

## LETTER

## Ecological persistence interrupted in Caribbean coral reefs

John M. Pandolfi<sup>1\*</sup> and Jeremy B.C. Jackson<sup>2</sup>

<sup>1</sup>Centre for Marine Studies and Department of Earth Sciences, ARC Centre of Excellence for Coral Reef Studies, The University of Queensland, St Lucia, Qld 4072, Australia

<sup>2</sup>Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA; and Center for Tropical Paleocology and Archeology, Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panamá

Correspondence: E-mail: j.pandolfi@uq.edu.au

### Abstract

The recent mass mortality of Caribbean reef corals dramatically altered reef community structure and begs the question of the past stability and persistence of coral assemblages before human disturbance began. We report within habitat stability in coral community composition in the Pleistocene fossil record of Barbados for at least 95 000 years despite marked variability in global sea level and climate. Results were consistent for surveys of both common and rare taxa. Comparison of Pleistocene and modern community structure shows that Recent human impacts have changed coral community structure in ways not observed in the preceding 220 000 years.

### Keywords

Barbados, Caribbean Sea, community ecology, community structure, Coral reefs, corals, ecosystem stability, habitat degradation, Pleistocene, rare species.

*Ecology Letters* (2006) 9: 818–826

### INTRODUCTION

Perhaps the most difficult questions in community ecology are those that deal with the ecological dynamics of communities over long temporal scales. Empirical investigation into the temporal variability of community structure is generally not possible beyond a few years or decades, so models are usually the most appropriate tools to investigate ecological stability or succession (Savage *et al.* 2000). This is especially true in long-lived organisms such as corals on reefs and trees in rainforests whose generation times may exceed 100 years. The only possibility for acquiring long-term empirical data comes from the fossil record.

On coral reefs, there are no quantitative data on the relative abundance of coral species for any tropical reef beyond four decades. Empirical work on limited temporal scales has shown dramatic fluctuations in species abundance through time and space (Connell *et al.* 1997, 2004). The general impression given by these studies is that coral reefs are disturbance driven systems that never reach an equilibrium state – community composition varies widely from time to time and from place to place (Karlson 2002).

In contrast, Late Pleistocene fossil reefs record a history of community structure over the past several hundred thousand years, and so provide one of the best ecological archives with which to compare modern trends in the variability of community structure (Pandolfi 1996; Pandolfi & Jackson 2001). The global extent of Quaternary reef deposits worldwide provides a reliable database with which to study both ecological predictions and long-term effects of habitat degradation over broad spatial and temporal scales (Pandolfi 2002).

The first tantalizing evidence for large scale patterns in the recent past history of living coral reefs came from a semi-quantitative analysis of Mesoellella's (1968) Pleistocene data from Barbados (Jackson 1992). Mesoellella (1968) recognized that the recurrent patterns in species dominance and diversity that he found in the raised terraces of Barbados were very similar to those being described in the living reefs of Jamaica (Goreau 1959; Goreau & Wells 1967). Jackson (1992) used this data to speculate that reef coral communities re-assembled after global sea level changes in similar ways throughout a 500 ka interval. Pandolfi (1996) found similar patterns in the raised reef terraces of Papua

New Guinea, using coral species presence/absence data collected over a 115 ka interval. Consistency in community structure is also characteristic of coral communities over the past 3000 years in the Holocene (Aronson & Precht 1997; Aronson *et al.* 2004). Thus, the few studies on ancient coral reef communities that do exist paint a dramatically different picture to modern ecological studies, one that involves persistence in coral communities through time.

In the present paper, we go beyond earlier work by presenting species abundance data of extant coral species over time spans of hundreds of thousands of years. Our first objective is to rigorously test for persistent species diversity and community composition through time in the raised reef terraces of Barbados (Fig. 1) using an ecological field-sampling program during four recent reef-building episodes aged 104, 125, 195 and 220 ka (thousand years). We gathered data on reef coral species abundance and distribution from the shallow reef crest habitat at Barbados. Our data was gathered using two different sampling techniques that captured the common and the rare species. Our Pleistocene data suggest that shallow water reef crest communities were dominated by a predictable abundance of species that was relatively invariant through time.

An understanding of the long-term patterns and processes affecting species co-existence is fundamental to activities that promote their preservation or restoration. In Caribbean coral reef communities, coral cover has declined (Gardner *et al.* 2003; Pandolfi *et al.* 2003) due to a number of factors, including overfishing (Jackson *et al.* 2001), climate change (Hughes *et al.* 2003), disease (Lafferty *et al.* 2004), and their interaction (Hughes 1994), resulted in a changed seascape. The most obvious manifestation is the virtual elimination of

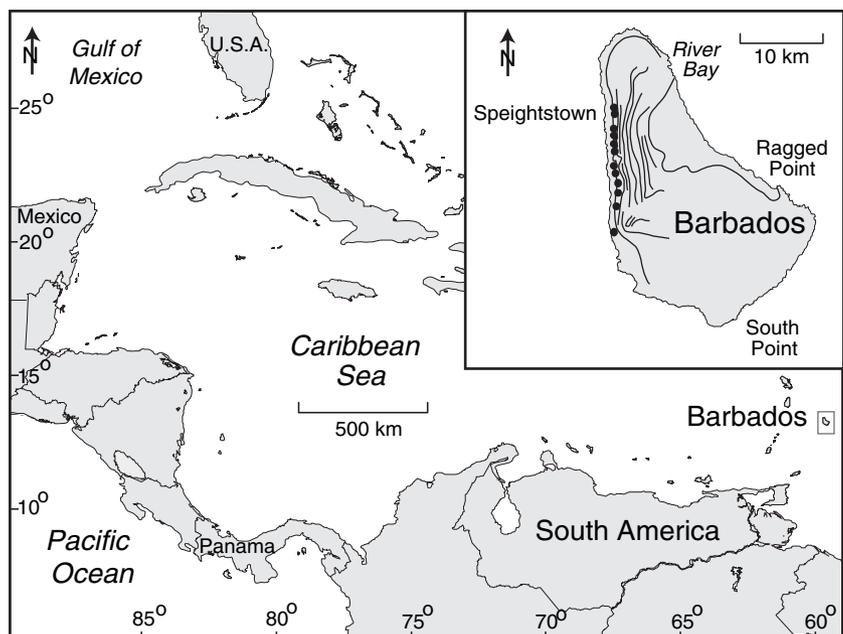
the once-dominant branching 'Elkhorn' coral (*Acropora palmata*) in shallow-water reef crest habitats (< 5 m depth), and the equally dominant branching 'Staghorn' coral (*A. cervicornis*) in mid-slope habitats (8–15 m depth). This has caused widespread loss of three-dimensionality to Caribbean coral reefs, and threatens their future viability.

The second objective of this paper is to investigate the magnitude of this impact at Barbados through a comparative analysis between the community structure we obtained from Pleistocene reef sequences and that obtained in the mid-1980s after severe human impacts (Lewis 1984; Tomascik & Sander 1987). The community composition of some Caribbean reefs that experienced recent mass mortality was quite stable over the past few thousand years (Aronson & Precht 1997; Aronson *et al.* 2004), but there are no comparable data for any Caribbean reefs that may have suffered comparable declines due to human impacts before modern surveys began. We find that human-induced degradation on Barbados has greatly modified the persistent community structure so typical of pre-human time. This is the first paleoecological study of Quaternary reef corals (still extant) conducted over a broad interval of geological time, using species relative abundance data gathered through hierarchical sampling, that relates community structure over time to modern species distribution patterns.

## MATERIAL AND METHODS

### Study site

We made a series of quantitative censuses of late Pleistocene reef coral assemblages in Barbados (West Indies) to examine



**Figure 1** Map showing location of Pleistocene reef crest coral assemblages sampled from the leeward side of Barbados. Censuses of coral assemblages were derived from the 104, 125, 195 and 220 ka leeward reef crests of Barbados. Closed circles denote sample localities for the 104 ka reef.

patterns of community structure over broad temporal scales (Fig. 1). We targeted the leeward reef crest habitat at this oceanic reef well away from highly influential continental land masses.

Barbados preserves a spectacular series of Pleistocene raised terraces with excellently preserved coral reef assemblages occurring over a wide range of reef habitats (Mesoella 1967; Mesoella *et al.* 1970; Jackson 1992; Martindale 1992). The raised reef terraces, formed through the interaction of Quaternary sea level fluctuations and local tectonic uplift, range in age from > 600–82 ka. Numerous authors have described the Pleistocene environments based on reef geomorphology, sediment characteristics (Mesoella *et al.* 1970), and epibionts (Martindale 1992). They have been extensively studied for sea level change during the last deglaciation (Fairbanks 1989) and for refining age dating methods (Bard *et al.* 1990). The magnitude and timing of Pleistocene global sea level fluctuations have been inferred from these reefs, and thus the stratigraphy, radiometric age dating, and models for Pleistocene reef development are among the best in the world. Coral species preservation is excellent, and the corals show clear depth zonation providing an ecological frame of reference. Thus, the raised reef terraces of Barbados provide an ideal setting to test for temporal stability in reef coral community structure during the Late Pleistocene.

Three lines of evidence suggest minimal preservation and sampling bias for the Pleistocene reef coral assemblages. The fossil reefs are characterized by excellent preservation of the sedimentary facies geometry, coral zonation patterns, and dominant taxa in similar environments to living reefs prior to the 1980s. Comparative taphonomic studies between life, death, and fossil assemblages show that depth zonation in live coral species abundance is preserved in adjacent death assemblages (Pandolfi & Minchin 1995; Greenstein & Pandolfi 1997; Edinger *et al.* 2001). Transects were placed where corals were predominantly upright and whole; in this way, we were able to avoid places where coral assemblages from adjacent habitats could be spatially mixed due to lateral transport.

### Sampling

We obtained coral species abundance patterns from transects 40 m long (line-intercept method, Loya 1972) from the shallow reef crest environment. After the transects were recorded, a 1-h search for additional (rare) coral species not intercepted along the transect was made using a belt-transect approach (Bianchi *et al.* 2004). The dimensions ( $L \times W \times H$ ) of each of these rare taxa occurring within 1 m of the transect tape along the entire 40 m were noted, giving an estimate of the relative abundance of rare taxa. Transects were normally separated from each other by 500–

1000 m. We obtained transects from each of four reef-building episodes, the 104 (12 transects), 125 (18), 195 (19), and 220 (13) ka, representing 115 ky along 25 km of the leeward western Barbados coastline. The number of transects obtained was dependent upon how much reef was available for study at each of the four different time periods, while maintaining the 0.5–1.0 km spacing.

We encountered 31 reef coral species from 62 transects from the four Pleistocene reef-building episodes in the shallow reef crest environment of Barbados. Species sampling curves showed that six to 10 transects (samples) per age were sufficient to capture > 95% of the coral species richness from all four reef-building episodes; thus sampling is adequate to estimate species diversity in the ancient shallow water environment (see Supplementary Online Material, Fig. S1). We found 20 species in the 104 ka, 17 species in the 125 ka, 22 species in the 195 ka, and 12 species in the 220 ka along the transects and 25, 22, 27 and 19 species, respectively, when the 1-h search data were included.

We also considered the transect data reported by Tomascik & Sander (1987) for seven modern fringing reef complexes adjacent to their fossil counterparts along the leeward west coast of Barbados. They reported average relative coverage in terms of % per transect for 24 scleractinian coral species (Table 2 in Tomascik & Sander 1987). The average represents transects conducted in the back reef zone from 0.5 to 1.4 m, the reef flat zone from 1.6 to 2.7 m and within the spur and groove structures. The water depths represented in these zones are comparable with those represented within the leeward Pleistocene reefs. Our results were the same regardless which modern zone or combination of zones the Pleistocene communities were compared. Here, we report results from the relative coverage averaged over the three reef zones.

### Data analysis

For each Pleistocene data set, comparison of taxonomic composition among all possible pairs of transects was calculated using the Bray-Curtis (BC) dissimilarity index. Abundance data were transformed to their square roots prior to the calculation to reduce the influence of occasional large abundance values for some taxa. The transformed abundance values for each taxon were then standardized.

Analysis of similarities (ANOSIM; Clarke 1993) was used to determine whether Pleistocene assemblages from different ages differed significantly in coral composition. The advantage to this test is that it does not assume any underlying distribution to the data, and it avoids using the BC index directly to compare sets of assemblages. Instead, it is a non-parametric test, based only upon the rank order of the matrix values. Where significant differences occur

pairwise tests provide an indication of where the differences among groups actually lie (Clarke & Warwick 2001). A separate ANOSIM was performed on the fossil plus modern data set.

We investigated whether the non-significant differences in community composition were meaningful by devising a test to determine whether the similarities among time periods on Barbados were any different than that predicted by chance, using bootstrapping. Although bootstrapping is also a component of the ANOSIM technique, further analysis was needed to determine if non-significant differences were any different from a random expectation of similarity; that is, are similar assemblages any more similar than a random association of species? Bootstrapping of the common and rare data matrices was completed in two ways: (1) shuffling, without replacement, the values of species abundances within columns, so that each sample retained its collective species abundance values, but values were shuffled among different species randomly (within sample shuffling); and (2) shuffling, without replacement, and simultaneously, the values of species abundances among columns and rows, so that species abundance values were randomized with respect to both individual species and individual samples (among species and sample shuffling). Data matrices were randomized 10 000 times and each matrix was re-analysed with respect to differences or not between times, based on BC dissimilarity index. The degree to which the observed BC dissimilarity values were significantly different from the BC dissimilarities of the randomized matrices was assessed using the Wilcoxin Rank-sum tests.

We applied non-metric multidimensional scaling (NMDS) ordination to the matrix of Bray–Curtis values to provide a visual summary of the pattern of Bray–Curtis values among the samples. Each ordination started with 20 random configurations, and proceeded through 200 iterations for each of four dimensions. To investigate any differences in community structure between fossil and modern communities, we performed another NMDS ordination on a data matrix comprised of the 62 Pleistocene transects plus mean values for transects completed at seven sites from the adjacent modern reef at Barbados reported in Tomascik & Sander (1987). For this analysis, the Pleistocene transect data was transformed to percent abundance per transect to standardize the modern and fossil data. Additionally, species of the *Montastraea* 'annularis' complex that were differentiated in the Pleistocene surveys were pooled for the fossil vs. modern comparison because Tomascik & Sander (1987) did not differentiate them for their study (they were still considered to be the same species when their modern surveys were undertaken). Calculation of BC indices, and ANOSIM and NMDS analyses were performed using PRIMER, v. 5.

Patterns of diversity among times were computed using two diversity metrics, species richness ( $S$ ) and Shannon–Wiener index of diversity ( $H'$ ) and analysed by ANOVA. To analyse for heteroscedasticity, probability plots of both variables and residual plots were examined. Heterogeneous variances were found for  $S$ , but not for  $H'$ . Thus,  $S$  was log-transformed prior to the ANOVA. When the ANOVA found a significant temporal effect, we used Fisher's Least Significant Difference *post hoc* hypothesis test to examine pairwise differences among the time periods, using a Bonferroni adjustment. Analyses were performed using DATA DESK, v. 6.1.

## RESULTS

Significant differences in relative abundance of coral species occurred among the leeward reef crest coral communities during the four time periods for analyses of common but not rare taxa (Table 1) due largely to the increased abundance of the organ-pipe *Montastraea* (Pandolfi 2007) in the 104 ka community. There were no pairwise differences among assemblages from the three older reefs for either analysis (Table 1). Moreover, the corresponding ordination of common taxa shows great overlap in

**Table 1** Results of ANOSIM analysis for significant differences in Pleistocene reef coral species composition within the leeward reef crest environment among the four Pleistocene reef-building episodes in Barbados and the modern reefs of Barbados

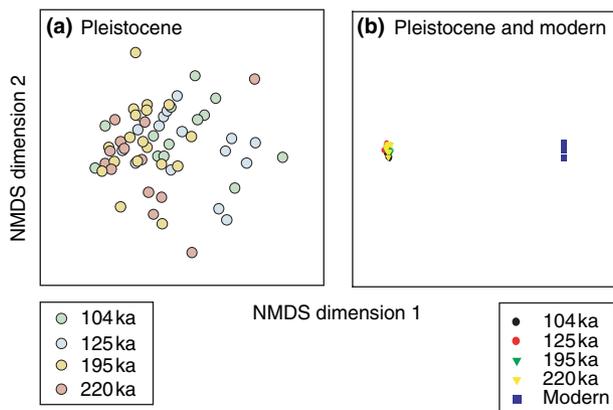
Main effect	Common taxa		Rare taxa	
	<i>R</i>	<i>P</i> -value	<i>R</i>	<i>P</i> -value
Barbados Pleistocene				
Overall	0.132	< 0.0001	0.023	0.223
104 vs. 125	0.386	< 0.0001	0.001	0.443
104 vs. 195	0.250	0.002	0.128	0.021
104 vs. 220	0.366	< 0.0001	0.092	0.089
125 vs. 195	0.014	0.250	−0.003	0.470
125 vs. 220	−0.021	0.605	−0.037	0.695
195 vs. 220	−0.017	0.550	−0.002	0.455
Barbados Pleistocene and modern				
Overall	0.328	<< 0.001		
104 vs. 125	0.379	<< 0.001		
104 vs. 195	0.265	0.002		
104 vs. 220	0.368	<< 0.001		
104 vs. Modern	1.0	<< 0.001		
125 vs. 195	−0.015	0.654		
125 vs. 220	−0.031	0.688		
125 vs. Modern	1.0	<< 0.001		
195 vs. 220	0.01	0.330		
195 vs. Modern	1.0	<< 0.001		
220 vs. Modern	1.0	<< 0.001		

*R*, ANOSIM test statistic.

taxonomic composition of reef coral communities through time (Fig. 2a). Similar ordination results were obtained for the rare taxa and whether or not we included data from the 104 ka assemblages.

When the coral data derived from Table 2 of Tomascik & Sander (1987) were included in the analysis, living communities were significantly different from all of the Pleistocene communities (Table 1). The corresponding ordination shows a marked separation between the Pleistocene assemblages and their modern counterparts (Fig. 2b). Again, similar ordination results were obtained whether or not we included data from the 104 ka assemblages.

For both the common and rare taxa in the Pleistocene data, bootstrapping by columns (samples), and by columns and rows (species and samples) both produced BC randomized distributions significantly different from the observed distribution (Supplemental Online Material, Fig. S2). Indeed, all of the results (100%) showed that the



**Figure 2** Non-metric multi-dimensional scaling (NMDS) ordination of the relative abundance of the common coral taxa in Pleistocene and modern assemblages from Barbados, West Indies. (a) Coral assemblages aged 104, 125, 195 and 220 ka from the Pleistocene leeward reef crest of Barbados. (b) Combined analysis of Pleistocene and modern coral assemblages surveyed in the 1980s by Tomascik & Sander (1987).

**Table 2** Atmospheric temperature and carbon dioxide values derived from the Vostok ice core during the reef building episodes studied on Barbados and modern values

Age	Delta temperature*	CO <sub>2</sub> (ppmv)†
Mid-1980s	0	350.0
104 ka	-4.16	230.9
125 ka	0.24	276.5
195 ka	-5.22	231.5
220 ka	-4.31	251.2

\* Temperature deviation (°C) relative to present.

† Parts per million by volume.

observed similarities are much greater than those of the randomizations. Thus, where pairwise ANOSIM tests were not significant between reef-building episodes (Table 1), similarity in community composition among time periods was greater than that expected by chance.

The same six most common coral species comprise > 97% of the total coral density for the four reef-building episodes on Barbados: *A. palmata*, *A. cervicornis*, organ-pipe *Montastraea*, *M. annularis* s.s., *Diploria strigosa*, and *M. faveolata* (Figs 3 and 4a). *Acropora palmata* was overwhelmingly the most abundant species at all four time periods (Fig. 3). These same six species are also the only ones that occur in > 50% of the Pleistocene transects (Supplementary Online Material, Fig. S3). However, these species only form around 20% (6/31) of the species encountered in the censuses. They occur in about the same abundance in the 125, 195 and 220 ka reefs, but *A. palmata* is reduced and organ-pipe *Montastraea* increased in the 104 ka reef (Fig. 3). Mean  $\alpha$ -diversity is eight species per transect, so the contribution of these coral species to the local  $\alpha$ -diversity is 75%. Most of the other coral species have low incidence in the censuses, with 68% of species occurring in < 25% of the transects (Supplementary Online Material, Fig. S3).

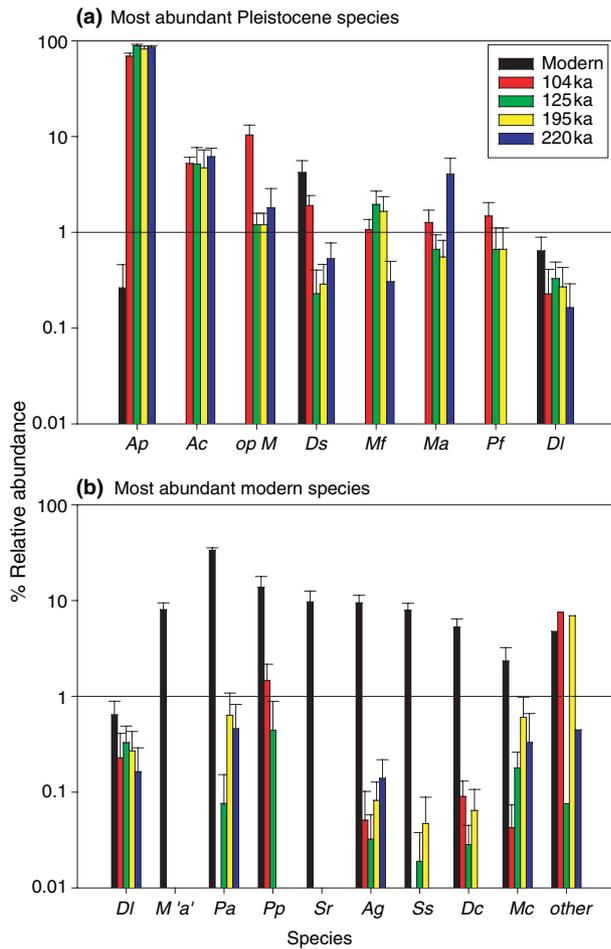
In marked contrast to the Pleistocene coral assemblages, those from the living reef on Barbados are dominated by species that are rare in the Pleistocene communities (Figs 3 and 4b). The most abundant coral is *Porites astreoides*, followed by *P. porites*, *Siderastrea radians*, and *Agaricia agaricites*. Living communities contained very little *A. palmata* and no *A. cervicornis*.

We found significant differences among the four reef episodes for both the log-transformed species richness ( $\log S$ ) [ $F_{(3,58)} = 9.74$ ,  $P < 0.0001$ ] and the Shannon–Wiener diversity index ( $H'$ ) [ $F_{(3,58)} = 5.58$ ,  $P = 0.002$ ] along the transects. Mean transect diversity in the 104 ka [ $S = 8.25$  (SE = 0.73),  $H' = 0.868$  (SE = 0.10)] reef is much higher than in the 125 ka [ $S = 4.61$  (SE = 0.44),  $H' = 0.398$  (SE = 0.07)], 195 ka [ $S = 5.37$  (SE = 0.50),  $H' = 0.553$  (SE = 0.08)] and 220 ka [ $S = 3.62$  (SE = 0.35),  $H' = 0.433$  (SE = 0.10)] reefs. Pairwise comparisons showed significant differences at the  $P < 0.008$  level (using a Bonferroni correction for six tests at 0.05 level) only between the 104 ka and other reefs (125, 194 and 220 ka reefs for  $S$ , and 125 and 220 ka reefs for  $H'$ ).

## DISCUSSION

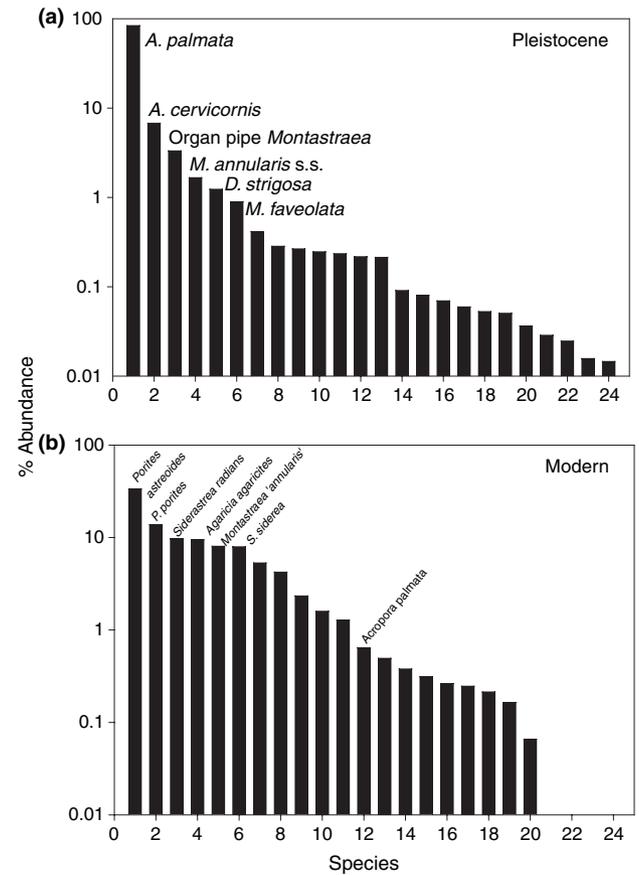
### Pleistocene variability in community structure

Pleistocene coral communities from Barbados show remarkable persistence in community structure and species diversity over tens of thousands of years through four episodes of reef development. Similarity in community composition among time periods was greater than that



**Figure 3** Relative abundance of reef corals occurring along 40-m transects from the Pleistocene reefs of Barbados from four different reef-building episodes, the 104, 125, 195 and 220 ka events and from the modern data collected by Tomascik & Sander (1987). For clarity, the plot is broken down into two components (a) and (b). (a) The relative abundance of the most abundant species from the Pleistocene transects. *Acropora palmata* is high in all of the Pleistocene reefs. (b) The relative abundance of the most abundant species from the modern transects. The most abundant species living on the reefs of Barbados today were rare to absent in the Pleistocene. Species shown are *Ap*, *Acropora palmata*; *Ac*, *Acropora cervicornis*; *op M*, organ-pipe *Montastraea*; *Ds*, *Diploria strigosa*; *Mf*, *Montastraea faveolata*; *Ma*, *Montastraea annularis* s.s.; *Pf*, *Porites furcata*; *DI*, *Diploria labyrinthiformis*; *M'a*, members of the *Montastraea 'annularis'* species complex undifferentiated; *Pa*, *Porites astreoides*; *Pp*, *Porites porites*; *Sr*, *Siderastrea radians*; *Ag*, *Agaricia agaricites*; *Ss*, *Siderastrea siderea*; *Dc*, *Diploria clivosa*; *Mc*, *Montastraea cavernosa*; and other, all other coral species. Error bars are standard error of the mean.

expected by chance (Supplemental Online Material, Fig. S2) so variance in community structure was not due to a random draw of species from the same species pool. These



**Figure 4** Overall abundance of reef coral species in Pleistocene and modern leeward reef crest environments of Barbados. (a) Pleistocene reef coral communities are comprised of a relatively small number of abundant species that make up over 99% of the occurrences in the Pleistocene reefs. (b) Living reef coral communities are comprised of a completely different set of abundant species than their Pleistocene counterparts.

Pleistocene data point to a high degree of order in coral communities over broad temporal scales and support the importance of local influences in determining reef coral community structure.

Remarkably, persistent patterns in community structure were shown not only by the most abundant species that represent only a small fraction of the number of taxa present (20%; Fig. 4a), but also for the separately sampled 'rare' taxa – the majority of coral species whose density on the reef was extremely small (< 5%). Persistent structure in both common and rare taxa invites investigation of whether or not the composition of the rare taxa is dependent, at least in part, upon that of the common, structurally dominant corals.

Persistence in community structure through time at Barbados is in marked contrast to previously documented variability in space at a single time period (125 ka) along a

> 2500 km southern Caribbean traverse (SOCA traverse of Pandolfi 2002). The similarity among communities from Barbados over 115 KA is much greater than among communities from the same habitat at San Andrés, Curaçao, and Barbados during the 125 ka reef-building event (Fig. 3 in Pandolfi 2002).

Long-term persistence of Late Pleistocene community structure of reef corals at Barbados is consistent with the much shorter-term studies of coral communities from the Late Holocene of Belize (Aronson & Precht 1997) and Panamá (Aronson *et al.* 2004), quantitative surveys of Pleistocene and sub-fossil communities of Florida and the Bahamas (Greenstein *et al.* 1998), and presence/absence surveys of species assemblages aged between 30 and 125 ka from Papua New Guinea (Pandolfi 1996). Similar patterns of long-term persistence in species abundance patterns have been observed for some temperate forest (Clark & McLachlan 2003) and small mammal (McGill *et al.* 2005) communities, but others have shown striking changes in community composition over the past 10–15 ka (Jackson & Overpeck 2000; Jackson & Williams 2004).

The overall pattern of persistence in relative abundance through time is due to the consistent abundance of coral species that form the three-dimensional structure of the reef, *A. palmata*, *A. cervicornis*, *D. strigosa*, and the members of the *Montastraea* 'annularis' species complex (Figs 3 and 4a). These corals broadcast their larvae and are characterized by either high growth rates that enable vertical extension above the surrounding substratum, or large body size that occupies a large amount of reef substrate. Fast-growing and robust corals that thrive in shallow-water, high light conditions and are able to withstand high wave energy were spatially dominant within the leeward shallow reef crest zone. The importance of large or fast-growing species in the structure of Caribbean coral communities over large time scales deserves careful consideration in the study of assembly rules in coral reef ecology.

Differences in composition through time were also driven by variability in the relative abundance of the six most abundant coral taxa (Fig. 3). On Barbados, the 104 ka reef showed an increase in organ-pipe *Montastraea* at the expense of a decrease in the abundance in *A. palmata*, demonstrating that ecological replacements among dominant coral species can and do occur. There were no obvious differences in preservation among the four time intervals (see Material and methods section) and no obvious correlation with global environmental parameters (the most distinct global atmospheric temperature and CO<sub>2</sub> combination actually occurs during the 125 ka reef – see Table 2), even though climatic conditions varied markedly among different glacial and interglacial maxima conditions (Table 2; Petit *et al.* 1999). Thus the reasons for the small differences we observed during the 104 ka reef remain unclear. Previous work on the

older terraces showed a marked increase in the organ-pipe *Montastraea* between 600 and 82 ka in the leeward buttress zone just seaward of the reef crest zone of this study (Pandolfi *et al.* 2002).

### Comparison with modern coral reefs

The community structure of Pleistocene corals is in marked contrast to that of present day corals from Barbados. Large species of branching *Acropora* corals dominated shallow reefs throughout most of the tropical western Atlantic for at least half a million years (Geister 1977) in the face of great geographic and temporal environmental variability. Caribbean coral reefs exhibited a distinct coral zonation controlled by exposure to wave energy. *Acropora palmata* formed dense, nearly single species stands in the highest energy environments, whereas *A. cervicornis* formed dense thickets in lower wave energy environments (Adey & Burke 1977; Geister 1977). The Elkhorn coral was an important component to Caribbean reef systems because it provided the major component of the three-dimensional structure characteristic of Caribbean coral reefs. Our study shows that *A. palmata* was a dominant coral species in shallow reef crest habitats for hundreds of thousands of years in Barbados.

Today, these two large branching coral species have been decimated all over the Caribbean due to a myriad of factors including trophic cascades resulting from overfishing (Hughes 1994; Jackson *et al.* 2001), coral (Patterson *et al.* 2002) and herbivore (Lessios *et al.* 1984) disease, and land erosion (Lewis 1984). On Barbados, the Elkhorn coral was dominant in the Pleistocene, and Nutting (1919) reported expansive tracts of living *A. palmata* in 1918. By 1939, Butsch (1939), and later Lewis (1960) reported this species as only a minor component of the living reef fauna. The live coral cover of *A. palmata* is now < 1% (Tomascik & Sander 1987) (Figs 3 and 4b). The greatest impacts on Barbados are probably related to increased turbidity resulting from land clearing and the development of sugar cane agriculture in the mid-17th century (Lewis 1984), although eutrophication is also a factor (Tomascik & Sander 1987).

Replacing *A. palmata* are much slower-growing corals that typically lie much closer to the reef substrate, and so may be less able to perpetuate the tall three-dimensional structure so typical of Pleistocene coral reefs. In fact, there has been significant loss of the geomorphological structure of the reefs of Barbados during the past 40 years (Lewis 2002). Thus, loss of the major reef builders has not only resulted in changes in community composition, but has also inhibited the ability of these reefs to maintain their bio-physical structural integrity.

We have shown that there has been a drastic change in coral community composition from long-term stability to recent declines. Such low abundance of *A. palmata* has no

historical precedent preserved in the Pleistocene fossil record. Throughout the Pleistocene fossil record on Barbados coral assemblages are strikingly different to that of 20th century reefs so the present is anomalous with respect to the past 200 ka. Pleistocene persistence in community structure through multiple episodes of global climate fluctuations argues against environmental variability as an exclusive force governing the nature and extent of coral communities. Human impacts have been the most important driving force in reef coral community change during the past several hundred thousand years. This historical perspective provides reef managers with the range in natural variability of coral reefs before the arrival of humans. While it may not be feasible nor ecologically possible to restore the coral reefs of Barbados to their Pleistocene state, recognition of this natural variability provides managers with goals as to the path such restoration might seek to embark upon, and a measure of success as to the length along that path management policy leads.

#### ACKNOWLEDGEMENTS

Financial support was provided by the Smithsonian Institution and the Australian Research Council Centre of Excellence in Coral Reef Studies. We are grateful to Gerardo Toro, Ghiselaine Llewellyn, Arturo Dominici, Melissa Frey, and Ruy Kikuchi for field assistance. Michael Bode assisted in the bootstrap analyses and drafted Supplemental Online Material, Fig. S2.

#### REFERENCES

- Adey, W.H. & Burke, R.B. (1977). Holocene bioherms of Lesser Antilles-Geologic control of development. *AAPG Stud. Geol.*, 4, 67–81.
- Aronson, R.B. & Precht, W.F. (1997). Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology*, 23, 326–346.
- Aronson, R.B., Macintyre, I.G., Wapnick, C.M. & O'Neill, M.W. (2004). Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology*, 85, 1876–1891.
- Bard, E., Hamelin, B. & Fairbanks, R.G. (1990). U-Th ages obtained by mass spectrometry in corals from Barbados: sea level during the past 130,000 years. *Nature*, 346, 456–458.
- Bianchi, C.N., Pronzato, R., Cattaneo-Vietti, R., Benedetti-Cecchi, L., Morri, C., Pansini, M. *et al.* (2004). Hard bottoms. *Biol. Mar. Mediter.*, 11 (Suppl. 1), 185–215.
- Butsch, R.S. (1939). The reef builders of Barbados. *J. Barbados. Mus. Hist. Soc.*, 6, 9.
- Clark, J.S. & McLachlan, J.S. (2003). Stability of forest biodiversity. *Nature*, 423, 635–638.
- Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Austr. J. Ecol.*, 18, 117–143.
- Clarke, K.R. & Warwick, R.M. (2001). *Change in marine communities: an approach to statistical analysis and interpretation*, 2nd edn. PRIMER-E, Plymouth.
- Connell, J.H., Hughes, T.P. & Wallace, C.C. (1997). A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.*, 67, 461–488.
- Connell, J.H., Hughes, T.P., Wallace, C.C., Tanner, J.E., Harms, K.E. & Kerr, A.M. (2004). A long-term study of competition and diversity of corals. *Ecol. Monogr.*, 74, 179–210.
- Edinger, E.N., Pandolfi, J.M. & Kelley, R. (2001). Community structure of Quaternary coral reefs compared with Recent life and death assemblages. *Paleobiology*, 27, 669–694.
- Fairbanks, R.G. (1989). A 17,000 year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature*, 342, 637–642.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, 301, 958–960.
- Geister, J. (1977). The influence of wave exposure on the ecological zonation of Caribbean coral reefs. *Proc. Third Intern. Coral Reef Symp.*, 1, 23–29.
- Goreau, T.F. (1959). The ecology of Jamaican coral reefs I. Species composition and zonation. *Ecology*, 40, 67–90.
- Goreau, T.F. & Wells, J.W. (1967). The shallow-water Scleractinia of Jamaica: revised list of species and their vertical distribution range. *Bull. Mar. Sci.*, 17, 442–453.
- Greenstein, B.J. & Pandolfi, J.M. (1997). Preservation of community structure in modern reef coral life and death assemblages of the Florida Keys: implications for the Quaternary fossil record of coral reefs. *Bull. Mar. Sci.*, 61, 431–452.
- Greenstein, B.J., Curran, A. & Pandolfi, J.M. (1998). Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective. *Coral Reefs*, 17, 249–261.
- Hughes, T.P. (1994). Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C. *et al.* (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929–933.
- Jackson, J.B.C. (1992). Pleistocene perspectives on coral reef community structure. *Am. Zool.*, 32, 719–731.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–638.
- Jackson, S.T. & Overpeck, J.T. (2000). Responses of plant populations and communities to environmental changes of the Late Quaternary. *Paleobiology*, 26 (Suppl.), 194–220.
- Jackson, S.T. & Williams, J.W. (2004). Modern analogs in Quaternary paleoecology: here today, gone yesterday, gone tomorrow? *Annu. Rev. Earth Planet. Sci.*, 32, 495–537.
- Karlson, R.H. (2002). *Dynamics of Coral Communities*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Lafferty, K.D., Porter, J.W. & Ford, S.E. (2004). Are diseases increasing in the ocean? *An. Rev. Ecol. Evol. Syst.*, 35, 31–54.
- Lessios, H.A., Cubit, J.D., Robertson, D.R., Shulman, M.J., Parker, M.R., Garrity, S.D. *et al.* (1984). Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs*, 3, 173–182.
- Lewis, J.B. (1960). The coral reefs and coral communities of Barbados, W. I. *Can. J. Zool.*, 38, 1133–1145.
- Lewis, J.B. (1984). The *Acropora* inheritance: a reinterpretation of the development of fringing reefs in Barbados, West Indies. *Coral Reefs*, 3, 117–122.

- Lewis, J.B. (2002). Evidence from aerial photography of structural loss of coral reefs at Barbados, West Indies. *Coral Reefs*, 21, 49–56.
- Loya, Y. (1972). Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar. Biol.*, 13, 100–123.
- Martindale, W. (1992). Calcified epibionts as palaeoecological tools: examples from the Recent and Pleistocene reefs of Barbados. *Coral Reefs*, 11, 167–177.
- McGill, B.J., Hadly, E.A. & Maurer, B.A. (2005). Community inertia of Quaternary small mammal assemblages in North America. *Proc. Natl. Acad. Sci.*, 102, 16701–16706.
- Mesolella, K.J. (1967). Zonation of uplifted Pleistocene coral reefs on Barbados, West Indies. *Science*, 156, 638–640.
- Mesolella, K.J. (1968). *The Uplifted Reefs of Barbados: physical Stratigraphy, Facies Relationships and Absolute Chronology*. Unpublished PhD Thesis, Brown University, Rhode Island.
- Mesolella, K.J., Sealy, H.A. & Matthews, R.K. (1970). Facies geometries within Pleistocene reefs of Barbados, West Indies. *AAPG Bull.*, 54, 1899–1917.
- Nutting, C.C. (1919). Barbados–Antigua expedition. *Univ. Iowa Stud. Natl. Hist.*, 8, 1–274.
- Pandolfi, J.M. (1996). Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. *Paleobiology*, 22, 152–176.
- Pandolfi, J.M. (2002). Coral reef ecology at multiple spatial and temporal scales. *Coral Reefs*, 21, 13–23.
- Pandolfi, J.M. (2007). A new species from the *Montastraea annularis* species complex from the Pleistocene of the Caribbean Sea. *J. Paleont.* (in press).
- Pandolfi, J.M. & Jackson, J.B.C. (2001). Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. *Ecol. Monogr.*, 71, 49–67.
- Pandolfi, J.M. & Minchin, P.R. (1995). A comparison of taxonomic composition and diversity between reef coral life and death assemblages in Madang Lagoon, Papua New Guinea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 119, 321–341.
- Pandolfi, J.M., Lovelock, C.E. & Budd, A.F. (2002). Character release following extinction in a Caribbean reef coral species complex. *Evolution*, 53, 479–501.
- Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G. *et al.* (2003). Global trajectories of the decline of coral reef ecosystems. *Science*, 301, 955–958.
- Patterson, K.L., Porter, J.W., Ritchie, K.B., Polson, S.W., Mueller, E., Peters, E.C. *et al.* (2002). The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata*. *PNAS*, 99, 8725–8730.
- Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I. *et al.* (1999). Climate and atmospheric history of the past 420 000 years from the Vostok ice core, Antarctica. *Nature*, 399, 429–436.
- Savage, M., Sawhill, B. & Askenazi, M. (2000). Community dynamics: what happens when we rerun the tape? *J. Theor. Biol.*, 205, 515–526.
- Tomascik, T.R. & Sander, F. (1987). Effects of eutrophication on reef-building corals II. Structure of Scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar. Biol.*, 94, 53–75.

## SUPPLEMENTAL MATERIAL

**Figure S1** Species sampling curves for the four Pleistocene reef building episodes of Barbados; 104, 125, 195 and 220 ka.

**Figure S2** Wilcoxin rank-sum statistics for Bray–Curtis comparison of observed vs. boot-strapped coral assemblages (125, 195 and 220 ka reefs).

**Figure S3** Histogram of the percent of the 62 transects in which each of the 31 observed species occurred through the four reef-building episodes on Barbados.

Editor, Helmut Hillebrand

Manuscript received 21 December 2005

First decision made 25 January 2006

Second decision made 22 March 2006

Manuscript accepted 24 March 2006