

## Community dynamics of Pleistocene coral reefs during alternative climatic regimes

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**Abstract.** Reef ecosystems built during successive periods of Pleistocene sea level rise have shown remarkable persistence in coral community structure, but little is known of the ecological characteristics of reef communities during periods of low sea stands or sea level falls. We sampled the relative species abundance of coral, benthic foraminifera, and calcareous red algae communities from eight submerged coral reefs in the Huon Gulf, Papua New Guinea, which formed during successive sea level fall and lowstand periods over the past ~416 kyr. We found that dissimilarity in coral species composition increased significantly with increasing time between reef-building events. However, neither coral diversity nor the taxonomic composition of benthic foraminifera and calcareous red algae assemblages varied significantly over time. The taxonomic composition of coral communities from lowstand reefs was significantly different from that of highstand reefs previously reported from the nearby Huon Peninsula. We interpret the community composition and temporal dynamics of lowstand reefs as a result of shifting energy regimes in the Huon Gulf, and differences between low and highstand reefs as a result of differences in the interaction between biotic and environmental factors between the Huon Gulf and Huon Peninsula. Regardless of the exact processes driving these trends, our study represents the first glimpse into the ecological dynamics of coral reefs during low sea level stands when climatic conditions for reef growth were much different and less optimal than during previously studied highstand periods.

**Key words:** *benthic foraminifera; calcareous red algae; coral reef; ecological dynamics; low-sea-level stand; paleoecology; Papua New Guinea; persistence; Pleistocene; Quaternary; regression; stability.*

### INTRODUCTION

The sudden and relentless impact of humans over the past millenium has caused rapid global degradation of living coral reef ecosystems (Pandolfi et al. 2003, Bruno and Selig 2007), which are now subject to the looming threat of anthropogenic climate change and ocean acidification (Hughes et al. 2003, Hoegh-Guldberg 2007, Lough 2008). Recent and rapid ecological shifts observed in tropical reef environments appear to be unique in the history of coral reefs (Jackson 1992, Aronson and Precht 1997, Greenstein et al. 1998, Pandolfi and Jackson 2006). In contrast, fossil assemblages of Quaternary reefs built during the optimal climate condition of rising sea level display remarkable persistence in their coral species composition over long time frames. For example, recent studies in the

Caribbean have found *Acropora*-dominated communities dating back thousands of years, broken only by recent dramatic shifts in species composition (Aronson and Precht 1997, Wapnick et al. 2004). Several longer term studies indicate that similar coral assemblages may have persisted virtually unchanged for hundreds of thousands of years on the Great Barrier Reef (to ~500 kya [kya = 1000 years ago]; Webster and Davies 2003), the Caribbean (to ~220 kya; Pandolfi and Jackson 2006) and Papua New Guinea (PNG; to ~125 kya; Pandolfi 1996, 1999).

Our current knowledge of Pleistocene reef ecosystems rests almost entirely on data from reefs built during sea level rise (transgression) up to a sea level highstand. Provided the reefs do not “drown,” glacially induced rising sea level represents the optimal condition for reef growth because it permits continuous upward accretion (Chappell and Polach 1991). However, these periods constitute only about 10% of the temporal duration of typical Quaternary sea level cycles (Pandolfi and Greenstein 2007). In contrast, very little is known about the ecological dynamics of reef species during periods of

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falling sea level (regression) or sea level lowstand (conditions not generally favorable for vertical reef accretion), other than that they surely must have survived somewhere in order for intervening highstand reef assemblages to be recorded so consistently in the Quaternary (Pandolfi 2002). These glacial low sea level stand reefs likely existed under less favorable conditions, including cooler temperatures, less available habitat, less connectivity among populations and reefs, and falling or lowstand sea-level, leading to very different environmental conditions for reef growth (Pandolfi and Greenstein 2007, Hopley et al. 2007). These differences bring to mind several key questions. What has happened to coral species during the transition from interglacial to glacial periods? Do reef communities survive as a whole, by tracking environmental shifts to new shallow water environments? Or do they survive in alternative ecological forms, still capable of maintaining species diversity, and later reassembling during highstands into the complex carbonate structures that we are most familiar with? Although little asked, the question of where do reef species go, and how, is highly relevant both for understanding the apparent persistence of these systems throughout the Pleistocene, and for better understanding how reefs might survive under the altered conditions (e.g., overexploitation and habitat loss) that humans are rapidly imposing on them (Pandolfi et al. 2003, 2005).

Although stable or falling sea level during glacial periods may not be ideal for reef development, subsiding tectonic plates (resulting in the deepening of the sea floor), found in tectonically active regions, or alternatively on the flanks of subsiding volcanoes (e.g., Webster et al. 2007), may promote vertical reef growth during these times of alternative environmental conditions. When subsidence is greater than the rate of sea-level fall, relative water depth above the plate will increase, providing a potential habitat for reef species and reef accretion (Webster et al. 2007). Fossil reef structures have recently been identified on such a subsiding plate in the Huon Gulf, Papua New Guinea (Webster et al. 2004b). The reefs formed stepwise as reef accretion migrated up the plate during successive regressions and lowstands over the past 450 kyr (kyr = 1000 years; Fig. 1), leaving a chronological series of submerged platforms (Webster et al. 2004a, b). In this paper, we outline and analyze the community structure of the coral, benthic foraminiferal, and calcareous red algal assemblages from eight of these temporally distinct submerged reefs. We then compare the coral communities from the lowstand reefs of the Huon Gulf to the highstand reefs of the Huon Peninsula 100–200 km to the north. The results show that persistence in community structure in lowstand reefs varies with ecological guild, with the reef coral community composition in the Huon Gulf varying in time with environmental change during successive glacial periods. These lowstand coral communities are

highly distinct from their highstand interglacial counterparts on the Huon Peninsula.

## METHODS

### *Study sites*

*Huon Gulf.*—A series of submerged Pleistocene coral reefs in the Huon Gulf, Papua New Guinea grew primarily during regressions and lowstands in response to rapid (2–6 m/kyr) tectonic subsidence (Webster et al. 2004b). The western Huon Gulf is an actively subsiding foreland basin characterized by 14 drowned carbonate platforms and numerous pinnacles/banks that increase in age (~20–450 kyr based on a combination of U/Th, <sup>14</sup>C-AMS, and numerical modeling data) and depth (0.1–2.5 km) northeast toward the Ramu-Markham Trench (Fig. 1). This configuration closely mimics the present-day Huon coastline and its seaward islands fringed by modern coral reefs. The platforms retain structural, morphologic, and sedimentary facies evidence of primary coral reef growth (e.g., raised reef crests, lagoons, spur and grooves, patch reefs, and mounds). The platforms are also composite features containing multiple terrace levels and notches, corresponding to multiple phases of growth, emergence, and drowning in response to rapid climatic and sea level changes during the evolution of each structure (Webster et al. 2004a).

*Huon Peninsula.*—On the Huon Peninsula of Papua New Guinea, a spectacular series of raised coral reefs has formed due to the interaction between tectonic uplift and Quaternary sea level changes (Chappell 1974). These late Pleistocene raised reefs are one of the best examples of reef growth during sea level rise that has been clearly related to the oxygen isotope record and eustatic sea level changes. Remarkable tectonically active, ongoing uplift during at least the last 340 kyr has left a record of reef terraces like “bath rings” along over 80 km of coast (Chappell 1994). The ecological dynamics of nine reef-building episodes, occurring between 30 and 125 kya during periods of highstand and sea level transgressions, and sampled across three sites, show remarkable constancy in coral composition (Pandolfi 1996).

### *Sampling*

*Lowstand reefs.*—We collected species abundance data from eight carbonate buildups in the Huon Gulf, PNG, aged 130–416 kya (Fig. 2A). Each reef represents a temporally distinct sea level regression approaching glacial lowstand, separated by intervening highstand periods. Species composition on each platform was sampled in 2001 using the Woods Hole ROV *Jason*. Limestone samples were collected (many broken off in situ) using the ROV manipulator from the shallowest part of each platform, near the paleo-reef crest or rim. Multiple samples were taken opportunistically from each reef platform (ranging from 14 to 54 samples), over scales ranging from 0.2 to 3.5 km, for a total of 279

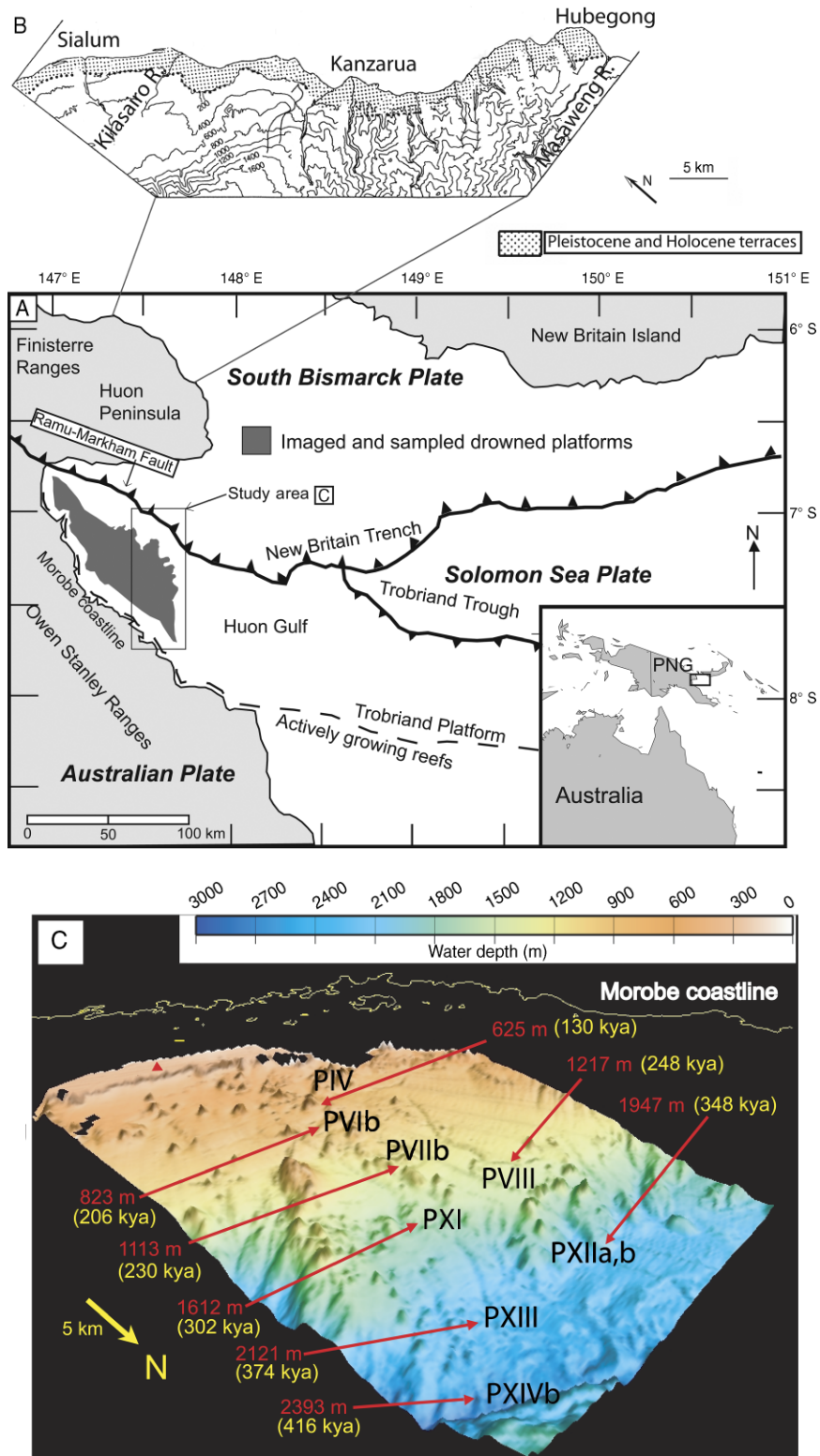


FIG. 1. Map showing (A) the tectonic setting of the Huon Gulf and the Huon Peninsula, Papua New Guinea (PNG). Also pictured is the (B) Huon Peninsula study area (adapted from Webster et al. [2004b] and Pandolfi [1996]). The vertical rectangle in panel (A) represents the Huon Gulf study area (panel C) from which lowstand reefs were sampled. In panel (C), the horizontal scale and north orientation are indicated by the length and direction of the yellow arrow; kya = 1000 years ago.

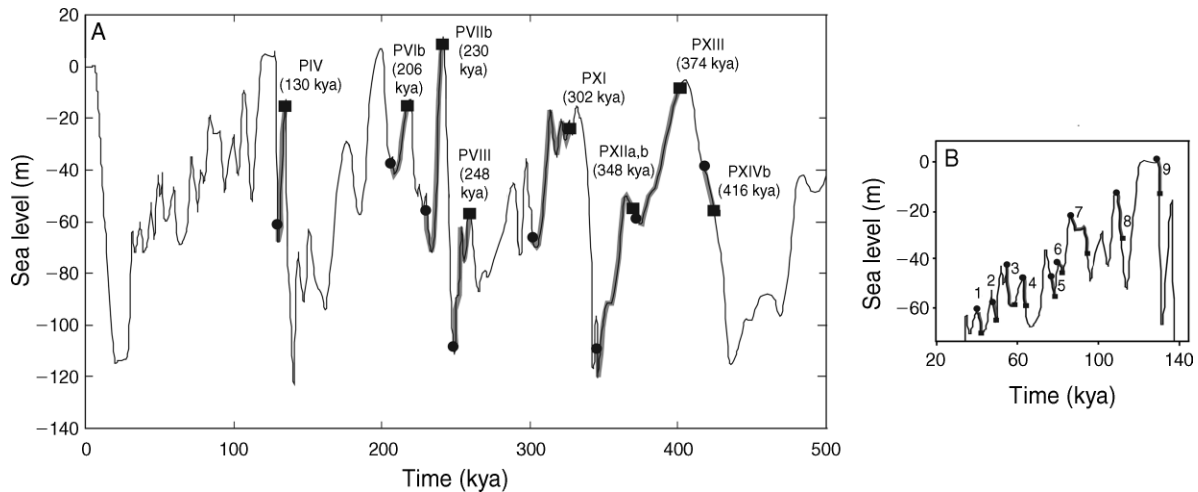


FIG. 2. Pleistocene sea level curves showing the intervals of reef growth for platform reefs examined from the (A) lowstand reefs of the Huon Gulf (adapted from Webster et al. [2004b]) and (B) the highstand reefs of Huon Peninsula, PNG (derived from Chappell et al. [1996] and Lambeck and Chappell [2001]). Squares show the start of reef growth, and circles show the end of reef growth. Platform names are as shown in Table 1.

samples, and averaging around 3.6 kg/sample (Table 1; see Webster et al. 2004b for detailed sampling methods, context, and sedimentary facies description). Corals, benthic foraminifera and calcareous red algae were identified to the lowest taxonomic level possible, either species or genus, and coral genera were further grouped according to growth form. For corals, both whole specimens and fragments were included. For benthic foraminifera, abundance was tabulated from the number of individuals found in thin section ( $\sim 2 \times 4$  cm). The

number of thin sections per reef platform varied between 5 and 19 (Table 1). Relative abundance of corals and benthic foraminifera was calculated for seven platforms, aged between 130 and 374 kyr (Table 1) as the number of individuals of a species/genus divided by the total number of individuals sampled at a platform. For calcareous red algae (Corallinales and Peyssonneliaceae), abundance was calculated as the percentage of limestone samples with a particular species/genus present for the seven platforms aged between 206 and

TABLE 1. Sampling attributes of lowstand and highstand coral reefs from Papua New Guinea.

Platform name†	Reef platform/ terrace	Age (kyr)	Spatial sampling scale (km)	No. limestone samples	Platform- depth (m)	Guilds sampled‡	No. thin sections	No. 100-m transects
Lowstand reefs (Huon Gulf)								
PIV	1	130	~1	30	625	c, bf	10	
PVIIb	2	206	~1	14	823	c, bf, ca	9	
PVIIb	3	230	~2	45	1113	c, bf, ca	8	
PVIII	4	248	~1	54	1217	c, bf, ca	19	
PXI	5	302	~3.5	47	1612	c, bf, ca	16	
PXIIa and PXIIb	6	348	~1	46	1947	c, bf, ca	10	
PXIII	7	374	~1.8	39	2121	c, bf, ca	17	
PXIVb	8	416	~0.2	9	2393	ca	5	
Highstand reefs (Huon Peninsula)								
IIa	1	35–42	25			c		3
IIIb	2	44.5	25			c		3
IIIa	3	46–61	16			c		2
IVb	4	?	~0.2			c		1
IVa	5	65–72	25			c		3
Vb	6	?	~0.2			c		1
Va	7	85	25			c		2
VI	8	107	25			c		3
VII	9	125	16			c		2

Note: For the Age column: 1 kyr = 1000 years; “?” indicates mean age unknown.

† Platform names are derived from Webster et al. (2004a) for the Huon Gulf and from Pandolfi (1996) for the Huon Peninsula.

‡ Key to abbreviations: c, coral; bf, benthic foraminifera; ca, coralline algae.

416 kyr (Table 1). Relative abundance for each of the three guilds was calculated per platform based on the pooled values of all samples, as there was not sufficient data to allow for spatial replication within each platform.

*Highstand reefs.*—Reef coral presence/absence data was previously reported from nine uplifted terraces of Pleistocene highstand reefs from the nearby Huon Peninsula, Papua New Guinea aged between 125 and 30 kyr (Fig. 2B; Pandolfi 1996). The terraces, each representing a single period of transgressive reef growth, span several geographic regions, allowing spatially independent replication for most time periods investigated (Table 1). Sampling occurred along 100-m transects from each of three sites (Fig. 1) where each uplifted terrace was represented (Table 1; see Pandolfi 1996 for full description of sampling techniques). To allow effective comparison to lowstand reefs, only data taken from the paleo-reef crest was used in the present study. As insufficient preservation of facies prevented sampling in some cases, this data was available for 20 of the 27 potential highstand sites sampled. Thus we compared the coral composition of seven lowstand reef platforms with permuted subsets of 20 highstand reef sites distributed over nine reef platforms, where each platform represents a distinct period of reef accretion.

#### Data analysis

*Lowstand reefs through time.*—Taxonomic sampling curves were constructed for coral, calcareous red algae, and benthic foraminifera, using 999 random permutations of platform by cumulative species/genus abundance (calculated in Primer 6.1.5, PRIMER-E, Ltd., Ivybridge, UK; Clarke and Warwick 1994). Relative abundance of each taxonomic grouping (coral, benthic foraminifera, and calcareous red algae) was compared separately amongst the submerged platforms in which they occurred to determine the dynamics of community composition over time. For each taxon, Bray-Curtis (BC) dissimilarity matrices (Bray and Curtis 1957) were constructed with relative abundance data that was square-root transformed, reflecting the pairwise dissimilarity between communities from each platform with every other platform. These matrices were then compared to a corresponding matrix of “time separating each pair of platforms,” using a Mantel test (Mantel 1967) for correlation between matrices based on random permutations of the dependent matrix. Each data point thus represents a comparison between a pair of reef building events, relating their assemblage dissimilarity to the amount of time separating them. The degree of change in taxonomic composition over time is expressed in bivariate plots that relate dissimilarity to time separating reefs, as calculated from their ages represented in Fig. 2A and Table 1. Regression was used to assess the relationship between Shannon’s evenness (calculated for corals only at each platform) and reef platform age. Bray-Curtis values were calculated in Primer 6.1.5

(Clarke and Warwick 1994). Regression analysis, mantel tests and NMDS were conducted in R, in the stats, vegan and ecodist packages, respectively (Goslee and Urban 2007, Oksanen et al. 2007, R Development Core Team 2007). The diversity index was calculated in the Excel add-on “diversity” (*available online*).<sup>8</sup>

*Comparison between highstand and lowstand species assemblages.*—Coral community composition of the lowstand Pleistocene reefs from the Huon Gulf was compared to that of their highstand counterparts on the raised terraces of the Huon Peninsula, 100–200 km to the north. To facilitate this, lowstand data were converted to presence/absence and reorganized into taxonomic groupings compatible with those used in Pandolfi (1996) for highstand assemblages. The difference in the species composition of the lowstand and highstand coral assemblages was tested using Analysis of Similarities (ANOSIM), which, by analogy to ANOVA, compares variation in the similarity of taxonomic composition within and between groups of samples (Clarke 1993). Significance was assessed by comparing the global R statistic to a null distribution based on 1000 permutations of the dissimilarity values of the seven lowstand reefs compared to a subset of nine randomly chosen highstand reefs, each drawn from a single reef-building episode. Spatial variation in the highstand reefs is thus eliminated in the null distribution, making this data directly comparable to that of the lowstand reefs which also lack spatial replication. The final *P* value was obtained by running this comparison 500 times using different randomly selected subsets of the highstand reefs, then calculating the mean significance value.

Coral communities from low and highstand reefs were represented using a nonmetric multidimensional scaling (NMDS) ordination, and recognition of key taxa using a SIMPER (SIMilarity PERcentage) analysis. ANOSIM was conducted in the vegan package of R (Oksanen et al. 2007), and SIMPER using Primer 6.1.5 (Clarke and Warwick 1994).

#### RESULTS

*Lowstand reefs through time.*—We found 29 coral genera that we further subdivided by growth form, leading to 49 taxonomic units. Together with 18 benthic foraminifera, and nine calcareous red algae, our study is based upon 76 taxonomic units. For all three taxa, cumulative taxonomic richness by platform began to level off at the end of sampling, indicating adequate, though imperfect, representation across lowstand samples (Appendix A). Bray-Curtis dissimilarity values between pairs of lowstand platforms ranged from 49.66% to 81.42% for corals, 18.39% to 79.93% for benthic foraminifera, and 17.39% to 59.91% for calcareous red algae. Mantel regression revealed that

<sup>8</sup> (<http://www.ssc.rdg.ac.uk/software/diversity/diversity.html>)

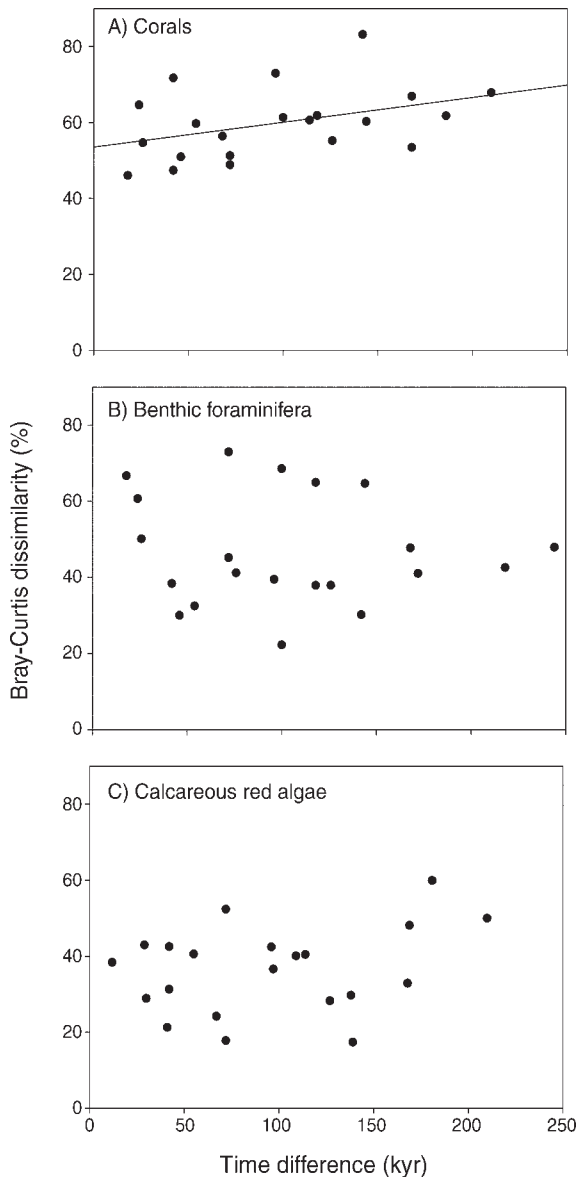


FIG. 3. Bray-Curtis dissimilarity of Pleistocene coral reef assemblages plotted against time differences for each pair of submerged platforms from the lowstand reefs of the Huon Gulf, PNG. (A) Differences between coral communities increased with time, while (B) benthic foraminifera and (C) calcareous red algae assemblages showed no temporal trends.

dissimilarity in coral composition correlated significantly with the amount of time separating the reefs ( $R = 0.65$ ,  $P = 0.002$ ; Fig. 3A). However, there were no significant temporal trends in the taxonomic composition of benthic foraminifera ( $R = -0.13$ ,  $P = 0.761$ ; Fig. 3B, Appendix B) or calcareous red algae ( $R = 0.28$ ,  $P = 0.10$ ; Fig. 3C, Appendix C). For the corals, Shannon evenness ranged between 0.95 and 1.00 and showed no correlation with time ( $F_{1,7} = 3.08$ ,  $P = 0.14$ ,  $R^2 = 0.26$ ; Appendix D).

Coral communities from the seven lowstand reefs apparently underwent a shift from older communities containing higher proportions of branching and stout branching *Acropora*, to younger reefs containing higher proportions of encrusting *Porites* and an increased proportion of platy *Acropora* (Fig. 4, Table 2, and Appendix E). Massive *Porites* and encrusting *Montipora* had high abundance in many of the lowstand reef communities, with no discernable trends.

*Highstand/lowstand coral community comparison.*— Significant differences in coral composition occurred between lowstand reef assemblages from the Huon Gulf and highstand assemblages from the Huon Peninsula (ANOSIM, Global  $R = 0.81$ ,  $P = 0.005$ ). The two groups are also clearly differentiated on the NMDS ordination plot (Fig. 5). These differences are primarily due to the relative dominance of massive *Platygyra* and digitate and stout branching *Acropora* in highstand compared to lowstand assemblages, and a higher abundance of *Montipora* and Agariciidae in lowstand reefs (Appendix F).

Despite the differences in the sampling strategy (transect vs. random sampling via an ROV manipulator) between the highstand and lowstand reefs, respectively, we believe that the observed variations reflect real taxonomic differences between the coral reef communities and not sampling bias. Firstly, the coral samples recovered from the lowstand reefs were mainly collected from *in situ* colonies attached to the paleo-reef crests. Secondly, using this strategy and the ROV manipulator we were able to recover a wide spectrum of coral taxa and growth forms and are therefore confident our sample suite is not biased towards a particular growth form or taxon. Quaternary fossil reefs have been shown to preserve a significant component of their original coral community structure (Greenstein and Pandolfi 1997, Edinger et al. 2001).

## DISCUSSION

Our study provides a rare glimpse into the long-term ecological dynamics of multiple trophic groups in Pleistocene coral reef ecosystems. Few studies have assessed reef composition over such long periods of time, and none has quantified the relative dynamics of multiple trophic guilds. Submerged lowstand reefs from the Huon Gulf, Papua New Guinea, built when sea levels were lower and reef habitats were less available than their highstand counterparts, show variation and change in the taxonomic composition of coral communities through time (Figs. 3A and 4). However, the taxonomic composition of benthic foraminifera and calcareous red algal assemblages showed no significant temporal trends (Fig. 3B, C; Appendices B and C), indicating possible community stasis within each of these two guilds over the 286 kyr time frame studied. The independent trajectories of coral vs. non-coral taxa indicate a lack of integration across coral reef guilds, an absence of “community unity” defined as “exclusive

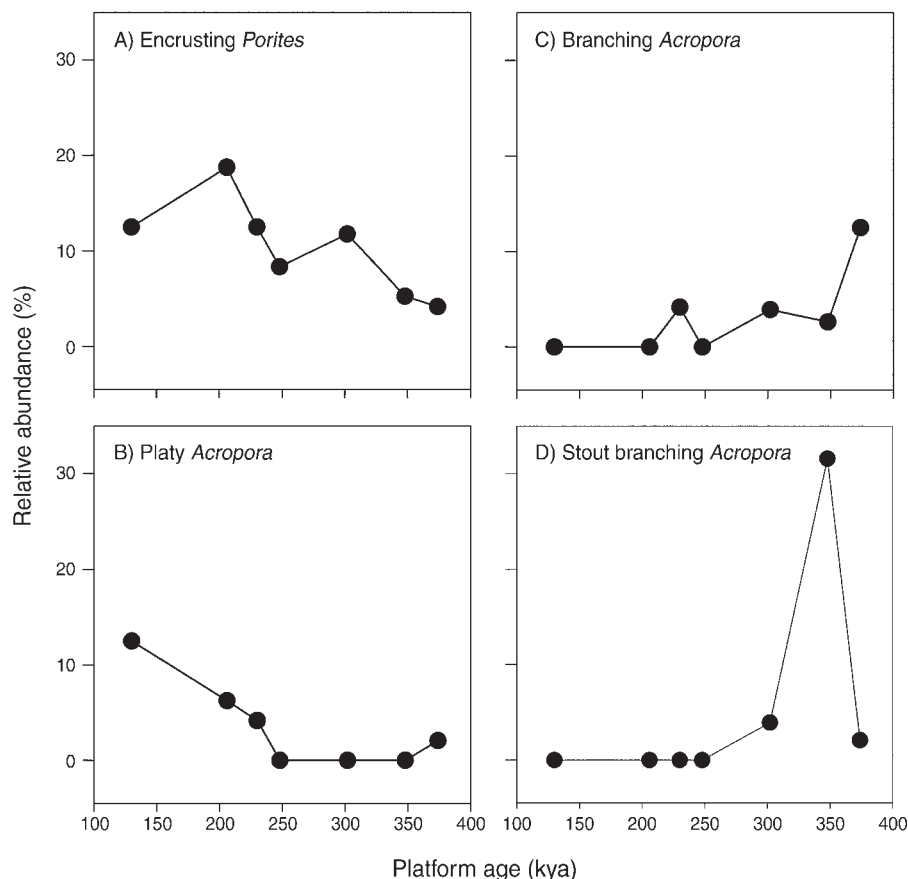


FIG. 4. Relative abundance of coral species showing temporal trends through the lowstand reef-building episodes examined in the Huon Gulf, PNG.

associations of closely dependent and coevolving species” (Jackson 1994). Both persistence (Gardiner 2001) and change (Paulay 1990) have been reported in the taxonomic composition of tropical Pleistocene molluscan communities. Our results indicate that persistence in the non-coral components of reef communities cannot be predicted from persistence in their coral counterparts, or we would have expected to see simultaneous community persistence or change across all three taxa

at the Huon Gulf. Thus, the different trajectories of lowstand taxonomic groups may not be compatible with the notion of a stable, integrated ecosystem, at least among disparate ecological guilds.

Shifts in the taxonomic composition of lowstand coral communities were subtle, and mainly due to differences in the relative abundance of four of the most abundant taxa (Table 2). Specifically, branching and stout branching *Acropora* decreased in abundance through

TABLE 2. Most abundant reef-building species/genera for benthic assemblages sampled across all Pleistocene lowstand reefs of the Huon Gulf, Papua New Guinea.

Coral	Benthic foraminifera	Calcareous red algae
Massive <i>Porites</i> (16.8)†	<i>Amphistigina radiata</i> (30.5)	<i>Neogoniolithon</i> (25.2)
Encrusting <i>Montipora</i> (14.2)	<i>Heterostegina depressa</i> (22.7)	<i>Hydrolithon</i> (23.2)
Encrusting <i>Porites</i> (10.5)	<i>Amphistigina lessonii</i> (14.4)	<i>Lithophyllum</i> (19.1)
Stout branching <i>Acropora</i> (5.4) ↓	<i>Gypsina</i> (7.5)	<i>Amphiroa</i> (8.5)
Platy <i>Montipora</i> (4.9)	<i>Peneroplis</i> (4.1)	<i>Peyssonnelia</i> (8.2)
Platy <i>Acropora</i> (3.6)†	<i>Homotrema rubra</i> (3.6)	<i>Spongites</i> (7.2)
Branching <i>Acropora</i> (3.3)↓	<i>Calcarina mayori</i> (3)	<i>Lithoporella</i> (6.7)
<i>Galaxea</i> (2.7)	<i>Amphisorus</i> (2.9)	<i>Mesophyllum</i> (1.1)
<i>Pocillopora</i> (2.3)	<i>Planorbulinella</i> (2.2)	<i>Polystrata</i> (0.8)
Massive <i>Cyphastrea</i> (2.3)	<i>Cycloclypeus carpenteri</i> (1.9)	

Note: Arrows indicate coral taxa displaying consistent increasing or decreasing abundance through time; mean relative abundance (%) is shown in parentheses.

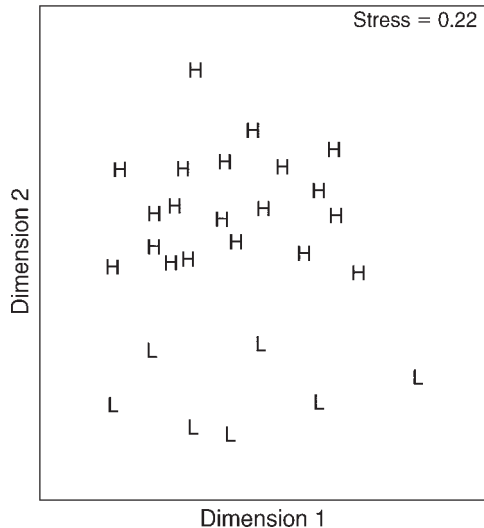


FIG. 5. Nonmetric multidimensional scaling (NMDS) ordination of coral presence/absence for 20 sites from nine reef platforms of the Pleistocene highstand reefs of the Huon Peninsula (after Pandolfi [1996]) and seven reef platforms of the Pleistocene lowstand reefs of the Huon Gulf, PNG. Key: H, highstand reefs; L, lowstand reefs.

time, whereas greater abundances of platy *Acropora* and encrusting *Porites* occurred on the more recent reef platforms (Fig. 4; Appendix E). However, patterns of diversity as measured by Shannon's evenness remained constant. The change in community structure is coincident with gradual closure of the Huon Gulf, as indicated by tectonic models (Webster et al. 2004b). The high abundance of branching and stout branching *Acropora* found in older platforms occurred during a higher wave energy regime, while the later increase in platy *Acropora* and encrusting *Porites* occurred in a lower wave energy setting (Webster et al. 2004b). This correlation of coral species assemblage and wave energy is consistent with paleocommunities found in similar energy regimes elsewhere in the Indo-Pacific (Montagioni 2005). Thus, it is likely that the observed changes in coral community structure may be due to shifting energy regimes in the Huon Gulf over the last ~375 kyr.

Our sampling design of the lowstand reefs, constrained by submersible scheduling, was unable to evaluate intra-reef variability. Thus, it is plausible that species distribution patterns of lowstand coral assemblages were more variable in space than time. For example, temporal changes detected in the coral assemblages might simply have been the result of changes in the proportion of space occupied by various weakly detected or undetected sub-assemblages (spatial variation) under a directionally changing set of physical conditions. If so, persistence in community structure would have been characteristic of the coral, calcareous algae and foraminiferal components of lowstand reefs, even under conditions of environmental change. However, we doubt that such random sampling of a spatially

variable community could ever result in the incremental increases in community disparity we observed over time; as such, we believe that our results most probably represent true shifts in coral community structure from lowstand reefs.

Coral communities of lowstand reefs of the Huon Gulf showed shifts in community composition through a 244-kyr interval, whereas those of the later highstand reefs of the Huon Peninsula displayed persistence through a 95-kyr interval (Pandolfi 1996). The highstand reefs we studied occupied a significantly shorter, and later time interval than their lowstand counterparts, and occurred in a more consistent (high-energy) environmental setting, though both systems were subject to global changes in sea surface temperature and  $p\text{CO}_2$  (Pandolfi 1999). There also appears to be clear differences in the coral species composition between high and low sea stands (Fig. 5). Although lowstand reefs cannot be easily characterized due to their changing nature, and sampling technique varied from lowstand to highstand reefs, apparent differences between the systems can be attributed largely to greater dominance of *Platygyra* and digitate and stout branching *Acropora* in highstand reef assemblages, and greater abundance of *Montipora* on lowstand reefs (Appendix F).

The differences in the ecological dynamics of coral communities between high- and lowstand systems can be attributed to one of two possibilities. The first possibility is that the maintenance of diversity on high- vs. lowstand reefs was somehow different: the relative influence of various ecological processes over coral community structure differed between the two systems. For example, dispersal limitation might have increased during low sea level stands under conditions of reduced habitat that was more scattered than during high sea level stands. This dispersal limitation might also have increased through time as restriction of the Huon Gulf gradually increased, making lowstand reefs communities more susceptible to incremental change in taxonomic composition.

Alternatively, the variation in coral community composition through time observed in lowstand reefs might be entirely dependent upon community response to changing environmental parameters. In contrast to their highstand counterparts where local environments remained relatively constant through time, lowstand reefs changed in response to shifting energy regimes over time as the Huon Gulf narrowed. Thus it is likely that the difference in the species composition and temporal dynamics of coral community structure between the highstand and lowstand reefs is simply a reflection of environmental differences between the Huon Gulf and Huon Peninsula, rather than ecological differences manifested in the different meta-population structure between the reef types. However, differences in community composition between the two reef settings may have involved variation in both biotic and abiotic controls. Understanding the relative role of these controls will



require replicate, hierarchical sampling of Pleistocene low- and highstand reefs that have occurred in similar energy environments and across comparable time frames.

Regardless of whether lowstand reefs were extensions of highstand reefs that continuously tracked changing environments, or they were characterized by different underlying ecological dynamics, an important discovery in our work is that coral reef systems were viable during the periods of altered environmental conditions resulting from dramatic lowering of sea level. Coral reefs have the ability to maintain diverse and dynamic reef building structures under favorable tectonic conditions, even during low and falling sea levels. These dynamic systems would surely have played a significant role in the re-seeding of highstand reefs as rising sea level led to subsequent reef growth. However, a further question highlighted by the incongruence between the corals of lowstand and highstand reefs is the source of species of the highstand coral communities that were not found on lowstand reefs. Perhaps re-seeding of Huon Peninsula highstand reefs from lowstand reefs occurred on a more local scale than the distant Huon Gulf (Fig. 1) or later Huon Gulf communities were more similar to their coeval highstand counterparts on the Huon Peninsula than were those we studied that existed earlier.

Understanding the resilience of coral reefs, and the ways in which they respond to major disturbance has become a central issue in marine management (McCook et al. 2007). One prediction associated with climate change is a possible order of magnitude reduction in coral reef habitat as low latitude reefs succumb to mortality events associated with temperature-induced bleaching events (Lough 2008). Reduced areal extent of Pleistocene coral reefs during lowstands may provide an analogue for such a future scenario. Just as Pleistocene reefs may have survived regressions at tectonically favorable locations, modern reefs may well be able to exist in refugia long enough to reseed low latitude belts when temperatures become more favorable (Greenstein and Pandolfi 2008). However, present reefs may well have different composition and biotic influences than their former counterparts, and are certainly under enormous stress from anthropogenic impacts (Pandolfi et al. 2003, 2005). It is only through taking a long-term view of coral reefs that we can hope to understand how these ecosystems might respond to changes of the scope and magnitude that are occurring today.

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#### APPENDIX A

A figure showing taxonomic sampling curves for coral, benthic foraminifera, and calcareous red algae for lowstand Pleistocene reefs from the Huon Gulf, Papua New Guinea (*Ecological Archives* E091-016-A1).

#### APPENDIX B

Graphs showing the relative abundance of the most abundant benthic Foraminifera taxa at seven of the eight Pleistocene reefs examined from the submerged lowstand reef platforms of the Huon Gulf, Papua New Guinea (*Ecological Archives* E091-016-A2).

#### APPENDIX C

Graphs showing the relative abundance of the most abundant calcareous red algae taxa at seven of the eight Pleistocene reefs examined from the submerged lowstand reef platforms of the Huon Gulf, Papua New Guinea (*Ecological Archives* E091-016-A3).

#### APPENDIX D

A graph of Shannon evenness of lowstand corals over time from the submerged Pleistocene reef platforms of the Huon Gulf, Papua New Guinea (*Ecological Archives* E091-016-A4).

#### APPENDIX E

Graphs showing the relative abundance of the ten overall most abundant coral taxa at seven of the eight Pleistocene reefs examined from the submerged lowstand reef platforms of the Huon Gulf, Papua New Guinea (*Ecological Archives* E091-016-A5).

#### APPENDIX F

SIMPER analysis of coral taxa that contribute most to taxonomic differences between highstand reefs of the Huon Peninsula and lowstand reefs of the Huon Gulf, Papua New Guinea (*Ecological Archives* E091-016-A6).