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Environmental change preceded Caribbean extinction by 2 million years

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Paleontologists typically treat major episodes of extinction as single and distinct events in which a major environmental perturbation results in a synchronous evolutionary response. Alternatively, the causes of biotic change may be multifaceted and extinction may lag behind the changes ultimately responsible because of nonlinear ecological dynamics. We examined these alternatives for the major episode of Caribbean extinction 2 million years ago (Ma). Isolation of the Caribbean from the Eastern Pacific by uplift of the Panamanian Isthmus was associated with synchronous changes in Caribbean near shore environments and community composition between 4.25 and 3.45 Ma. Seasonal fluctuations in Caribbean seawater temperature decreased 3-fold, carbonate deposition increased, and there was a striking, albeit patchy, shift in dominance of benthic ecosystems from heterotrophic mollusks to mixotrophic reef corals and calcareous algae. All of these changes correspond well with a simple model of decreased upwelling and collapse in planktonic productivity associated with the final stages of the closure of the isthmian barrier. However, extinction rates of mollusks and corals did not increase until 3–2 Ma and sharply peaked between 2 and 1 Ma, even though extinction overwhelmingly affected taxa commonly associated with high productivity. This time lag suggests that something other than environmental change *per se* was involved in extinction that does not occur as a single event. Understanding cause and effect will require more taxonomically refined analysis of the changing abundance and distribution patterns of different ecological guilds in the 2 million years leading up to the relatively sudden peak in extinction.

Isthmus of Panama | paleoenvironments | time-lag | macroevolution | paleocommunities

Increases in extinction rates are commonly correlated with major changes in environments (1–4). However, inference of cause and effect requires detailed stratigraphic control of the relative timing of events (5–7) as well as independent knowledge of the biological characteristics and fates of different taxa to tease apart the environmental factors responsible (8, 9). In addition, it has become apparent that the traditional paleontological approach to understanding macroevolutionary patterns by measuring temporal ranges of taxa reveals only part of the evolutionary narrative, and that addition of actual occurrence and abundance data significantly broadens our understanding of the ecological underpinnings of biological change (7, 10).

These problems are confounded by evidence that ecological and evolutionary responses to both natural and anthropogenic perturbations may not closely coincide. Modern ecosystems commonly exhibit large scale, rapid shifts between alternative community states because interactions among organisms and their environments are nonlinear and governed by critical threshold effects (11–13). These ecological shifts result in dramatic decreases in the relative abundance of taxa associated with displaced communities, as in the cases of modern reef corals killed by algal overgrowth, disease, and bleaching (12, 14). However, decreases in abundance are not extinction, and it remains unclear how long the new ecological conditions must persist before extinction occurs. Thus, considerable time lags should be expected between environmental and ecological changes and their effects upon extinction, and similar temporal asynchrony almost certainly occurred over macroevolutionary time (7).

The major extinction of Caribbean reef corals and mollusks at the end of the Pliocene (1) has been attributed to a collapse in planktonic productivity due to changes in circulation patterns and upwelling when the straits of Panama closed (15–18). This hypothesis is consistent with shifts in the trophic composition and growth rates of mollusks (9, 18) and life histories of reef corals (19) before and after extinction, but the timing is bad because the peak in extinction occurred 2 million years (My) after the major oceanographic changes in the Caribbean associated with the final stages of closure as measured in deep-sea cores (20, 21). However, the timing of changes in near-shore sublitoral environments inhabited by the affected mollusks and reef corals is much more poorly constrained (1, 16, 18).

Caribbean and Pacific coastal waters of Panama today differ dramatically (22–25). In the Pacific, interannual and seasonal variations in temperature and productivity associated with El Niño events and upwelling are great, planktonic productivity is high, corals and seagrasses are rare to absent, and suspension feeders overwhelmingly dominate benthic communities. In contrast, the Caribbean coast experiences no upwelling, much smaller interannual and seasonal variability (24), and lower planktonic productivity. However, localized increases in planktonic productivity occur in some Caribbean coastal waters that are heavily influenced by terriginous runoff (25). Because of these local effects, as well as the patchy distributions of coral reefs, seagrass meadows, and carbonate sedimentation, Caribbean coastal environments are much more heterogeneous than in the eastern Pacific.

We used these differences across the Isthmus today as a model for interpretation of the paleoecological and macroevolutionary events in the Caribbean over the past 10 My. To this end, we constructed the first stratigraphically well constrained time series of changes in near-shore environmental conditions and total benthic ecosystem composition based on replicate quantitative sampling of the same sites used for determination of extinction rates. Coastal environments and benthic communities changed from Pacific to Caribbean conditions between 4.25 and 3.45 My ago (Ma), in phase with offshore waters and the near final closure of the isthmian straits. These results confirm that extinction occurred 2 My after the environmental and ecological changes that were most likely responsible.

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The authors declare no conflict of interest.

Abbreviations: My, million years; MART, mean annual range of temperature; PCA, principal components analysis.

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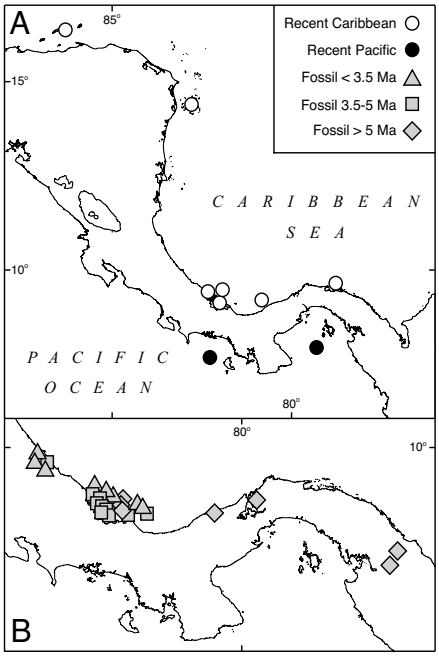

Fig. 1. Location of Recent (*A*) and fossil (*B*) faunules from which dredge and bulk samples were taken.

Rationale

Our study differs from most previous work by the incorporation of abundance data for the biota and measurement of environmental characteristics independently of, but in the same environments as, the organisms affected by extinction. Abundance data provide an essential measure of ecological success that may be unrelated to the number of taxa, which is the most common paleontological metric (7, 9, 10). Independence of environmental and biological measurements is necessary to avoid circular reasoning, and environmental measurements have to be made where the organisms once lived because conditions in near-shore environments vary much more among sites than in the open ocean.

We first characterized environmental and ecological variability along the coasts of the Isthmus of Panama today and then applied the same methods to ancient Caribbean sediments and fossils to document patterns of change through time. Recent data were derived from dredge and grab samples, whereas fossil data came from geological bulk samples from outcrops on land. Recent samples from the same geographic region and geological samples from the same region, age and formation were grouped into ecological units termed "faunules" for statistical analysis (refs. 1 and 26 and Fig. 1). Environmental conditions measured include the mean annual range of temperature (MART), sediment composition, and water depth. MART was determined from measurements of seasonal fluctuations in the size of cupuladriid bryozoan zooids with a precision of ±1°C (27, 28). High MART is a proxy for upwelling, which is the only known oceanographic mechanism that causes strong seasonal cooling of surface waters in the tropics. Measurements of sediment composition included mean % carbonate and mean % mud. Water depths were based on benthic foraminifera. The bulk ecological composition of faunules was measured as the percentage composition of >2-mm skeletal remains of higher taxa of the most frequently occurring fossils defined as calcareous algae, corals, bryozoans, bivalves, gastropods, and others (mostly echinoderms and crabs). Principle components analysis (PCA) was used to ordinate the faunules on the basis of ecological composition. The environmental variables (MART, % carbonate, % mud and depth) were then applied *a priori* to the resulting ordination to evaluate which factors explain the majority of biotic variation (see *Materials and Methods* for details).

Environments and Ecology Today

Environmental data and average bulk ecological composition for each faunule are presented in Table 1. Environmental proxies closely correspond to detailed instrumental observations of environmental variability in the two oceans (24, 25, 27). Estimated values of MART strongly correlate with the strength of regional upwelling along both coasts today. Moderate to high values of MART in the Pacific reflect the spatially variable seasonal cooling of surface waters that occur during times of upwelling, whereas consistently low values of MART along the Caribbean coast reflect the absence of upwelling-induced cooling of surface waters (24, 25). Percent carbonate is negatively correlated with upwelling and planktonic productivity that inhibit growth of corals and calcareous algae. However, planktonic productivity and % carbonate are also strongly influenced by runoff of sediments and nutrients from the land that increase planktonic productivity and dilute the carbonate content of sediments, albeit on a more local scale than upwelling (29). Due to the interplay of all these factors, sediments along the Pacific coast are uniformly low in carbonate, whereas sediments along the Caribbean coast exhibit a more complex patchwork of high- and low-carbonate environments (Table 1).

These environmental differences between the Pacific and Caribbean correlate well with variations in the proportional representation of major taxa of biotic assemblages from both oceans as demonstrated in the PCA of skeletal remains from Recent faunules (Fig. 2*A*). The first principal component explains 61.8% of the biotic variation and reflects the dominance of Pacific sediments by bivalve and gastropod mollusks versus the dominance of corals and calcareous algae in the Caribbean (Fig. 2*B*). The two exceptional Caribbean faunules most similar to the Pacific are from lagoonal environments in Bocas del Toro Province that are strongly affected by high levels of runoff (24, 25). As expected, the biotic differences between the two oceans are driven principally by the opposite trends of MART versus % carbonate (Fig. 2*B*). Thus, PCA axis 1 describes a trophic gradient along which the predominance of heterotrophic benthos corresponds to high MART and that of mixotrophic and autotrophic benthos corresponds to high carbonate.

Caribbean Environments and Ecology Through Time

Values of MART and % carbonate from fossil faunules reveal the dramatic transformation of Caribbean coastal environments over the last 10 My (Table 1 and Fig. 3 *A* and *B*). Faunules older than 5 Ma are characterized by high levels of MART and consistently low values of carbonate, strongly suggesting a coastal ecosystem influenced by upwelling and similar to the Eastern Pacific today. Considering that waters probably flowed through the straits of Panama from west to east (30), these high values of MART suggest that upwelling Pacific waters were entering and influencing the Caribbean coasts, although local Caribbean upwelling may also have occurred.

The first clear evidence of environmental change occurs at Cayo Agua 4.25 Ma (Table 1 and Fig. 3 *A* and *B*). Between then and 3.45 Ma, Caribbean environments went through a highly variable period of transition characterized by declining MART and increasing range of % carbonate (Fig. 3 *A* and *B*). These changes coincided with the final stages of the formation of a continuous Isthmus when the connections between the oceans became increasingly constricted (21, 30, 31) and the major shifts in open ocean water conditions occurred as recorded in deep ocean cores (20, 21). The occurrence of low values of MART during the transition mark the declining effects of Pacific waters upon the Caribbean coast of the Isthmus although the straits may not have been entirely closed. Consistently low values of MART

Table 1. Ecology and environment of Recent and fossil faunules

Faunule	Geological formation	Median age ± SD, Ma	Proportional weight of skeletal fraction >2 mm, %							MART, °C			% Carbonate		
			n	Bivalves	Gastros.	Bryos.	Corals	Algae	Others	Mean	CI	*n*	Mean	SD	*n*
Los Cochinos	Recent		16	16.01	9.41	7.17	12.23	55.01	0.17	2.60 (43)			62.83	26.26	16
Cayos Mosquitos	Recent		13	16.75	19.01	7.83	10.97	45.20	0.24	1.80 (43)			84.15	25.84	13
San Blas	Recent		22	26.38	26.24	19.17	8.18	18.82	1.21	3.13	0.52	8	67.37	24.64	61
Laguna Chiriqui	Recent		30	69.62	10.09	2.43	1.59	12.93	3.35	3.80*			35.24	17.87	87
Golfo de los Mosquitos	Recent		35	44.00	18.85	6.02	17.91	6.30	6.92	2.20 (43)			44.29	26.10	117
Bocas del Toro	Recent		54	38.98	25.12	8.18	10.88	3.15	13.69	3.39	0.38	10	33.58	27.46	72
Bahía Almirante	Recent		17	79.28	9.04	3.36	7.59	0.30	0.43	3.80*			28.06	10.39	51
Golfo de Panamá	Recent		26	56.86	32.14	8.75	0.70	0.00	1.55	8.38	1.46	10	30.09	23.55	74
Golfo de Chiriquí	Recent		55	71.02	24.85	0.75	1.12	0.38	1.88	5.92	1.77	10	24.99	12.63	112
Swan Cay	Swan Cay	1.4 ± 0.2 (26)	11	25.14	30.64	17.09	15.74	0.29	11.09	3.22	0.88	6	63.49	8.88	6
Upper Lomas del Mar	Moin	1.6 ± 0.1 (26)	27	12.45	22.38	24.98	35.70	2.02	2.46	2.82	0.90	5	43.28	10.71	9
Lower Lomas del Mar	Moin	1.7 ± 0.2 (26)	4	6.61	14.97	6.34	38.45	32.17	1.45	3.08	0.61	10	38.83	19.66	4
Northwest Escudo de Veraguas	Escudo de Veraguas	2.0 ± 0.1 (26)	6	31.11	62.38	2.58	0.27	0.01	3.65	3.88	0.76	10	37.66	12.25	4
Wild Cane Cay	Ground Creek	2.05 ± 0.15 (39)	8	12.48	24.99	2.29	52.62	5.09	2.53	4.19	1.00	6	45.76	23.84	7
Fish Hole	Ground Creek	2.6 ± 0.4 (26)	4	22.92	29.28	11.86	34.64	0.03	1.27	2.36	1.00	5	19.55	6.13	3
North central Escudo de Veraguas	Escudo de Veraguas	2.75 ± 0.85 (26)	7	14.59	57.35	9.31	9.42	0.00	9.32	2.68	1.14	5	35.44	15.29	5
Bomba	Rió Banano	3.05 ± 0.15 (26)	7	50.68	34.78	10.35	1.65	0.00	2.54	3.13	0.64	11	68.96	12.72	5
Bruno Bluff	Shark Hole	3.45 ± 0.15 (26)	6	52.06	41.73	1.69	3.05	0.00	1.46	6.95	1.05	10	13.52	3.74	5
Isla Solarte	Old Bank	3.55 ± 0.05 (26)	5	40.67	14.73	39.34	3.28	1.09	0.89	6.68	1.13	10	54.10	7.64	2
Santa Rita	Rió Banano	3.55 ± 0.05 (40)	11	42.99	22.71	21.49	5.86	4.11	2.84	5.73	1.01	10	44.40	11.47	7
Cayo Agua, Punta Nispero south	Cayo Agua	3.55 ± 0.05 (26)	4	58.85	25.54	8.68	3.00	0.00	3.93	7.23	1.07	10	26.10	15.87	8
Cayo Agua, Punta Nispero west	Cayo Agua	3.55 ± 0.05 (26)	3	34.98	57.62	3.30	1.56	0.06	2.47	7.23†	1.07	10	26.10†	15.87	8
Northeast Escudo de Veraguas	Escudo de Veraguas	3.55 ± 0.05 (26)	9	23.37	42.95	11.06	15.45	1.81	5.35	2.68	1.14	5	41.40	6.12	6
Cayo Agua, Punta Norte east	Cayo Agua	4.25 ± 0.75 (26)	5	49.40	43.84	4.18	1.60	0.00	0.98	4.11	0.79	10	18.87	5.63	6
Cayo Agua, Punta Piedra Roja	Cayo Agua	4.25 ± 0.75 (26)	9	49.04	25.87	6.53	17.32	0.03	1.22	3.52	0.51	10	27.73	9.43	9
Cayo Agua, Punta Norte west	Cayo Agua	4.25 ± 0.75 (26)	5	44.43	30.89	12.01	8.08	0.59	4.00	6.25	1.08	10	15.93	3.65	3
Isla Popa	Cayo Agua	4.25 ± 0.75 (26)	7	80.12	15.25	2.60	0.02	0.00	2.01	6.65	1.16	10	19.77	4.95	5
Shark Hole Point	Shark Hole Point	5.65 ± 0.05 (26)	6	23.53	72.60	0.00	0.11	0.00	3.75	5.22	0.90	11	14.25	7.29	11
South Valiente west	Shark Hole Point	6.29 ± 0.97 (41)	8	61.12	38.37	0.01	0.00	0.00	0.50	6.16	1.52	9	18.22	8.85	7
Rió Tupisa	Tuirá	6.35 ± 0.75 (42)	6	70.77	28.13	0.05	0.00	0.00	1.05	6.65	2.25	8	15.28	2.80	6
Rió Chico N17	Tuirá	6.35 ± 0.75 (42)	9	78.32	19.42	0.15	0.00	0.00	2.11	8.67	0.58	8	20.11	9.73	8
Finger Island	Nancy Point	6.9 ± 1.3 (26)	5	42.88	56.11	0.07	0.06	0.00	0.88	6.17	1.14	7	16.55	6.43	5
Rió Calzones	Unnamed	8.25 ± 2.95 (26)	7	80.50	9.09	0.48	1.11	0.18	8.64	5.96	0.83	11	15.02	4.57	5
Mattress Factory	Gatun	9.0 ± 0.4 (26)	3	67.12	32.88	0.00	0.00	0.00	0.00	6.18	0.59	11	24.55	7.61	6

Relative composition of taxa, MART estimated from cupuladriid bryozoans, and % carbonate are shown. CI, 95% confidence intervals.
*Temperature data from Smithsonian Tropical Research Institute Environmental Science Program.
†MART and carbonate data from Cayo Agua, Punta Nispero south were used.

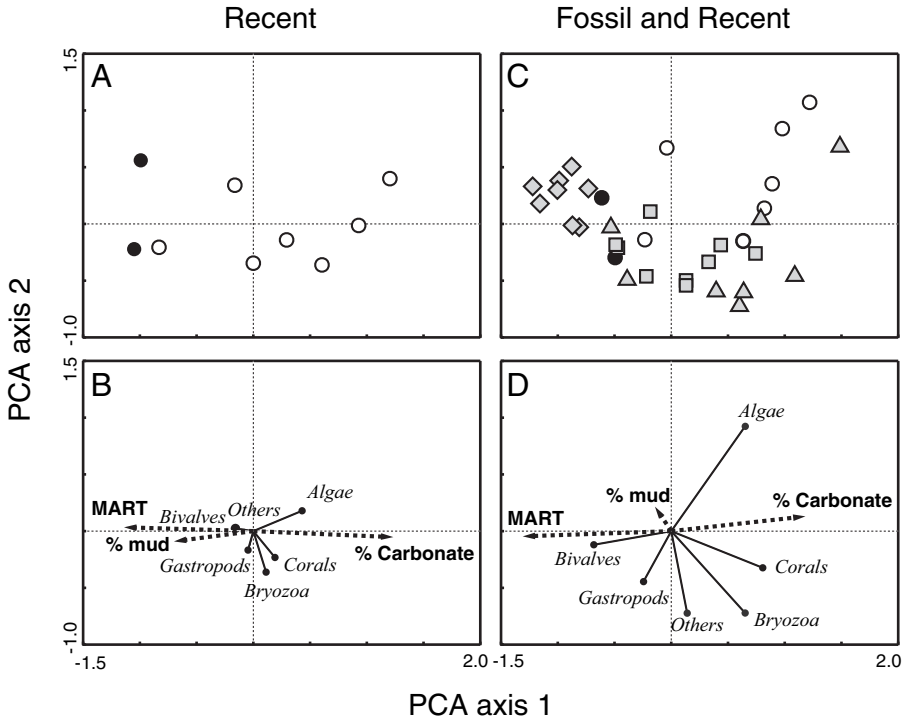

Fig. 2. Ecological structure of Central American Recent (*Left*) and fossil and Recent faunules (*Right*). (*A*) Ordination of Caribbean recent faunules based on biotic composition. (*B*) Taxa and environmental variables that best explain the ordination. PCA axis 1 describes a gradient from predominantly heterotrophic bivalves to mixotrophic corals that closely correlates with carbonate production and mean annual range of temperature (MART). (*C*) Adding the fossil Caribbean faunules to the ordination produces a similar pattern with scores of most fossil faunules intermediate between those for Recent Caribbean and Pacific faunules that again (*D*), reflects the opposite distributions of bivalves and corals correlated with MART and % carbonate. In *B* and *D*, solid lines with terminal spots are ordinations for different taxa. Dashed lines with arrows are environmental correlations that best explain the ecological variation observed. See Fig. 1 for legend.

after 3.45 Ma indicate that sustained upwelling could not have occurred, whereas the wide range of carbonate levels during this time are consistent with the mosaic of depositional environments typical of the southwestern Caribbean today (23–25, 29).

PCA of both Recent and fossil faunules together produces the same general pattern that we observe in the Recent, with faunules spread out along PCA axis 1 which accounts for 56.8% of the variation in biotic composition and again represents a gradient from heterotrophic to auto- and mixotrophic biotic assemblages (Fig. 2*C*). Just as in the Recent, these differences reflect the opposite distributions of bivalves and gastropods versus corals and algae that are best explained by opposite trends in MART and % carbonate (Fig. 2*D*).

Environmental and community changes with time are plotted together in Fig. 3*A–C*. Faunules older than 4.25 Ma as described by the first principal component of community composition closely resemble recent Pacific assemblages dominated by mollusks (Fig. 2*B*), whereas fossil faunules younger than ≈3.45 Ma resemble Recent Caribbean faunules that are wide-ranging in ecological structure from heterotrophic communities dominated by mollusks to auto- and mixotrophic communities rich in corals and coralline algae. The causal relationship between community composition and the environmental factors is strongly supported by the highly significant linear regressions between community composition as measured by PCA axis 1 and both MART and percent carbonate from the same samples (Fig. 4).

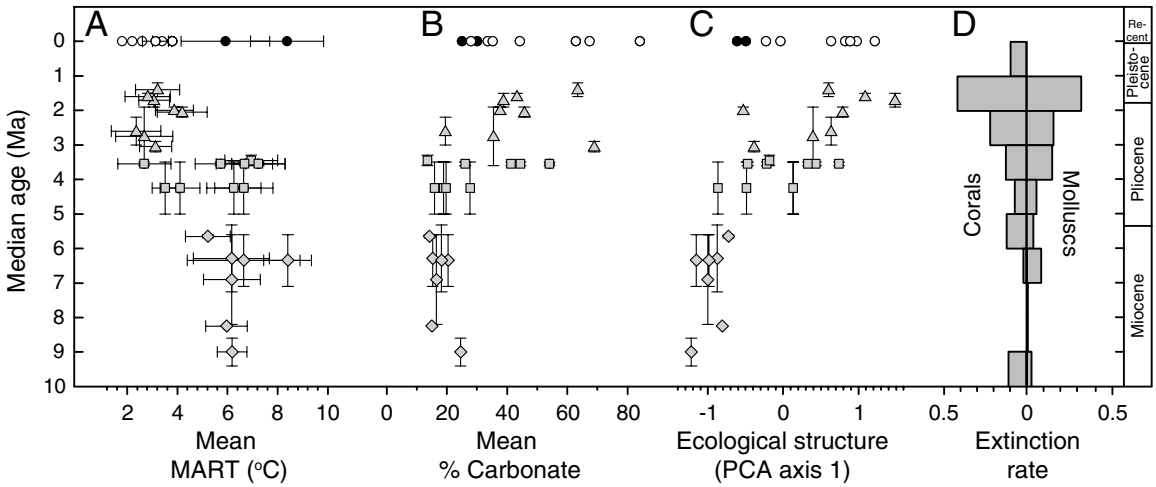

Fig. 3. Chronology of environmental and ecological changes in the coastal southwestern Caribbean over the last 9 My. (*A*) Ecological structure of biotic assemblages estimated by PCA axis 1 in Fig. 2. (*B*) Percent carbonate of ≤2 mm fraction. (*C*) Mean annual range of temperature (MART) estimated by using the zooid size profiling technique on cupuladriid bryozoans. (*D*) Extinction rates for coral species (1) and molluscan genera and subgenera (13). See Fig. 1 for legend. Horizontal error bars indicate 95% confidence intervals. Vertical error bars indicate maximum and minimum age estimates of faunules.

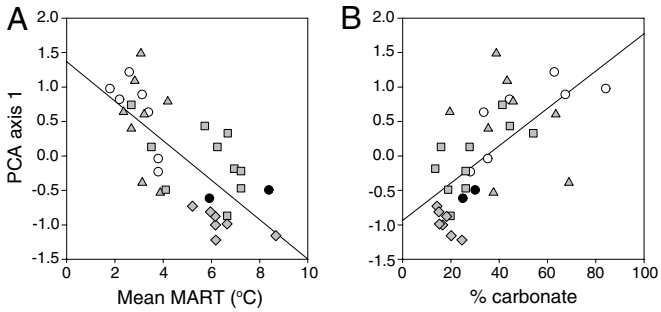

Fig. 4. Relationship between environmental variables and ecological structure measured as PCA axis 1 scores for each recent and fossil faunule. (*A*) MART ($y = -0.286x + 1.3665$, $R^2 = 0.52$, $F = 35.30$, $P < 0.001$). (*B*) Percent carbonate ($y = 0.0271x - 0.9363$, $R^2 = 0.42$, $F = 23.34$, $P < 0.001$). See Fig. 1 for legend.

Evolution and Environment

Our analysis places real constraints on the timing of near-shore environmental and ecosystem change in the southwestern Caribbean based on independent data for environments and organisms. Environments and benthic communities defined in terms of the relative abundance of different major taxa turned over in apparent synchrony between 4.25 and 3.45 Ma (Fig. 3 *A–C*). In striking contrast to this straightforward result, the peak in extinction of corals and mollusks did not occur until 2–1 Ma, although extinction rates began to rise as much as 2 My before (Fig. 3*D*). This gradual rise before the peak is probably real because sampling of Late Pliocene faunas is generally excellent (1, 10, 19, 26), and although extinction began earlier, the major peak may have occurred even later than our estimate of 2–1Ma, due to lack of Pleistocene samples <1.5 Ma (Table 1).

Thus, most of the extinction of corals and mollusks during the past 4 My occurred 2 My after the dramatic decline in seasonality (and by inference upwelling and productivity). This finding is remarkable because extinction most severely affected taxa associated with high productivity, including filter-feeding and predatory mollusks (9, 17, 18) and small corals, which inhabited deep seagrass habitats dominated by abundant bryozoans and other suspension feeders (19, 32). This time lag naturally begs the question of what other environmental changes besides a collapse in productivity may have been responsible. Alternatives suggested previously include cooling due to the onset of Northern Hemisphere glaciation (17, 33) and increasing variance in oceanographic conditions and rates and magnitude of sea level fluctuations due to Late Pleistocene intensification of glacial cycles (34, 35). However, coincidence of these events with extinction is also poor, and there is no paleobiological evidence comparable to the decline of suspension feeders (9, 17) to suggest a causal link. Barring evidence of any reasonable alternative mechanism, the massive extinctions in corals and mollusks must somehow be related to the drop in productivity despite the 2-My delay between the environmental change and hypothesized biological effects.

Our data reveal the general sequence of events in Tropical America but can only hint at the underlying causes. The first clue is that extinction was not a distinct event, despite the striking peak in extinction rates 2–1 Ma, but was more drawn out, suggesting a chain reaction of ecological events that affected different taxa at different times and with varying intensity of extinction over several My. For example, large differences in timing and intensity of extinction occurred among encrusting, erect, and free-living cheilostome bryozoans (32). The second clue is that our coarse ecological groupings are almost certainly missing important ecological information. For example, although the relative proportion of corals reached present-day Caribbean values in the Cayo Agua formation ≈3.5 My (Table 1), these corals are typically ahermatypic or small hermatypic species associated with deep seagrasses, rather than the large, light-loving hermatypic corals that dominate the Caribbean today. However, this clear ecological difference is too fine to be picked up in our analysis.

Thus, the key to understanding the extinctions will be to more finely dissect the tempo and mode of ecological changes that occurred between the initial environmental perturbation associated with the collapse of upwelling and productivity and the peak in extinction 2 My later. This can be achieved by analyzing the abundance and extinction rates of different ecological guilds of species of all of the major benthic taxa, defined by their similarity in modes of resource acquisition and ecological roles within the community (36, 37).

Materials and Methods

Sampling. Dredge samples were collected from shelf depths along the Caribbean and Pacific coasts of Panama from 1995 to 1998 [see Fig. 1 and supporting information (SI) Table 2]. Samples were washed on deck with an 8- and 2-mm mesh and dried for sorting and picking of skeletal remains in the laboratory. Approximately 10-kg geological bulk samples were obtained from Panamanian and Costa Rican Neogene shelf and shallow slope deposits (see Fig. 1, Table 1, and SI Table 2). Ages of samples are median values of minimum and maximum ages based on microfossils from the sample or interpolated from ages of samples stratigraphically above and below (Table 1). Samples were disaggregated by soaking, and then sieved with a 2-mm mesh, dried, sorted, and picked for skeletal remains using the same methods as for the Recent samples. Recent sediment samples were obtained by using a Van Veen grab sampler. For both Recent and fossil samples, ≈100 g of sediment was removed from each grab or bulk sample for analysis of % carbonate and % mud. See SI Table 2 for details on the distribution of sampling in space and time.

Data Collection. The MART of faunules was estimated from seasonal variations in zooid area measured along axes of growth of 38 recent and 218 fossil cupuladriid colonies. Variation in zooid area within single colonies closely reflects variation in temperature in which the bryozoan lived with a precision of about ±1°C (27, 28). Percent carbonate was determined by acid digestion (HCL 1:1) of the <2 mm fraction of 753 sediment samples. Percent mud (<63 μm) was measured from grain size analysis of the <2-mm fractions of 448 dry samples. All skeletal remains of organisms ≥2 mm were separated into corals (overwhelmingly reef building taxa), calcareous algae (mostly corallines and *Halimeda*), bivalve mollusks, gastropod mollusks, bryozoans, and all others combined. Each skeletal fraction was weighed to obtain its relative abundance in each sample (Table 1).

Data Analysis. Biotic and sediment data were transformed by using $y' = \log^{y+1}$ to correct for nonnormality of proportional weight data. The mean weight % of each taxon from each faunule was used to ordinate the faunules by PCA. Average values of MART, % carbonate, and % mud for each faunule were added *a priori* after ordination of samples to explain the variation observed (38). Mean depth of each faunule was used as a covariate because environment and ecology are known to vary with respect to depth. The resulting ordinations show the relative importance of taxonomic groups across samples, and the relationship with environmental variables. Per-taxon extinction rates are numbers of last occurrences divided by the total numbers of taxa present per My interval (1).

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