ECOLOGY

Coral reef diversity losses in China's Greater Bay Area were driven by regional stressors

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Observations of coral reef losses to climate change far exceed our understanding of historical degradation before anthropogenic warming. This is a critical gap to fill as conservation efforts simultaneously work to reverse climate change while restoring coral reef diversity and function. Here, we focused on southern China's Greater Bay Area, where coral communities persist despite centuries of coral mining, fishing, dredging, development, and pollution. We compared subfossil assemblages with modern-day communities and revealed a 40% decrease in generic diversity, concomitant to a shift from competitive to stress-tolerant species dominance since the mid-Holocene. Regions with characteristically poor water quality—high chl-a, dissolved inorganic nitrogen, and turbidity—had lower contemporary diversity and the greatest community composition shift observed in the past, driven by the near extirpation of *Acropora*. These observations highlight the urgent need to mitigate local stressors from development in concert with curbing greenhouse gas emissions.

INTRODUCTION

Contemporary environmental monitoring has documented that the biosphere and associated biogeochemical cycles therein have been human-dominated for decades (1–4). Concomitant to increasing human influence is a decline in global biodiversity (1), resulting from an exponential rise in species extinctions (3), as well as documented losses in genetic, phylogenetic, and functional diversity (2). Coral reefs, rich in both biodiversity and economic value, are severely affected by global change (4). The branching and plating corals that have been the dominant carbonate producers and framework builders on tropical coral reefs for almost 2 million years may be "living dead" in the midst of a major Anthropocene extinction event (5).

Over the last few decades, the impact of anthropogenic activities on coral reefs has been widely researched. Recent studies consistently highlight a global state of coral reef loss (6–9). Reef degradation is caused by widespread mortality and limited recruitment of scleractinian corals linked to bleaching (10), disease (11), susceptibility to predators such as the crown-of-thorns sea star (6), physical destruction (12), and other land-use oriented impacts (13). However, the main driver(s) of these impacts, their relative importance in causing coral mortality, and how they interact with one another are still debated (14). Global meta-analyses aimed at resolving this debate have resulted in conflicting conclusions. Studies have shown the main causes of coral mortality to be (i) global factors such as ocean warming that are not associated with local population density (15), (ii) human activity such as overfishing leading to decreased coral cover (16), (iii) cumulative impacts from the "human density effect" causing a reduction in reef-building organisms (17), or (iv) variable impacts dependent on location and management (18). However, some have argued that the natural variability inherent to coral reefs makes generalizing a single, "smoking gun" stressor impossible, particularly at a global scale. What is more productive is the understanding that the future of coral reefs will continue to be controlled by the interaction of multiple local (e.g., overfishing and eutrophication) and global (e.g., climate change) human factors (19).

A critical gap that pervades coral reef ecological analyses is a lack of historical baselines from which to assess the relative impact of human development before the emergence of anthropogenic ocean warming. Without knowledge of pre-Anthropocene coral community composition, studies using only contemporary data fail to understand the historical context that shaped modern coral community assemblages. Therefore, it is difficult to know whether current ecosystem dynamics are unique, or part of a system's natural variability (20). These baselines also provide a necessary framework to better conserve and manage reef ecosystems for the future (21, 22). When a study only analyzes modern communities, conclusions about changes in biodiversity may be confounded by historical human impacts (23, 24) and the shifting baselines syndrome (25).

We argue that the most effective approach for understanding mechanisms of recent coral declines are case studies that integrate data from modern and past times at a local to regional scales. This approach can also be a powerful tool for crafting effective conservation strategies. Several examples of this approach have highlighted the role humans have played in causing coral reef degradation before modern observations (7, 24, 26, 27). Specific studies have identified the unprecedented decline in fast-growing *Acropora* (27–29), which can lead to decreased accretion rates (30) and lower habitat complexity (31–33) on reefs. Some studies have gone further, leading to the implementation of successful reef management actions.

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By integrating modern ecological surveys with historical data, Jackson *et al.* (*34*) concluded that local factors, mainly overfishing of herbivorous parrotfish, were associated with Caribbean reef loss/decline. In response to these findings, areas that have enacted rigorous fishing management have seen increases in parrotfish abundance and subsequent improvement in reef health and resilience relative to areas without similar management. Although it is clear that climate change will ultimately make many reef habitats inhospitable to corals, the method used by Jackson *et al.* (*34*) could identify areas that would most benefit from local interventions by distinguishing the relative impact of various stressors at regional scales. Yet, the majority of ecological studies investigating human impacts on reefs have been focused in eastern Australia and the Caribbean (*35*). Other regions of the world that harbor higher coral diversity, such as the Central Indo-Pacific, are now lacking in research, creating a knowledge gap that could inhibit successful management and conservation of reefs in the future (*35*).

Here, we start to fill this gap by looking at spatial diversity variation through time within China's "Greater Bay Area" (GBA). The GBA in China's southern Guangdong Province is located within the South China Sea (SCS), ~700 km from the Coral Triangle that harbors the greatest coral diversity in the world (Fig. 1). The GBA itself was created as part of a national development initiative, aimed at physically and economically linking 11 different megacities into one megalopolis by 2050 (*36*). This large-scale development plan could have catastrophic consequences for the GBA marine environment, which accounts for more than 25% of all of China's marine biodiversity records (*37*). This biodiversity includes ~90 species of scleractinian corals (*37, 38*), which is relatively high for marginal reefs that commonly host less than 50 species (*39–41*). The co-occurrence of high diversity and extreme urbanization [an increase of >100 million people in the last 40 years; (*42*)] makes the GBA an appropriate choice for investigating historical trends in coral communities as a result of severe local stressors and more recent global change. Corals are a model system to study impacts to the marine environment as they are fragile animals that can be highly susceptible to human perturbations (*43, 44*). Presently, the GBA coastal marine environment includes both coral communities affected by highly polluted waters outflowing from the Pearl River, as well as communities influenced by ocean currents with oligotrophic water just tens of kilometers away. These unique "regions" occur across a spatial scale small enough to be exposed to identical global forces. Collectively, they represent an experimental gradient across which the historical and contemporary impacts of urbanization can be investigated. Although ideal for investigating regional and local scale impacts to marine life, there is presently a dearth of coral reef data for this area (*7, 45*).

We analyzed coral community composition and diversity across time and space within the GBA to achieve three main goals: (i) establish a historical baseline for coral biodiversity in the GBA, (ii) assess spatial changes in diversity (number of genera) and community composition (proportion of coral morphologies) through time, and (iii) identify the major stressors influencing present coral biodiversity. We determined poor water quality driven by increased urbanization to be the main stressor influencing local coral composition and identified a specific target for future management interventions. This investigation is timely. Global development is projected to triple the urban land cover and its associated negative effects to the surrounding environment by 2030, with many newly urbanized areas occurring adjacent to coastal environments especially in eastern and southeastern Asia (*46*).

MATERIALS AND METHODS
Study area and historical context
The Hong Kong Special Administrative Region (Hong Kong) is approximately 130 km south of the Tropic of Cancer with a subtropical climate. It is located at the mouth of the Pearl River in the southeastern part of the GBA (Fig. 1). The Pearl River stretches for ~2200 km with a drainage area of 453,700 km^2 and releases 80% of its annual discharge during the wet season (March to October). This discharge forms a fresh, nutrient-rich plume that extends eastward as far as the Taiwan Strait (*37*). During the dry season, this plume is reduced and isolated to the southwest of Hong Kong, leaving wind, tidal forcing, and oceanic currents to be the dominant forces in the east. This water regime causes areas of the marine environment to be eutrophic and presents a strong gradient of dissolved inorganic nitrogen (DIN) concentrations ranging from >100 μM in the south and west to >2 μM in the east (*38*). The nutrient sources from this expanding urban area are diverse, including industrial effluent, sewage, fish farming wastes, DIN derived from atmospheric deposition, and oceanic DIN (*37, 38*). This gradient in water sources and human pollution leads to a spatially divided marine ecosystem around Hong Kong, with southern communities influenced by Pearl River effluent and eastern communities influenced by oceanic water mixing (*47*). As expected, scleractinian coral cover and diversity follow this same gradient (*38*). Hong Kong is home to more than 90 species of hard coral, supporting only about 1 coral species in the south, to more than 50 species in the east (*38*). This paper used these two regional distinctions (South and East, Fig. 1) for statistical comparisons of coral communities.

Historically, anthropogenic stressors in the GBA, including coral mining, fishing, dredging, development, and pollution, have affected coral communities for more than 200 years. The earliest documented impact to coral communities was mining for slaked lime, which extracted live corals and carbonate deposits (*48*). This industry likely spanned centuries and, at its peak in the mid-1900s, crews of more than 200 boats would extract more than 36 metric tons of coral annually (*49*). Despite coral mining inflicting substantial damage to the local coral communities, the ecosystem was assumed to have recovered when ecological surveys began in 1980 (*47*). Yet, the true impact of coral mining in the GBA is poorly understood.

Indirect stressors to coral communities increased later via agriculture, then by local and destructive fishing practices, and, last, through urbanization. Agriculture in the 1950s, particularly with the rise of pig farming and the introduction of more than 1 million animals to supply growing demand in China, resulted in the increase of coastal pollution through to the 1970s (*50*). This period also saw the rise and fall of the local fishing industry. Between 1950 and 1998, fishing catch per unit effort dropped over 60% (*51*), and annual landings from Hong Kong waters went from a high of 31,400 tons in 1979 to just 13,200 in 2010 (*52*), both due to an overexploitation of the local fishing stock (*51, 52*). Destructive fishing, including the use of explosives (blast fishing), was a common practice in Hong Kong from the early 1900s until it was banned in the mid-2010s (*53*). These damaging agricultural and fishing practices likely had major ecological effects on marine communities of the GBA, such as decreasing herbivory and associated negative impacts as observed in Caribbean reefs (*54*).
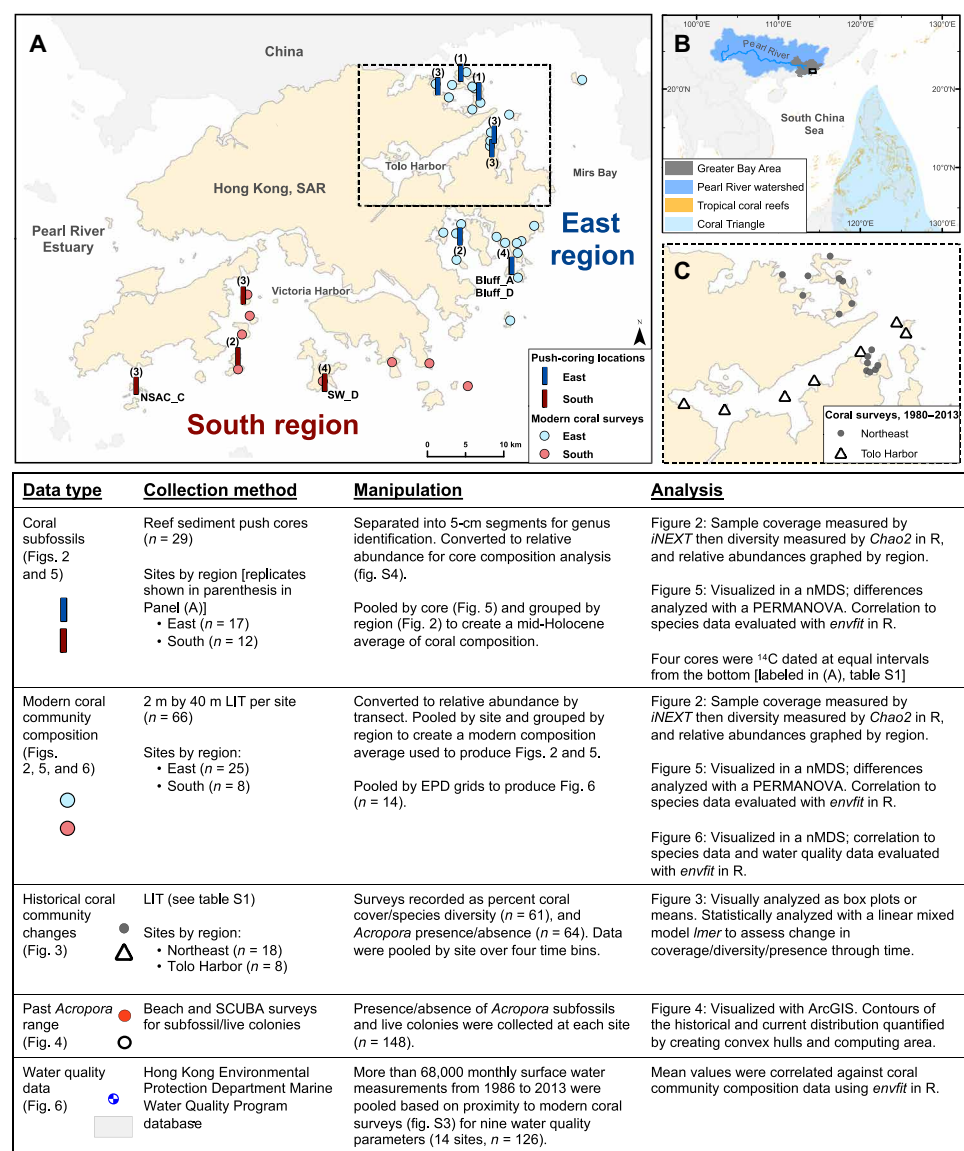
Fig. 1. Map of Hong Kong SAR. (**A**) Close-up of the study area and the sampling effort. Elongated rectangles denote locations where replicate sediment push cores were taken, and circles denote areas where replicate benthic transects were surveyed. The sampling effort is separated into the South region (red hues) and the East region (blue hues) for analysis. Cores with ^{14}C dated subfossils are labeled next to their sampling location. (**B**) The study area and its location in the southeastern portion of the GBA of China, approximately 700 km from the coral triangle. (B) also highlights the Pearl River watershed that discharges just west of Hong Kong into the Pearl River Estuary. (**C**) Close-up of the area and sampling effort for coral surveys from the 1980s. The gray circles and the black outlined triangles highlight the northwest area of Mirs Bay and Tolo Harbor survey sites, used to produce Fig. 3 (A and B). Descriptions of the data and analyses used to produce figures throughout this study are detailed in the table below the map.

More recently, further degradation of water quality has ensued from explosive urbanization. Excessive heavy metal contamination has been implicated in the complete eradication of corals from inner Tolo Harbor in the 1980s (*55*, *56*). The Pearl River outflow is highly turbid from high levels of sediment, another known coral stressor (*57*, *58*). Although sedimentation has been decreasing due to upriver damming over the last 50 years (*59*, *60*), low light continues to limit primary productivity in western waters (*61*). Extensive land reclamation throughout the 1980s increased silt loads and caused a documented loss of 40% of coral cover in two marine embayments (*47*). However, much of the impact from these stressors on corals within the GBA is poorly understood since local benthic surveys did not begin until the 1980s, well after the putative impacts.

Subfossil assemblage collection

To reconstruct past coral communities (Fig. 2), 29 sediment push cores were collected from 11 sites in 2016 (Fig. 1). The core internal barrel diameter was 7.6 cm, and lengths ranged from 2 to 3.5 m. When possible, three to four replicate cores were taken at each site ~5 m apart from the first core, which was chosen haphazardly adjacent to the shoreline and within present-day coral habitats. All cores were taken at water depths of 3 to 5 m, immediately adjacent and as close to live coral communities as possible without causing damage (<1 m). Following collection, cores were extruded, sediment was split into 5-cm segments, and coral subfossil fragments were identified to genus for diversity analysis (see Supplementary Methods).
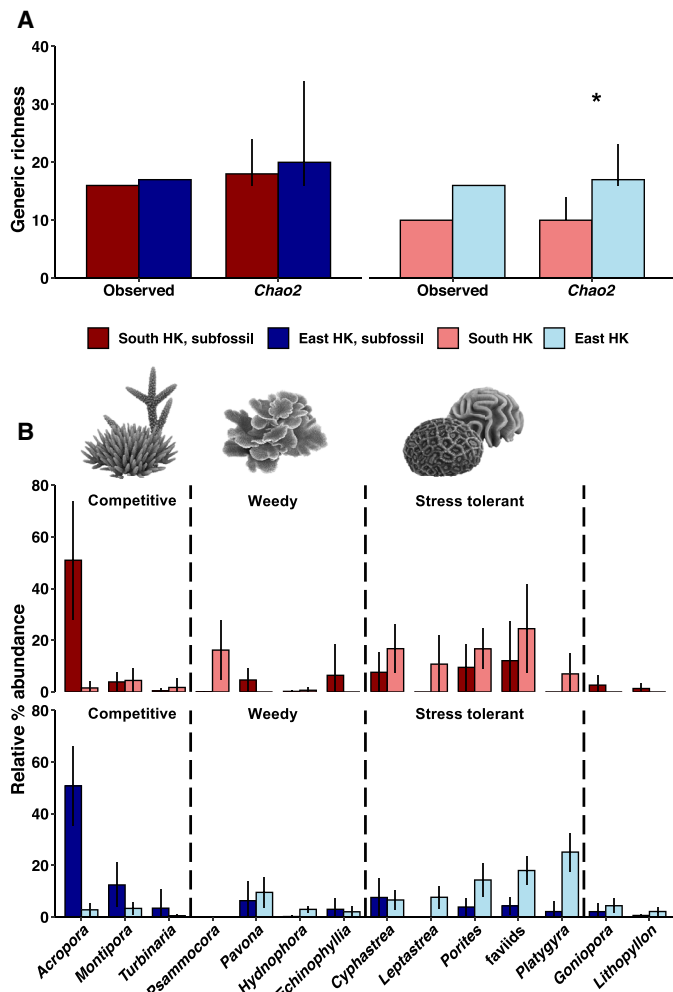
Fig. 2. Coral community composition through time. (**A**) Observed generic richness between the South and East regions in the past (subfossil) and modern (transect) datasets. The *Chao2* diversity index was used to extrapolate generic richness for the region. The error bars represent 95% confidence intervals. A log transformation was used for all estimators so that the lower bound of the resulting interval is at least the number of observed species. Asterisks indicate significant differences in coral diversity in the modern data. (**B**) Relative abundances of coral from the South and East regions in Hong Kong, for subfossil and modern data. The dashed lines separate the genera into three different coral life-history strategies as outlined in Darling *et al.* (*72*): competitive, weedy, and stress tolerant. The two genera *Goniopora* and *Lithophyllon* were not included in the Darling *et al.* (*72*) analysis and are not grouped accordingly. The error bars represent 95% confidence intervals.

Modern assemblage collection

In 2013, coral diversity and benthic cover data were collected from 33 sites (Fig. 1). At each site, a quick underwater visual census was first conducted to locate areas with highest coral coverage to obtain the highest possible estimate for coral cover and diversity for each location. Two 40-m transects were then placed parallel to the shore over coral colonies at water depths ranging from 3 to 6 m. A line intercept transect (LIT) method was used to determine the diversity of coral assemblages and coral colonies were identified to genus level on-site. These identifications were verified by photographs, which were checked against a local coral taxonomy guide book (*62*) as well as *Corals of the World* (*63*).

Historical coral community surveys

Modern quantitative coral surveys began in Hong Kong in 1980 and were only focused in areas of known high diversity and cover at that time (northwestern Mirs Bay, Fig. 1). To assess changes in coral communities since 1980, all known published surveys that had both coral cover and identified genera were compiled (*56, 64–71*) (table S5). Data were then binned between Tolo Harbor and the northwestern portion of Mirs Bay (Fig. 1). In general, Tolo Harbor is defined by a strong west-to-east pollution gradient, driven by effluent outflow and long retention times, whereas the northwestern portion of Mirs Bay has more oceanic flushing, leading to better water quality (*47*). To make accurate comparisons from the varying studies, only those that used line transects to determine benthic composition were compiled. Because of low sampling effort between 1999 and 2009, one study that used remote operated vehicle (ROV) video transects was incorporated (*64*). To determine *Acropora* presence/absence throughout the surveys, all sites were pooled for analysis (Fig. 3).

Past *Acropora* range

To help determine community structure change in coral assemblages, 148 beaches and dive sites were surveyed between 2013 and 2016 to document the presence or absence of remnant *Acropora* skeletal fragments (Fig. 4). *Acropora* was the genus chosen for this analysis for five reasons: (i) its known importance as a reef-building coral, (ii) its importance as one of the only competitive genera for the study area (*72*), (iii) its known global decline (*29*), (iv) its susceptibility to perturbations making it a good indicator of environmental quality (*39*), and (v) its focus in numerous other regional studies (*24, 26, 28, 29, 73*). This mapping aimed to reconstruct the past distribution of *Acropora*; as such, only fragments visible at the surface of the beaches and seafloor were included. At each location, some fragments were collected and brought to the laboratory to confirm the genus identification. We assume that the coral fragment distribution shown in Fig. 4 represents in situ mortality, and therefore a local range collapse, rather than postmortem relocation owing to storms and currents (see Supplementary Methods).

The current distribution of *Acropora* was based on observations of living specimens while scuba diving and complemented by an extensive compilation of survey data used in Duprey *et al.* (*39*), which covers the period of 1998–2006. The Global Positioning System coordinates of each site were recorded, and the data were visualized with the geographical software ArcGIS. The contours of the historical and of the current distribution of *Acropora* were defined by creating a convex hull from each dataset. The area of each distribution was then calculated.

Water quality data

The Hong Kong Environmental Protection Department (EPD) water quality database includes data from 76 locations within Hong Kong waters that have been collected since 1986 (fig. S3). At each station, 24 water quality parameters are monitored monthly at three different depths: bottom, mid-depth, and surface. Surface parameters measured at 1 m below the surface were used in this study because symbiont bearing scleractinians are typically found at shallow depths in Hong Kong (*47*). Nine physiochemical and nutrient-related water quality parameters were selected as potential drivers of coral diversity based on previous studies (*38, 74*). Physicochemical parameters chosen were salinity, sea surface temperature (SST), pH, and

dissolved oxygen concentration (DO), and nutrient parameters were chl-*a* concentration, DIN concentration (DIN = $NH_3 + NO_2 + NO_3$), dissolved inorganic phosphorus concentration (as phosphate; DIP), particulate suspended matter concentration (PSM), and turbidity. The dataset used in this study includes more than 65,000 monthly measurements ranging from 1986 to 2013 (when the modern coral assemblages were surveyed, table S2).

Radiocarbon dating
Fourteen radiocarbon dates were produced from six coral fragments and eight marine bivalve shells in four different cores (South region: two sites; East region: two replicate cores from one site; Fig. 1, fig. S4, and table S1). For all coral samples, *Acropora* spp. fragments were used, as they represent the dominant genus in all cores (fig. S4). Five-centimeter core segments to be dated were selected starting from the deepest segment of the core and then moving up in an evenly spaced distribution (fig. S4). Then, from each selected core segment, samples that were greater than 2 g were randomly chosen and cleaned of any encrustation and visible bio-eroders before being sent for dating. Accelerator mass spectrometry (AMS) ^{14}C analyses were conducted at National Ocean Sciences AMS laboratory of the Woods Hole Oceanographic Institute and the University of Tokyo.

Statistical analysis
For quantitative diversity analysis, both subfossil and modern datasets were converted to relative abundance. To better understand core composition, relative abundances of *Acropora* versus all other taxa in each individual 5-cm segment were calculated and plotted by depth (fig. S4). To determine a Holocene average for the subfossil communities collected, relative abundances of subfossil data were pooled and calculated per sampling unit (one core) by dividing the weight of each genus of coral by the total weight of coral fragments. Relative abundances of living coral recorded in modern transects were determined by dividing the number of colonies of a certain genus by total colonies for that sampling unit (one transect). To investigate relative abundances in three temporal bins, the cores were subsampled into two sections: the top 10 cm of each core (youngest subfossils) and the remaining lower sections (oldest subfossils). Relative abundance was then recalculated for each of these sections. We assumed that this created three temporal bins for our data: the modern surveys (modern), the top 10 cm of the cores (recently dead), and the lower of the cores (subfossil).

To assess the extent that coring and modern survey sampling methods captured the species richness of the study area through time, sample-based rarefaction analysis was conducted using the iNEXT package in R (fig. S1). The analysis followed the methods described in Chao *et al.* (*75*), allowing for the creation of both rarefaction and extrapolation curves (reliable to twice the sampling number). Once sampling coverage was determined to be complete for each time period, generic richness was calculated and compared for both datasets using the bias-corrected *Chao2* index with the *SpadeR* package in R (Fig. 2). This estimator provides a nonparametric lower bound of true species richness (*76*).

Before further analysis, "rare" taxa (those accounting for <0.5% of total mass of identified coral genera: *Acanthastrea*, *Alveopora*, *Caryophylliidae*, and *Galaxea*) were excluded, as it has been shown that the inclusion of rare taxa in historical datasets can result in unreliable statistical analysis, since their occurrence in the fossil record could be due to chance alone (*77*). All remaining taxa were then categorized based on coral life-history stages discussed by Darling *et al.* (*72*).

To visualize the differences of coral assemblages between regions and through time, data were plotted using non-metric multidimensional scaling (nMDS) and overlaid with SD ordination ellipses based on Bray-Curtis dissimilarity matrices (Fig. 5A) (*78*). Ordination ellipses were calculated and plotted based on 1 SD from the centroid. Stress vectors were overlaid onto the nMDS using the *envfit* function within the *vegan* package (*79*), using genus scores derived from the coral relative abundances. The purpose of this analysis is to identify the variables that are driving the compositional differences in coral assemblages. To assess the possibility that time averaging within the cores could be the cause of increased diversity in subfossil assemblages, the three data groupings (modern, recently dead, and subfossil) were rerun in the same nMDS analysis as described above (fig. S5).

Inherent sampling biases may exist when comparing spatial transect and temporal sediment push-core data, which could make direct statistical comparisons inappropriate. Therefore, only the pattern of a spatial separation between the East and South regions (i.e., the regions being more similar in the past and less similar in the present) could be inferred. This approach of using spatial patterns rather than absolute numerical changes has been shown by Tyler and Kowalewski (*80*) as a successful way to draw reliable comparisons between modern and past taxa datasets. To further investigate this potential bias, we also analyzed the subfossil and modern datasets in separate nMDS ordinations (fig. S2). The finding of regional separation in the modern data, as well as the coral genera driving this change, was unaltered.

To quantitatively test the hypothesis that past and modern coral assemblages are different, a two-way permutational multivariate analysis of variance (PERMANOVA) was conducted with 9999 permutations (table S3A). To further test that the regions (East versus South) were different in each time point (past and modern), a post hoc pairwise PERMANOVA with sequential Bonferroni significance correction was conducted (table S3, B to E). The assumption for the PERMANOVA of homogeneous spread was checked with the *betadisper* function and a subsequent ANOVA; the results were not significant ($P = 0.173$), indicating even spread among regions.

To test whether coral richness, coral cover, and the presence/absence of *Acropora* had changed since modern surveys were initiated in 1980, data were grouped into four time bins based on data availability: the first full surveys in 1980, 1981–1989, 1990–2009, and 2010–2013 (incorporating the modern dataset used in this study). If more than one independent survey was conducted for a site within that time bin, both the percent coral cover and the total generic richness were averaged. The data were visualized using *ggboxplot* in R, grouped by site and by time bins. Data for *Acropora* presence/absence were grouped together to assess overall change for the area. Changes in coral richness, cover, and the presence/absence of *Acropora* were analyzed using the *lmer* (*81*) linear mixed model function in R, with time as a fixed effect and site as a random effect. Pairwise post hoc comparisons to determine significant differences between time bins were performed using the "Tukey" test and "Holm" significance level correction.

To investigate the effects of environmental factors (nutrient: chl-*a*, PSM, DIN, DIP, and turbidity; physiochemical: DO, temperature, pH, and salinity) on coral community composition, modern coral abundance data and EPD environmental parameters were divided into approximately 5 km by 5 km grids around Hong Kong [fig. S3;

(*38*)]. Each grid contained at least one EPD water sampling station and at least one modern coral community sampling location (fig. S3). For each grid, the monthly EPD water quality data were pooled and averaged for the period of 1986–2013. Similarly, the modern coral transect data were pooled and the corresponding community composition based on relative abundance was recalculated. The resulting pooled coral community data were then projected on an nMDS plot (Fig. 5). All nine water quality parameters were incorporated into the *envfit* function in the *vegan* package in R to determine those that were significant. The function *envfit* evaluates how each environmental variable individually correlates with nMDS1 and nMDS2. Generic community composition was also analyzed against the community composition data using the *envfit* function in the *vegan* package in R. Statistical significance was assessed based on 9999 permutations.

Taphonomic considerations

Postmortem taphonomic bias of coral skeletal preservation can affect estimates of biodiversity used in this study. For example, varying physical (e.g., skeletal density and morphology) and environmental (e.g., grazing/bio-eroding preferences) properties can alter the perceived biodiversity of the past by preferentially eroding or eliminating the skeletons of certain coral species. Furthermore, using the push-coring method could lead to a bias against the collection of massive corals' subfossils due to their large size and density, making core penetration through them difficult. This could result in a subfossil record biased toward branching taxa. Although it is difficult to fully alleviate these biases, the pattern of decreased prevalence of *Acropora* through time is most likely ecological and not taphonomic for five reasons: (i) Our live and subfossil assemblages collected are very similar in total generic composition, indicating that we were successful in capturing the subfossils of those taxa that would typically be considered massive (Fig. 2); (ii) consistency of the observed trend (i.e., high-relative abundance of *Acropora*) throughout most of our cores and individual core segments, even when accounting for other branching genera present in the study area that would have been subject to the same fragmentation bias (fig. S4); (iii) the historical decline of *Acropora* documented in both benthic surveys from 1980 (Fig. 3) and death assemblages (Fig. 4); (iv) consistency with the greater global fossil record that spans multiple environments and climates (*29*); and (v) the knowledge that the early life stages (*82*) and overall resilience (*27*) of *Acropora* are highly sensitive to human perturbations and have been shown to be at risk in our study area (*38*). We therefore argue that the most parsimonious interpretation of the change in relative abundance of *Acropora* between the fossil and modern record is mortality due to changes in the marine environment.

RESULTS

Diversity and composition of coral assemblages from mid-Holocene to modern day

[14]C dating of two cores from each region revealed that the subfossil record spanned the period from ~5000 years before present (ybp; present is 1950) to modern (table S1). Estimates for vertical accretion rates were calculated for each region, averaging about 4.6 mm/year in the East and 0.45 mm/year in the South (see Supplementary Methods and table S1). Analysis of coral subfossils collected in 29 sediment push cores (Fig. 1) shows a clear past dominance of the relative abundance of competitive genera (*Acropora, Montipora,* and
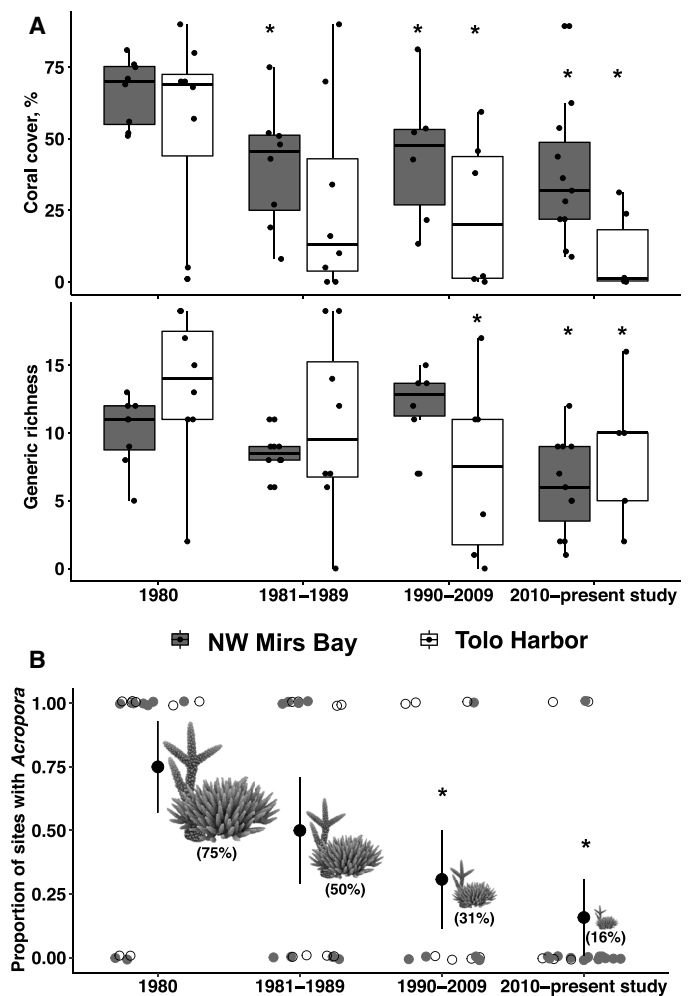
Fig. 3. Recent declines in coral communities. (**A**) Generic richness and coral cover for the northwest area of Mirs Bay (gray) and Tolo Harbor (white). Data were pooled into four time bins based on available surveys collected from 1980 to 2013 (*56, 64–71*). Asterisks indicate significant differences in means from the first surveys in 1980. (**B**) Proportion of sites that recorded *Acropora* for all surveys from (A) combined. Jittered points for each time bin represent the raw presence/absence data (1 or 0, respectively) and are color-coordinated to locations from (A) (Northwest Mirs Bay: gray; Tolo Harbor: black with white outline). The error bars represent 95% confidence intervals. The sizes of the *Acropora* animations are proportional to 1980, which represents presence in 75% of surveys. The asterisk indicates significant differences in means from the first surveys in 1980.

Turbinaria; Fig. 2B). Competitive corals are typically branching and characterized as highly productive and fast-growing in ideal conditions, but extremely sensitive to external stressors (*72*). This observation differed from modern surveys (Fig. 1), which showed a greater relative abundance of stress-tolerant genera (*Porites*, faviids, *Platygyra*, and *Leptastrea*; Fig. 2B), slow-growing massive corals that can persist in chronically harsh environments with low light and high sedimentation (*72*). The observation of more competitive coral genera in the cores versus more stress-tolerant corals in the transect data was consistent across both East and South regions (Fig. 2B). The increase in stress-tolerant coral abundance could be a true overall increase in massive coral growth, or simply a relative increase concurrent with the decline of competitive genera.

Observed subfossil generic richness showed similarity between the South and East regions (16 and 17 genera, respectively; Fig. 2A); however, modern generic richness differed by 6 (10 in the South region and 16 in the East; Fig. 2A). Extrapolation of diversity using the *Chao2* diversity index verified this pattern, with similar values across regions in the past, but different values between regions recently (Fig. 2A). The strong agreement between the measured richness and *Chao2* estimated patterns of diversity demonstrates the robustness of this result (*83*), which shows a ~40% difference in generic richness between regions in the modern dataset. Because the

Chao2 estimator is a nonparametric estimator of the lower bound of true species richness (*75*), this is likely a conservative estimate of genera lost. The separation of the 95% confidence intervals of mean modern generic richness in the *Chao2* indicates this result is statistically significant (*75, 76*). In both time frames, the rarefaction (or species accumulation) curve (fig. S1) approaches 1 (~0.99 for both datasets), indicating that only ~1% of the genera in the study area were not sampled (*84*). Thus, the conclusions drawn for each region during both time periods are based on a sufficient sampling.

Both the northwest area of Mirs Bay and Tolo Harbor (Fig. 1C) have experienced significant declines in coral generic richness (*P* = 0.006 and *P* = 0.005, respectively) and cover (*P* ≤ 0.001 and *P* = 0.008, respectively) when compared to surveys in 1980 (Fig. 3A and table S4). This finding is based on analysis of the first surveys of coral communities in the study area (*47*) up to the most recent dataset collected in 2013 (table S5). Beyond this significant decline in cover and diversity, there has been a concurrent drop in *Acropora* occurrences (*P* ≤ 0.001; Fig. 3B). In 1980, *Acropora* was present in 75% of transects for the Northeast and Tolo Harbor combined; by 2013, only 16% of transects recorded living *Acropora* (*56, 64–71*).

Beach surveys that collected coral fragments revealed that the past *Acropora* distribution equaled about 759 km², with a western-most boundary located along the eastern coast of Lantau Island (Fig. 4). Now, living *Acropora* colonies are seen only on the eastern area of Hong Kong, with a western boundary located on the southern tip of Lamma Island, over an area of about 347 km². The distribution area of *Acropora* has thus experienced a reduction of 54% compared to its past range.

Community composition based on relative abundance of coral genera appear different between the subfossil and modern datasets, visible by their separation when plotted in multivariate space on an nMDS ordination (stress = 0.20; dimensions = 2; Fig. 5A). These datasets separate out not only temporally but also spatially between regions as shown by the SD ordinance ellipses; the ellipse centroids of the past South and East regions overlap, while those of the modern regions are completely separated (Fig. 5A). This overall difference in coral composition through time and space appears to be driven by different genera. This is indicated by the stress vectors, which showed
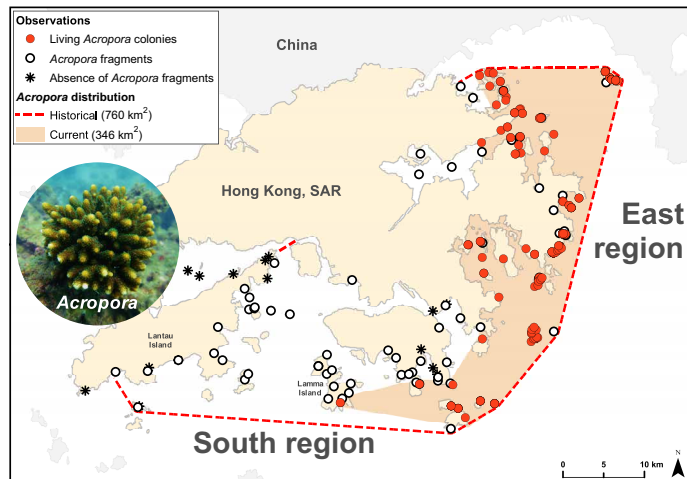
Fig. 4. *Acropora* range contraction within the Hong Kong SAR. This map encompasses the same study area as Fig. 1, with the Pearl River discharging to the west. Red filled circles indicate sites where live *Acropora* were found during diving surveys; white open circles indicate areas where *Acropora* subfossils were found among seafloor sediments during dive surveys, or on the nearest beach. Asterisks indicate sites where no live or dead *Acropora* were found. The red dashed line and light-red shaded area are interpolations of the past and modern *Acropora* range, respectively. The past range determination was made by considering sites where only subfossils were found to be those that have hosted live *Acropora* in the past, but presently do not support live populations.
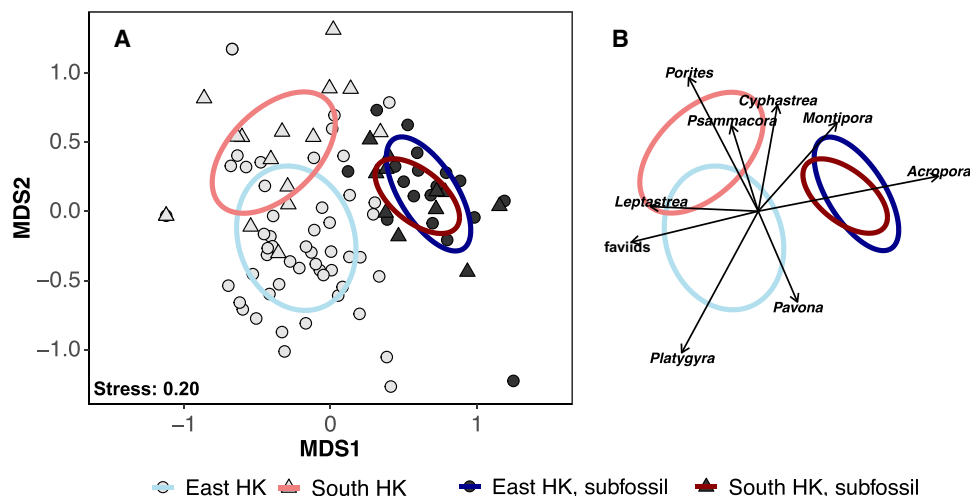
Fig. 5. nMDS of coral community composition. (**A**) nMDS showing subfossil (black) and modern (light gray) community composition data for East (circles) and South (triangles) regions. Ellipses are of SD. (**B**) Stress vectors created using *envfit* with the coral genera scores, shown only for genera that are statistically significant in driving the spread shown in the nMDS.

Acropora to be significantly associated with subfossil assemblages, whereas stress-tolerant genera are associated with modern assemblages (Fig. 5B). These patterns are maintained if the subfossil and modern datasets are plotted separately as well (fig. S2). Separating the data into three temporal bins (modern, recently dead, and subfossil) did not change this finding of regional and temporal separation (fig. S5). Analysis conducted to produce fig.S5 shows that the recently dead corals are most similar to the subfossil dataset, with their composition being driven by *Acropora*.

The PERMANOVA tests (table S3) quantitatively verified the nMDS results, showing that the relative abundance of coral assemblages differed significantly for age ($F = 24.12$, $P < 0.001$) and across sites ($F = 2.97$, $P < 0.001$). Pairwise post hoc tests with Bonferroni correction (hypothesis = 2) were applied to the modern and subfossil data, to compare differences between the South and East regions in each time period. The past South and East regions were not different ($F = 0.43$, $P = 0.91$), whereas the modern South and East regions differed significantly ($F = 5.20$, $P < 0.001$). This pattern was maintained if the data were split into three time bins (modern, recently dead, and subfossil) as well, showing that the relative abundance of coral assemblages differed significantly for age ($F = 16.98$, $P < 0.001$) and across sites ($F = 2.45$, $P = 0.001$). Pairwise post hoc tests with Bonferroni correction (hypothesis = 5) showed that this was driven by differences between the East and South regions in the modern ($P < 0.001$), with no differences between regions in the recently dead ($P = 1$) or the subfossil ($P = 1$) and no difference between the recently dead and subfossil for the South region ($P = 1$) and East region ($P = 1$). All tests were run with 9999 permutations.

Water quality is the major driver controlling modern coral community composition

Water quality was the main factor driving the dissimilarities in community composition in the modern dataset between the South and East region, represented by chl-*a*, DIN, and turbidity—all proxies for eutrophication (Fig. 6; permutations = 9999). However, since these are all nutrient-related parameters, they are highly correlated (Pearson's correlation between 0.81 and 0.88), and it is inappropriate to assess

them together. Therefore, depending on the individual parameter chosen, 42 to 48% of the variation in coral community composition was explained by water quality (turbidity: $r^2 = 0.48$, $P = 0.03$; chl-*a*: $r^2 = 0.46$, $P = 0.03$; DIN: $r^2 = 0.42$, $P = 0.05$).

DISCUSSION

"*Taking a rowboat…I went further down the harbor than ever before. In a bay near the N.E. part of Hong Kong Island I found a considerable variety of corals (Astreae, Madreporae, etc.) many of large size, attached to the boulders below low water mark.*"

—William Stimpson, naturalist and marine biologist, 28 May 1854 (*85*)

Stimpson's observations prove that corals once thrived in what is now one of the most species-poor and urbanized harbors of the GBA. Our study quantified past changes in these communities with implications for future management of the region. Remnant skeletal fragments were used to improve the spatial, temporal, and taxonomic resolution of coral reef decline as the area transformed from small fishing villages to a global trade megalopolis. Today, much of the GBA coastline is heavily urbanized and defined by high nutrients and turbidity, generally poor water quality that is typical of many cities in Southeast Asia (*86*). Our results illustrate that local stressors, particularly those that degraded water quality, were the main forces that have led to the coral community composition found today. Thus, the GBA presents an area of great potential for high return on investment into local stressor mitigation, specifically improvements in water quality and targeted restoration toward defined historical baselines (*22*). With aggressive conservation interventions, it is possible that marginal reef communities can act as climate refugia for reef-building corals in the coming decades despite continued warming (*87*) as suitable habitat will continue to decrease for corals closer to the equator (*88*).

Subfossil assemblages were more similarly diverse than modern communities

Coral communities between the East and South regions were more similar in the past in comparison to the present (Figs. 2 and 5
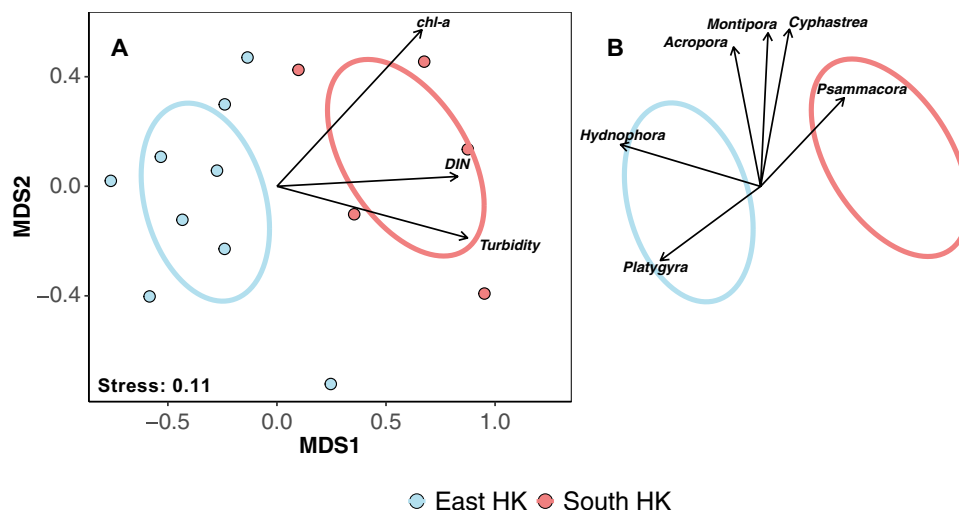
Fig. 6. nMDS of modern coral community composition versus EPD water quality parameters. (**A**) Modern coral community and water quality data (table S2) were combined based on their EPD grids in fig. S3. Ellipses represent SD ordinance ellipses. Stress vectors using *envfit* were calculated from the EPD water quality data and overlaid onto the coral composition data. Only the water quality parameters that were significantly driving coral composition were plotted. (**B**) Stress vectors created using *envfit* with the coral genera scores, shown only for genera that are statistically significant in driving the spread shown in the nMDS.

and figs. S1 and S2). In addition, we found that changes in coral community composition were driven by the loss of crucial habitat-building competitive corals, resulting in a present-day community composed primarily of massive, stress-tolerant corals (Figs. 2, 3, 4, and 5 and fig. S2). Sensitive *Acropora* have seen their range collapse by 54%, with the greatest losses occurring in areas with dense urbanization in close proximity to the Pearl River (Fig. 4).

This demise of *Acropora* is a trend that has been seen globally (*24, 26, 28, 29, 73*), and particularly in the SCS (*89, 90*), though the GBA specifically had previously been absent in meta-analyses owing to insufficient data (*7*). *Acropora* has experienced a global decline from being dominant within many reef systems for the last 2 million years (*29*) to local extirpation. Regional-scale declines in *Acropora* on major reef ecosystems including the Great Barrier Reef (*26*) and the Caribbean (*24, 73*) began almost a century ago (*28*). We believe that localized *Acropora* extirpation and community shifts occurred more recently in the GBA, paralleling the recent population boom: from 16 million people in 1980 to more than 55 million in 2012 (*91*). This population rise was concomitant to increased urbanization, maritime trade, and environmental degradation (*91*), which ultimately led to poor water quality driven by nutrient enrichment (*92*).

Acropora was consistently recorded when quantitative coral surveys first began in 1980 (Fig. 3B), although it was never shown to be the most abundant genus in those surveyed sites. Literature from the 1970s qualitatively recorded *Acropora* as a dominant genus in areas such as Tolo Harbor (*93*); however, the genus is now completely absent from these areas [Fig. 4; (*22*)], indicating its disappearance during the general community decline since that time. This is supported by more recent surveys taken in 1980–2013, which show the stepwise disappearance of *Acropora* (Fig. 3B) (*22, 65*) that occurs along the harbor's pollution gradient (*38*). Recent uranium-series dates of *Acropora* subfossils supports our hypothesis that death assemblages are just decades old [though some were hundreds of years old (*27*)]. This interpretation was bolstered by our binning of coral data by three time periods, which found the top 10 cm of the cores to be more similar to older subfossil data than to modern transects. Had the shift in coral community occurred earlier, there would have been time for dead coral skeletons from the newer community to accumulate and be represented in the top of the cores. We infer that the slight deviation in shape and centroid from the subfossil to the recently dead coral (fig. S5) means that this community change has occurred recently and is therefore not yet fully represented in the fossil data. Vertical accretion estimates of our cores from the South and East region (~0.45 and 4.5 mm/year, respectively; table S1 and fig. S4) are similar to those previously reported in the same areas [~0.2 and 4.6, respectively (*94*)]. Even at the slowest accumulation rate, this would mean that *Acropora* fragments collected (Fig. 5) would be covered with sediment after only a few decades, unless they were all stirred up by storms, which is unlikely. Taken together, we conclude that the *Acropora* range collapse (figs. 3 and 4) and consequential coral community shift (Fig. 5) occurred conservatively within the last 100 years, though it was more likely caused by GBA urbanization beginning in the 1980s. Similar findings of human perturbation leading to *Acropora* loss have been documented since the 1960s in Hainan Island about 650 km to the southwest of the GBA (*90, 95*) and since the 1980s in Daya Bay, northeast of Hong Kong (*89*). Our past reconstruction corroborates with these studies and shows the *Acropora* decline to be regionally consistent and expands upon them by showing this occurrence to be unique on a millennial time scale.

Loss of ecosystem function due to widespread decline of *Acropora*

The loss of fast-growing *Acropora* and other competitive, branching morphospecies within coral assemblages often results in a decrease in reef accretion rates (*30*), though accretion can vary widely from high to low even in non-acroporid dominated reefs (*96*). It can also result in lower habitat complexity (*31–33*) as slower-growing, more stress-tolerant massive corals and algae begin to dominate (*33*). Shifts from branching to massive morphologies decrease reef structural complexity and can lead to substantial changes in biotic processes such as predation and competition, and can decrease overall fish biomass and diversity (*97*). Complexity loss can also decrease diversity of coral-associated invertebrates, which represent the highest biodiversity on reefs (*98*). Under the current levels of local eutrophication and high turbidity that are known stressors to competitive genera (*72*), it is unlikely that the dominance of *Acropora* observed in the historical record and their associated ecosystem functions can be recovered regionally. Combined with future projections of climate change, regional stressors will continue to exacerbate the global decline of *Acropora* (*10, 99*).

The loss of *Acropora* and its unlikely recovery have particularly drastic consequences for the GBA. *Acropora* represents the major competitive and only completely branching genus in the study area and therefore has a unique functional role by creating high rugosity. This lack of branching coral diversity means the region has low functional redundancy, a feature unique to "high-latitude marginal reefs" (*100*). For example, whereas tropical coral communities may be able to buffer the negative impacts associated with an *Acropora* loss by the succession of another branching coral genus, the GBA cannot. Although there are other competitive coral genera in the GBA, they occur in much lower relative proportions to *Acropora* (Fig. 2) and therefore contribute less to overall habitat complexity.

This shift from competitive to stress-tolerant dominated communities is expected based on the life-history strategies outlined by Darling *et al.* (*72*) and the water quality stressors affecting the GBA (Fig. 6). Competitive species, which are the fastest-growing and greatest carbonate producers for reef accretion, are only dominant in those environments "ideal" for coral growth and are highly sensitive to environmental change (*72*). Conversely, stress-tolerant species are those that have adapted to persist in chronically harsh environments and to a number of stressors, such as low light and high sedimentation (*72*). This shift in dominant taxa therefore indicates severe environmental change within the GBA. There are few weedy genera in the GBA, all of which occur in relatively low abundances (Fig. 2). These genera are those that are known to be opportunistic and can rapidly recolonize a recently disturbed area (*72*). This paucity of weedy species in the GBA indicates the unlikely event that future disturbances will result in rapid coral succession. Instead, it appears that the GBA coral communities have shifted almost completely to stress-tolerant genera, whose slow growth and simple complexity make them poor habitat builders. In short, the drop in *Acropora* abundance in the GBA represents not only a decline of a single genus but also the loss of a complete functional niche within the marine community.

Eutrophication controls modern coral community composition

Our data implicate that poor water quality, represented by increased chl-*a*, DIN, and turbidity, is the driving force shaping modern coral communities (Fig. 6). This conclusion corroborates with the findings

of Duprey *et al.* (*42*), which showed an increase in DIN concentrations that peaked in the 1980s during rapid urbanization. Their conclusions that local eutrophic waters have led to the present coral richness southeast gradient are supported by our subfossil baseline. There are well-known direct and indirect negative effects of increased dissolved inorganic nutrients and turbidity on coral health. Direct impacts to biological processes include declines in calcification and photosynthesis rates, as well as fecundity (*101*). Indirect impacts include increases in bioerosion, disease prevalence, competition from macroalgae, and decreases in facilitation by coralline algae (*101*). Furthermore, nutrient enrichment has been shown to disrupt the vital symbiosis between coral and their photosymbionts, resulting in negative effects to coral physiology (*102*). All of these adverse effects are likely playing a role to decrease coral health and extirpate highly sensitive coral from the GBA region.

However, coral sensitivity to water quality varies among different genera. *Acropora* is known to be a "highly sensitive" genus, susceptible to poor water quality induced by increased nutrients and decreased light penetration (*38*). Conversely, slower-growing stress-tolerant corals, such as *Platygyra*, faviids, *Porites*, *Pavona* (those genera that are associated with modern communities; Figs. 2 and 6), are more resilient to water quality degradations (*38*). This predicted community shift based on genus-specific resilience to degraded water quality is represented in our findings (Figs. 2 and 6) and shows stress-tolerant, slower-growing massive corals dominating the modern reefs.

The influence of global stressors on modern coral communities

Climate variability has also been linked to Holocene coral community shifts (*50*) and modern reef degradation (*9*, *15*). Yet, there is no evidence that climate is the dominant force controlling modern coral community composition in the GBA. Paleoclimatic reconstructions within the SCS have shown that sea level and seasonal water flows of the Pearl River have been stable since the mid-Holocene [~7000 ybp (*103–105*)]. SSTs within the SCS have varied during the Holocene, with waters 1° to 2°C higher during the mid-Holocene climatic optimum about 5500 ybp, leading to a long-term SST decline, which lasted until subsequent warming due to the industrial revolution in the 1860s (*87*, *106*, *107*). These high- and low-SST periods have been linked with increased and decreased coral growth, respectively, in both coral reefs south of the GBA (*87*) and marginal reef communities in Daya Bay (*106*). Although out of the scope of this study, it is possible that during the period of about 5500 to 200 ybp, corals within the GBA experienced a prolonged decrease in growth and productivity as seen elsewhere in the SCS due to decreased temperatures (*106*) and a weakening of the Asian monsoon (*108*). However, Clark *et al.* (*106*) found that recent SST warming due to global industrialization in the 1800s has actually led to an increase in coral growth and productivity in regional coral communities. In addition, Duprey *et al.* (*42*) found salinity and SST based on $\delta^{18}O$ proxies to be stable from 1820 to 2007 and concluded that global warming did not greatly affect coral communities during this time.

For GBA corals in modern times, there have been no documented temperature or nutrient-driven mass bleaching events or disease outbreaks; the only recorded bleaching events were linked to hypoxia and decreased salinity caused by a severe rainfall event (*109*). However, Xie *et al.* (*109*) showed that these events were small scale and localized (catchment scale), with bleaching typically resulting in less than 15% mortality. The trends in genus-specific decline in our study indicate regional-scale impacts, associated with areas of degraded water quality. Had global drivers been the cause of this decline, they would have affected our entire study area uniformly. It is possible that global stressors are causing impacts to coral communities that have yet gone undetected. However, because of the evidence outlined here, and the agreement with other studies in the area, we conclude that these impacts are yet minor.

Multiple stressors on local coral communities

Our evidence that local eutrophication is the dominant force shaping modern coral communities (Fig. 6), coupled with support from Duprey *et al.* (*42*) and other historical literature (Fig. 3A), adds yet another case study of how coral reefs have suffered from human development over the last two centuries. Similar studies worldwide are converging on a common observation that anthropogenic stressors were playing a major role in shaping global coral communities before modern-day surveys (*23*, *24*, *110–112*). The GBA, which had more than 8 million people living in the area before 1980, is certainly no exception. The collective past stressors from resource extraction (*49*), agricultural (*50*), destructive fishing practices (*53*), heavy metals (*56*), and riverine driven turbidity (*61*) all combined with the outflow of more than 1.5 million m³ daily of sewage that was untreated until 2001 (*92*), represents one of the most widespread and chronic suites of anthropogenic stressors to coral reefs in the GBA and perhaps all of the SCS.

Although high coral diversity for marginal habitats persists within the GBA today, our data clearly illustrate that past reefs were more diverse, more structurally complex, and had a greater spatial footprint (Figs. 2, 3, 4, and 5). In summary, we propose the following explanation of the evolution from past to modern-day coral composition in the GBA. Community composition between the East and South regions was homogeneous in the Late Holocene. With the permanent settlement of the area, local stressors to coral communities increased mainly through forms of resource extraction and local pollution, likely decreasing the community's resilience to future stressors. Then, as regional urbanization and population increased exponentially over the last few decades, coral communities were inundated with polluted water driven from increased anthropogenic nutrients, pushing them beyond their known tolerances (*38*). This impact was greater in the South region because of its close proximity to the Pearl River. The catchment effectively concentrates the anthropogenic footprint for Guangdong Province and releases it as a nutrient-rich plume into the GBA, creating a large water quality gradient over a small spatial scale. Localities with the worst water quality have lost entire genera, including an almost complete extirpation of susceptible *Acropora* (Fig. 4). These changes have led to a completely altered composition of modern coral communities, now dominated by stress-tolerant but slow-growing species.

This study serves as a reminder that reefs were already undergoing dramatic changes owing to local human activities before and concomitant with modern climate stressors. Although climate was not the dominant cause of past coral reef degradation in GBA, it remains a serious threat to their future survival. The coral communities of the GBA could potentially represent a climatic "bright spot," similar to those defined by Cinner *et al.* (*18*) as they have yet avoided any major climatic impacts. They may also act as refugia for coral diversity in the future (*106*). However, it is unlikely that they will escape the most pronounced effects of climate change

in the long term. What is more likely is that both local and global forces will work synergistically against the persistence of coral reefs. This is particularly likely to occur within the GBA as nutrient enrichment in the marine ecosystem has been shown to increase coral disease (*11*) and thermal bleaching (*113*). We therefore recommend accomplishing the most immediate goal of mitigating local stressors with a focus on improving water quality, which has been shown to increase the resistance and resilience of coral communities during the Anthropocene (*34*), while pressing forward with climate change mitigation strategies.

Conservation implications

This work combines subfossil, historical, and modern datasets to understand the context of reef-building coral communities in the GBA and complements a growing body of research investigating Holocene changes to reef ecosystems within the greater SCS region (*87*, *89*, *90*, *95*, *106*, *114–116*). We created the first historical biodiversity baseline for GBA corals using subfossil records from sediment cores. We show that assemblages in the past were more diverse but have recently seen a change in community composition with a decline in *Acropora* abundance. We also showed that degraded water quality is the main stressor that caused a shift from competitive to stress-tolerant dominated communities with the most pronounced effects in regions that experience the largest influx of eutrophic water from the Pearl River. These results show that local stressors were historically and now remain the primary threat to GBA coral health, and coral conservation and restoration efforts must start with the improvement of water quality. We recommend that, as China continues to rapidly develop the GBA, drastic water quality improvements upstream of the Pearl River estuary must be enacted to preserve biodiversity downstream. This need to alleviate the water quality crisis extends beyond China, as much of the world's marine biodiversity (*117*) is located in areas projected to see increased urbanization by 2030 (*46*). This study demonstrates how region-specific historical ecology research can directly inform local management decisions to help conserve ecosystems in the face of global change. To protect other areas of high-conservation potential, regional studies such as this are required to identify and alleviate local stressors that may be working either independently from or synergistically with global drivers.

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