U-Th dating reveals regional-scale decline of branching *Acropora* corals on the Great Barrier Reef over the past century

Tara R. Clark^{a,b,1}, George Roff^{c,d}, Jian-xin Zhao^{a,1}, Yue-xing Feng^a, Terence J. Done^e, Laurence J. McCook^{f,g}, and John M. Pandolfi^{c,d}

^aRadiogenic Isotope Facility, School of Earth and Environmental Sciences, The University of Queensland, Brisbane, QLD 4072, Australia; ^bResearch Centre for Human Evolution, Environmental Futures Institute, Griffith University, Nathan, QLD 4111, Australia; ^cSchool of Biological Sciences, The University of Queensland, Brisbane, QLD 4072, Australia; ^dAustralian Research Council Centre of Excellence for Coral Reef Studies, The University of Queensland, Brisbane, QLD 4072, Australia; ^eAustralian Institute of Marine Science, Townsville, QLD 4810, Australia; ^fAustralian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia; and ^gSouth China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou 510301, China

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Hard coral cover on the Great Barrier Reef (GBR) is on a trajectory of decline. However, little is known about past coral mortality before the advent of long-term monitoring (circa 1980s). Using paleoecological analysis and high-precision uranium-thorium (U-Th) dating, we reveal an extensive loss of branching Acropora corals and changes in coral community structure in the Palm Islands region of the central GBR over the past century. In 2008, dead coral assemblages were dominated by large, branching Acropora and living coral assemblages by genera typically found in turbid inshore environments. The timing of Acropora mortality was found to be occasionally synchronous among reefs and frequently linked to discrete disturbance events, occurring in the 1920s to 1960s and again in the 1980s to 1990s. Surveys conducted in 2014 revealed low Acropora cover (<5%) across all sites, with very little evidence of change for up to 60 y at some sites. Collectively, our results suggest a loss of resilience of this formerly dominant key framework builder at a regional scale, with recovery severely lagging behind predictions. Our study implies that the management of these reefs may be predicated on a shifted baseline.

U-Th dating | Acropora | coral | mortality | Great Barrier Reef

oss of hard coral abundance, diversity, and habitat structure as a result of numerous anthropogenic (1, 2) and climatic (3) factors is a problem faced by many reefs on a global scale (4-6). On the Great Barrier Reef (GBR), substantial losses in hard coral cover have been observed on the inshore (7), midshelf, and offshore reefs (8), with the most severe coral mortality event on record occurring as recently as 2016–2017 (9). Despite this, little attention has been paid to past coral mortality and changes in community structure, with most of our present knowledge about the ecology of the GBR coming from spatially and temporally limited data that have contributed toward a lack of consensus over its current state (10-14). Combined available monitoring data provide a time series spanning only the last ~ 30 y (7, 15–17), beginning after many of the human activities that had already started by the early 19th century. Thus, these data provide only a small "window" to examine how coral communities have responded to disturbances, both natural and anthropogenic, over time. As a result, the limited detailed longterm information has essentially given rise to what is known as the "shifting baseline syndrome," in which the state of coral reefs documented in the early pioneering studies of modern reef ecology may erroneously be considered as a "normal" reef, and used as a baseline to evaluate subsequent changes (18, 19). Without longer-term information, there is the risk that scientists and management bodies may make overoptimistic assessments of the state of the reef (10), or set lower or incorrect recovery targets (20). A more worrying consequence is that the transition of reefs away from a coral-dominated landscape may have begun decades ago before the onset of modern monitoring programs, with chronic stressors such as a decline in water quality (e.g., increased nutrients and other contaminants) lowering the resilience of reefs to recover from acute disturbances (6). What we may now be witnessing is the tail end of this transition where recent acute disturbance events, such as bleaching and cyclones, have pushed coral communities toward or past their tipping point (21).

The most widely reported example of modern reef decline comes from the Caribbean, where Acropora palmata and Acropora cervicornis communities that persisted during the Pleistocene and Holocene have within the past four decades been replaced by fleshy macroalgae due to both natural and human influences (2, 22, 23). This phase shift has subsequently resulted in a widespread loss of architectural complexity that threatens the future viability of these reefs (24). In the Palm Islands region, central inshore GBR, coral communities suffered extensive mortality following the 1998 mass bleaching event (25, 26), resulting in a shift from coral to macroalgal dominated states at some locations (27). Acropora communities were the hardest hit (15, 26) due to their susceptibility to thermal bleaching (28) and have since shown little sign of recovery in the Palm Islands (SI Appendix, Table S1). However, chronological and paleoecological evidence suggests that the timing of Acropora loss began much earlier at Pelorus Island, northern

Significance

Branching Acropora corals are highly sensitive to environmental change and warrant close monitoring to avoid irreversible changes in ecosystem health. For the Great Barrier Reef, limited baseline information of ecological dynamics prior to ~1980 makes it difficult to understand recent ecosystem trends. We demonstrate the use of high-resolution uranium-thorium dating, modern and palaeoecological techniques to improve our understanding of mortality and recovery dynamics over much broader scales. We found a loss of resilience in ecologically important branching Acropora corals at a regional scale. This work will prove valuable to reef managers by providing a reliable baseline for ongoing monitoring and identifying reefs at risk for deterioration, especially for those where modern observations are lacking. COLOGY

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¹To whom correspondence may be addressed. Email: t.clark1@uq.edu.au or j.zhao@uq. edu.au.

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Palm Islands, and is unprecedented for the past millennium (29). The reason for this demise has been attributed to a decline in water quality associated with widespread catchment clearing in the late 19th century following European settlement (29). However, with widespread coral-reef monitoring only beginning in the 1990s, there are few data available to be able to assess regional trends before the past few decades and whether or not inshore reefs of the GBR are following a similar trajectory as the Caribbean.

In the absence of modern monitoring data, paleoecological records can provide invaluable insight into past ecosystem states (22, 29, 30) with the discordance between living assemblages and dead skeletal remains proving to be a powerful tool in detecting recent changes in community structure as a result of anthropogenic disturbance (22, 31). Where a strong and persistent environmental change occurs, compositional changes can take place in the associated biota and can be recorded in the death assemblage (32). Here we use comparisons of modern and dead coral assemblages (termed "death assemblage") combined with highly precise uranium–thorium (U-Th) dating to provide an important baseline understanding of historical change in coral communities within the Palm Islands, and assess the timing and extent of mortality at a regional scale.

Results

In 2008, benthic surveys conducted within the Palm Islands region (Fig. 1 and *SI Appendix*, Fig. S1 and Table S2) revealed highly variable live coral cover ranging from (mean ± 1 SD) $3.4 \pm$ 0.6% at Havannah S3 (where S denotes "site") to 74.9 \pm 9.9% at Havannah S1. Significant differences in benthic community composition were observed among sites (*SI Appendix*, Tables S3 and S4). Sites with high live coral cover (>30%) were composed mainly of monospecific stands of *Pavona*, *Goniopora*, *Porites*, and *Echinopora* typical of modern turbid inshore reef



Fig. 1. Map of the Palm Islands and sampling locations. Pie graphs depict modern benthic cover (percentage) for categories live coral, dead coral, soft coral, algae, and other substrate (including sand) surveyed in 2008.

environments (33, 34; Fig. 2A). Sites with <30% live coral cover were dominated primarily by macroalgae (up to 89.5%), other substrate (including sand), dead hard coral, or soft corals, with low densities of *Turbinaria*, *Psammacora*, *Galaxea*, and *Acropora* colonies (Figs. 1 and 2 A and C, and *SI Appendix*, Fig. S2).

Comparisons between the living and death assemblages revealed significant differences in the relative abundance of coral genera between [permutational multivariate analysis of variance (PERMANOVA); $F_{1,99} = 18.399$, P = 0.001; *SI Appendix*, Table S3] and among sites (PERMANOVA; $F_{12,99} = 1.7755$, P = 0.001; *SI Appendix*, Tables S4 and S5). Acropora was consistently more prevalent in the death assemblage than the living assemblage, especially at sites with low coral cover (Fig. 2 B and C). Importantly, even where live Acropora were reported in 2008, these colonies were dominated by early successional caespitose and digitate colonies, which are functionally different from the once historically dominant framework building branching Acropora growth form.

dominant framework building branching *Acropora* growth form. The corrected ²³⁰Th age data obtained from 215 dead *Acropora* samples collected from seven sites in the Palm Islands region characterized by high dead coral and algal cover (Pelorus S1, S2, S3, Fantome S3, Havannah S2, S3 and Pandora S1) ranged between AD 1623.5 ± 6.3 and 2006.9 ± 2.0 (Fig. 3 and *SI Appendix*, Table S6). The timing of mortality across all sites at Pelorus occurred roughly over the same time period during the early to mid-20th century between AD 1922.5 \pm 9.6 and 1961.5 \pm 7.6. Of the 19 ²³⁰Th ages obtained from Pelorus S1 where most of the substrate was overgrown by living Pavona cactus, 14 dated to more recent times between 1988.0 \pm 7.9–1998.9 \pm 7.2. Twenty-six (out of 27) ²³⁰Th ages obtained from dead Acropora skeletons collected from Fantome S3 bracketed the period AD 1969.0 \pm 5.6–1999.3 \pm 1.9, and coincide with the timing of mortality determined from 54 (out of 56)²³⁰Th ages obtained from Havannah S2 and S3 (AD 1972.7 \pm 2.3–2001.7 \pm 0.5). A highly constrained chronology was obtained from Pandora S1, where 41²³⁰Th ages obtained from dead Acropora skeletons revealed the timing of mortality to be between AD 1994.1 ± 1.3 and 1999.1 ± 5.5 .

Discussion

Comparisons between living coral and coral death assemblages in the Palm Islands region indicate a dramatic change in coral community composition during the period (post-~1850) of expanded European urbanization, land clearing, mining, and agriculture in northern Australia. Most noticeable has been the loss of branching Acropora colonies accompanied by a shift toward turbid water corals and noncoral-dominated assemblages. Using the highly precise and accurate U-Th dating method, the timing of mortality for 215 dead Acropora colonies from seven sites was found to be occasionally synchronous between reefs and attributable to multiple acute disturbance events (high sea-surface temperatures, storms, flood plumes) over the past century of record (Fig. 3). The earliest period of mortality detected occurred at Pelorus between AD 1904.7 ± 8.7 and 1952.9 ± 6.6 (Fig. 3 and SI Appendix, Table S6), inclusive of two (possibly three) discrete mortality events and well before the first detailed surveys were performed on the leeward side of the island in 2001 (35). We hypothesize that the mortality observed at Pelorus may have resulted from (i) increased sediment loading from the nearby Herbert River during the transition from a positive to a strong negative Pacific Decadal Oscillation (PDO) phase (e.g., during the mid-1940s) (Fig. 3). Floods that follow periods of drought carry an increased loading of suspended sediment to nearby coastal waterways due to a loss of groundcover and enhanced erosion (36) with deleterious effects on the growth, survival, reproduction, and recruitment of hard coral colonies (for review see ref. 37). This time period also coincides with extensive land clearing of the Herbert catchment for grazing and sugarcane post-European settlement (there were two operating sugar mills on the Herbert River by the late 1800s) that may have contributed further to the amount of sediment being delivered to adjacent waters; and/or



Fig. 2. Comparisons between living and death assemblages. (*A*) Principal coordinates analysis (PCO) of living coral genera at each reef within the Palm Islands. Sites grouped by 40% similarity and Pearson correlation vectors overlaid to display coral genera responsible for the differences between sites. (*B*) PCO of death assemblage coral genera at each reef with most of the variation (47.8%) explained by dead *Acropora*. (*C*) Comparison of living vs. death assemblage (percentage cover) for several key genera. Note the overrepresentation of *Acropora* in the death assemblage compared with the living assemblage.

(ii) anomalous sea-surface temperatures (SSTs) similar to that seen during the latest positive PDO phase (Fig. 3). These events may have been less pronounced at the other three reefs as the extent of flood plumes varies over spatial scales (38). Alternatively, the other three reefs may have recovered from disturbance, which is undetectable within surface death assemblages that only reach ~10-cm depth. A second period of mortality also occurred between AD 1980 \pm 17 and 2006.9 \pm 2.0, although the majority of dates came from Pelorus S1. The absence of ²³⁰Th ages for the \sim 30-y period between the peaks in age data suggests that there was a window of opportunity for branching Acropora communities to recover at Pelorus S1; however, branching Acropora failed to reestablish in this time at Pelorus S2 and S3. For the other four sites at Havannah, Fantome, and Pandora Reef, mortality (determined from the surficial death assemblage) is largely restricted to AD 1970–2000. During this window, significant Acropora mortality events (evident in the synchronicity in ²³⁰Th age data between reefs) appear to have occurred around ~1983, ~1987, ~1994, and ~1998, coinciding with high SSTs and extensive flood plumes associated with Cyclone Sadie (39) (Fig. 3 and SI Appendix, Table S7). At Pandora Reef, the timing and cause of mortality is well constrained not only by 41 highly precise 230 Th ages (40), but also by the independently documented collapse of Acropora corals at this site due to El Niño-induced high SSTs (15, 26).

Perhaps one of the most sobering outcomes of this study is the observed lack of, or delayed recovery in, *Acropora* colonies on these nearshore coral reefs. For areas of reef in which a high cover of fast-growing corals such as *Acropora* is killed by major natural disturbances, including thermal bleaching, predisturbance levels of coral cover can reestablish in a narrow range of 5–10 y (41–44). However, these recovery rates were observed on clear-water, mid-, and off-shore reefs following acute natural disturbances. By contrast, recovery rates for the Palm Islands, and inshore reefs in general, that are exposed to both chronic and acute events, are poorly understood (but, see ref. 45). The longest study capturing disturbance/recovery dynamics was conducted by Done et al. (26) at Pandora Reef over a period of 24 y (1981–2005), where *Acropora* corals showed remarkable resilience following several disturbance events (including cyclones, thermal stress, and flood events), attaining 60%

coverage in a space of 10–15 y following disturbances in the 1970s. Following catastrophic losses during the 1997–1998 bleaching event, however, recovery rates have severely lagged behind predictions based on previous rates of recruitment and growth (26). For example, *Acropora* comprised only $0.5 \pm 0.4\%$ of the total live coral cover in 2008 when surveyed in this study, $2.1 \pm 3.1\%$ in 2013 at one of the nearby Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program sites, and 0.8% and 1% cover at 2- and 5-m depth, respectively, at the AIMS Marine Monitoring Program (MMP) site in 2014 (Fig. 4 and *SI Appendix*, Table S1).

Over longer time scales, the approach used here can provide a means to understand and quantify mortality and recovery in coral communities. By dating dead coral skeletal material that represents recent growth before mortality, the 230 Th age distributions produced from multiple fragments closely approximates episodes of mortality, with multiple peaks implying repeated episodes of mortality. Importantly, multiple peaks in the 230 Th age-distribution data could also be interpreted as being evidence of recovery [where enough source material was (re)generated to produce another age distribution]. As an example, the period between mortality events (or "recovery" period) based on 230 Th age data obtained from Pelorus S1 is ~30 y (~1950 to late 1980s–early 1990s), which would represent the minimum time period for recovery to allow for branching coral colonies to regrow [although this site is now overgrown by turbid water corals such as P. cactus (Fig. 2A and C) that may have outcompeted Acropora following disturbance in the late 20th century (Fig. 3D)]. While further dating of coral material is required (particularly from deeper within the reef matrix to capture older material that may have been buried as the reef recovered), this "fossil estimate" of recovery is not far off of modern observations and testifies to the utility of U-Th dating to measure recovery rates in areas where data are lacking. For Pelorus S2 and S3, recovery has been limited for more than 60 y since mortality in the mid-20th century, which far exceeds both modern and fossil estimates of recovery.

Low contemporaneous *Acropora* abundance is a common feature across the entire Palm Islands region (Fig. 4 and *SI Appendix*, Table S1), and is in stark contrast to observations made in the mid-1980s and early 1990s (26, 46). Since the concentration of *Acropora* EARTH, ATMOSPHERIC, ND PLANETARY SCIENCES

ECOLOGY



Fig. 3. Timing of branching *Acropora* mortality and comparison with environmental data. (*A*) PDO (source: research.jisao.washington.edu/pdo/PDO. latest.txt). (*B*) Annual rainfall in millimeters (mm) for Lucinda township, Station 32031 (source: Australian Bureau of Meteorology). (C) Annual maximum, average, and minimum SST anomalies (HaddSST2) for 5 × 5 grid 147.5 °E, 17.5 °S from 1900 to 2014 (source: Hadley Centre). Relative probability curves (72) produced from the U-Th age data obtained from the dead *Acropora* coral skeletons for (*D*) Pelorus S1, S2, and S3; (*E*) Fantome S3; (*F*) Havannah S2 and S3; and (G) Pandora S1. The height and width of the curves represent the number of samples that date to the same time period and associated error, respectively. Individual ²³⁰Th ages $\pm 2\sigma$ age errors are also

mortality in the mid- and late 20th century, between 16–60 y have passed with very little sign of recovery (less than 2% *Acropora* cover across the majority of reefs in the Palm Islands region surveyed by AIMS between 2012 and 2014; Fig. 4 and *SI Appendix*, Table S1). While an increased number of disturbances in recent years has been implicated as the primary driver behind the observed lack of recovery at many reef sites (10), these acute events cannot explain fully the reasons behind ongoing population decline (12) and the unusually long lag time between mortality and recovery.

Potential explanations for delayed recovery include a loss of parental broodstock and recruitment failure (12) due to increased SSTs and declines in water quality (e.g., ref. 47). Despite the widespread death of mature colonies in the Palm Islands region following the 1998 and 2002 mass coral bleaching events and resulting dramatic decline in the supply of larvae to reefs within the region (48, 49), recent studies have recorded moderate numbers of acroporid corals recruiting on settlement tiles (7, 35, 50), suggesting that larval supply is not entirely a limiting factor. However, many larvae fail to develop past the settlement phase into juvenile size classes (35, 51), ultimately contributing to the low density of juvenile corals on the leeward side of these reefs (51). Low rates of recruitment and postsettlement survival have been associated with high sedimentation and nutrient enrichment in the Palm Islands region (52, 53) and elsewhere on inshore reefs of the GBR (54). This is not surprising given the estimated 5- to 10-fold increase in sediment delivery since European settlement (41, 55). Monitoring of water-quality parameters in the region has also revealed a medium (10-20%) to high (20-50%) frequency of exceedance (total number of daily observations that exceed the threshold value) of chlorophyll *a* guideline trigger values (0.45 μ g L⁻¹) between the years of 2002-2012 (56). Fine sediments in such turbid and nutrientrich waters aggregate to form sticky flocs or "marine snow" that have been shown to exert detrimental to lethal effects on corals (57). Moreover, high macroalgal cover associated with enhanced levels of nutrients (58) can reduce recruitment and suppress fecundity and growth in hard corals (59). This, together with low abundances of key herbivorous fish (27) is likely to contribute to the high abundance of macroalgae (60) and low coral cover at some sites (viz., Pandora S1 and Havannah S3). However, it cannot explain the ubiquitously low level of Acropora cover at sites with low macroalgae cover, such as Pelorus and Fantome Island. For these locations, the lack of consolidation of large expanses of dead Acropora rubble may also limit larval settlement and increase mortality of recruits as it is rolled by waves, collapses, and/or crumbles (61, 62). Density of juvenile corals, structural complexity, herbivorous fish biomass, and nutrient conditions have all been found to be important predictors of recovery or regime shifts in coral communities that experienced regionwide mortality following thermal bleaching (63), so the reasons for the observed lack of recovery in areas with poor water quality might be equally complex.

Species of the genus *Acropora* play a significant role in reef ecosystems as key framework builders and habitat providers for numerous organisms (64). If we have learned anything from the decline of coral reefs in the Caribbean, it is that irreversible changes in coral communities may go unnoticed until it is too late (21). While mortality of *Acropora* corals at many sites in the Palm Islands can be attributed to multiple acute disturbances in recent years and even broad-scale climatic phenomenon such as the PDO, several factors such as low reef fish herbivory, dramatic changes in benthic

shown. Vertical dark gray lines indicate the timing of observed Acropora mortality associated with flooding (*F*) and thermal bleaching (*B*) in 1982/83, 1987/88, 1994, and 1998 (*SI Appendix*, Table S7). Vertical light gray lines highlight a further two (possibly three) mortality events at Pelorus. Samples HavS2T4.1, PelS1T2.2, PelS1T2.5, and PelS3T4.3 fall outside the *x* axis.



Fig. 4. Modern Acropora cover (AD 1981–2014). Live Acropora cover (percentage mean ±1 SD) surveyed by the AIMS, MMP and Done et al. (26) for (A) Havannah, (B) Orpheus, (C) Pandora, and (D) Pelorus. Solid black symbols represent data collected during this study in 2008.

structure, low rates of juvenile coral survival, and poor water quality in the region may be implicated in their delayed recovery over longer time frames and warrant close monitoring. Knowledge of rates of mortality and recovery will be critical under projected global warming scenarios, with the frequency and severity of coral bleaching and mortality expected to result in the long-term decline of susceptible genera (65). Where the time required for recovery exceeds the time between disturbance events, this may pose a serious threat to the long-term sustainability of coral abundance and reef health in the GBR and warrants further in-depth research. In this regard, high-resolution U-Th dating of surficial coral death assemblages (top ~ 10 cm of the reef matrix) coupled with systematic dating of reef matrix cores reaching greater depths, provides a means for benchmarking recovery rates and could also be used to assess the resilience of coral assemblages, especially for many other reef sites where modern observations are lacking.

Materials and Methods

Study Location and Sampling. The Palm Islands (18°30'-19°00'S and 146°25'-146°45'E) are located 20-40 km offshore in the central inshore region of the GBR, and include \approx 12 continental islands with fringing reefs and one platform reef (Pandora Reef). This region lies adjacent to the heavily modified Burdekin River catchment and is routinely exposed to sediment and contaminant-laden flood plume waters from the Burdekin, Herbert, and several other smaller rivers. In this study, three sites were selected from the leeward side of Pandora Reef and Pelorus, Orpheus, Fantome, and Havannah Islands (Fig. 1), where four 20-m transects per site were laid parallel to the reef flat at a depth contour of 5–6 m in May 2008 (SI Appendix, Table S2). This sampling depth was chosen to (i) avoid any confounding effects of depth, and (ii) standardize depth with previous longterm monitoring surveys. Surveys of community structure were performed along each of the 20-m transects using both a still camera and video, and later analyzed with CPCe at 1-m² increments using 30 points per quadrat (66). Community structure was categorized by quantifying total cover of: live hard coral, dead coral, soft coral, algae, other substratum (substrate and sediment), and unknown. To assess variability in coral assemblages at a coarse taxonomic level, coral cover was categorized into dominant genera typically found in the Palm Islands region (such as Acropora, Porites, Goniopora, and others). Where possible, the death assemblage was also divided into similar dominant genera. Samples of the death assemblage were taken from the sediment-water interface following similar procedures described in Greenstein and Pandolfi (67)

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to be able to determine their age. At each site, five grab samples were collected along each of the four 20-m transects where coral rubble was present. Approximately 5 L of coral rubble was collected in calico bags, excavated from the same point to a depth of 10 cm (which was logistically feasible for a diver to collect by hand as below 10 cm the rubble was often cemented), and within a 2-m radius of the initial excavation site until the bag was filled. Previous work on the GBR has proven that this method is sufficient to capture recent changes in community composition (37).

Sample Preparation and U-Th Dating. To constrain the timing of mortality of the dominant genera in the death assemblage (see *SI Appendix* for discussion on preservation bias), 215 dead branching *Acropora* corals were randomly selected from each calico bag (where present) collected from Havannah (S2, S3), Fantome (S3), Pelorus (S1, S2, S3), and Pandora (S1) and their age determined using the highly precise and accurate U-Th dating method. Approximately 1 g of material for dating was selected from within 16 cm of the branch tip (free from alteration) and was cut using a diamond blade saw, crushed into a 1-mm-size fraction using an agate mortar and pestle, rigorously cleaned and vetted using procedures described in Clark et al. (40). U-Th chemistry and dating was performed at the Radiogenic Isotope Facility, The University of Queensland, using thermal ionization mass spectrometry (68, 69) and a Nu Plasma high resolution multicollector inductively coupled plasma mass spectrometer (70). For further detail, please refer to *SI Appendix*.

Ecological Data Analysis. Multivariate analysis using PRIMER version 6.1.10 with PERMANOVA + extension was used to examine differences in live community structure as well as live and death assemblage community composition within and among sites (71). For further detail, please refer to *SI Appendix*.

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