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Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems

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average, 46% of the Sumatran smoke plume was located over the region of IOD upwelling, with the highest density of smoke consistently located over the Mentawai area (*38*). Deposition of these fire particulates (*19*) would have been assisted by the 500 mm of rainfall received by the Mentawai region during the 1997 wildfires and by atmospheric subsidence over the cold SST anomaly (*6*). Weakening and reversal of the monsoon and equatorial winds (*7*) in December 1997 also would have acted to further concentrate nutrients and plankton into the Mentawai region from the upwelling plume offshore.

Approximately 1.1×10^4 metric tons of Fe were released from the Sumatran wildfires during 1997 (*35*, *39*), and exposure to sunlight and acid conditions during atmospheric transport in the smoke plume (*36*) would have allowed up to 90% of the Fe to exist as bioavailable Fe(II) (*40*). Only 0.2 to 0.8% of the Fe released from the Sumatran wildfires was required as bioavailable Fe(II) in the Mentawai region to meet the total Fe requirements of the 1997 red tide (Table 1) (*13*, *41*). Although these calculations are estimates, it is clear that the 1997 Sumatran wildfires were a large potential source of Fe that could have promoted the extraordinary productivity in the upwelled water around the Mentawai Islands.

The proposed link between the death of the Mentawai Islands reef ecosystem and the 1997 Indonesian wildfires has implications for the future health of coral reefs. Widespread tropical wildfire is a recent phenomenon (*25*, *34*), the magnitude and frequency of which are increasing as population rises and terrestrial biomass continues to be disrupted (*34*). Where background nutrient supplies in reef waters are elevated or human activities have reduced upper trophic levels (*42*), reefs are likely to become increasingly susceptible to large algal blooms triggered by episodic nutrient enrichment from wildfires. Therefore, in addition to their impact on forest ecology and human health, tropical wildfires may pose a new threat to coastal marine ecosystems that could escalate into the 21st century.

References and Notes

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44. We thank B. Suwargadi, D. Prayudi, I. Suprianto, K. Glenn, T. Watanabe, K. Sieh, and the Indonesian Institute of Sciences (LIPI) for logistical support and technical assistance with fieldwork and T. Wyndham, H. Scott-Gagan, J. Cali, G. Mortimer, A. Alimanovic, and D. Kelleher for laboratory assistance. N.J.A. was supported by an Australian Postgraduate Award and a Jaeger scholarship.

Supporting Online Material
www.sciencemag.org/cgi/content/full/301/5635/952/DC1
Methods and Calculations
SOM Text
Figs. S1 and S2
Table S1
References

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Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems

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Degradation of coral reef ecosystems began centuries ago, but there is no global summary of the magnitude of change. We compiled records, extending back thousands of years, of the status and trends of seven major guilds of carnivores, herbivores, and architectural species from 14 regions. Large animals declined before small animals and architectural species, and Atlantic reefs declined before reefs in the Red Sea and Australia, but the trajectories of decline were markedly similar worldwide. All reefs were substantially degraded long before outbreaks of coral disease and bleaching. Regardless of these new threats, reefs will not survive without immediate protection from human exploitation over large spatial scales.

Coral reefs and associated tropical nearshore ecosystems have suffered massive, long-term decline in abundance, diversity, and habitat structure due to overfishing and pollution (*1*–*7*). These losses were more recently compounded by substantial mortality due to dis-

ease and coral bleaching (*8–12*). Although much longer records exist for some coral (*13*) and commercially important fisheries species (*2*, *3*), detailed ecological descriptions of reef ecosystems are less than 50 years old (*14*, *15*). The long-term historic sequence of ecosystem decline is unknown for any reef, thereby obscuring the potential linkage and interdependence of the different responsible factors that must be unraveled for successful restoration and management.

We reconstructed the ecological histories of 14 coral reef ecosystems worldwide (*16*) using consistent criteria throughout. We determined the ecological status of reefs ranging from pristine to globally extinct (Table 1) for seven general categories of biota (hereafter referred to as guilds) (*17*) for each of seven culturally defined periods ranging from prehuman to the present (table S1) (*18*). We used cultural periods rather than calendar years because the magnitude of human impacts depends primarily on technological prowess and economic structures that were out of phase geographically until converging in the 20th century. Guilds and ecological status were broadly defined so that the same standards could be used for all periods and regions examined and so that widely disparate paleontological, archaeological, historical, fisheries, and ecological data could be used in the same analysis (tables S2 and S3) (*17*).

The average ecological status of each guild for all regions combined (*17*) declined sharply over time (Fig. 1). In general, large animals declined faster than small animals and free-living animals declined more rapidly than architectural builders such as seagrasses and corals. Large carnivores and herbivores were almost nowhere pristine by the beginning of the 20th century, when these guilds were already depleted or rare in more than 80% of the 14 regions examined. The universal lag in decline of architectural guilds is consistent with earlier observations for Caribbean reefs (*19*).

We used principal components analysis (PCA) to ordinate the data and to describe the historical trajectories of change within each region in terms of the ecological status of all seven guilds combined (*17*). Reef regions were defined as pristine for the initial (prehuman) period, and for purposes of comparison, we included a hypothetical reef for which all seven guilds were ecologically extinct. Only the first principal component (PC1) was interpretable (*17*). The resulting trajectories (Fig. 2A) closely and consistently track PC1, which explains 91% of the total variation in the data. The key structures in the data set were thus effectively captured by a one-dimensional system, with each region's time periods mostly sequentially ordered along PC1, which is described overwhelm-

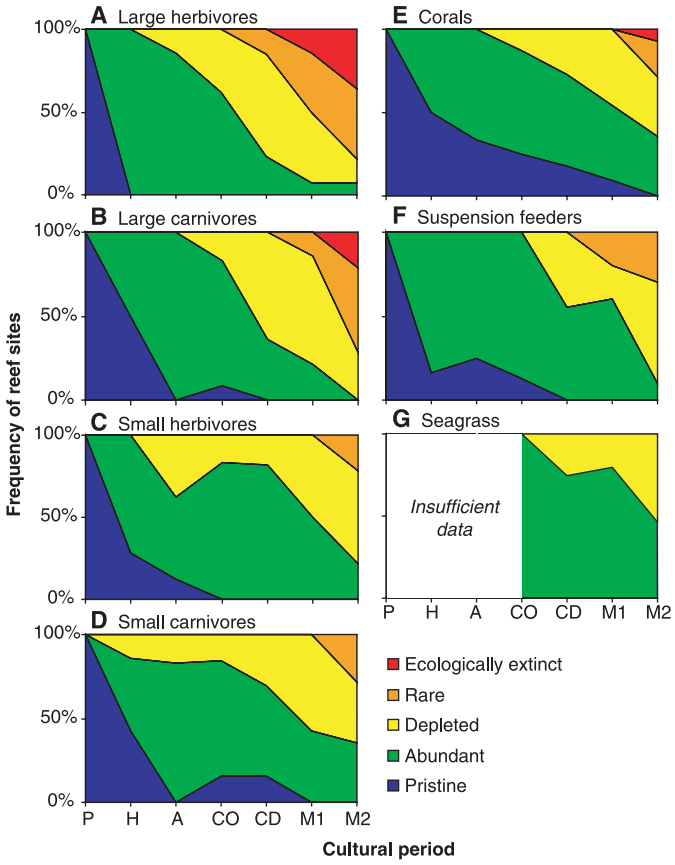

Fig. 1. (**A** to **G**) Ecological change in coral reef guilds through time. Time trajectories of ecological condition for each of seven guilds of reef inhabitants (*17*) expressed as the percentage of regions in each ecological state from 14 regions (*16*) in the tropical western Atlantic, Red Sea, and northern Australia. Cultural periods (*18*): P, prehuman; H, hunter-gatherer; A, agricultural; CO, colonial occupation; CD, colonial development; M1, early modern; M2, late modern to present.

Table 1. Ecological states and criteria used to assess the 14 tropical marine sites analyzed.

Ecological state	Criteria for classification
Pristine	Detailed historical record of marine resource lacks any evidence of human use or damage. Example: Fossil coral assemblages
Abundant/common	Human use with no evidence of reduction of marine resource. Example: No reduction in size of fish vertebrae in middens or relative abundance of species
Depleted/uncommon	Human use and evidence of reduced abundance (number, size, biomass, etc.). Examples: Shift to smaller sized fish; decrease in abundance, size, or proportional representation of species
Rare	Evidence of severe human impact. Examples: Truncated geographic ranges; greatly reduced population size; harvesting of pre-reproductive individuals
Ecologically extinct	Rarely observed and further reduction would have no further environmental effect. Examples: Observation of individual sighting considered worthy of publication; local extinctions
Globally extinct	No longer in existence. Example: Caribbean monk seal

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ingly by the status of large herbivores and carnivores (*20*).

PCA also provides a simple, objective index of present-day reef degradation as measured by the normalized scores for the end points of each regional trajectory along PC1 (Fig. 2B). As expected, reefs in the western Atlantic have declined more severely than in Australia or the Red Sea. The best-protected reefs in the world, on the Great Barrier Reef, are the closest to pristine. But these same reefs are also one-quarter to one-third of the way along PC1 to ecological extinction. Moreover, the reefs of Moreton Bay, at the extreme southern end of the Great Barrier Reef, are as close to ecological extinction for all seven guilds as the severely degraded reefs of eastern Panama and the Virgin Islands.

The overall historical trajectory of reef degradation across all cultural periods is markedly linear, despite the wide range of values within any one cultural period (Fig. 3). Most importantly from the perspective of reef conservation and management, most of the reef ecosystems were substantially degraded before 1900. Recent widespread and catastrophic episodes of coral bleaching and disease have distracted attention from the chronic and severe historical decline of reef ecosystems (*10*, *21–23*). However, all of the reefs in our survey were substantially degraded long before the first observations of mass mortality resulting from bleaching and outbreaks of disease (*10*, *11*). The only reasonable explanation for this earlier decline is overfishing (*3*), although land-derived pollution could have acted synergistically with overfishing in some localities.

Historical trajectories of reef degradation provide a powerful tool to explain global patterns and causes of ecosystem collapse, as well as to predict future ecosystem states, allowing managers to anticipate ecosystem decline through an understanding of the sequence of species and habitat loss. Management options will vary among regions, but there must be a common goal of reversing common trajectories of degradation. The maintenance of the status quo within partially protected areas such as the Great Barrier Reef is at best a weak goal for management, which should strive instead for restoring the reefs that are clearly far from pristine. Regardless of the severity of increasing threats from pollution, disease, and coral bleaching, our results demonstrate that coral reef ecosystems will not survive for more than a few decades unless they are promptly and massively protected from human exploitation.

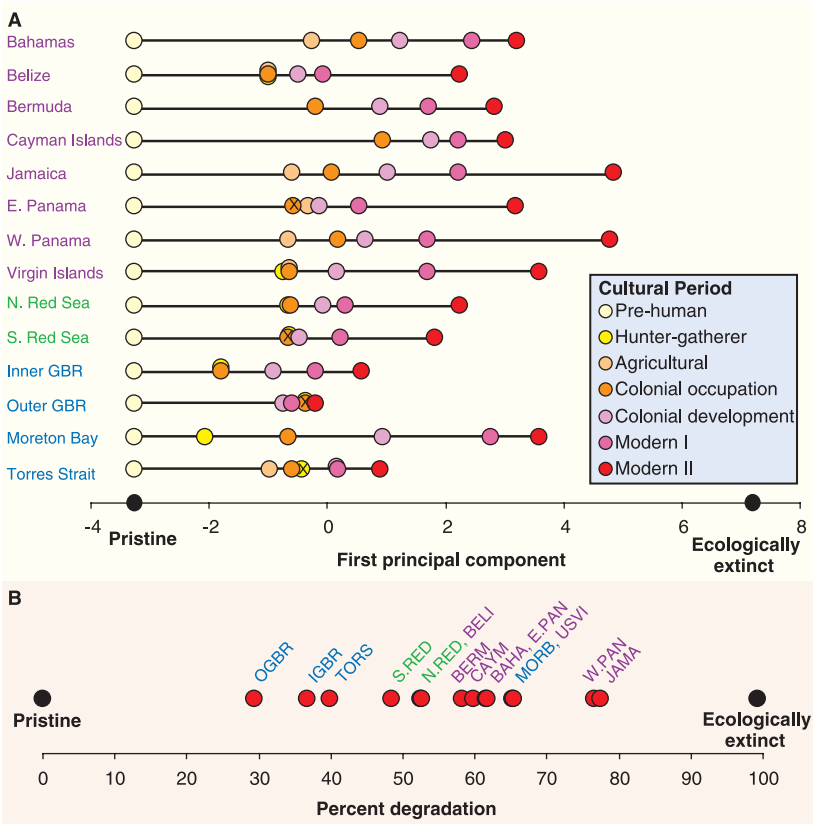

Fig. 2. PCA of ecosystem degradation based on the ecological state of all seven guilds of reef inhabitants at the 14 reef regions. Only PC1 was significant (*17*). (**A**) Time trajectories for each reef region over seven cultural periods. Each reef started at a single point to the left in the PCA space that is the pristine ecosystem state (Table 1) (*17*). Trajectories are mostly monotonic through time, but minor reversals occur in four regions (denoted with an "x" in the filled circle). The hypothetical ecologically extinct state, on the right, is one in which all seven guilds are ecologically extinct. PC1 is interpreted as an axis of historical degradation over time measured in cultural periods. The most important guilds influencing the trajectories of decline are large herbivores and carnivores (*20*). (**B**) End points (present ecosystem condition) of the 14 reef regions plotted along an axis of ecosystem degradation measured as the relative distance along PC1 between pristine and ecologically extinct. Oceanic regions are color coded: Australia, blue; Red Sea, green; western Atlantic, purple. OGBR, outer Great Barrier Reef; IGBR, inner Great Barrier Reef; TORS, Torres Strait Islands; S.RED, southern Red Sea; N.RED, northern Red Sea; BELI, Belize; BERM, Bermuda; CAYM, Cayman Islands; BAHA, Bahamas; E.PAN, eastern Panama; MORB, Moreton Bay; USVI, U.S. Virgin Islands; W.PAN, western Panama; JAMA, Jamaica.

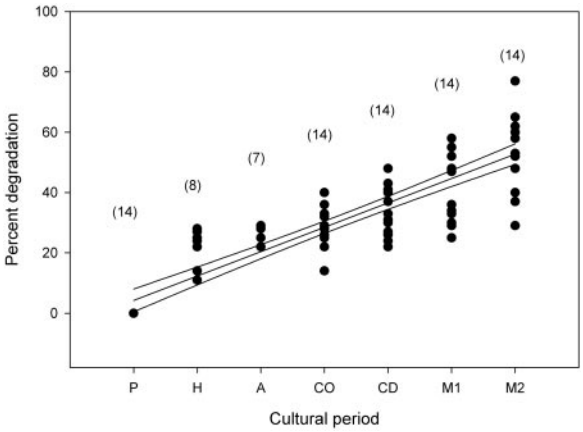

Fig. 3. Percent degradation of 14 reef regions over time. Data for each cultural period are derived from the PCA analysis plotted in Fig. 2A as measured along PC1 as the axis of reef degradation. Each point represents percent degradation of a particular site at a particular time. Numbers in parentheses are the numbers of reef regions recorded for each cultural period (*17*). Linear regression is plotted along with the 95% confidence interval. Abbreviations for cultural periods are as in Fig. 1.

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17. Materials and methods are available as supporting material on *Science* Online.
18. The seven cultural periods with their ranges of ages for the 14 regions studied are as follows: prehuman [40,000 years before the present (yr B.P.) to 1609 A.D.], hunter-gatherer (20,000 yr B.P. to 1824 A.D.), agricultural (3500 yr B.P. to 1800 A.D.), colonial occupation (1500 to 1800 A.D.), colonial development (1800 to 1900 A.D.), early modern (1900 to 1950 A.D.), and late modern (1950 to present). Not all cultural periods existed for all sites. For example, Bermuda was unpopulated until 1609, when colonial occupation began, and there was no agricultural stage in Australia before Western colonization.
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20. The values of descriptors (guilds) along PC1 represent the relative contribution to the position of sites along PC1 and are as follows: large herbivores, 0.45; large carnivores, 0.43; corals, 0.38; seagrass, 0.37; suspension feeders, 0.34; small carnivores, 0.33; and small herbivores, 0.33.
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24. This work was conducted as part of the Long-Term Ecological Records of Marine Environments, Populations, and Communities Working Group, which was supported by the National Center for Ecological Analysis and Synthesis (funded by NSF grant DEB-0072909), the University of California, and the University of California, Santa Barbara. The History of Marine Animal Populations Program of the Census of Marine Life, sponsored by the Sloan Foundation, and the Smithsonian Institution provided additional support. Support was also provided by NSF grant EAR-0105543 (J.M.P.) and the National Sea Grant College Program (NOAA, U.S. Department of Commerce) under NOAA grant NA06RG0142, project A/EA-1, through the California Sea Grant College Program. A. B. Bolten, P. J. Eliazar, A. McGill, R. Pears, and J. A. Seminoff assisted in literature compilations. A. M. Jabo assisted in the formatting of the figures.

Supporting Online Material
www.sciencemag.org/cgi/content/full/301/5635/955/DC1
Materials and Methods
Tables S1 to S3

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Long-Term Region-Wide Declines in Caribbean Corals

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We report a massive region-wide decline of corals across the entire Caribbean basin, with the average hard coral cover on reefs being reduced by 80%, from about 50% to 10% cover, in three decades. Our meta-analysis shows that patterns of change in coral cover are variable across time periods but largely consistent across subregions, suggesting that local causes have operated with some degree of synchrony on a region-wide scale. Although the rate of coral loss has slowed in the past decade compared to the 1980s, significant declines are persisting. The ability of Caribbean coral reefs to cope with future local and global environmental change may be irretrievably compromised.

It is becoming increasingly acknowledged that coral reefs are globally threatened (*1, 2*). Recent assessments suggest that 11% of the historical extent of coral reefs is already lost, while a further 16% is severely damaged (*3*). For the Caribbean basin, a wealth of quantitative, small-scale studies now exist that describe changes such as reduced coral cover, reduced physical and biological diversity, and increases in the spatial and temporal extent of macroalgae [e.g., (*4, 5*)] on individual reefs. These have contributed to qualitative summaries of regional and subregional scope (*3, 6*), which suggest a general pattern of decline and degradation. However, the extent and spatiotemporal variability of these changes have not been quantified on a Caribbean-wide scale. Here, we assess the extent of decline in coral cover across the Caribbean through the integration of existing data sets in a meta-analysis framework (*7*).

Data describing change in percent hard coral cover over time for monitored reef sites within the wider Caribbean basin were obtained from a range of sources (*8*). A total of 263 sites from 65 separate studies (table S1) across the Caribbean were included in the overall meta-analysis (Fig. 1).

Using the software Meta-Win (*9*), we carried out meta-analyses on the total data set to quantify two separate effect sizes: (i) overall absolute change in percent coral cover (C_A) as summarized across the duration of all studies, irrespective of year or length of study; and (ii) overall annual rate of change in percent coral cover (C_R) between surveys carried out at different points in time (calculated relative to the initial percent coral cover) (*8*). The latter has the advantage of partially accounting for differences in study duration and initial coral cover; however, it assumes a constant rate of decline between years. To allow for the possibility of nonlinear declines, we also calculated year-on-year rates of change in coral cover [$\Delta N = \log(N + 1)_{t+1} - \log(N + 1)_t$, where N is percent coral cover and t is year of study] for all studies with data from successive years (*8*). Finally, we calculated weighted (*8*) and unweighted mean absolute percent coral cover across all sites for each year between 1977 and 2001. We examined spatial and temporal variability in C_A and C_R by splitting the data set into subregions and time periods (*8*). Throughout, confidence intervals were generated by bootstrapping (*9*), corrected

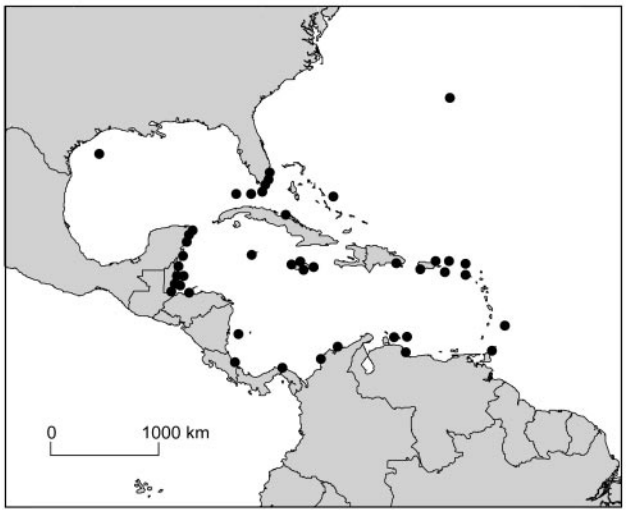

Fig. 1. Regional distribution of study sites in the wider Caribbean basin. The separate study sites from which monitoring data were sourced are shown as circles.

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