One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts

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Science **321**, 560 (2008);
DOI: 10.1126/science.1159196

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005.

signaling pathways. Although only BSK1 and BSK2 were identified in the proteomic study, additional members (BSK3 and BSK5) of this family of RLCKs appear to play a similar role in BR signaling. Our results support a model for the function of BSKs in BR signaling (Fig. 4F). In the absence of BR, BSKs are associated with BRI1. Upon BR activation of BRI1, BSKs are phosphorylated and then disassociate from the receptor complex to activate downstream signaling. Such ligand-induced disassociation from a preexisting receptor complex potentially provides faster signaling than does ligand-induced recruitment of a free component into the receptor complex.

Both BSKs and BAK1 are substrates of the BRI1 kinase, but several lines of evidence indicate that they play distinct roles in BR signaling. First, BR induces BRI1-BAK1 interactions (*6*) but reduces BRI1-BSK1 and BRI1-BSK3 interactions. Second, overexpression of BSK3 suppresses the *bri1-116* null allele, whereas overexpression of BAK1 only suppresses weak alleles but not a strong allele of *bri1* nor a double mutant containing the weak *bri1-5* allele and the BR-biosynthetic mutation *det2-1* (*19*). This suggests that BSK3 functions downstream of BRI1, whereas BAK1's action on the downstream BR response requires a functional BRI1. BAK1 and its homolog BKK1 are required in additional signaling pathways, and BAK1 is also a co-receptor for the FLS2 receptor kinase (a receptor for flagelin), suggesting that BAK1 is not a specific component of the BR pathway (*22*–*25*). BAK1 most likely mediates activation of BRI1 kinase rather than signal transduction to specific downstream components in the BR signaling pathway. In contrast, the BSKs directly mediate signal transduction from BRI1 to downstream BR responses (Fig. 4F). Identification of the downstream direct targets of BSKs will be the key to fully understanding how the BR signal is transduced from the cell surface to the nuclear transcription factors.

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26. We thank W. Briggs for commenting on the manuscript. Our research was supported by grants from NSF (NSF 0724688), the U.S. Department of Energy (DE-FG02-04ER15525), and NIH (R01GM066258). S.Z. and R.W. are supported by the Chinese Scholarship Council. The University of California, San Francisco, Mass Spectrometry Facility (A. L. Burlingame, Director) is supported by the Biomedical Research Technology Program of the National Center for Research Resources and grants NIH NCRR RR01614, RR012961, and RR019934.

Supporting Online Material

www.sciencemag.org/cgi/content/full/321/5888/557/DC1
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25 February 2008; accepted 24 June 2008
10.1126/science.1156973

One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts

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The conservation status of 845 zooxanthellate reef-building coral species was assessed by using International Union for Conservation of Nature Red List Criteria. Of the 704 species that could be assigned conservation status, 32.8% are in categories with elevated risk of extinction. Declines in abundance are associated with bleaching and diseases driven by elevated sea surface temperatures, with extinction risk further exacerbated by local-scale anthropogenic disturbances. The proportion of corals threatened with extinction has increased dramatically in recent decades and exceeds that of most terrestrial groups. The Caribbean has the largest proportion of corals in high extinction risk categories, whereas the Coral Triangle (western Pacific) has the highest proportion of species in all categories of elevated extinction risk. Our results emphasize the widespread plight of coral reefs and the urgent need to enact conservation measures.

Coral reefs harbor the highest concentration of marine biodiversity. They have high aesthetic, recreational, and resource values that have prompted close scientific scrutiny, including long-term monitoring (*1*, *2*), and face increasing threats at local and global scales. Globally, rapid buildup of carbon dioxide (and other greenhouse gases) in the atmosphere is leading to both rising sea surface temperatures (with an increased likelihood of mass coral bleaching and mortality) and acidification (*3*). Ocean acidification is reducing ocean carbonate ion concentrations and the ability of corals to build skeletons (*4*). Local threats include human disturbances such as increased coastal development, sedimentation resulting from poor land-use and watershed management, sewage discharges, nutrient loading and eutrophication from agrochemicals, coral mining, and overfishing (*1*, *2*, *5*–*9*). Local anthropogenic impacts reduce the resilience of corals to withstand global threats, resulting in a global deterioration of reef structure and ability of these ecosystems to sustain their characteristic complex ecological interactions (*1*–*3*, *5*–*9*).

In view of this ecosystem-level decline, we used International Union for Conservation of Nature (IUCN) Red List Categories and Criteria to determine the extinction risk of reef-building coral species. These criteria have been widely used and rely primarily on population size reduction and geographic range information to classify, in an objective framework, the extinction risk of a broad range of species (*10*). Categories range from Least Concern, with very little probability of extinction, to high risk, Critically Endangered (Table 1). The threatened categories (Vulnerable, Endangered, and Critically Endangered) are intended to serve as one means of setting priority measures for biodiversity conservation.

Our assessments of extinction risk cover all known zooxanthellate reef-building corals and include 845 species from the Scleractinia plus reef-building octocorals and hydrocorals (families Helioporidae, Tubiporidae, and Milleporidae). Corals have persisted for tens of millions of

years, and the many widespread species in particular are not obvious candidates for extinction. However, periods of mass coral extinctions are known from the fossil record (*11*, *12*), so conditions must have persisted that allowed populations to be reduced below sustainable levels. Up to 45% of all coral species went extinct around the Cretaceous-Tertiary boundary, with significantly more zooxanthellate than azooxanthellate extinctions (*13*). With reports of current widespread reef destruction (*2*) and unprecedented population declines in particular species (*14*, *15*), we used IUCN Red List Criteria to investigate whether present conditions have placed corals at elevated extinction risk.

Nearly all extinction risk assessments were made with the IUCN criterion that uses measures of population reduction over time (*10*). Most reef-building corals do not have sufficient long-term species-specific monitoring data to calculate actual population trends; consequently we used widely cited and independently corroborated estimates of reef area lost (*2*, *10*) as surrogates for population reduction. These estimates suffer from lack of standardized quantitative methodology, and so we interpreted them conservatively and weighted declines both regionally and by species-specific life history traits, including susceptibility to the threats causing reef area declines (*10*). Therefore, rates of population decline for each species have their basis in the rate of habitat loss within its range adjusted by an assessment of the species-specific response to habitat loss (so more-resilient species have slower rates of decline) (*10*).

Of the 845 reef-building coral species, 141 had insufficient data to complete a Red List assessment (Table 1) and were excluded from subsequent calculations. Of the remaining 704 species, 231 are listed in the threatened categories, whereas 407 are in threatened and Near Threatened categories combined (Table 1). Species in the families Euphylliidae, Dendrophylliidae, and Acroporidae are particularly at risk, with more than or close to 50% of species in a threatened category; the figures are around 40% for Meandrinidae and Oculinidae. *Heliopora coerulea*, the sole extant member of the ancient family Helioporidae, is rated as Vulnerable. The only species that do not fall within threatened categories are those that inhabit deeper, lower reef slopes and those not solely dependent on reef habitats (i.e., inter-reefal species). The Caryophyllidae, Astrocoeniidae, Merulinidae, and Fungiidae have the lowest proportions of threatened species.

In terms of species-specific vulnerability to impacts, about 40% of the 704 species are primarily reef-restricted, shallow water corals (<20 m depth) (*10*) that are susceptible to general anthropogenic disturbances. The remaining 60% of species can survive on deeper reefs (>20 m depth), in marginal reef habitats, or in off-reef areas. There are 303 species highly susceptible to bleaching, although 102 of these typically grow quickly and

Table 1. Current Red List Categories for reef-building coral species by family. Percentages in threatened categories (Thr) include all non–data-deficient species listed as VU, EN, or CR, whereas Near Threatened and threatened (NT + Thr) include all non–data-deficient species listed as NT, VU, EN, or CR.

Family	DD	LC	NT	VU	EN	CR	Total species	NT + Thr	Thr
Acroporidae	81	54	42	85	7	2	271	71.6%	49.5%
Agariciidae	3	26	5	11			45	38.1%	26.2%
Astrocoeniidae	4	9	1	1			15	18.2%	9.1%
Caryophylliidae		3					3	0.0%	0.0%
Dendrophylliidae	1	4	3	7			15	71.4%	50.0%
Euphylliidae	3		5	9			17	100.0%	64.3%
Faviidae	5	43	57	22	3		130	65.6%	20.0%
Fungiidae	2	32	5	5	2		46	27.3%	15.9%
Helioporidae				1			1	100.0%	100.0%
Meandrinidae	3	4		2	1		10	42.9%	42.9%
Merulinidae	1	7	3		1		12	36.4%	9.1%
Milleporidae	2	8	1	2	2	1	16	42.9%	35.7%
Mussidae	7	21	12	11	1		52	53.3%	26.7%
Oculinidae	6	3	3	4			16	70.0%	40.0%
Pectiniidae	5	12	6	5	1		29	50.0%	25.0%
Pocilloporidae	2	15	5	7	2		31	48.3%	31.0%
Poritidae	10	40	20	25	5	1	101	56.0%	34.1%
Rhizangiidae		1					1	0.0%	0.0%
Siderastreidae	6	15	6	4		1	32	42.3%	19.2%
Trachyphyliidae			1				1	100.0%	0.0%
Tubiporidae			1				1	100.0%	0.0%
Total	141	297	176	201	25	5	845		

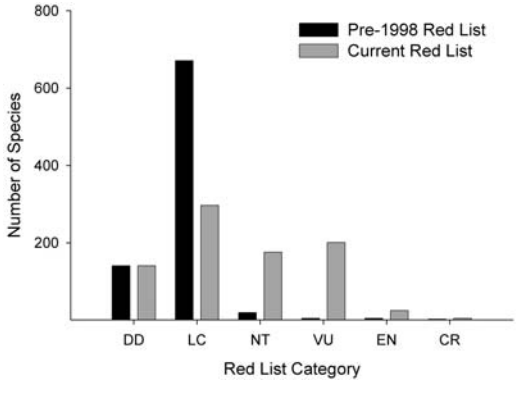

Fig. 1. Comparison of current Red List categories for all reef-building coral species to hypothetical Red List Categories back-cast to pre-1998. CR indicates Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; and DD, Data Deficient.

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populations recover within a few years (*7*). About 52% of the bleaching-susceptible species (mainly in the Acroporidae) are also heavily affected by disease and predation from the crown-of-thorns seastar, *Acanthaster planci*. Acroporid corals account for a high percentage of coral cover on reefs (*11*, *12*) and for a high proportion of the threatened species (Table 1). Eighty species are considered resistant to bleaching and include mostly members of the genera *Favia* and *Porites*.

Our results indicate that the extinction risk of corals has increased dramatically over the past decade (Fig. 1). By using the values from previous reports of the Global Coral Reef Monitoring Network (*16*), we determined extinction risk levels before the 1998 massive bleaching events (*10*). Before 1998, 671 of the 704 data-sufficient species would have been categorized as of Least Concern, 20 as Near Threatened, and only 13 in threatened categories. Although an estimated 6.4% of reefs recovered from the 1998 bleaching event about 5 years after it occurred, 16% were considered irreversibly destroyed after subsequent monitoring (*2*). Another study shows an increasing rate of coral cover loss in the Indo-Pacific of 1 to 2% per year since 1997 (*9*).

The proportion of threatened (not including Near Threatened) coral species exceeds that of most terrestrial animal groups apart from amphibians, particularly because of corals' apparent susceptibility to climate change (*10*). At slightly elevated sea surface temperatures, corals expel their symbionts, often resulting in colony death if the heat stress persists (*7*). Adult reef-building corals are restricted to well-lit tropical waters and are sessile, not having the option to move to cooler water. This also makes them susceptible to localized disturbances that can magnify the stress on a system already affected by warming seas.

Regionally, Caribbean reefs (Fig. 2) have been devastated by population declines of two key species, *Acropora cervicornis* (staghorn coral) and *A. palmata* (elkhorn coral) (*14*, *15*, *17*), which were recently listed as threatened under the U.S. Endangered Species Act. They were spatial dominants and primary framework builders during the Pleistocene and Holocene; their loss has had a major ecological impact (*14*, *15*). Another major Caribbean reef-builder, *Montastraea annularis*, has been listed as Endangered because of a rapid population decline over the past decade; on many

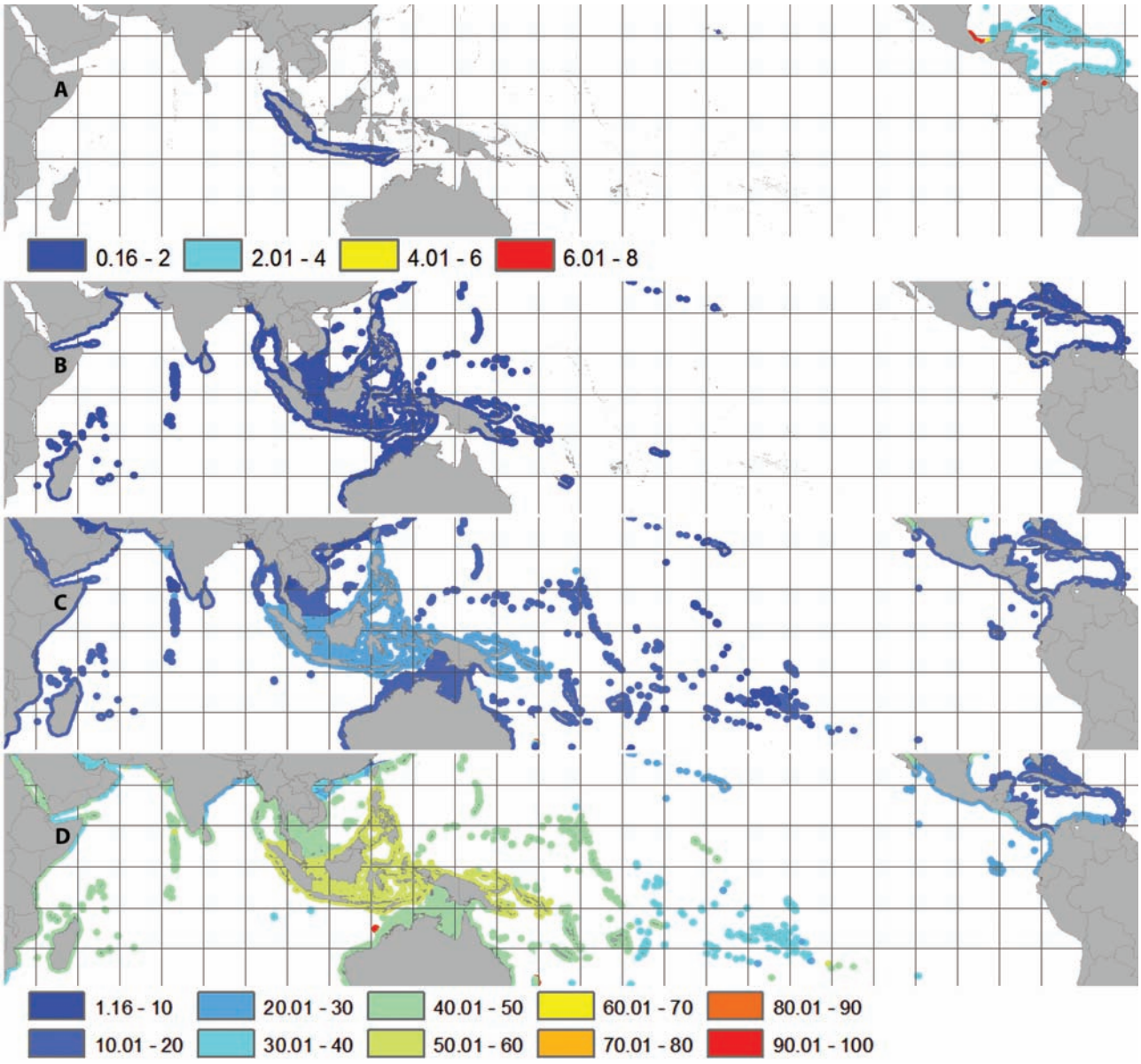

Fig. 2. (**A**) Critically Endangered species as percent of total species in area, (**B**) Critically Endangered and Endangered species as percent of total species in area, (**C**) species in all threatened categories (Critically Endangered, Endangered, and Vulnerable) as percent of total species in area, and (**D**) species in threatened and Near Threatened categories as percent of total species in area. Calculations are based on a cell size of 10 km^2.

reefs it is no longer dominant (*10*). It is the largest coral species in this region, has very slow recruitment (*18*), and is also highly susceptible to disease that can kill 500-year-old colonies within months, with recovery unlikely for decades.

In the eastern tropical Pacific, a high proportion of corals have been affected by warming events. However, subsequent monitoring has shown reefs are recovering in most areas across the region (*19*). Indian Ocean corals were the most affected by the 1998 warming event with two subsequent bleaching events in some places. Many of the shallow reefs have lost their three-dimensional rugosity, with cascading trophic and ecological effects including subsequent loss of fish populations (*20*). Other reefs are recovering their structure, but the time to complete recovery may range to decades and will be highly dependent on future climatic and local disturbance regimes.

The epicenter of marine biodiversity in the Indo-Malay-Philippine archipelago, the Coral Triangle (*11*, *21*), has the highest proportion of Vulnerable and Near Threatened coral species (Fig. 2, C and D). The chronic nature of anthropogenic disturbance in many parts of this region is compounded by the effects of climate change.

Corals in oceanic islands of the Pacific generally have the lowest proportion of threatened species (Fig. 2), and Hawaiian reefs have been spared extensive coral loss from bleaching or disease (*22*–*25*). However, Hawaii is an isolated archipelago with high levels of endemism (*23*), and several rare endemic species may prove especially vulnerable to future threats.

Our analysis indicates that the extinction risk for many corals is now much greater than it was before recent massive bleaching events. Whether corals actually go extinct this century (*12*) will depend on the continued severity of climate change, the extent of other environmental disturbances, and the ability of corals to adapt. If bleaching events become very frequent, many species may be unable to reestablish breeding populations before subsequent bleaching causes potentially irreversible declines, perhaps mimicking conditions that led to previous coral extinctions (*13*). If corals cannot adapt, the cascading effects of the functional loss of reef ecosystems will threaten the geologic structure of reefs and their coastal protection function and have huge economic effects on food security for hundreds of millions of people dependent on reef fish. Our consensus view is that the loss of reef ecosystems would lead to large-scale loss of global biodiversity.

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26. We thank T. Haas, the New Hampshire Charitable Foundation, CI, Esmée Fairbairn Foundation, and the Royal Caribbean Cruises Ocean Fund for their generous support of the IUCN Coral Red List Assessment. We also thank the following for help and support: M. Alava, J. Baillie, D. Bass, H. Reyes Bonilla, T. Brooks, H. Froyalde, P. Glynn, S. Henderson, C. Hickman, M. Hoffmann, D. Huang, R. McManus, M. Palomar, C. Pollock, R. Quicho, M. Smith, M. Syahrir, R. Trono, M. Vera, D. Zebrowski, Charles Darwin Foundation, CI Philippines, Darwin Initiative, First Philippine Conservation Incorporated, Gordon and Betty Moore Foundation, Walton Family Foundation, and the Zoological Society of London.

Supporting Online Material

www.sciencemag.org/cgi/content/full/1159196/DC1
Materials and Methods
Table S1

16 April 2008; accepted 24 June 2008
Published online 10 July 2008;
10.1126/science.1159196
Include this information when citing this paper.

Eco1-Dependent Cohesin Acetylation During Establishment of Sister Chromatid Cohesion

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Replicated chromosomes are held together by the chromosomal cohesin complex from the time of their synthesis in S phase onward. This requires the replication fork–associated acetyl transferase Eco1, but Eco1's mechanism of action is not known. We identified spontaneous suppressors of the thermosensitive *eco1-1* allele in budding yeast. An acetylation-mimicking mutation of a conserved lysine in cohesin's Smc3 subunit makes Eco1 dispensable for cell growth, and we show that Smc3 is acetylated in an Eco1-dependent manner during DNA replication to promote sister chromatid cohesion. A second set of *eco1-1* suppressors inactivate the budding yeast ortholog of the cohesin destabilizer Wapl. Our results indicate that Eco1 modifies cohesin to stabilize sister chromatid cohesion in parallel with a cohesion establishment reaction that is in principle Eco1-independent.

The cohesin complex provides sister chromatid cohesion from the time of DNA replication onward until mitosis (M) (*1*, *2*). A number of cohesion establishment factors that do not themselves form part of the cohesive structure that links sister chromatids (*3*–*9*) ensure that cohesin engages in productive linkages between sister chromatids during the synthesis phase (S phase), the period of DNA replication in the cell cycle. Of these factors, Eco1(Ctf7) is the only known essential protein. In its absence, cohesin associates with chromosomes before, during, and after S phase apparently normally (*3*, *10*), yet cohesion between sister chromatids is not established. Eco1 is a replication fork–associated acetyl transferase (*10*–*12*), suggesting a mechanistic link between replication-fork progression and cohesion establishment. How Eco1 promotes sister chromatid cohesion, and the role of its acetyl transferase activity in this process, have remained unclear.

When streaking *eco1-1* thermosensitive budding yeast cells (*3*) at their restrictive temperature, we noticed among the dying cells the outgrowth of colonies that had gained resistance to Eco1 inactivation (Fig. 1A) (*13*). Backcrossing of 20 such colonies revealed that spontaneous mutations in three complementation groups, ***a*** to ***c***, outside the *ECO1* locus, conferred thermoresistant growth. We

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