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18. The five lithic specimens (a few cm in size and weighing between 6 and 35 g) came from the upper phase of occupational deposits BBC M1: Samples BBC24 and BBC23 are from CA/CB and BBC15, BBC20, and BBC22 are from CC. Examination of thin sections revealed the presence of quartz grains embedded in a siliceous matrix. The time since they were burnt was computed from TL analysis of 100- to 160-μm grains obtained by crushing after the samples' outer surfaces had been removed with a diamond saw (*31*). The equivalent dose (D_e) was determined with a combined additive and regenerative dose protocol (*19*). U, Th, and K concentrations of the lithic samples were measured by neutron activation analysis (*32*). The total dose rates (*20*) were calculated assuming that the quartz grains were free of radioactive impurities and that all radioisotopes were confined to and uniformly distributed within the surrounding siliceous matrix. In computing the alpha and beta dose rates received by the grains, attenuation factors appropriate for the mean grain size in each specimen were taken into account. To determine the gamma dose rates, we buried 24 dosimeters in the cave deposits for 1 year at points no farther than 1 m from each previously excavated lithic. The ages combine to provide a mean age of 77 ± 6 ka, which is consistent with the OSL age for the overlying dune layer.
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22. The depositional age of the dune layer was determined by OSL dating. OSL analyses on Aber/52-ZB-15 were undertaken on quartz grains to measure the radiation dose that they had received since their last exposure to daylight. Their equivalent dose (D_e) was determined with the SAR procedure. The total radiation dose rate to the grains (*20*) was measured with a combination of thick-source alpha counting, beta counting, and atomic absorption spectroscopy for potassium determination, and a water content of 10 ± 5% (weight water / weight dry sediment) was used, based on current moisture contents in the cave. The calculated gamma dose rate was consistent with that measured in the field, and the cosmic ray dose rate of 45 μGy/year was based on the thickness of the overlying rock. Quartz grains were extracted after treatment with 10% hydrochloric acid to remove carbonates and 30 vol of H_2O_2 to remove organics. The sample was sieved to obtain grains from 212 to 250 μm in diameter. Feldspars and heavy minerals were removed by density separation at 2.62 and 2.70 g/cm^3. The alpha-irradiated outer layer of the grains was removed by etching in 48% hydrofluoric acid for 45 min. The initial set of luminescence measurements (stimulation at 470 nm with blue diodes) used 48 aliquots, each containing about 500 grains. A range of thermal pretreatments (preheats) from 160° to 300°C for 10 s was used. From 200° to 280°C, the D_e values from 30 replicate aliquots were reproducible and showed no systematic trend with temperature. A weighted mean was calculated, with the individual D_e values weighted according to their uncertainty. The uncertainty in the mean was divided by $\sqrt{N}$, where N is the number of independent estimates of D_e—in this case 30. D_e values were calculated with the package Analyst, which combines uncertainties due to the counting statistics of each OSL measurement and the error associated with the mathematical fitting of the growth curve to the luminescence data. The 30 aliquots gave a value of 47.9 ± 1.7 Gy, resulting in an age of 69 ± 5 ka.
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24. The single-grain SAR measurements were made in an automated reader based around a 10-mW, 532-nm Nd: YVO_4 laser, whose beam can be directed at individual grains (*23*). A single preheat at 220°C for 10 s was used, with the main OSL measurement (L) being followed by measurement of the OSL response (T) to a test dose as observed after a 160°C cut heat (*21*). Grains whose natural signal ratio (L_N/T_N) does not intersect the regeneration growth curve were not used in subsequent analyses. In addition, grains thought to contain some feldspar were also rejected. The presence of feldspar was identified by making additional measurements of a given regeneration dose on each grain. The first measurement is undertaken within the SAR procedure and yields the ratio L_1/T_1 used in the growth curve. For each grain, two additional measurements of L/T were made at the end of the SAR procedure. The first duplicates the previous measurement, as a test of the sensitivity correction. The second uses the same regeneration dose, but, before preheating, the grains are exposed to infrared (830 nm) radiation from a 500-mW laser diode for 100 s. If the grains contain feldspar, then the infrared exposure will have reduced the magnitude of L, and hence the ratio of these last two measurements of L/T will be substantially less than unity; for a quartz grain, the ratio will be consistent with unity. Of the 1892 grains that were measured, 22 were rejected on the basis of these criteria. The OSL signal from many of the remaining 1870 grains was close to instrumental background, and only 34 yielded reproducible growth curves.
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Marine Biodiversity Hotspots and Conservation Priorities for Tropical Reefs

Callum M. Roberts,[1,2]* Colin J. McClean,[2] John E. N. Veron,[3] Julie P. Hawkins,[2] Gerald R. Allen,[4,8] Don E. McAllister,[5]† Cristina G. Mittermeier,[4] Frederick W. Schueler,[6] Mark Spalding,[7] Fred Wells,[8] Carly Vynne,[4] Timothy B. Werner[4]

Coral reefs are the most biologically diverse of shallow water marine ecosystems but are being degraded worldwide by human activities and climate warming. Analyses of the geographic ranges of 3235 species of reef fish, corals, snails, and lobsters revealed that between 7.2% and 53.6% of each taxon have highly restricted ranges, rendering them vulnerable to extinction. Restricted-range species are clustered into centers of endemism, like those described for terrestrial taxa. The 10 richest centers of endemism cover 15.8% of the world's coral reefs (0.012% of the oceans) but include between 44.8 and 54.2% of the restricted-range species. Many occur in regions where reefs are being severely affected by people, potentially leading to numerous extinctions. Threatened centers of endemism are major biodiversity hotspots, and conservation efforts targeted toward them could help avert the loss of tropical reef biodiversity.

Coral reefs fringe one-sixth of the world's coastlines (*1*) and support hundreds of thousands of animal and plant species (*2*). Fifty-eight percent of the world's reefs are reported to be threatened by human activities (*3*). Terrestrial agriculture, deforestation, and development are introducing large quantities of sediment, nutrients, and other pollutants into coastal waters, causing widespread eutrophication and degradation of biologically productive habitats (*4*, *5*). Coral reefs are often fished intensively; and in regions of the Indian and Pacific Oceans, fishing with dynamite and poisons has devastated reef habitats (*6*). Coral reefs are also susceptible to climate change; 25% of the world's coral reefs have already been destroyed or severely degraded through problems arising from climate warming (*7*). Among marine ecosystems, tropical reefs represent a high priority for conservation action [Web note 1 (*8*)].

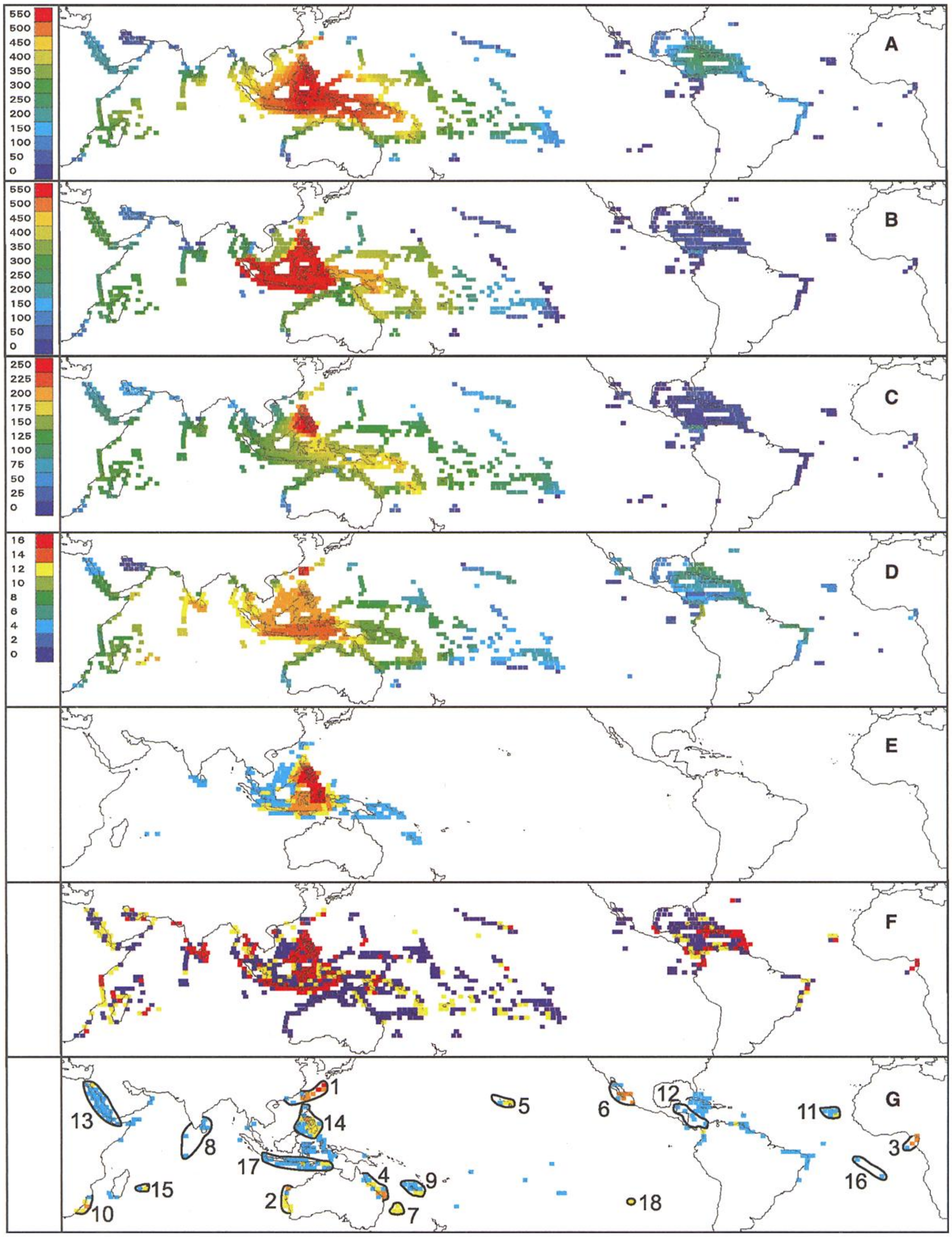

Fig. 1. Global clines in species richness of fish (**A**), corals (**B**), snails (**C**), and lobsters (**D**). Scales show number of species present. (**E**) Concordance of the top 10% most species-rich cells among taxa. Red cells were included for all four taxa, orange for three, yellow for two, and blue for one. (**F**) Threats to reefs in each grid cell, calculated using data from Bryant *et al.* (*3*, *13*). Blue represents low risk (average threat score between 1 and 1.67); yellow, medium risk (score between 1.68 and 2.33); and red, high risk (score ≥2.34). (**G**) Concordance in patterns of range rarity among the top-scoring 10% of cells for each taxon. Color codes are as in (E). Places outlined show multitaxon centers of endemism (*13*) [Web table 2 (*8*)], numbered as in Table 2.

We used data on the distribution of 3235 species from four phyla to explore the potential consequences of widespread reef degradation for biodiversity and to investigate ways to target conservation action to places where it is most needed and could have the greatest benefits. We mapped the geographic ranges of 1700 species of reef fish, 804 species of coral, 662 species of snail, and 69 species of lobster. We chose these taxa because they are well-known, good distributional data for them are available on a global scale, and they represent reasonable surrogates for reef diversity as a whole (*9*) [Web note 2 and Web table 1 (*8*)]. Figure 1, A through D, shows global clines in species richness of these taxa, mapped on an equal-area grid (*10*). There is a high level of concordance in patterns of total species richness across the four taxa (pairwise Spearman's rank correlations range from 0.78 to 0.89). For all taxa, species richness peaks in the so-called "coral triangle" of Southeast Asia (*11*), then falls off rapidly moving east across the Pacific, and less rapidly moving west across the Indian Ocean. In the tropical Atlantic, all taxa have highest richness in the Caribbean.

Figure 1E shows a high degree of overlap in the top 10% most species-rich cells for each taxon. 26.5% of the richest cells were shared by four taxa, 38.6% by three, and 38.6% by two (*12*). Cells in the southern Philippines and central Indonesia are in the top 10% richest locations for all four taxa, and degree of overlap declines moving away from this region.

Figure 1F shows the distribution of threats to coral reefs from human impacts, based on an analysis by Bryant *et al.* (*3*). They mapped threats to reefs from coastal development, overexploitation, and pollution from marine and land-based sources, then classified reefs as facing low, medium, and high levels of threat. Using their data, we calculated the average threat to reefs in each grid cell on a scale of 1 to 3 (low to high threat) (*13*). Areas of greatest species richness are exposed to significantly greater threats from human impacts than are less rich regions (Table 1).

Marine species have long been considered resilient to extinction because of their large geographic range sizes (*14*). Our data contradict this view for three of the four taxa. Figure 2 shows cumulative curves for species number versus range size, expressed as the number of cells within a species' extent of occurrence that contained reef habitat. Although most corals are widespread, most lobsters are geographically restricted, and fish and snails have roughly equal numbers of restricted-range and widespread species. Even among corals, 58 species (7.2%) had restricted ranges (≤10 cells). The figures were 26.5, 28.7, and 53.6%, respectively, for fish, snails, and lobsters. Hence, restricted-range species are common in the sea, and widespread reef degradation could lead to a gathering wave of extinctions. The low fraction of restricted-range corals should be treated with caution because we identified species by morphology (*15*). Corals and many other marine organisms with similar morphology conceal substantial genetic differences, even across regions without obvious barriers to gene flow (*16*, *17*). Future studies may reveal much cryptic speciation that could revise our conclusion that coral species are generally widespread. Extinction risk could be greater than suggested by our findings.

We examined the distribution of geographically restricted species to determine whether such endemics are clustered together into centers of endemism as they are in terrestrial environments (*18*). We used the reciprocal of the range size of each species as a measure of range rarity, and for each cell we summed the values of all species present (*19*). Maps of range-rarity scores reveal areas that are rich in restricted-range species [Web fig. 1, A through D (*8*)]. We mapped the top-scoring 10% of cells for each taxon, and Fig. 1G shows that there is high concordance among them. Of the top-scoring cells, 54.2% were shared by two taxa, 22.9% by three, and 3.6% by four (*12*).

Centers of endemism predominate in places isolated by distance or oceanography. For example, isolated islands rich in endemics include Mauritius and La Reunion in the Indian Ocean, Hawaii and Easter Islands in the Pacific, and St. Helena and Ascension Islands in the Atlantic. Centers of endemism also occur where nonreversing currents move water from tropical to temperate latitudes. Examples include east and west Australia,

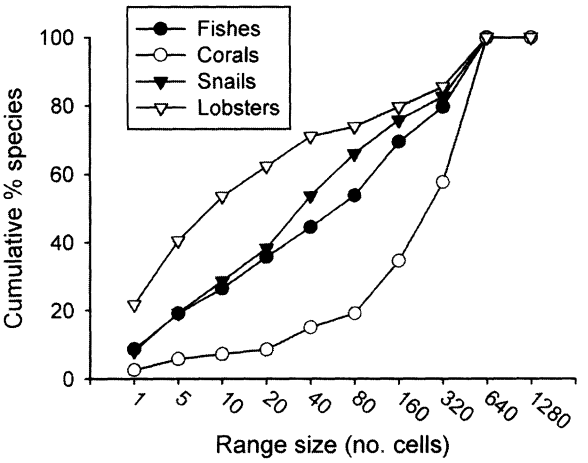

Fig. 2. Cumulative curves of species number versus geographic range size. Range size is expressed as the number of cells containing reef habitat within each species' extent of occurrence.

Table 1. Comparisons of threats to reefs from human impacts in the top 10% highest scoring cells versus the bottom 90% of cells. Threat scores for each grid cell were calculated with data from Bryant *et al.* (*3*, *12*) and range from 1 (low threat) to 3 (high threat). Figures show mean scores. For all taxa, the top 10% most species-rich cells were significantly more threatened than the rest. For the top 10% of range-rarity scores, this was the case only for corals and snails.

	Top 10% of cells	Bottom 90% of cells	Significance (Mann-Whitney U test)
Fish species richness	2.38	1.77	$P < 0.0001$
Coral species richness	2.54	1.75	$P < 0.0001$
Snail species richness	2.29	1.78	$P < 0.0001$
Lobster species richness	2.41	1.76	$P < 0.0001$
Fish range rarity	1.94	1.82	NS
Coral range rarity	2.23	1.79	$P < 0.0001$
Snail range rarity	2.14	1.80	$P < 0.0001$
Lobster range rarity	1.89	1.83	NS

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[1]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge MA 02138, USA. [2]Environment Department, University of York, York, YO10 5DD, UK. [3]Australian Institute of Marine Science, Private Mail Box No. 3, Townsville MC, Queensland, 4810, Australia. [4]Center for Applied Biodiversity Science, Conservation International, 1919 M Street, N.W., Suite 600, Washington, DC 20036, USA. [5]Ocean Voice International, Post Office Box 20060, Royal Post Office Perth Mews, Perth, Ontario, Canada K7H 3M6. [6]Eastern Ontario Biodiversity Museum, Box 1860, Kemptville, Ontario, Canada K0G 1J0. [7]United Nations Environment Programme–World Conservation Monitoring Centre (UNEP-WCMC), 219 Huntingdon Road, Cambridge, CB3 0DL, UK. [8]Western Australian Museum, Francis Street, Perth, WA 6000, Australia.

*To whom correspondence should be addressed at the Environment Department, University of York, York, YO10 5DD, UK. E-mail: cr10@york.ac.uk
†Deceased.

eastern South Africa, and southern Japan. However, there are also multitaxa centers of endemism in places that appear highly interconnected with other regions, such as the Philippines, Sunda Islands, and New Caledonia. This accords with growing evidence that species with pelagic larval stages do not always disperse widely (*20–23*).

We identified the 18 richest multitaxon centers of endemism (Fig. 1G) (*24*) [Web table 2 (*8*)]. They include 35.2% of the world's coral reefs and cover only 0.028% of the world's oceans (*25*), but include between 58.6 and 68.7% of restricted-range species from the four taxa (ranges ≤10 grid cells). The 10 richest centers of endemism cover just 15.8% of the world's coral reefs, but include between 44.8 and 54.2% of restricted-range species.

Terrestrial biodiversity hotspots have been defined on the basis of both endemism and threats facing them [the loss of >70% of primary vegetation (*18*)]. Figures for loss of primary habitat are unavailable for tropical reefs, but we can examine the risks of habitat loss based on threats estimated in Bryant *et al.*'s assessment (*3*, *13*, *26*). Many centers of endemism are deeply at risk and can be considered analogous to terrestrial biodiversity hotspots (Fig. 3). Without rapid conservation action, species will be lost. We define 10 marine biodiversity hotspots as those centers of endemism with average threat scores above 1.67 (that is, in the top two-thirds of the range of risk from human impacts) (Table 2 and Fig. 3). Focusing conservation effort on them could be highly effective in preventing species loss (*27*), but how good would it be as a strategy for protecting more widespread species?

Measures of range rarity and species richness are closely coupled for corals [Spearman's rank correlation (SR) = 0.86, $P < 0.001$, $n = 825$], loosely coupled for snails (SR = 0.51, $P < 0.001$), and largely uncoupled for fish (SR = 0.12, $P < 0.001$) and lobsters [SR = 0.06, not significant (NS)]. This means that although targeting centers of endemism for conservation would also benefit broader elements of coral diversity, it is likely to be less effective for other taxa. However, from the perspective of species' representation, the strategy looks better. The 10 richest centers of endemism include representatives of between 59.4 and 75.2% of all species in our sample, depending on taxon, whereas all 18 include from 73.9 to 96.1%.

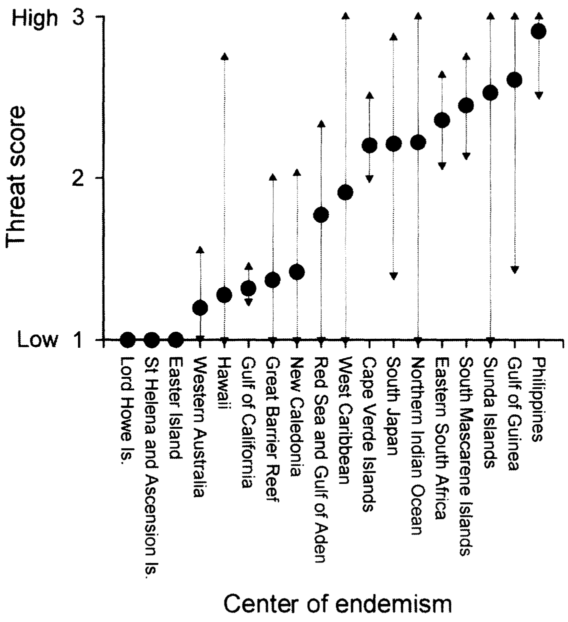
Figure 3 shows that even the most deeply

Table 2. Summary of attributes of centers of endemism [see Web table 2 (*8*) for details of places included in each]. We define marine biodiversity hotspots, indicated by bold type, as centers of endemism with average threat scores above 1.67 (*3*, *13*). na, not available.

Number	Location	Number of ≤10 cell range species present*	Rank based on number of ≤10 cell range species present	Number of more widespread species†	Rank based on number of more widespread species†	Average threat score for cells in center of endemism‡	Rank based on average threat to center of endemism	Area of coral reef in hotspot (km²)§	Adjacent terrestrial biodiversity hotspot(s)#
1	South Japan	75	1	1187	3	2.21	7	3136	Philippines
2	Western Australia	56	2	768	7	1.20	15	1713	Southwest Australia
3	Gulf of Guinea	45	3	33	15	2.61	2	na‖	West African forests
4	Great Barrier Reef	43	4	1080	4	1.37	12	23972	None
5	Hawaiian Islands	35	5	277	13	1.28	14	442	Polynesia/ Micronesia
6	Gulf of California	33	6	112	14	1.32	13	309¶	Mesoamerica
7	Lord Howe Island	31	7	493	11	1.00	16	103	New Zealand
8	North Indian Ocean	31	7	1053	5	2.22	6	9790	Western Ghats and Sri Lanka
9	New Caledonia	31	7	1011	6	1.42	11	5303	New Caledonia
10	Eastern South Africa	30	10	542	10	2.36	5	178	Cape floristic province
11	Cape Verde Islands	26	11	25	17	2.20	8	na‖	None
12	West Caribbean	20	12	430	12	1.91	9	4127	Mesoamerica
13	Red Sea	18	13	661	9	1.77	10	16194	None
14	Philippines	17	14	1471	1	2.91	1	21983	Philippines
15	South Mascarene Islands	16	15	746	8	2.45	4	205	Madagascar
16	St. Helena and Ascension Islands	13	16	27	16	1.00	16	na‖	None
17	Sunda Islands	13	16	1430	2	2.53	3	12639	Sundaland/ Wallacea
18	Easter Island	11	18	22	18	1.00	16	na‖	Polynesia/ Micronesia

*Results were qualitatively identical using ≤5 cells to define restricted-range species. †The number of more widespread species is based on those with range sizes >10 cells. ‡Based on Bryant *et al.* (*3*, *13*). Scores range between 1 and 3 (from low to high threat). §Calculated from the UNEP-WCMC database of coral reef area, Cambridge, UK (*25*). ‖These centers of endemism have limited rocky reef rather than coral reef habitat, and figures for habitat area are unavailable. ¶This center of endemism also has substantial areas of rocky reef habitat. #Terrestrial biodiversity hotspots defined by Myers *et al.* (*18*).

Fig. 3. Threats to reefs in centers of endemism. The figure shows mean (circles), maximum, and minimum threat scores for grid cells included within each center of endemism, calculated with data from Bryant *et al.* (*3*, *13*).



threatened centers of endemism often include places where threats are relatively low. Timely investment in the protection of these areas could yield good results. However, adopting a two-pronged conservation strategy, as Myers *et al.* (*18*) suggested for terrestrial ecosystems, would be better. Extensive areas of coral reef remain little affected by people, yet are rich in species (Fig. 1, A through F). Conservation efforts should extend to both marine biodiversity hotspots and reef "wilderness" areas and must include efforts to mitigate climate change.

Many threats to tropical reefs originate on land, including downstream impacts of forest loss, agricultural expansion, and construction (*3*). Our analysis reveals an opportunity for integrating terrestrial and marine conservation. Eight of 10 marine biodiversity hotspots and 14 of 18 centers of endemism are adjacent to terrestrial biodiversity hotspots (*18*) (Table 2). Extending terrestrial conservation efforts seaward in those places offers an effective and affordable strategy for protecting the planetary biota (*18*, *27*, *28*).

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9. Analyses are based on a sample of 1700 fish species from 28 families, representing approximately 40% of all known coral reef fishes (*29*). Mapping covered most of the characteristic families of coral reef fishes, including all known species of butterflyfish (Chaetodontidae), angelfish (Pomacanthidae), damselfish (Pomacentridae), surgeonfish (Acanthuridae), groupers (Serranidae), and wrasse (Labridae). Before analyses, experts checked maps for most families. All 804 known species of scleractinian corals, from 18 families, were mapped using a combination of museum records, literature sources, monographs, loan specimens, and extensive personal observations by one of us (J.E.N.V.), made during more than 30 years of research. Snails were mapped from three exceptionally well-known families that are both abundant on coral reefs and highly speciose: cone shells (Conidae), cowries (Cypraeidae), and volutes (Volutidae). Their ranges were mapped from taxonomic monographs, museum records, and extensive personal observations by one of us (F.W.). Lobster distributions (69 species from 7 families) were mapped from a taxonomic monograph of important fishery species [Web note 1 and Web table 1 (*8*)]. All sources used for mapping species' distributions are listed in Web note 3 (*8*). Range maps were interpolated, so that a species was assumed to be present on all reefs within a polygon bounded by the outermost records. Interpolation was necessary because large areas of reef tract remain poorly sampled. Interpolated ranges provide more realistic estimates of biodiversity clines than does the use of data directly from patchy sampling. For analyses, all range maps were input into ArcView as shape files.
10. For analyses, we used a grid that divides the tropics into a series of approximately 50,000-km^2 cells [edge length 2° latitude (*30*)] arranged in 2° latitudinal bands propagating north and south of the equator to 34°N and 36°S. The equal-area grid facilitated quantitative analysis of diversity clines, species ranges, and levels of threat. Only cells containing coral or rocky reef habitat were included.
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24. We identified multitaxa centers of endemism by including cells that were in the top 10% of range-rarity scores for two or more taxa. To them we added any adjacent cells in the top 5% of range-rarity scores for a single taxon. Cells were also included as centers of endemism if they scored in the top 5% for one taxon and in addition were in the top 20% for two or more other taxa. In this way, we obtained 18 centers of endemism [Web table 2 (*8*)], for which we calculated the number of restricted-range species present (range $\leq$10 cells); the number of other, more widespread species present; reef area; and levels of threat to reef habitat. Ongoing studies raise the possibility that our analysis omits some important regions. For example, Floeter *et al.* (*31*) show significant fish endemism in eastern Brazil, where approximately half the corals are also endemic (*15*). To ensure that centers of endemism were not artifacts of the range-rarity measure used (the reciprocal of the range size, summed across species present), we sought to confirm patterns by mapping the number of species per cell with ranges $\leq$10 grid cells. Web fig. 2, A through E (*8*), shows that patterns were virtually identical to those obtained using range-rarity scores.
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26. Myers *et al.*'s (*18*) analysis used historical loss of primary vegetation cover as a measure of impact, whereas Bryant *et al.*'s (*3*) threat scores identify areas at risk, some but not all of which have actually already witnessed human onslaught.
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