The calculated gamma dose rate was consistent with carbonates and 30 vol of H2O2 to remove organics. Treatment with 10% hydrochloric acid to remove dunes was determined with the SAR procedure. The total radiometric age of the dune layer was measured with 48% hydrofluoric acid for 1 year at a point 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.

Marine Biodiversity Hotspots and Conservation Priorities for Tropical Reefs

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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 distributors 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 focusing 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 ranges (14). Our data contradict this view for three of the four taxa. Figure 2 shows cumulative curves for species richness 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 with morphology (15). Corals and many other marine organisms with similar morphology conceivably 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 Réunion 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,

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.

<table>
<thead>
<tr>
<th></th>
<th>Top 10% of cells</th>
<th>Bottom 90% of cells</th>
<th>Significance (Mann-Whitney U test)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish species richness</td>
<td>2.38</td>
<td>1.77</td>
<td>P &lt; 0.0001</td>
</tr>
<tr>
<td>Coral species richness</td>
<td>2.54</td>
<td>1.75</td>
<td>P &lt; 0.0001</td>
</tr>
<tr>
<td>Snail species richness</td>
<td>2.29</td>
<td>1.78</td>
<td>P &lt; 0.0001</td>
</tr>
<tr>
<td>Lobster species richness</td>
<td>2.41</td>
<td>1.76</td>
<td>P &lt; 0.0001</td>
</tr>
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<td>Fish range rarity</td>
<td>1.94</td>
<td>1.82</td>
<td>NS</td>
</tr>
<tr>
<td>Coral range rarity</td>
<td>2.23</td>
<td>1.79</td>
<td>P &lt; 0.0001</td>
</tr>
<tr>
<td>Snail range rarity</td>
<td>2.14</td>
<td>1.80</td>
<td>P &lt; 0.0001</td>
</tr>
<tr>
<td>Lobster range rarity</td>
<td>1.89</td>
<td>1.83</td>
<td>NS</td>
</tr>
</tbody>
</table>
eastern South Africa, and southern Japan. However, there are also multixata 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 multixata 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 oceans, but include between 73.9 and 96.1% 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.

<table>
<thead>
<tr>
<th>Number</th>
<th>Location</th>
<th>Number of ≤10 cell range species present*</th>
<th>Rank based on number of ≤10 cell range species present</th>
<th>Number of more widespread species†</th>
<th>Rank based on number of more widespread species‡</th>
<th>Average threat score for cells in center of endemism§</th>
<th>Rank based on average threat to center of endemism</th>
<th>Area of coral reef hotspot (km²)¶</th>
<th>Adjacent terrestrial biodiversity hotspot(s)¶alom</th>
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<tbody>
<tr>
<td>1</td>
<td>South Japan</td>
<td>75</td>
<td>1</td>
<td>1187</td>
<td>3</td>
<td>2.21</td>
<td>7</td>
<td>3136</td>
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<td>56</td>
<td>2</td>
<td>768</td>
<td>7</td>
<td>1.20</td>
<td>15</td>
<td>1713</td>
<td>Australia, West African forests</td>
</tr>
<tr>
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<td>Australia</td>
<td>45</td>
<td>3</td>
<td>33</td>
<td>15</td>
<td>2.61</td>
<td>2</td>
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<tr>
<td>4</td>
<td>Great Barrier</td>
<td>43</td>
<td>4</td>
<td>1080</td>
<td>4</td>
<td>1.37</td>
<td>12</td>
<td>23972</td>
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</tr>
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<td>Hawaiian Islands</td>
<td>35</td>
<td>5</td>
<td>277</td>
<td>13</td>
<td>1.28</td>
<td>14</td>
<td>442</td>
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<tr>
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<td>33</td>
<td>6</td>
<td>112</td>
<td>14</td>
<td>1.32</td>
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<tr>
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<td>7</td>
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</tr>
<tr>
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<td>North Indian</td>
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<td>7</td>
<td>1053</td>
<td>5</td>
<td>2.22</td>
<td>6</td>
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<td>Western Ghats and Sri Lanka</td>
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<tr>
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<td>New Caledonia</td>
<td>31</td>
<td>7</td>
<td>1011</td>
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<td>10</td>
<td>542</td>
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<td>11</td>
<td>25</td>
<td>17</td>
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<td>8</td>
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<tr>
<td>12</td>
<td>West Caribbean</td>
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<td>12</td>
<td>430</td>
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<tr>
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<td>Red Sea</td>
<td>18</td>
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<td>15</td>
<td>746</td>
<td>8</td>
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<td>4</td>
<td>205</td>
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<tr>
<td>16</td>
<td>St. Helena and</td>
<td>13</td>
<td>16</td>
<td>27</td>
<td>16</td>
<td>1.00</td>
<td>16</td>
<td>na§</td>
<td>None</td>
</tr>
<tr>
<td>17</td>
<td>Sunda Islands</td>
<td>13</td>
<td>16</td>
<td>1430</td>
<td>2</td>
<td>2.53</td>
<td>3</td>
<td>12639†</td>
<td>Sundaland/Polynesia/Micrones</td>
</tr>
<tr>
<td>18</td>
<td>Easter Island</td>
<td>11</td>
<td>18</td>
<td>22</td>
<td>18</td>
<td>1.00</td>
<td>16</td>
<td>na§</td>
<td>None</td>
</tr>
</tbody>
</table>

*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).
threatened centers of endemism often include places where threats are relatively low. Time-
ly 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 ecossys-
tems, 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 “wil-
derness” 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 conserva-
tion. Eight of 10 marine biodiversity hotspots and 14 of 18 centers of endemism are adja-
cent to terrestrial biodiversity hotspots (18) (Table 2). Extending terrestrial conservation efforts seaward in those places offers an effec-
tive and affordable strategy for protecting the planetary biota (18, 27, 28).

References and Notes

1. C. Birkeland, Ed., Life and Death of Coral Reefs (Chap-
mann and Hall, New York, 1997).
8. Supplementary Web material is available on Science Online at www.sciencemag.org/cgi/content/full/295/5558/1280/DC1.
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 (Pomacentri-
daee), surgeonfish (Acanthuridae), groupers (Serranidae), and wrasse (Labridae). Before analyses, experts checked maps for most families. All 804 known species of scler-
actinian 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 (Voluti-
daee). Their ranges were mapped from taxonomic mono-
graphs, museum records, and extensive personal obser-
vations by one of us (F.W.L.). 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 be-
cause large areas of reef tracts 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 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 (Pomacentri-
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cause large areas of reef tracts 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.
11. To test the significance of differences using chi-square.
12. Threat scores were available for 642 of the 842 grid cells with reefs. Bryant et al.’s analysis (3) does not account for the problem of climate change, and this may add substantially to the levels of threat (7).
24. 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.
30. Supported by the Sir Peter Scott Trust for Education and Research in Conservation, Ocean Voice Interna-
tional, U.S. Agency for International Development, the Curtis and Edith Musson Foundation, the World Conservation Union (IUCN) Sir Peter Scott Fund, UNEP-WCMC, the UK Darwin Initiative/Tropical Ma-
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31. Dedicated to the memory of Don McAllister, who died during the writing of this paper.

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