



Coral Reef Biodiversity— Habitat Size Matters

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Coral reefs are the most diverse of all marine ecosystems (1), with estimates of reef species ranging from 600,000 to more than 9 million species worldwide (2, 3). This biodiversity is most pronounced in the western Pacific and Indian Oceans (1, 4), but decreases with increasing distance from the Indo-Australian archipelago. For example, reefs in the central Indo-Pacific have more than 10 times as many coral and fish species as reefs of the Galapagos Islands in the eastern Pacific (4) (see the figure). This striking gradient of biodiversity deserves an explanation (1, 4, 5). On page 1532 of this issue, Bellwood and Hughes (6) present their attempt to explain this biodiversity gradient by analyzing the numbers of coral and fish species associated with 113 reef communities stretching from the Red Sea to the Gulf of California. They discovered that the area of suitable reef habitat surrounding the study sites was by far the best predictor of biodiversity at these sites.

Despite sophisticated statistical analyses of large data sets, counting species remains at the heart of most modern biodiversity studies (7). Rather than count total numbers of species, Bellwood and Hughes counted the numbers of species in the 13 most species-rich families of corals and fishes associated with their reef study sites (they excluded gobies because of sampling problems). Using principal components analysis, the authors sought features of the coral reefs that could have contributed to the biodiversity gradient that they observed.

Much of the variation in diversity could be explained by the first principal component (PC1) of the analysis, which summarized the pattern of variation for those coral and fish families whose diversity varied the most across sites. This allowed the authors to then analyze the relationship between biodiversity (as measured by PC1) and four other reef site characteristics: latitude, longitude, reef type (offshore versus continental), and other suitable habitats within 600 km.

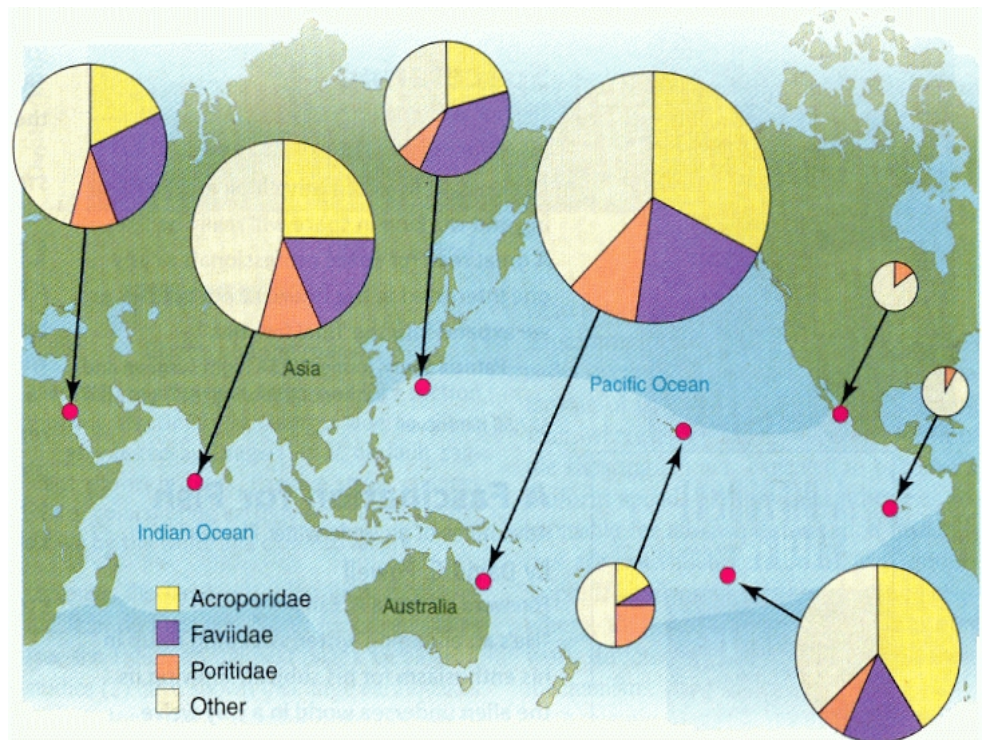
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Two surprising patterns emerged. First, the 13 species-rich fish and coral families represented remarkably similar proportions of total diversity for all but the most depauperate (species-poor) reef sites. This is illustrated by, for example, the constancy of proportions of dominant coral families at all sites except the depauperate sites of Hawaii, the Gulf of California, and the Galapagos Islands (see the figure).

Regardless of total diversity, such constancy—also observed in an earlier comparison of fishes from reefs near Madagascar and French Polynesia (8)—implies that the species found at any site may be a random sample of all the available species. However, the relative importance of different families in the global species pool might itself be highly nonrandom. Most members of fish families belong to just one or two feeding guilds—for example, most

groupers (Serranidae) are carnivores and most damselfishes (Pomacentridae) are plankton feeders or herbivores. If the proportions of fish species in different trophic groups (and hence families) are relatively constant among reef communities, this would affect the family composition of the global fish species pool. Although the ecological characteristics of corals correlate less well with family membership (because families are defined by microstructural features of the skeleton), there are some life-history differences among coral families that could also influence the composition of the global coral species pool (6).

The second pattern that Bellwood and Hughes observed was that the area of suitable habitat within 600 km of a study site was the most important predictor of variation in coral and fish species diversity as measured by PC1. Once local habitat area was factored out, longitude explained relatively little of the variation in diversity, and latitude even less (it was insignificant for corals); reef type was insignificant for both groups. This contrasts with previous analyses of coral reef diversity (based on numbers of species or genera), which revealed a significant relationship between biodiversity and either distance from the equator (9) or mean temperature (10). In the latter study



Rainforests of the sea. Biodiversity in the Indo-Pacific region was measured by counting the total numbers of species in the 13 most species-rich coral and fish families associated with 113 reef communities (data for coral species at 8 reefs are shown). Circle area is proportional to total number of coral species, which ranges from 13 associated with reefs of the Galapagos Islands to 321 associated with the Great Barrier reef. Fish species (not shown) exhibit a similar biodiversity gradient.

(10), temperature was found to be a much better predictor of variations in diversity than latitude. Bellwood and Hughes might have detected stronger effects had they used temperature rather than latitude in their study. These authors also used longitude as an estimate of distance (isolation) from the center of diversity (the Indo-Australian region), whereas earlier studies that did find strong associations between biodiversity and isolation (9, 10) used other measures, such as density of upstream islands within 5000 km of the reef site (10). Nevertheless, the discrepancy among these findings regarding the importance of isolation to biodiversity is puzzling because the various measures used to assess isolation are all related, as are the measures of diversity (6, 10).

The empirical finding of a relationship between habitat area and reef biodiversity is not without precedent (10). It is consistent with theoretical models based on the notion of metapopulations (that is, groups of partially isolated and partially interconnected populations) (11, 12). Recent studies of Pacific reef fishes and corals (13, 14) suggest that, as required by metapopulation models, new recruits to the reefs are a mixture of offspring produced by local and more distant parents.

The dependence of diversity on habitat area is particularly troubling in light of the progressive destruction of reef habitats worldwide (15), and this finding clearly has important implications for conservation. First and foremost, coral reefs need to be protected now in order to prevent future species extinctions. The fact that such extinctions are not yet conspicuous is no cause for complacency, because models predict a

substantial time lag between loss of habitat and species extinction (12). Moreover, these models also suggest that the coral species at greatest risk are the long-lived species that are rarely recruited to reefs but form the three-dimensional structure of reefs on which many other species depend. Finally, as noted by Bellwood and Hughes (6), low diversity regions may be especially vulnerable to damage and destruction because they lack entire families of species that might help the reef ecosystem to recover. The relationship between coral reef biodiversity and ecosystem productivity and resilience (16) is poorly understood (17). Thus, it is crucial that our conservation strategies err on the side of caution.

If reefs are the rainforests of the sea, then the corals and fishes counted by Bellwood and Hughes are equivalent to trees and birds. Even though most of the diversity in rainforests is contributed by insects, the insect equivalents that inhabit reefs have not been well characterized as yet. Indeed, the only estimates available for total reef biodiversity are based on an extrapolation from rainforests (2) and the counting of taxa found in a 5-cubic-meter reef microcosm in Baltimore harbor (USA) (3)! As we computerize and analyze existing taxonomic data and contemplate the contribution of reef loss to the global biodiversity crisis, we should remember that most of the organisms at risk on reefs are not only countless but also uncounted.

References and Notes

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