

Regional-Scale Assembly Rules and Biodiversity of Coral Reefs

David R. Bellwood* and Terry P. Hughes

Tropical reef fishes and corals exhibit highly predictable patterns of taxonomic composition across the Indian and Pacific Oceans. Despite steep longitudinal and latitudinal gradients in total species richness, the composition of these key taxa is constrained within a remarkably narrow range of values. Regional-scale variation in reef biodiversity is best explained by large-scale patterns in the availability of shallow-water habitat. Once habitat area is accounted for, there is surprisingly little residual effect of latitude or longitude. Low-diversity regions are most vulnerable to human impacts such as global warming, underscoring the urgent need for integrated management at multinational scales.

Globally, both terrestrial and aquatic ecosystems are experiencing declining biodiversity (1, 2). This decline highlights the need to understand processes regulating diversity and the consequences of species loss for ecosystem function (1–5). In marine systems, coral reefs are among the most diverse habitats on the globe (6, 7). Yet, our understanding of regional-scale patterns of biodiversity on coral reefs (and the processes underlying these patterns) has changed little since the seminal work of Stehli and Wells (6), which identified contours of decreasing diversity (measured as total generic richness) with increasing distance from the Indo-Australian Archipelago. Although recent studies have confirmed the existence of diversity gradients in the generic and species richness of numerous marine groups (7–10), the processes that shape these patterns remain elusive. We explore patterns of biodiversity and species composition of the two key taxa on coral reefs: fishes and corals. Our goals are to quantify for the first time biogeographic variation in species composition (as distinct from the pooled total generic or species richness) along biodiversity gradients and to explore several mechanisms that potentially shape the species composition of tropical reef corals and fishes across the Indo-Pacific Oceans.

First, we considered patterns of species loss along diversity gradients, determining the extent to which the patterns depart from a null model that depauperate assemblages merely represent a random subset of rich ones, using data (11) from 113 locations (Fig. 1). Our results show that the taxonomic composition of reef fishes and corals is remarkably conservative, that is, the species composition at each location across the Indian and Pacific Oceans is constrained within a surprisingly narrow range of configurations (Fig. 2). For example, across all sites with >100

species, 6 to 22% of the fish species are pomacentrids (damselfish) and 4 to 28% are serranids (groupers), whereas 14 to 43% of the corals are acroporids and 7 to 16% are poritids (12). Furthermore, for many families and locations, these values lie within the bounds predicted by random allocations of species to local sites from the global species pool (13) (see bootstrapped confidence limits in Fig. 2). Outliers occurred most frequently at depauperate sites (i.e., at high latitudes, or in the eastern Pacific and western Indian Oceans, farthest from the center of diversity in the Indo-Australian Archipelago) (Figs. 1 and 2).

All families exhibited highly correlated species richness, rising and falling in tandem along biodiversity gradients. Moreover, the correlation between the species richness of any two families across all locations (mean of r , fishes, 0.83; corals, 0.76) occurred even among families that differ markedly in life-history traits or larval duration (14–16). Indeed, direct comparisons between species richness of fish and coral families also revealed a modest positive correlation with a mean coefficient of 0.65 (16). Thus, we conclude that ecological traits (e.g., body size,

longevity, larval type) have surprisingly little impact on distribution patterns of species at a regional scale. However, deviations in species composition at depauperate locations do have a biological basis. For example, the dominant coral family Acroporidae is often underrepresented at low-richness sites and the Favidae is overrepresented (Fig. 2). This finding is consistent with observations that acroporids are less resilient in marginal conditions than favids, which can better withstand environmental stress and instability (17, 18).

These results indicate that large-scale assembly rules determine the species composition of reef assemblages throughout the Indo-Pacific: The proportion of species in each family is highly predictable, regardless of the location, based on a random allocation from the available species pool. Furthermore, our analyses highlight the vulnerability of low-diversity locations, where whole families or functional groups may be missing (Fig. 2). Thus, one might reasonably expect to lose, by chance alone, even the most speciose families (e.g., the serranid fishes or acroporid corals) in systems with a total species richness, for the 13 families, of <50 species. The loss of important families or functional groups has the potential to severely compromise ecosystem function, resilience, and stability (2–4). Such a scenario, with resultant ecosystem disruption, recently occurred in the Caribbean, where the decline of a guild of herbivores, scarid, and acanthurid fishes (due to overfishing) and sea urchins (due to disease) has led to widespread algal blooms and a phase shift in ecosystem structure (19, 20). Comparable records of major ecosystem changes on coral reefs in the Indo-Pacific have been recorded from depauperate, marginal sites [e.g., the Galápagos Islands, western Panama, Hawaii (21, 22)], whereas high-diversity locations such as the Philippines, Indonesia, or the Great Barrier Reef show a greater resilience to recurrent disturbances (23–25).

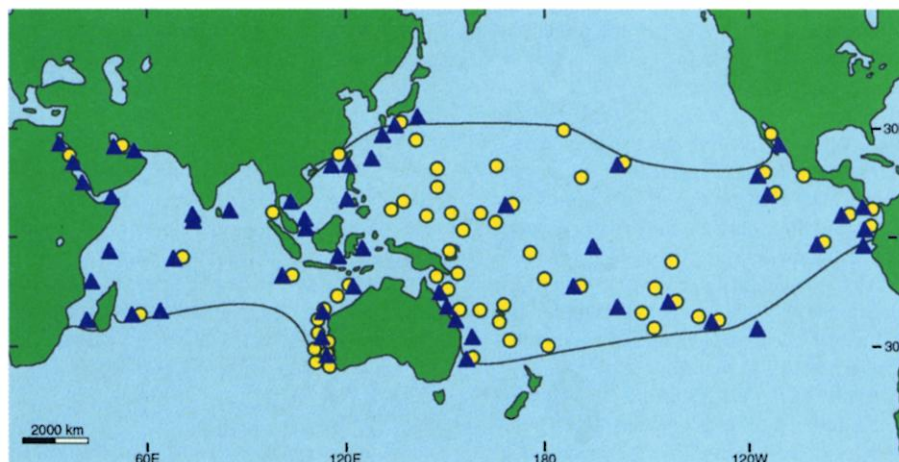


Fig. 1. The geographic distribution of survey sites used in our analysis of regional patterns of biodiversity of coral reef fishes (circles) and scleractinian corals (triangles) in the Indian and Pacific Oceans. The solid lines delineate the latitudinal extent of coral reef growth.

Centre for Coral Reef Biodiversity, Department of Marine Biology, James Cook University, Townsville, Qld 4811, Australia.

*To whom correspondence should be addressed. E-mail: david.bellwood@jcu.edu.au

REPORTS

There is a remarkable congruence between the regional-scale patterns of biodiversity of fishes and corals (Fig. 3). In both taxa, the Indo-Australian region between 120° and 170°E is characterized by the most taxonomically diverse assemblages, with a steep decline toward more depauperate assemblages eastward across the Pacific, and a shallower decline westward across the Indian Ocean (Fig. 3). Similar congruence among fish and corals occurs with latitude, with a region of diverse assemblages near the equator and a decline to more depauperate assemblages with increasing latitude.

The similarity in biodiversity patterns among corals and fishes indicates that the mechanisms that control the large-scale species composition of tropical reefs operate similarly across numerous taxa. We examined four variables (latitude, longitude, area of shallow-water habitat, and reef type) that may explain the variation in taxonomic composition of fish and coral assemblages (Fig. 4). Of these, regional-scale variation in habitat area stands out clearly as the major factor (26), explaining 57% of the variation in coral assemblages and 42% in fishes. The highest diversity sites occur in the Indo-Australian region, encompassing the vast continental reefs of Southeast Asia, the Philippines, Indonesia, Papua New Guinea, and the Great Barrier Reef. Once habitat area is accounted for, longitude remains an important factor for fish communities (17.2%), but it has a smaller impact on corals (10%). Biologically, the effect of longitude reflects the degree of isolation from the center of diversity. Latitude explains a further 15.0% of the variation in fish diversity, but it is surprising that changes in coral assemblages are not significantly correlated with latitude *per se*. Once habitat area and longitude are taken into consideration, latitude (with its correlates of temperature, seasonality, productivity, etc.) accounts for only a further 5.4% of the variation in diversity. Finally, we found no significant correlation between reef type (oceanic versus continental) and taxonomic composition. Once the other variables were accounted for, reef type explained only 1.3% and 1.8% of the variation in fish and coral assemblages, respectively. Collectively, the four variables explained >74% of the variation in taxonomic composition of reef fish and corals assemblages across the Indo-Pacific (Fig. 4).

An alternative hypothesis, which could account for similar latitude and longitudinal trends in all families in both fishes and corals, is the mid-domain effect, a product of the interaction between species geographic ranges and the maximum potential geographic range delineated by biogeographic barriers (27). However, the limited explanatory power of latitude and longitude revealed by our analyses (Fig. 4), and the relatively high diversity assemblages in the Western Indian Ocean (Fig. 3), suggest that mid-domain effects on coral reefs are relatively minor compared with the

overriding influence of habitat area. However, in the absence of an analysis of randomized range data, it is not possible to evaluate fully the contribution of mid-domain effects.

Habitat area may promote biodiversity, in both ecological and evolutionary time-scales, if larger areas have higher rates of speciation or reduced rates of extinction (28, 29). Habitat area

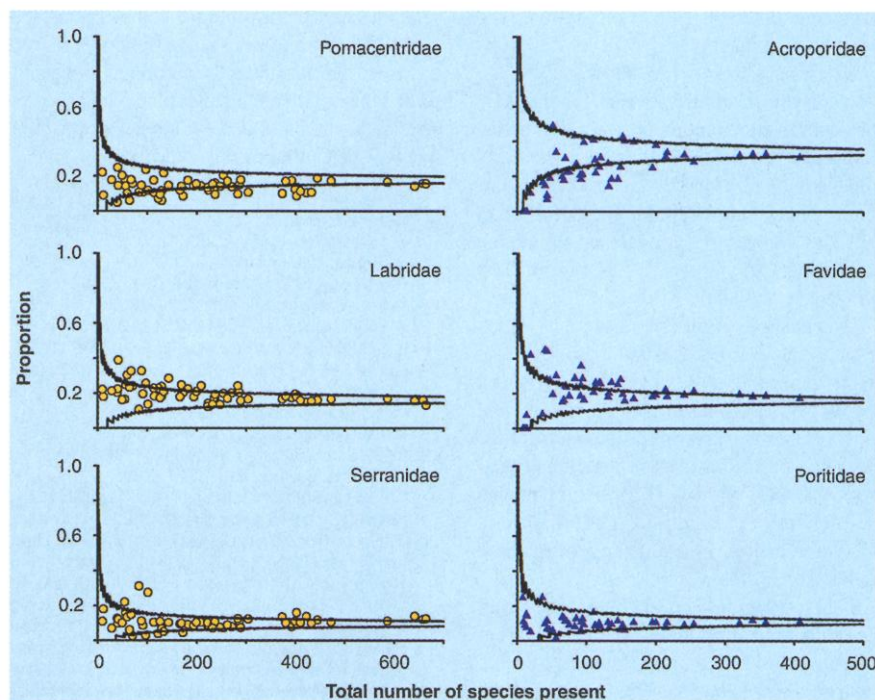


Fig. 2. Contribution to the total species pool of the three most abundant fish and coral families across a range of total species richnesses. Upper and lower lines are bootstrapped 95% confidence limits based on random selection of species from the total species pool (73). Other families show similar patterns (compare Fig. 3).

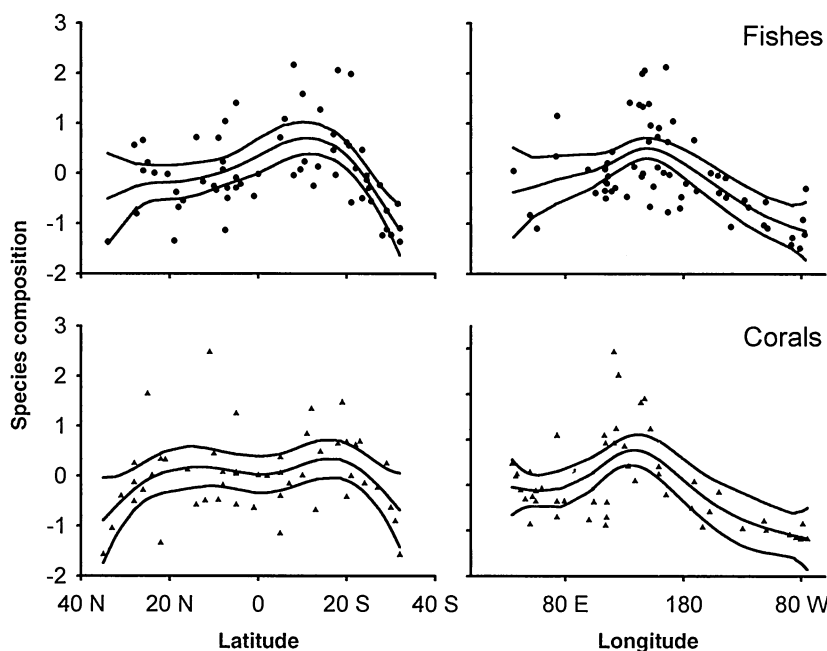


Fig. 3. Latitudinal and longitudinal changes in the taxonomic composition of fishes and corals. Taxonomic composition is expressed as the score on the first axis (PC1) of a principal components analysis (40), which provides a quantitative description of the degree of taxonomic similarity between fish or coral assemblages at different locations (Fig. 1). Two locations with the same PC1 score share similar species richness in those families that account for the greatest variation among sites. Latitude and longitude values are given in degrees from the equator or degrees east or west of Greenwich. Lines indicate the mean \pm 2 SEM.

has a crucial effect on population size (more area equates to larger populations; although recent population decline on degraded reefs may reduce the "effective" habitat area). Larger populations produce more offspring and support high genetic diversity (30). Furthermore, the probability of extinction is reduced for abundant, widespread species (31–33).

The strong relation between biodiversity, species composition, and habitat area offers direct evidence that the availability of large areas of suitable habitat is the key factor in maintaining high species richness in the Indo-Australian Archipelago (IAA). Historical biogeographic hypotheses to explain patterns of marine richness in the Indo-Pacific fall into three categories: (i) center of origin hypotheses, in which patterns are shaped by dispersal and degree of isolation from the IAA (1, 7), (ii) the IAA as a center of overlap or accumulation, or (iii) the IAA as a center of survival, providing a refuge from higher extinction rates in peripheral locations (8, 9, 34, 35). In all cases, the importance of the IAA for the origin or survival of species rests on the extensive availability of shallow water habitats in this region.

Global warming, coral bleaching, and overfishing are all capable of changing reef biodiversity and reducing the quality of reefs over large areas (20, 36, 37). Clearly, if we wish to protect global biodiversity, we must understand the processes that maintain diversity at this scale. We identify a major goal for management strategies: the protection of habitat over large, regional-scale areas. The results point to a need to shift our focus from individual taxa to broader habitat-based management strategies, and they highlight the need for international management of reef resources.

In conclusion, our approach provides a new

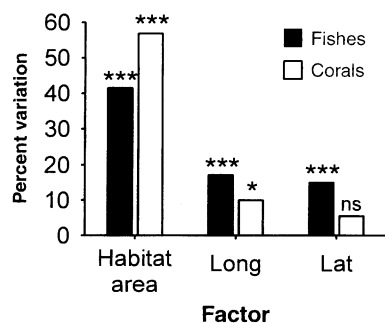


Fig. 4. Analysis of factors influencing biodiversity of coral reefs, illustrated by the percent variation in taxonomic composition of fish and coral assemblages explained by habitat area, longitude, and latitude. The score on the first axis of a principal components analysis provides a quantitative description of each assemblage (40) (Fig. 3). Of the four factors examined, the three shown here were significant in best-fit multiple regression models (*** $P < 0.001$, * $P < 0.05$), with habitat area explaining approximately half of the variation (26).

framework for examining regional patterns of biodiversity in reef systems and emphasizes the predictability of coral reef assemblages and the role of habitat area in shaping patterns of biodiversity. The challenge now is to identify the relation between taxonomic composition, species richness, and ecosystem function in reef systems. The formidable task of acquiring multiscale quantitative biogeographic data based on species abundances and functional characteristics will be central to this endeavor.

References and Notes

- K. J. Gaston, *Nature* **405**, 220 (2000).
- D. Tilman, *Nature* **405**, 208 (2000).
- F. S. Chapin et al., *Nature* **405**, 234 (2000).
- K. S. McCann, *Nature* **405**, 228 (2000).
- A. Purvis, A. Hector, *Nature* **405**, 212 (2000).
- F. G. Stehli, J. W. Wells, *Syst. Zool.* **20**, 115 (1971).
- J. E. N. Veron, *Coral Reefs in Space and Time: The Biogeography and Evolution of the Scleractinia* (UNSW Press, Sydney, Australia, 1995).
- G. Paulay, *Paleobiology* **16**, 415 (1990).
- S. R. Palumbi, *Coral Reefs* **16**, 47 (1997).
- F. G. Stehli, *Evolution* **53**, 326 (1999).
- We examined taxonomic composition (number of species in each family) across a range of sites with marked differences in total species richness. Data were drawn from 113 published species lists (63 fish, 50 coral) from locations spanning the Indian and Pacific Oceans between 33°N and 33°S (Fig. 1). 13 most speciose families of hermatypic scleractinian corals and fishes (excluding gobies, which are frequently underestimated). Published sources for species lists are provided in supplementary material available on Science Online at www.sciencemag.org/cgi/content/full/292/5521/1532/DC1
- Atlantic reef assemblages are completely different, reflecting a very different history of speciation and extinction (38). Among corals, for example, the dominant family in the Indo-Pacific (the Acroporidae) is represented by only three species in the Caribbean (7).
- Bootstrapping was based on 1000 iterations for each total species richness value, using estimated total species pools for the 13 families of fishes and corals (11).
- J. M. Leis, in *The Ecology of Fishes on Coral Reefs*, P. F. Sale, Ed. (Academic Press, San Diego, CA, 1991), pp. 183–230.
- D. J. Ayre, T. P. Hughes, *Evolution* **54**, 1590 (2000).
- Species richness in families with highly contrasting life-history modes and dispersal potentials were still highly correlated across all locations. In corals, species richness of the Acroporidae (95% spawners, mostly branching or encrusting colonies, generally short-lived) versus Poritidae (spawners and brooders, typically massive morphologies or finger corals, generally long-lived) were correlated with an r value of 0.93. Each family versus the Pocilloporidae (generally brooding, branching, short-lived) yielded an r of 0.70 and 0.68 respectively. In fishes, the Acanthuridae (surgeonfishes, broadcast spawners, long larval duration, strong swimming larvae) versus Apogonidae (cardinalfishes, mouth brooders with moderate larval duration and poor swimming abilities) correlated with $r = 0.73$. Values for all pair-wise correlations are provided in supplementary material that is available on Science Online at www.sciencemag.org/cgi/content/full/292/5521/1532/DC1
- B. E. Brown, L. S. Howard, *Adv. Mar. Biol.* **22**, 1 (1985).
- T. P. Hughes, J. H. Connell, *Limnol. Oceanogr.* **44**, 932 (1999).
- H. A. Lessios, *Annu. Rev. Ecol. Syst.* **19**, 371 (1988).
- T. P. Hughes, *Science* **265**, 1547 (1994).
- S. J. Dollar, G. W. Trumble, *Coral Reefs* **12**, 223 (1993).
- P. W. Glynn, J. S. Ault, *Coral Reefs* **19**, 1 (2000).
- B. E. Brown, Suharsono, *Coral Reefs* **8**, 163 (1990).
- J. H. Connell, *Coral Reefs* **16** (suppl.), s101 (1997).
- G. R. Russ, A. C. Alcala, *Coral Reefs* **17**, 399 (1998).
- Latitude and longitude are measured as the distance in degrees from the center of diversity in the Indo-Australian Archipelago (10°S 150°E fishes; 0° 150°E corals). Reef type was categorized as oceanic or continental. Reef type may act as a proxy for productivity, separating

continental reefs with relatively high productivity from oceanic reefs that are more oligotrophic and have low productivity. Available habitat was allocated into three categories (high, medium, low) based on the estimated area of shallow water (<50 m deep), >20%, 3 to 20%, 0 to 2%, respectively, within an arbitrary 600 km of each study site, using bathymetry indicated by the World Series Navigational Charts. Using a categorical estimate of habitat area was less subjective than a continuous measurement (e.g., km²) of locations with poorly known boundaries and avoided the problem of inadequate charts for many remote tropical regions. Despite the relative coarseness of our area estimates, this factor proved to be of overwhelming importance in explaining patterns of biodiversity. We used generalized additive regression models (GAMs) (39) to determine the best fit for each of the five dependent variables, utilizing a forward-backwards stepwise method to select the best sequence of predictors among the independent variables. At each step, the next variable added to the model with the highest F value and lowest P value was selected (provided $P < 0.05$). Independent variables were continuous (latitude, longitude) or categorical [area of habitat, reef type (oceanic versus continental)]. Continuous variables were entered into the model as nonlinear variables using spline functions with 4 degrees of freedom. The percentage of variation explained by each factor individually for fish and corals, respectively, was habitat area (41.5, 56.9), longitude (32.9, 35.8), latitude (30.3, 13.2), and reef type (<0.1, 4.1).

27. R. K. Colwell, D. C. Lees, *Trends Ecol. Evol.* **15**, 70 (2000).

28. M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995).

29. ———, *Science* **284**, 276 (1999).

30. S. R. Palumbi, *Coral Reefs* **16**, s47 (1997).

31. J. B. C. Jackson, *Am. Nat.* **108**, 541 (1974).

32. D. Jablonski, *Science* **231**, 129 (1986).

33. ———, *Science* **238**, 360 (1987).

34. J. B. C. Jackson, P. Jung, A. G. Coates, L. S. Collins, *Science* **260**, 1624 (1993).

35. M. E. J. Wilson, B. R. Rosen, in *Biogeography and Geological Evolution of SE Asia*, R. Hall, J. D. Holloway, Eds. (Backhuys, Leiden, Netherlands, 1998), pp. 165–195.

36. D. Bryant, L. Burke, J. McManus, M. Spalding, *Reefs at Risk: A Map-Based Indicator of Threats to the World's Coral Reefs* (World Resources Institute, Washington, DC, 1998).

37. J. B. C. Jackson et al., *Science*, in press.

38. D. R. Bellwood, in *Proceedings of the 8th International Coral Reef Symposium*, Panama, 24 to 29 June 1996, H. A. Lessios, I. G. Macintyre, Eds. (Smithsonian Tropical Research Institute, Panama, 1997), vol. 1, p. 379.

39. T. J. Hastie, R. Tibshirani, *Generalized Additive Models* (Chapman & Hall, London, 1990).

40. We used a principal components analysis to identify the main axis of variation in species composition among sites. In both fishes and corals, a very large proportion of the variation in the assemblages (fish 84%, corals 78%) could be explained on a single axis (PC1). Consequently, we are able to quantify fish and coral assemblages rigorously using PC1 to describe a range of assemblages ranging from high taxonomic diversity (strong representation of those families that exhibit most overall difference among sites) to low diversity (weak representation of these families). Furthermore, we used the PC1 axis as the independent variable in regression models to examine the potential causes of biogeographic patterns in diversity (27). Note that two locations with identical generic or species richness may have completely different taxonomic structures, a fundamental weakness of the Stehli and Wells approach (6) that our analysis explicitly addresses. Although the correlation between PC1 and total species richness was >0.99 in both groups, PC1 is not a simple proxy for species richness. A similar PC1 score at two locations means that they have a similar taxonomic structure, with similar numbers of species in those families that characterize most variation in biodiversity among sites.

41. We thank S. Blake, A. Hoey, and especially J. E. Tanner for technical assistance, and J. Caley, S. Connolly, N. Moltschanivsky, P. Munday, and R. Steneck for comments on earlier drafts. Supported by grants from the Australian Research Council to D.R.B. and T.P.H.

27 December 2000; accepted 5 April 2001