

## THE MAINTENANCE OF DIVERSITY ON CORAL REEFS: EXAMPLES FROM THE FOSSIL RECORD

John M. Pandolfi and Jeremy B.C. Jackson

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, República de Panamá

## ABSTRACT

Species membership in ecological communities is the result of many interrelated biotic and abiotic factors acting over a wide variety of scales. Ecological studies conducted over short spatial and temporal scales provide ample evidence of fluctuations in community membership but there are few studies to determine whether communities are more stable on much larger scales. We present results from two studies of Late Pleistocene coral reefs over large scales which show relatively constant species membership. Coral communities are similar in species composition through a 95 thousand year interval on the Huon Peninsula, Papua New Guinea, and show little decrease in similarity in taxonomic composition and abundance with increasing distance (up to 40 km) among communities of the same age at Curacao, Netherlands Antilles. The patterns in within-habitat species membership on broad spatial and temporal scales demonstrate much more order to coral reef communities than can be explained by disturbance and dispersal limitation alone.

## INTRODUCTION

How species are assembled into communities and how communities are maintained across time and space, are two of the fundamental questions in ecology. The great effort devoted to these topics has yielded a rich array of theories and hypotheses to explain how the taxonomic composition of communities varies over a variety of temporal and spatial scales.

Early theories emphasized niche differences that allowed species to coexist in an equilibrium world (Hutchinson 1959). But this view has come under increasing attack over the last 20 years due to: (1) the lack of clear evidence for niche diversification, and (2) the overwhelming evidence for rapid community change (Sale 1988). Two alternatives to niche diversification are the effects of disturbance and dispersal. Connell (1978) invoked the "intermediate disturbance hypothesis" to explain the apparent lack of order in coral reef communities at very small spatial scales. Connell reasoned that though niche differences might exist, the high frequency of major disturbances on reefs routinely prevented competitive exclusion. Thus Connell's coral reef communities appeared to be maintained in a nonequilibrium state. These views are really a restatement of Hutchinson's (1961) 'paradox of the plankton': communities are ever changing, in response to ever changing environmental conditions, with little temporal and spatial predictability. But in the case of coral reefs, we do not know how stable communities are over much larger scales of entire reefs or reef tracts (Jackson 1991). This suggests that we may falsify the dominant role of disturbance on coral reef community structure by demonstrating (1) no significant change in species membership or abundance in communities over large spatial and temporal scales, and (2) non-random persistence of species associations in space or time.

Another alternative view considers limitations to dispersal as the overriding factor in the species assembly of communities (Hubbell 1997a). In contrast to disturbance, dispersal assembly may or may not result in predictable community structure, depending on the presence or absence of widespread species that may dominate most local communities by virtue of their superior dispersal ability, rather than by niche differences. Community structure will drift through time and space, but long term compositional stasis can

arise as easily from the stabilizing effect of large numbers as from niche-assembly rules which limit species membership (Hubbell 1997b). Thus, we can falsify the exclusive role of dispersal for coral reef community structure by demonstrating large-scale non-random stability as for disturbance above, and that such stability is not due to dominance by a few highly dispersed species that are more widespread than non-dominant taxa.

Testing these ideas has been difficult for ecologists studying living ecosystems. Studies are usually no longer than the typical 2 or 3 years of most scientific grants, and even "long-term" studies rarely last beyond the two or three decades of a single scientific career. This is especially problematic for coral reefs because coral clones may live up to a thousand years or more (Potts et al. 1985), and different kinds of disturbance can act at a variety of temporal and spatial scales (Table 1 in Jackson 1991). To counteract the lack of long-term data, many ecologists have attempted to substitute variation in space for time. This is reasonable but limited in practice due to ignorance of the previous history of the ecosystems under study, especially when that history has involved degradation by human influence (Hughes 1989; 1994). In contrast, the fossil record of modern coral reefs provides ecological data on the order of hundreds to hundreds of thousands of years, long before human disturbance occurred. Preservation is potentially exceptional, in part because coral reef communities build a continuous, durable skeletal framework as they grow. The Quaternary fossil record provides an appropriate starting point for evaluating coral reef ecological patterns over large temporal and spatial scales (Jackson 1992; Pandolfi 1996).

In this paper, we summarize results from two studies examining large scale spatial and temporal patterns in the taxonomic composition of Late Pleistocene reef coral communities. Our first example is from the Huon Peninsula, Papua New Guinea (Pandolfi 1996), where reef coral communities have reassembled repeatedly after rapid fluctuations in sea level caused by global climate change during a 95 thousand year interval. Our second example is from Curacao, Netherlands Antilles (Pandolfi and Jackson, in prep.) where reef coral communities from the same environments are preserved around the island. The results clearly show consistent patterns of community structure and assembly that cannot be explained by disturbance or dispersal alone.

## METHODS

Environmental differences in taxonomic composition and abundance among living reef corals are faithfully preserved in their adjacent death assemblages in both the Caribbean and the Indo-Pacific (Pandolfi and Minchin 1995; Greenstein and Pandolfi 1997; Pandolfi and Greenstein in press). Moreover, patterns in Caribbean life assemblages appear well preserved in nearby Pleistocene deposits (Greenstein and Curran 1997). Therefore, we can survey fossil reef coral communities and analyze patterns statistically in much the same way as for Recent reefs (Pandolfi 1996; Jackson et al. 1996).

## (1) Measures of similarity

Replicate samples of Pleistocene coral species from different environments and times were gathered and then compared using the Bray-Curtis (BC) dissimilarity measure, a measure of the taxonomic similarity between

two different communities (Bray and Curtis 1957). The BC index, developed for both abundance and presence and absence data, has been shown to be one of the most robust and effective coefficients for the analysis of taxonomic composition data (Faith et al. 1987).

To assess whether BC dissimilarity values were significantly different we used the analysis of similarities procedure (ANOSIM; Clarke 1993; Clarke and Warwick 1994). ANOSIM is based only on the rank order of the BC values, and is thus a non-parametric test of the significance of taxonomic differences among groups of assemblages. The ANOSIM technique has been used extensively by marine ecologists, especially during the past 5 years, and is a proven ecological method to determine the degree of similarities and differences in taxonomic composition among communities. We used non-metric multi-dimensional scaling as an ordination technique to provide a visual summary of the pattern of BC values among the samples and to illustrate the results from the ANOSIM tests. Data management and analyses were performed using the DECODA (Minchin 1990) and PRIMER (Clarke and Warwick 1994) software packages.

When samples are shown not to be statistically significantly different from one another in reef coral species composition, it is necessary to conduct a null model test to understand the meaning behind community similarity. If similarity is no more than what we might expect from a random sample of the within-environment species pool, then we need look no further to explain it. If, however, similarity is greater than what we expect by chance, some other factor must be involved (e.g. dispersal assembly or niche assembly). Connor and Simberloff (1978, 1979) provide the appropriate null hypothesis for determining whether the observed number of shared taxa ( $S_o$ ) between two assemblages is any different from that expected based on chance alone:  $S_e = n_1 * n_2 / N$  where  $S_e$  = expected number of shared species,  $n_1$ ,  $n_2$  = the observed numbers of species in each sample, and  $N$  = the size of the species pool. Here it is essential that the species pool comprises only those coral species known to occur within the particular environment of interest, and not the entire Late Pleistocene fauna of the biogeographic region for all environments combined. This avoids the trivial result of underestimating  $S_e$  for an environment (e.g., the reef crest) where many species (e.g., exclusively deep-water forms) cannot survive. In practice, the species pool for any environment was probably somewhat greater than observed empirically, but increasing the size of  $N$  would make it more likely, not less, that  $S_o$  will be greater than expected by chance.

## (2) Influence of widespread species

It is possible that measures of community similarity are unduly biased by a few widespread species that may dominate most local communities within a particular environment (Hubbell 1997b). To test for this, we compiled present-day geographic occurrences for all of the Late Pleistocene Papua New Guinea (PNG) and Caribbean coral species encountered in our studies. The PNG compilations included 40 sites ranging from the Red Sea to Central America (Veron 1993). We used this information to determine whether the dominant taxa within each reef environment occurred in more or less of the 40 sites than the non-dominant taxa. The total number of sites occupied by each species was tabulated, and the number of sites occupied by the dominant species was compared to that of the remaining species using a Mann-Whitney U-test. Likewise, present-day geographic occurrences were compiled from 7 sites spanning the width and breadth of the Caribbean Sea for all of the Pleistocene coral species found from Curacao. As with the Indo-Pacific data, the total number of sites (1-7) occupied by each species was tabulated, and the number of sites occupied by the dominant species was compared to that

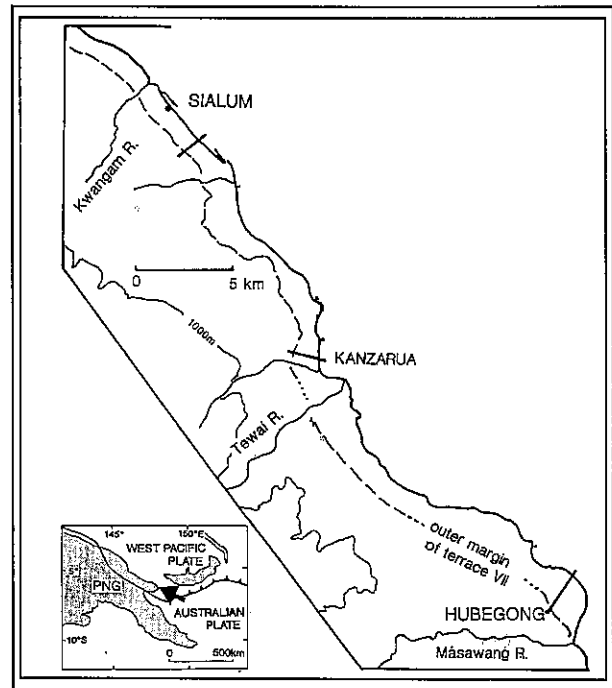


Fig. 1: Locality map of the Pleistocene raised reef terraces of the Huon Peninsula, Papua New Guinea. Geological sections from nine reef building episodes ranging in age from 125 - 30 thousand years were measured, described, and sampled for their coral communities at three sites: Sialum, Kanzarua and Hubegong. Large arrow in bottom map shows location of the Huon Peninsula.

of the remaining species using a Mann-Whitney U-test.

## CASE 1: COMMUNITY SIMILARITY THROUGH TIME

Pandolfi (1996) investigated the degree of community similarity through time of coral assemblages from the Pleistocene raised reef terraces of the north coast of the Huon Peninsula, PNG (Fig. 1). The stratigraphy, radiometric age dating, and models for Pleistocene reef development are well established (Bloom et al. 1974; Chappell 1974; Pandolfi and Chappell 1994), and excellently preserved reef corals occur over a range of reef habitats. The terraces formed through the interaction between Quaternary, glacially induced sea level fluctuations and local tectonic uplift (Chappell 1974; Pandolfi et al. 1994). This process has resulted in 9 separate ecological experiments of the development of reef communities after disturbance during the past 125 thousand years. Late Pleistocene communities that had reassembled after each successive rise in global sea level were sampled repeatedly from three sites. In general, the entire reef geomorphology is preserved for each reef building episode, from intertidal platform to deep foreereef. Here, we summarize results for the reef crest and reef slope environments. Details of the methods used, sampling, environmental interpretations and study sites are found in Pandolfi (1996).

The ANOSIM test showed no significant differences in species composition among assemblages from different reef-building episodes on the Huon Peninsula within both the reef crest and reef slope environments (Table 1). One-way analysis of variance of species richness also showed no significant differences between reefs of different ages for both the reef crest ( $F_{(8,19)} = 0.87$ ,  $p = 0.5664$ ) and reef slope ( $F_{(7,15)} = 0.80$ ,  $p = 0.5998$ ) environments. Thus, there appears to be constancy in the species richness as well as species

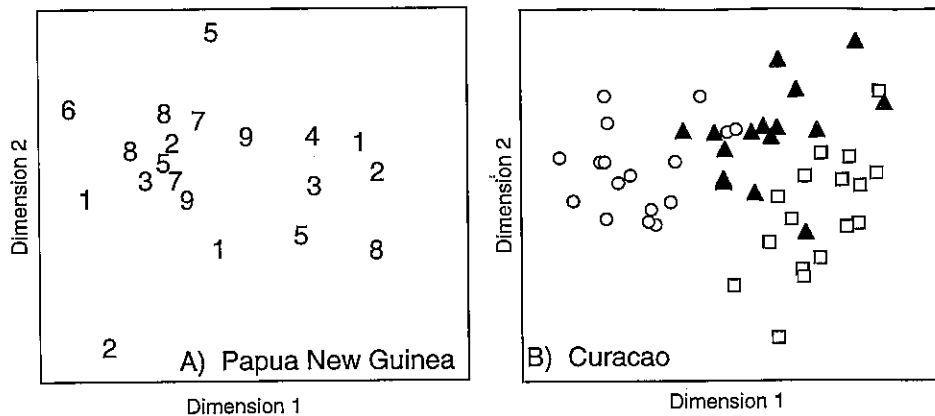


Fig. 2: Individual global non-metric multi-dimensional scaling (GNMDS) ordinations of Late Pleistocene coral reef communities. A) Ordination of coral assemblages from nine reef-building episodes (ranging in age from 30,000 - 125,000 ybp) based on presence or absence data from three sites along 35 km of coastline at the Huon Peninsula, Papua New Guinea. GNMDS plot of dimension one and two from the three-dimensional analysis of reef crest communities. Each number represents a coral community from a separate

reef-building episode; communities from up to three sites per reef-building episode are plotted (Reef 1 is the youngest, Reef 9 the oldest). Numbers closest to one another represent communities with more similar composition than numbers further away. There is greater dissimilarity among communities within a single reef-building episode than between reef-building episodes (for example, compare Reef 1 and Reef 9 which are separated by 95 thousand years). The GNMDS started with 20 random configurations, and proceeded through 200 iterations for each of four dimensions. The minimum stress value for the three-dimensional analysis was 0.12 (from Pandolfi 1996). B) Ordination of coral assemblages using species abundance data from three reef environments at Curacao: windward reef crest (circles), windward back reef (squares), and leeward reef crest (triangles). Windward reef crest and back reef assemblages show complete separation in reef coral community composition, suggesting distribution patterns in species abundances that are non-random with respect to reef environment. The leeward reef crest shows assemblages intermediate in composition between the windward reef crest and back reef assemblages. GNMDS plot of dimension 1 and 2 from the 3-dimensional analysis. The GNMDS started with 30 random configurations, and proceeded through 400 iterations for each of 6 dimensions. The minimum stress value for the 3-dimensional analysis was 0.13.

composition of the Papua New Guinean reefs through at least 95 thousand years (Pandolfi 1996).

Non-metric multi-dimensional scaling ordination showed no appreciable changes within either of the two reef environments throughout the nine reef-building episodes (Fig. 2A). The dissimilarity between communities from different times is less than that for communities during the same time. In the reef crest, for example, communities from Reef 1 are more dissimilar to one another than they are to those from Reef 9, but they are separated in time by 95 thousand years (Fig. 2A). In addition, there does not appear to be any temporal grouping or linear changes of communities; instead communities appear scattered throughout the plot.

Comparison of these results to those expected using the null model demonstrates that the observed number of shared species among assemblages from different reef-building episodes is highly significantly greater than expected for both the reef crest and reef slope environments (Table 2). Thus, it appears that random sampling of the within-habitat species pool cannot explain the high degree of temporal stability in the PNG reef coral assemblages (Pandolfi 1996).

The persistence of coral community composition is due, in part, to the consistent dominance of the same few species in the Late Pleistocene reefs that are also dominant on the living Huon Peninsula reefs (Nakamori

et al. 1994). In the reef crest environment, 11 of 66 species (17%) occurred in more than half of the Late Pleistocene samples and were considered dominants. However, these 11 species were no more or less widespread than the remaining 55 non-dominants (Table 3). Similarly, 23 of 92 species (25%) occurred in more than half of the reef slope samples and were considered dominants; but again their geographic distributions were the same as for the remaining 69 non-dominants (Table 3). Thus, widespread geographic distribution within the metacommunity does not explain the temporal recurrence of the same few dominant taxa over time in the local reef communities.

#### CASE 2: COMMUNITY SIMILARITY THROUGH SPACE

Curacao is located north of Venezuela (Fig. 3). As for the Huon Peninsula, tectonism and Pleistocene sea level fluctuations have resulted in a series of raised reef terraces. Coral communities were censused from the 125 thousand year old Lower Terrace (Schubert and Szabo 1978). Coral species abundances were estimated using a series of 17 transects (40 m in length) laid along the coastline in each of three fossil reef environments: the windward reef crest, the windward back reef and the leeward reef crest. The Pleistocene environments were interpreted independently from coral composition on the basis of position in relation to the present shoreline, position around the island (leeward versus windward), and lithologic characteristics (de Buissonjé 1974; Herweijer and Focke 1978; Pandolfi and Jackson unpub. data).

The ANOSIM test showed significant differences in species abundances among Pleistocene assemblages from the three different reef environments at Curacao (Table 4). These results are graphically illustrated by the multi-dimensional scaling ordination with all three reef environments showing distinct differences in taxonomic composition (Fig. 2B). Thus we can clearly define three distinct communities within the Late Pleistocene of Curacao based on the relative abundance of fossils. The patterns in species dominance and the differences in relative abundances of species among the three environments (Pandolfi and Jackson, ms) are very similar to those observed on

Table 1: Results of analysis of similarity (ANOSIM) test for significant differences in taxonomic composition among Late Pleistocene reef coral communities from different reef-building episodes at the Huon Peninsula, Papua New Guinea (from Pandolfi 1996).

Environment	Main effect	R stat	p
Reef crest	Time	- 0.3	0.99
Reef slope	Time	- 0.1	0.83

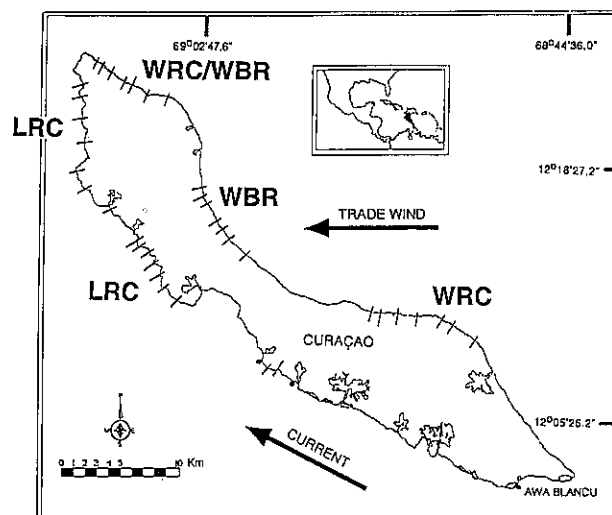
**Table 2:** Results of a null model to determine whether community similarity between time intervals is more than that expected from a random sampling of the within environment species pool. The analysis was performed on Pleistocene reef coral communities from the Huon Peninsula, Papua New Guinea (Pandolfi 1996).

	Reef crest	Reef slope
Species Pool (N)	77	109
Number of species in common:		
Expected - mean (SD)	4.3 (2.9)	10.2 (8.0)
Observed - mean (SD)	8.3 (4.1)	15.9 (10.2)
Two sample T-test	- 5.95	- 3.33
Degrees of freedom	100.9	108.0
p-value	< 0.00001	0.0013

modern reefs (Goreau 1959), including those from Curacao (Bak 1977; van Duyl 1985). From these results, we believe we can justifiably examine spatial patterns in species composition within the three established communities.

Examination of spatial patterns within each of these three communities demonstrates marked spatial similarity of reef coral community composition over distances ranging from 350 meters to over 40 kilometers (Fig. 4). This does not mean that there is no within-environment heterogeneity in reef communities along the Curacao coastline. Indeed, there probably are secondary environmental gradients in addition to the major environmental gradients we have documented. But for the present we assume any such gradients are randomly distributed with respect to our sampling. In reality, it is more probable that they vary linearly along the Curacao coastline which would tend to increase disparity in community similarity with distance. Thus, the Curacao spatial analysis is very conservative in that secondary environmental effects would make community differentiation more probable.

The high percent similarity within the same reef environments over 40 kilometers is due, in part, to the consistent dominance by the same few species in the Late Pleistocene as are dominant on reefs around Curacao today (Bak 1977). The top seven species in each of the three reef environments account for more than 90% of the relative abundance and were considered dominants. However, their geographic range was no greater than for non-dominants, which were also extremely widespread (Table 3). This was true even though we lumped together the different presumptive



**Fig. 3:** Locality map of Curacao showing sampling localities for the Pleistocene windward reef crest (WRC) and back reef (WBR), and leeward reef crest (LRC) environments. Seventeen transects were laid in each of the two windward reef environments, and 16 transects were laid in the leeward reef crest environment.

species of the *Montastrea annularis* complex (Knowlton et al. 1992), all of which are dominants, because they were not discriminated in most earlier studies. As with the temporal similarity in PNG, widespread geographic distribution within the metacommunity cannot completely explain the spatial similarity in the Late Pleistocene Curacao communities.

#### DISCUSSION

Our results demonstrate that Late Pleistocene reef coral community composition on opposite sides of the globe did not change significantly within environments over very large spatial and temporal scales, and was more similar than expected by chance. This was true even though high levels of disturbance due to tropical storms, earthquakes and sea level change have afflicted all of these communities from at least the Early Pleistocene to the present. Large-scale reef coral community composition is strikingly predictable

**Table 3:** Significance test for degree of geographic commonness of dominant versus non-dominant coral species from the Pleistocene of Papua New Guinea (PNG) and Curacao. The Indo-Pacific data source is Veron (1993). The Caribbean sites and data sources are Curacao (Bak 1977), Jamaica (Goreau and Wells 1967), San Andrés (Geister 1973; Kocurko 1977; Pandolfi unpub. data), Barbados (Lewis 1960), Florida (Pandolfi and Greenstein unpub. data), the Bahamas (Sullivan et al. 1994), and Panamá (Holst and Guzmán 1993). See text for explanation. Total diversity refers to the total number of species occurring within each environment where distribution data were available.

Environment	Dominants			Non-dominants		Mann-Whitney U stat	p	
	Total diversity	Number of species	Median occurrences	Number of species	Median occurrences			
PNG	Reef crest	66	11	15	55	15	276.0	0.64
	Reef slope	92	23	14	69	14	764.5	0.79
Curacao	WRC	24	7	7	17	7	56.0	0.73
	WBR	19	7	7	12	7	41.0	0.89
	LRC	24	7	7	17	7	65.0	0.62

**Table 4:** Results of analysis of similarity (ANOSIM) test for significant differences in species abundances among Pleistocene reef coral communities from Curacao, Netherlands Antilles. WRC = windward reef crest; WBR = windward back reef; LRC = leeward reef crest.

Main Effect	R stat	p
Environment		
Overall	0.601	< 0.0001
WRC vs WBR	0.850	< 0.0001
WRC vs LRC	0.539	< 0.0001
WBR vs LRC	0.413	< 0.0001

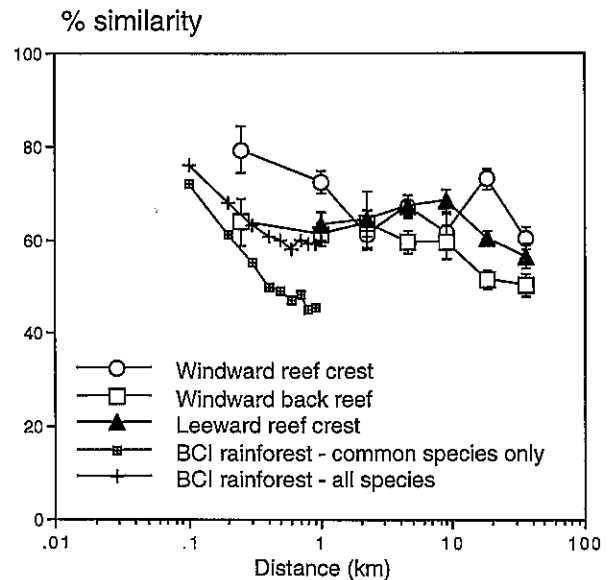
in spite of these disturbances (Jackson 1994a,b), that contrarily cause ecological anarchy at very small spatial scales (Connell 1978; Sale 1988). Small scale studies simply do not "scale up" unless placed in a landscape perspective (Paine and Levin 1981; Jackson 1991; Levin 1992; May 1994).

Likewise, the patterns we have observed cannot be explained by dominance of local communities by species that are especially widespread compared to non-dominants, as predicted by the dispersal limitation hypothesis (Hubbell 1997a,b). Corals differ greatly in their modes of dispersal (Richmond and Hunter 1990), including both broadcast dispersal of gametes and floating larvae into the water column and crawl-away dispersal of brooded larvae. Nevertheless, there are no differences in the geographic distribution of dominant and non-dominant species in any of the communities studied (Table 3).

However, the great majority of reef coral larvae almost certainly do disperse much farther than the seeds of trees in tropical rainforests. Such differences in dispersal might explain the much greater similarity in community composition observed for Late Pleistocene corals at Curacao compared with trees in Panamá (which were the inspiration for Hubbell's dispersal theory), where community similarity drops off exponentially over very short distances within an environmentally heterogeneous 50 hectare plot (Hubbell 1995; Fig. 4). However, Terborgh et al. (1996) observed much greater similarity in tropical forest composition over scales of tens of kilometers in Peru, and this might be maintained for up to several hundred kilometers (Terborgh, pers. comm. 1996). Hubbell (1997b) criticized the Peruvian results because they are based only on common species, but we obtained essentially the same results in our coral studies from PNG and Curacao using either all species or only common species (Pandolfi 1996; Pandolfi and Jackson, unpublished).

Connell (1978) and Hubbell (1995; 1997a,b) have dismissed niche diversification (i.e., adaptation) as an explanation for persistent community composition because of (1) lack of positive evidence for either persistence or adaptation, and (2) readily apparent alternative explanations. We have now provided evidence for large scale persistence in Late Pleistocene coral reef communities, and, at least partially, falsified Connell's and Hubbell's alternative hypotheses. Moreover, there is abundant evidence for adaptation of reef corals where biologists have bothered to look for it; most notably for the Caribbean elkhorn coral *Acropora palmata* (reviewed in Jackson 1991 and 1994b) and finely tuned photoadaptation with depth in the *Montastrea "annularis"* species complex (Rowan and Knowlton 1995).

We do not intend to revive the classical view of finely tuned niche diversification to explain large-scale community persistence. We do believe, however, that to ignore a significant role for adaptation is to ignore the obvious (Knowlton and Jackson 1994a,b).



**Fig. 4:** Similarity in species composition as a function of distance between communities for Pleistocene coral reef communities from Curacao and living forest communities from Barro Colorado Island (BCI; data from Hubbell 1995), Republic of Panamá. Note the smooth and exponential decay in community similarity in the modern tropical forest communities. In contrast species composition within the three Pleistocene reef environments of Curacao remains relatively constant over much broader spatial scales. Species abundance data were used in all plots. For the Curacao reef coral communities the Bray-Curtis index was used, and for the BCI rainforest communities % similarity was based on a spatial autocorrelation coefficient. Note that Hubbell's (1995) original curves are here represented with distance plotted along a logarithmic scale.

Rather, the most promising approach will be to incorporate both environmental and biological mechanisms into the analysis of community dynamics and stasis. Chesson (1997), for example, can predict long term species coexistence in model communities through the interaction between environmental variability and density dependence (e.g., competition), a result for which there is some empirical support from herbaceous plant communities (Chesson, pers. comm. 1996). Chesson (1997) believes that such a world view can accommodate the kind of long term community stability observed in Papua New Guinea (Pandolfi 1996). Our results indicate that coral reef communities cannot always be expected to behave as if species were equal in their per capita fitness, despite the very high local variance in species composition (Tanner et al. 1994), and the maintenance of their species diversity must involve some other biological processes than simply disturbance and/or dispersal.

#### ACKNOWLEDGMENTS

We are most grateful to Peter Chesson and Stephen Hubbell for very stimulating discussions during and after the 8th International Coral Reef Symposium. Of course, this doesn't imply that either of them agree with anything we have written.

#### REFERENCES

- Bak RPM (1977) Coral reefs and their zonation in Netherlands Antilles. AAPG Studies in Geology 4:3-16

- Bloom A L, Broecker WS, Chappell JMA, Matthews RK, Mesolella KJ (1974) Quaternary sea level fluctuations on a tectonic coast: new  $^{230}\text{Th}/^{234}\text{U}$  dates from the Huon Peninsula, New Guinea. *Quaternary Research* 4: 185-205
- Bray J R, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325-349
- Chappell J (1974) Geology of coral terraces, Huon Peninsula, New Guinea: a study of Quaternary tectonic movements and sea-level changes. *Geological Society of America Bulletin* 85: 553-570
- Chesson P (in press) Diversity maintenance by interaction of mechanisms over various scales. *Proceedings 8th International Coral Reef Symposium*
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117-143
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. National Environment Research Council. UK
- Connor EF, Simberloff DS (1978) Species number and compositional similarity of the Galápagos flora and avifauna. *Ecological Monographs* 48: 219-248
- Connor EF, Simberloff DS (1979) The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140
- de Buissonjé PH (1974) Neogene and Quaternary geology of Aruba, Curacao and Bonaire (Netherlands Antilles). *Uitg. Natuurwet. Studiekring Suriname Nederlandse Antillen (Utrecht)* 78
- Faith DP, Minchin FR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57-68
- Geister J (1973) Los arricifes de la Isla de San Andrés (Mar Caribe, Colombia). *Mitt. Inst. Colombo-Alemán Invest. Cient* 7:211-228
- Goreau TF (1959) The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology* 40: 67-90
- Goreau TF, Wells JW (1967) The shallow-water Scleractinia of Jamaica: revised list of species and their vertical distribution range. *Bulletin of Marine Science* 17:442-453
- Greenstein BJ, Curran HA (in press) How much ecological information is preserved in fossil coral reefs and how reliable is it? *Proceedings 8th International Coral Reef Symposium*
- Greenstein BJ, Pandolfi JM (in press) Preservation of community structure in modern reef coral life and death assemblages of the Florida Keys: Implications for the Quaternary fossil record of coral reefs. *Bulletin of Marine Science*
- Herweijer JP, Focke JW (1978) Late Pleistocene depositional and denudational history of Aruba, Bonaire and Curacao (Netherlands Antilles). *Geologie en Mijnbouw* 57: 177-187
- Holst I, Guzmán HM (1993) Lista de corales hermatípicos (Anthozoa: Scleractinia; Hydrozoa: Milleporina) a ambos lados del istmo de Panamá. *Rev Biol Trop* 41:871-875
- Hubbell SP (1995) Towards a theory of biodiversity and biogeography on continuous landscapes. In: Carmichael GR, Folk GE, Schnoor JL (eds) *Preparing for global change: a Midwestern perspective*. SPB Academic Publishing, Amsterdam pp 173-201
- Hubbell SP (in press) Niche assembly, dispersal limitation, and the maintenance of diversity in tropical tree communities and coral reefs. *Proceedings 8th International Coral Reef Symposium*
- Hubbell SP (in press) A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Proceedings 8th International Coral Reef Symposium*.
- Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. *Ecology* 70: 275-279
- Hughes TP (1994) Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551
- Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kinds of animals. *American Naturalist* 93:145-159
- Hutchinson GE (1961) The paradox of the plankton. *American Naturalist* 95:137-146
- Jackson JBC (1991) Adaptation and diversity of reef corals. *Bioscience* 41: 475-482
- Jackson JBC (1992) Pleistocene perspectives on coral reef community structure. *American Zoologist* 32: 719-731
- Jackson JBC (1994a) Constancy and change of life in the sea. *Phil Trans R Soc Lond B* 344:55-60
- Jackson JBC (1994b) Community unity? *Science* 264:1412-1413
- Jackson JBC, Budd A, Pandolfi JM (1996) The shifting balance of natural communities? In: Jablonski D, Erwin DH, Lipps JH (eds) *Evolutionary Paleobiology: Essays in Honor of James W. Valentine*. University of Chicago Press, Chicago, pp 89-122
- Knowlton N, Weil E, Weight LA, Guzmán HM (1992) Sibling species in *Montastrea annularis*, coral bleaching and the coral climate record. *Science* 255:330-333
- Knowlton N, Jackson JBC (1994a) New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? *Trends in Ecology and Evolution* 9:7-9
- Knowlton N, Jackson JBC (1994b) Taxonomy and coral reef ecology: a response to Sale. *Trends in Ecology and Evolution* 9:398
- Kocurko MJ (1977) Preliminary survey of modern marine environments of San Andrés Island, Colombia. *Tulane Studies in Geology and Paleontology* 13:111-134
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943-1967
- Lewis JB (1960) The coral reefs and coral communities of Barbados, W.I. *Canadian Journal of Zoology* 38:1133-1145
- May RM (1994) The effects of spatial scale on ecological questions and answers. In: Edwards PJ, May RM, Webb NR (eds) *Large-scale Ecology and Conservation Biology*. Blackwell Scientific, Oxford, pp 1-17

- Minchin PR (1990) DECODA users manual. Research School of Pacific Studies, Australian National University, Canberra
- Nakamori T, Wallensky E, Campbell C (1994) Recent hermatypic coral assemblages at Huon Peninsula. Contributions to International Geological Correlation Program 274:111-116
- Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and dynamics of pattern. Ecological Monographs 51:145-178
- Pandolfi JM, Best MMR, Murray SP (1994) The May 15, 1992, coseismic event, Huon Peninsula, Papua New Guinea: Comparison with Quaternary tectonic history. Geology 22: 239-242
- Pandolfi JM (1996) Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: Constancy during global change. Paleobiology 22: 152-176
- Pandolfi J M, Chappell J (1994) Stratigraphy and relative sea level changes at the Kanzarua and Bobongara sections, Huon Peninsula, Papua New Guinea. Contributions to International Geological Correlation Program 274:119-140
- Pandolfi JM, Greenstein BJ (in press) Preservation of community structure in death assemblages of deep water Caribbean reef corals. Limnology and Oceanography
- Pandolfi JM, Minchin PR (1995) A comparison of taxonomic composition and diversity between reef coral life and dead assemblages in Madang Lagoon, Papua New Guinea. Palaeogeography Palaeoclimatology Palaeoecology 119: 321-341
- Potts DC, Done TJ, Isdale PJ, Fisk DA (1985) Dominance of a coral community by the genus *Porites* (Scleractinia). Marine Ecology Progress Series 23: 79-84
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparison among the Caribbean, the tropical Pacific, and the Red Sea. Marine Ecology Progress Series 60:185-203
- Rowan R, Knowlton N (1995) Intraspecific diversity and ecological zonation in coral algal symbiosis. Proceedings of the National Academy of Sciences 92: 2850-2853
- Sale PF (1988) What coral reefs can teach us about ecology. Proceedings of the 6th International Coral Reef Symposium 1:19-31
- Schubert C, Szabo BJ (1978) Uranium-series ages of Pleistocene marine deposits on the islands of Curacao and La Blanquilla, Caribbean Sea. Geologie en Mijnbouw 57: 325-332
- Sullivan KM, Chiappone M, Lott C (1994) Abundance patterns of stony corals on platform margin reefs of the Caicos Bank. Bahamas Journal of Science 1:2-11
- Tanner JE, Hughes TP, Connell JH (1994) Species coexistence, keystone species, and succession: a sensitivity analysis. Ecology 75: 2204-2219
- Terborgh J, Foster RB, Percy NV (1996) Tropical tree communities: a test of the nonequilibrium hypothesis. Ecology 77: 561-567
- van Duyl FC (1985) Atlas of the living reefs of Curacao and Bonaire (Netherlands Antilles). Foundation for Scientific Research in Surinam and the Netherlands Antilles 117, Utrecht