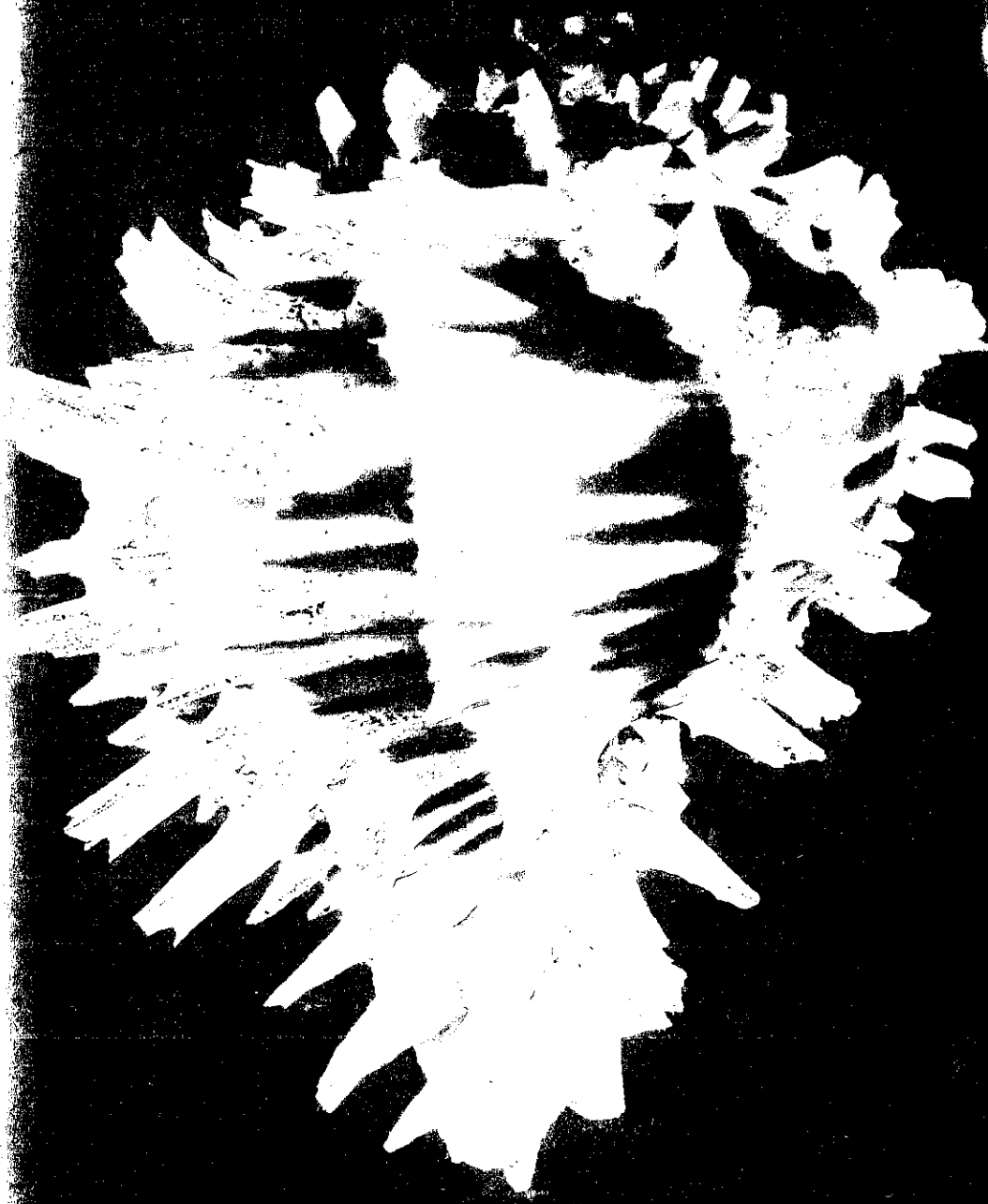


**E V O L U T I O N A R Y  
P A L E O B I O L O G Y**



**E D I T E D B Y**

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## *The Shifting Balance of Natural Communities?*

JEREMY B. C. JACKSON, ANN F. BUDD, and JOHN M. PANDOLFI

There has been a fundamental shift in community ecology over the past 25 years from a predominantly Eltonian to a Gleasonian perspective (Roughgarden 1989). In an Eltonian world, communities are exclusive associations of interdependent and coevolving species that exclude other forms, and every species has its own special role or niche. In contrast, in the Gleasonian view, communities are haphazard samples of a regional species pool that jointly happen to tolerate the environmental conditions of the moment, and there is enormous ecological redundancy of species. Increasing recognition that marine community membership varies greatly in space and time due to physical disturbances, predation and disease, and chance processes of transport and recruitment appears to better support the Gleasonian model (Connell 1978; Paine and Levin 1981; Underwood and Denley 1984; Roughgarden, Gaines, and Possingham 1988).

More recently, there has also been a shift from focusing in great detail on what happens in some very small place over a few years to recognition of the importance of larger scales of variation in space and time (Powell 1989; Levin 1992; Ricklefs and Schluter 1993; Edwards, May, and Webb 1994). Most environments exist as a physically discontinuous mosaic of patches in a landscape, so that the communities inhabiting different patches are connected only by migration or chance processes of transport and recruitment (Pickett and White 1985; National Research Council 1995). Moreover, recent environmental variance increases indefinitely and without apparent limit with distance between sites and the passage of time, so that overall differences among environments and their inhabitants also increase in space and time (Pimm and Redfearn 1988; Bell 1992).

An important consequence of these new perspectives has been the development of a series of conceptually related null models to explain community membership (Hutchinson 1961; MacArthur and Wilson 1967; Strong et al. 1984; Hubbell 1995) that virtually ignore the details of specific adaptations and relationships among species that are fundamental to the Eltonian perspective (e.g., Hutchinson 1957, 1959; MacArthur 1972). Models that consider only rates of colonization and extinction, the spatial distribution of environments, and historical regional differences in the size of the species pool have been successful in explaining most of the variance in community composition, even that among

highly diverse tropical forests (Hubbell and Foster 1986; Hubbell 1995) and coral reefs (Cornell and Karlson 1996).

The success of these models has led to the further null expectation by ecologists of gradual and continuous change in community composition over both ecological and evolutionary time (Bell 1992), comparable to the expectation of gradual speciation by natural selection (Darwin 1859). But this prediction is demonstrably false over geological time (Benton 1995), as epitomized by the Cambrian explosion of metazoan life (Whittington 1985; Gould 1989), Sepkoski's (1981) three great evolutionary faunas, Raup's (1991, chapter 16, this volume) kill curve, or any of the other well-known discontinuities in the history of Phanerozoic life (reviewed in Bambach and Bennington, chapter 6, this volume, especially their figure 6.1). Indeed, only 2 million years ago, more than half the Caribbean shallow-water coral and mollusk fauna turned over within 1 million years or less, after several million years of comparative evolutionary tranquility, and the same is probably true of many shallow-water, tropical marine communities elsewhere (fig. 5.1; Allmon et al. 1993, 1996; Jackson et al. 1993; Jackson, Jung, and Fortunato 1996; Rosen 1993; Budd, Stemann, and Johnson 1994; Budd, Johnson, and Stemann 1996; Jackson 1994b; Johnson, Budd, and Stemann 1995). Moreover, there has been little speciation and extinction afterward, despite repeated and intensifying cycles in climate and sea level throughout the Pleistocene (Potts 1984; Jackson 1994a,b). Many terrestrial faunas exhibited similar Quaternary evolutionary stasis (Coope 1970, 1995; Vrba 1985; Elias 1994; de Menocal 1995) until the advent of abundant *Homo sapiens* (Burney 1993; Lawton and May 1995).

Somewhere between the two extremes of the paleontologists' macroevolutionary punctuation and stasis and the ecologists' gradual and continuous community change lies a macroecological breakpoint. One possibility is that within-habitat changes in species composition are continuous both within and between pulses of macroevolutionary turnover. In this case, community membership would be Gleasonian on all scales, with species simply tracking their most favorable environments (Davis 1986; Webb and Bartlein 1992; Coope 1995), and changes in communities over geological time would be determined entirely by environmental forcing and whatever factors drive the evolutionary turnover of species. Alternatively, community membership may be limited, and therefore may vary less than expected from chance events and simple environmental tracking. Only in this case would so-called "coordinated stasis" be worthy of the name (e.g., Brett, Miller, and Baird 1990; Brett and Baird 1995; Morris et al. 1995), but, as we shall see, this hypothesis has not been tested.

Thus, a fundamental problem of paleoecology is to locate this macroecological breakpoint and determine whether or not community membership exhibits comparative stasis (i.e., low background origination or extinction rates *and* non-random associations of species) between pulses of macroevolutionary turnover. Here we examine this problem by investigating changes in tropical coral reef

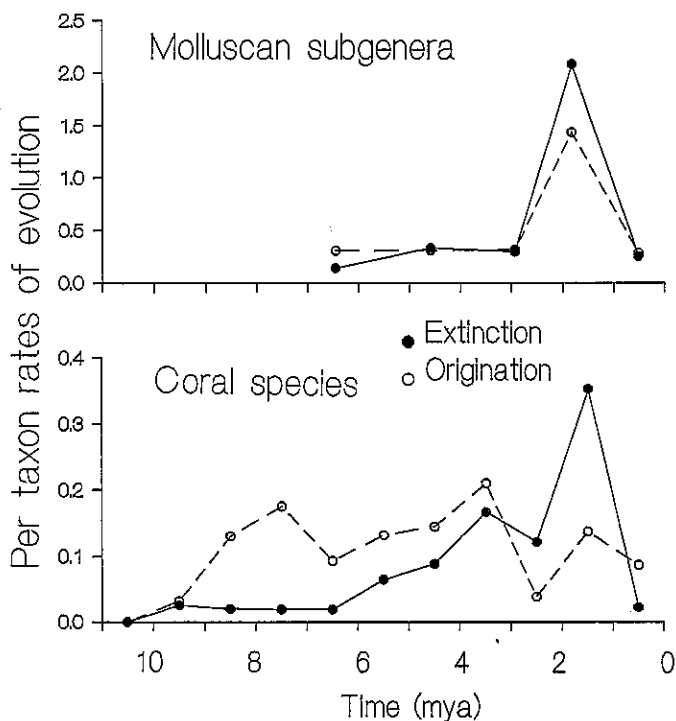


Fig. 5.1. Rates of origination and extinction of Neogene Caribbean mollusks and reef corals, normalized in relation to the numbers of taxa in each successive time interval and the amount of time in between (for details of calculations see Jackson 1994b; Budd, Johnson, and Stemann 1996). Mollusks are from the Limon, Bocas del Toro, and Canal Basins of Costa Rica and Panama (Coates et al. 1992; Jackson et al. 1993, unpublished data); corals are from the Dominican Republic, Costa Rica, and twenty-one additional localities throughout the Caribbean and Florida (Budd, Stemann, and Johnson 1994; Budd, Johnson, and Stemann 1996). Appearances and disappearances of coral taxa are not as well resolved stratigraphically as those of mollusks because of the much broader regional coverage and the uneven quality of age dating. Consequent weighting of the first and last occurrences (Budd, Johnson, and Stemann 1996) smooths out the curves and obscures the true magnitude of accelerated turnover. Nevertheless, coral origination preceded extinction, and was not as episodic as for mollusks.

communities over the past 10 million years. We first consider problems of spatial scale and the concept of metapopulations as a framework for thinking about community membership, as well as the appropriate null models for testing community persistence. We then present preliminary evidence for limited membership and community stasis on coral reefs during the Pleistocene. Similar community stasis during the Late Miocene and Early Pliocene was punctuated by

dramatic and rapid shifts in community membership during the faunal turnover in the Late Pliocene, which reflect changes in relative abundance and dominance out of all proportion to the simple changes in species and climate observed. Metapopulation models help to explain this punctuation during turnover and also, possibly, the stasis in between.

### Pattern and Scale in Community Membership

Early marine ecologists and paleoecologists were impressed by the repeated association of different species or higher taxa in different environments and called these recurrent groups communities (Petersen 1914; Thorson 1957; Moore 1958). The best-studied marine examples are the sessile communities of rocky shores in the temperate zone, where, moving down the shore, predictable associations of barnacles *usually* give way to dense stands of mussels, which in turn *usually* give way to beds of seaweeds and kelps (Lewis 1964; Ricketts and Calvin 1968; Stephenson and Stephenson 1972). Comparable examples from the Caribbean include dominance of reef crests on wave-swept coasts by coralline algae or the elkhorn coral *Acropora palmata* (Goreau 1959; Geister 1977a; Adey 1978; Jackson 1991) and dominance of the rhizome mat of shallow seagrass beds by large lucinid bivalves such as *Codakia* (Jackson 1972, 1973). Similar associations are widespread in Caribbean Pleistocene deposits. Indeed, the uppermost occurrence of dense elkhorn coral assemblages is routinely employed as a datum to establish ancient sea level in Pleistocene reefs (Lighty, Macintyre, and Stuckenrath 1982), an assumption that has held up well to subsequent investigation (Macintyre 1988; Fairbanks 1989).

More recently, however, marine ecologists and paleoecologists have used more quantitative methods to describe patterns of occurrence and association of species. Careful, detailed, and repeated observations of the same small areas of shoreline, especially when coupled with experimental manipulations of species abundances, have led to a revolution in the understanding of the ecological processes responsible for species distributions that was not possible using only qualitative or descriptive methods (Connell 1961, 1983; Paine 1966, 1984; Dayton 1971; Paine and Levin 1981). These new studies also revealed great variations in the local distribution and abundance of marine organisms that previously had been ignored (Sutherland 1974; Connell and Sousa 1983; Connell 1986). Even coral reef communities, whose high species diversity had been attributed to the supposed environmental stability of the Tropics (Odum and Odum 1955; Newell 1971; Porter 1974), turned out on closer examination to fluctuate wildly in response to storms, El Niño events, outbreaks of predators and disease, and the vagaries of larval recruitment (Loya 1976; Connell 1978; Woodley et al. 1981; Connell and Keough 1985; Knowlton, Lang, and Keller 1990; Doherty 1991; Jackson 1991; Sale 1991; Done 1992; Glynn and Colgan 1992; Knowlton 1992; Hughes 1993, 1994). Moreover, multivariate analyses of Petersen's origi-

nal data showed that benthos in sediments vary continuously in distribution and abundance across environmental gradients, rather than forming discrete communities (Stephenson, Williams, and Cook 1972). These discoveries led to the rejection of marine communities as anything but chance associations of species with overlapping ecological requirements (Connell 1978; Sale 1991; Bambach and Bennington, chapter 6, this volume).

The problem with most of this work, however, is its necessarily very small scale because of the intensity of the effort involved (Kareiva and Anderson 1988; Levin 1992; National Research Council 1995). Recognizing small-scale variation is essential for understanding the mechanisms of interactions among species and disturbance, as well as for recognizing the futility of ever-refined community classification based on local differences (Walter and Patterson 1994). However, the existence of great local variation says very little about the nature of community membership at larger scales. Does the noise of local variation obscure a signal of greater regional stability in community membership, or is there equivalent compositional variation over all spatial scales? Detailed experimental and descriptive study of intertidal landscapes suggests the former (Paine and Levin 1981), and the same is probably true of coral reefs (Jackson 1991, 1992). Therefore we need to look further at community membership on large spatial scales.

### The Metapopulation Perspective

A *species pool* comprises all species within some arbitrary biogeographic region that can potentially inhabit a particular environment, such as rocky shores, mudflats, or seagrass beds (Eriksson 1993). Consider, for example, the distribution of shallow-water mollusks on oceanic islands and continental margins (Valentine and Jablonski 1993). Within any environment, species with larvae capable of long-distance transport have similar distributions throughout the western Indian Ocean and western Pacific (Taylor 1968, 1971, 1978; Crame 1986; Paulay 1987, 1990). However, a higher proportion of the species pool tends to occur along continental margins than on isolated oceanic islands—a difference presumably caused by the vicissitudes of colonizing a small target in a big ocean. Indeed, entire assemblages of otherwise common taxa are missing from some islands. Lucinid bivalves, for example, particularly the genera *Codakia*, *Ctena*, and *Anodontia*, are the dominant infaunal mollusks of seagrass beds in the Seychelles and the Indian Ocean generally, but are virtually absent from seagrass beds at Aldabra (Taylor 1971, 1978). Similar variation occurs for lucinids among western Pacific islands and for other common mollusks in both oceans. Likewise, species alive on a given island today may be absent from Pleistocene deposits on the same island, or vice versa, and the same is true of the latitudinal ranges of mollusks along the north-south-trending coast of California (Taylor 1978; Valentine and Jablonski 1993).

Many of these differences among places and times may be due to differences

in environments, but others are probably just a matter of chance. For example, when lucinids are present, they occur in very similar habitats and associations (Taylor 1968, 1971; Stanley 1970; Jackson 1972, 1973), and the same appears to be true of other intensively studied groups. This may be just a matter of the "tendency for organisms, when they have the opportunity, to colonize and succeed in environments to which they are well adapted" (Bambach and Bennington, chapter 6, this volume). Alternatively, particular associations of species may occur more frequently than expected by chance sampling of the within-habitat species pool, in which case some higher-order process may be involved (Connor and Simberloff 1978; Rahel 1990). But the latter possibility is hardly ever tested in the sea, because it would require sampling of very large numbers of replicate islands or coastal localities for every stratigraphic or geographic horizon of interest, rather than the handful of samples usually available.

Because of this variation from site to site, we need to consider populations of sites and their inhabitants collectively, with emphasis on the discontinuity of habitats at different sites and the linkages between them (fig. 5.2; Paine and

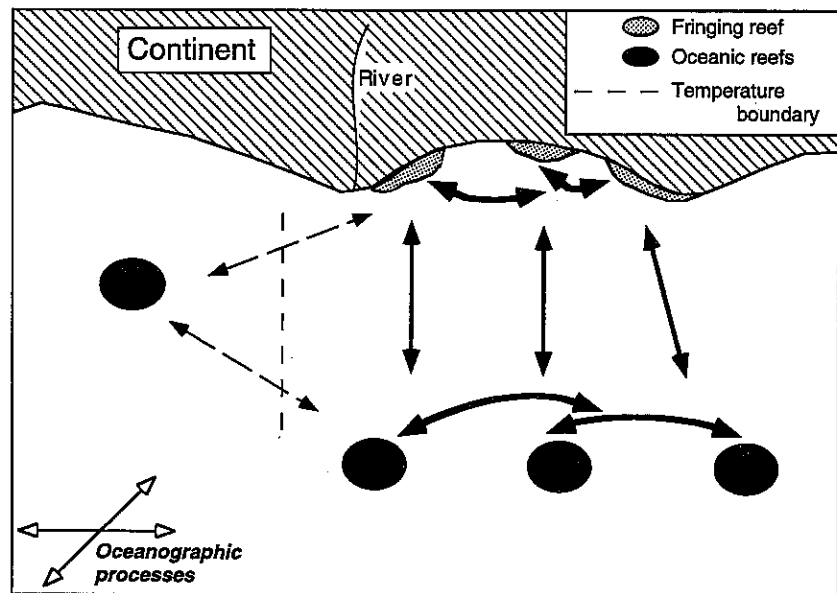


Fig. 5.2. Schematic relationship between habitat patches and metapopulations at different geographic scales. Metapopulations of reef corals may occur on a set of reefs along a single stretch of coast or on sets of reef tracts throughout a geographic region. These may also differ in relation to mainland and oceanic settings. The upper limit of the size of the region for any species is determined by the limits of individual movements (larval transport or adult migration), which vary widely among coral species with different life histories and modes of development. (After National Research Council 1995).

time in arid environments.

Each heading is subdivided into topics, and examples are given under each. The book

has an extensive reference list, including many recent review articles, and would provide a



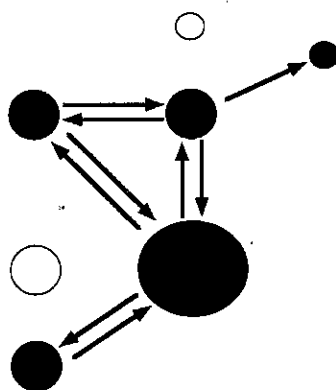


Fig. 5.3. A generalized metapopulation model. Solid circles represent habitat patches occupied by a species of interest; open circles, patches where the species is absent. Arrows indicate the direction of migration (colonization). There are many kinds of metapopulations depending on the scale and spatial relationships of patches and the degree of connectedness between them (see Harrison 1991).

Levin 1981; Roughgarden, Gaines, and Possingham 1988). Until recently, 95% of marine ecology was devoted to studying pinpricks on such a map, but now the goal is to study the entire map (National Research Council 1995). We can simplify and generalize this map to consider a set of habitat patches, which may or may not be inhabited by a particular taxon or taxa of interest from the species pool, such as a particular species of reef coral or all the corals of a particular reef environment (fig. 5.3). A *patch* is "the area of space within which a local population lives" (Hanski and Gilpin 1991), and may comprise a real habitat island or discontinuity within a continuous seascape. A *metapopulation* is a set of local populations that interact by means of the movement of individuals among populations (i.e., among different patches), and two or more species that occur in a similar set of habitat patches comprise a *metacommunity* (Hanski and Gilpin 1991). Thus a metacommunity is a subset of the species pool that occurs in a set of habitat patches, and not necessarily the entire species pool.

Figure 5.3 reduces all of ecology to two kinds of information: (1) what goes on inside any patch, and (2) the exchange functions between patches. The former comprises the full spectrum of traditional marine ecology, including the nature of interactions among species, the effects of environmental disturbances, and the nonlinear dynamics and threshold effects that may result in very different communities in identical environments. In a metapopulation context, however, one can express all this complexity as the factors responsible for the persistence or extinction of taxon *x* in any patch. Likewise, the exchange functions depend on oceanographic transport processes and the life histories and larval characteristics of taxa. There is a veritable growth industry of metapopulation models that attempt to describe the dynamics and persistence of species in a spatial mosaic of patches (Gilpin and Hanski 1991; Harrison 1994; Hanski et al. 1995). Local extinction is obviously inevitable, but regional persistence may be possible by dispersal into unoccupied patches.

Metapopulation models are at least heuristically important for paleontology because they shed new light on what may go on during extinction events. For

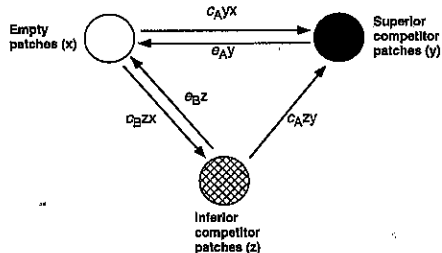


Fig. 5.4. The structure of a meta-population model used to examine the effect of patch removal on the coexistence of a dominant (A) and an inferior (B) competitor in a two-species community. The circles indicate the three categories of patches: x (empty), y (dominant competitor), and z (inferior competitor). Arrows indicate transitions between patch types by colonization and extinction (e.g.,  $c_{AYX}$  indicates colonization of empty patches by species A, and  $e_{BZ}$  indicates extinction of species B). (After Nee and May 1992).

example, Nee and May (1992) examined the effect of patch removal on the behavior of a two-species system comprising a superior competitor A and an inferior competitor B (fig. 5.4). It has long been known that A and B can coexist if B disperses better or is less likely to go extinct in any patch than A. The model considers three kinds of patches: x = empty patches, y = patches occupied by superior competitor A, and z = patches occupied by inferior competitor B. A displaces B, and B cannot invade A. The parameters  $c_A$  and  $c_B$  and  $e_A$  and  $e_B$  are the colonization and extinction rates for A and B respectively.

Consider now a system of many patches, some fraction of which are habitable. In this case the persistence of B is possible if the ratio  $c_B/e_B > c_A/e_A$ . Next, remove some of the patches. This has a direct negative effect on both species by lowering the number of new patches colonized per unit of time. If too many patches are removed, A will go extinct first because  $c_A < c_B$ . Recall that A has a direct negative effect on B in two different ways: it increases the overall extinction rate of B, and it decreases the number of patches available for B to colonize. Therefore, the removal of patches indirectly benefits inferior competitor B by decreasing the frequency of patches occupied by A. A decrease in the total number of habitat patches can decrease the total diversity of the system (loss of A) and cause a shift in community composition (a relative increase of B). The same is true of communities with many species, so the result appears to be quite general (Tilman et al. 1994).

The crucial point is that removal of patches should have these effects on community membership and diversity *even though many patches suitable for A are entirely unaffected by whatever process is affecting the system as a whole*. The implication for conservation biology is that extinctions to date are just the tip of the iceberg of the anticipated response to anthropogenic habitat destruction that has already taken place; this is the origin of the concept of an "extinction debt" (Tilman et al. 1994). Thus the shift to macroalgal dominance of Caribbean coral reefs at the expense of corals, due to the demise of grazers, has apparently not yet resulted in the Caribbean-wide extinction of any coral species. But such re-

gional extinction is to be expected, if present ecological trends continue, when the total number of patches occupied by any coral species drops below some critical minimum threshold value for its colonization potential. This will occur even though healthy and abundant populations of the species still exist locally on unaffected reefs.

The implications for paleoecology and macroevolution are equally profound. Modest changes in the distribution of habitat due to climatic change may drastically alter metacommunity structure and force alternative community states in local patches (Hanski et al. 1995). Thus climatic change inadequate to cause extinction directly may do so indirectly by altering the abundance of suitable habitat patches for particular species. In addition, species that were uncommon before such a shift may become dominant afterward as an epiphenomenon of local threshold effects and regional metapopulation dynamics that "lock" species associations into a limited number of alternative states once abundances rise somehow above critical levels (Knowlton 1992; Hanski et al. 1995). The success of such newly dominant species would therefore be an accidental side effect of characters evolved for other reasons (exaptation *sensu* Gould and Vrba 1982) rather than an adaptation to their newfound circumstances (Jackson 1994a). We will return to this subject at the end of the chapter, but first we need to reconsider community membership in a metapopulation context.

### What Should We Test For?

We need to ask two different questions about variation in community membership. First, does community membership change significantly over space or time? We address this question by using the Bray-Curtis dissimilarity coefficient with the ANOSIM procedure as a test of significance, and by ordination using multidimensional scaling for visual presentation of the results. Even if there is no change in community membership, however, similarity may simply be due to random sampling of the species pool (e.g., Buzas and Culver 1994). Therefore the second question is whether similarity among communities is greater than that expected by chance. We address this question using a null model of random sampling.

The Bray-Curtis dissimilarity coefficient ( $BC$ ) provides one of the most robust and powerful methods for analysis of taxonomic composition among samples (Bray and Curtis 1957; Faith, Minchin, and Belbin 1987). For two samples  $i$  and  $j$ :

$$BC_{ij} = (b + c)/(2a + b + c),$$

where  $a$  is the number of taxa common to both samples,  $b$  is the number of taxa restricted to sample  $i$ , and  $c$  is the number of taxa restricted to sample  $j$ . Values of  $BC$  range from 0 for a pair of samples with identical taxonomic composition to 1 for samples with no taxa in common.

The analysis of similarities (ANOSIM) procedure is a nonparametric test of the significance of taxonomic differences among assemblages from different samples based only on the rank order of *BC* values (K. R. Clarke 1993). *BC* values between all possible pairs of *n* samples are ranked in order from smallest to largest and values replaced by ranks. The mean of the ranks of sample pairs from different levels of the factor being tested (e.g., different times) is  $r_b$ , and the mean rank for all comparisons within the same level of the factor (e.g., the same time) is  $r_w$ . The ANOSIM statistic, *R*, is then calculated as

$$R = (r_b - r_w) / [n(n - 1) / 4].$$

The denominator is the maximum possible value of the numerator if all *BC* values representing comparisons between levels exceeded all those within levels, so that values of *R* range from -1 to 1. Values around 0 mean that the factor of interest has no effect on taxonomic composition (the null hypothesis), whereas values approaching 1 suggest that differences between levels exceed those within levels. The significance of *R* must be assessed by a permutation procedure because the rank dissimilarities are not statistically independent (Warwick, Clarke, and Suharsono 1990). Therefore, the proportion of simulated values of *R* that exceed or are equal to the observed value is used as an estimate of the probability of obtaining a value of *R* at least as great as the observed value under the null hypothesis (rejected by convention if the ratio is less than 0.05).

Global nonmetric multidimensional scaling (GNMDS) is one of the most effective methods for the ordination of data on the taxonomic composition of samples (Kruskal 1964; Kenkel and Orlóci 1986; Minchin 1987). GNMDS represents each sample as a point in a coordinate space such that the distances between each pair of points are, as far as possible, in rank order with their corresponding dissimilarities in taxonomic composition.

How much the distances depart from a perfect rank order fit is measured by a quantity known as "stress," and the ordination with minimum stress is found by a successive improvement algorithm that repeats the GNMDS procedure from a number of different starting configurations of the data. We applied GNMDS to the same matrix of *BC* values used in the ANOSIM tests. Ordinations were computed in from one to four dimensions, in each case using twenty randomly chosen starting configurations. In every case the three-dimensional solution provided an adequate summary of the pattern of dissimilarities among the samples. Scatter plots were then prepared to illustrate the placement of factors of interest (site, time) within the ordination.

The model of Connor and Simberloff (1978) provides a simple null hypothesis for asking whether the number of taxa shared between any pair of assemblages is different from that expected by random sampling of the available species pool. The expected number of shared species ( $S_e$ ) is

$$S_e = n_1 n_2 / N,$$

where  $n_1$  and  $n_2$  are the observed numbers of species in the two samples and  $N$  is the size of the species pool. Differences in observed and expected values of  $S_e$  for all possible pairs of samples from different levels of factors of interest (sites, times) can be tested by a two-sample t-test.

All of the above analyses are based only on the presence or absence of species because those are the only data available now. Rahel (1990) demonstrated that stability in community membership tends to decrease with the numerical scale of analysis (i.e., from presence/absence to ranked abundances to absolute abundance data), so that communities should be analyzed at more than one numerical scale. Traditionally paleoecologists have avoided relative abundance data, invoking problems of preservation, but recent results from the comparative taphonomy of life and death assemblages of reef corals indicate that the difficulties are surmountable (Pandolfi and Minchin 1995; Greenstein and Pandolfi, in press), and we are currently attempting quantitative censuses of Caribbean Pleistocene reefs. In the meantime, we believe that the present results are important because they consistently contradict the prevailing rhetoric of community ecology and paleoecology, which overwhelmingly denies any evidence for limited community membership.

### **Community Membership is Apparently Limited and Community Stasis is Apparently Real**

Early descriptions of Jamaican coral reef communities (Goreau 1959), as well as subsequent work there and at other islands around the Caribbean (summarized in Jackson 1991), suggested clear patterns of zonation with depth. The community in each zone was typically dominated by only one or a few species, even though most species of Caribbean reef corals occur over a very wide range of depths at even a single locality (Goreau and Wells 1967); for example, 32 of the 49 species of Jamaican reef-building corals listed by Goreau and Wells (1967) occurred in depths of 3 meters or less. Subsequent natural and anthropogenic events, which accelerated greatly during the 1980s, resulted in a precipitous decline of reef coral populations throughout much of the Caribbean (Woodley et al. 1981; Knowlton, Lang, and Keller 1990; Hughes 1994; Bak and Nieuwland 1995).

We applied GNMDS ordination to the few earlier census data available from the Caribbean (Liddell and Ohlhorst 1988). There is clear geographic separation of Antillean sites from the mainland and more northern localities. Nevertheless, our analysis demonstrates that forereef community composition at the same depth was highly variable well before the events of the 1980s (fig. 5.5), and that community membership is therefore more variable than recognized before.

The events of the 1980s removed the possibility of going back and adequately and consistently surveying large numbers of "pristine" Caribbean reefs within our lifetimes. Thus the only way to examine community membership at increasing spatial scales is to use the fossil record in place of living reef communities (Jackson 1992). The data are not yet what they should be because geologists have

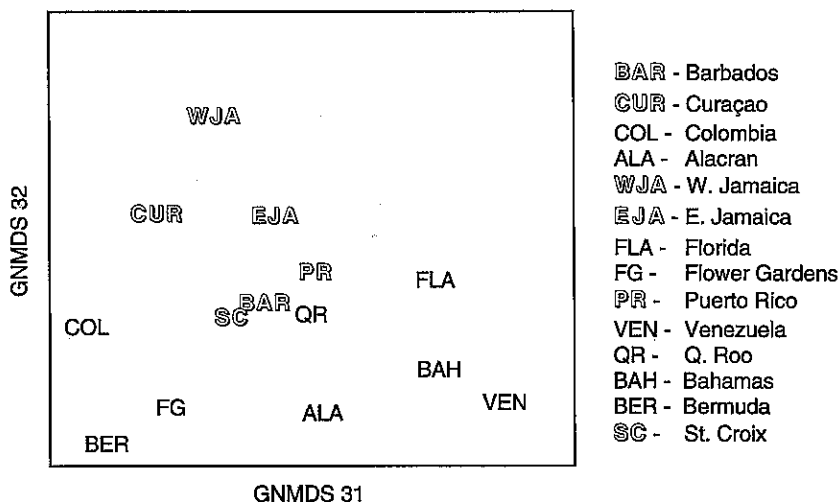


Fig. 5.5. Global nonmetric multidimensional scaling (GNMDS) ordination of fourteen Caribbean foreereef communities from approximately 15 meters depth. Each letter code on the graph represents a single coral community, and the distance between any two points is a measure of their dissimilarity in community composition based on the presence or absence of species. Antillean reefs (shadow font) aggregate toward the top, with mainland Caribbean and more northerly reefs (solid font) scattered across the bottom of the figure. The GNMDS ordination was applied to the matrix of Bray-Curtis values to provide a visual summary of the dissimilarity in taxonomic composition among the Caribbean samples. The GNMDS started with twenty random configurations and proceeded through two hundred iterations for each of four dimensions. Plots are of dimension 1 and 2 from the three-dimensional analysis. The minimum stress value for the three-dimensional analysis was 0.12. (Data from Liddell and Ohlhorst 1988.)

typically concentrated on common species and have not compiled thorough species lists. Nevertheless, what data there are support limited community membership and stasis over tens of thousands of years.

First, Mesolella (1967) showed that zonation on successive terraces of Pleistocene reefs on the emerging island of Barbados resembled that described by Goreau (1959) from Jamaica. Dense forests of the elkhorn coral *Acropora palmata* consistently gave way with increasing depth to a mixed zone of acroporids and brain corals, then to dense thickets of the staghorn coral *Acropora cervicornis*, which in turn were replaced by head corals (primarily the *Montastraea annularis* species complex) on most fossil reefs examined. The dominant species in each zone were extremely abundant, constituting roughly one-third to almost all of the coral limestone in Mesolella's measured sections (Jackson 1992). Moreover, the exceptions exhibited another familiar zonation pattern described by Goreau (1959) for the reefs at Ocho Rios in Jamaica, where development of complex buttresses replaced the mixed zone. Second, Geister (1977a, 1980) put Mesolella's results in geographic perspective by examining the 125,000-year ter-

race at many localities throughout the Caribbean. Windward and leeward shallow forereef communities closely resembled younger and older Pleistocene reefs at Barbados, as well as recent reef communities from the same environments.

The ecological importance of Mesoellea's and Geister's results is heightened because each reef terrace records the independent colonization by corals of a barren shore submerged by rising sea level. Thus comparison of coral communities from different terraces, sampled at several sites along the shore, constitutes a replicated natural experiment of reef community membership over time (Jackson 1992). Pandolfi (1996) has done a similar study of nine reef terraces deposited over a period of 95,000 years at three sites along the coast of the Huon Peninsula in Papua New Guinea. Like Barbados, the Huon is rising at an approximately constant rate, and the stratigraphy of the terraces is well established for calibration of global sea level curves (Chappell 1974; Chappell et al. 1994; Pandolfi and Chappell 1994). In contrast to the earlier studies, the data include all species encountered (presence/absence only) along 100-meter transects in two environments (reef crest from 0–5 meters depth; shallow forereef from 5–20 meters) for each terrace at each site. Not every terrace level preserved coral communities at every site, so there are only 20 out of a possible 27 (9 terrace horizons  $\times$  3 sites) samples for each environment.

A total of 122 coral species occurred in the transects, 77 in the reef crest and 109 in the shallow forereef (table 5.1). We used these numbers as estimates of the total available species pool for each environment, which is reasonable because there have been very few originations or extinctions of Indo-Pacific reef corals over the past million years (Potts 1984; Veron and Kelley 1988). Bray-Curtis dissimilarity coefficients were calculated for all possible pairs of reefs and subjected to the ANOSIM test of significance. Rare species recorded from only

TABLE 5.1 Summary statistics and analyses of community composition of Pleistocene reefs from the Huon Peninsula, Papua New Guinea

	Reef crest	Shallow forereef
Total number of species (= species pool)	77	109
Mean (SD) species per reef		
All species included	18.3 (8.1)	31.4 (16.3)
Rare species <sup>a</sup> excluded	15.4 (6.8)	28.1 (14.1)
Analysis of similarity (ANOSIM)		
$R_s$	-0.3	-0.1
Probability	$P = .99$	$P = .83$
Null model of random sampling of species pool		
Expected number of species in common ( $S_e$ )	4.3 (2.9)	10.2 (8.0)
Observed number of species in common ( $S_o$ )	8.3 (4.1)	15.9 (10.2)
Student's $t$	-5.95	-3.33
Degrees of freedom (unequal variances)	101	108
Probability of accepting null model	.0000	.0013

Source: Pandolfi 1996.

<sup>a</sup>Rare species are those found on only one or two reefs out of the twenty sampled for each environment.

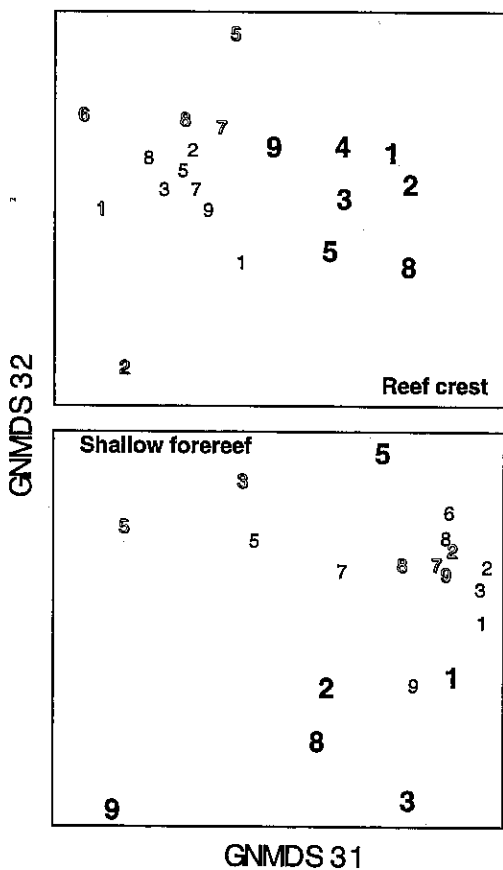


Fig. 5.6. GNMDS ordination of Pleistocene reef crest and shallow forereef coral communities from nine reef-building episodes over 95,000 years from three sites on the Huon Peninsula, Papua New Guinea. The numbers represent the different terrace levels from 1 (youngest) to 9 (oldest). The different fonts distinguish the three sites, with the site near the mouth of a river in boldface. Analysis and plots are as for figure 5.5. The minimum stress values for the three-dimensional analysis were 0.12 for the reef crest and 0.10 for the shallow forereef slope. Note that there is no tendency for communities to group by age, but that differences among sites tend to persist over the entire interval examined. (From Pandolfi 1996)

one or two reefs were excluded from this analysis, although including them does not change the results. There were no significant differences in community membership among the different reef crest or shallow forereef communities from different reef-building episodes during the entire 95,000-year interval (table 5.1). This was true even though an average of only 60% of the coral species from each time period colonized during the subsequent time period.

Ordination of the same BC values using GNMDS shows considerable scatter in each environment among the twenty reef terraces (fig. 5.6), much like the ordination of recent Caribbean reefs in figure 5.5. However, there are no trends in community membership over time, regardless of which GNMDS axes in the three-dimensional analysis are plotted. Differences among sites are consistently greater than those among times in both reef environments, a result that is due to the discharge of a river near one of the sites (Pandolfi 1996).

Finally, the observed number of species in common at different times *at the same sites* was significantly much greater than expected from random sampling



of the available species pool for each environment (see table 5.1). This was true even though the average number of species present on any reef at any one time was less than one-third of the total available. Moreover, we biased the analysis against the obtained result by including all the rare species in this analysis. This is because the same few species occur on the great majority of reefs, which is the basis for their similarity (table 5.2). Many of the dominant species occur almost equally frequently in both environments, although in strikingly different relative abundances as estimated in the field (boldfaced in table 5.2; there are no quantitative data). Thus the reef crest is dominated in rock volume by large, robust, and competitively dominant branching *Acropora gemmifera* and *Acropora cuneata*, with abundant large heads of *Goniastrea retiformis*; whereas the shallow foreereef is dominated by tall, branching, and competitively dominant *Acropora palifera*, with abundant large heads of *Porites* spp. and *Favia stelligera*.

TABLE 5.2 List of Pleistocene coral species from the Huon Peninsula, Papua New Guinea, occurring on half or more of the reefs sampled in each environment

Reef crest Species	Occurrence	Shallow foreereef Species	Occurrence
<i>Acropora gemmifera</i> (S)	<b>18</b>	<i>Acropora palifera</i> (B)	<b>18</b>
<i>Acropora cuneata</i> (B)	<b>16</b>	<i>Porites</i> spp. (S)	<b>18</b>
<i>Acropora palifera</i> (B)	16	<i>Acropora gemmifera</i> (S)	18
<i>Goniastrea retiformis</i> (S)	<b>14</b>	<i>Favia pallida</i> (S)	15
<i>Favia stelligera</i> (S)	14	<i>Platygyra sinensis</i> (S)	15
<i>Platygyra sinensis</i> (S)	13	Fungiidae (S)	15
<i>Favia pallida</i> (S)	12	<i>Favia stelligera</i> (S)	<b>14</b>
<i>Porites</i> spp. (S)	12	<i>Gardinoseris planulata</i>	14
<i>Favia laxa</i>	11	<i>Platygyra pini</i> (S)	14
<i>Platygyra daedalia</i> (S)	11	<i>Hydnophora microconus</i>	13
<i>Stylophora pistillata</i> (B)	11	<i>Montastraea curta</i> (S)	13
<i>Leptoria phrygia</i>	10	<i>Pocillopora</i> sp. (B)	13
		<i>Stylophora pistillata</i> (B)	13
		<i>Coeloseris mayori</i>	12
		<i>Leptoria phrygia</i>	12
		<i>Montastrea annuligera</i>	12
		<i>Platygyra daedalia</i> (S)	12
		<i>Acropora cuneata</i> (B)	12
		<i>Cyphastrea serialis</i> (S)	11
		<i>Favia laxa</i>	11
		<i>Goniastrea edwardsi</i> (S)	11
		<i>Diploastrea heliopora</i>	10
		<i>Goniastrea pectinata</i> (S)	10
		<i>Montastrea</i> sp.	10
		<i>Platygyra ryukensis</i>	10
		<i>Plesiastrea versipora</i>	10

Source: Pandolfi 1966.

Note: Occurrence refers to the number of reefs (out of 20) where the species was found. Species indicated in boldface are those that typically dominate the reef assemblage volumetrically. Spawning species (S) and brooding species (B) are based on Richmond and Hunter (1990).

gera. These distributions and dominance patterns are similar to those reported from living Australian reefs by Done (1982, 1983).

In summary, the above results provide strong support for coral metacommunity stasis in New Guinea over 95,000 years, under circumstances very similar to those in Barbados. Community membership in any environment was highly variable, but less so than expected by random sampling of the available species pool. Whether or not marine benthos other than coral reefs show similar metacommunity stasis has not been tested. Regardless, our results for coral reefs are strikingly different from those reported for temperate forest trees (Davis 1981, 1986; Webb 1987; Prentice, Bartlein, and Webb 1991) or temperate insects (Coope 1995), which exhibit wildly fluctuating community composition during the late Pleistocene.

Metacommunity stasis of coral reefs suggests an analogy to morphological or genetic variation in species populations over time (Jackson and Cheetham 1994; Cheetham, Jackson, and Hayek 1994, 1995). Coral community membership exhibits a great deal of local variation comparable to local population variation within species due to local adaptation and gene flow. Nevertheless, there is no net temporal trend in community membership, even though no single terrace community includes most of the possible species available. There are at least two explanations for this stasis, not necessarily mutually exclusive. First, pure community drift may explain metacommunity stasis if different reefs are sufficiently coupled by dispersal (Hubbell 1995, his fig. 3.12) and environments do not change (but see Harrison 1994 for an alternative view). Second, some ecological force analogous to stabilizing selection in population genetics (Lewontin 1974; Hubbell 1995) may help to keep metacommunity membership from a random walk through time (and space).

Community drift, which is essentially a metapopulation phenomenon in our context, is almost certainly a major factor given the broad larval dispersal of most spawning reef coral species (references in Knowlton and Jackson 1993). However, two of the three dominant *Acropora* species brood their larvae, which consequently should disperse very short distances; the same is true of many of the other frequently occurring species (indicated by the letter B in table 5.2). In addition, environmental conditions were almost certainly different each time sea level rose, as reflected in the varying magnitude of isotopic fluctuations (Webb and Bartlein 1992; Berger and Jansen 1994). Therefore the finding that community composition does not fluctuate significantly suggests some kind of stabilizing factor.

### What Happens to Metacommunity Membership During Faunal Turnover?

By analogy with the punctuated evolution of species, ecological stasis suggests that major shifts in metacommunity membership may occur in pulses during

time in arid environments.

Each heading is subdivided into topics, and examples are given under each. The rows have an extensive reference list, including names, recent reviews, articles, and would provide a

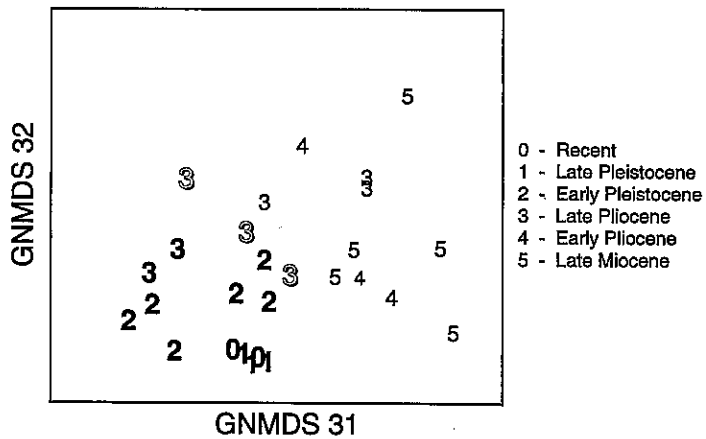


Fig. 5.7. GNMDS ordination of Caribbean coral reef faunas from twenty-seven shallow forereef environments (reef crest to 15–20 meters). Ages range from 0 = recent to 5 = Late Miocene. Large numbers in boldface indicate communities dominated by acroporids; smaller numbers, those dominated by pocilloporids; and large numbers in shadow font, mixed acroporid-pocilloporid communities. The minimum stress value for the three-dimensional analysis was 0.12.

faunal turnover (Gould and Eldredge 1993; Jackson 1994b; Jackson and Cheetam 1994). We investigated this possibility by comparing the species composition of twenty-seven Caribbean shallow forereef communities over the last 8 million years, using the ANOSIM test and GNMDS ordination on presence/absence data (fig. 5.7). The data are from Budd's surveys in Costa Rica, the Dominican Republic, the Bahamas, and Jamaica (Budd and Kievman 1994; Budd, Stemann, and Johnson 1994; Budd, Johnson, and Stemann 1996) and from San Andrés (Geister 1975). Sampling is sparse and replication limited. Nevertheless, the data are adequate to illustrate the kinds of methods that we believe are necessary to test claims of community stability and "coordinated stasis."

The communities are significantly different over the entire time interval (ANOSIM,  $R = 0.45$ ,  $P < .0001$ ), and this is well represented in the ordination (fig. 5.7). Each number in the figure represents a unique coral community, ranging in age from 0 = recent to 5 = Late Miocene. Reefs dominated by the large, tall acroporids *A. palmata* and *A. cervicornis* are indicated by large numbers in boldface; reefs dominated by finger-sized pocilloporid corals (*Stylophora* and *Pocillopora* spp.) by small numbers, and mixtures of the two groups by large numbers in shadow font. It is important to realize, however, that *relative abundance was not a factor in the GNMDS analysis.*

The results provide striking evidence for punctuated community change coinciding with the Late Pliocene turnover shown in figure 5.1. Late Miocene and

Early Pliocene communities are entirely distinct from early Pleistocene to recent communities (see fig. 5.7). In contrast, Late Pliocene communities overlap extensively with both younger and older communities. Moreover, the three communities with mixed acroporid-pocilloporid dominance occur exactly between the two temporally distinct groups, graphically illustrating the nature of the Late Pliocene faunal turnover. Pocilloporid dominance appears to have lasted between 5 and 6 million years, then turned over completely in about 1 million years. Afterward, acroporids were always more abundant, although they may not have achieved their extreme modern dominance until the late Pleistocene (Budd and Kievman 1994; Jackson 1994a), and *Pocillopora* did not finally become extinct until 60,000 years ago (Geister 1977b, Budd, Stemmann, and Johnson 1994). This was the acroporid revolution that swept through coral reefs at the end of the Pliocene worldwide (Rosen 1993).

In striking contrast to the ecological changes during the Late Pliocene, younger and older communities exhibit relative constancy in species composition. ANOSIM showed no significant temporal changes in community composition before ( $R = 0.226$ ,  $P = .18$ ) or after ( $R = -0.063$ ,  $P = .60$ ) the Late Pliocene turnover. Moreover, similarity among Pleistocene to recent communities was significantly greater than expected from random sampling of the species pool (Student's  $t = -3.06$ ,  $P = .003$ ), although this was not the case for Late Miocene and Early Pliocene communities (Student's  $t = 0.98$ ,  $P = .34$ ). The results are preliminary, but they are consistent with the hypothesis that the species composition of shallow Caribbean forereef communities has been stable since the early Pleistocene, and may have been stable before the turnover as well.

### Why Do Faunal Turnovers Occur?

Conventional forcing arguments are based on the correlation between faunal turnovers and changes in climatic or oceanographic parameters, such as the increasing fluctuations in temperature and primary productivity related to the intensification of Northern Hemisphere glaciation at the end of the Pliocene (Stanley 1986; Mix 1989; Allmon 1992; Jackson 1994b; Jones and Allmon 1995; Teranes, Geary, and Bemis 1996). In some cases, oceanographic changes were apparently so rapid and great that causality seems assured (Kennett and Stott 1991). But in other cases, such as the turnover at the end of the Pliocene, climatic changes in the Tropics were probably much less. This raises the physiological conundrum of how, for example, a drop of only a few degrees centigrade could result in such massive bursts of extinction and speciation of shallow-water species (A. Clarke 1993), especially since subsequently increasing fluctuations in climate had so little evolutionary effect (Valentine 1989; Valentine and Jablonski 1991; Budd, Stemmann, and Johnson 1994; Jackson 1994b). Similar questions arise for changes in sea level, primary productivity, upwelling, or any other factors tied to Pleistocene climate change.

Northern Hemisphere glaciation intensified 2.5 million years ago, about 0.5 million years before the peak in molluscan and coral extinctions (see fig. 5.1) and major shifts in coral community membership (see fig. 5.7). Assuming that climate change was somehow responsible for these events, the magnitude of climate change in the Tropics was not very great. Fluctuations in oxygen isotopic ratios, which reflect fluctuations in sea level and temperature, were less than during the last million years (Webb and Bartlein 1992; Berger and Jansen 1994). Isotopic data from reef corals at the end of the Pleistocene indicate a drop in tropical sea surface temperatures (SSTs) of  $5^{\circ}$ – $6^{\circ}$  C (Beck et al. 1992; Guilderson, Fairbanks, and Rubenstone 1994). Calibration of these data against oxygen isotopic fluctuations 2.5 million years ago suggests a maximum drop in tropical SSTs of only  $3^{\circ}$ – $5^{\circ}$  C below the preceding several million years, when SSTs were as warm as today (Dowsett and Poore 1991; Cronin and Dowsett 1996). This drop would have been sufficient to significantly compress the latitudinal ranges of tropical species, but probably insufficient to directly cause the mass extinction apparent in figure 5.1 (A. Clarke 1993).

Metapopulation theory provides a partial way out of this conundrum, based on the model of Nee and May (1992). The initial rapid fall in sea level must have greatly decreased the total habitat and number of suitable patches for all species (Valentine and Jablonski 1991). Moreover, declining temperatures would have further decreased the number of patches available to cold-intolerant species by compressing their latitudinal ranges, thereby causing local extinction at latitudinal extremes (fig. 5.8). For species with low colonization potential, the resulting decrease in number of patches could have been too great for the species to survive the usual cycles of local extinction and colonization of individual patches. This would result in a massive regional extinction debt (Tilman et al. 1994). Thus species extinction would lag behind local extinction, with the magnitude of the lag depending upon the particular life history characteristics of the species concerned. None of this, however, helps to explain why molluscan origination should have increased so much at the same time as the increase in extinction, or even before (see fig. 5.1).

The above scenario is compatible with what little we know about events in the Caribbean toward the end of the Pliocene. It also suggests that the life histories of species that survived the turnover should be different from those of species that became extinct. This idea has not been tested adequately, but it is increasingly apparent that life history patterns did shift dramatically across the turnover for some reef corals (Jackson 1994a,b; Johnson, Budd, and Stemann 1995) and mollusks (Jackson, Jung, and Fortunato 1996). Acroporids, for example, grow up to ten times faster than any other corals, sometimes even keeping up with sea level changes (Chappell and Polach 1991), and acroporids are the group that both radiated and increased in abundance most dramatically during the turnover (see fig. 5.7; Rosen 1993). The model also explains why turnover did not continue throughout the Pleistocene, because once the benthos had

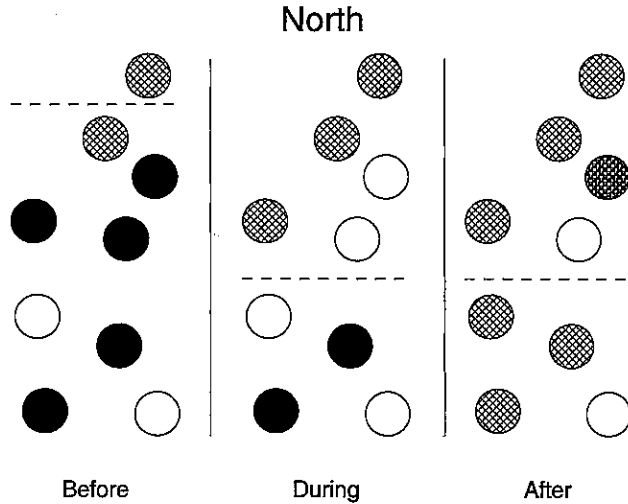


Fig. 5.8. A hypothetical model of the way metapopulation processes might affect the ecological and macroevolutionary consequences of global climatic change in a two-species system (ignoring for simplicity the effects of sea level change on the geographic arrangement of the patches, currents, or species interactions, which would presumably greatly hasten the replacement process during turnover). The left panel shows the distribution of patches and inhabitants before climatic change (open circles, both species absent; solid circles, species 1 present; hatched circles, species 2 present); the dashed line represents a latitudinal temperature isocline. Species 2 is more cold tolerant than species 1. The center panel shows the situation during the onset of climatic change. Species 1 is locally extinct in the north because it can no longer inhabit colder patches to the north of the isocline, and therefore inhabits fewer patches in total. Species 2 has moved southward because it does better than species 1 under cooler conditions and therefore occupies more patches. The right panel shows the situation sometime after the onset of climatic change. Species 1 is now regionally extinct because it has a colonization potential or patch persistence too low to maintain itself in a system with so few patches (an example of extinction debt), *not* because there are no suitable patches (there are four below the isocline). Species 2 has expanded further because it is more tolerant of the new conditions *and* because species 1 is gone. A new species (stipple pattern) has also evolved in the north (but could have evolved anywhere under the conditions of the model). (From Nee and May 1992.)

passed through the initial filter of climatic and sea level change, all that were left were eurytopic species (Jackson 1994b).

### The Shifting Balance of Communities?

Previous claims for or against stability of community composition have not been adequately tested in the fossil record. All of the examples of "coordinated stasis" cited by Morris et al. (1995) are based on the observation that most species

in a given stratigraphic interval tend to persist for millions of years before they are replaced by new species, with very little overlap between time intervals. This may be good evidence for punctuated *evolutionary* turnover and stasis (e.g., Jackson 1994b), but it says nothing about the relative stability of *ecological* communities between turnover events (Bambach and Bennington, chapter 6, this volume). Moreover, the communities listed in figure 1 of Morris et al. (1995) are simply ad hoc.

On the other hand, demonstrations of variation in local community composition over space or time (Valentine and Jablonski 1993; Buzas and Culver 1994; Roy, Jablonski, and Valentine 1995) do not really address the question of limited membership unless they (1) are based on well-replicated samples in space or time, so that the significance of the presence or absence of a species can be evaluated statistically, and (2) go beyond the simple demonstration of differences to ask whether the frequency of association is different from what we would expect by chance. Local and metacommunity composition obviously changed greatly in most environments during the Pleistocene, especially in higher latitudes, so the extreme Eltonian view of tightly integrated marine ecological communities is simply wrong (Jackson 1994a). But the more subtle, and we would claim more interesting, test of the extreme Gleasonian view has not been previously attempted with fossils.

Indeed, our analyses suggest that shallow forereef community membership did not change significantly for corals since the Late Miocene, except during the major faunal turnover at the end of the Pliocene. More importantly, community membership was more stable than expected by chance during the last 2 million years. By analogy to Wright's (1982, 1988) shifting balance theory, metapopulation processes alone may explain the breakdown of communities during turnover, although not necessarily their comparative stasis in between (e.g., compare discussions in Harrison 1994 with those in Hubbell 1995). If not, then metacommunity stasis implies some process analogous to stabilizing selection that keeps community membership within certain limits, except when the entire system breaks down.

What kinds of ecological processes could have such a stabilizing effect over geological time? There are at least three possibilities:

1. Rapid evolution of coadapted complexes, such as unique associations of corals and their hosts, host-parasite relationships, and behavioral symbioses (Glynn 1983; May and Anderson 1983; Knowlton and Jackson 1994; Rowan and Knowlton 1995), may occur during or shortly after turnover.

2. Short-term instabilities may lead to long-term stability when species differ sufficiently in their life history characteristics, habitat preferences, and sensitivity of competitive abilities to environmental conditions (Chesson and Huntly 1989). The dominance of the Huon Peninsula reef crest and shallow forereef environments by different small, competitively dominant subsets of the species

pool with differing growth forms and life histories is consistent with this hypothesis. Which species emerge as dominants may be an accidental consequence of extinctions during turnover and the balance of the life history characteristics of the survivors (Jackson 1994a).

3. Abundant habitat-structuring organisms such as mangroves, seagrasses, and acroporid corals provide the habitat for a great diversity of associated species (Jackson 1972, 1973; Chapman 1977; Kaufman 1977, 1983; Heck 1979; Zieman 1982; Cubit and Williams 1983; Glynn 1983; Abele 1983; Endean and Cameron 1990). Thus any factor affecting these organisms will inevitably affect their associates, as in host-parasite relationships (May and Anderson 1983). For example, corals and bryozoans associated with deep-water seagrasses suffered higher extinction rates in the Late Pliocene when those plants disappeared than did those in other environments (Johnson, Budd, and Stemann 1995; Budd, Johnson, and Stemann 1996; Cheetham and Jackson 1996). In contrast, large lucinid bivalves like *Codakia* enjoyed a burst of speciation in shallow seagrass beds at about the same time. Likewise, the most dramatic change in Caribbean forereef communities involved the replacement of one group of reef framework builders (pocilloporids) by another (acroporids).

Whether right or wrong, these kinds of ideas are testable by comparing the evolutionary fates, patterns of association, and relative abundances of different clades, functional groups, and species during turnover events and in between. For example, taxa closely dependent upon specific habitat-structuring organisms such as pocilloporid or acroporid corals might be expected to show greater changes during turnovers than those living well beneath the photic zone, where the biomass and the diversity of benthic habitat-structuring taxa are low.

Ecology is a young science, and few communities have been observed for more than a few decades, especially on a regional scale. Thus the controversy over community membership and stability cannot be resolved without paleontological data to provide the necessary time perspective and replication on appropriately large spatial scales. Even the wonderfully detailed histories of eastern North American vegetation since the last glacial maximum comprise only half of a single glacial cycle (Davis 1981, 1986; Webb 1987; Prentice, Bartlein, and Webb 1991), whereas the reef terraces from the Huon Peninsula record nine complete cycles (Pandolfi 1996). To use paleontological data effectively, however, we must greatly increase the sampling, stratigraphic precision, and statistical rigor of our analyses (Jackson and Budd 1996). Only then can we be confident that apparent departures from random associations of species are biologically significant and look for meaningful environmental correlations.

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