

Stability in coral communities: a natural experiment

Many models have been proposed to account for the continued existence of competing species. Of late, arguably the most important dichotomy for those studying coral and rainforest communities is between models that treat species as identical and those that require inter-specific differences ('niches'). The latter models emphasize mechanistic processes and natural history¹ and have promoted research into topics such as resource partitioning, variation in growth rates in relation to light intensity, and trade-offs between dispersal and competitive ability or tolerance. These models allow coexistence either because potential competitors divide up resources and avoid competition; or because there is spatial or temporal variation in competitive interactions and dispersal abilities, which either result in identical overall competitive ability, or reduced competition at low densities, which allows for recovery from small population size².

In contrast, the 'identical species' models emphasize stochastic events and history to explain community composition and are, in some respects, 'off the shelf' adaptations of models from neutral gene theory³. Although they do not predict indefinite species persistence, they suggest that the rate at which species competitively exclude each other is so slow that diversity could be maintained by a balance with speciation rates. These models have been pejoratively described as being 'exasperatingly devoid of biology'⁴. Maybe so, but they have successfully explained several patterns in species diversity in rain forests. Fifteen years of data from a 50 ha forest plot in Panama (in which every tree with a chest-height diameter of more than 1 cm is monitored) are consistent with the claim that local tree species composition drifts in a 'random walk' through time⁵. However, given that we know that trees show major differences in dispersal rates, flowering time, seed production, and so forth, do these models really tell us anything about communities? Peter Chesson, for example, has argued that the models' conclusions are too sensitive to the assumption of demographic equality to provide plausible biological explanations⁶. Another valid viewpoint is that they provide a parsimonious null model⁷. Perhaps we can ignore species differences and still accurately predict change in community composition through time and space? The responsibility lies with those who dissent to marshal

evidence that autecology is also needed to explain community structure¹.

One prediction of the null models is that local communities drift through time, showing variation in both species composition and richness. In contrast, niche-based models predict some level of consistency to community structure because not all species can co-occur⁷⁻⁹. At present, however, there are scant data to support claims for niche-based 'assembly rules'⁹. In part, this may reflect the usual timescale over which ecology is studied, with short-term noise obscuring longer-term stability. Ideally, we need a powerful experimental design involving repeated observation of community formation. This requires describing a community at a site and then removing every individual and waiting until the site is recolonized (allowing sufficient time for any niche-based successional processes to occur). If the new and old assemblages are sufficiently similar we may need to look beyond stochastic processes toward biological interactions. Of course, assemblages may look similar purely as a result of chance sampling⁷. We therefore need to observe repeatedly community formation to obtain sufficient replicates. Such a study is a daunting task, especially when dealing with long-lived species like trees or corals.

In a recent paper in *Paleobiology*, John Pandolfi has perceptively exploited a 'natural experiment' on the Huon Peninsula of Papua New Guinea to analyse changes in community membership of coral reefs¹⁰. Here, there have been repeated cycles of coral reef formation during the Pleistocene. Following a sea level drop, the then living reef dies and is fossilized; however, because northern New Guinea experiences tectonic uplift, when sea level returns to its former level the fossilized reef lies inland. Once sea level stabilizes a new reef then forms. This process has created a series of fossil reef terraces, marching uphill with a step-like topography. The youngest reefs studied were at the bottom, 20 m above present-day reefs; the oldest reefs were at the top, over 400 m above modern sea level.

An important aspect of this 'experiment' was the timescale it spanned. The oldest reefs examined were 125 000 years old, the most recent 30 000 years old. Across this time frame no new species evolved, and the study therefore recorded ecological rather than evolutionary dynamics. Furthermore, each reef had time

to develop (approximately 10 000–20 000 years) into a 'mature' reef that had passed through any initial successional phase. By examining coral species composition for each reef, Pandolfi determined whether coral communities at specific sites showed statistically significant similarity through time.

In total, data were obtained from nine reef-building cycles at three sites approximately 30 km apart. For each reef, he distinguished between the reef crest and slope using the geomorphology and distinctive sediment composition of shallower waters. In total, 20 reef crests and 20 reef slopes were sampled. Sampling involved searching a 100 m strip of each reef environment during which all species were identified. In total, systematic searching of 4 km of rock face yielded 122 fossil coral species.

Statistical analysis consisted of the use of a similarity index (Bray–Curtis) to compare spatial and temporal variation in species presence/absence in reef crests and slopes. The results were unexpected. The most surprising finding was that for both reef crest and slope communities at a given site there was no significant difference through time. In contrast, communities differed significantly among sites for reef crests ($p < 0.001$), and marginally so for reef slopes ($p = 0.08$). So, on average, the coral community at a site was more similar to the community at the same site tens of thousands of years ago than to a neighbouring site's community at the same point in time! Moreover, this similarity in composition at a site through time was not due to chance. Testing relative to a null model invoking random selection of species from a species pool drawn from all the species that were found in the reef crest or slope showed that, in both cases, the mean number of species shared between reefs at the same site at different times was more than expected by chance. Pandolfi has interpreted these results as showing niche differences between coral species such that not all species assemblages are equiprobable. In short, species can not be treated as identical entities.

Initially, the finding of community stability in corals is puzzling. Extant reefs display considerable unpredictable spatial and temporal variation in species composition¹¹. This discrepancy is understandable, however, when scales of analyses are considered. What is unpredictable at a small scale, say a 30-year study using 1 m² quadrats, need not be so over larger scales or paleontological timespans¹². By analogy, an insurance firm does not know when you will have a car accident, only that you will almost certainly have one in your lifetime. Likewise, they do not know which clients will have accidents this year, only that 9–10% will.

If the conclusion that coral communities are niche-based assemblages with limited membership is correct, we must then ask whether diversity in rain forests and coral reefs is maintained by different processes given the contrasting results from the Panamanian rain forest^{3,5}. A suitable fossil record is not yet available to test community structure through time in rain forests, but a new study by John Terborgh and colleagues substituting space for time also supports a niche-based view⁴. Sandbanks are deposited on the inner curve of meanders of the Manu river in Peru. Each bank is colonized by trees and eventually covered with a mature (high canopy) floodplain forest. Mature forests on these sandbanks showed marked similarity in the relative rank abundance of common tree species, implying 'assembly rules' for this forest community.

Perhaps rain forests and reefs are both niche-based communities. Hubbell has noted, however, that these conclusions may be premature. In a new null model synthesizing biogeography and relative species abundance theory (but maintaining the identical species assumption) he has shown that regionally common species are also likely to have similar abundance at local sites³. By focusing on these species the Manu study may have overestimated

community similarity. Likewise, with high dispersal ability, common species will reach all local sites. Given the wide dispersal abilities of many corals this may have led to similarity across time for New Guinean reefs (although this explanation can not account for the community differences between sites). The crucial question seems to be whether these studies would have produced the same results if they had confined their analysis to rarer species, and future studies will need to stare down this challenge. This is a dangerous game though. A null model of communities that requires data on rare species is likely to remain unfalsified for a very long time, regardless of its validity. Surely ecology has advanced sufficiently that a study documenting 95 000 years of community similarity¹⁰ allows us to distinguish between a niche- and dispersal-based view of community organization?

Michael D. Jennions

*Smithsonian Tropical Research Institute,
Apartado 2072, Balboa, Republic of Panama
(stri02.gamboa.gam128@ic.si.edu)*

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Timing is everything: new perspectives on floral phenology

Until recently, most research on floral phenology has focused on the interactions with pollinators or on the relationship between the timing of flower production and related characters, such as fruit production, fruit dispersal or requirements for seed germination. Recent work by evolutionary ecologists has begun to explore new aspects of floral phenology using a variety of new techniques. The vitality of research on floral phenology was highlighted at a symposium organized by Elizabeth E. Lyons and Gordon A. Fox at the Ecological Society of America meetings in Providence, RI, USA in August 1996. The symposium brought together scientists working on areas as diverse as developmental biology, quantitative genetics and ecological theory. The talks covered three areas within floral phenology: mechanisms, assortative mating, and phenotypic and genotypic variation.

Pamela Diggle (University of Colorado, Boulder, USA) asked how it is possible for

a plant to change its floral phenology. She noted that changes in timing or duration of flowering are contingent on modifications of overall ontogeny and suggested that plant architecture is, therefore, a critical determinant of phenological pattern. Diggle proposed two pathways for changes in timing of reproduction: (1) the rate of flower production can change through the disassociation of vegetative and reproductive development, or (2) there can be an insertion or deletion of nodes during development. By using markers to track the ontogeny of vegetative traits, one can distinguish between the two developmental pathways. She then reviewed several pertinent empirical studies of phenology. In particular, Diggle highlighted the work of Jones¹, who showed that differences in phenology between a mutant and parental squash were caused by an accelerated rate of flower production not changes in the architecture and ontogeny of the mutant. This study clearly demonstrated that

the change in phenology was because of a disassociation of vegetative and reproductive development.

Tom Meagher (Rutgers University, Piscataway, NJ, USA) and Lynda Delph (Indiana University, Bloomington, USA) described greenhouse experiments designed to examine the relationship between resource availability, flower production and flower longevity (lifespan). By treating the set of flowers produced within each plant as equivalent to a population, they were able to use simple population dynamic theory to examine differences in growth rate between male and female plants. They varied the resource demands within individual female plants by varying the levels of pollination. As the level of pollination increased, there was a concomitant decrease in flower production. Their studies clearly showed how different levels of resource use among male flowers, unpollinated female flowers and pollinated female flowers led to different phenological patterns of flower production. The resource demands for fruit production led to decreases in longevity of individual flowers or duration of flowering period in females.

Lisa Dorn (Brown University, Providence, RI, USA) and Tom Mitchell-Olds (University of Montana, Missoula, USA)