Community Unity?

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Are ecological communities exclusive associations of closely interdependent and coevolving species (*1*), or just a haphazard sample of species inhabiting a region that happen to jointly tolerate the environment of the moment (*2*)? Do all species matter for the function of marine ecosystems, or is there enormous redundancy? These questions are central to understanding not only how communities develop and persist but also the biological consequences of global change (*3*). To answer them, we need to know to what extent population interactions and resource specialization limit species abundance as opposed to fluctuations in environmental conditions, the availability of colonists, history, and chance (*4*). In this issue, Buzas and Culver (*5*) present new paleontological data that bear directly on these and other questions of long-term community membership and function.

Where ecologists stand on these issues is often a matter of taxonomic experience and the scale of investigation. For example, herbivorous insects occupy communities quite independently of one another and show little ecological convergence (*6*), whereas animals and plants living on rocky intertidal shores and coral reefs are strikingly similar worldwide (*7*). Coral reef species composition and succession after a hurricane vary much more within small quadrants than on entire reefs (*8*), and the same is true in other sessile communities (*9*). Interactions among species that are intensely competitive in the short term may lead to longer term positive interdependence, particularly for the amelioration of harsh physical conditions (*10*).

Recent data on the ecological consequences of marine species invasions provide strong support for the open community view (*11*). Interoceanic invasions have increased alarmingly in recent decades as an accidental consequence of introductions of oysters and other fisheries and indiscriminate pumping of ballast water by ships (*12*). Whether invasions cause extinctions of previous inhabitants is difficult to determine (*13*). But the resulting mix of newly established invaders and their predecessors forms communities as ordinary in appearance as those they replace, so that only an experienced taxonomist with earlier collections for comparison is likely to notice any difference (*11*).

The duration of most ecological investigations, however, is necessarily much shorter than that of the relevant environmental processes and generation times of the species involved (*14*). Thus, it is impossible to assess the persistence of different associations and whether, over time, particular combinations of species are more common than expected from a random sample of the regional species pool. Fortunately, these questions are eminently testable with the use of the excellent fossil record of many terrestrial and marine communities. For example, the histories of the reestablishment of forests and oceanic plankton communities after the last glaciation have been reconstructed in detail from sediment cores (*15*). In every case, individual species come and go in apparent response to changes in climate, and there is clear evidence for past communities without modern analogs; nevertheless, the vegetation and plankton are apparently in some form of dynamic equilibrium with climate. Likewise, paleontological studies of late Pleistocene mollusks have demonstrated that species associations were fluid over the last several hundred thousand years along the California coast (*11*) and on oceanic atolls (*16*), whereas those of the most abundant Caribbean reef corals were apparently more constant (*14*). Thus, with the possible exception of reef corals, fossil marine communities appear more open than closed.

Morphological diversity in benthic foraminifera. [Courtesy of S. J. Culver, digital images captured with the Paleovision system at the Natural History Museum, London]

Even these intervals are well within the limits of species' lifetimes. Now, Buzas and Culver (*5*) provide data on changes in marine community composition over the time scale of the origin and extinction of species based on benthic foraminifera (see figure). These abundant protists have been intensively studied by paleontologists because of their value for interpreting ancient environments and their use in oil exploration, so the patterns are robust. Buzas and Culver recorded six successive waves of colonization associated with marine transgressions of the mid-Atlantic Coastal Plain over the past 55 million years. With each new rise in sea level, the proportions of surviving species that reinvaded the same sedimentary basin as they had inhabited previously was highly variable, ranging from only one-quarter to two-thirds of the total species available. Thus, each community was only a subset of a much larger regional species pool. This is surely the death knell for the concept of tightly integrated marine ecological communities.

All of the above studies dealt with community membership on a local scale. In contrast, paleontological studies of entire regional biotas have demonstrated that speciation and extinction commonly occur in pulses, so that groups of species coexist in packages that persist in the same environments for millions of years (*17*). For example, dramatic turnover of mollusks and corals occurred throughout tropical America 2 to 3 million years ago in apparent response to the onset of Northern Hemisphere glaciation, so that the modern fauna is at least 2 million years old (*18*, *19*).

But species lists do not alone encompass ecological communities, as illustrated by the history of Caribbean coral reefs. For the past 500,000 years, until disrupted by an extraordinary combination of human and natural disturbances (*8*, *14*), shallow Caribbean reefs were dominated by dense, nearly monospecific stands of the elkhorn coral *Acropora palmata* and the staghorn coral *Acropora cervicornis* (*14*). Both of these species first appeared about 2 million years ago, but elkhorn was nowhere abundant until 500,000 years ago, and older abundant staghorn populations may have been restricted to the Bahamas (*19*). Moreover,

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smaller branching pocilloporid corals, which preceded elkhorn and staghorn corals in the same environments, persisted alongside the latter for nearly 2 million years before finally going extinct about 120 thousand years ago (*19*). Thus, modern Caribbean reef communities did not develop until at least 1 million years after the origin of the crucial species involved.

Why do such profound delays occur in the origin of novel communities? One possibility is that gradual evolution due to some process such as "neighborhood selection" slowly facilitates positive interactions among coexisting species that alter community structure (*20*). Alternatively, dominance by a few species that share a particular suite of characteristics may emerge as an epiphenomenon of local threshold effects (*21*) and regional metapopulation dynamics (*22*) that "lock" species associations into a limited number of states, once abundances somehow rise above certain critical levels. For example, staghorn and elkhorn corals grow up to 10 times faster than other Caribbean corals (*8*), which may have greatly increased their success relative to other branching species when glacial cycles and sea-level fluctuations intensified substantially about 1.0 to 1.4 million years ago (*23*). In the latter case, the success of these newly dominant corals is an accidental side effect of characters selected for other reasons rather than an adaptation to their present circumstances. The apparently punctuated evolution of most marine species (*24*) argues for the latter interpretation, except that life history traits and behaviors rarely fossilize, so it may be impossible to tell.

Paleoecologists need to pay more attention to the relative abundance of species if we are to resolve the issue of how much community structure is more than just the sum of the component species parts. But whatever the outcome, paleontology continues to contribute fundamentally to ecological and evolutionary theory, be it through the discovery of punctuated evolution of species or synchronous turnover of entire biotas, or the demonstration of the broadly open structure of marine communities. Paleontology still provides the only empirical test of the history of life and models of global change.

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A Biochemical Function for Ras—At Last

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Ras, a guanosine triphosphatase (GTPase), is a molecular switch for signal transduction pathways that control growth and differentiation. Its critical importance in growth control was known since the early 1980s when activated *ras* oncogenes were identified in certain human cancers (*1*). More recently, elegant genetic experiments in yeast, *Caenorhabditis elegans*, and *Drosophila* have established a universal function for Ras in controlling a cell's decision to grow or to differentiate (*2*). Tremendous effort has gone into characterizing the mechanism of action of this critical molecule. Like all GTP-binding proteins, Ras cycles between an inactive [guanosine diphosphate (GDP)–bound] and an active (GTP-bound) conformation, and a wide variety of extracellular signals can stimulate the formation of active Ras:GTP (*3*). The downstream function of Ras is to regulate a protein kinase cascade (*4*); two reports this week, one in *Science* from Hancock's group and another in *Nature* from Marshall's group, have finally pinned down exactly how Ras does this (*5, 6*).

In all eukaryotic cells so far examined (except *Saccharomyces cerevisiae*), Ras controls a mitogen activated protein (MAP) kinase cascade (*4*). After many false candidates came and went, it was eventually realized that stimulation of Ras invariably leads to an increase in the activity of two cytoplasmic serine-threonine MAP kinases, Erk-1 and Erk-2, which subsequently translocate to the nucleus where they phosphorylate key transcription factors such as elk (*7*). Unraveling the sequence of events that connects Erk-1 and -2 to Ras has, up to a point, been a relatively straightforward problem in protein biochemistry. MAP kinase activity depends on concomitant phosphorylation of a threonine and a tyrosine residue by a dual specificity kinase, MAP kinase kinase (MAPKK). MAPKK is itself activated by phosphorylation, and a number of MAPKK kinase activities have been detected in cell extracts.

One protein that clearly functions as a MAPKK kinase is Raf (*8*). This serine-threonine kinase was first characterized by Ulf Rapp's lab as the product of the *v-raf* retroviral oncogene, and in 1986 some elegant microinjection experiments by Stacey's group showed that transformation of cells by v-Raf is independent of Ras (*9*).

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