ECOSYSTEM RESEARCH

Taking a New Look at Life Through a Functional Lens

In the mid-1970s, ecologist Robert Steneck began to see a curious pattern of continuity in the face of drastic change among algae floating off the coast of St. Croix, an island in the Caribbean. The species within the algae clusters—mats—fluctuated wildly in abundance, recalls Steneck, who is now at the University of Maine: "Almost none of the dominant species I'd find in one season would I find as dominants in the next." But what was going on in the mats varied little: They consumed nutrients at a fairly constant rate and resisted similar types of predators. Different algae, apparently, were performing the same biological role. "Certain species were ecologically equivalent to one another," Steneck says.

And with the recognition of that equality comes awareness that small organisms in a system can wield a surprising amount of influence. Since the early 1960s, Steneck and dozens of other scientists have shown that in the plant and microbial kingdoms in particular, there are whole suites of organisms with equivalent functions, or what have come to be known as "functional groups." These investigations are forcing researchers to reassess the value of a long-cherished concept: that ecosystem integrity often depends on a single critical top predator, or "keystone," species.

The keystone concept, a notion championed by population biologists who saw the often drastic effects on such systems when a top predator was removed, dominated ecological thought for 3 decades. Removing a single starfish species from a stretch off the Washington state coast, in one classic example, led to the invasion of hundreds of new organisms. But, says Princeton University ecologist Simon Levin, "focusing on particular species often misses a great deal of what's important in an ecosystem."

Indeed, a growing body of work on functional groups, Levin and others say, is giving ecologists a more complete view of ecosystem processes, looking from the ground up as well as the top down. Take the lowly tussock plants in the Arctic tundra: These plants function as a group to create a "microtopography" above the permafrost that provides a home for insects and bacteria, says Gaius Shaver, an ecologist at the Marine Biological Laboratory in Woods Hole, Massachusetts. Functional similarity could also make life easier for ecosystem modelers, because they can perform one calculation for a whole group rather than for each species. "The concept of functional groups is very widely used and implicit in the thinking of most ecologists," says Shaver.

Beyond functional groups, a broader view of ecological processes is also allowing scientists to reassess the role that individual smaller, nonpredatory species have in shaping their communities, such as the way snails breaking down rocks into soil alter the habitat for the rest of the denizens of that particular ecosystem.

The keystone concept, however, is far from dead. Ecologists are trying to integrate it into the new view by formally expanding the definition of keystone species to include creatures not at the top of a food web, such as viruses, that have a big impact on their environment. "For years we've had population biologists who worry about keystone species and food webs doing their thing, and ecologists who worry about other ecosystem processes doing their thing," says Stanford University ecologist Harold Mooney. The goal now is to bring process and species together.

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Rugged individualist. Classic keystone species, such as this starfish (*Pisaster ochraceus*), can make or break an ecosystem.

Star species. The keystone species concept took the field by storm in the late 1960s, when University of Washington marine ecologist Robert Paine described removing dozens of *Pisaster ochraceus* starfish from the rocky intertidal zone. The starfish was the main predator of mussels, which took advantage of the absence to invade and occupy the area. These new mussel beds were fertile ground for more than 300 species of organisms, such as sea cucumbers, worms, and smaller starfish that had been scarce when *Pisaster* was around. Other starfish species and carnivorous snails, limited by size in what they could eat, could not produce this dramatic effect. Based on these observations, in 1969 Paine formulated the concept of a keystone species: one that determines "the integrity of the community and its unaltered persistence through time."

Scientists soon described other keystone species, such as the charismatic sea otter. In the early 1970s, ecologists James Estes, John Palmisano, and Charles Siminsted found that after Aleut islanders hunted the otters or otherwise drove them away from certain Aleutian islands off the coast of Alaska, sea urchins—a favorite otter food—began to proliferate. That was bad news for Pacific giant kelp forests and the myriad fish living in them. The urchins gnawed on the kelp roots, killing the huge plants and leaving fish-free "urchin deserts" behind on the sea floor.

The major thrust of the keystone concept has been to identify how the presence of certain predators determines the abundances of prey and competing organisms in an ecosystem. The effects ripple down the food web, and in this way, says University of Montana ecologist Jack Stanford, "a keystone species can identify the boundaries of an ecosystem."

Yet even as ecologists' attention was being captured by the dramatic effects of top predators, a small countermovement was taking form among scientists who had begun to notice that little creatures, too, exerted a large amount of collective power and influence. "As we move lower in the food chain, the concept of keystone species becomes less important," says Levin.

Looking beyond the species. Instead of finding keystone species of bacteria, for instance, ecologists are finding influential clusters: the functional groups. The concept has deep roots, emanating in part from efforts in the 1930s to look at functional similarities among species, such as how desert plants from Africa and North America look alike and conserve nutrients similarly even though each belongs to a different genus.

Microbiologists then picked up the thread in the 1960s and 1970s, with studies on bacteria indicating that vast numbers of species perform similar functions. One example is bacteria of the genus *Rhizobium*: Although many types of *Rhizobium* have not even been identified at the species level, it appears that all the species cataloged so far can fix nitrogen and many can substitute for one another in an ecosystem, says microbiologist Rita Colwell, president of the Maryland Biotechnology Institute. Thus, scientists believe, if a particular *Rhizobium* species were to decline or die out in a system, other species could take over the job of nitrogen fixation. In effect, plants that depend on legumes and symbiotic *Rhizobium* to fix nitrogen for survival have a safety net.

Steneck's continuing investigation of algal communities has produced similar results, pointing to at least seven discrete functional groups among the algae. For instance, one group, microalgae, can form mats close to shore that are highly photosynthetic and highly susceptible to predation by sea urchins and other organisms. Any one of several species of microalgae can form mats with these characteristics [*Oikos* **69**, 476 (1994)]. "You remove one member of a group, then another takes its place: It's like ecosystem insurance," says Mooney.

Today many ecologists are eager to put this insurance policy to practical use. Instead of simply describing functional similarities in an ecosystem, they are attempting to quantify them in order to get a better handle on ecosystem health and to make predictions about how ecosystems will change over time. The notion of functional groups aids such efforts by allowing ecologists to treat many different species as a single group.

One effort where this simplification is paying off is in the development of patch models, small plots of land on which rates of photosynthesis and carbon flow can be measured for all members of the species present. Patch models, on which Levin and Paine did pioneering work in the early 1970s, are now becoming "a marriage between demographics and systems," in that data on nutrient flow can be combined with data on how processes such as forest fires influence germination rates, says Tom Smith, an ecologist at the University of Virginia. A problem that has plagued this type of modeling, says Smith, is that researchers—and their computers—can be overwhelmed by the attempt to chart all the interactions between every species and every nutrient in an ecosystem. But he and his colleagues are hoping functional group data can help them simplify some of their calculations.

The traditional focus on how top predators affect the food web has also obscured the role that single, less dominant species play in shaping their environment, says ecologist Clive Jones of the Institute of Ecosystem Studies (IES) in Millbrook, New York. But as ecologists pay more and more attention to function and process within ecosystems, those roles are becoming more clear. Beavers building dams, microalgae absorbing light and reducing the strength of sea ice, and blind mole rats digging and tunneling are all species that can have a profound effect on the existence of the organisms around them. In an article last year in *Oikos* (vol. 69, p. 373), Jones, John Lawton of Imperial College in Berkshire, U.K., and Moshe Shachak of Ben Gurion University of the Negev in Israel outlined this idea. "Every ecosystem we looked at, we found a species modifying the environment in a manner important to the integrity of the ecosystem," says Jones.

ROBERT STENECK

Mob rule. Although individually not influential, clusters of functionally equivalent species, like these articulated algae (about 3 centimeters tall), can also have powerful effects.

Keystone revisited. Ecologists have not turned their backs on keystone species completely, however. "You can't get around the fact that some individual species are going to have much larger effects than others on their ecosystem," says Lawton. As a result, some researchers are trying to tie species and process together in a broader sense than was used in the traditional keystone concept.

One such attempt is to look at what IES ecologist Rick Ostfeld calls "keystone processes." He and IES colleague Charles Canham have found that population fluctuations of meadow voles can determine the species of trees gaining a foothold in agricultural land now slowly reverting to forest in upstate New York [*Ecology* **74**, 1792 (1993)]. The researchers have found that the voles ravage seedlings of red maples, sugar maples, and white ash, as well as tree of heaven, an aggressive Chinese invader. A healthy vole population "can eliminate an entire cohort of tree seedlings," he says, which clears the way for the growth of tree seedlings the voles eschew, such as acorns, oak, and pine.

A major attempt to refine the keystone concept took place at a meeting in Hawaii last December, where 15 prominent ecologists, including Paine, met to discuss how the notion of a keystone species might be extended beyond creatures sitting atop a food web. One way, says University of Minnesota ecologist David Tilman, a conference participant, might be to define a species as a keystone based on the ratio of its biomass to its effect on an ecosystem. A high ratio would merit a keystone classification.

The advantage of this definition, says Tilman, is that it encompasses the effect of a species on any ecosystem process. For instance, ecologists could identify keystone viruses. In the past, no ecologist would dream of describing a distemper virus that kills lions as a keystone species in the African plains community. But the virus does have large effects on the ecosystem considering its biomass. In line with this idea, the "keystone cops," as the Hawaii group called themselves, drafted a new definition of keystone species: "a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance."

Even a more traditional notion of a keystone species can be put to valuable use in conservation biology when linked to a basic understanding of ecosystems processes, says Stanford. He suggests such an approach could be useful in the effort to bring back two fish in the upper Colorado River, the Colorado squawfish and the humpback chub, which have been on the federal endangered species list for more than 20 years. There are myriad roots of the fishes' decline, Stanford says, including tourist traffic, overfishing, exotic species, and increased ultraviolet radiation that all reduce the food web supporting the fish. But which of these is most important, how many other factors there are, and which would yield the greatest payoff from remediation are open questions.

So Stanford envisions a two-pronged approach. While neither the chub nor the squawfish is a classic keystone species, a real keystone fish, such as a salmon, can be used to define the limits of the food web enmeshing the two endangered species. Once those limits are set, researchers can begin to investigate the processes occurring within those limits. "People lost sight of the very complex interactions that must be preserved to bring the fish back," he says.

Keystone species "may not be important in every ecosystem," says Michigan State University ecologist Gary Mittelbach, but "ecologists should not be too quick to abandon the idea entirely." The bottom line, he and other ecologists say, is not to cordon off research on these "gifted" organisms. If scientists can place keystone biota in the context of the processes that maintain an ecosystem, says Levin, they can "begin to understand what maintains ecological functioning." And that, after all, is what ecology is all about.

–Richard Stone