

A controversial push to focus on positive ecological interactions rather than competition and predation has ignited a debate among ecologists

## Conflict Over Cooperation

A brightly colored starfish with a voracious appetite for mussels occupies a key niche in ecological theory. In a series of seminal papers starting in 1966, Robert Paine of the University of Washington, Seattle, showed that by preying on mussels, *Pisaster ochraceus* creates an opening for other rock-dwelling shellfish, dramatically increasing the diversity of these sessile species. Take *Pisaster* out of the picture, and the riot of anemones, limpets, and barnacles on Washington's rocky shores would be replaced by a monotone of mussels. Paine

of Brown University in Providence, Rhode Island, argue that much of modern ecological theory stems from a misleading fixation on the roles of competition, predation, and externally imposed stress in shaping natural communities. Missing from core concepts, they argue, is the growing realization that species can interact in positive ways—a process called facilitation—with major consequences for community structure. This more benign view of species interactions, the trio points out, can have profound implications for deciding which species to focus

*Pisaster*, the so-called keystone, was absent, says Bertness. “The classic keystone species example is wrong,” he says. This prompted the *TREE* authors to propose a theoretical alternative to the keystone species: the “foundation species,” which shapes communities by creating and enhancing habitat.

Not surprisingly, this challenge to fundamental concepts is creating perturbations in the community of ecologists. Most of them agree that the subject has suffered undeserved neglect. “I have no problems with any of [Bertness’s] work on positive effects,” says ecologist Bruce Menge of Oregon State University in Corvallis. But he and many other ecologists say that they have long recognized facilitation and have made up for earlier biases. Adds Paine, now a professor emeritus: “It depends [on] how [Bertness] casts it. If he says new sorts of facilitative mechanisms are going to turn ecology on its head, he’s clearly wrong.”

### A different perspective

That’s exactly what Bertness and his colleagues are arguing. They note that competition and predation became the dominant forces in ecological theory beginning in the 1950s, when ecology began a transformation from a descriptive to an experimental science. Appreciation of the “largely unanticipated yet striking” influence of facilitation on the organization of terrestrial and aquatic communities came long after the core theories were well established, they write. And those theories have been slow to incorporate positive interactions, largely because their impacts are only now being put to the test. “We seem to finally be making headway, because we have unleashed experimental ecology to settle the debate,” says Bertness.

Bertness and a parade of students built their case on experiments in marine systems, where harsh environments—salinity, pounding surf, alternating wet and dry conditions—are the norm. A study published online on 2 July 2002 by *Oecologia*, for example, shows that on the relatively saline south side of Cape Cod in Massachusetts, growth of transplanted salt marsh plants is more often enhanced by neighbors than on the milder north side, where growth suppression is more common. Facilitation is easier to find in such environments, which could bias



**Ecological superstar.** The starfish *Pisaster ochraceus* spawned the concept of keystone species; it shapes communities by feeding on mussels, opening the way for other rock-dwelling species.

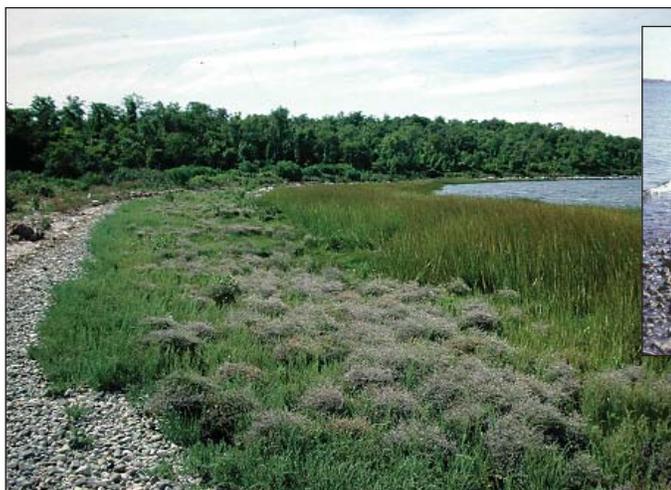
called the starfish a “keystone” species because, like a keystone in architecture, it is crucial for maintaining structure. Since then, Paine’s notion of keystone species has become a fundamental concept in ecology.

But a group of renegade ecologists is now arguing that the concept is flawed. And they are taking shots at other long-standing bulwarks of ecology. In a provocative article in the March issue of *Trends in Ecology and Evolution* (*TREE*),\* John F. Bruno of the University of North Carolina, Chapel Hill, John Stachowicz of the University of California (UC), Davis, and Mark Bertness

on in conservation efforts. “It is time to bring ecological theory up to date by including facilitation,” they write. And they warn: “This process will not be painless, as it will fundamentally change many basic predictions and will challenge some of our most cherished paradigms.”

Take *P. ochraceus*. Bertness argues that the positive side—facilitation by mussels—is at least as important as the negative, predation by starfish. Mussel beds are home to hundreds of invertebrates that do poorly in the presence of the mussels’ competitors. In studies that measured overall diversity, rather than the diversity only of sessile species, diversity was actually greater when

\* Now available online at [www.sciencedirect.com](http://www.sciencedirect.com)



**Foundation species.** The intertidal grass *Spartina alterniflora* facilitates a community of plants and invertebrates on New England cobble beaches.



it tackles the ecological-niche concept. According to this time-honored theory, the distribution of a species is restricted to a range of food sources and

their perspective.

But some of the newest support for their views comes from plant ecology. Ragan Callaway of the University of Montana, Missoula, and his colleagues measured the effect of thinning out neighboring vegetation on the growth of small herbaceous plants on 11 mountain ranges from Alaska to Argentina to the Republic of Georgia. The standard competitive view would predict that the remaining plants should benefit from reduced competition for limited resources. That's what Callaway found for low-altitude plants: They grew 22% faster than controls did. But, as Callaway reported in the 20 June 2002 issue of *Nature*, high-altitude plants whose neighbors were removed grew 25% less, because neighbors improved microclimate, sheltered plants from wind, or stabilized the soil. "There's a ton of new evidence that has come out just within the last 10 years," he says. For example, recent studies show that plants can change communities by providing shade or soil oxygen for neighbors.

Despite such findings, and anecdotal evidence dating back as far as the 1960s, most ecologists still see facilitation as a collection of "cute little evolutionary stories," says Bruno. "We're not saying people aren't aware of it; we're saying ecological theory doesn't account for it." Most ecologists "definitely don't think of it as structuring communities in the way disturbance or competition or predation does," he says. The new *TREE* article sets out to redress the balance.

With its confrontational tone and its attacks on some of ecology's most sanctified ideas, the article is guaranteed to attract attention. First,

environmental conditions—a "fundamental niche"—that is whittled down by competition with other organisms to a "realized niche."

But the concept could be even more powerful if it included facilitation, the authors argue. Realized niches could turn out to be larger than fundamental niches, because some species create habitat or beneficial conditions for others. For example, the *TREE* authors note, by providing shade and moisture, intertidal seaweed canopies extend the distribution of many organisms to higher tidal heights than they would otherwise be capable of occupying.

The authors also take on the intermediate-disturbance hypothesis. This pillar of ecology states that species diversity is highest when disturbance of an ecosystem is moderate: frequent enough to prevent the best competitors from dominating, but not so frequent that only fast-growing or resistant species survive. A classic 1979 study of algae living on intertidal boulders supports this idea. The boulders roll with the changing tides at a frequency determined by their size, crushing resident algae and providing a ready-made gradient of disturbance to study.

It turns out that small boulders, which roll frequently, and large boulders, which rarely roll, both have low algal diversity. But medium-sized boulders have the highest diversity, because both dominant competitors and new colonizers have opportunities to survive.

The *TREE* article points to little-noticed research on the same ecosystem in 1987, which took a broader view of diversity than just focusing on algae. The study, by Richard Dean and Joseph Connell, now at UC Santa Barbara, concluded that diversity of mobile invertebrates was highest at low levels of disturbance. The reason is facilitation: Less-disturbed algae provided more habitat for invertebrates.

The challenge to the keystone-species concept is similarly based on the argument that ecologists should broaden their focus to include a wide variety of species and positive interactions. In the kelp forests off the West Coast of the United States, for example, sea urchins' appetite for kelp may increase the diversity of other seaweeds. But most ecologists recognize that kelp is a foundation species, and its removal greatly reduces the amount of habitat available for anemones, fish, and other dependent species.

These arguments are more than academic. Bertness and company propose that facilitation may help devise strategies for dealing with invasive species, which cost billions of dollars a year in damages and can drive natives extinct. A large body of research suggests that diverse communities are less easy to invade because they are more competitive. But other research indicates that diverse communities can be easier to invade if they promote facilitative interactions (*Science*, 5 May 2000, p. 785). And if invaders facilitate one another, one invasion can open the door for others, precipitating what Daniel Simberloff

of the University of Tennessee, Knoxville, calls an "invasional meltdown." The *TREE* authors say conservation efforts that simply promote native diversity may therefore be doomed to failure. Managers might want to think twice, for example, before trying to restore

**Facilitating debate.** Mark Bertness, John Bruno, and John Stachowicz (left to right) are challenging "some of our most cherished paradigms."



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grasslands by adding a diverse mixture of native species without knowing which are likely to facilitate invaders and which will enhance habitat for natives.

### Competing pressures

Ecologists widely recognize and applaud the research by Bertness and his colleagues, but many question whether facilitation really is as important as competition or predation is. First in line with such questions is Paine himself. He praises Bertness's experimental work, but he questions his intense focus on habitat-forming species. "If you want to call that facilitation, fair enough, but it's boring," Paine says. "His [Bertness's] current hobbyhorse ... is much less studied and much less understood and much less experimentally tractable than the one that has made me famous—but not rich."

Paine argues that keystone interactions are actually the most important kind of positive interaction. *Pisaster*, by preying on the enemies of sessile invertebrates, facilitates those invertebrates. "When you add it, it's like hitting the system with a ball-peen hammer," says Paine. In the kelp-forest example, Paine says that sea otters, not urchins, are the keystone. Otters eat urchins, which is what allows kelp to thrive and facilitate other species.

Bertness's own research in fact underscores the importance of keystone species, Paine claims. In a study published online on 29 July 2002 by the *Proceedings of the National Academy of Sciences*, Bertness and student Brian Silliman attribute the decline of salt-marsh cordgrass in parts of the southeastern United States to herbivory by snails, which are plentiful because humans have overfished snail-eaters such as the blue crab. Paine calls this a clear example where a keystone species, the blue crab, is more important than the so-called foundation species, cordgrass.

"I agree that our blue-crab work is a spectacular example of a keystone," Bertness says. But "strong keystone species effects are almost always associated with predators controlling important foundation species."

To an outsider, the debate may seem like semantic wrangling, and some ecologists are inclined to agree. "I personally think the whole idea of positive versus negative interactions is not intellectually productive," says Clive Jones of the Institute of Ecosystem Studies in Millbrook, New York. The struggle over which is more important "comes from a very strong desire: physics envy." Ecologists would like to predict what happens in an ecosystem based on very simple data, he says, and Bertness and company may just be swapping the obsession with competition for an obsession with facilitation. Ecologists should focus on the condi-

tions that foster positive and negative interactions, not on deciding which predominates, he says.

Shahid Naeem of the University of Washington, Seattle, a veteran of a war of words over diversity in ecology (*Science*, 25 August 2000, p. 1282), says he is also bemused by the argument. One group focuses on the keystone species and the type of diversity it promotes, the other on foundation species and another type of diversity, he says: "But that's simply changing what you think of as diversity. ... It serves us poorly

to have people championing one cause over another." In other words, strong words are no substitute for strong science.

That may be one of the few points of agreement in this fractious discipline: Only creative, rigorous experiments can decide the outcome. "If you ask me if it's worth doing experiments [on facilitation], the answer almost certainly is 'yes,'" Paine says. But ask him if he knows how they will turn out, and he answers, "I don't have the faintest idea."

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## Neuroscience

# Singing in the Brain

Researchers flocked here in December 2002 for the first international conference devoted to birdsong. New findings presented at the meeting shed light on the neural circuits that coordinate the intricate movements needed to create song

**NEW YORK CITY**—Songbirds have long captivated certain humans. The English composer George Henschel, for instance, reportedly kept a highly trained bullfinch that sang "God Save the Queen." Henschel was intrigued when an untrained canary kept in an adjoining room picked up the tune and finished it off properly whenever the bullfinch paused too long in midmelody.

In recent decades, the fascination with songbirds has hatched a remarkably productive niche in neuroscience. By studying how male birds learn and produce their song (females generally listen and judge; see sidebar, p. 648), researchers have gleaned insights into the neural mechanisms of learning and motor control. Birdsong researchers were the first to discover that—contrary to

decades-old dogma—new neurons can be born in the adult brain (*Science*, 3 January, p. 32). They've also revealed many mechanisms by which sex hormones set up differences between the brains of males and females during development.

Despite all this interest, birdsong researchers had never come together for a conference of their own until last month, when 200-plus scientists from around the world gathered for a soggy few days at Hunter College in Manhattan. It felt something like a family reunion. The grand patriarchs of the field were there, including Peter Marler, whose work with sparrows in the 1950s pioneered the scientific study of birdsong; nearly all in attendance could trace their academic lineage to him. "It's like being at your wedding," one researcher said. "Everyone you ever wanted to see in the whole world is there, but you only get to see them for 5 minutes."

Presentations covered everything from genetics to behavior to theories on song evolution. One area in particular, though, that has taken wing of late is research on the motor-control circuits in the songbird brain. New work has revised the view of how birdsong is produced and may yield clues about how the brain generates other



**Prepare to be serenaded.** Male zebra finches are some of birdsong researchers' favorite subjects.

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