ECOLOGY

Biodiversity Is a Boon to Ecosystems, Not Species

Long before conservationists and developers began skirmishing over the value of biodiversity, ecologists were having their own debate about the issue. Pack an ecosystem with species and its future should be safer, some ecologists have insisted. Not so, said opponents, citing a paucity of experimental data as well as theoretical work that seemed to predict the opposite—that complex ecosystems are likely to be more vulnerable to disturbances such as drought. Now new evidence has raised hopes of a truce among ecologists by showing that both views have merit.

In a recently published pair of papers, ecologist David Tilman of the University of Minnesota, Minneapolis, reports that while diversity benefits an ecosystem as a whole, stabilizing it and boosting its overall productivity, populations of individual species can fluctuate more widely in diverse ecosystems than in simpler ones, even to the point of disappearing. Other ecologists are hailing the results and the years of meticulous fieldwork that went into them. "Tilman has teased apart the impact of diversity on total community biomass from that on individual species," says mathematical biologist Robert May of Oxford University (who is also chief science adviser to the British government). "In 10 years, this work will become a classic."

One pole of the debate was set in 1958, when the British ecologist Charles Elton suggested that less diversity results in less ecological stability. Elton cited the greater frequency of pest outbreaks in simple ecosystems like croplands than in complex ones like grasslands and forests; he also noted that invading species disrupt the relatively small, simple ecosystems of islands more than they do those of continents. A smattering of field experiments, including ones by Syracuse University biologist Sam McNaughton, seemed to confirm Elton's view.

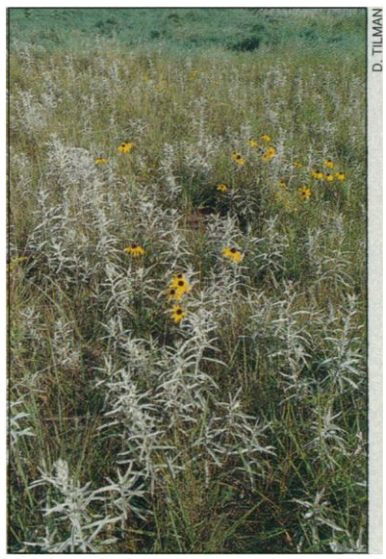
In 1973, however, May presented mathematical evidence that diverse systems are less stable than simpler ones. His model showed that the more diverse an ecosystem is, the more complex the web of interactions among its species—and the larger the repercussions of any disturbance on the abundance of individual species. A drought that kills off key plant species in a complex ecosystem, for example, will have widespread effects on the animals that feed on them.

A year later, May offered a brief caveat, arguing that although diversity may make individual species more vulnerable, it can stabilize the total biomass of an ecosystem by allowing prospering species to compensate for damaged ones. A drought may harm specific plants and animals, but overall productivity in a diverse ecosystem won't suffer much because certain plants, such as those with deeper root systems or the ability to store water, can take over from less drought-tolerant species. May wrote, "If we concentrate on any one particular species, our impression will be one of flux and hazard, but if we concentrate on total community properties ... our impression will be of pattern and steadiness."

For 2 decades, however, many ecologists overlooked this caution and interpreted May's work as implying that the lower stability of individual species in a diverse ecosystem would lower the stability of the whole assemblage of species. Says Tilman, "They made an incorrect leap of faith and believed that the ecosystem responded as a total of all its species." The controversy festered for years in part because of the difficulty of the experiments needed to resolve it: Ecologists would have to keep a close eye on ecosystems of varying complexity for years, observing both the fate of individual species and each ecosystem's total biomass.

In recent years, however, researchers have begun to do just that. Several small studies, in the field or in greenhouses, suggested that diversity could boost ecosystem productivity. But "nowhere are there such extensive field tests" as the ones that Tilman has conducted, says Princeton University ecologist Simon Levin. One study, done in collaboration with David Wedin of the University of Toronto and Johannes Knops of the University of Minnesota, examined the relation between biodiversity and ecosystem stability in 147 experimental plots 50 kilometers north of Minneapolis that had been planted with varying numbers and combinations of prairie species. For 2 years, the group measured the plots' productivity, resistance in the face of environmental stresses, and ability to retain nutrients in the soil. On all counts, the group reports in the 22 February issue of *Nature*, the more diverse plots did better.

That finding might seem to tip the scales toward Elton's view of the value of biodiversity. But a different set of field experiments, begun in 1982, moves the picture back toward the middle ground. In this study, which Tilman reports in the current issue of *Ecology*, he looked at the impact of diversity on the fate of individual species as well as on the ecosystems' overall health.



Strength in numbers. High-diversity plot of prairie species includes sage *(silvery leaves)* and brown-eyed Susan *(yellow flowers)*.

The project, which followed 207 patches of grassland over 11 years, is "the most massive and careful work" of its kind, says McNaughton.

Instead of seeding and weeding the plots, as in the *Nature* work, Tilman began with natural growth, then adjusted its diversity by adding varying amounts of fertilizer. High fertilizer levels reduced diversity by favoring certain very productive species at the expense of others, but otherwise he allowed the mix of species and the abundance of each one to vary freely. For each plot, he did an annual census of species and populations in late summer and tracked changes in total biomass by harvesting and weighing all the growth in a small section of the plot.

In a finding that complemented the 2-year study, high diversity increased the plots' resistance to disturbance, as Tilman learned when a 2-year drought hit about midway through the study. The species-rich plots suffered lower declines in total biomass during the drought than did the species-poor plots. But Tilman also found that the biomasses of individual species varied more from year to year in species-rich plots than in species-poor plots, as May had predicted. Concludes Tilman, "Ecosystems with more species tend to be more stable. However, populations within them can have great variability."

The results, he says, confirm the biological value of diversity in agriculture, rangelands, and conservation areas. But they also suggest that for individual species, diversity is no guarantee of survival. Paradoxically, says University of Tennessee ecologist Stuart Pimm, individual instabilities help stabilize the whole system: "There is a dance going on of compensatory changes. Something always benefits from a disaster, providing you have enough species."

–Anne Simon Moffat