CONSERVATION

Ecologists Dare to Ask: How Much Does Diversity Matter?

ASILOMAR, CALIFORNIA—Human beings depend on ecosystems for an array of vital services: soaking up carbon dioxide, preserving soil fertility, controlling pest outbreaks, and retaining water, among many others. But what does it take to preserve a working ecosystem? Would the loss of biodiversity—now a hot topic among environmentalists—affect an ecosystem's ability to carry out those functions? The fact is that researchers just don't know. As Stanford University ecologist Harold Mooney puts it, "If we lose biodiversity, what else are we losing? No one has tried to answer that before." Ian Noble of the Australian National University adds that ecologists have convinced policymakers of the importance of biodiversity to ecosystem health, and now "we find ourselves having to produce the evidence."

One effort to do so was a workshop* sponsored here recently by the Scientific Committee on Problems of the Environment (SCOPE) as part of a United Nations Environment Program assessment of Earth's biodiversity. None of the 50 participants expected consensus would be easy to reach, partly because, as Mooney notes, ecology has been a "Frank Sinatra science," divided into specialties that each do things "my way." The ecosystem ecologists generally measure the cycling of energy and materials through a forest or a prairie without taking specific organisms into account. The population biologists, on the other hand, examine individual species and the food webs they form—but generally ignore these creatures' roles in the larger cycles of energy and materials.

In the past two years, however, SCOPE ecologists have pulled together what data they could find—from experimental studies as well as observations in tropical forests, tundra, coral reefs, and a dozen other natural systems—about how species richness affects the workings of an ecosystem. For many functions, such as nutrient cycling and decomposition, there's next to no clear evidence about the role of species diversity. But for one key ecosystem function, its ability to turn carbon dioxide and water into plant matter, the Asilomar group saw evidence that greater diversity does make a difference. More diverse ecosystems are more productive—at least up to a point.

Most natural ecosystems are well beyond that threshold, however, and they can often sustain some species loss without a drop in productivity. As soil scientist J. M. Anderson of the Rothamsted Experimental Station in England concluded, "It's impossible to say we need every beetle to maintain function." And that left the participants with the toughest job of all: formulating guidelines for deciding which species really are crucial, and which ecosystem functions they're needed for. The workshop showed that researchers are far from reaching a consensus about such guidelines. Yet the relentless pressures imposed on biodiversity by agriculture, development, and population are making some kind of species triage unavoidable—and ecologists would like to provide guidelines to help policymakers make the best cuts.


MICHAEL GIANNECHINI/ PHOTO RESEARCHERS

Keystone. Moose, by munching hardwood shoots, alter an ecosystem.

Rivets or passengers? Shaping the discussions at Asilomar were two contradictory theoretical predictions about the importance of species diversity. One, made in 1981 by Stanford ecologists Paul and Anne Ehrlich, has become known as the "rivet popper" hypothesis. The diversity of life, said the Ehrlichs, is something like the rivets on an airplane, with each species playing a small but significant role in the working of the whole. The loss of each rivet weakens the plane by a small but noticeable amount—until it loses airworthiness and crashes.

A contrary proposal, the so-called redundancy hypothesis, came a decade later from ecologist Brian Walker of Australia's Commonwealth Scientific and Industrial Research Organization. Contrary to the Ehrlichs, Walker asserted that most species are superfluous—more like passengers than rivets—and that only a few key species are needed to keep the system in motion.

Several studies have now lent support to the "rivet" hypothesis. One was an experiment last year in controlled-environment chambers at the Ecotron facility near London. Ecologists Shahid Naeem, now at the University of Minnesota, and John H. Lawton of Imperial College tested the effect of diversity on productivity by setting up 14 artificial ecosystems. Each housed the same number of individual plants, chosen from either two, five, or 16 annual species. Under identical growing conditions, Naeem and Lawton found, the most species-rich systems consumed the most carbon dioxide and produced the greatest weight of plant material (*Science*, 3 December 1993, p. 1511).

To make sure the result wasn't a fluke, the team resorted to the roomier setting of a greenhouse, where they grew another 150 combinations of two, five, and eight species, picked at random from the thousands possible with their 16-species pool. The result: As species numbers went up, the mean productivity level climbed. Says Naeem, "On average, polyculture turns out to be more productive than monoculture."

The reason, Naeem believes, is that a larger number of species usually generates a more diverse plant architecture—from tall herbs to creepers—which allows the system to capture more light and produce more plant material. Support for that notion comes from agronomists studying multicrop systems: The most productive assemblages, they find, are usually those with the greatest number of functional types. Michael J. Swift of the United Nation's Tropical Soil Biology and Fertility Program in Nairobi, Kenya, for example, pointed out that the best way to raise productivity in a maize field is not by packing in more cereal grains but by adding melons, trees, or nitrogen-fixing beans.

Naeem notes that humans might be able to select a reduced set of species that would be highly productive under the right conditions. But, he notes, "Even if we could engineer our world to be incredibly productive—to clean up CO_2 emissions and produce lots of food and timber—if a pest or climate change wipes out our few chosen species we'll have nothing to back them up."

The idea that diversity imparts resilience gained support from another experimental result discussed at the meeting. David Tilman, another University of Minnesota ecologist, and John Downing of the University of Montreal spent several years monitoring the productivity of prairie grassland plots containing different numbers of species. The site, 30 miles north of Tilman's St. Paul campus, had been under study for other reasons since 1982, and natural variations in species richness among the plots had been exaggerated by varying the levels of nitogen fertilizer—a treatment that tends to reduce species numbers even as it boosts productivity. During

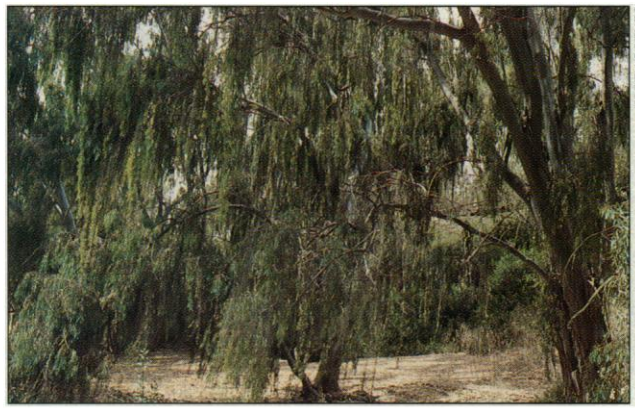
*SCOPE/Global Biodiversity Assessment Synthesis Conference, 27 February–3 March.

a drought in 1987 to 1988, productivity in all the plots fell drastically, Tilman reported, but it dropped only a fourth as much and recovered in one season instead of four in the most species-rich plots. Concludes Tilman: "Biodiversity is a way to hedge bets against uncertainty, even in managed systems."

But Tilman, like other investigators studying the relation of diversity to ecosystem function, saw evidence that, beyond a certain level of diversity, these effects reach a point of saturation. He noted that the biggest gains in stability came with the first 10 species in his system; beyond 10, additional species didn't seem to add much stability, perhaps because the essential functional niches had already been filled. Similarly, Swift noted that agronomists see little gain in productivity when they exceed four or five plant species. When it comes to productivity and resilience, some species in managed ecosystems may indeed be more like passengers than like rivets—as Walker had proposed.

Diminishing returns. Reports from natural ecosystems—temperate and tropical forests, for example—led workshop participants to conclude that the same may be true there: Although biodiversity is valuable up to a certain point, most ecosystems contain more diversity than is needed to reach peak productivity. On the largest scale, that idea is borne out by the fact that although the temperate forests of the Northern Hemisphere show vast differences in species richness (the forests of East Asia include 876 tree and shrub species, those of North America 158, and those of Europe 106) they are virtually identical in productivity, as German plant ecologist Ernst-Detlef Schulze of the University of Bayreuth reported.

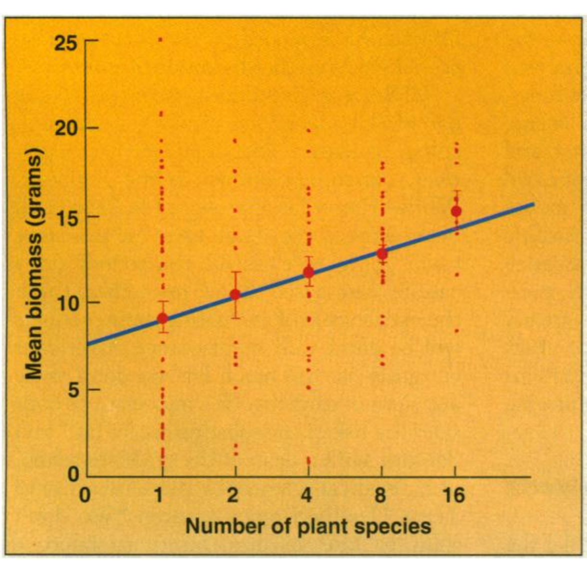
Similarly, a group analyzing what is known about growth and photosynthetic rates in tropical forests concluded that carbon consumption would probably top out with only 10 or so tree species—"a species richness far below that found in any tropical forest, even the most fragmented and highly disturbed," noted population biologist Gordon Orians of the University of Washington. By the end of the week, the workshop participants had extended those conclusion from forests to most other kinds of ecosystems. As Christopher Field of the Carnegie Institution of Washington put it, average annual productivity "saturates somewhere in the range of 10 to 40 species," as long as those species maintain the structural complexity of the vegetation.


EARTH SCENES

Top producer. Eucalyptus, a nonnative species, may boost the productivity of California scrubland by tapping into deep water.

This overall conclusion is hopeful, implying that in theory, loss of species need not impair ecosystem productivity. But that doesn't mean the extinctions now underway won't take a toll on function. Tilman notes that while random extinction might leave behind a few species in each structural category—understory palms and ferns, vines, epiphytes, and canopy trees in a tropical forest, for example—most extinctions caused by human beings are far from random. Grazing, logging, and burning always affect a specific subset of species, and Tilman thinks this probably has a larger impact on function than random extinctions would.

Which leaves ecologists looking for principles to help pinpoint the species that must be saved to keep ecosystems healthy. A model proposed at the meeting by ecologist Osvaldo E. Sala of the University of Buenos Aires and colleagues would judge the impact of a species by how abundant it is compared to other members of the same functional group—decomposers, photosynthesizers, or predators, for example. The assumption, says Sala, is that "a small number of abundant species account for a large fraction of ecosystem function."



SOURCE: LAWTON AND NAEEM

Strength in numbers. Artificial ecosystems with more species generally produced more biomass.

But Sala noted that his model leaves no room for so-called keystone species—species whose impacts can't be judged by their abundance. Another participant, F. Stuart Chapin of the University of California, Berkeley, suggested a rule of thumb for picking out these special cases: They are the species that change the total amount of water, nutrients, or other resources available to a community or the frequency of major disturbances such as disease or fire. Chapin noted, for instance, that moose in northern forests prefer to dine on aspen and birch, thinning them and encouraging the succession of spruce and balsam fir. The resulting cycle shapes the character of the whole ecosystem by varying its productivity, altering soil properties, and boosting the frequency of forest fires. Likewise, in California, deep-rooted eucalyptus trees tap into water supplies unavailable to other species and probably raise the overall productivity of the ecosystem.

Chapin's second example shows, however, why many ecologists at the meeting remain uncomfortable with trying to tie species conservation to ecosystem "performance"—it can favor species that conservationists wouldn't otherwise put at the top of their list. Eucalyptus may boost the productivity of California scrublands, but it is an alien invader that has disrupted many natural ecosystems. Conversely, participants emphasized, even a species that seems to be a fifth wheel in the workings of an ecosystem might be worth saving for economic, moral, or aesthetic reasons.

And if the goal of conservation is to maintain the performance of Earth's life-support systems, many at the meeting said a focus on critical species isn't enough. Just as important is the diversity and balance of entire ecosystems across the landscape—wetlands, forests of varying ages, tundra, grasslands. Each element in the mosaic has different roles in renewing Earth's air, water, and soil, said ecologist Indy Burke of Colorado State University. That mosaic is more likely to be disrupted by activities like swamp draining or forest clearing than by species loss.

But without some minimum number of rivet species, the components of that mosaic would disintegrate. Clearly ecologists aren't ready to pinpoint the rivets that keep any given forest or savanna working. But by "raising the level of discussion" on a very contentious topic, Mooney said, he and his colleagues had taken a first step.

–Yvonne Baskin

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