ECOLOGY

Rift Over Biodiversity Divides Ecologists

An acrimonious dispute has broken out over whether the data on biodiversity are robust enough to inform public policy

A long-simmering debate among ecologists over the importance of biodiversity to the health of ecosystems has erupted into a full-blown war. Opposing camps are dueling over the quality of key experiments, and some are flinging barbs at meetings and in journals.

The dispute pits an outspoken group of ecologists against some of the leading lights in the field. In one camp are ecologists such as David Tilman of the University of Minnesota, St. Paul, and John Lawton of Imperial College at Silwood Park, U.K., who have devoted their careers to large and costly experiments that have indicated that healthy ecosystems depend on diversity. Some ecologists have long questioned the validity of these experiments, but what had been a relatively low-key dispute ignited last fall when the Ecological Society of America (ESA) distributed a pamphlet to Congress and federal agencies touting the importance of biodiversity—and citing the research in question.

Critics—including ecologists Michael Huston of Oak Ridge National Laboratory in Tennessee, Phil Grime of the University of Sheffield, U.K., and David Wardle of Landcare Research, an independent research institute in New Zealand—fired off a letter to the ESA's *Bulletin*, alleging that Tilman, Lawton, and colleagues are using inconclusive research to push their policy agenda. Some of these same scientists also take issue with a recent experiment this week in a *Science* Online Technical Comment (see www.sciencemag.org/cgi/content/full/289/5483/1255a). Huston calls the diversity studies "irrelevant" and "politically manipulated." The critics even go so far as to allege bias at the major journals, which they say favor the more "politically correct" research plugging the value of biodiversity. "The results of these studies provide just the answers that many environmentalists want to hear," says Wardle.

Tilman calls such charges completely "off base." Although he and others acknowledge that the experiments have limitations, they argue that the evidence is still convincing.

Other ecologists safely outside the fray say there is more at stake in this dispute than personalities and egos. Beyond the legitimate scientific question about how much can be learned from the experiments is the nagging question—by no means limited to biodiversity—of when scientific data are strong enough to form the basis of policy decisions. "There's a lot of unease" about how this research is being used, says ecologist Daniel Simberloff of the University of Tennessee, Knoxville. Even so, others defend its merits. "Scientific criticism is good, but rather than trash these experiments, we need to say, 'What do we need to do to learn more?' " says ecologist David Hooper of Western Washington University in Bellingham.

Flourishing dispute. Some ecologists question the relevance of biodiversity experiments such as those at Cedar Creek.

CREDIT: G. DAVID TILMAN

Strength in numbers?

At the heart of the debate is the notion that the loss of plant or animal species will bring an ecosystem closer to collapse. Ecologists have long pondered how species contribute to ecosystem stability; in the early 1970s theoretician Robert May concluded that diversity has no consistent effect. Just 6 years ago, experimental evidence indicated the opposite.

One study, the Ecotron experiment, investigated what happens to plots of plants as more species are added. As reported in *Nature* in 1994, Shahid Naeem and others on Lawton's team at Silwood Park planted various plants in enclosed chambers, added insects and worms, and measured how biomass—simply the leaves, roots, and other organic matter produced by plants—changed with the number of species. To the surprise of much of the ecological community, they found that the more species there were, the more biomass the plot yielded—hence, the more productive the ecosystem was.

That same year, Tilman's group at the University of Minnesota published in *Nature* results from their grassland plots at Cedar Creek, 65 kilometers north of Minneapolis, showing that species-rich plots were more resistant to drought than were species-poor ones. The upshot, Tilman and other ecologists concluded, was that the more species the better, in terms of buffering ecosystems against disruptions.

But the studies soon came under heavy attack. Scientists including Huston and Grime charged in letters to *Nature* and in subsequent papers that the experiments were flawed: Variables other than species number could explain the rise in productivity, they argued. For example, the Ecotron team planted taller plants in more species-rich plots than in the sparser plots, which made the diverse patches more productive. Even experiments such as those at Cedar Creek that added species randomly suffered from a "statistical artifact," critics claimed: The higher productivity seen with more species could be explained by simply adding a few highly productive species to the mix, a phenomenon known as the "sampling effect." To show a real benefit from diversity, these ecologists argued, the plots would have to demonstrate "overyielding"—put simply, productivity would have to be greater than that of the single most productive species grown in isolation (see sidebar).

"Answer" yields more questions

The BIODEPTH experiment was supposed to resolve these problems. "We were partly prompted by criticism of earlier work that didn't separate [the effects of] biodiversity from other processes," says Andy Hector of Imperial College at Silwood Park, a protégé of Lawton and lead author on this massive study, which involved 34 authors in eight European countries. The 2-year experiment, reported in *Science* last year, found that in plots of up to 32 species, productivity rose in step with diversity (*Science*, 5 November 1999, p. 1123). Moreover, in many plots, the researchers saw the much-desired overyielding. In a Perspective accompanying the piece, Tilman, who was not an author on the study, called it a "landmark."

But rather than resolve the debate,

When Do Many Species Matter?

Ecologists agree that experimental plots of grasses are sometimes more productive when they harbor more species. But some disagree passionately about whether it matters—in other words, whether this proves that biodiversity is critical to ecosystem health (see main text).

If the rise in productivity is simply due to a phenomenon known as the "sampling effect," then it is a meaningless statistical artifact, argues Michael Huston of Oak Ridge National Laboratory in Tennessee. The sampling effect is an arcane term to explain a rather simple process: As more species are randomly added to a plot, the odds rise that one of those species will be productive—because it's leafier or uses nutrients more efficiently, for instance. And just a few highly productive plants can drive up the overall productivity of a plot. So, say Huston and others, this does nothing to prove that an array of species is any better than planting a monoculture of the most productive species.

Not necessarily so, answers David Tilman of the University of Minnesota, St. Paul, who argues that the sampling effect is a legitimate explanation for why more species make an ecosystem more productive and resilient. Even if a few more productive species were thrown in the mix, it is not certain that the entire plot would be more productive, because some species might outcompete each other, he says.

Both camps agree that the most convincing evidence that biodiversity is beneficial would come from a demonstration of an effect called "overyielding." This means that the productivity of a species mixture has to be higher than the productivity of any individual species within it grown in isolation. If it is, then something synergistic is at work. One plant might fix nitrogen for the other plants, for example, or a tall plant might provide shade for a sun-intolerant species. But to demonstrate that high numbers of species are beneficial, one has to show overyielding with many species, not just a few, asserts Phil Grime of the University of Sheffield, U.K.

Tilman says the latest results from his grassland plots, now 6 years old, may help bring the two sides together. Overyielding "totally dominates the patterns," a result that, he says, would be "a lot more interesting biologically" than the sampling effect. **–J.K.**

BIODEPTH added more fuel to the fire. In this week's Technical Comment, Huston, Grime, and 10 other critics argue that the BIODEPTH experiment also suffers from technical problems. On closer inspection, they say, the sampling effect does explain most of the productivity gain. The critics attribute the few cases of overyielding that the study authors report to an obvious explanation—addition of a legume. That "is a well-known phenomenon, and it occurs at very low species numbers," Huston says. "There's no evidence from this experiment that 200 species is any better than 50 species." Hector agrees that BIODEPTH results could benefit from more detailed analysis. "There are some good points, and I'm working on some of them now," he says. "But I think technically the work was correct, and there was nothing [in the Technical Comment] to change our conclusions."

Propaganda blitz?

The last straw for Huston and other critics—and what drove the dispute beyond science—was ESA's pamphlet on the importance of biodiversity to ecosystem functioning. A section of the pamphlet summarized work from Ecotron, Cedar Creek, and BIODEPTH—with scarcely any mention of doubts raised about the experiments, skeptics say. Part of a series called "Issues in Ecology" aimed at policymakers, students, and the public, the pamphlet was written by a panel of ecologists led by Naeem, now at the University of Washington, Seattle, and was translated into lay language. Copies were sent to members of Congress and agencies. Tilman was the series editor and one of the 12 co-authors. Finding that "both the magnitude and stability of ecosystem functioning are likely to be significantly altered by declines in local diversity," it recommends "the prudent strategy of preserving biodiversity in order to safeguard ecosystem processes vital to society."

Skeptic. Michael Huston says that biodiversity studies are "irrelevant."

Huston and the other critics hit the roof. In a commentary published in the July 2000 ESA *Bulletin*, which goes to all 7700 ESA members, they mince no words, charging that the pamphlet is "biased," "states opinions as facts," and sets "a dangerous precedent"—especially as it appears to represent the position of the entire society. It is "a propaganda document," they claimed, "and an advertisement for some authors' research." By promoting "unjustifiable actions" based on a "house of cards," they wrote, "scientific objectivity is being compromised."

In response to this broadside, some of the pamphlet's authors are backtracking. In a written response, Naeem defends the report as "objective." But, he told *Science*, he argued for including some material that would have made the piece more balanced, such as a graph showing conflicting studies. It was lost in the condensing process. Tilman, for his part, says he strove to satisfy two sides—ecologists who wanted more decisive language, and others who felt it should be more cautious. In the end, he concedes, "nobody was happy." Tilman says that in retrospect a scientist from "the other side" should have been invited to review the document; he has since added another layer of review to the series.

Ecologists who are less critical of the disputed studies argue that a different line of research might be more fruitful. Hooper suggests that rather than simply counting numbers, experimentalists should devote more attention to what a plant does—whether it sequesters a mineral for other plants, or how deep its roots are. "Composition matters more than diversity," he says. Wardle, too, suggests that a better way to get at what might happen to ecosystems as species are lost is to remove plants from established plots, rather than study plots started from seed.

Optimist. David Tilman says the two sides aren't so far apart.

In spite of the temperature of this dispute, Tilman doesn't believe the two sides are that far apart: What's different, he says, is the ardor with which they disagree. "We have a case where everybody is partly right, and some people are vehemently partly right."

If there's any hope for ecologists to reach some sort of consensus about what diversity experiments mean and how best to study the issue, it may come this December. Calling a cease-fire, Michel Loreau, a French member of BIODEPTH, has invited both sides to a meeting in Paris. "The opinions are so disparate, I don't think it's likely that everyone will converge," says Hector. "But we can maybe clear away some of these issues."

–JOCELYN KAISER

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