Biography of David Tilman

David Tilman describes himself as both a theoretical and an experimental ecologist. Currently the McKnight Presidential Chair in Ecology and Regents Professor at the University of Minnesota (St. Paul), Tilman has spent his career developing theories of biodiversity and species composition that he has tested in carefully designed and controlled experiments. His work on resource competition in both algal and grassland ecosystems has helped shape ecology into a more predictive and quantitative science. For this and numerous other contributions, Tilman was elected to the National Academy of Sciences in 2002. In his Inaugural Article, featured in this issue of PNAS (1), Tilman presents a new theory of species diversity and abundance within ecosystems. The theory was inspired, in part, by data he gathered over the past two decades at the Cedar Creek Natural History Area (Bethel, MN), where he currently serves as director. Through his new stochastic niche theory, Tilman offers an explanation for the patterns seen during the assembly of species into ecosystems, including what controls the number of species and their abundances, and why some ecosystems are more readily invaded by exotic species than others. The article suggests that stochastic niche theory offers a resolution to the controversy between whether it is "neutral" or "niche" processes that determine the diversity and composition of ecosystems.

David Tilman

A Budding Mechanist

Born in 1949, Tilman grew up on the shores of Lake Michigan. As an undergraduate at the University of Michigan in Ann Arbor, he was immediately attracted to physics and its use of simple mechanistic theory to make testable predictions. However, a week-long ecology section in his first biology course encouraged him to switch tracks. Steven Hubbell, an ecologist now at the University of Georgia (Athens), taught the section and showed Tilman ecology's potential. Tilman was attracted to ecology because he saw a chance to imbue a field rich with natural history observations with mechanistic and predictive theory. Ecology held added appeal because "it was so relevant to life on Earth and to its sustainability in the face of the growing pressures of humanity."

Tilman went on to major in zoology, because there was no program at the University of Michigan for ecology at the time. After earning his bachelor's degree in 1971, Tilman remained at the university for his doctoral work, studying under aquatic ecologists Peter and Susan Kilham. It was during his doctoral studies that Tilman first experimentally explored the mechanisms of resource competition and their implications for species diversity and coexistence. Such competition is especially fierce among plant species because all plants require sunlight and the same mineral elements. Tilman wanted to know whether the outcomes of competition could be predicted by looking at the traits of individual species, and whether these mechanisms might offer an explanation for the paradoxically high diversity of life on Earth.

For his thesis, Tilman decided to investigate the mechanisms of resource competition among algae of Lake Michigan, a question motivated, in part, by the effects of phosphorus pollution on algae in that and many other lakes. By looking at the traits of some common species, such as their nutrient uptake rates and efficiencies of nutrient use, Tilman found that he could predict abundances of competing species both in laboratory experiments and along a gradient of nutrient loading in Lake Michigan. In 1976, *Science* published one of his doctoral studies (2) detailing experimental confirmation of resource-based competition theory in algae. The experiments showed that two species could coexist on two resources, specifically on phosphate and silicate, if there was a tradeoff such that each species was a better competitor for a different resource. This theme, that ecosystems are structured by evolutionarily unavoidable tradeoffs, was developed and elaborated in much of Tilman's subsequent work.

Home on the Range

Tilman completed his Ph.D. in 1976 and went directly to an assistant professor position in the department of ecology, evolution, and behavior at the University of Minnesota. As his geographic location changed, so did the focus of his ecological studies. On the shores of Lake Michigan, Tilman had studied freshwater algae. In Minnesota's prairies, he turned to grasslands as his model system but remained focused on resource competition.

In the early 1980s, Tilman began experiments to determine which nutrients might be limiting various grassland species. One hectare of prairie can sustain more than 150 species of plants, all competing for the same resources. Tilman's early experiments showed that nitrogen was the only limiting nutrient in these ecosystems, raising, again, the question of how so many species could coexist while seemingly competing for just a single factor. His nitrogen-addition experiments, which have continued now for 22 years, have shown that nitrogen availability greatly influences competition and species abundances (3, 4). Moreover, chronic addition of even low levels of nitrogen causes the loss of plant diversity (5). This work, he says, "means that nitrogen deposition can have just as severe an impact on terrestrial ecosystems as phosphorus pollution has on lakes." Atmospheric deposition of nitrogen deposition is of growing concern globally, Tilman notes, because, as the work by Peter Vitousek and others (6) has shown, humans now produce more biologically active nitrogen than do all natural processes combined, and they are on a trajectory to triple this production during the next 50 years.

Besides these findings, the prairie at Cedar Creek gave rise to some of Tilman's most influential ideas in the field of ecology. In 2000, Essential Science Indicators deemed Tilman the most-cited environmental scientist from 1990

This is a Biography of a recently elected member of the National Academy of Sciences to accompany the member's Inaugural Article on page 10854.

More than 100 people, including summer interns, graduate students, postdoctoral researchers, faculty, and staff, perform research at Cedar Creek Natural History Area each summer. Much of this research is supported by a National Science Foundation Long-Term Ecological Research grant to Cedar Creek.

to 2002. His most-referenced article, a 1994 *Nature* article (7), rejected a 20-year-old ecological paradigm that suggested diversity is a destabilizing force on individual species and, thus, presumably, on entire ecosystems. This article, along with another published that year (8), asserted that diversity might have unexpectedly strong impacts on the functioning of ecosystems. In a study of the effects of drought on plant abundances in 207 plots of his long-term nitrogen-addition experiment, Tilman and his collaborator John Downing saw that, as was long thought, individual species dynamics became less stable at higher diversity. However, just the opposite happened for the system as a whole. Drought caused the productivity of the most diverse plots to fall by a factor of 2 but caused productivity to fall by a factor of 12 in the least diverse plots (7).

This initial finding sparked controversy as the discipline began to reexplore a long-rejected idea. The controversy kindled new theory and large-scale, well replicated experimental studies of biodiversity, including biodiversity experiments at Cedar Creek (9–11) and an experiment replicated across eight European nations (12). "Diversity is now recognized as one of the three or four major factors controlling the functioning of ecosystems," said Tilman.

Fertility for Thought

Issues of diversity and abundance (13) continue to be the focus of Tilman's career. He still is challenging existing paradigms, investigating paradoxes, and searching for explanations that address the individual species' role in shaping entire ecosystems. In his Inaugural Article (1), Tilman describes a new theory, stochastic niche theory, to explain the diversity and relative abundance of species within ecosystems.

His idea builds on existing theories for why some species are more successful, and thus more abundant, than others. Classical niche theories suggest that species thrive because each occupies a different niche. Although classical niche theories can explain why species are found separated along resource gradients, like moisture in the case of plants, they predict no limit to diversity and cannot explain the relative abundance of species. To fill in the gaps of classical niche theory, "neutral theory" was put forward in 2001 by Tilman's former undergraduate teacher, mentor, and friend, Steven Hubbell. Hubbell's neutral theory (14) ascribes species abundance solely to random chance. It offers what Tilman calls "an elegantly simple explanation for relative abundances and species diversity," but it does not account for the frequently observed connection between a species' traits and its success (15).

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Tilman's new stochastic niche theory, like neutral theory, is rooted in the mathematics of chance but adds a component of resource competition. The result is a theory that seems to resolve many of the conflicts between neutral theory and niche theory. Tilman's theory predicts that as more and more species coexist during the assembly of an ecological community, there are fewer resources left for new species, thus making invasion less likely. Stochastic niche theory also helps explain what Tilman (16) and others (17) have observed in the field over the years: that, in general, many new plant species can survive and grow in a habitat once a stochastic barrier to their establishment is overcome.

In 1991, Tilman added thousands of seeds from 5–54 prairie species to plots in a prairie and added no seeds to other plots. "A single addition of seed was able to almost double plant diversity in our most diverse prairie grassland, and most of these species are still present in these plots more than a decade later," he says. Paradoxically, though, most of the added species already were growing and producing seed in nearby areas of the field but had not colonized the plots on their own. Seeing this, Tilman realized that coexistence of species seemed to be the norm in nature (17) but that this coexistence was limited by the difficulty that plants had establishing from seed.

Consequently, Tilman wondered what factor was limiting diversity in the control plots. He found an answer in two elements: chance and competition. The vast majority of seeds do not make it to adulthood. An established plant drops thousands of seeds during its lifetime but, in effect, just ends up replacing itself with one new adult. The ability of an invading plant to establish itself, he reasoned, should depend on the resources left unused by the established species and on the resource needs of the invader. As diversity increases, he notes, "the odds of any given seed becoming an adult become very, very small because diverse communities use up almost all of the resources. Even those small odds are stacked in favor of invaders that have different resource requirements than the established species."

The stochastic niche theory is only the most recent example of Tilman's ability to interlock theory with experimental practice. "I rarely do an experiment that is not inspired by theory and rarely develop theory that is not inspired by an experiment," he said. Tilman shares this dual existence with several other senior ecologists, including Hubbell and Stephen Pacala, who works at Princeton University (Princeton, NJ). He is especially delighted that a growing cadre of younger ecologists is combining experimental and theoretical approaches, but he holds that there is no one right way to do ecology. "There's room for all different approaches in the discipline," he says, adding that intellectual diversity is crucial to addressing ecology's biggest problems.

The Price of Diversity

Tilman has not lost sight of the broader societal implications of his work on diversity. He has an interest in communicating the results of his work and the principles of ecology to the public and others who might be able to effect positive change. During his tenure as a Pew Fellow from 1995 to 1998, Tilman started *Issues in Ecology,* a publication of the Ecological Society of America. Each publication reports on a major ecological problem or issue. The articles are written by teams of scientists and edited to be understandable to nonscientists.

Tilman sees similarities between his studies of how individual species effect ecosystem functioning and how the choices of individual consumers influence the economy. "The mechanisms and mathematics of the economy of nature," he notes, "are amazingly similar to those of the economy of society." The economic analogy is important, he believes, because economic choices of consumers may be driving global environmental damage. Tilman currently is working with economists, such as Stephen Polasky, also at the University of Minnesota, to put economic values on what ecosystems do for humanity. For example, forests, oceans, and other ecosystems, for instance, provide an economically valuable service to society by removing about two-thirds of the carbon dioxide released by the combustion of fossil fuel. "All my theories and explanations assume tradeoffs, but humans have not been good at recognizing the tradeoffs that we face," he says. "If we can put a value on the services of nature, we can use the same currency to evaluate the costs and benefits of policies and actions. We can then find paths that provide society with the greatest long-term sustainable net benefits."

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