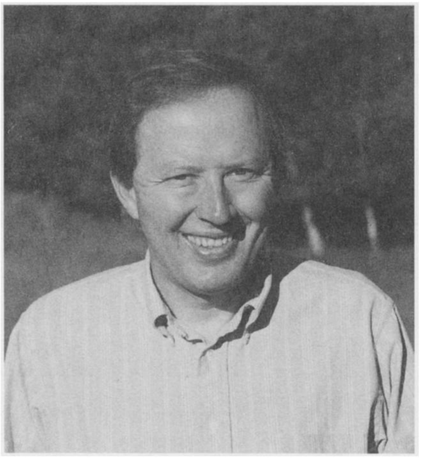
MACARTHUR AWARD



David Tilman

David Tilman is the 1996–1997 recipient of the Robert H. MacArthur Award, which honors distinguished ecologists in the middle of extraordinary careers.

From the beginning as a graduate student at the University of Michigan, advised by Peter and Susan Kilham and by Stephen Hubbell, to the present as Distinguished McKnight University Professor and Director of the Cedar Creek Natural History Area at the University of Minnesota, Dave Tilman has focused on broad questions related to biodiversity, including interspecific competition, succession, community composition, and ecosystem functioning.

His initial inspirations came from G. Evelyn Hutchinson's questions about the diversity of species (*American Naturalist* 95:137). Early ecological theory—the competition equations of Lotka and Volterra—imply that only as many species can coexist as the number of limiting resources available to them. But aquatic and terrestrial plant communities support far more species than the early theory allowed. That theory, strictly interpreted, presented a paradox of diversity. In principle, only two possibilities could account for such a paradox: Either (a) systems in ecology are too complex ever to be understood mathematically, or (b) natural ecological systems violate one or more crucial assumptions of the theory, hence the theory must be refined. A large part of Tilman's career has been a systematic experimental and mathematical investigation of these two possibilities, followed by application of the resulting science to problems of the environment.

Tilman's first step, undertaken as a graduate student, addressed the first possibility—whether mathematical theory can work in ecology even when the assumptions are met. That is, can ecological theory be predictive? He determined the resource requirements of diatom species grown in separate laboratory cultures, then used a theory of resource competition to correctly predict how the species would fare when they lived together in competition, both in the same laboratory culture and in Lake Michigan (*Science* 192:463–465). Results helped demonstrate that mechanistic theory does work in simple ecological systems and meant that the solution to the biodiversity paradox must lie in the simplifying assumptions of the theory itself.

The next step, therefore, called for more complex models with fewer simplifying assumptions. In 1980, Tilman switched to terrestrial plant communities and has worked at the Cedar Creek Natural History Area with many collaborators ever since. He successfully interlaced theory, observations, and experiments, inspiring and testing more advanced theories of competition, succession, and multispecies coexistence. One by one, assumptions of early theory were examined, both experimentally and mathematically, and through his studies and those of others, the paradox of diversity dissolved. Each crucial assumption, when relaxed, allowed an almost unlimited number of species to coexist. His conclusions form two books in the Princeton Monograph Series (*Resource Competition and Community Structure,* 1982; *Dynamics and Structure of Plant Communities,* 1988) and over 100 papers. By sustained systematic investigation combining long-term observations, rigorous experiments, and theory, Tilman has thus been a major force not only in settling fundamental questions in ecology, but also in helping establish a firm scientific basis for ecological theory.

Success in the first two steps led to the third—applying the resulting knowledge to global environmental problems. In a long collaboration with Wedin, study of nitrogen response has shed light on ecosystem functions, including the importance of individual plant species in ecosystem nitrogen dynamics (*Oecologia* 84:433–441). Expanding his 1994 theory of diversity in spatial habitats (*Ecology* 75:2–16) to include habitat destruction, he and collaborators warned that as habitat is increasingly destroyed, it may be that the most competitive, most abundant species are in greatest danger of extinction (*Nature* 371:65–66). Combining theory with a decade and a half of field experiments, he helped resolve the long-standing problem of whether complexity in ecosystems enhances their stability, as Elton and other early investigators maintained, or whether it upsets stability, as May showed mathematically. Remarkably, experimental work done as part of the Cedar Creek LTER showed that both groups were right—they each simply had addressed subsets of a broader question (*Ecology* 77:350–363). Most recently, large-scale experiments he and collaborators started two years ago have already demonstrated in a clear and simple way how biodiversity—in and of itself—affects ecosystem functioning, increasing productivity and reducing nutrient leaching. These experimental results (*Nature* 379:718–720) were the first such demonstration in a natural environment since Darwin suggested a connection between biodiversity and productivity over a century ago. Tilman is now following with theoretical treatments of why this connection may exist. Nor have these applications, of such importance to the public, remained isolated in the scientific realm. They have inspired public discussion, with attention in The New York *Times,* National Public Television, National Public Radio, and local papers around the world. Thus, in addition to its merit as basic science, Tilman's work has helped provide a

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firmer basis for environmental policies.

Among the qualities that have allowed Tilman to achieve such an effect on our discipline are these: a fluency in both the experimental and theoretical realms of ecology, a precise focus on the tasks at hand, patience to perform long-term studies, a vision of the important questions facing our discipline, a deep faith in the methods of science, and a resolve to apply them to the problems of our planet. He has contributed to the field by service on the editorial boards of *Limnology and Oceanography, Ecology* and *Ecological Monographs, The American Naturalist, Acta Oecologia,* and *Science,* and is the founding editor of *Ecological Issues.* For sustained contributions he has received grants, honors, and awards too numerous to list completely, but including a Guggenheim Fellowship, Fellow of the American Academy of Arts and Science, the W. S. Cooper Award, and Pew Scholar in Conservation Biology.

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