2013 Alexander von Humboldt Medal
David Tilman

By Jason Fridley

Few ecologists of our time have driven forward their discipline as has Dave Tilman, recipient of the 2013 Alexander von Humboldt Medal, presented to honor scientists of extraordinary contributions to the development and advancement of vegetation science. Indeed it is impossible to imagine plant ecology over the past three decades without him, and I am honored to speak on his scientific achievements.

Like many icons of North American ecology, Dave hails from the northern Midwest near the prairie-forest border in Illinois. He was from the outset drawn to the elegance of scientific theory and the expression of scientific principles in the language of mathematics, combining early interests in physics and a love of the outdoors into a PhD thesis at the University of Michigan exploring interactions of lake phytoplankton, under Steve Hubbell and Peter Kilham. His impact on the field was immediate. Taking inspiration from the theoretical work of G. Evelyn Hutchinson and Robert MacArthur, Dave forever changed the way we think about species interactions, formally developing a "mechanistic theory of resource competition" in several key publications as a grad student and then assistant professor at the University of Minnesota. This culminated in his groundbreaking Princeton Monograph in 1982, Resource Competition and Community Structure. Of course I needn't tell any of you this, as we are now all so accustomed to the "overlapping ZNGIs" of resource ratio phase planes in our introductory ecology courses that we could teach it in our sleep, and indeed this remains the principal way undergraduates are introduced to plant competition.

By the mid-1980s, Dave had started to apply his resource ratio theory to the grassland at Cedar Creek Natural History Area, a leap from algae to vascular plants that would transform plant ecology and ignite a series of controversies that drove a number of young scientists, including myself, into our discipline. It began by applying the R* concept - the level to which a species can reduce the concentration of a limiting resource - to dominant grasses at Cedar Creek, to determine whether this single unifying parameter accounting for both resource use and tissue loss rates could predict community dynamics. This principle could also be applied to succession, providing an elegant mechanism for Connell and Slatyer's ‘tolerance’ model of species turnover through competitive dominance. In both cases Dave was able to show that R*, particularly with regard to soil nitrogen, was a significant driver of community dynamics at Cedar Creek, evident in classic papers from the mid-80s to mid-90s and detailed in his second Princeton Monograph, Plant Strategies and the Dynamics and Structure of Plant Communities, in 1988.

By this time it had become clear that Dave's perspective on plant competition was not shared by all ecologists. In particular, the core argument that competition is driven by tolerance of low resource levels stood in strong opposition to existing theory, most notably by Phil Grime, which argued that competition is about resource preemption, or the speed at

which resources could be captured to prevent the growth of neighboring species. There were also fundamental disagreements about related issues: To what extent did assumptions about equilibrium conditions matter? Is competition intense even in sites of few resources? Do plants alter their allocation to above versus belowground tissues in response to limiting light or soil nutrients? To this day I still have a diagram I created my first year in grad school, labeled "The Grime-Tilman Competition Debate", which lists no less than 13 different areas of fundamental disagreement between the perspectives of our two inaugural Humboldt awardees. This debate has been described in detail by many others since, including contributions to the volume Perspectives in Plant Competition, which Dave co-edited with Jim Grace in 1990.

The early 1990s also saw Dave's work expand into spatial ecology, adding dispersal-based considerations to coexistence theory. Among his most cited papers is "Competition and biodiversity in spatially structured habitats", published in *Ecology* in 1994, where Dave showed that the coexistence of many species could be generated by a simple tradeoff between a species' ability to displace others versus how quickly it could colonize open sites. This was extended into another classic paper, published in *Nature* the same year, arguing that such tradeoffs may produce 'extinction debt', or the time-delayed extinction of dominant competitors in fragmented landscapes due to their inability to re-colonize patches. This work would culminate in a third Princeton Monograph, Spatial Ecology, edited with Peter Kareiva in 1997, which I think to this day is one of the clearest expositions of the contributions of spatial dynamics to community structure.

Cedar Creek experienced a severe drought in 1988. Among the communities affected were experimental plots of differential nitrogen addition established by Dave in 1982 that had diverged in species richness. In what he would describe as a series of serendipitous insights in the years that followed, Dave was able to show that, contrary to Robert May's classic theoretical treatment, more diverse plant communities were more stable - that is, more resistant to drought impacts and able to recover more quickly afterward. Published in *Nature* in 1994 with John Downing, the study was to be the first offensive in what would become the "biodiversity wars", with Dave as a leading proponent that species richness was not simply a function of the environment but a driver of function itself. In a series of grand experiments at Cedar Creek that followed, Dave and collaborators would publish several classic papers examining the effects of plant species and functional group richness on productivity, stability, and invasibility, all of which generated significant heat both inside and outside the literature that spilled over into the public arena. For those of us trained in this era, it is difficult to exaggerate how much this debate dominated grad student seminars and conference proceedings. Biodiversity experiments became 'all the rage', copied around the world and particularly in Europe, and accompanied by an explosion of theoretical research, some by Dave himself, revisiting old niche-based concepts in the new light of ecosystem functioning. Dave would write several popular syntheses during this time, including his MacArthur Award Lecture in Ecology in 1999 and a fourth Princeton monograph in 2002 with Ann Kinzig and Steve Pacala, The Functional Consequences of Biodiversity. Although the heat of the debate has largely dissipated, textbooks now routinely carry another of Dave's iconic figures, the saturating diversity-function curve, a testament to his influence in the biodiversity-ecosystem functioning era.

Dave's most recent work involves agricultural sustainability, biodiversity conservation, and renewable energy through the use of biofuels, using biodiversity as a tool for managing ecosystems in the face of strong energy demands and climate change. As Regents Professor

and McKnight Presidential Chair in Ecology at the University of Minnesota, director of the Cedar Creek Ecosystem Science Reserve LTER, and professor at the Bren School of Environmental Science and Management at UC Santa Barbara, Dave is working with collaborators on a global scale to forecast future human demands for food and fuel, and how those demands will impact land use, global carbon budgets, and conservation. He also continues to challenge accepted ideas about fundamental ecological processes, including a recent paper in *The American Naturalist* suggesting a "universal trade-off" surface for plants and animals across biogeographical realms.

Looking back on these achievements, it is hardly surprising that Dave is among the most highly cited environmental scientists of all time, or that he has been honored with some of the world's most prestigious scientific awards, including a Guggenheim Fellowship, Cooper and MacArthur Awards from the Ecological Society of America, the Centennial Award from the Botanical Society of America, a Pew Scholarship in Conservation Biology, the Princeton Environmental Prize, the International Prize for Biology from the Japanese Society for the Promotion of Science, and the A. H. Heineken Prize for Environmental Sciences. He is an elected Fellow of the American Association for the Advancement of Science, the American Academy of Arts and Science, and the US National Academy of Sciences, all rare honors and a testament to the reach of his science well beyond ecology.

I finally want to reflect on what our first two Humboldt medal winners have in common, despite their polarized viewpoints on so many themes in vegetation ecology. The obvious commonality, and one that I think speaks to how much vegetation science has progressed over the past century, is that both Dave and Phil are at their core experimentalists. Every significant theoretical advance made by both men has been subject to their own extensive experimental trials, and I would not be the first person to suggest that the debates that persist could be due in large part to differences in how plant communities are structured in calcareous pasture versus the Minnesota sand plain. But even more significant to our science is that Dave and Phil epitomize what it means to have a career that matters - both have forced others to have an opinion about their work, to take a side, to test claims with their own experiments and decide for themselves whether the world is structured according to resource ratios and local niches or CSR theory and infrequent disturbance. The lesson to young ecologists should be: at the end of the day, have you stuck your neck out enough? How bold is your claim? Dave's career, like Phil's, has involved a series of debates with very high stakes at the core of environmental sustainability. Perhaps more than anyone, Dave has brought what were once academic disagreements into the forefront of the modern environmental movement. I can think of no higher achievement for an ecologist in our era.

Please join me, on behalf of the IAVS Awards Committee, in recognizing David Tilman as the 2013 recipient of the Alexander von Humboldt Medal.