UNDERSTANDING PLANT ECOLOGY

An interview with David Tilman, 2014 Balzan Prizewinner for Basic/Applied Plant Ecology, by Charles Godfray, Member of the General Prize Committee

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Charles Godfray: My name is Charles Godfray and I'm in conversation with David Tilman, who is visiting Oxford at the moment. David, welcome.

David Tilman: Thank you. It's a pleasure to be here.

C.G.: David was the winner of the Balzan Prize for Plant Ecology in 2014. Dave, throughout your career you've worked on very many things, but am I right that one of the themes that has run through your career is the relationship between biodiversity and different ecological and ecosystem functions?

D.T.: Absolutely. Biological diversity – the ecological and genetic diversity within each ecosystem on earth – is one of the most unique features of life on earth, and it's amazing that the world has come to have so many species. With human impacts threatening species with extinction, and causing extinctions at an unprecedented rate in the last century or so, a question arose twenty-five or thirty years ago: does it matter? What are the impacts of losing diversity, of simplifying ecosystems, and how does it affect how they function? That question intrigued me and my students and I have been pursuing it in a variety of ways for the last three decades.

C.G.: It's always struck me that when I started as an animal ecologist, animal ecology was easy, because animals were mobile and populations mixed. In contrast plant ecology was hard. Plants stayed in one place; it mattered who you were, who you happened to be beside, and it was difficult to model. But as the mathematics has become more tractable, plants have become a better system for answering hard questions in ecology than animals.

D.T.: Actually, it's precisely because they sit still, and therefore it's much easier in field experiments to know how abundant they are, how they're changing through time, which organism is interacting with which. On the animal side, all my degrees are in zoology so I understand it, the dilemma is that the ecological mechanisms often come down to behaviors, which are harder to quantify. Behaviors can be quite variable, but there's a certain mean tendency that organisms have, whereas the «behaviors» of plants are things such as how much root do they create, how tall is a plant, how many leaves do they have, how many seeds do they put out, how are they dispersed. Those are more readily quantified traits and more easily put into logical mathematical structures.

C.G.: And you of course have worked both on experiments and theory. I guess I first started reading your work when you were writing your very influential Princeton monographs. Are you a theorist who's become an experimentalist, or the other way around?

D.T.: I was probably a theorist who became an experimentalist. Theory was what drew me into ecology to begin with. But I had wonderful mentors as an undergraduate and a graduate student. They insisted that, although theory can be mathematically elegant, it's only relevant if it actually applies to nature. So I was always challenged to show them why this mattered.

C.G.: I was going to ask you about the mid-twentieth century thinkers who most influenced you. Am I right that Robert MacArthur from Princeton was one?

D.T.: Robert MacArthur, G. Evelyn Hutchinson from Yale was a big influence, Bob Paine from Washington, Joe Connell from Santa Barbara.

C.G.: All animal ecologists, which is interesting.

D.T.: All my degrees are in zoology. Although interested in plants, I chose a zoology program for my degrees because, at least at that time, zoologists were the ones who were mechanistic. They had a strong, or a growing, theoretical basis, and I was excited by ecology because I saw the opportunity and the need to have a more mechanistic look at how species interacted with each other and their environment, to have the potential ability to predict how ecosystems would respond to various changes. And at that time, I was concerned about human impacts. I grew up on the edge of Lake Michigan, which is a very large body of water, one of the Great Lakes. I'd seen that it had become quite polluted; I saw the change in the algae in the lake. I actually did my PhD on algae from Lake Michigan, and how they responded to nutrient loading, but tried to make it a predictive model, with the traits of each of these species. I quantified those traits, and then used that in what I call resource competition theory, to predict who would win and under what kinds of conditions, and when they should coexist. I then tested that both in the laboratory and in Lake Michigan, and saw a pretty good confluence of results.

C.G.: Then there is the famous R* [r-star] result. Now, is it possible to summarise that in a couple of sentences?

D.T.: R*: «R» refers to resource, and R* refers to how low a population of a species can reduce its limiting resource when that population has reached a level density and is no longer growing. If one resource were to limit many species, whichever species could drive that resource to the lowest level – to the lowest R* – in theory should win. When we tested that in the laboratory where we had just one limiting resource, that did happen – that was on algae. Later we tested the same idea on perennial prairie plants. We grew them in the field, in monocultures and mixtures, and again we found that when we created soils in which nitrogen was the most limiting nutrient (by adding other nutrients so they weren't limiting), the species which could drive nitrate to the lowest level in monoculture that had the lowest R*, was the one which won in competition.

C.G.: I remember reading that work, and as an animal ecologist being jealous, because you understood the relatively small number of limiting nutrients from plants. You could do both the theory and the mechanistic understanding of why that was happening.

D.T.: The dilemma with animals is that, at least for herbivores, plants are their resources. But there are about as many or often more species of plants than there are herbivores eating them, so it becomes much more complex.

C.G.: You're also famous for the very long-term series of field studies you've done at Cedar Creek, in Northern Minnesota. Could you describe exactly what the Cedar Creek facility is? How did it start?

D.T.: It started with a very generous family foundation that donated enough money in 1950 to buy twenty-seven square kilometres of land, a nine-square-mile piece of land. It was chosen because one of the leading botanists of the era, who was at Minnesota, had seen an incredible array of different kinds of ecosystems at that site. It's on a sand plain. Oak savannah is one of the dominant vegetation types, with patches of prairie, but it also has mixed hardwood stands with maple and bass wood. It has stands of white pine, red pine, jack pine, and a black spruce stand. It has quaking bogs; and contains three lakes within the boundaries of our land. When I arrived in Minnesota, a more senior ecologist took me under his wing and said, «You've got to come see this place». I fell in love with it, and started working there.

C.G.: I'm going to ask you about the science you've been doing at Cedar Creek, but am I right that a veritable army of undergraduates descends on the study site each summer to take multiple measurements?

D.T.: Yes, we've grown a lot in the last forty years. When I first arrived, there were maybe two undergraduates doing work there – it was a pretty lonely site. But now, we have between forty-five and seventy undergraduates who live on site every summer. We have housing for all of them and housing for postdocs and graduate students as well. There is some housing for visiting faculty, and we have a full-time staff that is there year-round. But the majority of the action happens in the summer, when all the plants are growing, and the insects are out. We have experiments on bison now. Wolves have come back, and repopulated our lands. We have set up camera traps to follow what wolves are doing and what they're eating. Turkeys have reintroduced themselves, and they're in high abundances. It's really an amazing natural place. There are also bears, some bobcat, mink, otter... it's amazing.

C.G.: Extraordinary! You've done a huge number of experiments there over the years, but the one that everyone probably knows about is where you manipulated biodiversity, and measured a variety of different ecosystem functions. Could you just remind me when that started, and some of the important results that you found?

D.T.: We planted it in 1994. We started to prepare the site in 1993. We had a paper that we were sending off to *Nature*, with results from earlier work that suggested that more diverse ecosystems were more stable, which went contrary to the then generally accepted wisdom of ecology. The results were supportive of this alternative idea, that greater diversity led to greater stability. But there are many reasons why someone could object to them. We ourselves tried to test everything we could to get rid of all the objections we had when we first saw these results. Knowing this paper was coming out, and knowing that reasonable scholars would object to it, we decided to set up an experiment at the same time that we knew this result, because we thought that if this really is happening, it was incredibly important for us to understand it at the level of ecological mechanism. Whether we supported or refuted the idea, the experiment would be of great interest to us and to the rest of the field. So we set up an experiment, planted out several hundred plots, nine by nine metres in size, each planted out with one species, or two, or four, or eight, or sixteen, and each plot having randomly chosen species. We randomized the whole experiment, and that allowed us to look at – on average – how ecosystems function when they have one plant species, or two, or four, or eight, or sixteen.

C.G.: When you say «function», can you just explain what you mean by that term in this context?

D.T.: That's a really good question. We measured many different things that happened in these ecosystems. One major function of an ecosystem is how productive it is, how much biomass it can produce every year. We found a surprisingly large effect of plant diversity on how productive an ecosystem is. It took three years for the plants to grow and become mature prairie plants. Once they were mature, the most diverse plots with sixteen species were about 80% more productive than the average species growing by itself in monoculture. Now, twenty-seven years later, the most productive plots are 200-240% more productive, depending on the year, than the average species growing in monoculture. So not only was productivity, this one function, highly dependent on diversity, but this effect has grown through time. One of the mysteries that we've been trying to understand lately is why it grew through time. Some of the Balzan scholars whom I've been able to support with my Prize funds – especially George Furry and Yi Yang, one a grad student and one a postdoc – have done a lot of work on this. The major bottom line to the story is that there are feedback effects of high productivity which increase the quality and quantity of organic matter that gets into the soil, which makes the soil have more carbon as well as more nitrogen, and so it becomes much more fertile through time. So high diversity has this feedback effect which makes the system even more productive. So we actually had an exponential increase in the amount of carbon in the soil and the amount of nitrogen in the soil for the first twenty years of this experiment. We don't know what'll happen next. It can't go on like that forever, but there's been an incredibly important feedback effect that we never could have imagined at the start.

C.G.: Is it the biodiversity *per se* that changes the quality and quantity of the organic matter that then feeds back to increase the productivity?

D.T.: Yes, it does. The quality in some sense is lower in order for microbes to consume it. Critical are the plants that do best when they're competing with many other species, and then become the dominant species; these are perennial grasses with what's called a C_4 carbon fixation pathway. They are very efficient at using nitrogen, and are good competitors because they put about three-fourths of their biomass into roots. Then the roots grow, and when autumn comes they shrink back to their long-term persistent parts while the fine roots die becoming organic matter. But this organic matter has carbon that doesn't decompose very quickly and that holds on to the nitrogen. That builds up through time, and the soils become richer and richer, with more humus, more organic matter in them, which in the long term leads to this feedback effect on fertility.

C.G.: It's the heterogeneity of the different carbon sources, the different structures of the organic material in the soil that is significant, isn't it?

D.T.: We've had some postdocs and visitors working on that issue, and they find that heterogeneity influences which microbes are dominant, but all the steps between that heterogeneity and what's happening to carbon accumulation isn't yet clear.

C.G.: Are you including studies of the microbial flora in your work?

D.T.: Yes. When we set this up, we realized there would not be many other experiments like this, and so our goal was to make the plots large enough and to make them open for collaborators. We've had collaborators from many different countries around the world, as well as many different universities in the United States. They come in and we give them all the data we've collected relevant for what they wanted to do, and it has allowed us to gain incredibly deep knowledge of these prairie grassland ecosystems and of the role that plant diversity plays in ecosystem stability. And the stability of an ecosystem measures how it responds when there are perturbations. A more stable system doesn't change as much when there is a alteration in this environment. Because we have twenty-some years of data now, year by year by year, we can look at what happens to each species in each plot as well as what happens to their total biomass, and the total production of each of these grassland systems. For a farmer, you might call it hay. But ecologists just call it production. It's much more stable. It doesn't change very much year to year when there are many species growing together. But when there are few species, it fluctuates a lot more in response to climate and other events. So there's greater stability and greater productivity at greater diversity. The greater diversity of plants leads to a greater diversity of insects. As there's higher and higher plant diversity, not only are there more species of insects, but the whole mixture of that insect community changes, with a greater dominance by predatory insects and parasitoids, and a lower dominance by the plant-eating herbivorous insects.

C.G.: As someone with a special affection for these creatures I knew that at some stage in your career, David, you would realize that parasitoids were the most interesting of all creatures! As you know, part of the Balzan Prize is a research project. Am I right that your Balzan research project involves Cedar Creek?

D.T.: Yes, it's almost solely at Cedar Creek. There is one exception, which was also dealing with diversity, but in a broader global sense.

C.G.: I know the project isn't finished yet, but could you give us an update on where it is and what the results are as they're coming in?

D.T.: My goal for the Balzan Prize, which was also the Balzan goal, was to use these funds to support younger scholars. In particular, so far we have supported PhD students and postdocs with these funds. There have been three major areas in which these scholars have been doing their work. One was on just why it is that there are so many species, or how these things compete with each other and coexist. Adam Clark, who did his PhD with me and is now a postdoctoral fellow in Leipzig, Germany, did some very important work. He looked at how each of these species grew in their monocultures in the biodiversity experiment, and used that to discover a three-way trade-off that these species face in terms of how a species becomes better at doing one thing when it's worse at doing something else. You discover that three axes are needed to describe the trade-off. This trade-off, defined by the observed traits, basically formed a very flat plane with the species lying very, very close to that plane. He then found that if the points representing different species were taken off this plane, when he used those traits in a mathematical model of how they would compete with each other, he would find that these species would coexist. This is what happens in the field. He found that when more species were taken off this trade-off plane, the system would be more productive, and he was able to predict how abundant each species would be. Although it's not a perfect prediction, there's a very strong correlation between what we actually see in each plot for how abundant each species is and what is predicted from this model based not upon observing and competing, but only on looking at how they respond in monoculture. So that was really important work, and it really gave us a much deeper understanding of what is going on and why in the biodiversity experiment.

Jane Catford, who is now a new faculty member at King's College in London, started working at Cedar Creek as a postdoc, but is now coming back as a collaborator. I can't claim too much of her in the sense that she doesn't need much money; we help support her field work when she comes, but her salary is paid elsewhere. She has also done very important work on the role that diversity and composition have in limiting the ability of other species to invade into a plot. We've also done some theory together on that. The other area I already mentioned briefly earlier is trying to understand the various feedback effects in these ecosystems which are causing the larger than expected effects of diversity on these ecosystems. Why is it that more diverse systems are so much more productive? Why are they more stable? Why do insect communities shift and so on? We don't have answers for all these questions yet, but the work so far has mainly focused on soils, and Yi Yang and George Furey have done a lot of interesting work on the mechanism involved in these feedback effects. George discovered things which I would never have imagined. Not only were these soils becoming more fertile in terms of nitrogen, but calcium, phosphorus and other micro-nutrients are being transported from the deeper soil to the soil surface. These elements are being moved into these upper, more organic rich soils, so they actually become more fertile in almost every single element the plants have to have because of these feedback effects. The pH is changing, becoming less acidic. It's really been surprising to us. He's gotten soil scientists in the next building very excited because they had no idea that diversity really mattered that much in soil development. They had no idea that these soils could develop as quickly as they have under high diversity conditions.

C.G.: That sounds really exciting. I'm going to finish by asking a question. You're well known as a theoretical ecologist, as a plant ecologist, but in the last ten years you've written a lot on much broader topics: on biofuel policy, on food security – topics that really impinge on a much broader array of different issues beyond just ecology. What brought you into this world, and how do you divide your time between your fundamental science and this really important applied work?

D.T.: I can barely tell the difference between these questions. My initial interest in ecology wasn't just a love of nature which I had, it was really a concern about nature. I was concerned by what I had seen as a child on the edge of Lake Michigan, and wanted to understand what was causing it and therefore how to overcome it and reverse it. I was intrigued by why the world had so many species, but also concerned about why we were losing them. So these issues are all tied together. Food is one of the major ways that humans affect the environment. There are 7.6 or so billion people now, most eating an adequate diet, many of us eating a more than adequate diet, and whenever seven-and-a-half billion organisms do something, when they're the size of a human, they're a huge impact. So we're having global impacts in ways we didn't have even fifty or one hundred years ago. My concern for the functioning of ecosystems, for the services they provide to society relates to my concern that humanity is able to persist on earth for the long term, and that humans have the right to have as high a quality of life ten thousand years from now as we have right now. I think those concerns come because I know that nature and how we treat nature is going to be critical to having that kind of quality of life in the long term for us on earth. So my work on agriculture, on biofuels, is all motivated by trying to find solutions to these problems, to trying to find a way for seven and a half billion of us to live more sustainably, such that nature and humans, which have to coexist together – we need nature to live – can be doing well on earth far into the future.

C.G.: Dave, as always it's a pleasure to chat to you, and so thank you very much for this very interesting conversation.

D.T.: My pleasure, Charles.