Causes, Consequences and Conservation of Biodiversity

David Tilman

It is a pleasure to be here. The ceremony yesterday was a joy.

The most unique feature of life is the amazing number of different shapes, types and sizes of plants and animals that coexist with each other on Earth. Indeed, there are at least 5 million, and perhaps as many as 10 million, different species on Earth. The existence of this biological diversity, or "biodiversity," has raised three major scientific questions. First, why is life so diverse? Second, does biodiversity matter, that is do changes in biodiversity impact the productivity, stability and other ways that ecosystems function? Third, why and how are human actions leading to the loss of biodiversity, and how might such losses be minimized or prevented?

Causes of Coexistence

The first of these questions is what attracted me to ecology. In the early 1970's, one of the major mysteries of ecology was how so many different species could compete with each other and coexist. This was called "Hutchinson's Paradox," since G. Evelyn Hutchinson had pointed out that the well-mixed waters of lakes and oceans often contained 100's of competing species of algae, but that ecological theory predicted that the single best competitor should outcompete all other species in such well-mixed and homogeneous habitats.

This paradox highlighted the state of the discipline at that time. Ecology was mainly an observational discipline then. Mathematical theory and experiments, a combination that had led to rapid advances in physics and chemistry, were rare in ecology. I loved both mathematics and the power of experiments. Two young ecology faculty members at the University of Michigan, Steve Hubbell and John Vandermeer, inspired me to pursue Ph. D. research that combined experiments and mathematical theory in ecology. I and many others at that time felt that ecology needed to take this step toward maturation. The early 1970's were also a time of increased awareness of environmental problems. I felt that ecology had to become a mechanistic and predictive science for it to adequately address such problems.

I was attracted to lakes and the effects of nutrient pollution on them. In many lakes, the growth rates of diatoms, which are a type of algae that makes its cell walls from silicon, are limited by concentrations of phosphate and silicate. Work I did with

Susan Kilham and Peter Kilham showed that the resource requirements of two dominant diatom species had evidence of a tradeoff. One species had a low requirement for phosphate but a high requirement for silicate. The other had a high requirement for phosphate but a low requirement for silicate. Based on some early theory of competition for two limiting resources, we realized that this type of a tradeoff between these two species might allow them to coexist in habitats that had a predicted range of phosphate to silicate ratios. In a laboratory study across about 80 different sets of environmental conditions, including different ratios of available phosphate to available silicate, we found that the theory correctly predicted the phosphate to silicate ratios for which each species won in competition and displaced its competitor, and for which the two species stably coexisted.

Next we looked at how the abundances of these two species of algae in Lake Michigan changed along a 50 km long nutrient gradient from low to high ratios of phosphate to silicate. I had grown up on the edge of Lake Michigan, and I had watched its water quality degrade from nutrient pollution. So, my work on algae was also motivated by my concern for the amazingly beautiful great lake that I loved. We found that the resource requirements we had measured in the laboratory for these two species predicted, in broad outline, where these species coexisted in Lake Michigan, and how their abundances were impacted by phosphate pollution.

The paper came out in the journal *Science* in 1976 (1) was among the first in ecology where someone had shown that by an understanding the mechanisms of interaction, the outcome of those interactions could be predicted in advance. However, at that time it was not at all clear if such mechanisms and seeming predictive ability were unique to the two species we had happened to study, or, alternatively, if similar processes might explain patterns in species abundances and the coexistence of the millions of species inhabiting Earth.

While continuing to do doing additional experiments on various species of algae, I also began to expand and generalize the theory of resource competition, which resulted in my first book (2), published in 1982. The book applied the ideas of interspecific tradeoffs and mechanisms of competition for resources to terrestrial plants, insects, and vertebrates. It predicted how patterns in species abundances and biodiversity for each of these types of organisms should change along major environmental gradients. Such predictions were compared to data available from some well-studied ecosystems, especially from the Park Grass Experiment at Rothamsted, England.

I sent G. Evelyn Hutchinson a draft of my first book before it was published, and he wrote back and said something like, 'David, this is all well and interesting, but why isn't there some species that disobeys these trade-offs? Shouldn't something be able to evolve and be better than this?' Hutchinson's question was incredibly insightful and motivating. I have pondered it and pursued it ever since.

A major conclusion from this book, which was bolstered by analyses in a second book that appeared in 1988 (3), was that the ability of many different competing species to coexist with each other was dependent on interspecific tradeoffs. Put simply, there seemed to be only one logically viable theoretical explanation for why the earth had so many competing and coexisting species. Coexistence of multiple species was predicted to require evolutionarily unavoidable tradeoffs. Motivated by Huchinson, I realized that an evolutionarily unavoidable tradeoff results if and only if a mutation or genetic recombination that causes an individual to better deal with some limiting aspect of its environment necessarily made that individual less able to deal with some other limiting aspects of its environment.

By this time I had switched from working on diatoms in lakes to studying perennial plant species of the native prairie grasslands and savannas that cover the middle of North America. A variety of our field experiments showed that, despite the great complexity of perennial plants relative to single celled diatoms, the same basic theory correctly predicted the outcome of competition among perennial prairie plant species. Such species, we found were limited by and had tradeoffs in their abilities to compete for soil nitrate versus light. We also found that another factor, the ability of seeds to disperse into open sites, was involved in these tradeoffs.

Habitat Destruction and Extinction

The tradeoff between dispersal ability and the ability to compete for a limiting nutrient led to new theory, and to two unexpected theoretical predictions. Species become better competitors for a limiting soil nutrient, such as nitrate, by having a higher proportion of their biomass in roots, but in so doing they unavoidably have proportionately less biomass in leaves, stems or seed. Since it takes leaves and stems to capture light and provide roots with the energy they need to survive, the main tradeoff the prairie perennials faced was between roots and seeds. Surprisingly, a simple mathematical model of competition predicted that a potentially unlimited number of species could coexist in a homogeneous but spatial habitat solely because of a competition versus dispersal tradeoff.

In collaboration with my colleague Clarence Lehmann, who honors me with his presence here today, and Robert May, an earlier recipient of a Balzan prize, we next used this model to predict how habitat destruction would impact extinction. We found that the model predicted that there need be no immediate extinctions caused by habitat destruction, but rather that even moderate habitat destruction caused time-delayed but deterministic extinction. More surprisingly we found that the species that were predicted to go extinct were the very species that were the best nutrient competitors and thus the most abundant species in the fragments saved from destruction. We suggested that global habitat destruction might thus be threatening the most efficient plant species on earth with eventual extinction.

Biodiversity and Ecosystem Functioning

After spending two decades studying how so many species could coexist with each other across the ecosystems of earth, two events conspired to focus my work on a different aspect of biodiversity. The first event was a small scientific meeting in Bayreuth, Germany, where we discussed the recently proposed idea that the number of species in an ecosystem might influence how an ecosystem functions, including the possibility that greater biodiversity should lead to greater ecosystem stability. Those discussions led me to evaluate, in collaboration with John Downing, how a major drought – the worst drought of the past 50 years for the region in which I was working – had impacted ecosystem stability. Analysis of data from more than 200 grassland plots showed that plots with many plant species (greater plant biodiversity) before the drought were more resistant to the drought and recovered from it more rapidly. This was the first rigorous evidence lending credence to the biodiversity and ecosystem functioning hypothesis (4).

I knew that this finding would be met with considerable skepticism and that only a well-designed field experiment that directly manipulated plant biodiversity could address the questions that would be raised by our drought study. By the time our drought paper appeared my colleagues and I had established the first plant biodiversity field experiment. Shortly after that we began using models of multi-species competition and coexistence to determine how changes in the number of coexisting species were predicted to impact ecosystem productivity, stability and susceptibility to invasion by exotic species. Within a decade more than a hundred other biodiversity experiments had been performed on a wide range of organisms by researchers from around the world.

Our biodiversity experiment and the vast majority of the other biodiversity experiments have shown that the number of plant species in an ecosystem is a major determinant of ecosystem productivity, stability and invasibility. In particular, greater plant biodiversity can lead to a doubling, or more, of ecosystem productivity, to greater ecosystem stability, to greater retention of limiting nutrients, and to much lower rates of invasion by exotic species (5).

Consequences of Biodiversity Loss

In 1990, few academic ecologists thought that the loss of biodiversity would have much of an affect on ecosystem functioning. However because of all the experiments that have been done on this issue, there is now perhaps more rigorous support for the effects of the loss of biodiversity on ecosystem processes than there is for any other issue.

Why does biodiversity matter? The basic answer is this. Biodiversity exists because of the interspecific tradeoffs that allow so many interacting species to coexist with each other. Tradeoffs mean that each species becomes specialized on doing something thing very efficiently, but at a cost. Specialization necessarily means that each species does many other things poorly. When species interact with each other, it is the strength of each species that defines the role it plays in an ecosystem. The weaknesses of a given species become irrelevant to ecosystem functioning when many other species are present. In essence, in the open and competitive interactions of nature, each additional species adds to the overall efficiency of the ecosystem, making it more productive and more stable. This is a simple verbal description of the predictions of mathematical models in which species coexist because of interspecific tradeoffs.

The most recent work that we have done shows how such effects of biodiversity are not limited solely to competitive interactions. For instance, we have studied the effect of plant biodiversity on the rest of the food chain -- such as the 500 or so species of insects that live in the plots of our biodiversity experiment. This work has shown that greater plant biodiversity led to greater insect diversity, and had an unexpected impact on the insect communities. When plant diversity was low, the insect community was dominated by insect species that ate the plant species, which are called herbivores. However, at high plant diversity, insects that were predators dominated the insect community. These insect predators kept the herbivorous insects at low levels, further increasing the positive effects of plant diversity on ecosystem productivity.

Three decades ago almost all ecologists would have told you that the most important variables determining ecosystem productivity were soil fertility, climate, and herbivory. At the same site where we have our biodiversity experiment, we also have experiments that manipulate soil fertility by fertilization, that change climate via warming and water removal or addition, and that manipulate the abundances of herbivores. When we compared the effects of these and other variables on ecosystem productivity with the effects of changes in plant biodiversity, we found that the effects of biodiversity were as large or larger than the effects of any of these other variables. Biodiversity is one of the key variables determining how ecosystem function.

Universal Tradeoffs

Although the results of numerous biodiversity experiments are consistent with the hypothesis that all organisms face unavoidable tradeoffs, this hypothesis raises its own paradox, much like the question that Hutchinson asked me. Darwin proposed that natural selection, by favoring heritable traits that were beneficial, should lead to the evolution of new species that were superior to existing species, and that these superior species, if they migrated to a new continent, would competitively displace the established species when they invaded.

Paleontologists have found that the number of species on Earth has been increasing in a roughly linear manner for hundreds of millions of years. This means that when speciation led to the appearance of a new species on Earth, on average, each new species did not cause an existing species to go extinct. If that had happened, diversity would have leveled off. Instead, each new species coexisted with the species that were there before. This pattern would seem to question the traditional concept of the process of evolution: are new species truly better if they do not displace existing species?

The fossil record also provides a different way to answer this question. It documents the dynamics of many major events, called biogeographic interchanges, when species that evolved in one realm have invaded a new region during the past 500 million years. Analyses of these interchanges fail to support the conjecture that newly evolved species were truly superior to established species. In none of these interchanges did the invasion of species that had evolved in one realm lead to the extinction of species in the new realm. Rather, the established and invading species consistently coexisted for periods of millions years. Such long-term coexistence is predicted to only occur if the established and invading species had all long been bound to a single, universal tradeoff curve (6).

The deeper meaning of this finding is that the evolution of new species has, for the past half a billion years, been more about evolution while bound to an unavoidable tradeoff surface than about any species gaining any traits without also experiencing concomitant costs. This tradeoff is the likely explanation for why almost all newly evolved species have coexisted with established species rather than outcompeting them.

Biodiversity Ethics

Given all that we now know about the causes of the Earth's great biodiversity, about how human actions are endangering biodiversity, and about the effects of the loss of biodiversity on ecosystem functioning, it should be clear that the preservation, conservation and restoration of biodiversity should be a high global priority.

Biodiversity is the "economic capital" of nature, the ecological endowment upon which human life depends. The world's marine and terrestrial ecosystems remove and store almost two-thirds of all the greenhouse gasses that we release by burning fossil fuels. We depend on thousands of species for our food and fiber. We depend on innumerable species for ecosystem services such as purification of water, decomposition of wastes, and the production of the fertile soils. The wild plants and microbes of the Earth's remaining ecosystems are the biodiversity from which we discover the majority of new medicines. We receive these services form nature for free, but only if we preserve biodiversity.

Human societies face tradeoffs. We have become the dominant force impacting ecosystems worldwide. Our impacts have outpaced our ethics. Our environmental and land-use ethics and laws were devised during an era when the human population, one-tenth its present size, tamed wilderness with ox and axe. Now, every ecosystem, and the fate of its biodiversity, is subject to the whims of society. The world needs an ethic that values the well-being of all future generations by preserving for them the greatest riches that the earth holds – its biodiversity.

Reference Notes

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Questions and Comments

Charles Godfray

Are there any questions from the audience? Marc, do you have one?

Marc Van Montagu

Don't you think that growth-promoting bacteria are also important for plants, that you also have then a much higher diversity of growth-promoting bacteria because the bacteria always goes in relation to species and that gives them hormones that help everybody? They are the mediator in what you observed.

David Tilman

Yes. We are working now with people who use wonderful modern molecular techniques, so they can identify the microbial biome, if you will, in the soil, and see how microbes respond to plant diversity, and try to understand what roles they're playing. So you ask a very important question. I have no reason to imagine anything other than the effects of biodiversity we see with plants happen with various bacteria and other elements of the food web. I think that in the next decade or so we should have lots of insights on this issue.

Charles Godfray

Another question from one of our science journalists.

Marco Ferrari

Thanks for the wonderful speech. If biodiversity means higher productivity, why in civilization, is the path of human civilization toward less biodiversity and less biodiverse agriculture?

David Tilman

Well, the simple answer is that much of what is produced when you talk about higher productivity is not edible. We don't eat grass ourselves. And we don't eat trees.

We tend to eat seeds of annual plants for some of our main crops. And in that regard, if you look within annual plants, such as wheat or other grains, there's good work now showing that having a diversity of genotypes actually leads to higher productivity than growing a single genotype. In crops that are hybridized, we put the genes inside the plant. Our hybrid plants have two different genes at every locus in their genome, and that diversity of genes actually lets those plants to be more productive than the lines that aren't hybridized.

So we use diversity in little ways right now in agriculture, but I think you ask a fundamental question that merits a lot more attention in agriculture. And that is, "How can we use diversity as a a tool to have agriculture be more sustainable and more productive. I don't have instant answers; we're at the beginning of these questions.

Charles Godfray

Thank you. Professor Brunori?

Maurizio Brunori

I have a short question. The struggle for food is a fundamental component of evolution and survival. I mean, at face value, would you say it sounds like a contradiction with evolutionary theory, unless there is something which is abundant in any event for all the species. Have you done some of these experiments under conditions in which the food – let's call it this way – of the different plants was limiting? Because that's the situation. When growing bacteria, if you have very little food, very little glucose, then there is the survival of one and the loss of the other. At face value it seems like a contradiction with Darwin's theory, but obviously it's not.

David Tilman

No, it's not a contradiction, but you ask a good question. In fact, one of the first criticisms of our experiment was that we did it on unusually nutrient-poor and therefore it wasn't relevant to the rest of the world. We did our work on sandy, low-nitrogen soils, and I defended myself by saying one third of the land surface has sandy soils. But a better answer is this - there are limiting factors for all organisms across the face of the world, and diversity can only exist when there are limiting factors. Because only when there are factors which limit fitness can many species coexist with each other. So coexistence depends not just on trade-offs, but on trade-offs for factors that limit fitness. Species have differentiated their use of nitrogen by time of year and climate as a result of their competitive interactions. So probably the same axes of differentiation that led to speciation cause multiple species to coexist.

Charles Godfray

Another question from the audience?

Member of the audience

I personally do think that GMO are a good opportunity for the future of agriculture. How about the relationship between the GMO and biodiversity?

David Tilman

Well, I also agree that GMOs are something which could be very important for letting us continue to produce food. The most serious problem that crop plants face are rapidly evolving diseases. Crop breeding goes on continually, with breeders trying to stay ahead of rapidly evolving diseases. What GMO allows us to do, among many other things, is to bring in genes from other kinds of grass than the ones we're growing, or maybe other kinds of plants, and in some cases other kinds of organisms that we couldn't bring in before. So I think in the long term, especially since we have a world where 60% of our calories only come from three species, we can't afford to lose any of these species. We need to keep them productive. I think it's going to be a very important tool. I would argue that some GMO were released too soon. They weren't used as wisely as they could have been, because we've had an evolution of herbicide resistance, evolution of resistance to *Bacillus thuringiensis* genes, and so on. We're losing important tools very, very quickly. We need these tools. We need to use them in a wise way that keeps them available for the long term. Thank you.

Charles Godfray

Dave, if I can ask you a question. Most of your experimental work has been on relatively short-lived perennial and annuals. Do you think if you apply your theory to longer-lived plants, especially trees, it will need to be applied in a different way? Will there be a greater role for random stochastic effects?

David Tilman

If I were to speak tongue in cheek, I might assert that everything we've found on our plants applies to every other organism in the world. However, clearly much more work will be needed to find out if, or how the responses of trees might differ from perennial grasses. I should mention, though, that I have never done any work on annuals. All of these prairie plants are long-lived perennials that may live fifty or a hundred years – perhaps as long as some tropical trees live.

Charles Godfray

Ok, so is there a final question? In that case, will you join me in thanking Dave for a fabulous presentation.

Enrico Decleva

I thank Charles Godfray very much for his extensive presentation, and Professor Tilman for his important speech. I don't know if it is correct to note it, but both of the winners that we have just heard, Professor Sullivan and Professor Tilman, make a great use of their hands. It's a signal, I believe, of the passion they put into their work and their research. It's important to have passion in research. Thank you very much.