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Source: BioScience, 55(10) : 828-831

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2005)055[0828:SALPFE]2.0.CO;2

Simon A. Levin's Passion for Ecology

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Simon A. Levin, professor in the Department of Ecology and Evolutionary Biology at Princeton University, was awarded the Kyoto Prize in 2005 for "the establishment of the field of spatial ecology and the proposition of the biosphere as a 'complex adaptive system.'" In this interview, Oksana Hlodan, editor of ActionBioscience.org (an education resource of the American Institute of Biological Sciences), explores Levin's research interests and insights.

Hlodan: *You have been honored with the 2005 Kyoto Prize in Basic Sciences for your contributions to environmental science. What do you consider your most fundamental contributions?*

Levin: My major interests, and I hope my major contributions, have been in recognizing that the dynamics of ecological systems take place on many different scales simultaneously, and the great challenges for us are to understand how processes change across scales, how our perspective on systems affects the dynamics that we see, and how processes on one scale relate to processes on other scales. That has involved utilizing whatever mathematical techniques I can muster to try to relate dynamics on different scales. I think that this recognition of processes on different scales and the development of mathematical methods to deal with them are what I would identify as my major interests and, hopefully, my contributions.

Simon A. Levin, 2005 Kyoto Prize winner.

Hlodan: *You were trained as a mathematician and worked in mathematical biology. How have you applied mathematics to studies of ecosystems?*

Levin: I was trained in mathematics, but from the beginning I had an interest in applying the mathematics—and, indeed, applying it to biological systems. I have worked on a variety of problems in biology. For almost 35 years my entire focus has been on ecological and evolutionary systems. This is a subject that has a rich history in terms of mathematical methods, going back to the great mathematician Vito Volterra. It really began to be developed in the '60s by people such as Robert MacArthur, bringing in a lot of people from mathematics and physics, like me, Robert May, George Oster at Berkeley, and others who recognized that in order to provide quantitative answers to systems that were so complex, in which phenomena were taking place on different scales, one had to use mathematical methods. We've seen the development of the field over the last 35 years. It relies a great deal on methods of applied mathematics, but there are novel mathematical techniques that are needed continually.

My approach has been to try to let the problems dictate the kind of mathematics used. For me it's a natural thing to think about these systems in quantitative terms, to recognize that the dynamical nature of these systems requires translation into mathematical models that can help to capture some of the essence. Nowadays, people can rely a great deal more on computer simulations, but 35 years ago that approach was much more limited. Today there is a partnership between computation and mathematical analysis, and I'm delighted to have been part of this transformation.

Hlodan: *Your paper "The Problem of Pattern and Scale in Ecology," published in* Ecology, *was the most cited paper in its field in the 1990s. Why was this paper so significant?*

Levin: I feel that I was fortunate enough to be in the right place at the right time. There are many people who have been thinking about issues of how to relate phenomena across different scales and the importance of the perspective that one imposes on the system. Apparently my paper hit a resonant [note] with lots of different people. It's been very rewarding to me because these are people coming from a variety of perspectives. I hope it's a readable paper that translates somewhat sophisticated mathematical concepts into terms that field biologists can understand. Basically, I think, coming into ecology as a mathematician, I began my career by listening, and hopefully listening well, to the problems we're confronting, and I was able to put these thoughts together into a framework that people found useful. I was delighted first of all to write that paper, because it allowed me to tie together things that I was thinking about a lot, and especially delighted that it found such a broad sympathetic audience.

Hlodan: BioScience *published an article in April 2004 in which Gary E. Belovsky and colleagues suggested that ecologists often forget the past of their subject and so reinvent wheels. Do you agree with their view?*

Levin: Well, there's no question—that's true. It's not all bad, in that we sometimes have to go down the same paths again to learn for ourselves the importance of certain approaches and ideas. But if the point of that article is that people should become more aware of the literature, then I entirely agree. It's harder to do now than it was 60 years ago, or even 35 years ago when I first started working in the field, because the literature has exploded since then. Even with the best of intentions, none of us can keep up with the whole literature. The authors are certainly correct that we keep reinventing the wheel. We do have an obligation to at least try to find out, as early as we can, how what we do relates to what others have done.

Actually, this has always been a fascination for me.... I like to read about how people have approached similar problems in other disciplines—developmental biology, economics, social systems, ecology, as well as physical systems—namely, how do systems become assembled from interactions among individual components, how does pattern form, what's the significance of pattern, and so on. We're all concerned with similar issues. I've learned a lot from what people have done in other disciplines. But I know that I also missed the work of others that would have made it easier for me to take the next step. I'm sure that the authors' point is well taken.

Hlodan: *The same authors point out that some ecologists do not see the pursuit of solutions to environmental problems as "real" science. Do you think that ecologists have a conflict between ecology as science and ecology as a basis for problem solving?*

Levin: Yes, but I think ecologists are better in that regard than people in most other disciplines. There is this conflict in any discipline—the conflict between the basic and the applied. Where I come from, mathematics, it is certainly the most extreme, in which the pursuit of pure research is valued above all else. The great mathematician G. H. Hardy, known in biology for the Hardy–Weinberg equilibrium, probably would have rolled over in his grave were he to learn how much influence his work has had in the applied context. We have this conflict imposed in part by the academic reward system and in part by the fact that most of us have been attracted to ecology because we're interested in understanding natural systems. However, we're also citizens of the world. We have to find ways both to advance basic science and to translate the science into terms that help to solve the great problems of the day. Ecologists, more than people in almost any other discipline, are in a unique position to do that.

I try to resolve the conflict for myself, sometimes by having a schizophrenic personality. I feel quite comfortable working on abstract things one day and then working on applications the next, and then finding ways to relate them. It's because my interest span is such that I have always enjoyed working on many things at the same time; I can switch back and forth easily between the pure and applied.

I think it's very important not only to recognize our obligation to do work that helps address problems society faces but also to recognize that there is a place for the basic work, for abstraction. Unless we get away from details of the particular problems we're working on, we don't develop any principles that allow us to address the next problem. There needs to be a place for applied work and basic work. It doesn't have to be the same people doing both, but we need to find ways to move between them.

I was drawn into ecology partly because I was interested in solving environmental problems. About 10 years after becoming an ecologist, I became the director of a center at Cornell, sponsored by the EPA [Environmental Protection Agency], whose mission was to help EPA administrators deal with applied problems. So I've always recognized this duality.

Hlodan: *Should scientists organize to increase their political influence, or should they retain academic detachment?*

Levin: Scientists are citizens. They have the right and obligation to become involved in the political process. Depending on the issue, scientists will have partnerships with others. But we all have an obligation to use our best knowledge and understanding of systems. For some problems a scientist will be in a better position to provide an expert opinion. We can use our best knowledge to try to guide the political process. The most prominent example today, perhaps, is the issue of stem cell research, but there is a whole list of issues related to the environment, such as climate change as well as antibiotic resistance, where it would be dereliction for a scientist not to translate his or her findings into the political debate. It doesn't necessarily mean organizing as a lobbying group. It can mean choosing the most effective way to get one's opinions and best judgment into the decisionmaking process.

The notion that science and policy must be separated, as some have suggested, is not valid. I was on the advisory committee for the restoration efforts of the Northwestern salmon. We wrote a paper in *Science* in 2004 on suggestions that somehow science and policy could be separated when it comes to making decisions on endangered species, which I think is nonsense. They can't be separated. Just as policymakers can't divorce their decisions from science, scientists cannot divorce their activities from policy implications. They have to enter into that arena if they're going to be responsible citizens.

Hlodan: *You and Giulio A. De Leo wrote a paper on environmental management in 1997. You posed a question in your conclusion: How do you "characterize the relationship between the structural features of ecosystems and measures of functionality?" Have you found part or all of the answer since then?*

Levin: I don't think we'll ever find all of the answer. It is one of the two essential questions in dealing not only with ecological systems but with any complex system. Five years before that paper, I edited a report for the National Science Foundation called *Mathematics and Biology: The Interface*, which examined the great challenges in mathematical biology. We identified this question as essential throughout biology. It's motivated by the fact that we usually observe only a snapshot of the system, a measurement, for example, of biodiversity. We don't observe the dynamics as easily. We'd like to infer the dynamics or something about the dynamics from snapshots. We'd like to be able to take reports like the Millennium Ecosystem Assessment and be able to infer...which ecological systems are most at risk and how important biodiversity is in terms of the robustness of those systems. We've made steps in that direction—I don't mean just me, I mean the field.

For example, there's been huge progress in understanding the relationship between biodiversity and ecosystem function. I single out the work of David Tilman in Minnesota and the work of Shahid Naeem and John Lawton in the [United Kingdom]. For example, my colleague Steve Pacala and I, along with others such as Tilman, Lawton, Naeem, Robert May, and Michel Loreau, have been concerned with theoretical approaches to understanding those relationships. Yes, I think that we have learned a lot about it. We've learned that the robustness or resilience of systems is fundamentally important. There is now an institution, the Resilience Alliance, that Brian Walker heads up, trying to understand what makes systems robust or resilient. All this emerged from a paper published 30 years ago by Buzz Holling.

I wrote a book in 1999 titled *Fragile Dominion* in which I explored this theme—the importance of static measures like heterogeneity and diversity, the redundancy in systems, the modularity of those systems, and the strength of feedback loops. These are all basically measures of the structure of systems, and I tried to summarize our understanding of how these structural features translate into functional properties. More recently, I have been interested in stoichiometry, whose study was pioneered by Robert Sterner and James Elser—that is, how organisms utilize crucial limiting nutrients such as carbon, nitrogen, and phosphorous and how the distribution of nutrient use within the ecosystem relates to functionality, et cetera. I think that the field of theoretical biology has made a lot of progress, but we have a lot more to do.

Hlodan: *Would your idea about a metacommunity model for the design of marine reserves be one of the answers?*

Levin: The notion of metacommunity design, and more generally the principles that underlie the design of reserves and the protection of endangered species, builds on the recognition that principles like modularity, redundancy, and heterogeneity are crucial to understanding what we need to do to preserve populations. These are general confusions from the science that has developed; but in any particular application, one has to do more than take things off the shelf, more than rely on generalities. So in that sense, it's exploring these issues.

Hlodan: *You've published papers with Paul Ehrlich. Do you hold similar views on sustainability issues?*

Levin: Paul and I see eye to eye on most things, but I know he wouldn't want his views represented as synonymous with mine, and vice versa. He and I are sure to come to different conclusions on some issues, but I always have the deepest respect for his views. We've been involved with a wonderful group called the Beijer International Institute in Stockholm, which brings together economists and ecologists. It is motivated by the need to develop a sustainable future for humanity. It would be hard for me to think of any place with these issues where Paul and I would disagree.

Hlodan: *In the June 2005 issue of* PloS Biology, *you and Ehrlich have called on scientists to model human cultural evolution. What model do you suggest and why?*

Levin: We're not suggesting a single model. It would be presumptuous. There have been lots of efforts, for example, by Luigi Cavalli-Sforza and Marcus Feldman, Robert Boyd and Peter Richerson, Samuel Bowles and Herbert Gintis, and others who have made substantial steps in that direction. We identify some of our own modeling efforts with Richard Durrett. Our main message is that the solutions to environmental problems are not to be found in ecological science alone. It has a great deal to do with society's will to address these problems, with the conflict between what individuals see as their own self-interests and what may be in the group's interests, the social norms that society imposes on individuals, some of which are not so good and lead to overconsumption, some of which are quite good and lead to altruistic behavior and behavior for the common good. In some situations we've been very successful in modifying social norms and the practices of society to achieve fairer, more equitable societies.

We need to understand the forces that have led to positive solutions or less attractive solutions. We need to understand what drives people's consumption patterns. More generally, we should understand the interrelationship between natural systems and the socioeconomic systems in which they're embedded. This will involve modeling in which we address questions such as the relationship between individual behaviors and environmental effects, what drives individual behaviors, and how individual behaviors relate to the practices of groups.

One problem of considerable current interest to Paul and me has to do with the frightening and rapid loss of the effectiveness of antibiotics due to antibiotic resistance, which to a large extent is driven by social practices of overusage of antibiotics and failure to follow best practices in hospital settings. There are a lot of different approaches to modeling that can be applied. Those approaches will need to span from the behaviors and incentives of individuals up to the collectives of which they are part and to the world community.

Hlodan: *Where do you see the most potential application of the science of ecology in the future?*

Levin: When it comes to the application of ecological principles, we know that these principles relate to the protection of our natural systems and the ecosystem services that we derive from them. Gretchen Daily, of Stanford University, has done wonderful work in helping to focus the efforts of lots of people on the issue of services that we are deriving from ecological systems, from biodiversity. That has led us all, including myself, Paul, and Gretchen, to work with economists to try to quantify these services, to work with complex systems people in trying to understand what preserves these services and, more generally, the robustness of complex adaptive systems.

But, in addition to thinking about ecological systems per se and the services we get from them, I see many other systems, which are basically ecological in character and require the same sort of thinking. I will single out two.

Epidemiology is one—the dynamics of infectious diseases pose serious problems that confront us, such as the evolution of the influenza virus, the evolution of HIV, the evolution of antibiotic resistance. You can tell by the words I've chosen to describe them that they are both an ecological problem, as Roy Anderson and Robert May have developed in their writings, and an evolutionary problem. I should mention too that part of this is understanding that how the immune system operates within an individual is an ecological problem where different clones compete with one another and so on.

The other area where ecological thinking is starting to have an impact and has a tremendous future is one that I've already mentioned, that is, the dynamics of social and cultural systems, in particular the evolution of social norms. I think virtually all systems are ecological systems, and all scientists ought to be paying attention to ecologists for what they can learn about their systems.

Hlodan: *What advice would you give a student thinking of ecology as a career?*

Levin: First of all I would say, "We need you, come on over to this exciting field!" Mainly, the advice I would give to any undergraduate or graduate student or anybody contemplating problems in ecology is to find problems about which you are passionate, about which you care, to which you want to have answers. Don't be driven by particular methodologies. Don't be restricted to particular problems unless you simply have to know the answers to them. Find something that you love doing and you will make a difference.

Hlodan: *Where do you intend to concentrate your academic efforts now?*

Levin: The word "concentrate" doesn't usually fit in the same box with the phrase "my academic interests." It seems to me I tend to become more and more diffuse. I'm really interested right now in three sets of problems. One is the relationship between biodiversity and ecosystem functioning. There I am concentrating more and more on marine systems as we collect tremendous amounts of information on marine biodiversity, especially marine microbial biodiversity. I'm interested in how all the information coming from genomics in particular can help us to understand the structure and function of those systems. Not surprisingly, this involves crossing scales.

The second area that I've been interested in for 20 years, and continue to be interested in, is the dynamics of infectious diseases. I think this is one of the great challenges facing humanity. I have been working on influenza for most of that time. That will continue, but I'm very interested in the problem of antibiotic resistance and what we can do about that.

Much of what we can do about it involves the social and cultural dimension, and therefore the third area, as reflected in the 2005 *PloS Biology* paper, is the dynamics of social norms, understanding why people do what they do, especially in relation to ecological and epidemiological problems, and how we can we change individual behaviors towards the common good. I don't mean to be arrogant here. I recognize that understanding what "the common good" means is going to involve essentially a democratic process. In this third area I will continue, as I have done in about the last 15 years, to work as closely as I can with those economists who see these problems, that is, problems of the environment, as great challenges that have to be addressed, and who recognize that markets don't hold the complete answer...because they don't adequately take into account the externalities, the social costs. So I see this as a major third area—namely, the interface between ecology and socioeconomics.

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