

When physics and ecology unite

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Professor Ehud Meron is a researcher at Ben-Gurion University of the Negev. Here, he discusses how his background in nonlinear physics has helped answer ecological questions.

Could you tell us a little about your academic background and how you came to study physics?

I did my undergraduate studies in chemistry at the Technion. This was a four-year physics-enhanced program, during which I also published my first two articles. During my PhD at the Weizmann Institute I moved to nonlinear physics.

I was fascinated by the beautiful patterns of chemical spiral waves that I first encountered in one of Ilya Prigogine's books. From there, I decided to study nonlinear partial differential equations (PDEs) that describe pattern-forming systems, such as convective fluids and chemical reactions. I pursued these research directions during my postdoctoral training at the University of Chicago (Physics Department) and at the Columbia University Astronomy Department. I continued on this path until my employment at the University of Arizona Mathematics Department, where I focused on the mathematical aspects of similar nonlinear PDEs. Although my academic background includes chemistry and applied mathematics, I approach scientific questions as a physicist and regard myself as such.

How did your background in physics lead to your interest in ecology? How are these areas connected in your research?

My interest in ecology started after I joined Ben-Gurion University in 1994. My affiliation with the Blaustein Institutes for Desert Research (jointly with the Physics Department) exposed me to interesting problems in the ecology of drylands. However, it was a few papers on vegetation patterns in semi-arid regions, which appeared sometime during 1997 and 1999 that got me actively involved. I realised the close relationship between these phenomena and the principles of nonlinear physics.

At first, my research group focused on applying these principles to vegetation pattern formation, identifying positive feedbacks that can destabilise spatially uniform vegetation to form periodic patterns, building mathematical models that capture these feedbacks, and

investigating the variety of patterns that can appear along the rainfall gradient, among others. More recently, our interests have shifted to the roles that pattern formation plays in the ecosystem function. Specifically, we aim to address questions that tackle the resilience of ecosystems to environmental changes, mechanisms of species coexistence, the restoration of malfunctioning ecosystems and the like. As we continue with these research directions, asking questions that ecologists would ask, we occasionally encounter new pattern formation problems that have not been studied before. In turn, this helps further expand our area of research.

Your research is characterised by interdisciplinarity. Why is this important?

Most phenomena in living systems intermingle biological, chemical and physical processes and the study of these processes further calls for integrating experimental sciences with mathematical and computational sciences. The shortcomings of disciplinary sciences to explain these phenomena have led to the emergence of interdisciplinary sciences such as biochemistry, biophysics and biomathematics, which have become themselves new scientific disciplines.

The emergence of these new disciplines that bridge over established disciplines is a continual process that goes along with the overall increase in scientific activity. At any period, truly interdisciplinary research occupies a very small percentage of overall scientific activity. However, this is only the case because of the subsequent consolidation of such research into new disciplines. In this sense, science is becoming more and more interdisciplinary, as it should be. My current research lies on the interface between two disparate scientific fields, spatial ecology and pattern formation. Whether research at this interface will result in a new discipline is an interesting question—we can do another interview in 10 years and find out.

We are living in a period of great biodiversity loss. How can your research be inserted in this context?

This question touches upon a wider concern - the impact of human intervention on ecosystem

dynamics. Pattern formation theory provides tools for identifying the inherent modes of undisturbed or disturbed ecosystem dynamics. Once such modes are identified, intervention along these modes can better maintain ecosystem function.

One such example is our current study on vegetation restoration by periodic landscape modulations. Our study deals with the likes of parallel embankments that intercept runoff and along which vegetation is planted. From there, we see that the inherent modes are a stripe mode dictated by the embankments, and two additional modes representing slanted stripes. Restoration that includes all three modes—which can be obtained by fragmented plantation along the embankments to form spot-like rhombic patterns—results in a better functioning ecosystem. This is reflected by high resilience to droughts and high biological productivity.

A similar approach may be applied to the question of biodiversity loss as a result of human intervention. The big and hard question in this context is this: What are the inherent spatial modes of self-organizing communities?

Have you experienced funding challenges in your career?

It is indeed harder to get funding for interdisciplinary studies. What has become easier throughout our research is finding which funding resources are more problematic, or which disciplinary section should be chosen when submitting a proposal to a given foundation.

I was lucky to receive a James S. McDonnell grant in the Studying Complex Systems Program in 2003, which helped me significantly upgrade the computational power available to my group. The Israel Science Foundation has also become a major funding resource for the interdisciplinary studies in my group. I was funded several times in the past by the US-Israel Binational Science Foundation on disciplinary topics. Also, I receive funding from an interdisciplinary H2020 EU project.

Understanding vegetation pattern formation and its roles in ecosystem function: What can mathematical models tell us?

To understand the dynamics of an ecosystem, it is necessary to consider the spatial relationships between biological, chemical and physical processes and, at the same time, identify possible positive feedbacks between these processes. In this sense, the spatial dynamics of ecosystems can be seen as a problem of pattern formation, which is a nonlinear physics subject. The research of Professor Meron is focused on understanding these dynamics and their implications for ecosystem function using mathematical modelling and model studies.

ECOLOGY AS AN INTERDISCIPLINARY FIELD

The composition and structure of the ecosystems we observe in nature are dictated by biological, chemical, and physical processes. Examples of such processes are biogeochemical cycling, species dynamics, and the physical forces that create wind and water regimes. In this light, Ecology must be seen as a cross-disciplinary field that bears different aspects of science. Because such natural processes do not distinguish between the traditional disciplines that humans have delineated, addressing a particular ecological issue by integrating multiple approaches can be highly advantageous.



We are living in a period of great biodiversity loss and mass extinctions—two aspects that have been mostly regarded as a consequence of human intervention on ecosystem integrity.

Ecosystem integrity is a relatively new concept that may be defined as the degree to which an ecosystem is self-organised. In other words, it measures the potential of an ecosystem to follow its inherent modes of development. Habitat degradation, whether by anthropic actions such as rural development and urbanisation or the conversion of natural ecosystems into agroecosystems, often results in the loss of ecological integrity. Professor Meron's research inserts into this context by approaching questions of spatial ecology using physics theories and mathematical modelling.

THE THEORY OF PATTERN FORMATION AND THE ECOLOGICAL CONTEXT

The main approach to studying the inherent modes of undisturbed or disturbed ecosystem dynamics lies in the theory of pattern formation. The theory addresses the spontaneous appearance of spatial patterns in nature. For example, such patterns may be animal-coats, spiral waves in the heart, vegetation bands or columnar lava patterns.

In the context of dryland ecosystems, the theory provides predictions about the mechanisms by which small, patch-scale processes lead to large, landscape-scale vegetation patterns. It also looks into the spatial modes that grow in these pattern-formation dynamics and the particular patterns that can form in different environments.

Such predictions are often hard to test with direct empirical experiments because of the long spatial and temporal scales that characterise such ecological processes. Through mathematical modelling, however, this difficulty can be circumvented. Rather than testing a particular pattern-formation mechanism directly, the theory can be used to test whether the behaviour implied by this mechanism agrees with available field observations.

Vegetation pattern formation is a key process not only in questions of landscape ecology, but since it involves the redistribution of critical resources like water and nutrients, it also affects interspecific interactions and species assemblage properties, such as biodiversity-productivity relations. "In studying vegetation patterns, we do not look for new ecological problems to address; rather, we ask the same questions ecologists ask, but make use of vegetation patterning in the process. We show that vegetation patterning is an inherent

ecological process that must be taken into account in many fields of ecology, including landscape ecology, community ecology, ecosystem ecology, and restoration ecology," said Professor Ehud Meron.

THE CURIOUS CASE OF THE NAMIBIAN FAIRY CIRCLES

Mathematical models can be a powerful tool to address questions of spatial self-organization of ecosystems. Using these techniques, Professor Meron and collaborators have recently provided exciting novelties about the peculiar Namibian fairy circle ecosystem. The ecosystem is relatively poor in animal and plant diversity, and consists of a uniform grassland punctuated by circular gaps of sandy bare soil, dubbed as the fairy circles. Local myths believe these fairy circles are footprints of gods or burn marks of dragons living beneath the ground. How exactly this spatial organization would have emerged is a question that has intrigued the scientists for decades.

Several explanations for the emergence of these circles have been suggested and some of the earlier ones have already been refuted. More recent explanations attribute fairy circles to microseepage of hydrocarbon gases that displace oxygen in the root zone. Other explanations have referred to grass or seed harvesting by social insects such as termites. These explanations all share one essential drawback - they do not account for the emergence of large-scale order. Could the fairy circles in the Namibian ecosystem be explained as a pattern formation phenomenon, in which small-scale processes induce large-scale order?

Combining mathematical modelling and empirical studies, Professor Meron and collaborators have provided two types of supporting evidence for the pattern-formation hypothesis. The first is based on comparative

model and empirical studies of statistical properties, such as the nearly hexagonal order of fairy circle patterns (any fairy circle is surrounded by six nearest-neighbour circles). The second evidence is dynamical by its nature and related to fairy circle birth and death events. According to the pattern formation theory, uniform vegetation and hexagonal gap (fairy circle) patterns can coexist as alternative stable ecosystem states. The theory further predicts that a multitude of additional stable hybrid states can exist, consisting of spatial mixtures of patterned and uniform domains.

Integrating satellite image and rainfall data analyses over a period of 10 years, from 2004 to 2013, with model simulations, and using initial conditions derived from satellite images taken in 2004, Professor Meron and collaborators have shown that, in essence, fairy circle birth and death events are transitions between hybrid states induced by droughts and spates respectively. This is a nice example of the indirect evidence that model studies can provide; the association of fairy circle birth and death events with hybrid-state transitions supports the view of fairy circles as a self-organisation pattern-formation phenomenon that is responsible for the appearance of hybrid states in the first place.

Besides providing a new kind of evidence for the pattern-formation hypothesis of fairy circles, the observation of hybrid states and hybrid-state transitions modifies the way we understand regime shifts.

Professor Meron explains: "Unlike the common view of regime shifts as sudden 'catastrophic' transitions between alternative stable states, our results indicate that regime shifts in pattern-forming systems can proceed gradually through cascades of hybrid-state transitions. Being fairly uniform and undisturbed, the Namibian fairy circle ecosystem provides an excellent field model for studying gradual regime shifts in general.

THE FUTURE PERSPECTIVES

Two broadly explored topics in ecological studies are how ecosystems respond to environmental variability and the impact of this response on ecosystem function. Addressing these issues can be very challenging, essentially because of the multiple spatial scales and organisation levels that characterise ecosystem complexity. While empirical studies usually

focus on particular scales and organisation levels, mathematical modeling allows more complex route.

"The model platform that our group has developed allows for integrative studies across spatial scales and organization levels. It does so by scaling up organism-level traits and small-scale spatial processes to higher levels of organization and larger spatial scales," says Professor Meron. On future studies, he plans to use this platform to combine the theory of pattern formation and biodiversity and understand this coupling in the context of ecosystem function. His team will also study how to achieve and maintain high ecological integrity in human-intervention contexts, such as restoration ecology and agro-ecology.

Researcher Profile

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Professor Ehud Meron is a researcher at Ben-Gurion University of the Negev. He received his PhD in nonlinear physics from the Weizmann Institute of Science. Later on, he followed this up with his postdoctoral research in the Physics Department of the University of Chicago and in the Astronomy Department of Columbia University. After a three-year term as a faculty member in the Mathematics Department of the University of Arizona, he joined the Blaustein Institutes for Desert Research and the Physics Department at BGU. Among his areas of expertise are nonlinear dynamics and pattern formation, complex systems and spatial ecology. Professor Meron has made significant contributions to the understanding of pulse and front dynamics in reaction-diffusion systems. He has also pioneered research in the response of pattern-forming systems to periodic temporal and spatial forces. During the past 15

years, he has been devoting his knowledge and expertise in pattern formation theory, to the mathematical modelling of dryland ecosystems and the understanding of the roles that pattern formation plays in their response to varying environments. Professor Meron has also authored the *Nonlinear Physics of Ecosystems* (CRC Press 2015), a monograph which aims to help in closing the gap between the two disparate research fields of spatial ecology and pattern-formation.

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