

Viewpoint

Microbial Ecosystem Follows Deterministic Dynamics

Otto X. Cordero

Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA 02139-4307, USA

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High-resolution tracking of the population abundances in a simple, closed microbial ecosystem shows that the intrinsic dynamics of the system are strongly deterministic.

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A Viewpoint on:

Strongly Deterministic Population Dynamics in Closed Microbial Communities Zak Frentz, Seppe Kuehn, and Stanislas Leibler *Physical Review X* 5, 041014 2015 – Published October 26, 2015

Do simple laws govern the dynamics of complex ecosystems? Are these dynamics predictable? These are hard questions to address because of the intrinsic complexity of ecosystems and the lack of data available. In a new study, Stanislas Leibler from the Rockefeller University, New York, and colleagues [1] take on this problem by tracking the population dynamics of a closed ecosystem of three microbial species at an unprecedented level of detail. Using a novel method of automated counting of single cells, which tracks the abundances of the species as frequently as every 400 seconds for 90 days, the authors find that the intrinsic dynamics of the three-species ecosystem are strongly deterministic, that is, the system's evolution is highly reproducible under controlled external conditions. Despite the high level of determinism, the observed abundances of the species don't have a simple dependence on position and time and, to current knowledge, are unpredictable. This means that although the dynamics of the system is not left to chance, we don't know how to model its future states.

To fully appreciate the importance of these findings, we need to put them in context. Life has different levels of organization, from molecules, cells, and organisms, all the way to collectives like populations, communities, and ecosystems. The higher the organizational level of a biological system, the more complex the behavior of the system's members is and the more difficult it is to find general principles that predict their dynamics. Over the past decade, quantitative biology has made enormous progress in mapping the dynamics of biological systems at ever-higher levels of temporal and spatial resolution. But this progress has mostly occurred at the lowest levels of organization; for example, it has allowed the precise quantification and modeling of molecular dynamics inside cells. However, ecology, the branch of biology that deals with the dynamics of groups of organisms, has remained fairly observational. This is because quantitative data of real ecosystems is hard to obtain and because there are few well-established model systems that can be replicated to distinguish deterministic factors (leading to reproducible dynamics and structures) from chance events within populations. As a consequence, there are plenty of conceptual models in ecology but very few with general predictive power [2].

To search for universal principles explaining the dynamics of multispecies collectives, Leibler and colleagues used one of the simplest possible closed ecosystems: a system of three microbial species (algae, bacteria, and ciliates) that can be maintained under highly controlled external conditions. Because it can be easily replicated, this model system provides the opportunity to study large ensembles of identical ecosystems. It also offers a chance to find out what would happen if the "tape of ecology" were "replayed"—a question that cannot be addressed in the context of traditional observational studies.

The first study on this three-species ecosystem dates back to 2012 [3]. Interestingly, at that time, the authors of that study (Leibler and Hekstra) did not observe the deterministic dynamics that Leibler and co-workers now report. Instead, they found that the population dynamics of replicates of this ecosystem diverged as time went by. Back then, the explanation for the observed divergence was that small differences between replicates amplified with time because of the ecosystem's many stacked levels of complexity.

As it turns out, the differing dynamics between the two studies stem from differences in the experimental setups. In 2012, measurements of the population dynamics required placing cuvettes containing the replicates under a fluorescent microscope for a short period of time each time a measurement was taken. Technically, this meant that measurements introduced very small perturbations to the external conditions of each replicate due to the movement of the cuvette. Could this be the reason

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FIG. 1: The digital holographic microscopes used by Leibler and colleagues to study the intrinsic dynamics of a threespecies microbial system. Each device observed one replicate of the system, allowing the replicate to be kept under highly controlled external conditions. (Seppe Kuehn and Zak Frentz)

why the dynamics diverged? To answer this question, Leibler and co-workers built digital holographic microscopes around each replicate (Fig. 1) and reconstructed holograms using computational algorithms. This approach bypassed the need to disturb the cuvettes during measurements and allowed data to be captured at rates of minutes, compared to days in the previous study.

It was only after this monumental effort to control extrinsic factors that the researchers discovered that the intrinsic population dynamics (those which emerge from processes that occur within the ecosystem, not outside of it) of the three-species ecosystem are highly deterministic. This is a remarkable result, because a large number of stochastic events take place across all levels of biological organization. One would think that all of these processes should contribute to creating significant variance among replicate ecosystems. Instead, the dynamics of this ecosystem seems to follow a prescribed "program."

What might this program be then? Theoretical ecologists may feel compelled to build a model; after all, the three-species ecosystem is just a trophic chain that can be described by three differential equations, one for each species. Wrong. The deterministic dynamics of the system depend on a multitude of microscopic factors. Algae,

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bacteria, and ciliates can swim, aggregate, and change their size and behavior. All of these factors contribute to shift the species abundance in a reproducible yet unpredictable manner. The upshot is that we know there is a program, but we don't know its rules.

Researchers could try and find some set of rules by measuring all the microscopic processes that take place in the closed ecosystem. But that exercise would most likely result in a model for this specific experiment, rather than in the scientific synthesis of the ecological forces that drive the system to its deterministic behavior. Experience from other complex systems shows that, to find a useful scientific synthesis, we need to identify order parameters, or "collective variables," that capture the macroscopic behavior that emerges from a myriad of microscopic details [4].

Finding those variables remains a challenging problem, and it is one of the main scientific frontiers in the physics of life. However, for physicists, as for biologists, it should be clear that despite the great advances in molecular systems biology, the most ambitious questions in biology remain at the highest levels of organization.

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Otto X. Cordero received a B.S. in computer and electrical engineering from the Polytechnic University of Ecuador, and a M.Sc. in artificial intelligence and a Ph.D. in theoretical biology from Utrecht University. His past research work has demonstrated the importance of ecological interactions between microbes in generating patterns of diversity and sustaining ecological function. He currently heads the Ecological Dynamics lab at the Massachusetts Institute of Technology, which uses a combination of experimental and computational approaches to reverse-engineer the microscale ecology of bacteria in the environment, and to learn how microscale processes impact ecosystems at global scales. http://www.corderolab .org