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Understanding chaos and diversity in complex ecosystems – insights from statistical physics

1. **Many-Species Ecological Fluctuations as a Jump Process from the Brink of Extinction**
   Authors: Thibaut Arnoulx de Pirey and Guy Bunin
   PHYSICAL REVIEW X 14, 011037 (2024)
2. **Spatiotemporal ecological chaos enables gradual evolutionary diversification without niches or tradeoffs**
   Authors: Aditya Mahadevan, Michael T Pearce, Daniel S Fisher
   eLife 12:e82734 (2023)

Recommended with a Commentary by Pankaj Mehta,
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In the mid 1970s, theoretical physicist turned theoretical ecologist Robert May published an extremely influential set of manuscripts on chaos, stability, and diversity in complex ecosystems [1, 2]. May was directly inspired by the work of Wigner and Dyson which used random matrix theory (RMT) to understand the properties of complex nuclei. May argued that the more diverse an ecosystem is (roughly defined as the number of species present), the less stable it becomes. To make this counter-intuitive argument, May considered an ecosystems consisting of S species whose abundances were given by N_i^* where $i = 1, \dots, S$. He then imagined perturbing the ecosystem $N_i^* \to N_i^* + \delta N_i$. In linear response, the dynamics of such an ecosystem are described by the equations:

$$\frac{d\delta N_i}{dt} = \sum_{j=1}^{S} M_{ij} \delta N_j. \tag{1}$$

Invoking Wigner and Dyson, he modeled M as random matrix whose diagonal entries were all -1 and whose off diagonal elements were drawn from a normal distribution $\mathcal{N}(0, \sigma^2)$ with mean zero and variance σ^2. The maximum eigenvalue of M can easily be calculate using results from RMT and is given by $\lambda_{max} = -1 + \sqrt{S}\sigma$. Stability requires $\lambda_{max} < 0$, yielding a criterion for the maximum size S^* for a stable ecosystem at steady-state, namely $S^*\sigma^2 < 1$. This has since become known as the May stability bound and, within May's framework, serves as an upper bound on ecological diversity.

One major deficiency of May's argument is that it does not allow for the possibility that complex ecosystems can self organize through immigration and extinction. The simplest model that contains all these processes is the Generalized Lotka-Volterra model (GLV) which takes the form

$$\frac{dN_i}{dt} = N_i(1 - N_i - \sum_{j \neq i} A_{ij} N_j) + \lambda, \tag{2}$$

where $i = 1, \ldots, S$ runs over the S species in the "regional species pool", N_i denotes the abundance of species i, A_{ij} encodes how species j affects the growth rate of species i (with positive elements indicating competition and negative elements indicating cooperation), and λ is the immigration rate of species into the ecosystem from the regional species pool and is assumed to be small ($\lambda \ll 1$). Note, that in writing this equation, we have already rescaled time by the species growth rate, species abundances by their carrying capacity, and interaction coefficients A_{ij} by their self interactions A_{ii}, so that all quantities are dimensionless. Despite its simplicity, this equation holds many surprises, especially when the number of species is large. The term in the parenthesis of Eq. 2, $g_i(N) = (1 - N_i - \sum_j A_{ij} N_j)$, can be interpreted as the growth rate of species i in the presence of all the other species. If $g_i(N)$ is negative, species i will go extinct in the absence of immigration and will persist at a low abundance of order $N_i \sim \lambda$ in the presence of immigration. Since the growth rate of every species depends of the abundance of every other species, this model represents a non-trivial complex, interacting system that becomes extremely hard to analyze analytically.

For this reason, it is again useful to analyze the statistical properties of Eq. 2, when the interaction coefficients A_{ij} are drawn from a random distribution with mean $\langle A_{ij} \rangle = \mu/S$ and variance $\langle \delta A_{ij} \delta A_{kl} \rangle = (\sigma^2/S)\,(\delta_{ik}\delta_{jl} + \rho\delta_{il}\delta_{jk})$. Here the parameter ρ measures the asymmetry of the interactions. When $\rho = 1$, the interactions are reciprocal – how species i affects species j is identical to how species j affects species i. However, when $\rho < 1$, the interactions are non-reciprocal. This non-reciprocity has important implications for the dynamical behavior of the equations. When interactions are reciprocal, the dynamics admit a Lyapunov function and the system always reaches a steady-state. However, in the presence of non-reciprocity the system can exhibit complex dynamical behavior including chaos [3–6]

Over the last decade, motivated by new experimental techniques for measuring properties of large microbial ecosystems, there has been a flurry of new theoretical works trying to understand these equations in high dimensions using techniques from the statistical physics of disordered systems such as the cavity method and dynamical mean field theory (DMFT). For a pedagogical set of lectures covering these developments, see our Les Houches lectures [7]. The phase diagram for these equations was first worked out using the zero-temperature cavity method in [8]. However, understanding the chaos that emerges for non-reciprocal interactions and its implications for diversity remained an open problem. Hints that this chaotic phase exhibited extremely interesting dynamics appeared in [4]. Numerical simulation in conjunction with DMFT calculations showed, that for the special case of completely anti-symmetric interactions ($\rho = -1$ in the equations above), the dynamics exhibited a "boom" and "bust" behavior where species would stay at low abundance before shooting up to high abundances. In the presence of some minimal spatial structure (multiple connected islands), the resulting chaotic dynamics supported much more diversity than would be possible at steady-state, an observation with important implications for understanding the origin of the fine grained diversity observed in sequencing experiments of microbial ecosystems [9].

Until recently, relatively little was understood about the chaotic dynamics outside this special anti-symmetric case. Two recent papers by Mahadevan et al. and de Pirey and Bunin have made significant progress towards answering this question by developing impressive new technical tools based on DMFT and scaling arguments [5, 6]. In [5], Mahadevan et al. build upon their earlier work to show that the spatiotemporal chaos with boom-bust dynamics observed in [4] can occur even when ecosystems are assembled through sequential invasions of new species and where the strict anti-symmetry condition is relaxed. This suggests that the increased diversity seen in the chaotic phase may be generic even in the presence of evolution. These impressive calculations (which are really too technical to discuss in this short format) open up the possibility of mathematically modeling eco-evolutionary dynamics – one of the biggest open problems in evolution and ecology.

In a complementary analysis, de Pirey and Bunin develop a new DMFT for the chaotic dynamics seen in the GLV (Eq. 2) [6]. This DMFT naturally explains the presence of the boom-bust chaotic dynamics seen in simulations, where species persist at low-abundance for extended periods of time, before shooting up to high abundance for a considerable duration, and then once again returning to low abundance. The authors start by performing careful numerical simulations that show that at any given time, the ecosystem consists of a mixture of high-abundance species and low-abundance species (species with $N_i \sim \lambda$). They derive analytic expressions for the steady-state abundance distribution and an analogue of the fluctuation-dissipation theorem for chaotic dynamics relating static and dynamics correlation functions.

To derive these results, Bunin and de Pirey consider the special case where interactions between species are uncorrelated ($\rho = 0$) and use an ansatz for the two time species-species correlation function $C_\lambda(t, t')$. Their key insight is that the natural variables for the problem are not the time t and abundances N_i, but the rescaled quantities $t/|\ln \lambda|$ and $z_i = \ln N_i/|\ln \lambda|$ (recall λ is the immigration rate and all quantities in Eq. 2 are dimensionless). With these rescaled variables, the two-time correlation function exhibits a data collapse $C_\lambda(t, t + s|\ln \lambda|) \to \hat{C}(s)$, allowing one to write a DMFT for $z_i(s)$. This DMFT shows that the dynamics can be thought of as a jump process where low abundance species first shoot up to high abundance and then slowly return to low abundances. They also show that the return of high abundance species to low abundances can be modeled by a biased random walk with an absorbing boundary condition. Using this DMFT solution, they derive a number of remarkable predictions. We focus on one of these: an unexpected relation between May's stability bound and chaos. Recall, that in the chaotic system the species fall into two groups: species at high abundances and species at low abundances near the immigration floor. de Pirey and Bunin show that even in the chaotic regime, the number of high abundance species in the ecosystem will always be less than the May stability bound. This result is quite surprising since it suggests that ecosystems self-organize in such a way that the high abundance species still follow May's diversity bound even when they are chaotic.

These papers highlight the exciting possibility that it may be possible to analytically understand complex eco-evolutionary dynamics. They also show how thinking about high-dimensional ecology offers a rich playground for statistical physics.

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