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Chaos may lurk under a cloak of neutrality

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The astonishing diversity of species on Earth has long puzzled ecologists and evolutionary biologists alike. For instance, why are there more than 300,000 species of beetles and only 10,000 species of mammals? Is it because the Creator is inordinately fond of beetles, as J. B. S. Haldane reportedly joked (1)? A somewhat more satisfying explanation can be based on the assumption of niche differences between species: When the self-limiting interactions of each species are stronger than interactions with its competing species, species cannot competitively exclude each other and biodiversity is maintained (2). However, metagenomic surveys increasingly reveal high diversity even within single microbial species (3, 4), for which the assumption of local niche differentiation seems less obvious. A prominent example of this fine-scale diversity is given by the phytoplankton *Prochlorococcus*, which, with an estimated 3×10^{27} cells, is among the most abundant photosynthetic cells in the oceans (5). A single milliliter of seawater can contain hundreds of *Prochlorococcus* strains that have diverged from thousands to tens of millions of years ago (6).

One way out of this dilemma is to argue that diversity simply is the result of the continual emergence of new strains, via an assumed constant rate of speciation or via immigration from other habitats, and their extinction via random demographic fluctuations, also called random genetic drift. This conjecture, which is the basis of neutral theory (7), has become one of the leading null models of biodiversity because it is remarkably successful in describing static observables related to the species abundance distribution in various ecosystems (7, 8). Yet, it is difficult to imagine that the dynamics of enormously abundant species like *Prochlorococcus* are controlled primarily by neutral processes, which could be disrupted by even tiny differences between strains (9). In PNAS, Pearce et al. (10) show analytically how alternative nicheless models can produce the same neutral abundance patterns from a dynamics that could hardly be more nonneutral: rapid spatiotemporal chaos generated by ecological interactions and random dispersal. Pearce et al. (10) highlight that widely observed static patterns, believed to be hallmarks of neutrality, are too insensitive to distinguish pertinent scenarios, reinforcing the need for spatiotemporal data (11, 12) in microbial ecology.

The analysis of complex ecosystems kicked off in 1972 when the great Robert May, who sadly passed away weeks ago, found a way to deal with the vastness of ecological parameter space (13). Even the simplest ecological model of S interacting species or strains, the generalized Lotka–Volterra model, requires fixing S^2 interaction parameters to describe how the presence of a given strain affects itself and the growth of all other strains. Naively, one would think that because of such a parameter deluge it may be hopeless to try to exhaustively characterize the behavior of systems of many species. However, May (13) found that, under relatively mild assumptions about the parameter statistics, surprisingly general statements can be made when S becomes large: Complex ecosystems are unstable unless niche differences encoded through self-limiting interactions

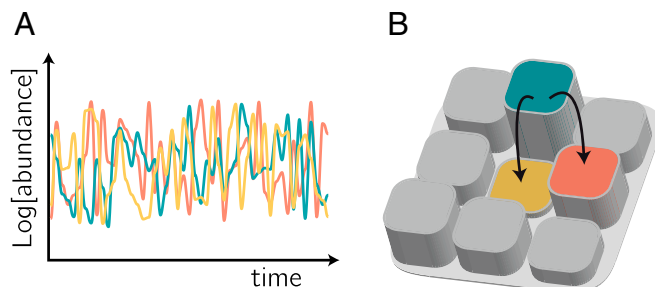


Fig. 1. Self-organized spatiotemporal chaos stabilizes high diversity in ecological systems. (A) When strains undergo negative feedback and small migration between islands, large communities self-organize into spatiotemporal chaos. Colors illustrate the chaotic dynamics of the logarithmic abundance of one strain on three different islands. (B) “Snapshot” of the chaotic state. While some islands experience a “bloom” (blue), others experience a “bust” (yellow). Desynchronized blooms and busts can stabilize high diversity. Bars represent different islands; their heights illustrate the abundance of a species on that island.

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are sufficiently strong—the minimal strength of self-limiting interactions required for stability increases with the number of interacting species and the variance in ecological interaction strengths. But what type of dynamics looms outside the regime of niche-stabilized coexistence? Do species go extinct en masse or become somehow stabilized dynamically? These are the central dynamical questions that Pearce et al. (10) set out to answer because populations of closely related strains are, with only weak niche differences, poised to be May-unstable.

Pearce et al. (10) develop analytical techniques within the framework of dynamical mean-field theory that, like May's approach, leverage the simplicity that emerges in the large S limit. Supported by simulations, they find that the population dynamics become chaotic outside the stability region, as the ecological interactions provide sufficient negative feedback to prevent any one strain from outcompeting most of the others. Negative feedback could be induced, for instance, by host–pathogen interactions, as is common to bacteriophage systems (14). Under such dynamics, single well-mixed communities are unable to maintain high diversity because most species undergo wild but deterministic number fluctuations and ultimately reach abundances so low that they drift to extinction. However, if spatial variation is permitted—as in a metacommunity of islands connected by weak migration—chaos is remarkably efficient in maintaining high diversity in a long-lived state of spatiotemporal chaos. In this state, most species experience local “bloom and bust” cycles, in which an individual species will go extinct locally, only to be rescued by migration from an island experiencing a bloom (Fig. 1). Through these dynamics, survival times increase exponentially with the number of islands, rendering the spatiotemporally chaotic phase very robust. Neutral theories typically assume the existence of a “mainland” from which species migrate, which serves to buffer species from purely stochastic extinction (7, 15). However, in Pearce et al.'s (10) self-contained metacommunity model, species self-organize into a dynamic state, without the need for imposing the presence of a mainland. This self-consistency allows them to equate a strain's long-time abundance distribution with its island-averaged abundance distribution, which in turn leads to fascinating analytic insights and testable quantitative predictions. Most notably, the observable time-averaged species abundance distribution turns out to be very similar to the abundance distribution predicted by neutral theory (7). Yet, the dynamics are fundamentally different. This is reflected, for instance, in the statistics of the high-abundance peaks or the rapid, superdiffusive meandering of the intermediate log-abundances over time, which in large populations is much faster than the fluctuations induced by neutral birth–death processes.

In summary, the conceptual and technical advances by Pearce et al. (10) support at least three important conclusions. First, large ecosystems with some amount of negative feedback and small migration generically self-organize into a long-lived state of spatiotemporal chaos. Chaotic dynamics have indeed been indicated in several microbial experiments with plankton (16), viruses (17), and oceanic bacteria (18). Crucially, while ecological models with assumed local chaotic dynamics have been studied before (19), Pearce et al. (10) provide a firm mathematical description of how

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the chaotic bloom–bust cycles actually emerge in a large class of ecological models. They further point out that spatiotemporal chaos may also emerge in communities with selective differences and in the presence of uncorrelated interspecies interactions or moderate niche-like interactions, as shown in parallel work (20).

Second, as spatiotemporal chaos can maintain long-lived diversity, Pearce et al.'s (10) bloom–bust paradigm provides a more plausible route to fine-scale diversity observed in microbial species, where random birth–death fluctuations are easily overshadowed by deterministic forces due to differential reproduction.

And third, “snapshots” of abundance distributions can give us only very limited insights into the ecological mechanisms that underlie complex ecosystems. Even if two ecosystems show the same static abundance distribution, the dynamics of individual species could be driven by fundamentally different mechanisms. Instead of static measurements, time series data from deep sequencing at multiple sampling sites are needed to learn about the underlying mechanistic scenarios. Pearce et al.'s (10) detailed analysis also suggests what to look out for in these data, such as the superdiffusion of log-abundances, as a telltale sign of chaotic boom–bust cycling.

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