

Self-organized disordered vegetation patterns with hidden order in arid ecosystems

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PNAS



Fig. 1. Schematics indicating circular sampling windows in two dimensions for three different images of scalar fields: a garden-variety disordered nonhyperuniform (*Left*), disordered hyperuniform (*Middle*), periodic (*Right*) patterns, as adapted from ref. 15. In each of these examples, the intensities of the fields within a window will fluctuate as the window position varies, which specifies the local field variance $\sigma^2(R)$. In the case of the disordered nonhyperuniform configuration, the variance $\sigma^2(R)$ decays to zero like $1/R^2$. By contrast, the disordered hyperuniform pattern, shown in the *Middle*, has a variance $\sigma^2(R)$ that decays to zero like $1/R^3$, which remarkably has the same decay rate as the periodic pattern, shown on the *Right*; and hence, both are hyperuniform of class I. The reader is referred to refs. 15 and 18 for details.

Understanding the formation mechanisms that lead to spatial patterns found in nature has intrigued scientists for centuries. Examples include leopard spots, zebra stripes, convection-cell motifs, honeycombs, sunflower-seed spirals, tessellations of cracks, and veins in a leaf, to mention only a few. In a seminal 1952 paper entitled "The Chemical Basis of Morphogenesis," Alan Turing introduced a theory to describe how highly symmetric spatial patterns in nature arise spontaneously via simple diffusion-reaction equations (1). He demonstrated that diffusion in an initially homogeneous chemical system can lead to instabilities that result in a variety of ordered spatial patterns with certain selected wavelengths. This work demonstrated how ordered patterns can arise out of "randomness" during morphogenesis. In the last 70 y, Turing-like reaction-diffusion equations and their generalizations have been employed to understand pattern formation in a variety of natural and synthetic systems (2-5). In a recent article in the PNAS (6), Zhengpen Ge explored unusual disordered Turing patterns in arid and semi-arid vegetation ecosystems with an exotic hidden order on large scales that has come to be known as "disordered hyperuniformity" (see Fig. 1).

Large-scale regular vegetation patterns are common in nature and play a critical role in the ecological functioning of arid and semi-arid ecosystems. The formation of these patterns has been explicated via solutions to a variety of different mathematical models that account for the mechanisms of plant-water interactions (7–13). Some of these models incorporate the activator-inhibitor principle that Turing first proposed in 1952 (1), which is also known as the scale-dependent feedback principle in ecology (8, 12). However, the identification of all of the key mechanisms underlying the origin and maintenance of vegetation patterns continues to be debated. For example, it has been suggested that regularity in vegetation patterns induced by interactions with animal populations is another critical mechanism that must be understood, stressing the need to integrate multiple mechanisms of ecological self-organization (13).

Notably, previous investigations of the spatial selforganization of vegetation patterns have primarily focused on features at short length scales, such as patch size and shape, rather than features spanning across large length scales. Drawing inspiration from the nascent field of hyperuniformity, Ge found that the disordered arid and semi-arid vegetation Turing patterns evolve toward the unusual

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Author contributions: S.T. wrote the paper.

The author declares no competing interest.

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Published November 27, 2023.

long-range property of hyperuniformity (14, 15), which he argues is linked to optimal water usage.

But, what is hyperuniformity? The study of hyperuniform states of matter is an emerging multidisciplinary field, impinging on developments in the physical sciences, mathematics, and biology (14, 15). The hyperuniformity construct was first introduced in the context of many-particle systems (e.g., atoms/molecules that comprise a liquid or solid, stars in a galaxy, or trees in a forest). Hyperuniform many-particle systems are characterized by an anomalous suppression of large-scale density fluctuations compared to those found in garden-variety disordered systems, such as ordinary fluids and amorphous solids. Hyperuniformity generalizes our established notion of long-range order to include not only all perfect crystals, perfect quasicrystals, but exotic disordered systems as well. While disordered hyperuniform systems were largely unknown in the scientific community two decades ago, there is now a realization that such systems arise in a host of contexts across the physical, mathematical, and biological sciences, including classical equilibrium liquids and ground states, classical nonequilibrium systems, quantum systems, sphere packings, random matrices, dynamical systems and guantum chaos, number theory, large-scale structure of the universe, biological and ecological systems, and novel materials (15, 16).

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The hyperuniformity concept was subsequently generalized to characterize heterogeneous media (17) and random scalar fields (18). Scalar fields can arise in a variety of physical contexts, including concentration and temperature fields in porous media, turbulent flows, laser speckle patterns, and temperature fluctuations associated with the cosmic microwave background (15). Other examples include spatial patterns that arise in biological and chemical systems, including Turing patterns, which is the subject of the PNAS article.

How is hyperuniformity quantified for random scalar fields? Such patterns are characterized by a spectral density $\Psi(\mathbf{k})$ (a nonnegative quantity) that tends to zero as the wavenumber |k| tends to zero (18), where k is the wavevector. The spectral density encodes information about characteristic spatial frequencies (wavenumbers) of the random scalar fields or, more precisely, the square of the Fourier transform of "images" of the fields. By contrast, garden-variety random scalar fields possess a spectral density $\Psi(\mathbf{k})$ that does not vanish at the origin, i.e., $\Psi(\mathbf{k} = 0) > 0$. Another way to ascertain hyperuniformity is to randomly place many large spherical sampling windows of radius R in the system and measure the integrated field intensities within the window. The fields within the randomly placed windows will fluctuate, enabling one to find the corresponding local variance associated with fluctuations in

the field $\sigma^2(R)$, as shown in Fig. 1. Run-of-the-mill disordered patterns are characterized by a local variance $\sigma^2(R)$ that decays to zero like $1/R^d$ for large R, where d is the space dimension; see the left panel of Fig. 1. A hyperuniform pattern has a variance that decays to zero faster than 1/R^d (15, 18). For example, all perfect periodic patterns have a variance that decays like $1/R^{d+1}$. Remarkably, there are disordered patterns (see Middle panel of Fig. 1) that have the same decay rate as periodic ones (see *Right* panel of Fig. 1) and hence are hyperuniform. This type of long-range order in a disordered hyperuniform pattern is said to possess hidden order (15) because it is often difficult to detect by eye. Patterns in which $\sigma^2(R)$ decays like $1/R^{d+1}$ are the strongest form of hyperuniformity and are called class I (15, 18). Fig. 1 contrasts a typical disordered nonhyperuniform pattern with two different class I hyperuniform patterns in two dimensions, one that is disordered and the other that is ordered. Class II systems are an intermediate form of hyperuniformity in which $\sigma^2(R)$ decays like $\ln(R)/R^{d+1}$. The weakest form of hyperuniformity is class III in which $\sigma^2(R)$ decays like $1/R^{d+\alpha}$, where $0 < \alpha < 1$.

Returning to the PNAS article, Ge studied four different Turing reaction-diffusion equations to model the spatial evolution of two-dimensional (d = 2) vegetation patterns over time and analyze their large-scale structural

characteristics. To quantify the latter, he utilized the aforementioned theoretical tools to calculate the degree of hyperuniformity as measured by the exponent β in the decay of the local field variance $\sigma^2(R) \sim 1/R^{\beta}$ for large *R*. (Note that Ge uses the notation b_{lr} for this exponent.) At steady-state conditions, he showed that the mean biomass (initially spatially uncorrelated and

hence nonhyperuniform) linearly decreases with rainfall and spatial patterns of "gaps," "labyrinths," and "spots" sequentially emerge. The gap and labyrinth patterns become hyperuniform of class III (2 < β < 3) and in the steadystate, the exponent β approaches the upper hyperuniform limit of 3 (class I hyperuniformity) with decreasing rainfall. When spots emerge, the exponent β becomes greater than 2 (class III) and always converges to the upper hyperuniform limit 3 (class I) with decreasing rainfall until a tipping point (rainfall threshold amount that separates desert states from recoverable states) is reached. Interestingly, the time taken for β to reach the value 3 increases exponentially with decreasing rainfall. As the ecosystem approaches the tipping point, the temporal changes in mean biomass show that decreasing rainfall causes the vegetation pattern to remain in a nonhyperuniform state, that is, $\beta \leq 2$, resulting in low biomass for an extended period of time. After the ecosystem evolves to achieve hyperuniformity (i.e., $\beta > 2$), biomass rapidly increases. Importantly, Ge observes that the time-evolution of the exponent β toward a hyperuniform state is accompanied by the spatial optimization of water acquisition by vegetation. Therefore, decreasing rainfall reduces the mean biomass in steady states and significantly slows down the spatial optimization of water-use efficiency by vegetation in long-time transient regimes.

In order to examine the effect of spatial patterns on resilience, Ge carried out numerical disturbance experiments on the models considered. He fixed the amount of rainfall and focused on how resilience responds to two kinds of disturbances: 1) the resilience of the transient patterns in response to homogeneous disturbances; and 2) the resilience of the steady-state pattern (β = 3) in response to both homogeneous and heterogeneous disturbances. A key finding is that the spatial resilience of Turingtype ecosystems after intense, short-term heterogeneous disturbances in hyperuniform states with β = 3 (which destroy hyperuniformity) leads to longer recovery times in the biomass to a pre-disturbance hyperuniform state with β = 3, in contrast to spatially homogeneous disturbances that maintain hyperuniformity. Therefore, Ge has proposed that the degree of hyperuniformity, as measured by the exponent β , could be used in future work as a metric for assessing spatial resilience after intense shortterm disturbances in the spatial evolution of vegetation patterns.

As mentioned above, Ge has shown a possible concomitant link between hyperuniform states and the spatial optimization of water-use efficiency by vegetation. It is noteworthy that disordered hyperuniformity can confer optimal or nearly optimal functionality (under certain constraints) in two other biological contexts: photoreceptor mosaics in the avian retina (19) and the immune system (20). It is likely there are many other disordered hyperuniform spatial patterns in nature that are waiting to be discovered by diagnosing them under the hyperuniformity "lens." If so, what are the possible hyperuniformity classes and how are they linked to the mechanisms leading to the spatial patterns? Does hyperuniformity in such instances always signify an underlying constrained optimization process due to the singular nature of such an exotic disordered state? The exploration of answers to these exciting open questions are fruitful avenues for future research.

ACKNOWLEDGMENTS. I am supported in part by the NSF CBET-2133179 and the US Army Research Office under Cooperative Agreement No. W911NF-22-2-0103.

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