PNAS COMMENTARY

Conservative or dissipative? Two distinct processes for spatial pattern emergence

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In PNAS, Siteur et al. (1) recently contributed to the topic of spatial patterns in ecosystems. This is of relevance since ecologists have long recognized that ecological variables (e.g., plant biomass, species abundances, etc.) display uneven distributions in space—i.e., patterns—that need to be accounted for and interpreted (2, 3). Although ecologists have historically favored external factors, such as preexisting substrate heterogeneity or disturbance as potential explanations, we have witnessed an increased awareness of the potential for self-organizing processes to account for various pattern types, some of them amazing (Fig. 1). Self-organized spatial patterns have now been evidenced or hypothesized in a variety of ecosystems. Yet vegetation in drylands has become paradigmatic for the introduction of pattern formation approach (sensu 4, 5) in the study of ecosystems. Notably, the most impressive patterns displaying both spatial periodicity and stability in time (2, 3) are observable worldwide across drylands in relation to predictable ranges of environmental conditions (6). Spatially periodic patterns inspired a first contribution that introduced in vegetation ecology methods from the field of morphogenesis in physical and chemical systems (7). This seminal approach proposed an integrodifferential modeling of plant biomass dynamics using spatial kernels to embody plant–plant interactions, whether positive (enhancement of scarce water resource by shading) or negative (resource preemption by roots). Pattern formation through spatial-symmetry breaking instability directly relates to relative strengths and spatial scales of these two types of interactions, a necessary condition being that positive and negative feedbacks predominate at short and longer ranges, respectively [further referred to as scale-dependent-feedbacks (SDF)] (1). In this approach, and deriving subsequent works (e.g., refs. 8–10), the fast dynamics of the limiting resource, namely water, remained implicit. In parallel, the subject inspired theoretical efforts that revisited and adapted the classical approach of morphogenesis from A. Turing (3, 11) and addressed the interacting dynamics of vegetation biomass and water (explicitly considered) through systems of reaction-diffusion equations (e.g., refs. 12 and 13). A comprehensive model integrating most relevant aspects of intertwined water-vegetation dynamics in drylands is detailed in refs. 4 and 5, while several specific contributions relate to it (e.g., refs. 14 and 15). Quickly too, patterns outside the arid lands alone were approached in ecosystems as varied as peat bogs, mussel beds, etc. (2, 3).

Despite that archetypal, strikingly regular spatial patterns inspired most of the aforementioned efforts, it is obvious that a dominant share of observable real-world patterns are irregular. Understanding patterns, whether regular or irregular, not only matters for grasping their role in ecosystem functioning but is also hypothesized as a way to get indicators, or "early warning signals" of possible ecosystem collapse under external stressors, such as drought, overgrazing, etc. (2, 16, 17). This question remains timely although several recent contributions have rather underlined how the relations between patterns properties and the dynamics in progress are often complex (13, 15, 17, 18). Irregular patterns are of different sorts and have been interpreted following different theoretical lines. "Localized structures" have been frequently highlighted as additional outcomes of models aimed at explaining regular patterns (9, 10, 15). In spite of irregular spatial distribution, localized structures display as signature a dominant patch size. Scale-free spatial patterns (14–16) have been studied and hypothesized as dynamical outcomes in ecological systems displaying strong positive feedbacks and devoid of negative feedbacks. This precludes regular pattern formation while enabling patchiness through long-lasting phase coexistence (1). In these systems, patch-size distribution is expected to follow power-laws (14, 16, 18). Considering the variety, the complexity, and the importance of the subject, it is obvious that the questions linked to nature, resilience, and stability of irregular patterns deserves increased attention.

In PNAS, Siteur et al. (1) highlighted a particular subset of patterning processes, which may result in irregular patterns having specific properties in terms of patch-size distribution and patch dynamics. Such process has been so far largely overlooked in ecology. It characteristically features the interplay between two forms of a given substance. One form is mobile and the other sessile, while the two corresponding quantities sum to a fixed amount assuming neither creation nor leakage in the whole system. This contrasts with most published models addressing patterning processes that are referred to as "dissipative" for featuring a critical substance flowing (explicitly or not) through the system. For instance, existing dryland models entail (or invoke) water dynamics that vegetation either consume or concentrate/preserve from evaporation or runoff.

From this premise, the authors propose a generic framework that may accommodate patterns resulting from phenomena as diverse as plant-nutrient cycling, picky grazing by herbivores, or sand movement in vegetated dune fields, with

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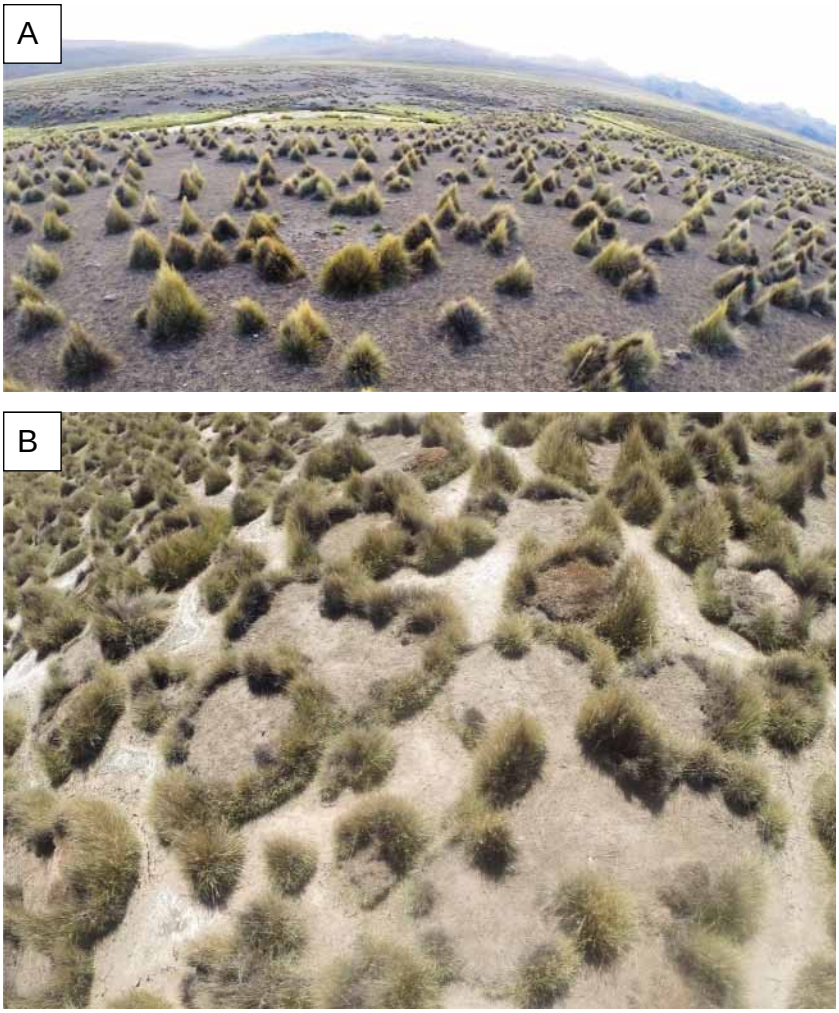

Fig. 1. Is this system dissipative with SDF or conservative with density-dependent aggregation? *A*—Top, Tussock grass pattern in the Andean Altiplano (Sajama National Park, Bolivia, see ref. 9 for context, photos: courtesy F. Anthelme). In this very case and apart from patch-size distribution, observations from a specific area (b—bottom) showing spiral patterns rather plead for localized structures and curvature instability (as in ref. 10) from SDF.

likely applicability to additional real-world examples. As idealized example, let us consider an ecosystem intrinsically poor in a key nutrient, such as nitrogen, as in many grasslands (e.g., ref. 19). The conceptual model assumes part of the nitrogen (say, u) trapped in plant biomass and part (say, v) mobile in the soil. Plants capture N from v and release it through death and biomass decay. Local N concentrations of the u and v forms may vary in space, but the overall quantity remains constant over the system/landscape (an assumption that we will not ecologically discuss here).

From this framework of conservative interplay between mobile vs. fixed forms, the authors defined the "density-aggregation" model as belonging to a specific category (namely, "conservative reaction-diffusion") of the well-known reaction-diffusion models. u and v being the fixed and mobile fractions, the density–aggregation model stands as (after appropriate scaling):

$$\begin{aligned}\frac{\partial u}{\partial t} &= f(u,v)+\delta\left(\frac{\partial^2 u}{\partial x^2}+\frac{\partial^2 u}{\partial y^2}\right)\\ \frac{\partial v}{\partial t} &= -f(u,v)+\left(\frac{\partial^2 v}{\partial x^2}+\frac{\partial^2 v}{\partial y^2}\right)\end{aligned} \qquad [1]$$

As first specificity, both equations have the same reaction term, $f(u,v)$ with converse signs, in accord with the conservation of $u + v$ as a constant amount (τ). Therefore, $f(u,v)$ includes both fluxes from v to u (demobilization, e.g., plant uptake) and fluxes from u to v (mobilization, e.g., via biomass decay). δ is the ratio of the u to v diffusion rates (i.e., diffusion ratio). In the field of reaction-diffusion systems, the authors placed the conservative system of type Eq. 1, in the class of "activator-depleted substrates" (u being called "activator" and v "substrate"). This can be illustrated in our idealized example of nitrogen-grass tussocks, simply saying that living plant biomass is autocatalytic ("activator") at least at low local density, depletes the N resource ("substrate") as it grows, and keeps it trapped until the plant tissues die and decay. The emergence of patterns requires as additional feedbacks that the activator (here plant biomass) reduces substrate release (e.g., through decreased tissue mortality) and/or amplifies depletion (e.g., through increased nutrient uptake).

Using qualitative analyses and complementary simulations of their general model, the authors established conditions for patterning from diffusive instability and drew characteristic properties of the patchy state, notably with respect to δ and τ as main driving parameters. Patches are here local maxima of the focal substance under its two forms. Without much loss of genericity, they specified (in Table 2) the form of a general model addressing examples of plant-nutrient and plant-sand dynamics (the "picky

gazing" modeling is a little bit specific). In these two cases, the plant density is supposed proportional to u, which induces proportionality between plant and patch covers (e.g., in figures 4 and 5 in Siteur et al.). Moreover, patch-size distribution is expected to be log-normal while there is a slow, overall patch coarsening through time. This is due to the intrinsic instability of the smallest patches that progressively release the focal substance and thereby allow larger patches catching it. Interestingly, coarsening leaves unchanged the shape of the patch-size distribution (once rescaled by mean patch radius). Any local disturbance is speeding up coarsening since smallest patches never recover (figure 4). For this reason, the authors highlight the higher vulnerability of patchy systems originating in the density-dependent aggregation (DDA) process compared with outcomes of SDF. This lack of resilience at local scale is not expected for the entire system in which the focal substance is assumed conserved in coarser patches. The concerns of disturbance mitigation or ecosystem restoration are thus shifted toward the broadest scales. In the real world, this may raise questions about boundary conditions and minimum extents for system viability.

The contribution of Siteur et al. (1), is another example of the fruitfulness of introducing physical methods in ecology. It installs DDA as a distinct patterning process, which may be of potential relevance to interpreting a vast array of ecological systems. Theoretical findings on patch-size distribution can provide clues that DDA is at play instead of other mechanisms, such as SDF or sole positive feedbacks. Coarsening may be more equivocal since it has already been encountered in some SDF models (see the "global competition model" in ref. 5 p.141, or ref. 8 relating to the Swift–Hohenberg equation). Moreover, in many real ecological systems (e.g., ref. 20), several patterning processes may simultaneously be acting. In the famous patterns of banded vegetation (tiger bush), some observers underlined the role of a "sandy veil" 21, which conservative dynamics may interact with the dissipative vegetation-water dynamics.

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In real-world systems that are intrinsically heterogeneous and experiencing disturbances, tracking signatures of specific processes through indicators is naturally tricky, yet necessary as to nurture the fascinating dialogue between models and nature. A snapshot of a certain pattern (as in Fig. 1*A* here), whatever its impressiveness is rarely unequivocal about the underlying mechanisms. Field knowledge remains essential along with replicated observations that are fortunately increasingly available from aerial or space remote sensing. Moreover, observing large systems is often useful to access different stages of pattern development (e.g., Fig. 1*B*). The evaluation of well-identified model classes in light of rich multitemporal data sets is essential to allow ecological pattern science to progress to maturity and to provide insights into the resilience of ecosystems in the face of global change.

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