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Review Article

Spatial patterns in ecological systems: from microbial colonies to landscapes

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Self-organized spatial patterns are ubiquitous in ecological systems and allow populations to adopt non-trivial spatial distributions starting from disordered configurations. These patterns form due to diverse nonlinear interactions among organisms and between organisms and their environment, and lead to the emergence of new (eco)system-level properties unique to self-organized systems. Such pattern consequences include higher resilience and resistance to environmental changes, abrupt ecosystem collapse, hysteresis loops, and reversal of competitive exclusion. Here, we review ecological systems exhibiting self-organized patterns. We establish two broad pattern categories depending on whether the self-organizing process is primarily driven by nonlinear density-dependent demographic rates or by nonlinear density-dependent movement. Using this organization, we examine a wide range of observational scales, from microbial colonies to whole ecosystems, and discuss the mechanisms hypothesized to underlie observed patterns and their system-level consequences. For each example, we review both the empirical evidence and the existing theoretical frameworks developed to identify the causes and consequences of patterning. Finally, we trace qualitative similarities across systems and propose possible ways of developing a more quantitative understanding of how self-organization operates across systems and observational scales in ecology.

Introduction

Ecological systems can spontaneously develop highly symmetric structures from seemingly disordered configurations. Examples span a broad range of observational scales, from bacterial [1,2] to social insect colonies [3–5], to landscapes in water-limited ecosystems, wetlands, or coral reefs [6]. These self-organized structures or patterns are hypothesized to result from the effect that nonlinear interactions among organisms, and between organisms and their environment, have on spatio-temporal population dynamics [7,8]. Inter-individual interactions may establish various positive and negative feedbacks on the organisms and the environment, which might locally enhance or diminish demographic rates and movement. If positive and negative feedbacks act at different spatial scales (scale-dependent feedbacks, SDF), they can drive the emergence of a regular self-organized spatial distribution in population density [6,8,9]. Although density-dependent feedbacks often act simultaneously on demographic rates and movement [10], depending on which of these two processes is more strongly shaped by nonlinear feedbacks, it is possible to classify emergent patterns in two broad categories: demography-driven patterns in which patterns form due to SDFs modulating birth/death dynamics, and movement-driven patterns, in which the total population size is mostly conserved and individuals rearrange in space and time due to active movement with density-dependent velocity.

Organismal responses to the interactions above are shaped by evolution. Hence, in living systems, the byproducts of group activity (i.e. self-organized patterns) might be adaptive and respond to changes in the environment (but see [11]). Another feature of ecological self-organized systems is that spatial patterns emerging from such interactions may have cascading consequences that can result in

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qualitatively new system-level properties, such as reversal of competitive exclusion [12–14] and the appearance of tipping points and hysteretic loops that are key to understanding the stability and diversity of ecosystems [7,15,16]. Because, consequently, self-organized patterns connect the individual, population, and ecosystem levels, two overarching questions naturally drive research on ecological self-organization. First, what are the causes of observed patterns (that is, what are the mechanisms and individual-level interactions that create the emergent patterns)? Second, what are the ecosystem-level consequences of such patterns (that is, how does the emergent structure influence the long-term dynamics of the whole system)? In the next sections, we review self-organized ecological systems at different observational scales, with the two questions above in mind.

Microbial colonies

Due to their manageability in laboratory settings and their fast timescales, microbes provide a unique model system to test many ecological and evolutionary processes [17–19]. Among these, range expansion, which enables populations to colonize a new habitat, presents an excellent opportunity to study self-organized spatial patterns [20,21]. For example, in bacteria, range expansions are generated in lab conditions by inoculating a drop or a stripe of cell culture on a substrate (agar plate) and tracking the profile and species composition of the expanding front through space and time. Experiments with *Bacillus subtilis* and *B. licheniformis* showed that expanding fronts of bacterial colonies are fractal objects [22]. These experiments further revealed that the fractal properties depend on nutrient availability and agar concentration, which determine cell division rate and mobility, respectively [2,23–25] (Figure 1A). At high agar concentrations, the hard substrate suppresses active cell movement, and only cell division drives range expansion. Thus, when nutrients are scarce, bacteria deplete resources locally but cannot disperse and forage; consequently, cells break the radial symmetry of the initial drop and create a branched structure with a fractal dimension similar to that produced by the diffusion-limited aggregation phenomenon in physics (DLA [26]) [27,28]. If nutrients are abundant, colonies expand instead to form Eden-like patterns, with radial symmetry but wave-like fronts that are more compact than DLA and thus have different fractality [29]. A quantitative analysis of these front irregularities shows that they are determined by competition for nutrients and space [30] and caused by mechanical stresses at the propagating front that create fingering instabilities [31]. At intermediate agar concentrations, cells can move actively, and the colony pattern consists of a sequence of concentric rings that result from alternating growth and movement-driven

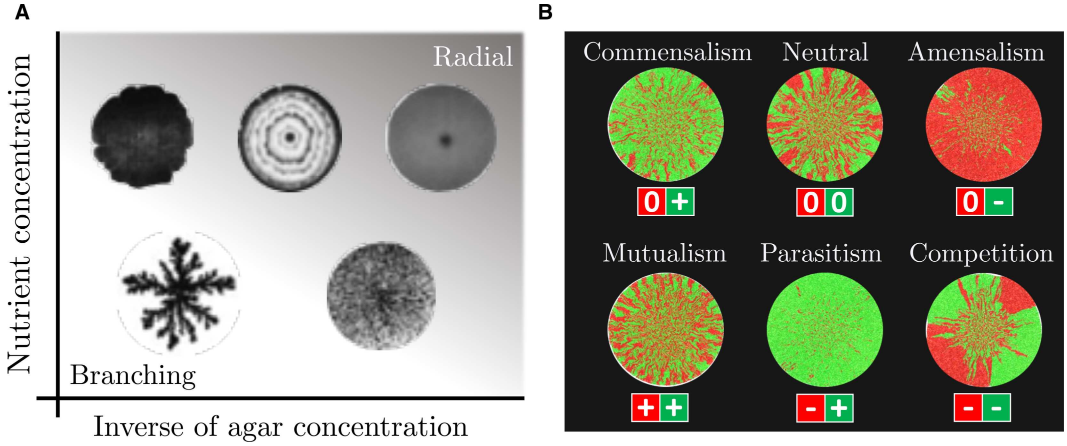

Figure 1. Emergent spatial patterns during microbial range expansion.
(**A**) Morphological phase diagram of the spatial patterns created by growing bacterial colonies of *B. subtilis*. As substrates get harder (higher agar concentration) and nutrients more limiting, the spatial symmetry changes from radial to branching. This transition is sketched by the gray-white gradient in the figure background (© (2004) The Physical Society of Japan, modified from [24]). (**B**) Community spatial structures resulting from different social interactions. Asymmetric interactions result in the extinction of the species affected negatively by the interaction whereas symmetric interactions promote species coexistence. For symmetric interactions, species mixing depends on whether the interaction is positive or detrimental for both species (adapted from [40], published under a license CC BY-NC 4.0).

expansion stages [32,33]. Finally, at low agar concentrations, cells are highly motile and expanding colonies display densely branched morphologies when nutrients are scarce and radial symmetries with smooth fronts when nutrients are abundant.

Mathematically, the simplest models that attempted to capture microbial range expansion relied on the Fisher-Kolmogorov equation, which couples logistic cell growth to constant cell diffusion [34]. These models failed to capture the rich variety of front shapes observed experimentally when agar and nutrient concentration are varied. Such variety of patterns was better explained by a more comprehensive family of models consisting of a system of coupled reaction-diffusion equations for the spatio-temporal dynamics of nutrients and active and inactive cells. Active cells move actively, grow, and divide, whereas inactive cells do nothing at all [35]. Focusing on substrate hardness and nutrient availability as the main determinants of colony shape, this framework reproduced the experimental patterns described above using different parameterizations [2,35]. Although more detailed than the Fisher-Kolmogorov equation, however, this framework still provides an oversimplified description of range expansion because it neglects many factors that could be potentially relevant during bacterial range expansions [36,37]. In colonies of sessile cells, which expand primarily due to cell growth and division, mechanical stresses at the front [38], mutations, and trophic and social interactions [39,40] are major determinants of the spatial pattern due to the dense packing and high demographic rates within the colony. In colonies of motile cells, cell movement is generally more complex than the purely random dispersal described by diffusion, and it might exhibit, for example, density-dependent speed or gradient-sensing navigation [32,41–44]. These additional processes will lead to more complex models that include advection terms to account for gradient sensing [45], the spatio-temporal dynamics of the attractant [46], density-dependent diffusion coefficients [47,48], or finite cell size (and hence excluded volume interactions) [49]. We review below the nuances associated with each of these two important drivers — demography versus movement — of microbial patterns. Other processes responsible for community structure during range expansions, such as microbial hitchhiking, are not considered here (see [21]).

Patterns driven by demographic processes

In the absence of active cell movement (e.g. high agar concentration for bacterial inoculations), colony expansion is driven by a SDF between long-range competition for nutrients and short-range mechanical stresses at the propagating front due to cell growth and division [21]. Any non-uniform spatial distribution of cells creates spatial heterogeneities in nutrient concentration, which makes cell growth rate location-dependent and ultimately creates local gradients in mechanical stress along the propagating front. These local differences create fingering instabilities that break the radial symmetry of the initial drop [31]. If the inoculum consists of a series of drop colonies randomly distributed on the substrate, expanding fronts belonging to different initial drops will eventually coalesce and generate a static spatial pattern [50]. The specific shapes of these patterns in the stationary state are determined by the shape of the fronts at coalescence, which is ultimately determined by total nutrient availability. Along a gradient of decreasing nutrient availability, bacteria transition from fully covering the surface uniformly, to forming a gap pattern, to labyrinths, to clumps. Following the clumped pattern, if nutrient concentration continues to decrease, the population collapses [50]. The long-term consequences of patterning in this case depend on whether the population is clonal or not and whether different strains are mixed or segregated in the inoculum. In clonal populations, bacterial biomass at the stationary state is accurately predicted by a well-mixed theory and hence spatial patterning does not affect system productivity. In non-clonal populations, when resources are scarce, the emergent self-organized spatial pattern and whether the different strains are inoculated in clonal groups or well-mixed affect key properties of the colony, such as the optimal spreading rate or carrying capacity [50].

Thus, the stage of colony growth at which different species interact with one another is critical to understanding pattern formation and the outcome of the interaction (i.e. pattern consequences). For example, neutral mutations occurring at the front of the expanding colony create well-defined clonal sectors that allow them to persist in large populations where they would go extinct in well-mixed scenarios [51]. Ecological interactions occurring as the colony grows from a well-mixed inoculum might change the spatial structure expected for neutral communities (Figure 1B) [40]. Asymmetric interactions (i.e. commensalism, amensalism, parasitism) tend to eliminate the species affected negatively by the interaction, and symmetric interactions (i.e. competition, mutualism) favor species coexistence at roughly equal abundance [40,52]. Furthermore, mutualistic interactions result in high species mixing, whereas competition enhances segregation (Figure 1B) [40,53–55]. If species interact on a

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stationary spatial pattern, the pattern geometry and the range of the interaction control the rate of intra and interspecific encounters, which ultimately determines the fate of the species within the colony [56–60].

Movement-driven patterns

Colonies of motile microbes (e.g. low and intermediate agar concentrations for bacterial inoculations), show a diversity of movement behaviors, including gradient-sensing navigation (such as chemotaxis) [61] or density-dependent speed [9,62]. These behaviors can lead to different colony-level spatial patterns, such as regular or elongated spots, stripes, concentric rings, branching patterns, or vortices [21]. *E. coli* cells inoculated on intermediate agar concentrations, for example, navigate gradients of cell-secreted attractants, which leads to a diversity of patterns of cell aggregates hypothesized to increase resistance to oxidative stresses [63]. Similarly, colonies of *P. aerugionsa* growing in poor nutrient conditions form a branching pattern in which branch thickness is regulated through chemotaxis to maximize biomass accumulation and colony fitness [64]. In multispecies colonies, chemotaxis allows cells to fine tune their velocity and exclude competitors from their territory [65], as well as to segregate from competitors and coexist with them in the same patch [66]. Finally, in the social amoeba *Dictyostelium discoideum*, cells respond to starvation by triggering an aggregation process that starts with the emergence of spiral waves of chemoattractant, and culminates in streams of chemotactic cells migrating towards an aggregation center where they form a multicellular fruiting body [67–69]. How many cells become chemotactic — and hence the pattern of streaming cells — depends on the community composition, and might impact its long-term ecological dynamics [70]. Chemotaxis is thus a well-documented pattern-forming mechanism in microbial systems, and chemotaxis-driven patterns are fundamental to optimizing community growth and survival, and species coexistence.

Many other microbial systems show non-trivial movement behaviors that allow them to establish spatial patterns by following attractant gradients. *Myxococcus xanthus* starving cells, for example, aggregate and form multicellular fruiting bodies similar to those observed in *D. discoideum*. Instead of following chemical gradients, however, they tune their velocity over time and aggregate because collisions between cells in crowded regions slow them down [71]. This aggregation process resembles a motility-induced phase separation (MIPS) process, which was first documented in physical systems of active particles [62]. Density-dependent cell velocity is observed in many other microbial systems and can stem from processes other than crowding, such as hydrodynamically mediated surface accumulation [72], the secretion of polymers that increase viscosity [73], or quorum-sensing regulated locomotion systems [42,74]. The latter are often linked to chemotaxis and used to initiate biofilm growth, and thus increase community resistance to external hazards [75]. Finally, some microbial systems, such as *B. subtilis* suspensions, develop chaotic spatio-temporal patterns at high population density that resemble inertial turbulence and are thus known as active turbulence [76,77]. The ecological implications of these turbulent patterns are yet unknown.

Landscapes and animal groups

At vastly larger, landscape scales, range expansions were among the first processes hypothesized as drivers for reported spatial patterns and symmetries, and typically justified using simple mathematical models. In 1905, a muskrat population escaped from a breeding farm near Prague and started to disperse through Europe. In its expansion over a heterogeneous landscape, this population created a pattern of concentric rings with irregular edges that resembles those of the Eden-like region of Figure 1A. A simple mathematical model based on the Fisher-Kolmogorov equation (and thus coupling logistic population growth to diffusive dispersal) reproduced the spreading speed of the front [78]. This model further revealed that, due to the feedback between population growth and dispersal, the muskrat invasion was super-diffusive (i.e. spreading faster than expected from a diffusive process). As a result, the area of the muskrat habitat grew faster than linearly with time. More generally, these results showed that spatio-temporal interactions between individuals could result in symmetries that are key to understanding longer-term ecological dynamics, such as the speed of a species invasion. We next review different systems in which patterns emerge within landscapes. As in the previous section, we catalogue these examples according to whether density-dependent feedbacks predominantly influence demography or movement behavior.

Patterns driven by demographic processes

Feedbacks affecting demographic rates can make population growth nonlinear and space-dependent and thus cause self-organized patterns [79]. For example, the growth and spatial distribution of seagrass is an

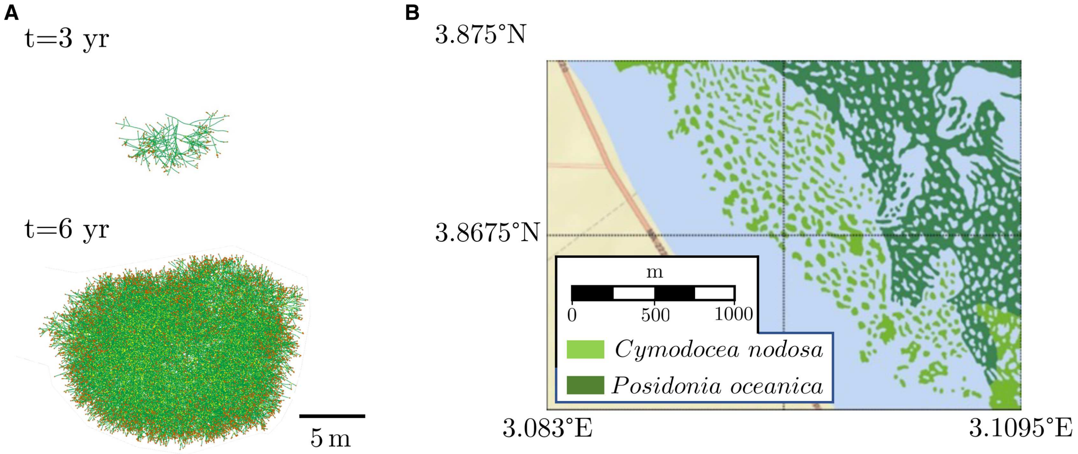

Figure 2. Seagrass spatial patterns.
(**A**) Expanding patches of the seagrass *Cymodocea nodosa* first show branch symmetry and then undergo a radial growth (image courtesy of *T. Sintes* and obtained with the model published in [82]). (**B**) Side-scan image of a seagrass meadow in Pollença bay (Mallorca Island, Spain, Western Mediterranean) showing different patterns in meadows of *Posidonia oceanica* and *C. nodosa* (adapted from [83], published under a license CC BY-NC 4.0*)*.

autocatalytic process in which patches first show a DLA-like geometry as observed in expanding bacterial colonies, and then become denser and radially symmetric (Figure 2A). This growth pattern allows patches to spread initially faster than predicted by simple radial growth [80–82]. In the long term, patches interact with each other and establish a potential SDF that results in a self-organized pattern covering kilometric submarine landscapes [83] (Figure 2B). The specific interactions that might control the SDF in seagrasses remain unknown, but it is assumed that interactions between seagrass switch from positive to negative when the distance between patches increases.

A similar SDF is also hypothesized to cause self-organized patterns observed in water-limited ecosystems, where vegetation arranges itself in gaps, labyrinths, and clumps in response to increased water scarcity [84–86] (Figure 3A). In these systems, however, models provide a more mechanistic explanation of how the SDF could operate. Vegetation patches enhance water infiltration locally, thereby favoring the growth of more plants and the transport of water from the surroundings toward densely populated patches. This water transport reinforces vegetation growth within the patch (short-range facilitation), limits plant proliferation far from it (long-range competition/inhibition) and, as a result, vegetation regular patterns emerge [87] (Figure 3B). These mechanisms agree, in a generic way, with those proposed by Turing for the patterning of animal coats [88,89]. Other hypotheses propose alternative pattern-forming mechanisms [90], including long-range competition alone [91,92]. Scale-dependent feedbacks between individuals and the environment (e.g. resource availability) are hypothesized to cause regular patterns in many other ecosystems (see [6] for a review), such as wetlands [93–96], savannas [97,98], and coral reefs [99,100]. Young mussel beds, for example, align in stripes perpendicular to the tidal flow driven by a hypothesized SDF between short-range protection against sea currents and waves and long-range competition for resources [101] (Figure 4A). When tidal flow rates are low and nutrient availability is affected by local interactions rather than by flow, stripes lose stability and become spots [102].

The ubiquity of self-organized patterns that could potentially emerge from SDFs across ecological systems prompted research to evaluate their ecological relevance. This effort has been mostly theoretical, owing to the large spatio-temporal scales at which these patterns arise. Many existing models that aim to capture these SDF rely on reaction-diffusion equations that describe the coupled dynamics between individuals and resources in space and time [6,103,104]. In these models, diffusion often accounts for biomass spreading through processes such as seed dispersal or patch growth due to demography. SDF model predictions for seagrass landscapes, water-limited ecosystems, and mussel beds suggest that regular patterning might increase system productivity and resilience to environmental change, such as precipitation decline, thus allowing patterned states to persist in regimes in which uniform landscapes would collapse [83,101,104]. The first analyses of these models further predicted that patterned ecosystems collapse abruptly if resource availability (e.g. rainfall for semi-arid

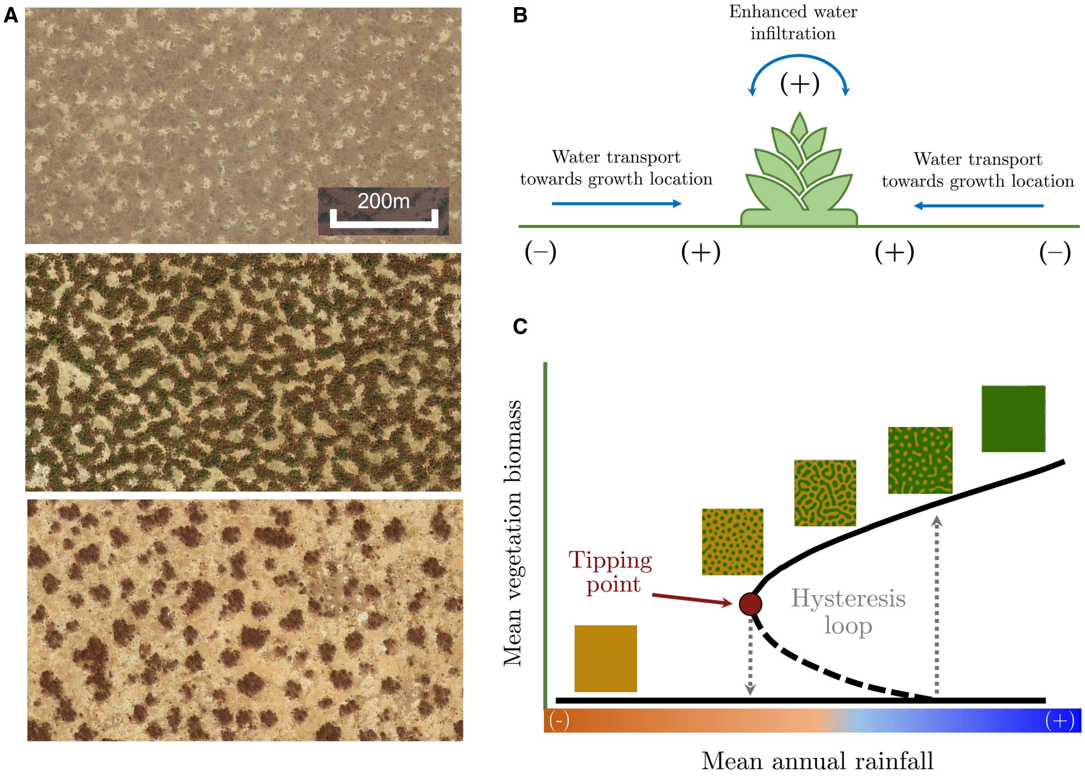

Figure 3. Vegetation spatial patterns in water-limited ecosystems.

(**A**) Aerial images of self-organized vegetation patterns. In all panels, vegetated regions are darker and bare-soil regions, lighter. (Top) Spot pattern in Sudan (11°34′55.2″ N; 27°54′47.52″ E). (Center) Labyrinthine pattern in Mali (12°27′50″ N; 3°18′30″ E). (Bottom) Gap pattern in Niger (11°1′12″ N; 28°10′48″ E). Microsoft product screen shot(s) reprinted with permission from Microsoft Corporation. Image Copyrights ©2021 Maxar. (**B**) Scheme of the mechanisms proposed for the hypothesized SDF underlying self-organized vegetation patterns. (**C**) Vegetation clumps as hypothesized early-warning indicators of abrupt ecosystem collapse in early models of vegetation pattern formation in water-limited ecosystem. Schematic illustration provided for visualization proposes, see [108] for a more rigorous picture.

ecosystems or algal concentration for mussels) falls below a certain threshold, with the population forming clumps triggered by resource scarcity close to that threshold. Moreover, these models report a hysteresis loop that hinders ecosystem restoration after collapse (Figure 3). Hence, according to these results, clumps could be early-warning indicators of ecosystem tipping points [105,106]. More recent work theorizes that spatial patterns allow water-limited ecosystems to evade abrupt desertification processes because the rearrangement of vegetation spatial structures as water availability decreases buffers the effect of environmental changes and prevents ecosystem-level vegetation extinctions [107,108] (Figure 3). However, the abrupt transition may instead be replaced by continuous desertification when demographic noise is added to these deterministic models [109,110]. Continuous desertification and the absence of a hysteretic loop are also predicted by models based on long-range competition alone that are able to qualitatively replicate the same spatial patterns [111]. Although data-driven studies have begun testing these opposing predictions using remote-sensed data [112,113], identifying the ecosystem-level consequences of these patterns remains an open question.

All patterns discussed above emerge from the coupling between demographic and environmental processes in homogeneous landscapes. When the landscape is heterogeneous, due to e.g. microreliefs created by geological feedbacks in expansive soils [114], soil-vegetation feedbacks such as plant autotoxicity [115,116], or the action of soil-dwelling macrofauna [117–120], heterogeneity will influence the feedbacks between organisms and the environment and can potentially affect the ecosystem-level consequences of the resulting pattern. In water-limited ecosystems, for example, plant autotoxicity can create traveling waves of vegetation density that might have a positive effect on species coexistence [115,116]. Soil-dwelling termites generate a hexagonal

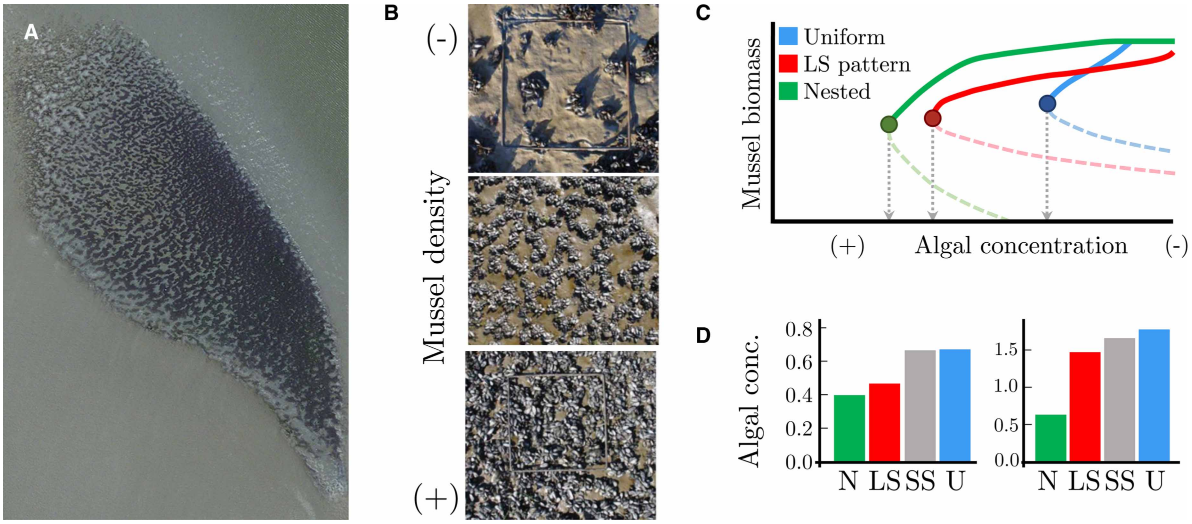

Figure 4. Spatial patterns in mussel beds.

(**A**) Large scale patterning in a mussel bed in the Dutch Wadden Sea. The image was taken from a topological map featured on BAG viewer, an interactive map powered by Kadaster, and is reproduced under the licence CC-BY Kadaster (adapted from [102]). (**B**) Small-scale patterns of mussel aggregation driven by density-dependent movement at different mussel densities (adapted from [123] with permission from the authors). (**C**) Schematic representation of how both large-scale (LS) patterns alone and combined with short-scale aggregation (nested) modify population collapses (sketched using results in [10]). (**D**) (Left panel) Algal concentration at which the mussel population collapses under different self-organization regimes. (Right panel) Algal concentration at which mussel biomass recovers following an external perturbation (data extracted from [10]). U: uniform population, SS: small-scale patterns, LS: large-scale patterns, N: nested patterns.

pattern for soil productivity emerging from competition between colonies [121]; such heterogeneity in soil productivity is hypothesized to strongly impact the way these ecosystems collapse, making this transition smoother and easier to revert [110,118,122].

Patterns driven by density-dependent and gradient-sensing movement

Macroscopic systems can also self-organize due to complex movement behaviors, and movement-driven patterns can form as independent structures or, sometimes, even within larger-scale patterns formed by demographic processes. Continued research on the large-scale mussel bed patterns discussed above found an additional, small-scale regular spatial pattern that was attributed to a concave-up relationship between mussel speed and conspecific density [123,124]. Mussel speed first decreases and then increases as mussel density increases locally around a focal individual. This nonlinear behavior makes mussels arrange into short-scale regular spatial patterns whose shape is determined by mussel density [123] (Figure 4B). The rules behind this aggregation process are the same as those governing phase separation, the physical process by which a homogeneous mixture separates into two different phases [123]. The joint action of density-dependent movement and the hypothesized SDF linking population dynamics, resource availability, and environmental processes, leads to mussel patterns with two characteristic scales, one per each of the pattern-forming processes. These nested patterns have important ecological consequences because they allow mussel beds to survive at lower resource concentrations [10] (Figure 4C,D).

More complex behavioral rules for individual movement that also include individual alignment with neighbors can create a diversity of patterns of collective motion. Examples include bird flocks, fish schools, or animal herds [5,125,126], subjects of intense research over the last decades. Early efforts to model these emergent phenomena used individual-level simulations in which each organism moved at constant speed in a direction that mimics, with some error, the mean orientation of its nearest neighbors [127,128]. When the error in alignment is high and population density is low, individuals move randomly. When the error in alignment is low and population density is high, however, individuals follow rectilinear trajectories that minimize collisions between individuals and facilitate group movement [127]. These simple simulation setups can be improved by

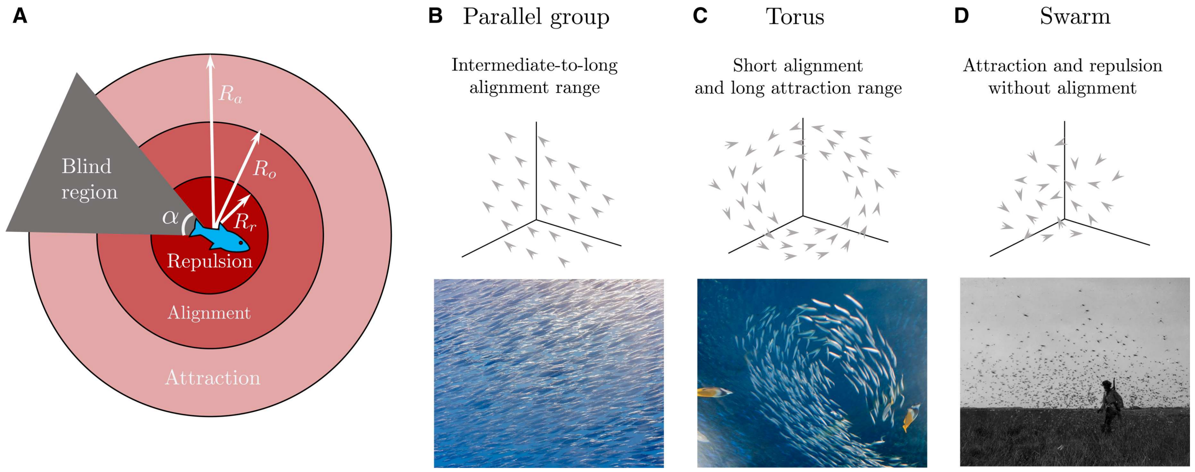

Figure 5. Emergent patterns of collective behaviors in animal groups.

(**A**) Representation of an individual in the model by Couzin et al., 2002 [129] with the three neighborhoods affecting attraction, orientation, and repulsion defined by their ranges. The possible ''blind volume'' behind an individual is also shown by the gray triangle. (**B**) (Top) Representation of a simulated parallel group. (Bottom) School of trumpetfishes (*Macroramphosus scolopax*), Faial-Pico Channel, Azores Islands, Portugal. Source: commons.wikimedia.org, contributed by Diego Delso under CC BY-SA 4.0 license. (**C**) (Top) Torus simulation outcome. (Bottom). Prey fish schooling or shoaling forming a circular bait ball in a defensive move against predation flanked by two larger butterfly fish. Source: commons.wikimedia.org, contributed by Lifefish under CC BY 3.0 license. (**D**) (Top) Swarm simulation outcome. (Bottom) A locust cloud over Juncus maritimus at Imililik, Western Sahara (April, 1944). Source: commons.wikimedia.org, contributed by Eugenio Morales Agacino's Photographic Archive and provided by the Universidad Autónoma de Madrid (Spain) under CC BY-SA 3.0 ES license.

considering anisotropic fields of perception and individual velocities that depend on the presence of others within different zones centered at the focal individual [129,130] (Figure 5A). The latter models exhibit diverse patterns of collective behavior depending on the relative weights of these three interaction zones/forces [129] (Figure 5B–D). Moreover, transitions between these emergent behavioral patterns are abrupt and triggered by small perturbations in individual movement, suggesting that animal groups moving collectively can respond effectively to both internal and external challenges — such as hunger or predation (following resource gradients through effective group chemotaxis, or spreading information about an impending predatory attack or the location of good-forage regions [131–133]) — and maximize their fitness by adopting the most efficient group structure in each scenario [129,134,135].

The spatio-temporal patterns of collective behavior discussed above are often influenced by environmental properties, especially in migratory species that show coordinated patterns while moving from one seasonal habitat to another. For example, every year, hundreds of thousands of herding wildebeest migrate, together with individuals from other species, on a loop path through Tanzania and Kenya tracking local gradients of high-quality forage [136]. Migrating herds show wavelike fronts similar to those formed by expanding bacterial colonies (Figure 1A) due to the presence of leaders with preferred direction of motion [125,137]. Over the years, migratory species maximize their annual fitness and grow larger population sizes than non-migratory species with which they share habitats [138]. Wildebeest are the most abundant herbivore in the Serengeti ecosystem, outnumbering all the other herbivores combined [136]. The spatial patterns emerging from these migrations have nontrivial ecosystem-level consequences, as migrants transport tons of nutrients every day and are source of food for multiple species of predator and scavenger [139–141].

Linking scales and future perspectives

The micro-scale and macro-scale patterns described above share important features, despite emerging at very different observational scales. Non-motile bacterial colonies expanding on nutrient-rich environments exhibit a fractal structure with wave-like fronts [24] that are qualitatively similar to those observed at much larger spatial scales in spreading seagrass patches [82], species invading into heterogeneous landscapes [78], biome transitions between savanna and tropical forest [108], and migrating wildebeest [137]. On the other hand, non-motile bacteria colonies growing on low nutrient concentration create branched patterns with very thin branches that are well described by diffusion-limited aggregation and are akin to those in young seagrasses [24,82]. At long time scales, bacteria and seagrasses, but also vegetation in water limited systems and mussels in their beds, can form regular static patterns whose shapes follow the same sequence as environmental conditions worsen (gaps, labyrinths, and clumps). Interestingly, these stationary structures often form when expanding populations coalesce, with the geometry of the expanding front determining pattern shape, which establishes a link between the short-term and long-term patterns discussed in previous sections. The fact that these patterns share some of their statistical properties has raised the possibility that pattern formation across ecological systems and scales could be quantitatively described by 'universal' physical principles and thus described by a unifying mathematical framework.

Turing scale-dependent feedback ('TSDF' henceforth, for concreteness) and its associated Turing instability have been proposed to be the unifying principle for spatial pattern formation across ecological systems [6]. Associated models have provided important insight into how self-organization could be operating in natural systems and how it could impact ecosystems at various levels. However, there is still very little direct empirical work supporting TSDF — or any other unifying mechanism — and very different processes, leading to mathematically different symmetry-breaking instabilities, can generate patterns similar to those of TSDF. For example, a SDF involving short-range mechanical pushing and long-range competition for resources might induce a fingering symmetry-breaking instability and generate gaps, labyrinths and clumps of bacteria in response to nutrient scarcity (see section 2). Other theories suggest that long-range negative feedbacks alone are enough to create these same patterns (see section 3). Importantly, these three pattern-forming mechanisms predict very different system-level emergent consequences of spatial patterning. TSDF-based models predict abrupt ecosystems collapses and the existence of hysteretic loops that hinder ecosystem recovery [86]. Models evoking different SDFs, such as those with short-range mechanical pushing and long-range competition for resources, predict a smooth collapse of the population without hysteresis following the clumped pattern characteristic of low-nutrient scenarios [50]. A similar smooth collapse is predicted by models that replicate observed vegetation patterns in water-limited ecosystems using only long-range negative feedbacks [111].

The heterogeneity in mechanisms described above for the same patterns sets a challenge for the development of any unifying framework for self-organized pattern formation in ecology. We envision a few promising directions of future research that, even if they might eventually negate the existence of general principles for self-organized patterns in ecology, would deepen our understanding of how patterns form across systems and observational scales. Recent progress in synthetic biology, for example, has enabled testing some of these principles in artificial microbial communities [142,143], providing a good starting point to design larger-scale experimental setups that can potentially unveil empirical evidence of the mechanisms driving self-organized patterns at those observational scales. The strength of some individual-level processes is hard to measure in macroscopic systems. Thus, microcosm experiments, especially engineered systems, might provide a good testing ground to discard or confirm their importance in driving self-organized pattern formation. Finally, data-driven approaches based on inference methods and machine learning used to extract directly from observational data the interactions underpinning observed patterns have already provided promising results [144,145]. Work in this direction has so far focused on small systems in which individuals are easily recognized and high-quality data can be recorded [146]. Extending these methods to more complex scenarios will hopefully result in powerful tools to quantitatively unveil the principles behind self-organized patterns in ecology.

Summary

- Self-organized patterns, resulting from interactions between individuals and the environment, are ubiquitous in ecological systems and can result in qualitatively new system-level properties.

- Seemingly identical pattern shapes are observed across observational scales, from microbial communities to landscapes.

- Seemingly identical pattern shapes might be caused by different underlying processes and thus result in qualitatively different system-level consequences.
- The question remains as to the extent to which the rich variety of self-organized patterns observed in nature can be explained by a set of common principles.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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Author Contributions

R.M.G. drafted the first version of the manuscript. All authors conceived and designed the work and revised the manuscript.

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Abbreviations

LS, large-scale; MIPS, motility-induced phase separation; SDF, scale-dependent feedbacks.

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