



Review

Phase separation driven by density-dependent movement: A novel mechanism for ecological patterns

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Abstract

Many ecosystems develop strikingly regular spatial patterns because of small-scale interactions between organisms, a process generally referred to as spatial self-organization. Self-organized spatial patterns are important determinants of the functioning of ecosystems, promoting the growth and survival of the involved organisms, and affecting the capacity of the organisms to cope with changing environmental conditions. The predominant explanation for self-organized pattern formation is spatial heterogeneity in establishment, growth and mortality, resulting from the self-organization processes. A number of recent studies, however, have revealed that movement of organisms can be an important driving process creating extensive spatial patterning in many ecosystems. Here, we review studies that detail movement-based pattern formation in contrasting ecological settings. Our review highlights that a common principle, where movement of organisms is density-dependent, explains observed spatial regular patterns in all of these studies. This principle, well known to physics as the Cahn–Hilliard principle of phase separation, has so far remained unrecognized as a general mechanism for self-organized complexity in ecology. Using the examples presented in this paper, we explain how this movement principle can be discerned in ecological settings, and clarify how to test this mechanism experimentally. Our study highlights that animal movement, both in isolation and in unison with other processes, is an important mechanism for regular pattern formation in ecosystems.

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1. Introduction

When left undisturbed, ecosystems can develop striking regular spatial patterns and patchiness, caused by the interactions among organisms or between organisms and their environment [1,2]. Such self-organized spatial patterns have been found in a wide range of ecosystems, ranging from arid bush lands to marine corals [2–4]. So far, most studies explaining spatial patterns in ecosystems highlight spatial variation in processes such as growth, birth, mortality or respiration, as the driving process (from hereon called growth-based processes). This variation is considered to result from the interplay of multiple interactions between organisms operating at different spatial scales. For example, localized facilitation between individuals in combination with large-scale competition for resources generates regular spatial patterns in for instance bushland vegetation just south of the Sahara as well as in mussel beds in the Wadden Sea [5–9]. Self-organized spatial patterns are considered key to understanding ecological stability [10], diversity [11] and ecosystems functioning [7,9,11–14]. Hence, understanding of the processes driving pattern formation is important to understand how these systems may respond to, for instance, climate change.

A multitude of studies have linked regular pattern formation in ecosystems to the activation–inhibition principle developed by Alan Turing [15] and Hans Meinhardt [16,17]. This general mathematical principle proposes that the interaction between a self-amplifying activation process operating at small spatial scales and an inhibiting process that operates at a larger spatial scale can explain pattern formation in a wide variety of chemical and morphological systems (see Box 1). Essential here are a *diffusive* or *differential flow* instability, meaning that the rate of spread of the inhibitor – either through diffusion or through flow – significantly exceed that of the activator. This causes the effect of the activator to remain local, while the inhibitor exerts its effect also at larger distance. As a result of this, there is a scale-dependent feedback of organisms on the *growth* of neighboring conspecifics. Locally, there is a positive feedback, where organisms promote each other's growth, but at a larger distance a negative effect on growth predominates.

Recent papers highlight the importance of adaptive animal behavior in explaining patterns observed in nature [12, 18–25]. Here, animals aggregate to form concentrated groups, clumps, herds, or schools in order to avoid predation, dislodgement of other losses they face increasingly when alone. Within the groups, they experience lower chances of predation by means of dilution of predator attention, can confuse predators in isolating an individual, or can benefit from the vigilance of others in the group and thereby improve food intake [26]. To form groups, animals must adjust their movement and other forms of behavior, in the first place by moving towards others when they are alone, but most importantly by adjusting their movement speed when they have merged to form a group [12,24,27–29]. This adaptive behavior is essentially density-dependent, as it adjusts to the local density of conspecifics. Density-dependent movement can lead to the formation of groups that, in combination with constraints on the total number of animals, leads to regular or semi-regular distribution of groups in the landscape [29]. This mechanism of pattern formation is fundamentally different from Turing's activator (facilitation)–inhibition mechanism. Rather than organisms affecting each other's growth rates, this mechanism centers around animal behavior, where animal movement adjusts to variation in density, amplifying this variation to form aggregations that in turn form coherent spatial patterns (see Table 1 for a summary for different ecosystems). Although the implications of density-dependent movement for population dispersal has been treated in studies going back to the classic work on clines and spread [30–34], it has received little attention as a general mechanism of self-organization in ecological theory.

In this paper, we review studies on movement-driven self-organization in ecological systems. We show that many recent studies adhere to the physical principle of 'phase separation' [35], either in a direct mathematical way [24,29, 36,37] or by revealing the characteristic movement patterns. So-far unrecognized in ecology, this principle explains movement-driven self-organization in a wide range of physical [28,29,38,39] and chemical systems [40,41] and as we will argue, also ecological systems [24]. To keep the scope of the paper manageable, we only consider the mechanisms that could reasonably be termed as 'density-dependent' movement, and that deal with self-organization dynamics.

First we briefly explain the limitations of the traditional models of spatial population dynamics that can be found in many textbooks [4,31,42]. We then review a number of studies on a diverse group of species that highlight how density-dependent dispersal can generate aggregation and – in some occasions – regular pattern formation. We discuss the conditions under which phase separation occurs and whether these conditions are likely to be common. We limit ourselves to the processes of animal aggregation and group formation, and will not extensively discuss the behavior and coordination of animal movement within groups, which is extensively discussed in the literature on collective animal movement [43].

Box 1: The activator–inhibitor and phase separation principles

The models of Turing (1953) and Cahn–Hilliard (1958) outline two fundamentally different principles of spatial self-organization. Turing’s model for pattern formation is based on the interaction between (minimally) two species, an activator and an inhibitor (Box 1: Fig. 1A), which disperse at different rates in space. The interplay between the activator and the inhibitor results in spatial variation in net growth of or rate of reaction between interacting species, which amplifies local variability, leading to the formation of spatial patterns. In contrast, the model Cahn and Hilliard for phase separation and subsequent pattern formation only requires a single species, whose net movement switches between aggregation and dispersion as a function of its own local density (Box 1: Fig. 1B).

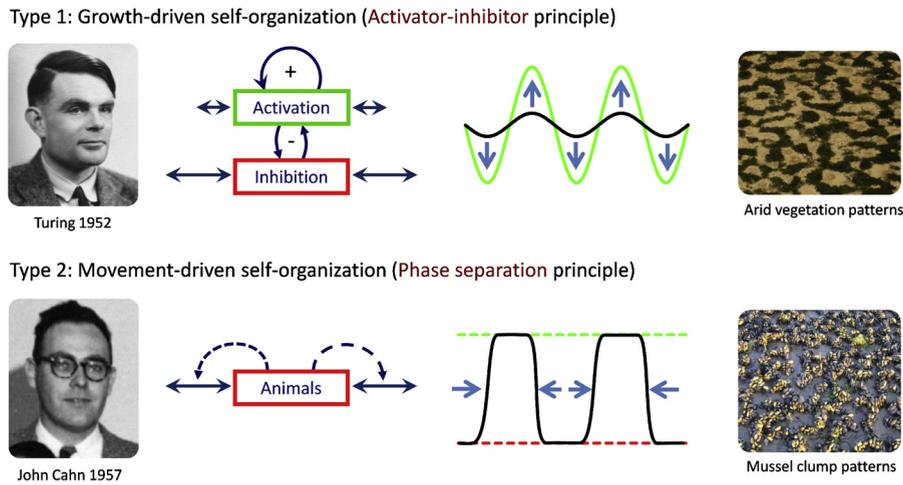


Fig. 1. (A) Alan Turing’s (1912–1954) principle for spatial pattern formation, based on the interaction of an activator and an inhibitor. Here, the activator promotes its own growth, but also generates an inhibitor that limits activator growth. The two species diffuse through the system at different rates, with the inhibitor moving faster than the activator. As a result, the activator has a net positive effect on itself at short distance, but inhibits itself at longer distance, via the inhibitor. (B) The Cahn–Hilliard principle (John W. Cahn, 1928–2016; John E. Hilliard, 1926–1987) for phase separation in pattern formation. This principle is based on density-dependent movement, where species tend to disperse at low and very high density, but aggregate at intermediate density. The patterns that then develop interpolate between two stable states, one with high, and another with low biomass (red and green dashed lines). The principle has been developed initially to explain self-organized patterns in metal alloys, and formation of minerals.

Table 1
A summary of the movement-driven mechanisms on spatial self-organization in ecosystems.

Ecosystem	Spatial self-organization mechanism	Pattern formation	Refs.
Mussels	Density-dependent movement behavior	Regular striped, labyrinth patterns	[7,12]
Ants	Density-dependent movement behavior	Aggregation to clusters	[18]
Bacteria (<i>E. coli</i>)	Density-dependent chemo-taxis behavior	Striped, spotted and circuits	[48,62,66]
Birds	Resource-dependent movement behavior	Spatial regular patches	[68]
Elk (<i>Cervus canadensis</i>)	Socially inform	Collective behavior	[75]
Zebrafish	Run-and-chase behavior movement	Striped or spotted patterns	[126]
Sperm	Integrated geometry with minima drag	Collective movement	[100]

2. Models of population dynamics

Models describing the spatial dynamics of animal populations often describe dispersal of animals using a diffusion term that follows Fick's law [44]:

$$\frac{\partial N}{\partial t} = f(N, R) + D\nabla^2 N.$$

Here, N is the local density of the population, $f(N, R)$ summarizes all local growth, birth and mortality processes as a function of local densities of N and other factors R such as food availability, D is a diffusion coefficient, and ∇^2 is the Laplace operator. This formulation implicitly presumes that individual movement can be approximated by random, Brownian motion [45]. A fundamental characteristic of the use of diffusion is that in the absence of population growth or mortality, animal movement always leads to dispersion, i.e. leads to an even distribution of the population over its spatial range. For concentrations of animals to form, the term $f(N, R)$ only needs to be slightly spatially heterogeneous at the onset, i.e. growth conditions need to vary over the landscape, as is the case in Turing's model. Hence, this general formulation of population dynamics is unable to describe aggregative movement by animals, and hence precludes group formation of animals in the form of clumps, schools or herds in the absence of environmental heterogeneity.

3. A physical principle for movement-driven pattern formation

In the physical and chemical sciences, it is widely recognized that aggregation of atoms and molecules can lead to the formation of self-organized patterns, a process called 'phase separation' [35,41]. Phase separation describes the spontaneous separation of mixed fluids [38], such as molten alloys, into their separate components [39]. During this process, spatial patterns are at first often fine-grained, but they grow coarser as time progresses due to spatial separation of the components of the alloys. The physical principle of phase separation has been captured by a simple partial differential equation by Cahn and Hilliard in 1958 [35]. Under this scenario, the dynamics of the density field is governed by

$$\frac{\partial N}{\partial t} = D\nabla^2(f(N) - \kappa\nabla^2 N),$$

where $f(N)$ describes the energetic state of N , reflecting its tendency to move in response to local variation in density, and κ accounts the nonlocal diffusivity or tension in ecology and physics, respectively. Essential to the Cahn–Hilliard (CH) principle is a switch from dispersive to aggregative movement of particles as the local concentration of similar particles increases. In other words, particles move towards concentrations of similar particles, amplifying the formation of these aggregations. The Cahn–Hilliard model has become the standard description of phase separation driving pattern formation in metal alloys [39,41,46], fluid flow [40,47], and microbiology [28,48]. Moreover, recent developments in theoretical physics expand this principle to "self-propelled particles", e.g. the movement of (often microbial) organisms [28,29,36,49–51]. Here, a number of studies argue that active Brownian particles, e.g., a bacterial or algal suspension, can spontaneously separate into a concentrated and a dilute phase resulting from the movement behavior of the microbes [27,28,38].

Central to the explanation put forward by the Cahn–Hilliard model is a density-dependent relation between particle movement and the local concentration or density of similar particles. In this review, we highlight that this phenomenon is also very general to ecological systems, where animals adjust their movement speed directly or indirectly to the behavior of conspecifics. Here, it can lead to a wide range of aggregative phenomena, ranging from the formation of regular patterns, to animal concentrations such as herds and fronts, and to highly organized phenomena such as the collective movement of organisms as swarms of birds or schools of fish. Below, we review examples of each of these three categories.

4. Regular pattern formation driven by density dependent movement

Mussel beds. The blue mussel (*Mytilus edulis*) is a common filter-feeding animal living on rocky shores and intertidal flats. Mussels develop net-shaped or clumped spatial patterns at small spatial scales (less than 1 m), especially in mussel beds on soft sediments (Fig. 1a). Laboratory experiments demonstrate that both net-shaped and clumped patterns

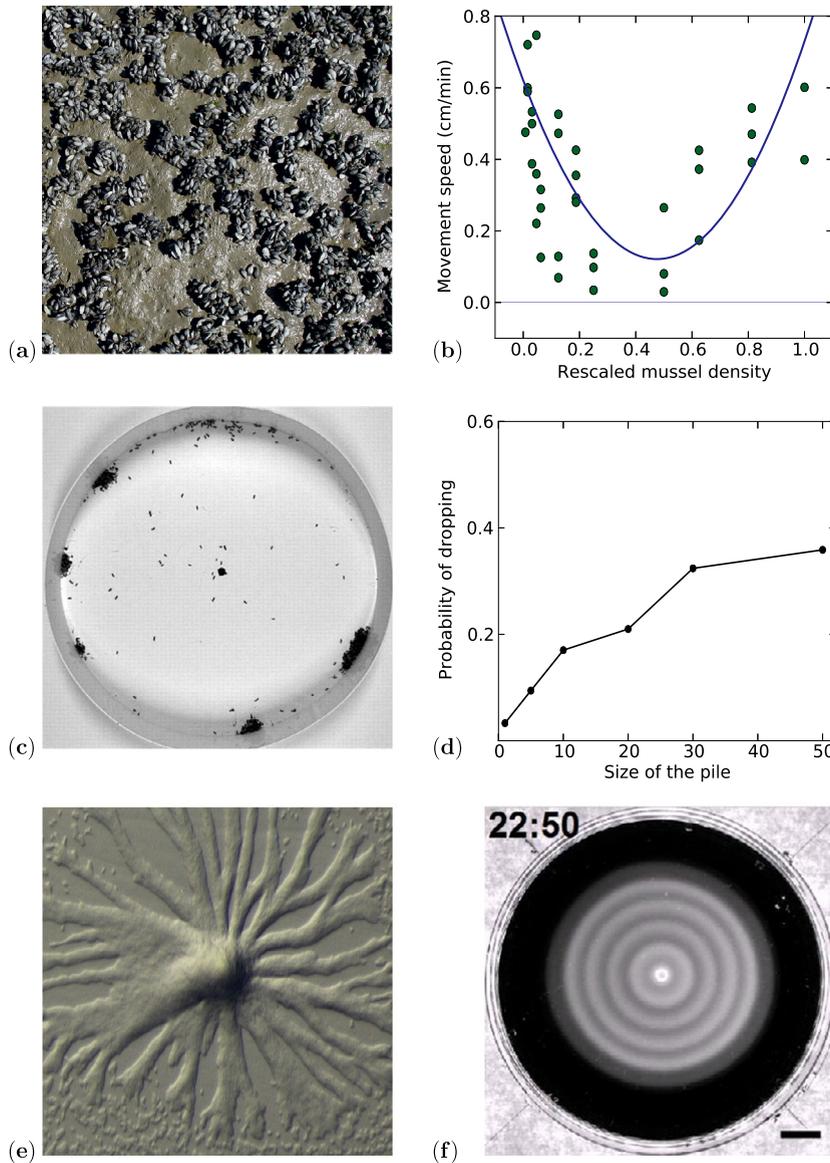


Fig. 1. **Observations of regular patterns from density dependent movement processes.** (a–b) Labyrinth patterns of small-scale mussel beds on intertidal flats (scale about 50 cm), and experimental data show that mussel-movement speed reveals a quadratic function of mussel density. (c–d) Self-organized cluster formation in ants driven by aggregation starting from a random initial condition. The probabilities of dropping a corpse remarkably depend on the local density. The data come from experiments in Ref. [18]. (e) Self-organized branching patterns in *Dictyostelium discoideum*. The cells produce alternatively lower and higher levels of cAMP concentrations as a two dimensional spiral (scroll) waves from the mutant center (later as aggregation center) to outwards, the cells move inwards from flat territories. (f) Typical circular patterns obtained for the engineered strain CL3, *Escherichia coli* [62] where the CL3 cells spotted at the center of a semi-solid agar plate, scale bar about 1 cm. Photo (a) by Johan van de Koppel; photos (c) by Guy Theraulaz; photo (e) copyright Bioayuda in Microbiología, Noticias, <http://bioayuda.wordpress.com/tag/amebas-que-comen-bacterias>; photo (f) copyright with Science, 334, 2011, 238–241.

can develop from a homogeneous initial distribution due to a behavioral response of the mussels to the local density of conspecifics [12]. Mussels move fast at both low and high density, but move much slower at intermediate densities. This leads to aggregation into clumps of intermediate size. Laboratory experiments, lasting for only a day, highlight that pattern formation at the clump scale is a purely movement-driven process; no change in mussel numbers occurs within these short experimental timescales. This process of behavioral self-organization, explaining the emergence of

regularly distributed mussel clumps, is adaptive in that it simultaneously reduces predation and dislodgment risks, and minimizes competition for algae [12].

Interestingly, our recent study of the aggregative movement of mussels demonstrates that the Cahn–Hilliard principle can be applied to spatial pattern formation in mussels [24]. Results from quantitative experiments of mussel movement revealed that mussel movement speed decreases in a characteristic fashion with local mussel density (Fig. 1b). Mathematical analysis revealed that a decrease of movement speed at intermediate density translates into a shift from dispersive movement at low mussel density to aggregative movement at intermediate density, which is an essential condition for pattern formation in the Cahn–Hilliard principle. We showed that the model of density-dependent aggregation and pattern formation in mussels is mathematically similar to the original model of Cahn and Hilliard [24]. Hence, aggregation and pattern formation in mussels is a process that is equivalent to the familiar process of phase separation in physics.

Ants. Movement-driven self-organization processes are an important factor in the building of spatial structures by social insects [18,52]. For instance, the ant *Messor sancta* creates regular patterns of ant corpses within ant cemeteries, a specific place where they gather their dead corpses. This process is completely spontaneous, as there is no prior information, nor a leader, among ants. A single cluster (pile) is gradually built as the result of a collective effort, where ants pick up a corpse from a small pile of dead bodies and then deposit the corpse in an already existing cluster. Experimental observation of ant behavior shows that ants pick up or drop corpses with a probability that increases with the local density of corpses, as shown in Fig. 1d. The unladen ants pick up corpses with a probability that significantly declines at larger cluster sizes, whereas corpse-carrying ants drop corpses with a probability that increases with cluster size [18]. In addition, ants drop corpses with a fixed probability outside piles, leading to a limited range of transport. If the size of the experimental arena is limited, or if the area contains spatial heterogeneities, ordered clusters will develop along the borders of the arena or more generally along the heterogeneities [18,53]. Such a self-organized pattern is shown in Fig. 1c. Similar to the mussel example, movement is the dominant process of pattern formation, as corpses are aggregated by density-dependent movement of the ants. Here, the chance of movement is a function of the local density of other corpses, making the net movement density-dependent.

Slime molds. Movement plays likewise an important role in the formation of fruiting bodies in colonies of the cellular slime mold, *Dictyostelium discoideum*. *D. discoideum* is a social soil amoeba with a complex life cycle. It morphs from a collection of unicellular amoebae into a multicellular slug, and finally into a fruiting body [54]. The movement of the cells of *D. discoideum* during the aggregation and the migration stages is controlled by cAMP, which is produced by the cells themselves [55–57]. At an early stage a few scattered cells spontaneously secrete a single pulse of cAMP (cyclic adenosine monophosphate), followed by cells in the surrounding vicinity secreting more cAMP. This disturbance initially triggers the movement of *D. discoideum* into a cellular aggregation, later to form connected banding that migrates towards the higher concentration of cAMP, like a traveling wave [58]. Cells in dense concentrations produce more cAMP, leading to a higher rate of aggregation for amoeba until saturating (setting a maximal speed) at high cell density [55,59]. Hence, the underlying mechanism of aggregative movement is indirectly controlled by local cell densities. The typical patterns are spiral waves in the cAMP concentrations and branching patterns in *D. discoideum* cells as shown in Fig. 1e, where the spiral wave propagates outwards, the cells move inwards [55,58].

Bacteria. The bacterium *Escherichia coli* and similarly other bacteria may form a wide variety of colony structures ranging from arrays of spots to radially oriented stripes and arrangements of more complex elongated spots [60, 61]. Alternative patterns include regular stripes and circular rings when bacteria are grown in a matrix of agar with the inducer anhydrotetracycline [62]. The traditional explanation of pattern formation in bacteria is that it is based on chemotactic behavior [63,64]. Bacteria emit a chemoattractant when they experience oxidative stress conditions. Bacterial cells are thought to sense this chemical and swim up a gradient, creating spatial concentrations of bacterial cells, after which eventually the bacteria turn nonmotile, freezing the pattern into space. However, recent studies show that the key process explaining aggregation is deceleration of movement at high cell density [27,48,62,65,66]. It can be captured by density-dependent mobility, where the swimming speed of *E. coli* changes with the density of conspecifics in the local environment. This process will lead to a net cell flow toward the high density region and spatial pattern formation (Fig. 1f).

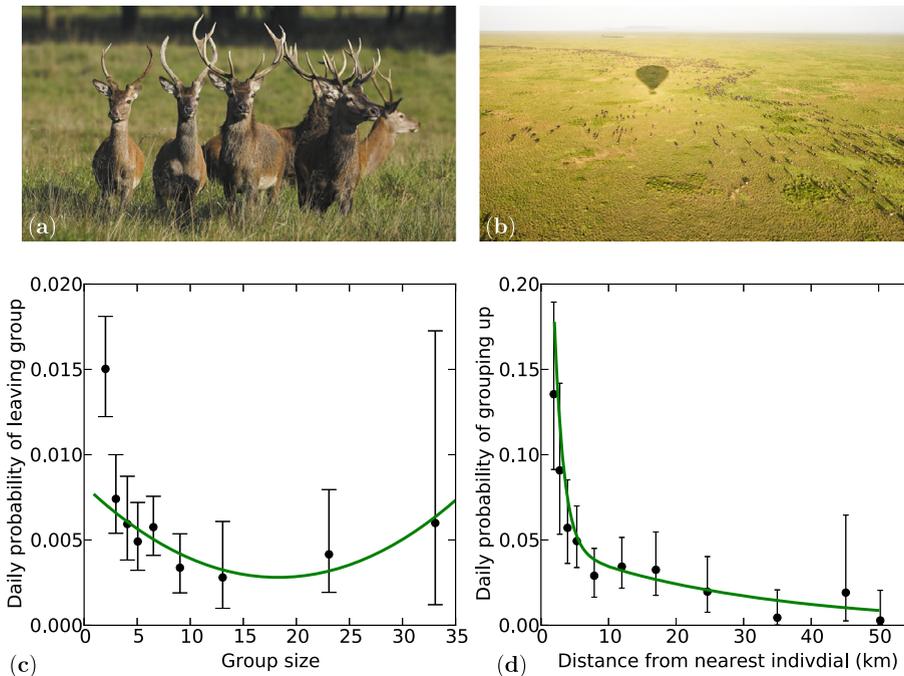


Fig. 2. **Density-dependent aggregation in mobile patterns.** (a) An aggregation of elk formed by density dependent movement. (b) Massive consumer front of wildebeest on grasslands in Africa extending tens of kilometers in length and commonly more than 1 km in width. (c–d) The daily probability of leaving a group versus group size on elk (error bars shown 2 s.e. around each point); The probability of a solitary individual grouping up with another elk versus the distance (error bars shown 2 s.e. around each point), where the fitted curve is a four-parameter exponential model, data from the Haydon et al. [75]. Photo (a) copyright with Nature, 490, 2012, 182–183; photo (b) copyright Serengeti Balloon Safaris, <http://www.balloonsafaris.com>.

5. Herds and schools: mobile aggregations

The formation of aggregations such as schools of fish or herds of mammals is very general in nature as an anti-predator defense, and is, like the mussel system, driven by movement. Hence, beyond providing a general principle for the formation of regular patterns as was described in the above mentioned examples, the principle of phase separation may extend to aggregation in mobile groups such as flocks of birds, herds of grazing mammals, and schools of fish, which are known to aggregate in response to mobile predators [67–70]. Below, we review studies that reveal that – similar to mussels and ants – density-dependent movement is a crucial mechanism behind the formation of such mobile groups.

Elk. The elk (*Cervus elaphus canadensis*) is one of the largest and most widespread land mammals in North America, Europe, and eastern Asia. Both sedentary and migratory populations have been repeatedly identified, often within the same ecosystem [71,72]. In contrast to the classic correlated random movement used in many population models, elk movements have been clearly demonstrated to be density-dependent [73,74]. Elk with GPS satellite radio-collars that were introduced into a novel ecosystem were studied over time in relation to group structure and group status (Fig. 2a). Haydon et al. [75] and Yott et al. [74] demonstrate that elk movement is driven by two important processes, described as fission (individuals leaving groups) and fusion (individuals joining up with a group) respectively. Ungrouped elk individuals were found to move greater distance than grouped animals, grouped animals were more likely to leave small groups than larger groups, and single individuals were more likely to join nearby groups than those that were more distant [75], shown as in Fig. 2c and 2d. As dispersing individuals spread out from the initial introduction site, they randomly encountered clusters of other elk individuals. Over a matter of weeks the rate of population spread slowed appreciably [73], but more importantly small clusters of individuals coalesced into local herds. Hence, similar to the other examples, density-dependent rates of movement by elk rapidly led to group formation and spatial patterning across the landscape.

Logically, the movement of aggregated (e.g., herd-forming) consumers is not only dependent on the density of conspecifics, but also on the density of their food. Here, they move more extensively when food density is low. In this case, the formation of mobile animal aggregation such as herds and schools due to density-dependent movement may have important complications for the stability of grazing systems. While aggregation of mussels has no immediate consequence for food availability because of continued supply of algae by the tidal water, herds of grazing mammals can locally deplete their sessile food. Hence, there is an immediate necessity to move as a group to avoid food depletion. This behavior has been observed in herds of grazers, for instance in the Serengeti ecosystems [76–79], where ungulates aggregate as an anti-predation adaptation, and move as a front to through the Serengeti plains as shown in Fig. 2b. The movement of individual wildebeest dramatically slows once they encounter ungrazed lands. Dense wildebeest herds rapidly deplete the grass resources available locally, leading to continual relocation of groups across the Serengeti Plains [80]. This complex combination of resource and conspecific-dependent movement behavior results in transient aggregations of wildebeest in extensive grazer fronts that track seasonal changes in the spatial gradient of food availability, often termed the green wave [77,78,81–84]. This aggregative process helps stabilize an otherwise unstable grazing interaction [85,86]. Studies of other species show that restriction of group movement by vegetation [82,83] or immediate danger of predation when moving, can cause local depletion of food sources leading to the formation of grazing fronts that can strongly destabilize consumer-resource interactions [87], such as those observed in snail-grazed salt-marshes [88] and urchin-grazed kelp beds [89].

6. Collective animal movement

Density-dependent movement can also generate remarkably complex patterns when animals not only influence each other's rate of movement, but also the directionality. This has been studied extensively in the field of collective animal behavior, a field that studies the joint movement of animals in schools and flocks. For instance, using density-dependent movement features, Farrell et al. [90] and Buhl et al. [91] showed that a group of individuals (locusts) that align their direction and patterns with that of their neighbors undergo a rapid transition from random motion to coherent motion where all individuals move in a common direction to form spotted and striped patterns. In parallel, biophysicists [92–95] showed that collective cell migration in 2-dimensional cultures reveals a similar density-dependent movement, when beyond a threshold density. These theoretical and experimental studies demonstrate that density-dependent movement is a universal ecological feature generating a multitude of complex spatial configurations, not only regular patterns. Moreover, this work suggests that collective changes in the orientation of individuals within groups could potentially be just as profound as density-dependent changes in movement velocity in generating spatial patterning. It seems quite likely both behavioral processes are relevant in explaining pattern formation in mobile group-forming organisms.

Although many studies imply that density-dependent relationships exist in collective behavior [90,92,94–96], direct experimental verification remains elusive. A very interesting example has recently emerged in a study on Sperm movement. Sperm cells race via their flagella to reach an egg in a viscous medium and the first one to get there will be able to fertilize it [97]. A solitary sperm cell is more vulnerable to deviations from a straight trajectory owing to the rotational fluctuations caused by imbalanced torque exerted by their flagellum, whereas sperm can group together to form cooperative bundles that make it easier for them to swim along straighter paths. Sperm groups have been observed in several vertebrate and invertebrate taxa, ranging from sperm pairs to massive aggregates containing hundreds of sperm [98,99]. Using the fine-scale imaging of spermatozoa of deer mice, Fisher et al. [100,101] have revealed that the sperm cells in the rodent genus *Peromyscus* form motile aggregations of 2–30 cells by adhering to one another at sperm head or head hook to midpiece (See Fig. 3a). The increased number of sperm cells within an aggregated cluster significantly increased group average velocity because the group exhibits greater linearity in its movement path, without an increase in speed. Hence, sperm cooperation allows them to migrate more quickly through the female reproductive tract. The average movement velocity would be expected to decrease once the clusters grew larger than seven cells, due to sperm cells swimming against each other, a prediction consistent with density-dependent velocity measurements (Fig. 3b). Obviously, this process does not adhere to the phase separation principle, as movement is maximal at intermediate densities, but it highlights that density-dependent movement is a crucial element in a variety of complex aggregative phenomena.

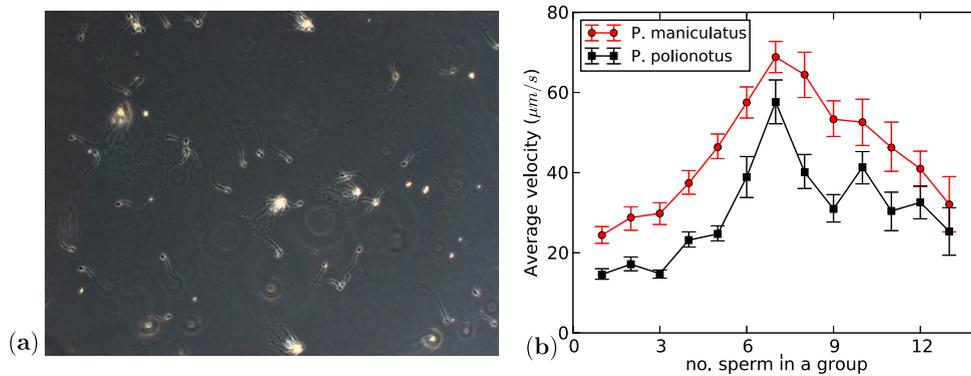


Fig. 3. **Density-dependent collective behavior of sperm cells of deer mice.** (a) Scanning electron micrographs of group formation of *peromyscus* sperm cells, starting from initial release with highly motile (more than 90% progressively motile) single cells. (b) The relationship between aggregate size and average movement velocity of the sperm cells of two species of deer mice. Figure and data courtesy of Heidi S. Fisher.

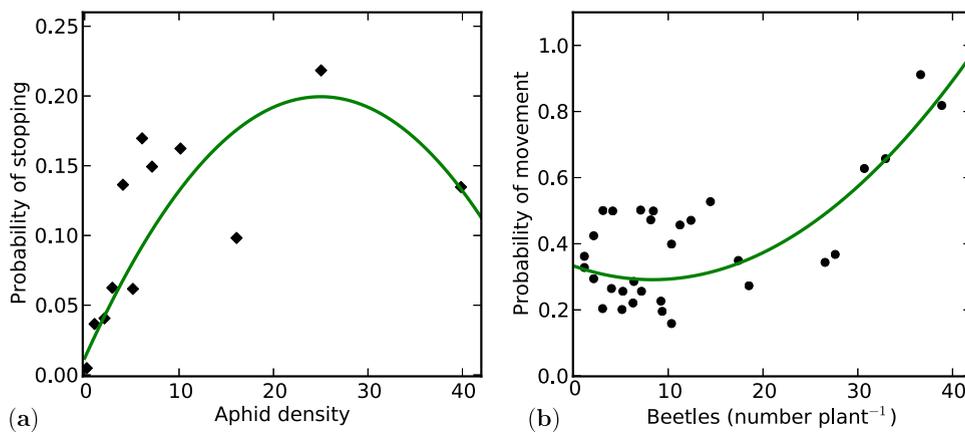


Fig. 4. **More evidence for density-dependent movement in ecology.** (a) The probability of stopping as a function of local aphid density, where the curve is a quadratic polynomial fit, data come from Ref. [102]. (b) The density-dependent motility in the Mexican bean beetle, data from Ref. [103].

7. Further examples of density-dependent movement

Empirical evidence suggests that density-dependent movement is a common phenomenon in ecology. An extensive literature exists on density-dependent movement in animals [31,33,34,102]. However, little attention has been given to how density-dependent movement affects spatial self-organization processes. Density-dependent movement rates have been recorded in social insects such as aphids and beetles [103,104] and even zooplankton [105,106]. Empirical data of aphid movement were obtained using marked *aphids varians* on fireweed flower stalks. The data show that settlement of moving aphids increased as a function of local aphid density during the first 6–8 hours following aphid released. The probability of termination of movement by the aphids increased by more than an order of magnitude as the local density increased from 1 to 40 individuals (see Fig. 4a). Similar to the aphids, the movement of Mexican bean beetles is affected by the density of conspecifics. Experimental trials show that the probability of movement was not affected by the number of conspecifics on the plant at densities lower than 20 beetles per plant (Fig. 4b). However, dispersal rates went up rapidly when beetle density was increased beyond 20 beetles per plant. Such behavior data suggest that at high population densities, beetle movement becomes overdispersive. This example, together with the others described earlier in this paper, highlights that density-dependent movement behavior is a common, yet rarely unacknowledged, phenomenon in biology [90] and ecology [12,18,103,104], and its effects of spatial patterns formation and self-organization needs further investigation.

8. Indicators of phase separation dynamics in animals

Although the model of Cahn and Hilliard can generate similar spatial patterns as those predicted by models based on Turing's activator–inhibitor principle, there are several crucial differences. First, phase separation is essentially mass conserving, as it only involves movement or diffusive processes, at least when following the standard definition and equations [35]. The activator–inhibitor principle is, to the contrary, not a mass conserving process per se, as spatial variation in growth and mortality are the essential processes. Secondly, Turing patterns exhibit a characteristic wavelength, or a number of characteristic wavelengths, under constant environmental conditions. This is the consequence of limitations in the scale of interaction between organisms [107], as the rate of movement of water or nutrients is limited by physical restrictions. In contrast, patterns arising from phase separation do not exhibit a characteristic wavelength, but pattern development is characterized by a continuously increasing wavelength, which follows a power law relationship with time, referred to as the Lifshitz–Slyozov law [41,108,109]. This process is well known as *coarsening*. In other words, the phase separation process, in mass-conserving systems, will not develop stationary patterns. However, this time-dependent power law may collapse in the long term if other process come into play that limit movement, such as in mussels where food competition limits the formation of very large clusters [24].

Going beyond the movement-driven patterns elucidated here, the pattern coarsening that is observed in the phase separation process can in principle also be found in activator–inhibitor systems when the inhibitor process is global, e.g. when there are no physical restrictions in the range of negative, inhibitory interactions between the organisms [107,110,111]. These conditions have been suggested for the FitzHugh–Nagumo (FHN) model and for semiarid vegetation when competition for limiting water resources is global [111]. However, for most ecosystems with regular patterns, such as those observed in arid ecosystems, this is likely unrealistic, as there are physical limitations in the extent that organisms can influence each other via the depletion of water. In systems with moving animals, global limitation of plant growth via the interaction with animals is more easily conceivable [112,113]. Whether mobile grazers can generate coarsening dynamics in patchy plant–herbivore systems is an important topic for future study.

A negative effective diffusivity is a prerequisite for phase separation to occur in the original Cahn–Hilliard model [24], as well as in later physical studies on abiotic particles [32,35,48]. This requirement, however, was broadened in recent physical studies highlighting that a negatively density-dependent swimming speed is a sufficient condition for phase separation to occur in case of 'active Brownian particles', i.e. organisms [27,28,37]. In case of 'self-propelled active matter', physics theory highlights, a decreasing motility with increasing local density will trigger a positive feedback, whereby an increase of the local density of individual particles leads to local slowdown, causes further accumulation of these particles. Hence, negative density dependence can cause phase separation even without explicit taxis or other orientational processes [29,49], which is confirmed by both simulations [36,50] and experiments [24,51]. The application of phase separation principles to the movement of larger organisms, as put forward in this overview, will expand the scope of this novel theory beyond the field of theoretical physics.

Classical, mass-conservative phase separation exhibits coarsening dynamics, but simple modifications of the Cahn–Hilliard phase-separation model with a linear dissipative term (i.e. mortality and birth processes in ecological terminology) may inhibit the coarsening and lead to steady state patterns with a fix wavelength [46,48]. Yet, a fundamental difference exists between pattern formation as predicted by Turing's and Cahn–Hilliard's principles [24]. The patterns arising with a Turing instability develop from a homogeneous background state, which becomes unstable with respect to small spatially perturbations, leading to the formation of regular patterns [114]. In phase separation, there is no such unstable background state, but patterns arise from the spatial mixing of two stable states (see Box 1 and Fig. 5), creating patches of either high or low biomass. There are, in general terms, only local attractive or repulsive forces among individuals that cause biased movement in case of phase separation, and that drive the dynamic development of the patterns.

The difference between the two mechanisms becomes clearer when comparing the feedback effects on net growth by the activator–inhibitor interaction with the effect of local density on the effective diffusivity in the phase separation process. A switch between activation and inhibition of either net local growth or movement characterize both mechanisms (Fig. 5). However, in Turing's model this alternation occurs in response to increased scale, while in the Cahn–Hilliard model this alternation occurs in response to biomass or density (cf. Fig. 5a and 5b). As a consequence, Turing-type systems adhere to specific scales, while no characteristic scales are observed in phase separation.

Although many Turing models include explicit activator and inhibitor components [15,42], an explicit configuration is not essential to generate a Turing instability. Spatial patterns can also develop from perturbations of an

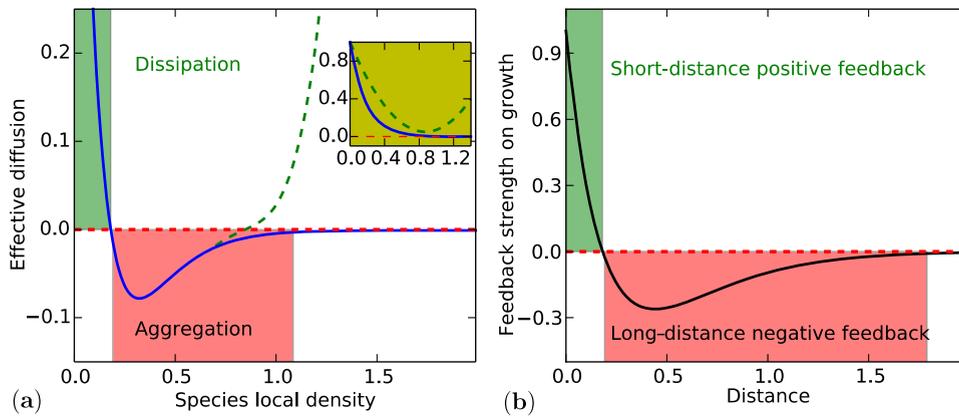


Fig. 5. Schematic representation of the feedback in the phase separation and the activator–inhibitor principles. (a) The dispersion relation of the spatial pattern between the effective diffusivity and species local density, where the two curves corresponding to the lines in the inset panel. (b) The scale-dependent feedback in the activator–inhibitor principles.

unstable homogeneous state in single-species systems, as is observed in the Swift–Hohenberg model, and in non-local competition models [114–116]. In the past decades, non-local growth and interaction effects have been proposed to produce observed regular spatial patterns in ecology and biology [115–119], which consider non-local competition for resources in a variety of biological fields [120,121]. In a population-dynamical context, these nonlocal growth and interaction models have two features in common with Turing systems, i.e. growth- and mortality-driven demographic processes and scale-depend feedback [2].

9. Outlook

Our review reveals that density-dependent effects on movement velocity and coordinated turn frequency is a ubiquitous mechanism for the formation of self-organized spatial patterns in ecosystems. Density-dependent movement, where speed declines over at least some range of local population density, can readily generate pattern formation in a wide range of ecological settings. Moreover, density-dependent movement is broadly observed in ecological systems, affecting the spatial dispersal of many organisms [103,104,122–124]. Hence, the principle of density-dependent movement can be usefully extended to other ecological systems that do not exhibit conspicuous regular patterns, but nonetheless reveal more complex forms of aggregations, such as animal herds.

Many real ecosystems exhibit complex spatial organization, revealing patterns and patches at multiple spatial scales. Such complexity does not typically stem from a single underlying process. Multiple pattern-forming processes involving movement on short time scales, and demographic and habitat-modifying processes at longer time scales are superimposed to generate complexity. Little is known about how these processes interact to shape ecosystems, and how this affects ecosystem functioning in terms of the established population sizes, and their resilience against disturbances [46,125]. Possibly, the benefits of aggregation, in terms of for instance reduced predation risk, can affect demographic process such as population losses. This has important implications, as by influencing survival, movement-driven spatial patterns are likely to affect evolutionary processes that in turn shape movement behavior [23]. Hence, to understand the functioning of complex ecosystems, research should not focus on a single process driving pattern formation, but should address how behavioral, demographic and evolutionary processes interact.

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