Chapter 6

Movement as a new process of pattern formation in ecosystems

When one has finished a substantial paper there is commonly a mood in which it seems that there is really nothing in it. Do not worry, later on you will be thinking “At least I could do something good then.”

John Edensor Littlewood, 1885—1977

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Abstract

Many ecosystems develop striking spatial patterns. This is caused by small-scale interactions between organisms, a process called spatial self-organization. Originating from the selection pressure on the participating organisms, patterns are important determinants of the functioning of the systems, promoting growth and survival, and affecting the capacity to cope with changing environmental conditions. Until recently pattern formation was explained by spatial heterogeneity in demographic processes such as growth, birth and mortality. However, a number of recent studies have led to the recognition that density-dependent movement comprises an important mechanism for pattern formation. Here, we review the studies that detail movement-based pattern formation in contrasting ecological settings. These studies highlight a common principle, well known to physics as the Cahn-Hilliard principle of phase separation. We provide a heuristic procedure explaining how this movement principle drives regular pattern formation and how to test this mechanism experimentally. Our study highlights that a behavioural process such as movement, both in isolation and in unison with demographic processes, can determine spatial complexity in ecosystems.
When left undisturbed, many ecosystems develop natural spatial organization caused by self-organizing processes (Sole and Bascompte, 2006; Rietkerk and Van de Koppel, 2008). Such self-organized spatial patterns are characteristic of a wide range of ecosystems, varying from arid bushlands to marine corals (Rietkerk and Van de Koppel, 2008). So far, spatial patterns in ecosystems have been explained by spatial variation in demographic processes such as local growth, birth, mortality or respiration (see Rietkerk and Van de Koppel, 2008, for a review). This variation is considered to result from interactions between organisms operating at different scales. An example of such a scale-dependent interaction is localized facilitation between individuals in combination with large scale competition for resources, found for example in patterned arid bushland and mussel beds (Klausmeier, 1999; Rietkerk et al., 2002; van de Koppel et al., 2005; Liu et al., 2012). Spatial self-organized patterns are considered key to understanding ecological stability, diversity (Sole and Bascompte, 2006) and ecosystems functioning (van de Koppel et al., 2005, 2008; Scheffer et al., 2009; Pringle et al., 2010; Liu et al., 2012).

In the past decade, various mechanisms of spatial self-organization in ecology have been proposed, mechanisms that are strikingly different (Theraulaz et al., 2002; van de Koppel et al., 2008; Liu et al., 2012; Klausmeier, 1999; Rietkerk and Van de Koppel, 2008; Liu et al., 2011; Cates et al., 2010). In these papers, organisms such as mussels, bacteria and ants respond to local density when moving, leading to the formation of regular patterns, or even more complex spatial structures (Liu et al., 2013, chapter 3). The net effect of such a behavioural adaptation is that organisms aggregate into clumps or colonies even in the absence of demographic self-organization processes. While demographic self-organization can take years to decades for patterns to develop, movement-driven, behavioural, self-organization can occur on very short timescales, for mollusks such as mussels even shorter than a day (Theraulaz et al., 2002; van de Koppel et al., 2008) and for flocking birds within hours or even minutes (Folmer et al., 2012). Because of its seeming ubiquity, movement-driven self-organization may be of particular relevance to the resilience of ecosystems, especially when considering disturbances that affect spatial structure.
In this paper, we review studies on movement-driven self-organization in ecological systems. We show that these examples follow the physical principle of *phase separation* (Cahn and Hilliard, 1958). So-far unrecognized in ecology, this principle explains movement-driven self-organization in a wide range of physical, chemical and as we will demonstrate, ecological systems. We discuss the conditions under which phase separation occurs and whether these conditions are likely to be common.

**Empirical evidence of behaviourally-driven spatial self-organization**

*Mussel beds.* The blue mussel (*Mytilus edulis*) is a common filter-feeding animal living on intertidal flats. Mussels develop net-shaped or clumped spatial patterns at small spatial scales (less than 1 m), especially found in mussel beds on soft sediments (see Figure 6.1A). Laboratory experiments demonstrate that both net-shaped and clumped patterns can develop from a homogenous initial distribution due to a behavioural response of the mussels to the local conspecifics densities, where their movement speed changes with local mussel density (van de Koppel et al., 2008). 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. The laboratory experiments, lasting maximally a single day, highlight that pattern formation at the clump scale is a purely behavioral process; no demographic processes are at play at these short experimental timescales. Such a process of behavioural self-organization that explains the emergence of regular distributed mussel clumps are adaptive in that they simultaneously reduce predation and dislodgment risks and minimize competition for algae (van de Koppel et al., 2008).

*Ants.* Movement-driven self-organization processes are an important factor in the building of spatial structures by social insects (Camazine et al., 2003; Theraulaz et al., 2002). For instance, the ant of the species *Messor sancta* gather their corpses at a specific place to form an ant cemetery. 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 effect, 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 behaviour shows that ants pick up or drop corpses with a probability that depends on the local density of corpses, where 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 (Theraulaz et al., 2002). 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 (Bonabeau et al., 1999; Theraulaz et al., 2002). Such a self-organized pattern is shown in Figure 6.1B. Similar to the mussel example, movement is the dominant process of pattern formation, as corpses are aggregated by density-dependent movement of the ants.

**Slime molds.** The cellular slime mold, *Dictyostelium 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 (Tyler, 1994). 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 (Tyson and Murray, 1989; Plisson and Cox, 1996; Dormann and Weijer, 2006; Hofer et al., 1995). At an early stage a few scattered cells spontaneously secrete a single pulse of cAMP (cyclic adenosine monophosphate), followed by cells in the surrounding secreting more cAMP. This disturbance initially triggers the movement of *D. discoideum* into aggregation, later to form connected banding that migrate toward the higher concentration of cAMP, like a travelling wave. Thus, cells in dense concentrations will produce more cAMP, lead to a higher movement speed for amoeba until saturating at a maximal speed at high cell density (Tyson and Murray, 1989; Hofer et al., 1995; van Oss et al., 1996). Therefore, the underlying mechanism of this aggregative movement is indirectly controlled by local cell densities. The typical patterns are spiral waves in *D. discoideum* as shown in Figure 6.1C.

**Bacteria.** The bacterium *Escherichia coli*, and other bacteria as a consequence of different movement patterns, may form a wide variety of colony structures ranging from arrays of spots to radially oriented stripes and arrangements of more complex elongated spots (Budrene and Berg, 1991, 1995). Alternative patterns include regular stripes and circular
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Figure 6.1: Observations of self-organization patterns from visible ecology. (A) Labyrinth pattern of small-scale mussel beds in intertidal flats (scale about 50 cm). (B) Self-organized cluster formation in ants driven by aggregation starting from a random initial condition (Theraulaz et al., 2002). (C) Self-organized spiral wave pattern in Dictyostelium discoideum (Palsson and Cox 1996). (D) Typical patterns obtained for the engineered strain CL3 (Escherichia coli, (Liu et al., 2011)), where the CL3 cells spotted at the center of a semi-solid agar plate, scale bar about 1 cm.

rings when bacteria are growth in a matrix of agar with the inducer anhydrotetracycline (Liu et al., 2011). The traditional explanation of pattern formation in bacteria is that it is based on chemotactic behaviour (Tsimring et al., 1995; Mittal et al., 2003), where bacteria emit a chemoattractant when they experience oxidative stress conditions. Bacterial cells are thought to sense this chemical environment 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 (Brenner, 2010; Cates et al., 2010; Fu et al., 2012; Liu et al., 2011). Specially, the direct interaction of bacteria with attractant or nutrient fields can be ignored completely (Liu et al., 2011; Cates et al., 2010). Instead, 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 in the long run (Figure 6.1D).

**A physical principle**

The studies reviewed reveal movement-driven aggregation as a new mechanism for spatial self-organization patterns, something that was not recognized within ecology beyond the work on moving vertebrates (Couzin and Krause, 2003; Folmer et al., 2012). In physics, however, it is widely recognized that aggregation can lead to the formation of self-organized patterns, in a process called *phase separation*. Phase separation describes the spontaneous separation of mixed fluids, such as molten alloys, into their separate components. During this process, patterns emerge which grow coarser in time. The physical principle of phase separation has been conceptualized into a simple partial differential equation by Cahn and Hilliard in 1958 (Cahn and Hilliard, 1958). Central to the CH principle is a switch from dispersive to aggregative movement of particles as the local concentration of similar particles increases. The Cahn-Hilliard model has become the standard description of phase separation driving pattern formation in metal alloys (Bray, 2002), fluid flow (Falk, 1992), and biological applications (Cohen and Murray, 1981; Chomaz et al., 2004).

Interestingly, our recent mathematical study of the aggregative movement of mussels demonstrates that the Cahn-Hilliard principle can be extended to understand how spatial patterns develop from the aggregative movement of organisms (see Box I). 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 CH principle. In chapter 3, we showed that the model of density-dependent aggregation and pattern formation in mussels is mathematically equivalent to the original model of Cahn and Hilliard. Hence, aggregation and pattern formation in mussels is equivalent to the physical process of phase separation.

**Box I: The activator-inhibitor and phase separation principles**

The models of Turing (Turing, 1952) and Cahn-Hilliard (Cahn and 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 I: Fig A), which disperse at different rates in space. The interplay between the activator and the inhibitor results in spatial variation in the net growth of reaction between the interacting species, which amplifies local variability, leading to the formation of spatial patterns. In contrast, the Cahn and Hilliard model 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 I: Fig B).

**Figure I:** (A) Alan Turings (1912-1954) principle for spatial pattern formation, based on the interaction of an activator and an inhibitor. Here, the activator can generate by itself-activation process and also activates the inhibitor. 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. This principle has been used to explain regular pattern formation in morphological development, chemical interactions, and ecosystems. (B) The Cahn-Hilliard principle (John W Cahn, 1928-present; 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 principle has been used to explain self-organized patterns in metal alloys, formation of mineral, and in mussel beds.

The process of phase separation as outlined by Cahn and Hilliard might provide an alternative mechanism driving regular pattern formation to the activator-inhibitor principle that was proposed by Alan Turing in 1952 (Turing, 1952; Meinhardt et al., 2003). In contrast to the movement-based CH principle, the activator-inhibitor principle is based on demographic processes, where spatial differentiation in birth rate, growth, mortality rate and decay explain the formation of patterns (see Box I). So far, this mechanism has successfully been applied to a wide range of self-organized ecosystems, such as arid lands, boreal peat lands, wetlands and intertidal mudflats (Klausmeier, 1999; van de Koppel et al., 2005; Rietkerk and Van de Koppel, 2008), describing how spatial patterns develop spontaneously resulting from of facilitative and inhibiting processes on organismal growth.

Although the model of Cahn and Hilliard’s can generate similar spatial patterns as those predicted by models that follow Turing’s activator-inhibitor principle, there are several crucial differences between them. Firstly, phase separation patterning is essentially mass conserving, as it only involves movement or diffusive processes, at least when following the standard definition and equations (Cahn and Hilliard, 1958). However, the activator-inhibitor principle is not a mass conserving processes per se, as spatial variation in growth and mortality are the essential processes. It typically involves a substance that changes in state, such as in arid systems, e.g., where surface water, essential to plant growth, infiltrates underneath vegetation to become soil water with a much lower horizontal
mobility, facilitating local growth. Secondly, Turing patterns exhibit a characteristic wavelength, or a number of these, under constant environmental conditions. In contrast, in phase separation patterns there in not such saturated wavelength, where it gradually changes, showing a power law relation between wavelength and time, which is referred to as the Lifshitz-Slyozov law (Lifshitz and Slyozov, 1961; Bray, 2002). However, this power law may collapse on the long term due to biological interaction beyond movement, as was found in mussel beds ecosystems (see Liu et al., 2013, chapter 3).

**Movement driving the spatial distribution of animals in other systems**

Aggregation at intermediate density in mussels is driven by the need for protection from wave actions and predation. The formation of aggregations such as clusters of sessile animals or herds of mammals as an anti-predator defence is very general in nature, and is, like the mussel system, driven by movement. Hence, beyond providing a general principle for the formation of patterns as was described in the above mentioned examples, the principle of phase separation may extend to aggregation in mobile organism such as birds, mammals, and fish, which are known to aggregate in response to predator presence in order to increase predator sighting efficiency (Folmer, 2012; Folmer et al., 2012), and mobile predators (Couzin and Krause, 2003; Handegard et al., 2012; Ioannou et al., 2012).

Many studies have pointed out that density-dependent movement behavior is a universal phenomenon in biology (Farrell et al., 2012) and ecology (Turchin, 1989; Turchin and Kareiva, 1989; Theraulaz et al., 2002; van de Koppel et al., 2008). Next, we highlight quantitative experimental results that reveal density-dependent movement behavior in animals under a wide range of circumstances. We start with discussing quantitative measurements of density-dependent movement during pattern formation in mussels, and show that other examples of self-organization that involve animal movement reveal similar density-dependent movement patterns (Theraulaz et al., 2002; van de Koppel et al., 2008), as well as further evidence that reveals this behavior under non-selforganizing
conditions (Turchin and Kareiva, 1989; Turchin, 1989).

Results from quantitative experiments of mussel movement revealed that mussel movement speed changes in a characteristic fashion with local mussel density (Figure 6.2A). These data were further analyzed to confirm that the relative drop in movement speed leads to negative diffusion at intermediate densities, or in other words, aggregation of mussels into intermediate-sized clumps (see chapter 3). Similar results were found for ant colonies, where experimental results reveal that the probability of dropping an ant corpse increased with pile size in the ants, as shown in Figure 6.2(B). However, unlike with mussel movement behavior, ant movement displays a monotonic relationship with local ant density.

Beyond self-organized pattern formation, empirical evidence suggests that density-dependent movement is a universal phenomenon in ecology, as was found in social insects such as aphids and beetles (Turchin and Kareiva, 1989; Turchin, 1989). Empirical data of aphid movement were obtained using marked *aphids varians* on fireweed flower stalks. The data show that settlement of moving aphids increases as a function of local aphid density during the first 6-8 hours after aphids 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 Figure 6.2C). Similar to the aphids, the movement of beetles (Mexican bean beetle) is affected by the density of conspecifics. The experiment shows that, at low beetle densities (less than 20 beetles per plant), the probability of movement was not affected by the number of conspecifics on the plant (Figure 6.2D). However, it fast went up when the beetle density increased beyond 20 beetles per plant. Such behavior data suggest that at high population densities beetle movement becomes overdispersive.

**Collective behavior.** Density dependent movement is found in a wide range of ecological settings. For instance, using density-dependent movement features, Farrell et al. (2012) and Buhl et al. (2006) showed that a group of individuals 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 and form a spotted and stripped patterns. In parallel, Méhes et al. (2012) showed that collective cell migration in 2-dimensional cultures also
Figure 6.2: Experimental evidence for density-dependent movement. (A) Experimental data showing that mussel-movement speed reveals a quadratic function of mussel density. (B) Density-dependent probabilities of dropping a corpse, the data come from experiments in literature (Theraulaz et al., 2002). (C) The probability of movement stop as a function of local aphid density, where the curve is a quadratic polynomial fit (Turchin and Kareiva, 1989). (D) The density-dependent motility in the Mexican bean beetle (Turchin, 1989).

reveal a similar density-dependent movement principle, when beyond a critical density. These theoretical and experimental studies demonstrate that density-dependent movement is a universal ecological feature generating a multitude of complex spatial configurations.
Discussion and outlook

In this paper, we review the movement as new mechanism for spatial self-organized patterns formation. Here, density-dependent movement, where movement speed varies with density of the involved organism, explains pattern formation in a wide range of ecological settings. Yet, direct experimental evidence supporting this form of pattern formation is still scarce relative to the traditional activator-inhibitor patterns as observed in, e.g., arid bush lands or boreal peat lands. Density dependence of movement is nevertheless broadly observed in ecological systems, affecting the spatial dispersal of many organisms (Turchin and Kareiva, 1989; Turchin, 1989; Ims and Andreassen, 2005; Cote and Clobert, 2007; Bitume et al., 2013). Hence, the principle of density-dependent movement can potentially be extended to other ecological systems that do not exhibit conspicuous patterns, e.g., as found in social organisms.

On longer timescales, many real ecosystems exhibit a complex development of their spatial organization. This complexity does not result from a single underlying process. Multiple mechanisms involving behavior, and movement on short time scales, and demographic and habitat-modifying processes at longer time scales are superimposed. Little is known about how these processes interact to shape ecosystems, and how this affects ecosystem functioning in terms of the establish population sizes, and their resilience against disturbances. Moreover, the benefits of aggregation, in terms of for instance reduced predation risk, feedback to affect demographic processes such as population losses. This has important implications, as the emergent, movement-driven spatial pattern is likely to affect the evolutionary processes that in turn shape movement behavior (de Jager et al., 2011; Liu et al., 2013). Hence, to understand the functioning of complex ecosystem, research should not focus on a single process driving pattern formation, but should address how behavioral, demographic and evolutionary processes interact.