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**Running title:** Movement-driven pattern formation

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- Phase separation is introduced as a universal mechanism for movement-driven self-organized patterning in ecology.
- Density-dependent movement appears to be a ubiquitous process in a wide variety of aggregating organisms, explaining their aggregation and pattern formation.
- We provide guidelines to integrate the physical principle of phase separation within ecological studies on the movement and aggregative behavior of animals.

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# **Phase separation driven by density-dependent movement: a novel mechanism for ecological patterns**

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## **Abstract**

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

20

## 21 **Introduction**

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

37 A multitude of studies have linked regular pattern formation in ecosystems to the  
38 activation-inhibition principle developed by Alan Turing [15] and Hans Meinhardt [16,  
39 17]. This general mathematical principle proposes that the interaction between a self-  
40 amplifying activation process operating at small spatial scales and an inhibiting process  
41 that operates at a larger spatial scale can explain pattern formation in a wide variety of  
42 chemical and morphological systems (see Box 1). Essential here are a *diffusive* or  
43 *differential flow* instability, meaning that the rate of spread of the inhibitor – either

44 through diffusion or through flow – significantly exceed that of the activator. This causes  
45 the effect of the activator to remain local, while the inhibitor exerts its effect also at  
46 larger distance. As a result of this, there is a scale-dependent feedback of organisms on  
47 the *growth* of neighboring conspecifics. Locally, there is a positive feedback, where  
48 organisms promote each other's growth, but at a larger distance a negative effect on  
49 growth predominates.

50 Recent papers highlight the importance of adaptive animal behavior in explaining  
51 patterns observed in nature [12, 18-25]. Here, animals aggregate to form concentrated  
52 groups, clumps, herds, or schools in order to avoid predation, dislodgement of other  
53 losses they face increasingly when alone. Within the groups, they experience lower  
54 chances of predation by means of dilution of predator attention, can confuse predators in  
55 isolating an individual, or can benefit from the vigilance of others in the group and  
56 thereby improve food intake [26]. To form groups, animals must adjust their movement  
57 and other forms of behavior, in the first place by moving towards others when they are  
58 alone, but most importantly by adjusting their movement speed when they have merged  
59 to form a group [12, 24, 27-29]. This adaptive behavior is essentially density-dependent,  
60 as it adjusts to the local density of conspecifics. Density-dependent movement can lead to  
61 the formation of groups that, in combination with constraints on the total number of  
62 animals, leads to regular or semi-regular distribution of groups in the landscape [29]. This  
63 mechanism of pattern formation is fundamentally different from Turing's activator  
64 (facilitation) - inhibition mechanism. Rather than organisms affecting each other's growth  
65 rates, this mechanism centers around animal behavior, where animal movement adjusts to  
66 variation in density, amplifying this variation to form aggregations that in turn form

67 coherent spatial patterns (see Table 1 for a summary for different ecosystems). Although  
68 the implications of density-dependent movement for population dispersal has been treated  
69 in studies going back to the classic work on clines and spread [30-34], it has received  
70 little attention as a general mechanism of self-organization in ecological theory.

71 In this paper, we review studies on movement-driven self-organization in ecological  
72 systems. We show that many of recent studies adhere to the physical principle of 'phase  
73 separation' [35], either in a direct mathematical way [24, 29, 36, 37] or by revealing the  
74 characteristic movement patterns. So-far unrecognized in ecology, this principle explains  
75 movement-driven self-organization in a wide range of physical [28, 29, 38, 39] and  
76 chemical systems [40, 41] and as we will argue, also ecological systems [24]. To keep the  
77 scope of the paper manageable, we only consider the mechanisms that could reasonably  
78 be termed as 'density-dependent' movement, and that deal with self-organization  
79 dynamics. First we briefly explain the limitations of the traditional models of spatial  
80 population dynamics that can be found in many textbooks [4, 31, 42]. We then review a  
81 number of studies on a diverse group of species that highlight how density-dependent  
82 dispersal can generate aggregation and – in some occasions - regular pattern formation.  
83 We discuss the conditions under which phase separation occurs and whether these  
84 conditions are likely to be common. We limit ourselves to the processes of animal  
85 aggregation and group formation, and will not extensively discuss the behavior and  
86 coordination of animal movement within groups, which is extensively discussed in the  
87 literature on collective animal movement [43].

88

## 89 **Models of population dynamics**

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

$$92 \quad \frac{\partial N}{\partial t} = f(N, R) + D \nabla^2 N.$$

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

## 105 **A physical principle for movement-driven pattern formation**

106 In the physical and chemical sciences, it is widely recognized that aggregation of atoms  
107 and molecules can lead to the formation of self-organized patterns, a process called 'phase  
108 separation' [35, 41]. Phase separation describes the spontaneous separation of mixed  
109 fluids [38], such as molten alloys, into their separate components [39]. During this



110 process, spatial patterns are at first often fine-grained, but they grow coarser as time  
111 progresses due to spatial separation of the components of the alloys. The physical  
112 principle of phase separation has been captured by a simple partial differential equation  
113 by Cahn and Hilliard in 1958 [35]. Under this scenario, the dynamics of the density field  
114 is governed by

$$115 \quad \frac{\partial N}{\partial t} = D \nabla^2 (f(N) - \kappa \nabla^2 N),$$

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

129 Central to the explanation put forward by the Cahn-Hilliard model is a density-dependent  
130 relation between particle movement and the local concentration or density of similar  
131 particles. In this review, we highlight that this phenomenon is also very general to

132 ecological systems, where animals adjust their movement speed directly or indirectly to  
133 the behavior of conspecifics. Here, it can lead to a wide range of aggregative phenomena,  
134 ranging from the formation of regular patterns, to animal concentrations such as herds  
135 and fronts, and to highly organized phenomena such as the collective movement of  
136 organisms as swarms of birds or schools of fish. Below, we review examples of each of  
137 these three categories.

### 138 **Regular pattern formation driven by density dependent movement**

139 *Mussel beds.* The blue mussel (*Mytilus edulis*) is a common filter-feeding animal living  
140 on rocky shores and intertidal flats. Mussels develop net-shaped or clumped spatial  
141 patterns at small spatial scales (less than 1 m), especially in mussel beds on soft  
142 sediments (Fig.1a). Laboratory experiments demonstrate that both net-shaped and  
143 clumped patterns can develop from a homogenous initial distribution due to a behavioral  
144 response of the mussels to the local density of conspecifics [12]. Mussels move fast at  
145 both low and high density, but move much slower at intermediate densities. This leads to  
146 aggregation into clumps of intermediate size. Laboratory experiments, lasting for only a  
147 day, highlight that pattern formation at the clump scale is a purely movement-driven  
148 process; no change in mussel numbers occurs within these short experimental timescales.  
149 This process of behavioral self-organization, explaining the emergence of regularly  
150 distributed mussel clumps, is adaptive in that it simultaneously reduces predation and  
151 dislodgment risks, and minimizes competition for algae [12].

152 Interestingly, our recent study of the aggregative movement of mussels demonstrates that  
153 the Cahn-Hilliard principle can be applied to spatial pattern formation in mussels [24].

154 Results from quantitative experiments of mussel movement revealed that mussel  
155 movement speed decreases in a characteristic fashion with local mussel density (Fig.1b).  
156 Mathematical analysis revealed that a decrease of movement speed at intermediate  
157 density translates into a shift from dispersive movement at low mussel density to  
158 aggregative movement at intermediate density, which is an essential condition for pattern  
159 formation in the Cahn-Hilliard principle. We showed that the model of density-dependent  
160 aggregation and pattern formation in mussels is mathematically similar to the original  
161 model of Cahn and Hilliard [24]. Hence, aggregation and pattern formation in mussels is  
162 a process that is equivalent to the familiar process of phase separation in physics.

163 *Ants.* Movement-driven self-organization processes are an important factor in the  
164 building of spatial structures by social insects [18, 52]. For instance, the ant *Messor*  
165 *sancta* creates regular patterns of ant corpses within ant cemeteries, a specific place  
166 where they gather their dead corpses. This process is completely spontaneous, as there is  
167 no prior information, nor a leader, among ants. A single cluster (pile) is gradually built as  
168 the result of a collective effort, where ants pick up a corpse from a small pile of dead  
169 bodies and then deposit the corpse in an already existing cluster. Experimental  
170 observation of ant behavior shows that ants pick up or drop corpses with a probability  
171 that increases with the local density of corpses, as shown in Figure 1d. The unladen ants  
172 pick up corpses with a probability that significantly declines at larger cluster sizes,  
173 whereas corpse-carrying ants drop corpses with a probability that increases with cluster  
174 size [18]. In addition, ants drop corpses with a fixed probability outside piles, leading to a  
175 limited range of transport. If the size of the experimental arena is limited, or if the area  
176 contains spatial heterogeneities, ordered clusters will develop along the borders of the

177 arena or more generally along the heterogeneities [18, 53]. Such a self-organized pattern  
178 is shown in Fig.1c. Similar to the mussel example, movement is the dominant process of  
179 pattern formation, as corpses are aggregated by density-dependent movement of the ants.  
180 Here, the chance of movement is a function of the local density of other corpses, making  
181 the net movement density-dependent.

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

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

### 213 **Herds and schools: mobile aggregations**

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

222 such mobile groups.

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

241 Logically, the movement of aggregated (e.g., herd-forming) consumers is not only  
242 dependent on the density of conspecifics, but also on the density of their food. Here, they  
243 move more extensively when food density is low. In this case, the formation of mobile  
244 animal aggregation such as herds and schools due to density-dependent movement may

245 have important complications for the stability of grazing systems. While aggregation of  
246 mussels has no immediate consequence for food availability because of continued supply  
247 of algae by the tidal water, herds of grazing mammals can locally deplete their sessile  
248 food. Hence, there is an immediate necessity to move as a group to avoid food depletion.  
249 This behavior has been observed in herds of grazers, for instance in the Serengeti  
250 ecosystems [76-79], where ungulates aggregate as an anti-predation adaptation, and move  
251 as a front to through the Serengeti plains as shown in Fig.2b. The movement of individual  
252 wildebeest dramatically slows once they encounter ungrazed lands. Dense wildebeest  
253 herds rapidly deplete the grass resources available locally, leading to continual relocation  
254 of groups across the Serengeti Plains [80]. This complex combination of resource and  
255 conspecific-dependent movement behavior results in transient aggregations of wildebeest  
256 in extensive grazer fronts that track seasonal changes in the spatial gradient of food  
257 availability, often termed the green wave [77, 78, 81-84]. This aggregative process helps  
258 stabilize an otherwise unstable grazing interaction [85, 86]. Studies of other species show  
259 that restriction of group movement by vegetation [82, 83] or immediate danger of  
260 predation when moving, can cause local depletion of food sources leading to the  
261 formation of grazing fronts that can strongly destabilize consumer-resource interactions  
262 [87], such as those observed in snail-grazed salt-marshes [88] and urchin-grazed kelp  
263 beds [89].

#### 264 **Collective animal movement**

265 Density-dependent movement can also generate remarkably complex patterns when  
266 animals not only influence each other's rate of movement, but also directionality. This has  
267 been studied extensively in the field of collective animal behavior, a field that studies the

268 joint movement of animals in schools and flocks. For instance, using density-dependent  
269 movement features, Farrell et al [90] and Buhl et al [91] showed that a group of  
270 individuals (locusts) that align their direction and patterns with that of their neighbors  
271 undergo a rapid transition from random motion to coherent motion where all individuals  
272 move in a common direction to form spotted and striped patterns. In parallel,  
273 biophysicists [92-95] showed that collective cell migration in 2-dimensional cultures  
274 reveals a similar density-dependent movement, when beyond a threshold density. These  
275 theoretical and experimental studies demonstrate that density-dependent movement is a  
276 universal ecological feature generating a multitude of complex spatial configurations, not  
277 only regular patterns. Moreover, this work suggests that collective changes in the  
278 orientation of individuals within groups could potentially be just as profound as density-  
279 dependent changes in movement velocity in generating spatial patterning. It seems quite  
280 likely both behavioral processes are relevant in explaining pattern formation in mobile  
281 group-forming organisms.

282 Although many studies imply that density-dependent relationships exist in collective  
283 behavior [90, 92, 94-96], direct experimental verification remains elusive. A very  
284 interesting example has recently emerged in a study on Sperm movement. Sperm cells  
285 race via their flagella to reach an egg in a viscous medium and the first one to get there  
286 will be able to fertilize it [97]. A solitary sperm cell is more vulnerable to deviations from  
287 a straight trajectory owing to the rotational fluctuations caused by imbalanced torque  
288 exerted by their flagellum, whereas sperm can group together to form cooperative  
289 bundles that make it easier for them to swim along straighter paths. Sperm groups have  
290 been observed in several vertebrate and invertebrate taxa, ranging from sperm pairs to



291 massive aggregates containing hundreds of sperm [98, 99]. Using the fine-scale imaging  
292 of spermatozoa of deer mice, Fisher et al [100, 101] have revealed that the sperm cells in  
293 the rodent genus *Peromyscus* form motile aggregations of 2-30 cells by adhering to one  
294 another at sperm head or head hook to midpiece (See Fig.3a). The increased number of  
295 sperm cells within an aggregated cluster significantly increased group average velocity  
296 because the group exhibits greater linearity in its movement path, without an increase in  
297 speed. Hence, sperm cooperation allows them to migrate more quickly through the  
298 female reproductive tract. The average movement velocity would be expected to decrease  
299 once the clusters grew larger than seven cells, due to sperm cells swimming against each  
300 other, a prediction consistent with density-dependent velocity measurements (Fig. 3b).  
301 Obviously, this process does not adhere to the phase separation principle, as movement is  
302 maximal at intermediate densities, but it highlights that density-dependent movement is a  
303 crucial element in a variety of complex aggregative phenomena.

#### 304 **Further examples of density-dependent movement**

305 Empirical evidence suggests that density-dependent movement is a common phenomenon  
306 in ecology. An extensive literature exists on density-dependent movement in animals [31,  
307 33, 34, 102]. However, little attention has been given into how density-dependent  
308 movement affects spatial self-organization processes. Density-dependent movement rates  
309 have been recorded in social insects such as aphids and beetles [103, 104] and even  
310 zooplankton [105, 106]. Empirical data of aphid movement were obtained using marked  
311 *aphids varians* on fireweed flower stalks. The data show that settlement of moving aphids  
312 increased as a function of local aphid density during the first 6-8 hours following aphid  
313 released. The probability of termination of movement by the aphids increased by more

314 than an order of magnitude as the local density increased from 1 to 40 individuals (see  
315 Fig. 4a). Similar to the aphids, the movement of Mexican bean beetles is affected by the  
316 density of conspecifics. Experimental trials show that the probability of movement was  
317 not affected by the number of conspecifics on the plant at densities lower than 20 beetles  
318 per plant (Fig. 4b). However, dispersal rates went up rapidly when beetle density was  
319 increased beyond 20 beetles per plant. Such behavior data suggest that at high population  
320 densities, beetle movement becomes overdispersive. This example, together with the  
321 others described earlier in this paper, highlights that density-dependent movement  
322 behavior is a common, yet rarely unacknowledged, phenomenon in biology [90] and  
323 ecology [12, 18, 103, 104], and its effects of spatial patterns formation and self-  
324 organization needs further investigation.

### 325 **Indicators of phase separation dynamics in animals**

326 Although the model of Cahn and Hilliard can generate similar spatial patterns as those  
327 predicted by models based on Turing's activator-inhibitor principle, there are several  
328 crucial differences. First, phase separation is essentially mass conserving, as it only  
329 involves movement or diffusive processes, at least when following the standard definition  
330 and equations [35]. The activator-inhibitor principle is, to the contrary, not a mass  
331 conserving process per se, as spatial variation in growth and mortality are the essential  
332 processes. Secondly, Turing patterns exhibit a characteristic wavelength, or a number of  
333 characteristic wavelengths, under constant environmental conditions. This is the  
334 consequence of limitations in the scale of interaction between organisms [107], as the rate  
335 of movement of water or nutrients is limited by physical restrictions. In contrast, patterns  
336 arising from phase separation do not exhibit a characteristic wavelength, but pattern

337 development is characterized by a continuously increasing wavelength, which follows a  
338 power law relationship with time, referred to as the Lifshitz-Slyozov law [41, 108, 109].  
339 This process is well known as *coarsening*. In other words, the phase separation process,  
340 in mass-conserving systems, will not develop stationary patterns. However, this time-  
341 dependent power law may collapse in the long term if other process come into play that  
342 limit movement, such as in mussels where food competition limits the formation of very  
343 large clusters [24].

344 Going beyond the movement-driven patterns elucidated here, the pattern coarsening that  
345 is observed in the phase separation process can in principle also be found in activator-  
346 inhibitor systems when the inhibitor process is global, e.g. when there are no physical  
347 restrictions in the range of negative, inhibitory interactions between the organisms [107,  
348 110, 111]. These conditions have been suggested for the FitzHugh-Nagumo (FHN) model  
349 and for semiarid vegetation when competition for limiting water resources is global  
350 [111]. However, for most ecosystems with regular patterns, such as those observed in arid  
351 ecosystems, this is likely unrealistic, as there are physical limitations in the extent that  
352 organisms can influence each other via the depletion of water. In systems with moving  
353 animals, global limitation of plant growth via the interaction with animals is more easily  
354 conceivable [112, 113]. Whether mobile grazers can generate coarsening dynamics in  
355 patchy plant-herbivore systems is an important topic for future study.

356 A negative effective diffusivity is a prerequisite for phase separation to occur in the  
357 original Cahn-Hilliard model [24], as well as in later physical studies on abiotic particles  
358 [32, 35, 48]. This requirement, however, was broadened in recent physical studies  
359 highlighting that a negatively density-dependent swimming speed is a sufficient condition

360 for phase separation to occur in case of 'active Brownian particles', i.e. organisms [27, 28,  
361 37]. In case of 'self-propelled active matter', physics theory highlights, a decreasing  
362 motility with increasing local density will trigger a positive feedback, whereby an  
363 increase of the local density of individual particles leads to local slowdown, causes  
364 further accumulation of these particles. Hence, negative density dependence can cause  
365 phase separation even without explicit taxis or other orientational processes [29, 49],  
366 which is confirmed by both simulations [36, 50] and experiments [24, 51]. The  
367 application of phase separation principles to the movement of larger organisms, as put  
368 forward in this overview, will expand the scope of this novel theory beyond the field of  
369 theoretical physics.

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

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

391 Although many Turing models include explicit activator and inhibitor components [15,  
392 42], an explicit configuration is not essential to generate a Turing instability. Spatial  
393 patterns can also develop from perturbations of an unstable homogeneous state in single-  
394 species systems, as is observed in the Swift-Hohenberg model, and in non-local  
395 competition models [114-116]. In the past decades, non-local growth and interaction  
396 effects have been proposed to produce observed regular spatial patterns in ecology and  
397 biology [115-119], which consider non-local competition for resources in a variety of  
398 biological fields [120, 121]. In a population-dynamical context, these nonlocal growth  
399 and interaction models have two features in common with Turing systems, i.e. growth-  
400 and mortality- driven demographic processes and scale-depend feedback [2].

## 401 **Outlook**

402 Our review reveals that density-dependent effects on movement velocity and coordinated  
403 turn frequency is a ubiquitous mechanism for the formation of self-organized spatial  
404 patterns in ecosystems. Density-dependent movement, were speed declines over at least

405 some range of local population density, can readily generate pattern formation in a wide  
406 range of ecological settings. Moreover, density-dependent movement is broadly observed  
407 in ecological systems, affecting the spatial dispersal of many organisms [103, 104, 122-  
408 124]. Hence, the principle of density-dependent movement can be usefully extended to  
409 other ecological systems that do not exhibit conspicuous regular patterns, but nonetheless  
410 reveal more complex forms of aggregations, such as animal herds.

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

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433 **Figure Captions:**

434 **Fig 1: Observations of regular patterns from density dependent movement**  
435 **processes.** (a-b) Labyrinth patterns of small-scale mussel beds in intertidal flats (scale  
436 about 50 cm), and experimental data show that mussel-movement speed reveals a  
437 quadratic function of mussel density. (c-d) Self-organized cluster formation in ants driven  
438 by aggregation starting from a random initial condition. Their probabilities of dropping a  
439 corpse remarkably depend on the local density. The data come from experiments in Ref.  
440 [18]. (e) Self-organized branching patterns in *Dictyostelium discoideum*. The cells  
441 produce alternately lower and higher levels of cAMP concentrations as a two dimensional  
442 spiral (scroll) waves from the mutant centre (later as aggregation center) to outwards, the  
443 cells move inwards from flat territories. (f) Typical circular patterns obtained for the  
444 engineered strain CL3, *Escherichia coli* [62] where the CL3 cells spotted at the center of  
445 a semi-solid agar plate, scale bar about 1 cm. Photo (a) by Johan van de Koppel; photos  
446 (c) by Guy Theraulaz; photo (e) copyright Bioayuda in Microbiología, Noticias,  
447 <http://bioayuda.wordpress.com/tag/amebas-que-comen-bacterias>; photo (f) copyright with  
448 Science, 334, 2011, 238-241.

449 **Fig 2: Density-dependent aggregation in mobile patterns.** (a) An aggregation of elk  
450 formed by density dependent movement. (b) Massive consumer front of wildebeest on  
451 grasslands in Africa extending tens of kilometers in length and commonly more than 1  
452 km in width. (c-d) The daily probability of leaving a group versus group size on elk (error  
453 bars shown 2 s.e. around each point); The probability of a solitary individual grouping up  
454 with another elk versus the distance (error bars shown 2 s.e. around each point), where



455 the fitted curve is a four-parameter exponential model, data from the Haydon *et al.* [75].  
456 Photo (a) by John Fryxell; photo (b) copyright Serengeti Balloon Safaris,  
457 <http://www.balloonsafaris.com>.

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

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

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

472 **Box 1: The activator-inhibitor and phase separation principles**

The models of Turing (1953) and Cahn-Hilliard (1958) outline two fundamentally  
474 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  
476 inhibitor (Box 1: Fig. A), which disperse at different rates in space. The interplay  
between the activator and the inhibitor results in spatial variation in net growth of or  
478 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  
480 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  
482 density (Box 1: Fig. B).

**[Figure box at here]**

484 Fig I. (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 it's own  
486 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  
488 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  
490 (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  
492 species tend to disperse at low and very high density, but aggregate at intermediate  
density. The principle has been developed initially to explain self-organized patterns  
494 in metal alloys, and formation of minerals.

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

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

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