Comment

Pattern, process, scale, and model's sensitivity
Comment on "Phase separation driven by density-dependent movement: A novel mechanism for ecological patterns" by Quan-Xing Liu et al.

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Spatial distribution of ecological populations is rarely homogeneous. Typically, the population density exhibits considerable variability of space, in an extreme yet not uncommon case creating a "patchy" pattern where areas of high population density alternate with areas where the population density is much lower or close to zero [1]. This phenomenon, often generically referred to as ecological patterning or ecological pattern formation, has long been a focus of interest in ecology and a number of theories and models have been developed aiming to explain it under different ecological and/or environmental conditions and on different spatial and temporal scales; see Table 1. A straightforward explanation of the heterogeneous distribution of population density relates it to the heterogeneity of the environment (e.g. to nonuniform distribution of resources) and this is indeed often the case [2]. However, a closer look reveals that this is not enough and in many cases the heterogeneity of population density is only weakly correlated to the heterogeneity of the environment [3,19]. Understanding that biological interactions play, on the relevant spatial and temporal scales [20], as important role in shaping the ecological patterns as the physical/chemical forcing resulted in a number of theories. The earliest one that used the idea of Turing's instability [4] was followed by several others [5,6,21] including theories where pattern formation was due to a non-Turing mechanism [8,9] and theories where the movement behavior and/or density dependence was an essential factor [12,14].

Due to the ubiquitous complexity of ecological interactions and the multiplicity of possible situations, the long list of relevant mechanisms of pattern formation (as is briefly reviewed in Table 1) is by no means complete. Existing theories do not yet provide a complete description of the phenomenon. New theories and models are therefore required (as is evidenced by some recent publications, e.g. see [10,11,22,23]) and this is where the work by Liu et al. [17,18] is likely to make an important contribution. The review by Liu et al. [18] begins with introducing a novel model of pattern formation (a modification of the Cahn–Hilliard model widely used in physics of alloys) which is described mathematically by a fourth order partial differential equation; see Eq. (2) in [18]. The Cahn–Hilliard model describes pattern formation by the so called phase separation mechanism which is claimed to have a considerable similarity to the dynamics of mussels on the sea bed [24]. Since an essential condition for their model to work is the density

Table 1
Mechanisms of pattern formation in ecological populations.

	Name of the pattern-forming mechanism	Temporal scale	Spatial scale	Are patterns self-organized (i.e. not related to environmental heterogeneity)?	Movement behavior important?
1	Response to heterogeneity of resources [2]	Within generation as well as multi-generation	Intermediate to large	No	No
2	Response to turbulent environmental flows [3]	Within generation as well as multi-generation	Small to large	No	No
3	Classical Turing diffusive instability in activator–inhibitor-type systems (e.g. prey–predator) [4]	Multi-generation	Intermediate to large	Yes	No
4	Turing-type differential flow instability [5]	Multi-generation	Intermediate to large	Yes	No
5	Dissipative structures more generally [6,7]	Multi-generation	Intermediate	Yes	No
6	Biological turbulence ("wave of chaos") [8,9]	Multi-generation	Intermediate to large	Yes	No
7	Delayed-induced spatiotemporal chaos [10]	Multi-generation	Intermediate to large	Yes	No
8	Fokker–Planck diffusion [11]	Within generation	Intermediate	No	No
9	Stratified diffusion [12]	Within generation as well as multi-generation	Intermediate	Yes	Yes
10	Animal aggregation (formation of schools, herds, swarms etc.) due to taxis and density-dependence [13,14]	Within generation	Intermediate	Yes	Yes
11	Aggregation and pattern formation due to nonlocal interactions [15,16]	Within generation as well as multi-generation	Intermediate	Yes	Yes
12	Animal aggregation due to Cahn–Hilliard-type phase separation [17,18]	Within generation	Intermediate	Yes	Yes

dependence of the individual animal movement (resulting in the dependence of the diffusivity on the population density), the authors then proceed to present a collection of ecological examples where some form of density dependence was observed. Although both the existence of density dependence and its potential effect on the population dynamics are by themselves rather old news, cf. [7,12], apparently these issues have not yet been sufficiently appreciated in the existing literature, so the effort made by Liu et al. [18] to highlight their generality and importance is very useful indeed.
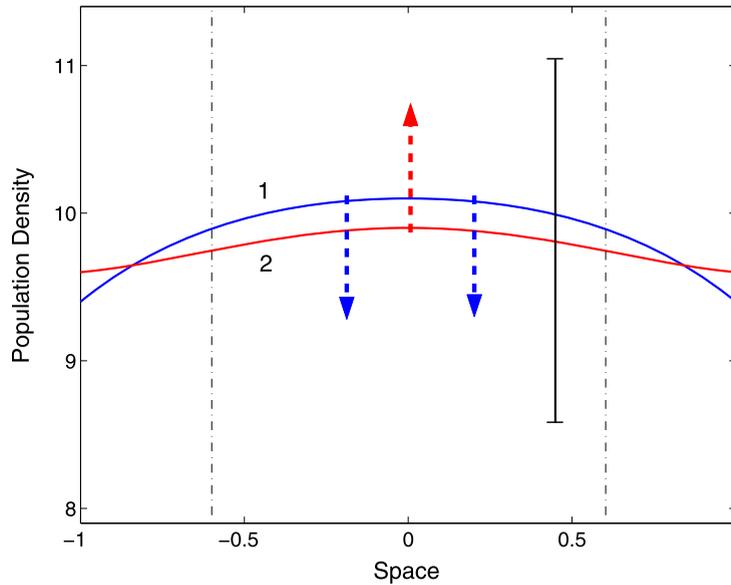
Fig. 1. (Color online.) Sensitivity of phase separation mechanism to minor details of density distribution. Two hypothetical population distributions over the domain $-1 \leq x \leq 1$ at a certain moment t are described by a fourth order polynomial, $N(x,t) = u_0 - |a_2|x^2 + a_4 x^4$ where $a_4 < 0$ for distribution 1 (blue curve) and $a_4 > 0$ for distribution 2 (red curve). The Cahn–Hilliard model (Eq. (2) in [18] considered here for a special case $D = \kappa = 1$ and $f(N) = N$) predicts different dynamics for these two apparently close population distributions: while the distribution 1 will decrease (as symbolized by the arrows), i.e. $\partial N/\partial t < 0$ over the domain, the distribution 2 will grow in the most of the domain ($\partial N/\partial t > 0$ in the area between the two vertical dashed-and-dotted lines). The error bar shows the typical error range for ecological data (as can be seen, for instance, in Figs. 1–3 in [18]).

Having that said, the ecological relevance of the Cahn–Hilliard model remains a matter of discussion. The model modifies the diffusion equation by adding a term that is proportional to the spatial partial derivative of the fourth order. It means that the rate of increase in the local population density N, i.e. as given by $\partial N/\partial t$ in the model, depends on some subtle, minor details of the spatial distribution. As a result, close spatial distributions may correspond to a different dynamics; an example is shown in Fig. 1. Whilst this sensitivity may be a genuine property in physics where the accuracy of data is usually high, it is hardly manageable in ecology where uncertainty is inherent and the measurement error of twenty percent (cf. the error bar in Fig. 1) is usually regarded as excellent. The accuracy of ecological data might be sufficient to distinguish between concave and convex shape of the density profile (as is needed by the diffusion model) but hardly sufficient to detect the acceleration in curvature, as is implied by the fourth derivative. Moreover, there is a more fundamental problem of scale as the actual value of the population density depends on the size of the spatial window [25,26]. In the situation when the population density is not well defined, a model where the dynamics depends on minor details of the shape may appear to be impractical.

The authors' claim that the Cahn–Hilliard model provides the best description of the mussels patterning does not seem to be well justified either. There are other models (e.g. "auto-taxis" [14]) that predicts similar dynamics under similar conditions and on the same spatial and temporal scales, in particular resulting in the self-organized, mass-conserving formation of an aggregated population distribution [16]. Unfortunately, Liu et al. [18] does not compare the predictions of their phase separation model with predictions of other relevant models. Hopefully, it will become a focus of future research.

References

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