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Liu, Quan-Xing; Rietkerk, Max; Herman, Peter M J; Piersma, Theunis; Fryxell, John M; van de Koppel, Johan

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Reply to comment

Bridging physics and biology

Reply to comments on “Phase separation driven by density-dependent movement: A novel mechanism for ecological patterns”

Quan-Xing Liu^{a,b,g,*}, Max Rietkerk^c, Peter M.J. Herman^b, Theunis Piersma^{d,e},
John M. Fryxell^f, Johan van de Koppel^{b,e,**}

^a State Key Laboratory of Estuarine and Coastal Research, East China Normal University, 200062 Shanghai, PR China

^b Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research, and Utrecht University, PO Box 140, 4400 AC Yerseke, The Netherlands

^c Department of Environmental Sciences, Copernicus Institute, Utrecht University, P.O. Box 80155 TC Utrecht, The Netherlands

^d Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, Post Office Box 59, 1790 AB Den Burg, The Netherlands

^e Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

^f Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario N1G 2W1, Canada

^g Center for Global Change and Ecological Forecasting, East China Normal University, Shanghai 200062, PR China

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We would like to express our thanks to all commentators for their important and thought-provoking commentaries. We appreciate that commentators from a diverse array of expertise including mathematics [1], statistical physics and biological physics [2], biomathematics [1,3], computational and systems biology [4], evolutionary biology and ecology [5], as well as the recently thriving realm of the soft matter [6], have provided different perspectives on the use of the phase separation principles in ecology and biology. The commentaries have also identified important open

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* Corresponding author at: State Key Laboratory of Estuarine and Coastal Research, East China Normal University, 200062 Shanghai, PR China.

** Corresponding author at: Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research, and Utrecht University, PO Box 140, 4400 AC Yerseke, The Netherlands.

E-mail addresses: qxliu@sklec.ecnu.edu.cn (Q.-X. Liu), Johan.van.de.Koppel@nioz.nl (J. van de Koppel).

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Fig. 1. Derivation of the double-well energy potential function from the individual movement of animals. Based on original data from Liu et al. [26], $V(m)$ in panel A depicts the experimentally determined movement speed of mussels as a function of rescaled mussel density, $D(m)$ in panel B describes the population dispersal, and is derived from $V(m)$ as follows $D(m) = \frac{1}{2} V \left(V + m \frac{\partial V}{\partial m} \right)$, and $P(m)$ in panel C describes the free energy potential, and is in turn derived from $D(m)$ as follows: $P(m) = \int D(m) dm + \mathcal{H}$. When the diffusion rate in panel B becomes negative, population flux switches from dispersive and aggregative, which is the driving force behind the phase separation process. The solid balls in the valleys indicate the steady states where the free energy potential is minimal.

questions on this novel mechanism for self-organized ecological patterns. Below, we discuss some of the important issues and observations raised by Petrovskii [3], Kuperman [7], Lutz [5], Reynolds [4], Silverberg [6], Vicsek [2], and Maini and Garikipati [1].

The comments emphasize that we did not provide extensive coverage of models that can be found in the literature on -among others- collective animal behavior [8–13], insect dynamics [14–16], and single-species models with nonlocal interaction [17–22]. Much of this was by choice. First, we aimed to give a review of studies with empirical evidence for density-dependent movement in aggregating populations, to point out that this process is an important general mechanism for aggregation in real-world animal populations. Moreover, some of the alternative models that were suggested, such as the non-local interaction models, fit better in the Turing framework, as they act on growth and mortality processes rather than movement, and have an explicit scale. Second, the incredibly rich and active field of collective animal behavior focuses for a large part on movement within aggregations, rather than on the formation of patterns and clusters. It provides a detailed perspective on how interactions between organisms can create a phase transition from a disordered state with uncoordinated movement to an organized state with coordinated, collective movement [8,23]. This level of organization goes far beyond the formation of self-organized heterogeneity that we addressed in our review and we therefore regarded it as beyond the scope of our paper. Finally, with respect to insect aggregation, we highlight in our review that density-dependence in insect movement may align well to the Cahn–Hilliard framework, as both experimental work and modeling of pattern formation in insect corpses reveals coarsening, a hallmark signature of phase separation [24,25]. This might provide an interesting avenue for further research.

Petrovskii [3] appears to have misinterpreted the fourth-order spatial derivative in the Cahn–Hilliard model. The fourth order derivative is not the driver behind the aggregative dynamics. It is the second order-part, labeled $\mathcal{P}(s)$ in our previous paper [26] and $f(N)$ in the comment by Maini and Garikipati [1] that creates negative diffusion at intermediate local population density. The self-organization process only depends on energetic state of the species, $f(N)$, which is further clarified by Maini and Garikipati [1]. $\mathcal{P}(s)$ describes the well-known “double-well energy potential”, which can be derived from either individual movement properties, or from the relation between population dispersal and density (Fig. 1). It reveals that free energy is minimized at the curve’s minima, reflecting the two phases of the phase separation process. Moreover, we would like to stress here that one could also have ‘Turing instabilities’ in systems with fourth-order derivatives [27–29]. The fourth-order derivative does not in any way distinguish between the principle outlined by Cahn and Hilliard [30] and the Turing principle with short-range excitation/activation and long-range inhibition [31].

As was stressed by Petrovskii [3] in one of his final remarks, we were not the first to point to the possibility of pattern formation in animal population in response to direct or indirect density-dependence of movement. A number

of very nice experimental and theoretical studies can be found in literature predating ours [e.g., [32]]. Yet, as of now, the formation of self-organized patterns in real-world ecosystems is for the most ascribed to Turing's local-activator, long-range inhibitor principle [33], even when it involves only aggregative movement as the driving force [34,35]. With the current review [36] and the earlier paper on which it builds [26], we have put forward an alternative paradigm for movement-driven pattern formation in the form of the original Cahn–Hilliard model and many following model studies that have expanded on it. The phase separation literature provides a distinct set of predictions which can help in testing for the most appropriate model, even in experimental settings [26]. Moreover, the general understanding of the phase separation process in the physical literature will help scientists in ecological and biological fields in studying aggregative dynamics.

Kuperman [7] highlights that “density-dependent” movement in animals is more often related to the local density of food, or gradients in environmental conditions, and not necessarily related to the local density of conspecifics. This is obviously true, as most movement is aimed to find food. Yet, searching for food would lead to dispersal of organisms in response to resource depletion and competition. Yet, many foragers have strikingly aggregated distributions, for instance in the form of clumps, herds or schools, independent of underlying gradients in resource availability or environmental conditions. To explain these aggregations, there must either be a direct relation between movements and the local density of conspecifics, or an indirect relation via some chemical, physical or biological property that in turn reflects the local density of the aggregating species itself. An example of this is the clumping of the Great Spruce Bark Beetle (*Dendroctonus micans*), which aggregate in response to a pheromone they jointly excrete [37]. Obviously, in many real-world ecosystems, a single principle may not be enough to explain observed self-organized patterns, as both growth-driven and movement-driven processes interact to shape the spatial distribution of species [38]. A prominent example is the formation of bacterial colony patterns in a particular strain of *Bacillus subtilis*, which is highlighted in the commentary of Vicsek [2].

Kuperman [7] and Petrovskii [3] both highlight that nonlocal interaction model should be considered as an alternative mechanism to explain self-organized patterns in ecosystems. Specially, non-local effects could generate similar spatial patterns in the distribution of a population [17–22]. We agree that the concept of nonlocal interaction provides a simple and effective approach to modeling self-organization processes in ecosystems. However, as we state in our original paper [36], nonlocal growth and interaction models have two features in common with Turing systems, i.e. growth- and mortality-driven demographic processes and strict scale-dependence. Hence, it would be less suited to describe patterns that originate from the movement of organisms.

In their comments, the authors collectively emphasize that the Cahn–Hilliard equation, and more generally non-linear diffusion, has been applied to other biological fields, highlighting the universality of the process it describes. Maini and Garikipati [1] emphasize that the Cahn–Hilliard equations have been applied to tumor dynamics, wound healing, and the development of capillary network that develops during the process of angiogenesis. Silverberg [6] highlights that phase separation can be applied to extreme human collective motion, as observed at heavy metal concerts, where people gather and “mosh” in a centralized region of a larger crowd [13,39]. Vicsek [2] and Lutz [5] highlight that density-dependent methods have already been applied to living systems about two to three decades ago, referring to the literature on collective animal behavior. Here, early theoretical work [40] and the classical Vicsek model [41] stimulated extensive research on the coordination of animal movement within aggregation patterns [10,42,43] and active particles motion [44,45]. Collective animal behavior has since developed into a field of its own. Here, a common feature is that adaption of a range of movement properties (i.e. speed, direction) to local neighbors leads to a phase transition from a disorder state characterized by uncoordinated movement to an ordered, coordinated state in which collective behavior emerges from the local interactions. The properties and functions of collective movement have been under intense theoretical and experiment investigation, but their similarities and differences with original atoms and molecules are still unexplored [2].

The most intriguing comment – to our opinion – comes from Silverberg [6] and Maini [1]. They wonder whether the energy-based arguments on which the Cahn–Hilliard equation rests are actually valid for movement of organisms or even cells within a tissue [46]. The link between animal movement and the Cahn–Hilliard equation that we present in [26] is based on a mathematical derivation, but the underlying processes of segregation and aggregation in solids and fluids may differ greatly with that in animal populations. This points to a fundamental difference between physical and biological systems: while physical particles might move to minimize free energy, organisms move to – on the long run – maximize their Darwinian fitness, and they may scale energetic slopes to obtain this long-term fitness benefit.

Whether maximization of fitness and minimization of free energy can be gathered under a general unifying framework is an important question to be addressed by scientist working on the interface of biology and physics.

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