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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”

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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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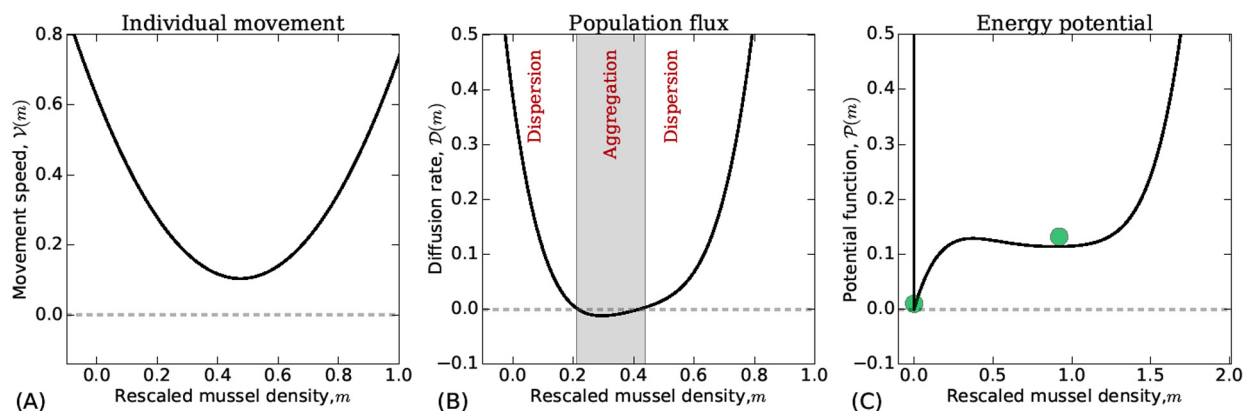


Fig. 1. Derivation of the double-well energy potential function from the individual movement of animals. Based on original data from Liu et al. [26], $\mathcal{V}(m)$ in panel A depicts the experimentally determined movement speed of mussels as a function of rescaled mussel density, $\mathcal{D}(m)$ in panel B describes the population dispersal, and is derived from $\mathcal{V}(m)$ as follows $\mathcal{D}(m) = \frac{1}{2}\mathcal{V}\left(\mathcal{V} + m\frac{\partial\mathcal{V}}{\partial m}\right)$, and $\mathcal{P}(m)$ in panel C describes the free energy potential, and is in turn derived from $\mathcal{D}(m)$ as follows: $\mathcal{P}(m) = \int \mathcal{D}(m) dm + \mathcal{H}$. 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

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