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Mechanisms and phenomenology of phase separation Comment on: “Phase separation driven by density-dependent movement: A novel mechanism for ecological patterns” by Quan-Xing Liu et al

Jesse L. Silverberg

Wyss Institute for Biologically Inspired Engineering, Harvard University, Boston, MA 02115, USA

There is a striking resemblance between animal herding behaviors and phase separation physics. Admittedly, this language is imperfect. However, my one-sentence summary of Liu et al.’s detailed article [1] attempts to capture their essential message and distill it into a convenient form. To elaborate more, “animal herding behaviors” is my catch-all phrase for the commonalities observed in organismal groups ranging from *E. coli* colonies to elk herds. Similarly, “parallels to phase separation physics” refers to the tendency for these organismal groups to either aggregate into coherent clusters or spread sparsely as individuals. When viewed this way, the behavioral patterns Liu et al. discuss are reminiscent of water separating from oil, or an alloy freezing into its component domains. Such remarkable similarities between living and non-living systems have inspired a great deal of research in the field of *active matter* where collective behavioral dynamics are connected to foundations of condensed matter physics. Arguably the most interesting observation to emerge from this intersection of biology, physics, and material science is the recurrence of a small number of self-organized patterns that arise in wildly different animal populations. Without a doubt, this broad consistency across organisms lies at the heart of Liu et al.’s review.

The general similarities between organismal group collective behavior and phase separation have been recognized more than once in the active matter community [2–4]. Liu et al. have done the hard work of formally surveying the literature in order to establish the analogy’s specific details and underlying principles in an ecological context. This synthesis is a significant contribution to the community as a whole and provides firm evidence for a pattern of otherwise loosely connected results. In crafting their argument, the authors cite the seminal work on phase separation of heterogeneous materials by Cahn and Hilliard as inspiration [5]. Without hesitation, I agree that this is the right starting point for the analogy Liu et al. advance, because it allows one to establish a correspondence between measurable quantities and observable phenomenology. However, I disagree with their interpretation of the physical mechanism driving Cahn–Hilliard phase separation and its applicability to organismal collective motion.

The crucial details in Cahn and Hilliard’s original work can be found early in their derivation for the equilibrium behavior of heterogeneous materials [5]. In essence, they

performed a free energy functional expansion, and using Landau-esque symmetry arguments, wrote the leading energetic terms as the sum of two contributions. The first contribution is a double-energy well that defines two preferred densities for the system. The second contribution is an energetic penalty for density gradients that both drives the formation of homogeneous domains and maintains their stability through time. It must be stressed that density *gradients* are the important factor for Cahn–Hilliard phase separation, owing to the fact that uniform density fields are incapable of generating a flux. In addition, two of the theoretical works on phase separation in active matter systems cited in Liu et al.’s review derive mechanisms that are also based on density gradients [6–8]. In both cases, the particle velocity function contains a leading correction proportional to factors of the local density gradient. With this information in mind, I found it surprising that Liu et al. repeatedly refer to a “density-dependent relation between particle movement and the local concentration” as the driving mechanism of Cahn–Hilliard phase separation. My understanding is that the bare density alone is incapable of driving the fundamental phenomenology at hand.

Putting aside the question of whether Cahn–Hilliard phase separation and ecological herding behaviors are driven by the same causal principles, Liu et al. are successful at highlighting a broader point: *density*-dependent motion appears to be a fundamental mechanism that drives many dissimilar organisms to exhibit phase-separation-like behavior. Generally, this principle functions as a positive dynamical feedback loop where increased densities lead to reduced speeds, which in turn, stabilizes the formation of high-density clusters. Thus, organismal groups that start in a spread out state eventually condense into spatially localized clusters. Some of my collaborative research on extreme human collective motion has observed similar behavior at heavy metal concerts, where people gather and “mosh” in a centralized region of a larger crowd [9,10]. This self-segregation of moshers from non-moshers is driven by a preference for moshers wanting to mosh with each other, while non-moshers prefer to avoid moshers. As Liu et al. highlight for the specific examples of mussel beds, ants, slime mold, bacteria, and elk, positive feedback loops like the one observed in heavy metal concert attendees have a dramatic impact on the overall spatial organization of groups.

From an abstract point of view, it’s fascinating to see multiple different microscopic mechanisms giving rise to similar phase-separation-like phenomena. A possible explanation could be the existence of a fixed point in model space that different coarse grained theories flow towards [11]. While this would explain the similarities between density and density-gradient driven processes, a significant amount of work is required to determine if the idea holds up to scrutiny. Regardless of the outcome, the essential phenomenology of phase separation still holds utility for studies of ecological pattern formation, as it provides a guide for quantitative measures and research strategies that can be introduced to a wide range of new problems. Needless to say, there is still much more to do.

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