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Balancing general principles with fine-scale interactions in understanding the emergence of movement-driven spatial patterns

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ACCEPTED MANUSCRIPT

<u>Title:</u> Balancing general principles with fine-scale interactions in understanding the emergence of movement-driven spatial patterns [Comment on "Phase separation driven by density-dependent movement: a novel mechanism for ecological patterns" by Liu et al.]

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Comment:

With their broad overview of spatial patterns driven by density-dependent movement [1], Liu and colleagues have put forward a novel framework for describing certain aspects of selforganization and pattern formation in biological systems. The review makes an important contribution to the literature by identifying two distinct classes of self-organized spatial patterns, which previous reviews [2, 3] have not necessarily made explicit. The first class, exemplified by the activator-inhibitor principle outlined by Turing [4] and developed by Meinhardt [5], consists of processes driven by differential growth and mortality, while the second class, exemplified by the Cahn-Hilliard principle of phase separation [6], consists of movement-driven processes. The authors introduce and describe the Cahn-Hilliard principle, and, having applied this model in previous work on self-organization in mussels [7], discuss how the principle of phase separation driven by density-dependent movement may capture the dynamics of many other systems. While it remains unclear how closely each of the examples cited might conform to the specifics of the Cahn-Hilliard model, the general principle of phase separation provides a useful framework for understanding the emergence of movement-driven spatial patterns.

The authors state that the first of these classes (growth-driven processes) represents the "predominant explanation" for the emergence of self-organized patterns in ecosystems. While this may hold true for some previous studies, particularly at the landscape scale [8-10], the idea that the movement of organisms following simple rules can lead to the emergence of complex patterns at higher levels (including the landscape scale) is not a new one. The claim that density-dependent movement "has received little attention as a general mechanism of self-organization in ecological theory" is unnecessarily broad, and is contradicted by many of the references cited [11-14]. Perhaps what the authors refer to here as "ecological theory" does not include work on social insects, collective behaviour or behavioural ecology in general, but this seems an arbitrary rhetorical distinction.

Although the scope of their review is necessarily limited, some additional examples of self-organization through density-dependent movement from the collective behaviour literature would serve to extend and further inform the proposed framework. To manage the scope, the

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