Robust ecological pattern formation induced by demographic noise
Authors: Thomas Butler and Nigel Goldenfeld
Physical Review E, Rapid Communications **80**, 03092(R) (2009)

Stochastic Turing patterns in the Brusselator model
Authors: Tommaso Biancalani, Duccio Fanelli and Francesca Di Patti
arXiv:0910.4984v2 (2010)

Recommended with a commentary by Mehran Kardar, MIT

Fluctuations are expected to reduce the stability of ordered states; mean-field approaches in statistical physics (which neglect spatial fluctuations) typically exaggerate the extent of order in a phase diagram. This is well known for standard models, such as the Ising system, for which mean field theory overestimates the critical temperature. In contrast, the above articles demonstrate that in some out of equilibrium reaction-diffusion systems, fluctuations arising from the discreteness of the degrees of freedom (termed intrinsic noise), such as organisms or molecules, promote spatio-temporal ordering (pattern formation).

In the first paper above, Butler and Goldenfeld study corrections beyond mean field to the phase diagram of a simple reaction-diffusion model of plankton-herbivore dynamics. This model was originally intended to capture the formation of short length scale ($\sim$1m) patchy domains observed in real planktonic ecosystems [1]. Typically, such models are studied by following the evolution of *deterministic* partial differential equations. Within this framework, the model requires fine tuning of parameters, or a separation of scales between the diffusivities of the plankton and herbivores, in order to lead to the formation of patterns. This is common to most mean field models of diffusion driven pattern formation and has been a major obstacle in their application to real systems. However, corrections to mean field present a far different picture. At leading order, the beyond mean field calculation predicts the emergence of spatio-temporal patterns in regions of parameter space where mean field predicts a random distribution of organisms. In the new phase diagram (Fig. 1) the pattern forming phase occupies a much larger region of parameter space than expected in mean field theory. This change in the phase diagram makes it much more likely that real systems satisfy the requirements for diffusion driven pattern formation since the wide separation of diffusivities is no longer required. This is in line with observations that Turing type patterns seem to be quite common in real ecosystems (for a review, see [2]). Thus the stochastic fluctuations in fact promote the formation of patterns.

Butler and Goldenfeld conjecture that similar mechanisms should enhance spatio-temporal order in other systems. This is now confirmed in the second paper above, where Biancalani and coworkers replicate Butler and Goldenfeld's results on the Brusselator model of chemical pattern formation. As in the plankton-herbivore dynamics, this calculation shows that intrinsic noise due to the discreteness of molecules drives the formation of patterns in large regions of the phase diagram previously predicted on the basis of mean field theory to contain only a trivial

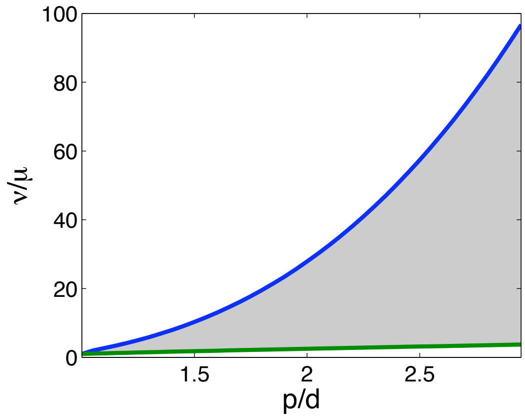

Figure 1: Phase diagram of the plankton-herbivore model from the first recommended paper above (Figure courtesy of Thomas Butler). The vertical axis is the ratio of the diffusivities of herbivore and plankton, while the horizontal axis is the dimensionless ratio of two kinetic parameters. The mean-field solution predicts pattern formation only in the limited interval above the upper curved line (a form of 'fine tuning'). By contrast, beyond mean field calculations indicate the formation of fluctuation driven patterns also in the shaded region (where patterns are absent in mean field).

steady state.

The reason these computations lead to such distinct departures from mean field theory is clear in retrospect. Typical individual trajectories of the systems contain spatio-temporal patterns with a definite wavelength and period. However, random variations in wavelength and period cause the spatio-temporal patterns in different trajectories to cancel when the trajectories are summed for an ensemble average. Since mean field theory models the dynamics of average concentrations, it fails to capture the patterns present in the individual trajectories.

Comparing mean field theories to data has been the standard way of applying mathematical models to ecosystems, and other biological systems with low local copy numbers, for many years. Thus the discovery that fluctuations can play a key role in the formation of spatio-temporal patterns in experimentally relevant parameter ranges will lead to the reexamination of the role of generic reaction-diffusion mechanisms in biological pattern formation, as well as a deeper understanding of the diverse effects of fluctuations in non-equilibrium statistical mechanics.

References

[1] Simon A. Levin and Lee. A. Segel, Nature **259**, 659 (1976).

[2] Max Reitkerk and Johann van de Kopppel, Trends in Ecology and Evolution **23**, 169 (2007).