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Tommaso Biancalani

The Influence of Demographic Stochasticity on Population Dynamics

A Mathematical Study of Noise-Induced Bistable States and Stochastic Patterns

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A Mathematical Study of Noise-Induced Bistable States and Stochastic Patterns

Doctoral Thesis accepted by
the University of Manchester, UK

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Author
Dr. Tommaso Biancalani
Department of Physics
University of Illinois at Urbana-Champaign
Urbana, IL
USA

Supervisor
Prof. Alan J. McKane
School of Physics and Astronomy
The University of Manchester
Manchester
UK

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  The linear noise approximation for reaction-diffusion systems on networks
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  Diffusion of two molecular species in a crowded environment: theory and experiments
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  Stochastic waves in a Brusselator model with nonlocal interactions
  Phys. Rev. E **84**, 026201 (2011).
- T. Biancalani, D. Fanelli and F. Di Patti
  Stochastic Turing patterns in a Brusselator model
  Phys. Rev. E **81**, 046215 (2010).

Supervisor's Foreword

It gives me great pleasure to write the foreword for Tommaso Biancalani's Ph.D. thesis. The thesis is concerned with observable phenomena that arise due to the noise which is generated as a consequence of the discrete nature of entities (atoms, molecules, individuals, …) which make up a system. This is called intrinsic noise, or in a biological context, demographic noise. Tommaso had already worked on one type of phenomenon induced by demographic noise (stochastic Turing patterns) for his master's thesis with Duccio Fanelli in Florence, before coming to Manchester, and so was already familiar with the concept. During the period he was in Manchester, several new features of noise-induced structures were uncovered, some of which appear in this thesis.

All these phenomena are fascinating, rather general and we have mathematical and computational tools at our disposal to analyse them. However, this latter point is not widely appreciated and the ideas have frequently been developed by theoretical physicists, rather than by those trained in the biological sciences. One reason for this is not hard to find: the dynamics of the processes are stochastic, and the subject of non-equilibrium statistical physics has stochastic dynamics at its core. Another factor, which is just as important, is that the theory of stochastic processes can be presented in a very mathematical way, essentially as a branch of pure mathematics. The gap between this way of viewing stochastic phenomena and the way empirical biologists work is usually too great for effective communication. In my experience, theoretical physicists have just the right mix of intuition and mathematical background to successfully analyse stochastic systems found in the biological sciences. Tommaso's thesis is very much in this tradition.

There has been a long history of theoretical physicists moving into theoretical biology. In recent years this trend has grown and a trickle has become, if not a flood, at least a sizeable flow. There are many statistical physics groups around the world in which many or all the members of the group apply the ideas and techniques of statistical physics to biology and related fields. This area has become known as "Biological Physics"—to distinguish it from the older field of "Biophysics", which concerns itself more with the physical properties of biological materials. Those trained in theoretical physics focus rather more on general principles and unifying features—synthesis as well as analysis. They also tend to favour bottom-up approaches to modelling: in the biological literature there is frequently little attempt to make any connection between "microscopic models"—in which the number of individuals of a given type define the state of the system, and which are used in numerical simulations—and "macroscopic models"—which are average, deterministic, descriptions and are used in many traditional analytic treatments. Yet it is vital to do this to get the correct form of noise and so the correct form for the noise-induced structures. In practice, this is usually achieved by working with "mesoscopic models" which have the structure of the macroscopic model, but with the correct form of noise inherited from the microscopic system added on.

A simple example of a noise-induced structure is found in models of predator-prey systems. This kind of dynamics is meant to favour cyclic behaviour, but the simplest textbook models do not generically show this. It turns out that at least some of the predator-prey cycles empirically observed are noise-induced. These so-called quasi-cycles can be found by application of the linear-noise approximation, which as its name suggests linearises the noise about the macroscopic (deterministic) equations. It is found that the amplitude of the cycles is amplified by this noise, which has its origin in the discreteness of the fundamental constituents of the microscopic model. Thus, while one would naively expect the amplitude of the quasi-cycles to go like $1/\sqrt{N}$, where N is the number of individuals that can fit into the system, the resonant amplification multiplies this by a large factor, so that cycles which have an amplitude of order one are seen even for quite large values of N.

In the last decade quasi-cycles have been found in many different contexts, and several other effects of demographic stochasticity which can be observed have been identified. Tommaso discusses two of these effects in his thesis. The first is stochastic waves, which have both a spatial and temporal aspect. The quasi-cycles discussed above were found in well-mixed systems and consisted only of temporal oscillations. Microscopic models which are defined on a lattice or network, and so allow individuals not only interact with each other, but also to migrate to neighbouring sites, lead to reaction–diffusion equations on the macroscale, and to stochastic spatio-temporal patterns on the mesoscale. In fact mesoscopic reaction–diffusion models may also contain stochastic versions of deterministic Turing patterns, but as Tommaso explains these are not such natural generalisations of quasi-cycles as are stochastic waves. However, all these phenomena can be successfully analysed using the linear noise approximation, with all the advantages that working with a linear system bring.

The second main topic of Tommaso's thesis is noise-induced bistable states. The classic picture of bistability is of a double-well potential with weak noise permitting rare transitions between the two (meta)stable states. Noise-induced bistable states, by contrast, may occur in situations in which only a single stable state exists in the deterministic limit; now the noise not only causes the transitions, but also creates the metastable states between which the transitions occur. The model used to illustrate this effect in this thesis had its genesis in the study of a model of Togashi and Kaneko on autocatalytic reactions. The noise is multiplicative, and so the linear noise approximation cannot be used, at least without carrying out a nonlinear change of variables. These ideas are not new: in the 1980s there was a great deal of interest in the possibility of multiplicative noise causing transitions of this type. Much of the work of that time is summarised in the book "Noise-Induced Transitions" by Horsthemke and Lefever. However, the work carried out then started with a mesoscopic description—with all the ambiguities that entails—rather than with microscopic and biologically (or physically) motivated processes.

I am sure that there are many new effects to be uncovered, as well as new theoretical formalisms to be developed to understand them. I hope that the work presented here will allow many more people to understand, and eventually contribute to, the theory of phenomena induced by intrinsic noise.

Manchester, April 2014 Prof. Alan J. McKane

Abstract

This thesis presents a mathematical analysis of two classes of behaviours which occur in systems of populations: noise-induced bistability and stochastic patterning. Both behaviours have their origins in the intrinsic stochasticity possessed by a population system due to the discreteness of the individuals: the intrinsic noise.

In the study of noise-induced bistability, we analyse a system which exhibits switching between two states. These states do not correspond to fixed points of the corresponding system of deterministic equations, but instead are the states at which the system stochasticity is minimal or vanishing. This feature suggests that the mechanism is intrinsically different to the traditional paradigm of bistability, in which a system with two stable fixed points is subject to noise. Through our mathematical analysis we highlight some characteristic properties of the dynamics, suggesting a way to distinguish, in a real system, the presence of noise-induced bistable states from other types of bistability.

Stochastic patterning arises when noise acts on a reaction–diffusion system which exhibits pattern formation via an instability of the homogeneous state. If the system is close to the onset of the instability, whilst still in the stable regime, then patterning occurs due to a combination of stochastic agitation and the exponential decay of the underlying stable homogeneous state. We investigate the case of the stochastic travelling waves on both regular lattices and complex networks. In both cases, a complete analytical treatment is provided via the power spectra of fluctuations.

The spirit of the thesis is to propose a simple model which is representative of an observed behaviour, and then solve the model analytically. Numerical simulations are used throughout to verify the accurateness of the analytical approximations. Thus the analytical treatments constitute the core of the work and have two purposes. They are explanatory, in the sense that they help to develop intuition about how the noise leads to a certain behaviour. Moreover, they give quantitative understanding, as we provide the explicit expressions for various quantities \(stationary distributions, mean times, etc.). In some cases, the formulas that we have obtained do not rely on the details of the model, so that we would expect them to fit experimental data. In other cases this is not so, yet the analytical treatment may give insight into how to attack more realistic models.

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To the people who proofread this thesis lol.
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