

## Special Issue on Spatial Moment Techniques for Modelling Biological Processes

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Published online: 18 April 2015  
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Over the last two decades, there has been an increasing awareness of, and interest in, the use of spatial moment techniques to provide insight into a range of biological and ecological processes. Models that incorporate spatial moments can be viewed as extensions of mean-field models. These mean-field models often consist of systems of classical ordinary differential equations and partial differential equations, whose derivation, at some point, hinges on the simplifying assumption that individuals in the underlying stochastic process encounter each other at a rate that is proportional to the average abundance of individuals. This assumption has several implications, the most striking of which is that mean-field models essentially neglect any impact of the spatial structure of individuals in the system. Moment dynamics models extend traditional mean-field descriptions by accounting for the dynamics of pairs, triples and higher  $n$ -tuples of individuals. This means that moment dynamics models can, to some extent, account for how the spatial structure affects the dynamics of the system in question.

Previous applications of moment dynamics models have focused on several application areas, such as: ecological dynamics (Bolker and Pacala 1997; Law et al. 2003; Lewis and Pacala 2000); epidemics (Keeling et al. 1997; Sharkey 2008); surface chemistry reactions (Mai et al. 1993, 1994); herding behaviour (Levin 1994); and clustering of organisms (Young et al. 2001). Two examples of applications where moment dynam-

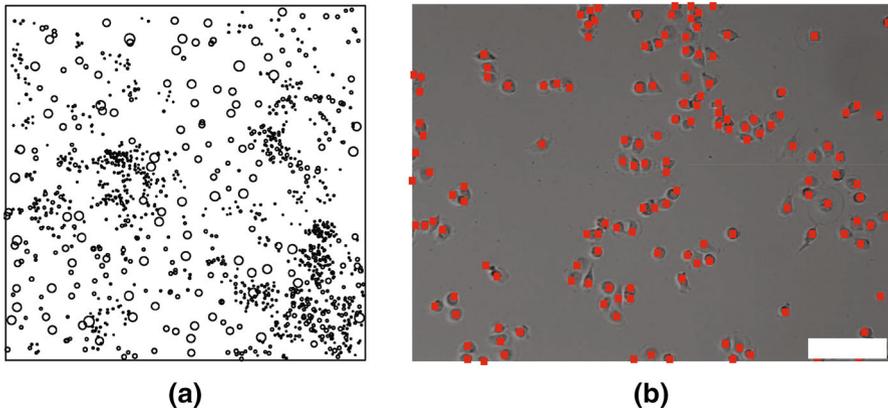
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**Fig. 1** Clustering and patchiness in biological and ecological systems. **a** Dispersal and competition processes in a beech forest give rise to patchiness in the distribution of trees (see [Law et al. \(2009\)](#) for full details). **b** Rapid cell proliferation, relative to the rate of cell motility, in a population of initially spatially uniform breast cancer cells gives rise to patchiness and clustering during the growth-to-confluence process (see [Simpson et al. 2013](#) for full details). The image in **a** is reproduced with permission from John Wiley and Sons

ics models are relevant are shown in Fig. 1. The image in Fig. 1a shows some field data illustrating patchiness and clustering in the spatial distribution of trees in a beech forest ([Law et al. 2009](#)), while the image in Fig. 1b shows an in vitro growth-to-confluence assay for a breast cancer cell line where the cells are initially distributed uniformly and, as the population grows towards confluence, we observe significant clustering and patchiness in the spatial distribution of cells ([Simpson et al. 2013](#); [Agnew et al. 2014](#)).

Understanding in the field of moment dynamics techniques is advancing on several concurrent fronts. A common feature of moment dynamics models is the need for some kind of closure approximation. This arises because moment dynamics approaches often lead to large (or possibly infinite) systems of coupled equations, for example for the dynamics of  $n$ -tuples for  $i = 1, 2, \dots, n$ . For such models to be tractable, these hierarchies of equations need to be truncated, or closed, before an approximate solution describing the dynamics of the system of interest can be obtained ([Singer 2004](#)). As a result, the development of new closure approximations or the development of new understanding of existing closure approximations is an active area of research, and results are often published in the physics and mathematics literature ([Murrell et al. 2004](#); [Karrer and Newman 2010](#); [Raghib et al. 2011](#); [Rogers 2011](#); [Wilkinson and Sharkey 2014](#)). Another front of research concerns the application of moment dynamics descriptions to dynamic processes taking place on networks. These network applications can be similar to ecological applications since the system of interest often takes the form of either individuals that can compete with other individuals ([Adams et al. 2013](#)), or individuals that can change their status via contact with neighbouring individuals. One broad feature lacking from these ecological and network models is the incorporation of a motility mechanism that allows individuals to move between network nodes. This has recently been incorporated into our work which seeks to use

moment dynamics descriptions to explore the collective behaviour of cell populations (Baker and Simpson 2010, 2011). Explicitly incorporating a motility mechanism into a moment dynamics description of the evolution of a population of cells is essential since very often cell motility is the dominant mechanism that drives their collective behaviour. As the development of moment dynamics models has become more specific to particular applications, another area of interest is how these kinds of models can be integrated with experimental/field data to provide additional insight into the particular application. Several recent studies have made particular progress on this front, with applications involving plant ecology (Detto and Muller-Landau 2013) and cell biology (Simpson et al. 2014).

One of the issues which we have sought to address in this special issue of the *Bulletin of Mathematical Biology* is that studies which detail developments in moment dynamics techniques and their application to various biological processes are often published in separate sections of the scientific literature. For example, results concerning ecology and forestry applications are often published in the theoretical ecology literature, new results focusing on moment closure approximations are often published in the theoretical physics and mathematics literature, whereas results from the application of moment dynamics models to observations in cell biology have been published in the mathematical biology literature. Therefore, it is possible that researchers working in one area might be unaware of parallel developments in different areas of the literature. To address this, we sought to gather a very general collection of articles about moment dynamics techniques and models that are motivated by, and applied to, biological processes, and publish them together in a special issue of the *Bulletin of Mathematical Biology*.

This special issue combines several articles which illustrate the diversity of interests in this broad field. In particular, the special issue covers incorporate a broad review paper by Plank and Law (2015), which documents a general framework that can be used to model movement, birth, and death of multiple types of interacting agents in a non-homogeneous setting, which is relevant to a range of biological conditions, such as moving population fronts. The studies presented by Sharkey (2015) and House (2015) focus on describing dynamics on discrete structures, such as a graph, since these kinds of structures are thought of as being representative of the heterogeneities that exist in contacts between individuals. More specifically, House (2015) introduces an approximate algebraic method to describe population dynamics on a discrete network that avoids the use of special features (such as the absence of loops), which are often used in similar contexts, and the new results are validated using an SIR model. Sharkey et al. (2015) also consider an SIR model on a contact network and prove that a new pair-based moment closure representation is consistent with the infectious time series for networks with no cycles in the associated graph. Hiebeler and co-workers consider a moment dynamics description of an SIS model, and they specifically focus on the influence of population size, where the population is partitioned into groups or communities (Hiebeler et al. 2015). Using their moment dynamics model, Hiebeler et al. carefully study the role of population size, variability in infection levels among communities and variability among stochastic realizations. Markham et al. (2015) explore methods for determining the validity of mean-field and moment dynamics models interacting populations in a setting that is relevant for interpreting experimental data



**Fig. 2** Contributors to the special issue sharing dinner after the ESMTB 2014 mini-symposium. From *left to right*: Michael Plank, Thomas House, Kieran Sharkey, Frédéric Barraquand, Deborah Markham, Matthew Simpson and Ruth Baker

from cell biology experiments, paying particular attention to difficulties encountered when these models are applied to co-culture experiments in which more than one cell type is present in the system. Finally, Mente et al. (2015) describe a discrete model of collective cell behaviour, which can include spatial dynamics and clustering, and focus on the properties of individual trajectories in their model and approximating the properties of these individual trajectories using stochastic differential equations.

To gather together interested researchers and promote the special issue in the field, we organised a mini-symposium at the 2014 ESMTB meeting in Gothenburg. The mini-symposium consisted of seven speakers, and it generated a number of interesting discussions in the area (see Fig. 2 for a picture of the post-symposium dinner). Many of these speakers also made contributions to this special issue.

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