Math. Model. Nat. Phenom.
Vol. 9, No. 3, 2014, pp. 1–4
DOI: 10.1051/mmnp/20149301

Modelling Biological Evolution: Introduction to the Special Issue

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The crucial role of theoretical approaches in studying evolutionary processes in biosystems is now well recognized. Indeed, even Charles Darwin, although himself not being a mathematician, derived his revolutionary ideas using theoretical methodology [4]. Combining mathematical modelling with empirical studies can provide a good understanding of the underlying biosystem which is unobtainable by means of laboratory experiments and field observations alone (for few recent examples see references in [14]). On the other hand, the number of publications in literature on modelling biological evolution is tremendously large and is constantly growing each year: it is rather hard to deal with such an immense flux of information.

The main aim of the current Special Issue is to provide a useful guide to important recent findings and developments in few key areas of the modelling of biological evolution. This Special Issue addresses the following topics in particular: (i) the origin of genetic diversity in populations and communities; (ii) dynamics of replicator equations; (iii) evolution of biological macromolecules; (iv) evolutionary population ecology and (v) evolution and adaptation of animal behaviour and strategies. It is important to emphasize that the individual contributions to the Issue are not limited to one of the mentioned areas but rather combine several of them, so it may be hard to assign a particular paper to a single topic. Finally, most of the studies presented here are actually papers from the international conference "Modelling Biological Evolution" (MBE 2013), which was hold in Leicester, UK in May 2013. This conference brought together a number of mathematicians and empiricists with the key objective of creating stimulating discussions and productive debates between them.

Understanding the mechanisms of genetic diversity (both within a single population and in ecological communities) has been the central topic in modelling biological evolution since the revolutionary work of Charles Darwin on the origin of species. In their study, Bessonov *et al.* [1] revisit the famous evolutionary diagram suggested by Darwin showing patterns of species creation [4]. Bessonov *et al.* provide a novel mathematical interpretation of this diagram and show how it can be reproduced using a set of generic mathematical models of reaction-diffusion type. The authors argue that to correctly reproduce Darwin's diagram, one needs to take into account local, nonlocal and global competition of interacting species in the hypothetic space of the phenotype. They also argue that the coefficients describing interaction of species in this space should be not constant but phenotype-dependent as well as time-dependent.

The work of J. Farkas and A. Morozov [6] explores evolution in a predator-prey system, where the prey population is genetically structured. The evolutionary process is considered to be rapid since it takes place on the same time scale as ecological dynamics. There is a growing body of empirical evidence for such rapid evolution in nature (see [20] and many other papers). Interestingly, previously published results show that rapid evolution in such structured predator-prey system can stabilize the system even with an unlimited carrying capacity of the prey [15]. These findings, however, were only based on direct numerical simulation using particular parameterizations of model functions, which obviously calls into question their correctness and generality. J. Farkas and A. Morozov treat the model analytically and consider various parameterizations of the inheritance kernel. The stabilizing role of structuring and rapid evolution is analytically demonstrated for the first time, and in particular, it is shown that selectivity of predation according to the life trait of prey is necessary for stabilization of the predator-prey interaction [6]. Thus this work emphasizes once again the importance of genetic structuring and animals personality in population persistence.

An important requirement for an evolving biological system is the ability to reproduce itself which can be mathematically described by so-called replicator equations [5,7]. S. Bratus and co-authors [2] consider a replicator system with diffusion: an important application is the modelling a hypercycle of macromolecules in a non-mixed system such as a living cell. By introducing a novel analytical technique, Bratus *et al.* investigate the properties of stationary solutions of the distributed replicator system. The results demonstrate that, surprisingly, whereas in a well-mixed system some of the species/macromolecules go extinct, the spatially heterogeneous replicator system can supports the co-existence of all species/macromolecules. The analytical conditions of persistence and stability in the replicator equations with diffusion are elegantly derived.

In their insightful review, G. Karev and I. Kareva [12] consider a general method for investigating evolution in genetically heterogeneous populations based on the replicator equations framework. This method seems to be rather promising: it allows us to easily follow the evolutionary dynamics of complex genetically structured populations, while the system can be treated with the help of the analytical tools of bifurcation theory. The main idea of the method is to introduce new 'keystone' variables with a further reduction of complex multi-dimensional models to low dimensional systems which in many cases can be easily explored analytically. This framework is applicable to both continuous time systems and discrete models. A set of insightful examples illustrates the theoretical findings. These include studies of evolution of life trait distributions within a single population as well as in interacting populations, preventing the tragedy of commons and, finally, some important applications to cancer therapy.

Evolution of key biological macromolecules is another focus of modern mathematical biology and the two following contributions of the current issue are devoted to this hot topic [16, 18]. In her work, R. Retkute [16] explores the fundamental question of duplication of DNA in all three domains of life (the bacteria, the archaea and the eukarya) with the main objective being to reveal and quantify major evolutionary forces shaping the patterns of genome replication observed in modern organisms. The author uses evolutionary simulation, taking into account random genome sequence shuffling, mutation, selection and DNA replication. The simulation results are compared to the genome data in *E.coli, P.calidifontis* and *S. cerevisae*. Interestingly, the results of the evolutionary simulation demonstrate that under assumption of a fixed cost per replication origin it becomes more beneficial for a genome to reduce the number of replication origins in the case of high uncertainty in origin activation timing.

The contribution of A. Terry [18] explores the response of cells to various stresses (such as oncogene activation, thermal shock or DNA damage), regulated by the p53 protein. This protein is supposed to play a crucial role in preserving genomic integrity and protecting cells from becoming cancerous [13, 19]. The author suggests a novel mathematical model of the p53 pathway using the reaction-diffusion framework. A particularly interesting new feature of the model is that it takes into account the appearance and repair of DNA damage. The model results suggest that with the existence of DNA repair, spatio-temporal oscillations of densities of p53 become severely dampened. Interestingly, a minor change to the location of the DNA damage can highly affect the spatial distribution of p53 within the nucleus. This finding

https://doi.org/10.1051/mmnp/20149301 Published online by Cambridge University Press

is important since uneven spatial distribution of active p53 within the nucleus of a real-world cell could strongly influence the response of the entire cell to stresses via activation of a large number of competing p53-inducible genes [18] .

The contribution of K. Parvinen [9] explores the evolution of a particularly curious type of parasitism: sperm parasitism in asexual populations. The study organism is Amazon molly (*Poecilia formosa*) whose females reproduce asexually, but still need sperm to initiate the reproduction. All offspring of asexually reproducing females are females, thus they should potentially outcompete sexually reproducing females, however, their own persistence will be threatened by the absence of males in the population. This provides an amazing biological paradox: why Amazon mollies or any similar species exist in nature, whereas according to "common sense" reasoning they should become extinct [8]? K. Parvinen provides his own solution to this paradox. He considers the evolution of sperm parasitism in a structured metapopulation model, which incorporates both realistic local population dynamics and patterns of individual dispersal. In the considered metapopulation model, the coexistence of sexual and asexual behaviour becomes possible in the case of the existence of a trade-off between the reproduction and dispersal traits. Interestingly, a non-spatial model always predicts an evolutionary suicide of the whole population.

The papers by Broom *et al.* [3] and Teichmann *et al.* [17] address the problems of optimality in shaping animal behavioral and signalling strategies using the mathematical framework of game theory. M. Broom and co-authors model kleptoparasitism (food stealing) in animals competing for a vital resource, which is a well known phenomenon in nature [10]. An important novelty of the approach by Broom *et al.* is that they consider non-homogeneous animal populations: each individual is characterized by its Resource Holding Potential (RHP). The mathematical results emphasize the importance of the relationship between RHP and resource value for each individual, with different relations between RHP and resource value determining the probability of potential fighting between the individuals. The theory is demonstrated to work well in describing the kleptoparasitic behaviour of Olrog's gulls.

Teichmann *et al.* [17] model the evolution of secondary anti-predator defense. This type of defense is a widespread in nature and often consists in producing toxins along conspicuous warning signals (known as aposematism). The optimal energy allocation into the secondary defence of an individual is a result of co-evolution of toxin production and warning signalling strategy. The paper by Teichmann *et al.* develops a new methodology in assessing the outcomes of this co-evolution by considering finite populations (the previous models were focused on infinite populations) and including the effects of genetic drift as an extra evolutionary force. Using evolutionary simulations the authors find the existence of a negative correlation between strength of warning signal and that of secondary defence, and demonstrate that the introduced genetic drift can promote stable aposematic behavior. The results maybe useful for a better understanding of the origin of mimicry in some species.

Acknowledgements. I thank the contributors and reviewers for their collaboration in producing this Special Issue. Professor A. Gorban (University of Leicester) provided valuable suggestions which helped to prepare this Issue. I am very grateful to the London Mathematical Society (LMS) for providing a supporting grant which was vital for organising the international conference "Modelling Biological Evolution", Leicester, UK May 2013.

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