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Editorial

Modelling biological evolution: Linking mathematical theories with empirical realities

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Mathematical modelling has long been recognised as a powerful, efficient and ethically justifiable research tool for exploring various aspects of biological evolution and adaptation in biosystems ranging from biomolecules to human societies. Theoretical models and computer simulations are now regarded as a low cost and convenient supplement to empirical studies, but modelling often can even provide an alternative to biological experiments which can hardly be done at all. For example, in the case where we explore the evolution and spread of particularly severe diseases or when we study acclimation of the human body to severe stress conditions. Using a model-based style of thinking in biology can bring outstanding results—for example, Charles Darwin, although not himself a mathematician, derived his revolutionary ideas based on theoretical methodology—and the mathematical modelling of biological evolution has a long and illustrious history starting from the pioneer publications by J. Haldane in the 1920s (Haldane, 1990) and followed by the seminal works of Fisher (1999) and Wright (1986). Currently, hundreds of theoretical studies are being published each year; novel mathematical and computational approaches are being rapidly developed to cope with the existing and newly emerging challenges. It is often hard to avoid getting lost in such an immense flux of current publications on modelling biological evolution!

The aim of the present Issue of the Journal of Theoretical Biology is to provide a useful guide to important recent developments in some key-areas in modelling biological evolution and adaptation. In particular, the following topics are presented: (i) evolution of decision-making in animals; (ii) the origin of life and various mechanisms of species creation; (iii) links between evolutionary and ecological processes; (iv) evolution of cooperation; (v) acclimation and adaptation of organisms to severe stress conditions and (vi) evolution of human culture. Most of the works presented here are in fact contributed papers from the international conference ‘Modelling Biological Evolution: Linking Mathematical Theories with Empirical Realities’ (MBE 2015), which took place in Leicester, UK, in May 2015 and brought together about 130 theoreticians and empirical evolutionary biologists with the main aim of creating debates and productive discussions. As an outcome of the conference, it was concluded that making substantial progress in modelling evolution would require better links between our sophisticated models and available empirical data. The current Special Issue fully supports this conclusion: a large proportion of the theoretical models presented here are closely related to concrete biological study cases. The Special Issue also emphasizes the need for a more constructive dialogue between theoreticians and experimentalists to be able to aid with linking theory and empirical data.

The first two papers of the Issue (Caiado et al., 2016 and Morozov and Kuzenkov, 2016) consider modelling of animal decision making. In their work, Caiado et al. (2016) explore the optimality

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of decisions made by social animals (including humans) in the case where these decisions are affected by social aspects—for example, by the popularity of a particular option within the population as well as transparency of information on the costs and benefits of different options. In this case, the decision making process should necessarily involve cultural learning, and the authors show how the fitness landscape function can be constructed over a two-dimensional surface representing transparency of option choice and social influence. The authors consider an arbitrary number of possible decision options. It is shown that the expected optimal decision can be reached based on a hill-climbing algorithm by finding peaks of the fitness landscape function. The authors show how one can estimate the transparency, social influence and related fitness landscape from data. It is demonstrated that due to complexity of the fitness landscape function, the optimal behaviour of social organisms would depend on initial conditions even for a fairly small number of possible options.

Morozov and Kuzenkov (2016) explore diel vertical migration of zooplankton (DVM) in the ocean and lakes—the largest synchronized movement of biomass on Earth (Hays, 2003). Unlike previous approaches suggesting optimization of some factor (e.g. reproductive value, venturous revenue, energy gain/mortality ratio, etc.), the authors demonstrate that the optimal strategy of DVM can be unambiguously derived as a result of selection processes in the underlying system of equations for the frequency dynamics of the genotype or traits. Using this novel approach, they obtain the optimal DVM in the infinite dimensional space of spatial trajectories chosen by zooplankton in the water column. For a set of plankton models, it is shown how functionals generating the evolutionarily stable behavioural patterns can be derived. The mathematical tools used by Morozov and Kuzenkov are based on the variational principle for self-replicating systems (Gorban, 2007; Kuzenkov and Ryabova, 2015) which is different from the standard adaptive dynamics formalism (cf. Parvinen et al., 2006); notably, it allows the authors to take into account long-range or non-rare mutations.

The next two contributions of the Issue focus on revealing the origin of life and species creation (Hubai and Kun, 2016; Yamaguchi and Iwasa, 2016). The work of Hubai and Kun addresses the famous paradox of Manfred Eigen which states that neither the accurate copying of genomes, nor the building of long genomic sequences could be possible without the prior establishment of the other. This produces a fundamental obstacle for the acceptance of the hypothesis of a spontaneous formation of life (Eigen, 1971; Maynard Smith, 1979). Hubai and Kun propose a partial solution to this paradox by considering an array of small individually replicating genes under multilevel selection. The paper explains how an ensemble of such genes might overcome the principal challenges: the non-synchronicity in replication and the randomness in assortment to daughter cells. Using the Stochastic Corrector Model framework, it is found that multilevel selection can support a large number of genes (e.g. 100) and that this system can also allow for a limited amount of competition asymmetry of genes (about 10%). The authors carefully explore the limit to the enzymatic diversity (the second error threshold), which can be maintained in ancient cells, and suggest a particular plausible scenario of incorporation of novel genes during early stage evolution.

In their study, Yamaguchi and Iwasa (2016) investigate mechanisms of species creation via allopatric speciation caused by accumulating genetic divergence due to geographic isolation of populations. Allopatric speciation has been considered in the literature as a major process in species creation (Rosenzweig, 1995). Here, Yamaguchi and Iwasa investigate a more realistic scenario of speciation known as parapatric speciation, in which the populations are not completely isolated from each other, but are related by rare migration. The authors introduce some assumptions on genetic mixing and haploid-type species as well as free recombination between loci within the population. By using different modeling approaches, they show that species creation can be maximized at an intermediate rate of migration between the sites. It was also found that a decrease in the number of loci would increase the optimal migration rate and considerably shorten the time to speciation, thus accelerating creation of species. The study is an extension of previous work on the same topic by the authors (Yamaguchi and Iwasa, 2013).

The next five contributions explore links between evolutionary and ecological processes (Lion, 2016; Mazzucco et al., 2016; Ritterskamp et al., 2016; Dean et al., 2016; Świerniak et al., 2016). The detailed review of Lion (2016) addresses modelling of evolution in spatially structured populations based on the spatial moments technique. Currently, it is well recognized that spatial structuring would greatly affect evolution processes (Rousset, 2004; Lion and van Baalen, 2008), however, evolutionary models including spatial dynamics are often difficult to handle analytically. The review shows how master equations for the species densities can be derived from first principles for various spatial configurations in network-based models and how spatially structured models can be connected to the general adaptive dynamics framework. It is demonstrated that the selection gradient of the invasion fitness can be written in terms of neutral measures of genetic and demographic structure. The review explores connections between the given spatial modelling approach and inclusive fitness theory. The author concludes that by combining the spatial moments technique with the adaptive dynamics framework one can perform efficient modelling of the evolution of life-history traits even in the case where populations exhibit complex life cycles.

The work by Mazzucco et al. (2016) continues the topic on modelling evolution in spatially structured populations. The authors investigate the possibility of efficient eradication of infection diseases in spatially structured populations in the case where pathogen evolution counteracts eradication measures. The particularity of the study consists in including the trade-off between infectivity and mobility among groups of individuals which has been neglected in the previous works. The model predicts that pathogen evolution would generally extend the eradication tail. It is also demonstrated that the cost structure of eradication procedure and timing of interventions can greatly affect the shape of eradication tails. Since disease eradication is often time consuming and expensive, the results of Mazzucco et al. (2016) can be useful to assess whether or not it is worth implementing such a procedure at all.

Ritterskamp et al. (2016) consider the role that spatial heterogeneity and predator-prey and/or competition interactions play in speciation and biodiversity in food webs, a fairly new area of research. The authors explore an eco-evolutionary model consisting of integro-differential equations and demonstrate that adding space to evolutionary food webs can result in the emergence of communities with complex structures both in terms of life traits and spatial distribution. Interestingly, the outcome of evolution can be either a static configuration or a constantly evolving structure. The relative simplicity of the model allows the authors to reveal key factors shaping the network structure. In particular, it is shown that the ratio between competition or predation and interaction between small groups of species should play a crucial role in the evolutionary outcome. The authors argue that the obtained biodiversity patterns are in a good agreement with those typically observed in the wild.

In their study, Dean et al. (2016) construct and investigate a detailed mathematical model of photosymbiosis, which is a well-known type of symbiotic relationship. Although photosymbiosis is widely addressed in the literature, its exact mechanisms are still poorly understood. Here the authors are interested in how the