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Mathematical Modelling in Theoretical Ecology: Introduction to the Special Issue

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Mathematical modelling in ecology has a long and illustrious history leading back to the famous works of Malthus [16], Quetelet [19] and Verhulst [28] on principals of demographic regulation. These early models, although rather naïve, formulated fundamental questions and challenges in population dynamics, which were addressed in many later works. In the first part of the 20th century, the classical works of Lotka [13] and Volterra [27] on dynamics of interacting species radically transformed the entire idea of modelling in ecology. In fact, their works, along with many other important contributions, (for a short history of the implementation of mathematics in ecology, see [9]) eventually resulted in the emergence of theoretical ecology as a new science. The fundamental ideas of Lotka and Volterra on the principles of ecological modelling have not lost their importance even now and are implicitly present in a large number of newly created models. Currently, theoretical ecology is a rapidly developing area of research (with thousands of new publications appearing each year) and mathematics continues to play a fundamental role in understanding the generic mechanisms shaping dynamics of populations, communities, metacommunities and ecosystems. Mathematical modelling in ecology is so important because it provides a thorough investigation of a problem without a need for large-scale experiments with ecosystems, which can be costly, time consuming and potentially dangerous for nature. Interestingly, the questions on the main mechanisms of populations regulation addressed by Lotka and Volterra as well as by the earliest modelers Malthus, Quetelet and Verhulst are still in the focus of theoretical ecology!

The main goal of the current Special Issue is to provide a useful guide to important recent findings and developments in several key areas of mathematical and theoretical ecology. In particular, the contributions to this issue are centered around the following four topics: (i) influence of spatial heterogeneity on population dynamics and species persistence; (ii) modelling biological invasion and biological control; (iii) reduction of complex ecological models to simpler tractable models; (iv) applications of bifurcation theory to the dynamics of interacting species. It is worth mentioning that most of the contributions to this issue are not limited to only one of the above topics, but rather lie at the interface of several of them.

One of the most important achievements in mathematical ecology since the works of Lotka and Volterra is the recognition of the role of space. It has been convincingly demonstrated that heterogeneity in the distribution of organisms across the environment can play a key role in shaping ecosystem dynamics and enhancing persistence of populations [6, 8, 9, 15]. In the current issue, four contributions [4, 12, 20, 23] directly focus on the role of space in population dynamics.

Understanding the mechanisms of biological aggregation and patchiness is a hot topic in theoretical ecology with various models suggested [6,18,21]. In her work, R. Eftimie [20] investigates the movement of aggregations of organisms mediated by various signals as a result of communication and social interactions. The mathematical framework used in [20] is based on nonlocal hyperbolic equations with integral kernels. It is demonstrated that animal groups using communication can travel in a zigzagging manner and the maximal speed of group movement is estimated using analytical techniques. Since the constructed model allows us to link different modes of communication and the density structure of zigzags, R. Eftimie argues that the given framework can provide new insight into an understanding of the complex patterns of collective motion observed in nature.

Lewis *et al.* [12] consider mutitrophic interactions in a spatially extended ecosystem in the case where the release of infochemicals by prey can provide feeding cues for predators and thus can affect the trophic structure of this system. As a study case, the authors investigate the dynamics of a tri-trophic planktonic food chain model consisting of phytoplankton, microzooplankton and carnivorous copepods (the prey, intermediate and top predators, respectively), where the phytoplankton release chemicals following grazing by microzooplankton and thus attract copepods who can remain and feed on biologically productive patches of microzooplankton in the water column. Lewis *et al.* [12] elaborate a 1-d reaction-diffusion food-web model of this ecosystem (based on the earlier non-spatial model [11]). Model results demonstrate that utilization of infochemicals for foraging provides fitness benefits to the top predator and stabilizes the ecosystem at high nutrient load. Interestingly, the model shows that the use of infochemicals by copepods can be an evolutionarily stable strategy which promotes their persistence in the water column.

The work of Gauduchon *et al.* [4] explores the effect of habitat fragmentation on population dynamics and persistence. The authors consider predator-prey cyclic dynamics in a fragmented landscape and use a reaction-diffusion modelling framework. An important extension of [4] compared to the previous works on this topic (e.g. [24]) is adding edge-mediated behavior - organisms exhibit a behavioral response to the interface between different habitat types. Gauduchon *et al.* show that habitat fragmentation generally results in a drop of densities of interacting populations in terms of both cycle amplitudes and average densities of species. Gauduchon *et al.* demonstrate that the response to fragmentation is different for the edge and the middle of a favorable patch, showing an increase and a decrease in population density, respectively. Thus, measuring population density in just one location (e.g. at the edge of the patch) can give a misleading interpretation of the effects of habitat loss.

In their study, M. Semplice and E. Venturino [23] investigate the propagation of population waves in a reaction-diffusion model of interacting planktonic species in the ocean. The interacting species include toxin-producing and toxin-free phytoplankton as well as herbivorous zooplankton consuming both algal species, which is a fairly typical ecological scenario in marine ecosystems [7]. Using analytical and numerical techniques the authors show the existence of travelling waves of species, and variation of diffusion coefficients demonstrates the possibility of a variety of dynamical patterns after the propagation of the travelling wave.

Biological invasions and biological control are key topics in theoretical ecology [15]. Two contributions to this issue directly deal with this problem. In their study, Tyutyunov *et al.* [26] explore the efficiency of biological control of ragweed by its natural enemy, the ragweed leaf beetle. They develop a 2-d spatial reaction-diffusion-advection demogenetic model which describes both ecological interactions between the species and evolution of the dispersal ability of the biocontrol agent. Using their model Tyutyunov *et al.* demonstrate the existence of a solitary population wave of high beetle density as a result of its deliberate introduction into the ragweed-invaded ecosystem, accompanied by a rapid evolution in the flying ability of the beetle, enhancing its dispersal. Additionally, the theoretical prediction of Tyutyunov *et al.* seems to be in good agreement with available empirical data on the introduction of ragweed leaf beetle in the South of Russia. The contribution of L. Rodrigues and D. Mistro [22] explores biological invasion in a spatially heterogeneous environment. The novelty of the study comes from the fact that they formulate a spatially discrete 2-d model of invasion in a fragmented landscape, while earlier models were focused solely on continuous space. They analyse the model using the Coupled Map Lattice framework, considering two important types of heterogeneity: a stripe-like and a randomized environment. It is shown that invasion success in an environment containing hostile regions is predetermined by the connectivity between the favorable regions, and not only by the relative proportion between favorable and unfavorable regions as was previously believed.

Attempts to make our models of ecosystems more realistic often results in an essential increase of model complexity, and thus in a loss of mathematical tractability. Therefore it is desirable to develop techniques of model reduction and approximation, which can allow us to transform a complex model into a simpler one without losing the essential system properties. For example, complex spatially explicit systems can be sometimes reduced to mean-field models (see [17] for an introductory review). In this special issue, Bravo de la Parra *et al.* [2] consider the aggregation of variables method for the reduction of discrete dynamical systems, in which the reduced model can be formulated in terms of only a few global variables. The reduction method suggested by Bravo de la Parra *et al.* takes advantage of time scale separation by considering slow and fast processes, but the method is substantially different from similar methods developed for continuous models (e.g. [1]). Indeed, when defining slow and fast processes in a discrete population model we cannot go beyond a certain minimal time unit: the time between consecutive breading seasons, for instance. The authors explain how the problem of the existence of this minimal time unit can be resolved, and address both the cases of linear and nonlinear population models. In their work, Ly *et al.* [14] implement the method of aggregation of variables to a model of multi-site fishery in the case of a variable price of fish. The implementation of the reduction technique is justified since both the movement of boats and the variation of price take place on a fast time scale, whereas the population dynamics occur on a slower scale. Analytical tractability of the aggregated model allows us to fulfill a thorough bifurcation analysis. A particularly interesting result of Ly *et al.* [14] is that variation of the total number of fishery sites can result in a switch between the regimes of over-exploitation and sustainable fishing.

The final two contributions [5] and [10] clearly demonstrate the important role that bifurcation theory of ODEs plays in understanding patterns of dynamics in population models. In their insightful review, E. González-Olivares and A. Rojas-Palma [5] consider the possible patterns of dynamics in a generic predator-prey model with an Allee effect in the prey growth. The Allee effect in a population occurs when the per-capita growth rate is an increasing function of species density, and is a rather widespread phenomenon in nature [3]. Mathematically, the family of models considered in [5] is a modification of the Lotka-Volterra system with various parametrizations of the predator functional response with the prey growth described by standard cubic parametrization of the Allee effect. Surprisingly enough, this apparently ‘simple’ model can possess a rather complex bifurcation structure, with multiple limit cycles. Using bifurcation theory, González-Olivares and A. Rojas-Palma derive the conditions for the existence of a unique equilibrium and multiple limit cycles and then compare the dynamics of the system with similar models without an Allee effect. Kooi *et al.* [10] use bifurcation theory to develop a framework for the analysis of resource competition models in a chemostat environment. The classical method of analysis of resource competition models is Tilman’s well-known graphical approach [25], which is now routinely included in standard theoretical ecology textbooks. Kooi *et al.* [10] argue, however, that their approach is complementary to Tilman’s since it allows for a different interpretation of the classical results on competition. Additionally the approach of [10] can be applied to exploring multiple resources-multiple species communities with both stable and oscillatory dynamics, providing an interesting new interpretation of Tilman’s approach for those systems.

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