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Modelling in Ecology, Epidemiology and Ecoepidemiology: Introduction to the Special Issue

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Mathematical modelling in ecology, epidemiology and eco-epidemiology is a vast and constantly growing research field. This is perhaps unsurprising since mathematical models can provide a wide-ranging exploration of the biological problem without a need for experiments which are usually expensive and can be potentially dangerous to ecosystems. The current Special Issue of MMNP presents recent findings and developments in the following areas of theoretical ecology and epidemiology: (i) revealing the biological processes behind observed complex patterns; (iii) modelling the role of dispersal and spatial heterogeneity in species persistence; (ii) applications of bifurcation theory in population dynamics and epidemiology; (iv) the role of selection in self-replicating biological and ecological systems; (v) sensitivity, predictability and control of biological models in a noisy environment. It is important to emphasize that many of the contributions to this issue are not limited to one of the above topics, but rather lie at the interface of several of them.

The work of D. Ahmed and S. Petrovskii [1] studies the movement of insects whose spatial dispersal is a random variable and is described by a certain probability distribution. Understanding the mechanisms of insects movement behaviour is a highly relevant problem from the practical point of view, since it can help us to correctly interpret the results of insect trapping, which is the basis of many current pest monitoring programs [17]. There is a lively ongoing debate in the literature regarding the possibility of Lévy-type movement behaviour by animals, as opposed to the Brownian motion, and various mechanisms have been proposed to explain the observed patterns [3, 16, 24]. Ahmed and Petrovskii provide an alternative description of Levy-type movement by introducing time-dependent diffusivity. In particular, the authors claim that the trap counts of insects whose dynamics is given by an example of a Lévy-type distribution -a Cauchy type random walk - can be successfully modelled via a different movement pattern: classical Brownian motion with a time- dependent diffusion coefficient. Thus, the authors provide an excellent example of how two completely different mechanisms can describe the same pattern of field observations.

Among the central topics in theoretical ecology is the understanding of the role of space in population dynamics and species persistence across different time scales [6, 7, 11, 12]. In this issue, three contributions [2, 4, 20] directly focus on the role of space in population dynamics.

Modelling the mechanisms of biological aggregation and patchiness is a pertinent topic in theoretical ecology, with various models suggested [6, 14, 19]. In their work, R. Eftimie and A. Coulier [4] explore the effects of communication between organisms on the formation and structure of large biological aggregations. In particular, the authors consider the effects of avoidance behaviour by a fraction of the population on the spatial dynamics of the whole population. They demonstrate that avoidance behaviour results in the emergence of new spatio-temporal patterns, which are characterized by spatially separated aggregations of individuals or by segregation of individuals within the same aggregation. In the case where individuals learn to tolerate their neighbours, this can result in even more complicated dynamics: spatial segregation into tolerant and intolerant subpopulations.

P. Carmona and D. Franco [2] investigate the dynamics of a meta-population in a heterogeneous environment and the role that species dispersal plays in species persistence and the long-run average amplitude of density oscillations (called the 'fluctuation range' by the authors). The authors consider a standard system of coupled difference equations: they explore a system of two patches (sites) connected by dispersal, where the local population dynamics on each patch is different (e.g. a stable equilibrium on one site and chaotic dynamics on the other site). Two cases of dispersal: unidirectional and bi-direction are considered. It is shown that the response of this meta-population to variation of dispersal rates can be quite complicated, and largely depends on the intrinsic dynamics of each subpopulation and the type and strength of dispersal. The authors show that multistability in the resultant meta-population model can strongly affect the behaviour of the mean total population size and its fluctuation range. They conclude that efficient control and sustainable management of this system via variation of the connectivity between the patches is possible only when a sufficient knowledge of the local population dynamics is available: the lack of such knowledge can results in a severe drop of the population size.

In their study, Y. Sekerci and S. Petrovskii [20] explore how the dynamics of marine planktonic ecosystems are influenced by oxygen production due to photosynthetic activity of phytoplankton. This is a novel approach to modelling plankton communities since most of the existing literature complectly ignores the oxygen-plankton interactions. The authors first develop a generic model of oxygen-phytoplankton-zooplankton dynamics and then provide an extensive bifurcation analysis of this model. The model predicts oxygen depletion in the water under certain environmental conditions, which can seriously impede the survival of plankton. Sekerci and Petrovskii demonstrate the possibility of various complex spatio-temporal patterns in the planktonic system including travelling fronts of oxygen depletion, dynamical stabilization of unstable equilibrium and spatiotemporal chaotic dynamics in the species densities.

The contribution of Hieu *et al.* [8] investigates the behaviour of the Kernack - MacKendrick epidemiological model in a noisy environment. The authors consider a particular case of noise: the telegraph noise, which switches between two values at random in both the transmission rate and the recovery rate. Such noise can represent sudden changes in environmental conditions. The authors provide the conditions for the persistence of the disease, and it is shown that the asymptotic behavior of the system is determined by a certain threshold value λ (which can be explicitly calculated using model parameters), which is a function of the probabilities of switching between the two different environmental states, the total size of the population, the transmission rate and the recovery rate. Depending on the value of λ, the system can globally tend towards the endemic state or the disease free state.

Sen *et al.* [21] consider a novel epidemiological model where the predator is a generalist and the alternative food supply is a dynamical variable. This approach is quite different to most ecoepidemiological models, where the predator is generally considered to be a specialist [23]. Another important new feature of the model is that the authors investigated the role of predator-dependent disease transmission, since although there are various known mechanisms through which the predation on the infected host can affect the transmission of disease (see [13]), the existing literature only considers predator-independent disease transmission. Sen *et al.* [21] extensively explore how the predator-dependent transmission in the presence of a second dynamical prey can affect the resultant behaviour of the system. Paradoxically, even if the second prey cannot establish itself in the system in the long term, and therefore formally the equilibrium species densities are equivalent to the model with a single prey, the overall system behaves differently to the case of a specialist predator, where the second prey is always absent.

The work of O. Kuzenkov and E. Ryabova explores the fundamental issue of relating natural selection to variational principles in biology [5,9,15,25]. Traditionally, variational principles in biological evolution have often used conventional wisdom without any strict mathematical justification. Here the authors attempt to justify the variational principal in general self-replicating systems by introducing the order of preference on the set of hereditary behavioural strategies as a result of selection. The proposed order of preference is based on the comparison criterion, and its maximization gives a variational principle for a generic self-replicating system. The newly introduced criterion has some particular properties which are considered in the paper. For instance, the evolutionary outcome may depend on initial conditions of the phenotype frequency; in particular, the transitivity principle might not be satisfied. Additionally, it is shown that the best strategy can lead to system-wide extinction. The paper discusses how to take into account the above peculiarities when modelling optimization of self-replicating systems.

The final two contributions [18] and [22] consider the fundamental issues of sensitivity and predictability of biological models in a noisy environment. In their work, L. Ryashko and I. Bashkirtseva [18] suggest a new approach for preventing catastrophic shifts in ecosystems with a stochastic environment. The approach proposed takes advantage of the stochastic sensitivity function technique, which is applied to a stochastically forced predator-prey system with a strong Allee effect. The authors assess the possibility of a noise-induced extinction of both species by constructing the confidence domains, and a method of robust control is suggested to prevent noise-induced extinction in the system with Allee effect. The method seems to work well even in the case where the stationary state in the underlying deterministic system is globally unstable. Stollenwerk and co-authors [22] explore the prediction uncertainty (the authors call it 'prediction insecurity') in stochastic systems in epidemiology (which can be also implemented in ecological modelling) using available information from available time series. By considering a set of examples with increasing complexity, the authors emphasize the apparent difference between the prediction based directly on data and the prediction based on a model with parameters of best fitted on data. In particular, prediction insecurity becomes larger in the case of conditioning on the data directly, as would be the case in empirical studies. The authors discuss prediction insecurity in more complicated stochastic models, in which the deterministic skeleton shows chaotic dynamics. The framework developed here can be implemented for analysis of ecological and epidemiological systems with time dependent and state discrete stochastic processes.

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