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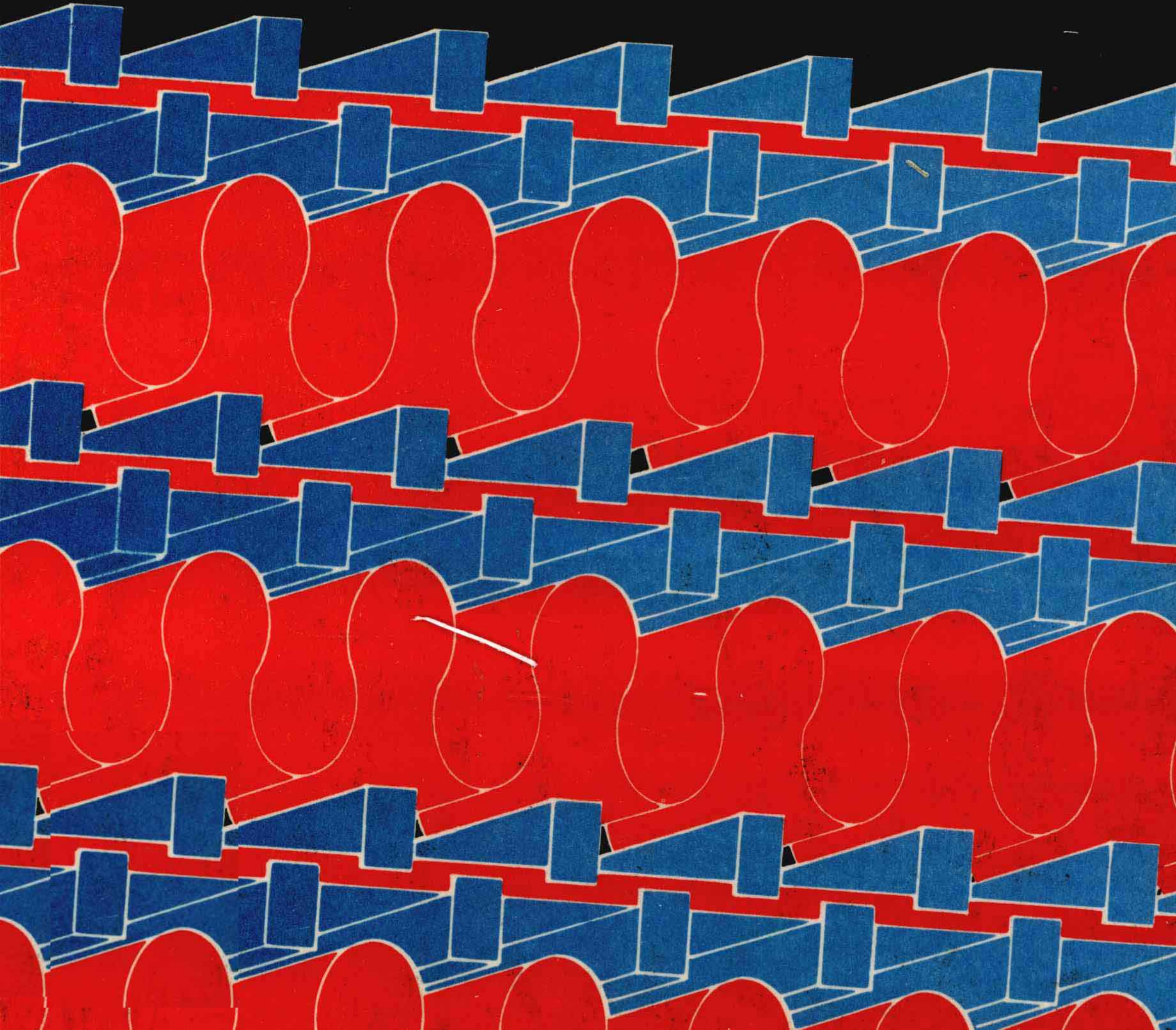
A MATHEMATICAL TREATMENT OF DYNAMICAL MODELS IN BIOLOGICAL SCIENCE

Kristína Smítalová and Štefan Šujan



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Preface

Mathematical ecology as a biological science accumulates information concerning the evolution of biological communities. On the other hand, as a mathematical science it gains a systematic character. In comparison with other mathematical specializations it utilizes methods of different parts of mathematics.

The main aim of the authors was to write an introductory book concerning the mathematical theory of biological community models. This book is not intended to be encyclopaedic in character, but nevertheless describes the main developments of mathematical ecology in parallel with the mathematical ideas which were stimulated by ecological modelling.

Unfortunately, Š. Šujan died in January 1985, but fortunately left notes of individual chapters and sketches of some parts. I have tried to respect his intentions concerning the contents and their presentation.

The first three chapters — except for those parts dealing with stochastic process — presuppose only an elementary knowledge of mathematical analysis and algebra: The fourth chapter, however, is a little more pretentious.

I am very grateful to I. Bajla for providing me with the notes of

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K. Smítalová

Introduction

A quarter of a century ago the term ecology was used only in the specialist biological literature. Today ecological problems excite the interest not only of specialists but also the general public, at large.

'Ecological problems' are concerned with questions relating to the protection and sustenance of life in the environment and the rational exploitation of natural sources. The solution to these problems demands a detailed investigation of the phenomena under study including their intrinsic structure and relation to the environment. The development of the theoretical elements of nature conservancy proceeds by the integration of different disciplines, the most important of which is ecology — a science concerning conditions of existence and the mutual interactions of living organisms with the environment.

The complexity of ecological relations underlines the growing need for wider penetration of mathematical methods into biology. Indeed, the number of papers devoted to various mathematical models of ecological phenomena continues to increase. It is therefore not surprising that mathematical ecology has arisen as a relatively independent science.

Living organisms of single species do not live separately, but form groups which are called populations. Several populations of different species form a biological community. An ecological system — or ecosystem for short — is the union of a biological community and the environment in which it lives.

The term 'ecology' was first used by E. Haeckel in 1866 to denote a science dealing with the conditions for existence of organisms and their relation to the environment. However, attempts to use mathematical ideas to describe living objects appeared much earlier.

In the Middle Ages the Italian mathematician Fibonacci considered the problem of how many pairs of rabbits are born to one pair of rabbits during a year. He supposed that a pair of offspring is born to any pair during a month and that this process starts after the second month of life. The number of rabbits after one, two and successive months then forms a sequence of natural numbers in which every next member is equal to the sum of two preceding members. This sequence is well-known in mathematics as the Fibonacci sequence.

In this example rabbits served only to give a contrived biological interpretation to an abstract mathematical idea. Later, however, attempts were made to model realistic evolutionary processes from theoretical considerations. For instance, in 1798 T. Malthus constructed a general model of the evolution of the number of individuals in a single-species community in which he assumed the growth-rate to be linearly dependent on the number of individuals. This assumption, however, is only valid in the case where resources are unlimited and the age structure of the population and the environment remain unchanged. Such circumstances rarely occur except possibility under laboratory conditions or in the first phase of evolution of the lower organisms.

Population dynamic models describing a number of real evolutionary situations were constructed in the first half of the 19th century including the well-known logistic or Pearl–Verhulst equation which originated in the following way. Since real resources are limited, the population density $x(t)$ cannot be greater than some constant K and if the population density increases, then the growth-rate decreases. In the case that this process is linear, the population dynamics equation has the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = ax\left(1 - \frac{x}{K}\right)$$

in which a stands for the relative growth-rate. This simple equation is appropriate for modelling the evolution dynamics of a number of real populations. Later, models of two-species biological communities with interactions were also constructed.

During World War I fishing was limited and in the northern Adrian region predatory types of fish became widespread. In order to understand this phenomenon the mathematician V. Volterra constructed an analytical model describing a two-species predator–prey community. This model consisted of a system of two non-linear differential equations exhibiting periodic solutions. When applied to the fish populations in the northern Adrian region the model suggests that the observed growth of the density of the predator population could be caused by a mechanism of reciprocal interactions of species rather than the lack of fishing. This hypothesis was confirmed by a subsequent decrease in the predator population without any external intervention.

The same system of differential equations was investigated by A. Lotka in his book *Elements of physical biology* of 1924. Based on models of chemical kinetics Lotka derived a system of differential equations applicable to the dynamics of the densities of two interacting populations.

V. Volterra may be considered to be the founder of the mathematical theory of biological communities. In his book *Leçons sur la théorie mathématique de la lutte pour la vie* of 1931 Volterra's mathematical analysis of his models led to results with realistic interpretation. Indeed, his models of biological communities became not only a means of description, but also provided a means for predicting the behaviour of the modelled system.

It is intuitively clear that a biological community which exists in a constant state a long time has an intrinsic ability to resist disturbances in its environment. Such communities are said to be stable. A stable community should conserve the number of species. This is a natural requirement, since a community represents an organized system of populations. A stable community should also be resilient, in that it should conserve its intrinsic relations under perturbations. Moreover, it should be resistant to small changes of the environment.

Those intuitive requirements could be compared with the physical notion of the equilibrium of thermodynamical systems. Changes of the system are dependent on its interaction with the environment and according to this interaction there are three possible groups: namely isolated, closed and open systems. A system is isolated if it exchanges neither matter nor energy with the environment. More generally, a closed system is one which exchanges only the energy within the environment. A system which exchanges both energy and matter is called an open system. Biological communities are usually open systems.

The equilibrium state of a system is the state the system achieves if it is isolated from the environment. Open and closed systems do not usually exhibit equilibrium, since they interact with the environment.

An important case of a non-equilibrium state is the so-called stationary state. This state arises in the process of energy and matter exchange in open systems. Hence in general, a stationary state is no equilibrium, but every equilibrium state is stationary. Biological communities exist predominantly in stationary states which correspond to an optimal adaptation to the environment. After a deviation from the stationary state, the community tends to return.

If a non-zero stationary state is stable, then we say that the community is stable. Similarly as in the predator – prey system there may exist a periodic regime which is formed as a result of effects of individual factors of the system. Hence fixed regimes are represented by stationary and periodic states.

A biological community is considered to be stable if some non-zero fixed regime is stable and the stability theory of differential and difference equations enables one investigate the stability of models of communities. A fixed regime of the model will be considered to be a fixed regime of the community.

Note that in mathematical terminology the notions of equilibrium and stationary solutions are synonymous and both terms may be used.

An appropriate form of the model is determined by the properties of the community (i.e. size and structure of individual populations, the sufficiency or otherwise of resources or the character and intensity of the environmental influences). Parameters of the model are determined by the specific situation and are obtained either experimentally, or by a simulation on a computer.

In this book we shall not discuss methods of processing experimental data, but rather make the object of our considerations the qualitative properties of the model; namely, the existence and stability of fixed regimes. These properties are usually dependent on some parameters.

Dynamical models of biological communities are interesting also from the mathematical point of view. They may have properties which are difficult to interpret and may also have properties which have yet to be investigated mathematically. Some models (especially discrete) lead to further theoretical investigations.

The book is divided into 4 chapters. The first three chapters deal with models of single-, two-, or more-species communities and survey the fundamental results of mathematical ecology. The authors hope that these chapters are of interest to non-mathematicians. The last chapter "From determinism to randomness" is purely mathematical. It describes the mechanism of the appearance of chaos in one-dimensional discrete dynamical systems. These systems represent one of the two fundamental models of population dynamics. Whether chaos exists in real biological systems is still open to debate.

Some ecological notions

age structure of the population	— differentiation of the population into groups with respect to age
amensalism	— a relationship between two individuals which is disadvantageous for one of them and indifferent for the other
biomass	— mass of organisms
birth-rate	— the number of individuals in a given population born in a unit of time
comensalism	— a relationship between two individuals which is advantageous for one of them and indifferent for the other
community	— a system of populations which live a long time in a certain region
competition	— competition for food, habitat or other necessities between individuals
interspecies competition	— competition between individuals of different species
intraspecies competition	— competition between individuals of the same species
death-rate	— the number of individuals in a given population which die in a unit of time
diversity	— the number of species in a given com-

		munity together with the relative densities of individual populations
ecosystem	—	the union of a biological community and the environment in which it lives
mutualism	—	a relationship between two individuals which is advantageous to both of them
population	—	all individuals of the same species living in a given habitat
population density	—	the number of individuals per unit area or volume of habitat
resilience	—	an ability of the ecosystem to resist disturbance
survival-rate	—	the number of individuals which survive to a given age
trophic level	—	organisms on the same degree of the food chain