

Preface

The anthropogenic pressure on the environment evidently increases steadily. By all accounts, this development will continue in the foreseeable future. This makes it necessary to minimize the devastating consequences of anthropogenic influences on natural systems. The first step in this direction consists of learning how to estimate the character and size of the impact of these influences and to predict their consequences. A system of ecological monitoring is now being developed both on the global and national scales to meet these objectives (Izrael', 1976, 1977; Izrael' *et al.*, 1981).

Assessing environmental influences and predicting their consequences are closely related problems despite some significant differences. Predicting the consequences of influences would remain a special and very complex task, even if we had reliable "snapshots" of natural systems and knew their dynamics over a certain period of time. There are many possible reactions of ecosystems, none of which are yet studied well enough. However, we can distinguish, although somewhat artificially, the two most important ones (Bazykin, 1978; Holling, 1978).

1. *Buffered reaction of natural systems to external influences.*

For a very wide range of systems, we know that there exists a level of external influences which is called a *threshold* (or *critical level*). Relatively weak influences below threshold, are, in a sense, absorbed by natural systems. The result is only a small, quantitative change, which is undetectable for an external observer in many cases. This ability of ecological systems to withstand, up to a certain extent, external influence is called *resilience* of ecological systems (Holling, 1973). If the intensity of an external influence exceeds the threshold then the system cannot endure the pressure any longer. It breaks down and turns into a qualitatively different and, as a rule, undesirable state.

The significant feature of such a qualitative transition consists of its practical irreversibility. A disappearance of the external influence does not lead to the restoration of the original state of the ecosystem, and it is not possible to get the system back to that state artificially. Only the process of ecological succession,

which requires tens and hundreds of years, can contribute to the restoration of the original state.

The distinction between qualitative and quantitative, as well as between gradual and abrupt changes, depends of course on the point of view. In the first place, it is a question of the time required for those changes to occur as compared to characteristic times of the system. In the case of ecological systems, changes must be considered as abrupt (or qualitative) that evolve in the course of several years or decades. On the one hand, this length of time is most relevant for making predictions while, on the other hand, changes that occur over such long periods seem to be gradual from the conventional human point of view. It poses psychological difficulties to perceive such changes as abrupt.

2. *Counter-intuitive reaction of natural systems to external influences.*

The term *counter-intuitiveness* was introduced by J. Forrester (1971), the recognized American expert in the field of systems analysis, as applied to the management of economic, demographic and social processes in large cities, in particular. It refers to reactions of complex systems to external influences that go against common sense. In natural systems they are the rule rather than the exception: excessive application of insecticides leads, in due course, not to the suppression of an insect pest, but to a series of outbreaks; the extermination of predators may lead not to an increase, but to a drop in the numbers of key-industry animals; redundant irrigation entails, in many cases, not improved fertility of agricultural land, but its salinization, etc. The eutrofication of freshwater ponds can serve as a striking example of counter-intuitive consequences of anthropogenic influences. Fertilizers arriving at lakes and storage ponds from fields frequently do not lead, as might be expected, to an increasing productivity of the ponds. Instead they induce a fundamental structural reorganization of the ecological system of the pond resulting in its ecological destruction.

In situations like this, mathematical modeling may be regarded as the most promising tool for predicting the reaction of natural ecosystems to external influences. However, scientists run into serious obstacles when taking this path, obstacles that are intrinsic to any attempt to apply mathematical methods to biology. However, in mathematical models the ecological effects appear, perhaps, in their purest form with all their specific features. Difficulties are mainly the result of two closely related circumstances.

First, the structure of ecological systems is very complicated: they consist of many tens and hundreds of populations of separate species interconnected by thousands of different and, what is particularly important, essentially nonlinear interactions.

Second, all biological systems are unique, and this uniqueness becomes strikingly apparent when we examine natural ecological systems. Therefore, the contradiction between the adequacy and precision of a model on the one hand, and its size on the

other hand, is most pronounced when we undertake the mathematical analysis of ecological communities.

This contradiction is clearly reflected by two kinds of methods of mathematical analysis of ecological communities which are, to a considerable extent, independent of each other. The first kind is called *simulation modeling* and aims at achieving the best approximation of a single ecological object, as well as at describing it as concisely as possible. The second kind is called *mathematical modeling* (proper) and tries to describe and to analyse mathematically the characteristics typical for the widest conceivable range of ecological systems (Smith, 1974).

One of the most urgent problems demanding our attention is the stability of ecosystems (see, for example, May, 1974; Svirezhev, Logofet, 1978). Although it is usually considered a property of an ecosystem itself, it would be more correct to regard stability as a property intrinsic to a particular functional regime of an ecosystem. In light of this, there is an urgent need for a systematic study of all models of ecosystems with more than one possible locally stable functional regime. Such models are most adequate for describing qualitative changes of regimes of ecosystems under external influences.

Here it is natural to consider two classes of phenomena (Bazykin, 1982). The first class consists of qualitative changes of the functional regime as a result of a single, non-permanent external disturbance. Such an influence can move the ecosystem away from one stable regime and to another, qualitatively different one. The second class consists of qualitative changes that occur under the influence of a constant external change of gradually increasing intensity. When this intensity exceeds a certain threshold, the basin of attraction of a regime may for instance shrink to a point and disappear. As a result, the ecosystem reorganizes itself, which is practically irreversible: it changes its functional regime. Adequate mathematical tools to analyse such changes are the qualitative theory of differential equations and bifurcation theory (Andronov *et al.*, 1971, 1973; Arnol'd, 1983).

The purpose of this book is the systematic analysis of different dynamic regimes in models of two or three interacting populations that are interconnected by different biological interrelationships. Primary attention is given to the nonlinear dynamical effects in the modeled systems, depending on their initial state and the external conditions. They allow for different possible functional regimes, as well as for qualitative restructuring under the influence of external factors.

A careful, systematic study of greatly simplified interaction models of only two or three populations may be of interest for theoretical and practical ecology for the following reasons:

1. There are serious reasons to believe that the fundamental behavioral characteristics of a natural ecosystem (such as the above-mentioned buffered and counter-intuitive reactions to external influences) are due not so much to its complexity (number of components or species), but to the pronounced nonlinear character of the relationships between separate components of the

ecosystem. This may be observed even in a model ecosystem consisting of only two or three components. Analysing and classifying counter-intuitive behavior and criteria for when a threshold of external influences is approached for simple models is also of use for real, incomparably more complex ecosystems.

2. The near-threshold behavior of a complex system may be well described by the respective approximating system consisting of few variables (Molchanov, 1975*a,b*).
3. The study of interacting populations consisting of only two or three species extracted from an ecosystem seems to be ecologically justified as well as of practical interest in a number of important cases. Systems, as “forest-pest”, “agricultural crop-agricultural pest”, “valuable marketable animal species-its main resource-its major predator”, and so on, serve as examples.

The largely nonlinear dynamics of interacting populations require using both analytical and numerical methods. The analytical study allows us to apply results from the qualitative theory of differential equations and bifurcation theory (Arnol'd, Il'yashenko, 1988). These are essentially used for analysing the bifurcations of codimension one, two and three that occur in population models. A numerical study was carried out by applying two software packages (Levitin 1989; Khibnik, 1990; Khibnik *et al.*, 1993) developed at the Institute of Mathematical Problems of Biology (formerly Research Computing Centre), Pushchino: the TRAX package for analysing the phase space of dynamical systems depending upon parameters, and the LOCBIF package for constructing their bifurcation diagrams.

Some results of the numerical analysis are presented in the appendices after the individual chapters. We would like to draw special attention to the correspondence between the figures appearing in the book itself and the computer pictures presented in the appendices. In our opinion, both of them complement each other, giving a new understanding of dynamical models. Moreover, it seems to us that the behavior of strongly relaxational systems cannot be understood without an analytical prediction of the phase portraits which, in a sense, serves as a guide. Furthermore, the numerical study of systems gives an insight into dynamical characteristics which could hardly be discovered within the framework of analytical studies.

Finally, it is necessary to emphasize that this book could never have appeared without the enormous assistance of my closest collaborator, Faina S. Beresovskaya. I can never hope to repay her for her support. The present work has been greatly influenced by long-time scientific collaboration with researchers of the Institute of Mathematical Problems in Biology, (formerly R. A. S.) especially with A. I. Khibnik, Yu. A. Kuznetsov, E. A. Aponina and Yu. M. Aponin, as well as with my colleagues from the Ecological Centre, Pushchino. The computer-generated figures of the book were prepared with the assistance of S. L. Zudin who spent a lot of his time on that. This book was translated into English with great consideration and diligence by Vladimir V. Ievenko. The immense work of producing the camera-ready manuscript

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¹This refers to a previous version of the book.