



# **MATHEMATICAL MODELS IN ECOLOGY: THE ROLE OF CRITICAL REGIMES**

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Introduction

Ecology is one of the most complex biological disciplines. And ecosystems, of all the systems with which one deals in science, are among the most difficult to study. The dimensions of the problem are vividly demonstrated by the fact that only in the twentieth century has it become possible to pose the question of ecosystem study.

Any ecosystem consists of both biotic and abiotic elements. Thus ecosystem study is impossible without direct participation of the sciences of geology and geography in describing and investigating geological, topographical, hydrographical and climatic characteristics. So too the tools of chemistry and physics are absolutely necessary (and, unfortunately, completely insufficient) to study the constituent elements of an ecosystem's abiotic component. For study of the sum and substance of any ecosystem--animals, plants and microorganisms--the entire complex of all biological sciences must be employed.

Nor can one manage in the study of ecosystems without the socio-economic sciences, since the basic goal of ecology

is use of the biosphere for the needs of mankind. A mankind, I might add, which strives to rise above its role as a self-centered consumer, and seeks to understand its task as guardian of the biosphere. The interaction of ecosystems with a rapidly growing technology which urgently needs the multitude of raw materials it draws from these systems--this is not a simple problem. On the other hand the notion of the danger of irrevocable environmental pollution has already become a paradoxical platitude.

The mathematical sciences also have a role in the study of this important problem. One may, for example, point to statistical methods for quantitative evaluation of ecosystem structures; to the systems approach for description and classification of the multiform internal and external linkages of ecosystems; and to the more traditional studies of how systems change on both an evolutionary time scale and on a successional one.

This quick summary gives an idea of the full magnitude of this problem. One cannot help but wonder, "Is today's science, consisting as it does of almost entirely disconnected divisions, ready to solve such multifaceted complex problems?" To this one may only note that life itself has presented this problem, and a "natural" solution would cost mankind and the biosphere dearly. The best procedure

apparently is to single out the most pressing, crucial problems for study.

### Properties of Biological Systems

To isolate correctly the main approaches to research and modeling in ecology, a clear understanding of the specific features of biological systems is essential. Broadly speaking, one may point to four paramount features of living things: (1) the complexity of internal structure of each separate individual; (2) the multifaceted nature of the external environment (the conditions under which vital activity takes place); (3) the open nature of biological systems, as regards energy as well as structure and information; (4) intrinsic non-linearity--the tremendous range of external parameters within which the viability of systems is maintained. Let us now make a few observations concerning each of these points.

#### 1. Complexity of internal structure

This section might just as well be entitled "Respect for the biological system." Any complete description of even the simplest biological system requires the full sum of knowledge accumulated in the "pre-biological" natural sciences. Let us explicate this idea with a simple example. It is common in the popular literature while

flattering mankind's collective vanity to point out that nature never got around to "inventing" the wheel. Yet if one understands as the "principle of the wheel" the idea of replacing slipping friction with rolling friction, then any walking, jumping, or running animal realizes this principle far more subtly than the inefficient and awkward device we call the wheel. In a more far-reaching sense, with regard to cyclic energy transformation processes, nature "invented" the magnificent "chemical wheel," whose transformation of chemical into mechanical energy may be observed in any muscle contraction. For now, a man-made equivalent of such an energy converter is no more than a dream.

From a purely mathematical point of view, complexity in a system's structure means that in order to describe it or represent its structure, the values of many state variables must be assigned. In the language of mathematics this may be put as follows: *the phase space of a biological system is multi-dimensional.*

## 2. Multi-faceted nature of the external environment

Biological systems are complex not only internally. They function in a complex, often rapidly changing environment. Moreover, there are solid grounds for believing that the very complexity of their structure

possesses a compensatory character. They are complex precisely so that, responding to any external impact, internal defense reactions develop which preserve internal structure to the maximum. Especially well protected, of course, is the genetic hereditary structure. One may say of today's complexity for any given individual that it is the accumulated stock of "experience in interacting with its environment" for that individual's "mother," "grandmother," and "great-great . . . grandmother."

*Mathematical consequence:* a model of a biological system should contain many parameters (continuous and discrete) assigning the complex environment in which the given system functions.

### 3. The open nature of biological systems

Biological systems are never closed as regards energy--even school children know this nowadays. There are even more subtle aspects of this important property, however. Thus, for example, most higher plants have the leaf as their organ of photosynthesis. But at the same time, in the winter in the temperate zone trees shed their leaves, which then become part of the surrounding environment. An even more intricate interaction with the surrounding environment is manifested by insects which pass through larval and pupal stages. This feature of living things may be termed

"morphological, structural openness." Examples of informational openness are obvious, say, the "chemical intercourse" among social insects. And from this proceeds the fundamental (even if unhappy for the mathematical modeler) conclusion: *it is necessary to jointly model both a biological system and the environment in which it functions.*

#### 4. Intrinsic non-linearity

The range of variation for conditions under which biological systems usually operate (consider, for example, organs of sight and hearing), is significantly greater than, say, that of laboratory or industrial equipment used in measuring amplitudes and frequencies. For the purposes of many theories in physics, a linear approximation that describes small deviations from a state of equilibrium is fully effective. Taking into account quadratic terms usually significantly increases the exactness of such a model. The need to introduce non-linearity of a higher degree infrequently arises in the "pre-biological" natural sciences.

An entirely different situation exists in biology. Here it is insufficient to introduce polynomial terms of no matter how high an order. Non-linearity in biology is of an *exponential character*. The clearest expression of



this is the Weber-Fechner Law in physiology which establishes the logarithmic dependence of a reaction on an action. *The evolutionary significance of such powerful non-linearity is quite easily understood: one must be able to hear the rustle of an approaching snake and not be blinded by nearby lightning.* Those biological systems not able to embrace the enormous range of environmental impacts relevant to their existence simply become extinct, having lost the battle for existence. On their graves one might write: "They were too linear for this world." And the same fate, as well, awaits mathematical models which fail to take into account this important feature of life.

Complex Pre-Biological Systems. The Limits of Computer Technology

There are systems in the natural sciences for which sufficiently complete mathematical models have been built. Thus celestial mechanics predicts planetary movements with all the precision which modern observation techniques have at their disposal. In this sense one may speak of an exact model of a phenomenon. In the other extreme we have the case of quantum mechanics and its description of atomic structure. In principle there is no reason to doubt that Schroedinger's wave equation describes the behavior of

molecules with great accuracy, at least in the case of small molecules such as the benzene ring,  $C_6H_6$ .

On the basis of this example it is possible to graphically demonstrate the limits of computer technology. Let us consider what it would require to compute an extremely simple quantum mechanical model for benzene--Schroedinger's equation for 24 electrons. We will take only 4 valence electrons for each of the 6 carbon atoms, dispensing with the inner (paired) electrons and ignoring the motion of nuclei. Even with such simplification one gets an equation in partial derivatives for the  $\psi$  function which depends on 72 variables. Applying standard computational methods let us use a difference scheme carrying out to only 10 places (and this is not very many; one should go to at least 100) for each of the variables. In all we get an impressive number:  $N = 10^{72}$ .

To get an idea of the enormous magnitude of this number one should note that modern computers complete not more than a billion ( $n = 10^9$ ) operations per second. Supposing that engineers succeed in increasing computer speed by a billion times ( $n = 10^{18}$  operations per second). Even at this (at present) fantastic speed, a time,  $T = 10^{54}$  seconds, would be required in order to take a single step in the computation of a benzene ring using direct methods.

This is unimaginably longer than the lifetime of the Earth,  $T_0$ , i.e.:  $T \gg T_0 = 5 \cdot 10^9$  years  $= 1.5 \cdot 10^{17}$  seconds.

#### Exact, Approximate and Elementary Models

Direct computation by computer of exact models of various phenomena is, of course, unrealizable not only in biology but in other fields as well. In biology, however, this fact is very often apparent. This in no way is to say that exact models are useless. It does, however, presume the need for close, reciprocal ties between pure and applied mathematics. A good approximate model often dramatically reduces computational workloads. In this regard, quantum chemistry is nothing other than an approximation method for solving Schroedinger's equation for molecules. Quantum chemistry permits one to calculate the most important (usually energetic) characteristics of less complex but sufficiently representative molecules and radicals. Although we are not able to find the solution of an exact quantum mechanical problem, knowledge of Schroedinger's exact equation permits theoretical evaluation of any approximate solution.

An exact, granted it be even extremely complex, mathematical model of a phenomenon permits the construction of approximate models which answer special questions. Here

occurs a kind of "emancipation" of theory from experiment. Experiment, of course, continues to have the final word. But suitably designed systems of models can empower "King Experiment" to yield an unambiguous, "unclouded" answer. Thus the correctness of quantum mechanics need not be verified at the molecular level. The theory is verified on an elementary system (here, the atom) and by means of sufficiently simple and exact experiments.

*Moral for the mathematician: special and marginal cases of a theory are important not only in their own right, but as a means of verifying experimentally detailed, exact models.*

#### Is an Axiomatic Approach to Biology Possible?

Until recently the development of mathematics has been stimulated largely by the needs of mechanics, physics, and engineering. The expression has even become current, "exact natural sciences." And it is precisely in this narrow scientific framework that the axiomatic ideal for the development of science has been formulated. The essence of this ideal is the establishment (even if only experimentally) of basic postulates and the subsequent strict logical construction of all remaining theory. Its crystallization as a concept can be traced in the entire

history of the natural sciences as a developing social and intellectual force. Its attractiveness is obvious. Only a comparatively small number of postulates are submitted to meticulous refinement and scrupulous experimental verification. Their corollaries (models of specific phenomena) automatically improve as the postulates are refined. The most perspicuous, classical manifestation of this ideal is Hellenic (Euclidian) geometry. And significantly more complex is the axiomatic structure of the next major achievement in scientific thought--celestial mechanics. Here the role of axiom is played by motion equations based on the law of universal gravitation. And, although not all corollaries are obvious (as, for example, the "three body problem" which to this day has not had a satisfactory solution), nevertheless any motion can be found without difficulty using present-day means of computation.

Still more complex are the axioms of quantum mechanics, whose basic postulate--Schroedinger's equation--is an equation in partial derivatives. Here exact solutions are possible only in the most simple (although also the most important) cases, and purely computational methods, as was already mentioned, are extremely time-consuming and for now unrealizable.

All this apparently shows that the axiomatic ideal is, unfortunately, applicable only for the "pre-biological" natural sciences. However, this unhappy conclusion relates only to biology taken as a whole. *It is beyond all question that its salient branches (and not necessarily those paralleling its present subdivision into individual disciplines) not only can, but should be structured along axiomatic lines.* Below are some considerations in favor of this idea.

#### "Hierarchy" and the Small Parameter

In the last century the cell theory of animals and plants was developed--probably the most onerous and fundamental step to "atomism" in biology; an historic move forward in understanding hierarchical nature, and the discreteness and discontinuity of life's forms. A population consists of organisms. An organism consists of cells. For all the fundamental difference between populations and organisms, they nevertheless share a profound similarity, one which in both instances allows use of one and the same verb, "to consist of." The cells of an organ (or tissue), of course, interact with one another, yet intercellular ties are significantly weaker than intracellular ones. Experimenters take advantage of the comparative weakness of intercellular ties when they

select external influences (mechanical, chemical, electrical and so on) sufficiently strong to dissociate separate cells within a tissue. It is significant that this can be accomplished while preserving unharmed the structures and functions of individual cells.

The ratio of the value of an influence which "dissociates" (it is not important what this value may express--force, acidity, voltage, or temperature) to the value of an influence which "destroys" is, as mathematicians say, the "dimensionless small parameter  $\epsilon$ ." Similarly, small parameters characterize quantitatively the individuality of a cell in its tissue. The generalization of this idea "upwards and outwards" to biogeocoenoses and the biosphere, and also "downward and inwards" to cell organelles and macromolecules, is obvious. *It is impossible to over-emphasize the significance of this remarkable peculiarity of living things for the effective application of mathematical methods in biology.*

### Neighboring Levels

Mathematics deals with the same reality as all other natural sciences. There are distinctions, however, between methods, approaches, and points of view. Mathematics more often studies the ties, relationships, and analogies between phenomena rather than the actual embodiment or realization of these phenomena. This inevitably involves

a loss in specificity--a loss, on the other hand, which is compensated for many times over by a gain in generality and number of applications. An ichthyologist, for instance, who is forecasting the population size of a certain species of fish usually works on the population level, never "descending" to the molecular level nor "rising" to the level of the biosphere. This possibility to ignore neighboring (whether above or below) levels has a general character and is closely tied with the idea of the small parameter, or more precisely the idea of two small parameters with kinetic and temporal interpretations.

The surrounding environment may be held to be almost constant and uniform: it varies quite slowly within the temporal and spatial scales characteristic for the system under study. And with this fact we see another--a kinetic--aspect of the small parameter, of the measure of individuality. The internal environment of a system may also be considered constant, or more exactly, dependent only on essential variables which describe the given system. However the reason for this fact is in a certain sense paradoxical. Sub-units (for example, individuals in a population or cells in an individual) move, undergo change, oscillate so rapidly that only average values of these variables have meaning. The most profound expression of this idea is found in the well-known theorem of Tikhonov regarding



equations with a small parameter in a higher derivative. Its special applications, however, were apparently formulated independently: for example, the "steady-state concentrations method" in chemical kinetics.

Is it worth "beating upon an unlocked door" and attempting to "prove mathematically" the feasibility of scientific research within the confines of a single level? Certainly it would not be worth it were it not for two circumstances. *Firstly, it is impossible to remain within the confines of a single level: one must know the limits of applicability of any "single-level" scheme. It is impossible, for instance, to understand the laws governing the most important migrational phenomena only at the population level without a physiological (and even biochemical) analysis of stress factors. Mathematics helps understand the general reasons for any "breach" of a neighboring level--the loss of a given system's stability. Secondly, mathematical analogies sometimes permit the modeling of a given phenomenon at another (more accessible to the experimenter) level. The mere mention of the "avalanche-like" character of certain migrational processes points to a possible physical model--an analogy.*

Critical Regimes, in Particular Oscillatory Ones

The complexity of biological phenomena is usually very great. Even within the confines of a single level, even "nullifying" all additional small parameters, simplifying and dispensing with everything that it is possible to simplify and dispense with, one seldom obtains a transparent model. In such cases it can help to modify the parameters of a model (or, better yet, of the conditions of an experiment) so as to consciously and purposely bring the system to the limits of its stability. In such critical situations the number of essential variables is usually not great, often only two. Of course with a different set of conditions it would be possible to get an entirely different pair (or more) of "critical variables," but nevertheless, if one manages to achieve a "line of neutrality" or "boundary" the properties and structure of a system will become largely clarified.

It is now possible using mathematical procedures alone to find all conceivable types of kinetics for any system which has attained such a critical situation. There are the (well-known from the field of electronics) soft and hard regimes for generating auto-oscillation. Also possible are either a relaxation analogy of these regimes (explosion or monomolecular decay) or a combination of

these regimes (for example, tissue differentiation in embryogenesis). All these regimes, of course have been well examined theoretically for a long time.

The essential point, however, is that with whatever complex system one is dealing, the most simple losses of stability for a steady-state regime will, without fail, occur according to one of the four types indicated above. *Mathematical models of radioactive decay (the most important example of a monomolecular reaction) or of the operation of a thermionic oscillator--these are not special cases, but typical representatives, canonical forms of the most complex systems.* It is clear how our respect for such models must grow as we come to understand the significance of this idea.

#### The Ecological Side of the Critical Regime Method

Ecological systems deal with objects for which it would behoove one to categorically forbid the application of those methods so sympathetically described in the preceding section. Herein lies one of the major tenets of the entire program "Man and the Biosphere"--learning not to bring ecosystems to the edge of destruction. In the same regard it is necessary to "drive" their models to crisis states. "Know the edge and you won't fall off!"

It is well known that no small number of ecosystems are already in critical states (and by now it's unimportant whether due to ignorance or some other cause). It is necessary, therefore, to make the best of things and direct ourselves to the immediate, careful, maximally objective study of the problems and to judiciously intervene in crisis situations. *Thus critical regime modeling methods are most effective in precisely those situations where modeling is the most necessary.*

Systems analytic methods, the careful consideration of all conceivable, multifaceted, hard-to-identify interrelationships, should be supplemented by quantitative evaluation of the roles of these interrelationships. Different models proceeding from different hypotheses as regards essential variables should be compared with one another, and the models' conclusions should be compared with field data.

#### "Bottlenecks" and Regulation

Since Darwin's theory of evolution we have had a rather clear picture of how regulatory mechanisms emerge. The idea of the small parameter, which also came to light independently in chemistry (and especially biochemistry) under the name "reaction bottleneck," helps us to understand the evolution of control systems, or at least some of them.

Initially they are the "most exposed," the "most vulnerable" places or stages. Here a system either dies out (e.g., a species) or it "takes into its own hands" control over the bottleneck (as, for example, in the case where an increase in carbon dioxide gas concentrations stimulates a respiratory center). In general, the checking of a former "poisoning agent" and its gradual transformation into "controlling agent" is, apparently, one of the most remarkable inventions of evolution.

Perhaps, then, one should leave everything to the beneficial effects of time? This, of course, is one conceivable course of action. The question is only what price the biosphere, mankind and, especially, civilization would have to pay for a natural regulation of the situation. *Unfortunately, in dealing with ecosystems we do not have evolutionary time at our disposal. We must replace sequential evolution with parallel analysis.* If, however, we wish (and we do wish!) that by the end of the analysis there is something left to regulate, and, more importantly, someone to do the regulating, then this analysis must inevitably use models.