THE ROLE OF CHANCE AND CHAOS IN THE EVOLUTION OF SPECIES, POPULATIONS, AND ECOSYSTEMS

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ABSTRACT. Living organisms as well as ecosystems can be regarded as *dynamical systems* (in the physical sense), and thus the theory of deterministic chaos can be applied to them, to elucidate both the ontogenesis of individuals, the phylogenesis of species, the growth and decay of populations, and the development and maintenance of ecosystems. Although all single steps occurring in dynamical systems are determined by physical and chemical laws, these systems are so complicated that mostly predictions are very uncertain and often chaotic behaviour occurs. But in spite of unpredictable, unordered and random-like chaotic behaviour of such systems, in special cases, ordered, self-maintaining states can arise which can be predicted, at least roughly. Such ordered states can occur spatially, temporally, and spatiotemporally such as patterns, structures, and characteristic time courses, both in individuals, in populations, and in ecosystems (growth, maturation processes, metabolism, oscillations, equilibria, climaxes, etc.).

INTRODUCTION

That all biological events which have ever occurred on earth are historical events and are due to incidents, to chance, is well known although very often there seems to be some destinative force in history, also in biological history. It is much more interesting to learn the role of chaos in biology and history. The existence of something what is called *chaos* or *deterministic chaos* is the result of system theory which has developped recently out of several origins. This paper gives a short overview of the facts connected with chaotic behavior of dynamical systems without going into the details too much - due to lack of space. Neither proofs nor examples are given here.

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ECOSYSTEMS AND INDIVIDUALS

Ecosystems and individuals differ of course in most of their properties but they have also a lot of properties in common: Both are hierarchically structured. Both contain several different populations of elements which interact with each other, and each of these elements may itself consist of different populations of elements which interact with each other, too. There is a whole hierarchical set of ecosystems starting from the whole biosphere down until a particular local biocenose.

Ecosystems consist of several populations of individuals belonging to different species and containing subpopulation of several age or other classes. Each (sub)population inhabits an ecological niche, and the individuals interacts with each other and with individuals of other (sub)populations. Thus they form networks exchanging matter, energy, and information such as the trophic network (mostly called trophic scale or trophic pyramid) or social networks. Some of these interactions are described mathematically by the well-known LOTKA-VOLTERRA equations with different degrees of refinement.

In the sense of thermodynamics, ecosystems are *open systems*. Ecosystems have dynamical functions: They develop, migrate and propagate, and can change or be destroyed. An ecosystem can neither propagate or migrate as a whole; only its individual components migrate or propagate with their own individual rates. Ecosystem changes can be brought about by *external changes* such as climatic changes, geographic changes, immigration of new species or *internal changes* such as species extinction or evolution of new species, changes in food web and niche structure, internal changes of abiotic factors. Ecosystems also show a tendency of maintenance, under changing condicions. This is circumscribed by WALTER'S so-called "law of relative biotope constancy" (WALTER & WALTER 1953).

Also *individuals* consist of several populations of elements which are arranged in hierarchical order, from organs over cells and subcellular organelles down to molecules and atoms. These subsystems interact with each other. Especially the chemical components react with each other thus creating internal metabolism. Metabolism itself is structured hierarchically too. It consists of functional elements which are interdentated in a rather complicated way. So individuals can be regarded as chemical factories, *i.e.*, structured chemical reactors. In the sense of thermodynamics, individuals are open systems, too.

Individuals can propagate and undergo a development (ontogenesis, morphogenesis). Shape and functions are encoded in the genome which is expressed during ontogenesis. The so-called diffusion-reaction hypothesis (BEYHL, to be published) explains how morphogenesis is worked out by mere biosynthesis, diffusion, concentration gradient formation, and reactions of particular chemical compounds which have triggering functions in the body.

DYNAMICAL SYSTEMS

Both ecosystems and individuals as well as the other components of the cosmos are treated by modern system theory as so-called *dynamical systems*. This allows the application of the same scientific methods to any hierarchical level of both kinds of systems.

Dynamical systems have, *inter alia*, the following properties: They consist of elements which are structured hierarchically and which interact with each other in ways that are described mathematically by nonlinear equations. The interaction of these elements is therefore a very complicated one. Each state of the system is determined by the previous state and determines the following one. As is known since long time the whole is always more than the sum of its parts.

Dynamical systems typically dissipate energy for maintenance of themselves, and are by no means in an equilibrium state. They can show so-called chaotic behaviour. Also they very often obey to *fractal geometry*. Within dynamical systems, information processing (generation, exchange) occurs, and they can show feedback, self-organization, and self-optimization phenomena. There are inherent constraints within dynamical systems which may select between several possible states.

CHANCE

If a system which is going to change its present state can thereby obtain one of several states all dependent on the single previous state, it does of course obtain only one of these different states. If we do not know the cause why the system chose this very state we speak of *chance* (or incident). Especially ecosystems develop out of their elements in a way where causes mostly cannot be detected. This means, they develop mostly by chance. There are probabilities for slow (secular) and rapid (catastrophic) climatic or geographic changes, for mutations (and by that for evolution of new species or for species extinction), for selection, and for other events. Thus one can calculate the probability for an event and predict it, at least in some cases. If one waits long enough, depending on the probability, one will experience this particular event. Very often events cannot be predicted, however, or their probabilities cannot be evaluated.

CHAOS

Chaotic behaviour, i.e., deterministic chaos, is a kind of behaviour of dynamical systems where every change of state of a system is fully determined but cannot be predicted. Chaotic behaviour is characterized by so-called *strange attractors*. Chaotic behaviour is connected with fractal geometry. Normally, chaotic processes are as unpredictable as those caused by chance although they are totally deterministic. In special cases, order can arise unexpectedly out of unordered, chaotic systems.

Chaotic behaviour very often occurs in nature. Especially, ecosystems show a tendency to express chaotic behaviour. This is due to the mathematical nature of the Lotka-Volterra equations which govern the individual numbers of the species which constitute the ecosystem. They are typical examples of nonlinear equations, also in their simplest forms.

Even in a "theoretical" ecosystem which consists of only one species, chaos can arise under particular condicions. The more, chaos is possible in "theoretical" ecosystems consisting of more than one species, and naturally also in really existing ecosystems.

Biological communities consisting of several species can show the following types of behaviour during time course: Extinction of one or several species, periodic population cycles with one or more frequencies, quasi-periodic population cycles with frequency bands, and irregular ("chaotic") population fluctuations. Only in the case of periodic population fluctuations, stable mean values of the species' abundancies do exist. But no population mean values can be predicted during chaotic states of the system. That means, no population mean values can be expected in those cases. Therefore species abundancies in a certain community may fluctuate considerably during time course. Extinctions may occur which might be obscured by immigration of the same species from external sources. There are lots of examples of such irregular population changes. Therefore, any ecosystem stability is not garanteed forever. It only exists for some short time period.

Abundancies of long-living species do not fluctuate as rapidly as those of short-living species. Populations of long-living species of an ecosystem such as trees or other perennials make observers erroneously believe in the longlived or even everlasting stability of this ecosystem and to construct sophisticated ecotaxonomical systems. During longer time periods, there are always chaotic changes as well as climatic changes, geographic changes, immigration and extinction events, mutations, and larger catastrophes to be expected in an ecosystem which will invalidate syntaxonomic work.

This statement based on chaos theory seems at first sight to contradict the experiences of synecological taxonomists, of several schools and their guru-like heads who pretend ecosystems to be stable and durable so to allow to elaborate sophisticated syntaxonomies, especially with plants (characteristically, zoological syntaxonomy never obtained such a high degree of oversophistication as botanical). Paleontologists showed that there always have been and are floristic as well as faunistic changes. This stability of ecosystems supposed by synecological taxonomists to exist in reality is both denied and nevertheless may be explained, at least partly, by the theory of dynamical systems (see below).

Another system where order and "spherical harmony" seem to exist is the planetary system. Since prehistoric times, this system was the paradigm of eternal constancy and predictability for generations. But it was shown recently that the observed ordered behaviour which until now was believed to be eternal is only transitional.

Another quasi-periodically fluctuating system is the geoclimatic system which causes glacial and interglacial periods. It oscillates between two possible states, in a kind of sweeping oscillation, and can be simulated very simply by mathematical functions, on a computer.

A further quasi-periodically fluctuating system is formed by the rates of the stock exchange market. Human economy seems to oscillate between two states: Boom (*hausse*) and depression (*baisse*).

There are also chaotic processes within individuals, such as chaotic fluctuations in biochemical reactions and chaotic fluctuations in electrocardiograms and electroencephalograms which go back on corresponding functional chaos. Such chaotic fluctuations may endanger the proper function of the components of the individual and even its further existence. But they also can give rise to fundamentally new shapes or functions in individuals and thus to beginning speciation, up to "macroevolution" which is postulated by many authors to exist.

The last aspect of chaos is that of "order out of chaos". Under very particular circumstances, a system which behaves chaotically can obtain an ordered, regular, and fully predictable behaviour or a quasi-ordered, roughly predictable one, at least for some time. Temporally, periodic or at least quasi-periodic oscillations evolve. Spatially, regular or quasi-regular patterns are formed. And also, some kind of "transient equilibrium" between several species can exist. Such kinds of ordered states can be relatively stable or relatively unstable, depending on the characteristic parameters of the corresponding system.

FRACTAL GEOMETRY

The last item in this context is fractal geometry (MANDELBROT 1991). Dimensions of fractal bodies are nonintegers. Fractal bodies are beased geometrically on repetitive imageing processes (recursions, iterations). Fractal bodies are *self-similar*.

Mathematical examples for fractal bodies are: Mandelbrot's apple figure, Julia's figure, Peano's curve, Koch's snowflake-like figure, Sierpinski's carpet-like figure, Menger's sponge-like figure (form inutes, see MANDELBROT 1991). Many of such artificial fractal figures are very similar to some natural structures or to *Art Déco* products.

Natural examples of fractal bodies are: boundaries of islands and lakes, courses and networks of rivers, shapes of clouds, sponges and trees, dendritic and treelike growth, lightnings. Empirical examples of fractal curves are: weather record curves, animal abundancy time records, electrocardiograms, seismographic curves, sunspot number records, curves of stock exchange rates, numbers of islands of an archipelago larger than a given area, numbers of lakes in a country larger than a given area, species numbers on archipelagos larger than a given number, numbers of souvereigns of a country ruling longer than a given time, numbers of taxa in dependence of area (BEYHL 1990).

Also strange attractors which are active in chaotic behaviour obey to fractal geometry.

Fractal bodies show self-similarity: Each part of a fractal body is similar both to the whole body and to smaller parts of itself, for infinite magnifications of any section. There is geometrical self-similarity and statistical self-similarity. Fern leaves, *Euphorbia* plants (BEYHL 1994) and "Federbusch" plants show self-similarity.

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