NON-LINEARITIES IN MATHEMATICAL ECOLOGY:
PHENOMENA AND MODELS

Yuri M. Svirezhev

Potsdam Institute for Climate Impact Research
P.O. Box 601203
D-14412 Potsdam, Germany
Phone: +49 331 288 2671
Fax: +49 331 288 2695
E-mail: Yuri.Svirezhev@pik-potsdam.de

"When we study the History of Science we discover
two mutual contrary phenomena: either behind
an apparent complexity a simplicity is hidden or,
on the contrary, an evident simplicity conceals within
itself an extraordinary complexity"

H. Poincarè

1. Introduction

The linear world of classic mathematical physics was harmonious and consistent. Almost the entire evolution of this world proceeded in small neighbourhoods of stable equilibrium where linearisation principle held true. This was a smooth differentiable world, in which there was no room for instabilities, catastrophes, and other inconvenient phenomena. Certainly, the complete harmony did not exist and nature produced now and then surprise packets with unpleasant non-linearities; nevertheless, the situation was saved due to the fact that those non-linearities could be regarded as minor ones, so that one could manage with small non-linear additions to the main linear solutions. To explain all those non-linear phenomena, viz. jumps, discontinuities, catastrophes, hysteresis, and dynamic chaos, was the task to philosophy rather than mathematics.

In contrast to many fields of mathematical physics, where linear models have been used very extensively and effectively (recall, for instance, the wave equation, the heat conduction equation, the Schrödinger equation, etc.), mathematical ecology is principally non-linear science. The fact is that almost all interactions in ecology, both competitive and trophic, are non-linear. Perhaps, the only linear model is the model of exponential growth by T. Malthus. Even the classic Volterra "prey - predator" model demonstrates a typical non-linear pattern, while in more sophisticated
models, for instance, in trophic chains, we can see non-linear oscillations, "quantum" effects, and dynamic chaos.

A vast variety of non-linear problems generated by ecology is described in many books, and there is not need to repeat their descriptions here; I would like to dwell in more detail on the problems yet unsolved, trying to predict or, strictly speaking, to guess the potential results and offer their informal interpretation.

2. Models and realities in ecology

Nowadays a lot of classic models in mathematical ecology, which are the basis for applied ecological modelling, are subject to severe revision. This process is going in two directions: first, a "canonisation" of canonical models is taking place, and second, new descriptions are proposed, using either new mathematical subjects and concepts or well forgotten ones.

Also, the models of mathematical ecology themselves, coming from physics and chemistry or elsewhere, are subject to revision. It is clear, that Lotka - Volterra models (later on I shall omit the first name as it is usually done in mathematical ecology) have their "genetic" origin in the models of chemical kinetics. Also, the origin of ecological models that account for spatial movement of individuals is clear. They are called models of the "reaction-diffusion" type (in spite of the fact that we are not sure that the physical process of diffusion is a good model for biological movement). Constructing both Volterra models and diffusion ones, we use first of all all conservation laws (matter and energy), and after that, knowing really nothing about the mechanism of behaviour of individuals in the populations, use different physical and chemical hypotheses for their description. In fact, the "collisions" hypothesis in the Volterra models is a typical hypothesis of chemical kinetics about collision of molecules.

What is the "diffusion" hypothesis? It is an assumption about stochastic movement of individuals over their areal, which is equivalent to an assumption from statistical physics about random movement of atoms and molecules. But an individual in a population is not a molecule; it is a complex organised system, having "freedom of choice", with complex behaviour even in some average situations. Therefore, for more adequate models we should use some other, more realistic hypotheses about the behaviour of individuals. This leads to more complex models. As an example we can mention "Schödinger's systems" suggested for the description of self-thinning processes in plant communities (Svirezhev, 1978, 1987). On the other hand, even if we agree that the diffusion model is a fairly good approximation for the description of spatial migrations of individuals in populations, there are still strong local non-linearities in the processes of competition, trophics, inheritance, reproduction, etc., which generate such phenomena as non-linear waves and dissipative structures in models of spatially distributed systems described by the reaction-diffusion equations. It is interesting to observe how spatially ordered structures such as the dissipative ones appear from random (diffusive) movements of specimens (Nicolis and Prigogine, 1989).

Generally, the problem of choosing an adequate mathematical description in ecology is very acute today. Physical and chemical ways of description are already exhausted; it is necessary to look for some new non-traditional methods, which can be based on already known mathematical concepts and new forms of description for ecological realities.
For instance, one of the main difficulties in ecological modelling is how to obtain discrete structures over the set of continuously changing parameters. The point is that all vegetation on the Earth is the mosaic of discrete forms. There are biogeocoenoses (having the same boundaries as phytocoenoses), and some larger taxonomic units like biomes (for example, taiga or steppe). Analysing geographical distribution of vegetation, we can see the following: while temperature, moisture, precipitation, and other climatic characteristics are changing continuously, biological characteristics (like storage of aboveground and underground phytomass, etc.) change by jumps from one community to another. Why is it so? In my opinion, the answer is either in particular properties of principally non-linear functions, describing dependence of biological processes on abiotic parameters of the environment, or principal non-linearity of such processes as, for instance, inter- and intraspecific competition.

From the mathematical point of view, the first type of models should be of the kind that we find in the theory of catastrophes. We can hope, that it is the mechanisms with non-linearities of cubic type that are responsible for sudden changes of any biological parameter when abiotic parameters are changing continuously, and the task of modeller is to define these critical parameters correctly. Second type of mechanisms, which can lead to the formation of discontinuity, is the destruction of some unstable equilibrium under perturbation in a system that has some hysteresis. As we show later, it may be the classic Volterra model for two competing species imbedded into a slowly changing environment.

We see that the world of non-linear phenomena in mathematical ecology is very rich in terms of different complex behaviours, but in this lecture I would like to attract your attention only to some of them.

3. "Canonical models" in mathematical ecology

If we consider any (more or less) complex simulation models of ecosystems, we can see that all them contain some elementary “bricks”, or building blocks. Let us call them Canonical Models. These may be:

a) a model of a single population with simple (for instance, logistic) or more complex laws of population growth (for instance, Alle's principle of aggregation, etc.),
b) a prey - predator model,
c) a model of two competing species,
d) a model of two populations bound by migration (linear or non-linear), so-called “migranon” – as suggested by G. Alexandrov,
e) a demographic model (Leslie model).

All these models may be both with overlapping generations (continuous-time models) and non-overlapping generations (discrete-time models). It is clear that the general dynamic properties (dynamic behaviour) of the "large" model can be determined by both its general structure (so-called emergent properties) and the specific dynamic properties of its components, i.e., by the dynamics of canonical models.

Unfortunately, the history of mathematical ecology and ecological modelling is such that ecological modellers use the canonical (elementary) models as the “laws” (like in physics). However these models are not the laws; they are only some "phenomenological descriptions"
having a very narrow field of implementation. For instance, whereas in mechanics we have
Newton's laws to derive equations of motion from the general conservation laws, in ecology we
have no such laws (or, to be more accurate, their analogues). What is the meaning of the
dissipative energy of competition? What is the relation between energy utilised in reproduction,
and energy consumed for life-support of an individual? Certainly, the list of similar questions
may be continued. Clearly, as long as we do not know the mechanisms governing the processes
of interaction between individuals in the ecosystem and the quantitative expressions for them, all
the attempts to apply the global properties of energy and matter in ecosystems to this local
behaviour will be speculative. Notice that this is the case not only in mathematical ecology, but
say, in mathematical economics, too. Attempts to introduce some global energetic characteristics
there also did not pay off.

In some special cases we managed to look at the results of stability analysis for dynamic models
of communities from the viewpoint of extreme principles. And what is more, we could use some
optimal general principles in order to close the input balance. For instance, instead of using some
allocation principle, which must describe the energy allocation among various species in the
community (which is usually unknown), we use the adaptation principle, which, as a rule, has a
very "scientific" formulation (which the case for most teleological principles in biology).

Discussion of the role of teleological principles in biology and about their applicability goes far
back in history, and now they are as heated as before. However, we are still nowhere near to the
clearness and transparency achieved, say, in classic mechanics.

I would quote just one statement ascribed to von Brücke, in which teleology is characterised as
"a lady no biologist can live without, but whose company seems shameful in society".

The usage of phenomenology was often leading to special (interesting from theoretical
viewpoint) dynamic effects in complex models, which did not reflect reality, being in fact
consequences of either the usage of wrong elementary models, or their non-motivated expansion
beyond the field of their validity. For instance, the usage of population models with the biomass
as a continuous state variable for low densities where the discrete allocation of the biomass
(among individuals) becomes important. Thus, when we come across an unexpected dynamics in
a complex model, we should consider three possibilities:

1. This dynamics is a direct consequence of the dynamic properties of canonical (elementary)
models.
2. This dynamics is an emergent property of the whole model.
3. This is a "false dynamics", or an artefact of modelling.

In order to make the right choice, one has to know in detail:
- dynamic properties of canonical models,
- domains of their validity,
- dangerous effects of parameterisation, when we attempt to approximate some
  phenomenological relations by empirical formulas ("parameterisations traps")

In other words, a canonising procedure (canonisation) for canonical models is needed. This
procedure would provide a tool for testing reliability of ecological modelling. Unfortunately, up
to date nothing systematic is done in this important area. The "canonisation" would allow
modellers to choose the elementary (canonical) model blocks basing on some regular rules rather
than traditions. It would also be a filter for wrong interpretations of the results that, at first glance,
seem unexpected.
4. Logistic equation

It seems like there is nothing simpler than the logistic equation

\[
\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right),
\]

where \( r \) is the intrinsic growth rate and \( K \) is the population capacity. It is interesting that Eq. (1) has an analytical solution even if \( r = r(t) \) and \( K = K(t) \), i.e. these parameters depend explicitly on time. Indeed, the substitution \( y = 1/N \) transforms Eq. (1) into the linear equation with respect to \( y \):

\[
\frac{dy}{dt} + r(t)y = \frac{r(t)}{K(t)},
\]

that has the solution:

\[
y(t) = e^{-\int r(t)dt} \left[ Const + \int \frac{r(t)}{K(t)} e^{\int r(t)dt} dt \right],
\]

where the constant is found from the initial condition \( y = (1/N_0) \) at \( t = 0 \). Finally, denoting \( r/K = \gamma \) and \( \exp \int_0^t r(\tau)d\tau = \psi(t) \), the general solution for a logistic equation with variable coefficients is represented in a very elegant form:

\[
N(t) = \frac{\psi(t)}{(1/N_0) + \int_0^t \gamma(\tau)\psi(\tau)d\tau}.
\]

It is especially convenient when we have to analyse behaviour of a logistic population in periodically changing or random environment.

If we assume that periodical changes of the environment become apparent only in the form of periodical changes of capacity, \( \tilde{K}(t) = K_0(1 + k \sin \omega t) \), i.e., as its linear oscillation (see the dotted curve in Fig. 1), then, as seen from direct integration of the corresponding logistic equation, in this case there is a “smoothing” effect in the oscillations of the population size (solid line). It is interesting that the average value of the population size, \( \tilde{N} \), is shifted with respect to the mean capacity, \( \tilde{K} \). For instance, \( \tilde{K} = 100 \), while \( \tilde{N} = 68 \).
Fig. 1. Oscillations of the environmental (carrying) capacity (---), and corresponding oscillations of population size (——). The period \( T = 10 \), \( \omega = 2\pi / T = 0.628 \), \( r = 0.25 \), \( K_0 = 100 \), \( k = 0.8 \).

5. Different types of growth functions and corresponding population dynamics

Before we consider different laws of population growth (different Malthusian functions) we introduce one very useful concept: the graph of \( dN/dt \) as a function of \( N \) we shall call a phase portrait of the system described by the equation \( dN/dt = F(N) \). For instance, the phase portrait of logistic population (Eq. (1)) is shown in Fig. 2. It is obvious that in its upper part, where \( dN/dt > 0 \), the representing point moves to the right, in the low part, where \( dN/dt < 0 \), to the left. Points, in which the phase trajectory intersects the axis \( N \), and where \( dN/dt = 0 \), correspond to equilibriums. These are the points \( N^* = 0 \) and \( N^* = K \). If the derivative \( dF/dN \) at some equilibrium point is negative then the equilibrium is stable (and vice versa). Therefore, in the logistic population the trivial equilibrium \( N^* = 0 \) is unstable, and the non-trivial equilibrium \( N^* = K \) is stable.

Let us represent the Malthusian function as a difference between two functions, \( B \) and \( D \). Then
\[
\frac{dN}{dt} = N(B - D),
\]
where \( B \) is the birth-rate, and \( D \) is the mortality. In fact, accepting this form of Eq. (5) we postulate that two processes determine the population dynamics: birth and death.
As to a dependence of the mortality function on $N$, for almost all populations $D(N)$ is a monotonous increasing function, and $D(0) = m > 0$ where $m$ is the natural mortality. An increase of mortality with growth of $N$ is explained by an increase of competition with respect to a limited resource (food, space, etc.). The situation is more complicated when we deal with the birth function, $B$. For many species it is determined only by some upper physiological birth rate, and it does not depend on $N$, so that $B(N) = f = \text{const}$ where $f$ is so-called natural fecundity. However, there are other species, in particular, species–migrants, which occupy their areals very sparsely. So for them this assumption is not quite correct. For low densities the reproduction is determined by the probability for a reproductive pair to meet rather than by their physiological fecundity. In this case, the dependence of $B$ on $N$ has the form shown in Fig. 3. Populations with such type of $B(N)$-dependence are usually named “Alle-type populations”\(^1\). A physiological limit of birth-rate is attained for them only at a certain density. The birth rate for low density is usually very small, but still it is not zero.

**Fig. 3.** Allee-type curve. Note that in reality it should go down again for higher densities, because of stronger competition. However in our models this effect is described by the mortality increase, therefore the birth curve is regarded as monotonous with saturation. Points mark experimental values of fecundity for a species of butterfly; number of eggs per female and number of butterflies per cage are shown on the ordinate and abscissa axes, correspondingly.

Let $B(N) = \text{const} = f$. The simplest form of $D(N)$ is linear, $D(N) = m + \mu N$, then the equation of population dynamics is written as $dN/dt = N(f - m - \mu N)$, or, substituting $f - m = r$, and $(f - m)/\mu = K$, we get $dN/dt = rN(1 - N/K)$. But this is the logistic equation, which we already dealt with. We generalised the “logistic” concept, taking into consideration the following definition:

any population with the local law of its growth, $dN/dt = F(N)$, where $F(N)$ satisfies the following conditions:

a) $F(0) = F(K) = 0, \quad 0 < K < +\infty$;

b) $F'(0) = r > 0$;

c) $F'(N) < F'(0)$ for any $N > 0$.

is a generalised logistic population.

A phase portrait of this population is shown in Fig. 4.

![Fig. 4. Phase portrait of the generalised logistic population.](image)

It is obvious that it has two equilibriums: unstable, \( N_1^* = 0 \), and stable, \( N_2^* = K \), and the whole trajectory lies under the line \( dN/dt = F'(0)N \). Note that the dynamics of generalised logistic population qualitatively is very similar to its classic analogue.

Let us return to the Alle-type populations and consider different relations between the functions of birth and mortality.

![Fig. 5. Different relations between the birth-rates and mortalities for the Allee-type populations.](image)

![Fig. 6. Phase-portraits of the Allee-type populations: a – population with a single stable equilibrium, \( F'(N_1) > F'(0) \); b – population with a single threshold of density; population with two thresholds of density](image)

1. Let \( f > m \), i.e., the natural mortality is very low, and the mortality caused by competition increases with the growth of density either very slowly (the \( D_1(N) \) in Fig. 5a) or very quickly (the \( D_2(N) \) in the same figure). In the latter case the population is logistic, however, with an
extremely low value of the environmental “capacity”, \( K_2 \). In the first case the population also has two equilibriums: the zero equilibrium that is unstable, and the stable non-trivial equilibrium, \( N^* = K_2 \), but it is no longer logistic. The latter is obvious since there is such \( N \) that \( F'(N) > F'(0) \), i.e., condition b) in (5) does not hold. This is seen in Fig. 6a, where the corresponding phase portrait is shown.

2. Let \( f < m \), i.e., for low densities the natural mortality is higher than the fecundity (Fig. 5b). One can see from the phase portrait of this population (Fig. 6b) that it has three equilibriums: \( N^*_1 = 0 \), \( N^*_2 = k \), \( N^*_3 = K \), where \( N^*_1 \) and \( N^*_2 \) are stable, and \( N^*_3 \) is unstable. If the population density is lower than some critical threshold \( N_{cr} = k \) then the population goes extinct. We know a population with this type of local law of growth as a population with a single critical threshold of density. If its local law of growth is described by the equation \( \dot{N} = F(N) \) then the function \( F(N) \) has to satisfy the following conditions:

\[
\begin{align*}
\text{a) } & F(0) = F(k) = F(K) = 0, \quad 0 < k < K < +\infty; \\
\text{b) } & F(N) < 0 \text{ for } 0 < N < k \text{ and } K < N < +\infty; \\
\text{c) } & F'(0) < 0, \quad F'(k) > 0, \quad F'(K) < 0. 
\end{align*}
\]

3. Let, as above, \( f > m \), but suppose the mortality rate due competition is increasing moderately (see Fig. 5c). A phase portrait of the population is shown in Fig. 6c. In this case there are 4 equilibriums: \( N^*_1 = 0, \ N^*_2 = k_1, \ N^*_3 = k_2, \ N^*_4 = K \), where the 1st and 3rd are unstable, and the 2nd and 4th are stable. The lower equilibrium \( N^*_2 = k_1 \), is attained for all \( 0 < N < k_2 \), but as soon as the density becomes higher than \( k_2 \), then the population begins to move to the steady state with the higher density, \( N^*_4 = K \). We name such type of population: population with two critical thresholds of density. Its local law of growth, \( F(N) \), has to satisfy the following conditions:

\[
\begin{align*}
\text{a) } & F(0) = F(k_1) = F(k_2) = F(K) = 0, \quad 0 < k_1 < k_2 < K < +\infty; \\
\text{b) } & F(N) < 0 \text{ for } k_1 < N < k_2 \text{ and } K < N < +\infty; \\
\text{c) } & F'(0) > 0, \quad F'(k_1) < 0, \quad F'(k_2) > 0, \quad F'(K) < 0. 
\end{align*}
\]

In the simplest population model, the Malthusian model of exponential growth, one assumes that the increment of the population density is proportional to its value, \( \dot{N} \sim N \). Apparently, when we deal with asexual reproduction, this is really so, but if there are two sexes, then the reproductive act implies an encounter of two individuals of one species, belonging to different sexes, i.e., a cooperative act.

From this point of view, it is clear that competition is a typically cooperative process. Moreover, the specific form of dependence of the fecundity on the population density in Allee-type populations is a consequence of specimens’ cooperative interactions in such population.
Let us consider the simplest model of reproduction, taking into account the probability for one specimen to encounter its reproductive partner. If \( 2n \) is the number of offspring produced by one fecund female during a time unit, and \( p(N) \) is the probability for the female to find its reproductive partner, then the increment of the population number due to fecundity is equal to \( \Delta N = n \cdot p(N) \cdot N \cdot \Delta t \). We implicitly assume here that the sex ratio is 1:1.

Let the process of the reproductive partner search be random of the Poisson type. We consider as successful all the events when the encounter with one, two, etc. partners takes place, then

\[
p(N) = 1 - e^{-\mu N}.
\]

So we have

\[
\frac{dN}{dt} = \left[ n(1 - e^{-\mu N}) - D(N) \right] N.
\]

(9)

It is obvious that for small values of \( N \) we have \( \dot{N} = n\mu N^2 - D(N)N \), for large values of \( N \), when \( \dot{N} = [n - D(N)]N \), we deal with a logistic population.

Returning to Eq. 5 we see that if \( D(0) = m > 0 \) then such a population is the population with a critical threshold of density (see above). However, if we can neglect the natural mortality compared to the “competitive” one, even for low densities, so that \( D(N) = dN^\beta \), \( \beta \geq 1 \), then the population has a single stable equilibrium, attained for any non-zero value of density. In this case for small \( N \) we have \( \dot{N} = aN^2 \) and \( N(t) \approx N_0/(1 - aN_0 \cdot t) \), i.e., at the beginning the population density growth is hyperbolically, rather than exponential. We shall name such populations “hyperbolic”.

If we now require that this population is logistic (in the “narrow” sense) for large \( N \), then we must postulate \( D(N) = d_0 N \), so that

\[
\frac{dN}{dt} = \left[ n(1 - e^{-\mu N}) - d_0 N \right] N.
\]

(10)

Note that \( p(N) \) is approximated by a hyperbolic function, \( N/(\gamma + N) \), where \( \gamma = 1/\mu \), instead of an exponential one with a saturation, \( 1 - e^{-\mu N} \). For our purposes, it is sufficient to use some simplified description, which, however, retains the basic qualitative characteristics of the population dynamics with hyperbolic growth:

\[
\frac{dN}{dt} = \alpha N^2 \left( 1 - \frac{N}{K} \right).
\]

(11)

Indeed, \( \dot{N} \sim N^2 \) for small \( N \), and \( N(t) \to K \) as \( t \to \infty \). Thus, this population belongs to some intermediate type between the logistic population and the population with a critical threshold of density. It is obvious that, on the one hand, it is not logistic since \( F(0) = 0 \); on the other hand, its critical threshold is zero, so that \( N(t) \to K \) as \( t \to \infty \) for any \( N_0 > 0 \). A phase portrait of the population, described by Eq. (9), is shown in Fig. 7.
6. “Predator – prey” system as a classic subject of mathematical ecology

Beginning with Vito Volterra’s works, the “prey-predator” system has been a classic subject of mathematical ecology. Let \( x(t) \) and \( y(t) \) be the populations of preys and predators, respectively; then a sufficiently general (so-called "Kolmogoroff") model of this system takes on the form:

\[
\frac{dx}{dt} = \alpha(x)x - V(x)y, \quad \frac{dy}{dt} = [kV(x) - m]y, \quad (12)
\]

where \( \alpha(x) \) is the Malthusian function for the prey population, \( V(x) \) is the trophic function (functional response), \( m \) is predator natural mortality, \( k \) is the efficiency of converting prey biomass into predator reproductive biomass. In classic Volterra’s model \( \alpha(x) = \text{const} \) and \( V(x) = \lambda x \).

The first assumption means that there are no self-regulation mechanisms in the prey population; only the predator controls it. The second assumption is not “ecological”; the most popular types of (really observed) functions \( V(x) \) are shown in Fig. 8.

\[
V(x) = \frac{V_{\infty}x^n}{K^n + x^n}, \quad n = 1,2,... \quad (13)
\]

If we shall use the following popular parameterisation for trophic functions:
then for $n = 1$ we have the trophic function of Type 1; for $n = 2,3,\ldots$ - Type 2.

By introducing the new variables:

$$\alpha t \Rightarrow t, \ x/x^* \Rightarrow x, \ y/y^* \Rightarrow y, \ V/V_e \Rightarrow V, \ m/\alpha \Rightarrow \mu,$$

where $x^*$ and $y^*$ are co-ordinates of the equilibrium point, determined from the equation $V(x^*) = m/k$ and $y^* = (\alpha k/m)x^*$, we get a dimensionless version of Eq. (12):

$$\frac{dx}{dt} = x - V(x)y, \quad \frac{dy}{dt} = \mu y[V(x) - 1].$$

(14)

Stability of the equilibrium $x^* = y^* = 1$, which is a topological knot, is determined by the value of the derivative $v = \frac{dV}{dx}(1)$: if $v < 1$, it is unstable, and if $v > 1$, it is stable. When the representative point crosses the value of $v = 1$ we deal with the Andronov-Hopf bifurcation, and in the "general position" case, a limit cycle is born out of this equilibrium. At first glance, it is a trivial situation, and there are no problems here. However, we can prove that if the trophic function $V(x)$ is represented in parametric form (13), then system (14) has no limit cycles! (see Svirezhev, 1988). Periodic regimes cannot arise from any closed trajectories surrounding such a singularity as the centre (the latter is typical for classic Volterra' model).

So, the parameterisations trap closes, and all our and other authors’ results about different stable oscillations in the prey – predator systems (see, for instance, Svirezhev, Logofet, 1978) are wrong, aren’t they? This was quite a disaster for me: what to do now? Apparently, the best strategy in such a situation: before we do something let’s think.

Further investigation showed that this result is a so-called “non-rough, non-robust” one, i.e., if we subject the trophic function to small finite deformations then our statement fails, and we can observe the birth of a cycle from closed trajectories.

That was close. The point is that before we have used some asymptotic methods (for instance, Krylov-Bogolubov one) to find the periodic solutions of Eqs. (14). Obviously, the expansion of their right hand sides – including the trophic function - by the powers of some small parameter is equivalent to a small deformation of the function that, as shown above, leads to the destruction of the "non-rough" situation. As a result, we do obtain stable cycles. Moreover, by choosing different deformations we can generate the birth of an arbitrary number of cycles from the equilibrium by means of Andronov-Hopf bifurcation.

In other words, after the $\epsilon$-deformation of the trophic function (13), system (14) becomes structurally stable, while this system with trophic function (13) is structurally unstable. In the structurally stable system the bifurcation of the “parameter of deformation” can provide limit cycles from both equilibriums and closed trajectories. A number of these cycles can be arbitrary, whatever we wish.

It is very interesting that the parametric form of the trophic function, described by (13), generates the entire class of structurally unstable phase portraits. Really, the probability to “bump” into a "non-rough", structurally unstable situation is very low, but nevertheless we have found one.

So, system (14) with trophic function (13) is structurally unstable. My question is: Is this structural instability a principal emergent property of the prey-predator system, which ensures the high degree of adaptation and the high sensitivity to environmental changes, or is this an artefact
of parameterisation, i.e., the effect, which can be called a "parameterisation trap"? It seems to me the first statement is more probable. As an argument the following Gedankenexperiment can be carried out.

a) Let us embed the structurally unstable "prey-predator" system into some random environment. This is the same if we assume that random perturbations impact the system. These perturbations destroy the structurally unstable equilibrium (without any cycles) in the original system, and, as a result, stochastic limit cycles (stable and unstable) arise. It can be interpreted as follows: although the random environment is deterministically unpredictable we can still predict behaviour of the structurally unstable system embedded in this environment.

b) Let us embed this system into a periodically changing (i.e., predictable) environment. One can prove that there is such set of parameters in the original structurally unstable system that its dynamics becomes chaotic. In other words, behaviour of this system becomes principally unpredictable in the predictable environment.

So, we can formulate the following speculative hypothesis: Structural instability is one of the many evolutionary mechanisms, which allows the "prey-predator" system to predict its fate in a random environment.

7. Hysteresis in a system of competing species

"Struggle for Life is a permanent reality in the Nature and the Society."  
T. Malthus

The second classic model in mathematical ecology is the model of a system made of two species competing for a single resource:

\[
\begin{align*}
\frac{dx}{dt} &= x(\varepsilon_1 - \alpha_{11}x - \alpha_{12}y), \\
\frac{dy}{dt} &= y(\varepsilon_2 - \alpha_{21}x - \alpha_{22}y),
\end{align*}
\]

(15)

where \(x(t)\) and \(y(t)\) are population sizes (or biomasses) of these species. After rescaling:

\[
\varepsilon_1 t \Rightarrow t, \quad \varepsilon_2 / \varepsilon_1 = k, \quad \frac{\alpha_{11}}{\varepsilon_1} x \Rightarrow x, \quad \frac{\alpha_{22}}{\varepsilon_2} y \Rightarrow y, \quad \frac{\alpha_{12} \varepsilon_2}{\alpha_{22} \varepsilon_1} \Rightarrow \gamma_1, \quad \frac{\alpha_{21} \varepsilon_1}{\alpha_{12} \varepsilon_2} \Rightarrow \gamma_2,
\]

system (15) can be re-written as:

\[
\begin{align*}
\frac{dx}{dy} &= x(1 - x - \gamma_1 y), \\
\frac{dy}{dt} &= k y(1 - y - \gamma_2 x).
\end{align*}
\]

(16)

System (16) has been studied in detail: there are no limit cycles, only 4 equilibriums:

\[
\sigma_0 = (0,0); \quad \sigma_1 = (1,0); \quad \sigma_2 = (0,1); \quad \sigma_3 = \left(\frac{1 - \gamma_1}{1 - \gamma_1 \gamma_2}, \frac{1 - \gamma_2}{1 - \gamma_1 \gamma_2}\right).
\]
Their phase portraits are shown in Fig.9. Stability of these equilibriums depends on $\gamma_1$ and $\gamma_2$; the corresponding domains of stability in the plane $\Gamma = \{\gamma_1, \gamma_2\}$ - $\omega_i, \ i = 1, 2, 3, 4$ - are shown in Fig. 10. It seems to us that at first glance there is nothing interesting in this situation. However, it is more than that. Let us embed the original problem into the following more general one. For this we suppose that the parameters $\gamma_1$ and $\gamma_2$ evolve - slowly - in the positive quadrant of the plane $\Gamma = \{\gamma_1, \gamma_2\}$ (slowly as compared with the fast dynamics of $x$ and $y$).

To describe the dynamics of the joint system we have to add to Eqs (16) the two equations for slow variables:

$$
\frac{d\gamma_1}{dt} = \varepsilon g_1(x, y; \gamma_1, \gamma_2), \quad \frac{d\gamma_2}{dt} = \varepsilon g_2(x, y; \gamma_1, \gamma_2), \quad \varepsilon \ll 1,
$$

Thus, we have to consider the behaviour of the joint system in the extended phase space $U \times \Gamma, \ U = \{x, y; x, y \geq 0\}$. What kind of surprises should we expect here?

Let the system move along a phase curve $\xi$, which passes through an arbitrary point $\xi(t_0) = G_0$. After an initial fast movement the point $G \in \xi$ gets into the neighbourhood of an equilibrium manifold, and then slowly moves within its neighbourhood. The movement corresponds to changing the parameters $\gamma_1$ and $\gamma_2$ within the domain $\omega_i$, where $i$ may take any value from 1 to 4. When the curve $f(\xi)$ - the projection of $\xi$ onto $\Gamma$ - crosses the boundaries between the domains $\omega_i$, and the representing point approaches to the corresponding equilibrium, then it either disappears or becomes unstable.
In this case the phase trajectory may leave the domain of applicability in the Tikhonoff theorem. As a result, the system immediately gets into the layers over other stable equilibriums, whereto it will pass immediately and quickly, to move again slowly in the neighbourhood of another equilibrium manifold. Let us consider the following example.

Let the system move from the initial state $I \in \omega_2$ to the final state $F \in \omega_2$ across the domain $\omega_1$ along the path $\xi_1$ ($f(\xi_1)$ being its projection onto $\Gamma$) - see Fig. 10. At the moment of crossing the boundary $\gamma_2 = 1$ between $\omega_2$ and $\omega_1$ at point $B$ the equilibrium $\sigma_1$ loses stability, simultaneously $\sigma_3$, a new stable equilibrium originates. The transition from this equilibrium to another occurs slowly, and the change of the ecosystem structure proceeds smoothly. Replacing equilibrium $\sigma_3$ with equilibrium $\sigma_2$ proceeds in a similar way when $f(\xi_1)$ crosses the boundary $\gamma_1 = 1$ between $\omega_1$ and $\omega_4$ at the point $C$. The entire transition $\sigma_1 \rightarrow \sigma_3 \rightarrow \sigma_2$ is reversible in the sense that if the system performs a return transition from $F$ to $I$, and $f(\xi_1) = f(\xi_1)$, then trajectories $\xi_1$ and $\xi_1$ are close in the phase space $U$.

The situation is quite different when $f(\xi_2)$ passes across the domain $\omega_3$. Upon crossing the boundary $\gamma_1 = 1$ at point $D$, the equilibrium $\sigma_1$ retains its stability, but at the same time the equilibrium $\sigma_2$ becomes unstable, and the unstable saddle $\sigma_3$ separates from $\sigma_2$. The part of phase trajectory which is projected into $\omega_2$, is in the neighbourhood of the equilibrium manifold corresponding to $\sigma_1$, the part which is projected into $\omega_3$ remains in the same neighbourhood.

However, upon crossing the boundary $\gamma_2 = 1$ at point $E$ the equilibrium $\sigma_1$ loses its stability and the slow movement along this manifold changes into a fast one, which leads the trajectory $\xi_2$ into
the neighbourhood of the equilibrium manifold corresponding to $\sigma_2$. In this case the observed variables $x$ and $y$ change quickly, the ecosystem structure makes a jump, and the transition $\sigma_1 \to \sigma_2$ is irreversible. The *irreversibility* is understood in the sense that if there exists a trajectory $\xi_2$ leading in the opposite direction (from $F$ to $I$), such that $f(\xi_2) = f(\xi_2)$, then fast movement along $\xi_2$ will take place at the point $E$ rather than $D$, i.e., the trajectories $\xi_2$ and $\xi_2$ will no longer be close. This is *hysteresis*, which typical for non-linear systems.

We have considered the simplest model of a two-species competitive community. It is clear that hysteresis effects and possibly other catastrophes will take place in case of multi-species competitive communities. Stratification of the phase space, typical for these systems, results in different characteristic times (different time-scales) for different groups of species: while the population sizes of some species will be almost constant, the population sizes of other species change quickly and abruptly. Slow evolution of parameters, caused, for instance, by genetic processes, or changes in environment, will generate various structural ecological “*perestrokas*”, and non-linear effects like the hysteresis will make these evolutionary reconstructions irreversible.

8. Border between two vegetation zones

I would like to show how we could use this simplest model of two competing species to describe a rather complex phenomenon such as the boundary between two different vegetation zones.

Suppose in Eqs. (15) the coefficients depend on some spatial coordinate $s$, moreover, only the coefficients $\varepsilon_1$ and $\varepsilon_2$, which we could interpret as the NPPs of these plants, depend on this coordinate; the coefficients $\gamma_{ij}$ are constant and do not depend on $s$. We also suppose that $\varepsilon_1$ and $\varepsilon_2$ change continuously along $s$, as shown in Fig.11.

![Fig. 11. The NPP or growth functions $\varepsilon_1(s)$ and $\varepsilon_2(s)$ of two plant species.](image)

After the change of variables $\alpha_1x \Rightarrow x$, $\alpha_2y \Rightarrow y$, $\alpha_{21}/\alpha_{11} = a_1$, $\alpha_{12}/\alpha_{22} = a_2$, we get

\[
\frac{\partial x}{\partial t} = x[\varepsilon_1(s) - x - a_2y], \quad \frac{\partial y}{\partial t} = y[\varepsilon_2(s) - y - a_1x].
\]  

(17)
Let \( a_1a_2 < 1 \), i.e., interspecific competition is very weak in comparison to intraspecific one. Then the movement along the axis \( S \) corresponds to the movement from point \( A \) up to point \( D \) (see Fig. 12).

\[
\varepsilon_2 = (1/a_2) \varepsilon_1 \\
\varepsilon_2 = a_1 \varepsilon_1
\]

**Fig. 12.** Case \( a_1a_2 > 1 \): movement in the parametric space \( \{\varepsilon_1, \varepsilon_2\} \), corresponding to the movement along the space axis \( s \).

For the quasi-stationary movement when the steady-state equilibriums are not broken, there is a transition zone, where the both species co-exist with continuous change in their biomasses. The interval \( BC \) in the parametric space \( \{\varepsilon_1, \varepsilon_2\} \) corresponds to this zone. This is the so-called "soft" border; it is very often observed in the nature, when the biomass of first species decreases up to zero level at that time the biomass of second species increases as we are going into the region more and more favourable for the second species. Domain I (see Fig. 12) corresponds to the area covered by the first species solely; domain II, corresponding to the transition zone, contains plants of the both species, where the abundance of the first species at the beginning smoothly and continuously is replaced by the abundance of the second species at the end of the transitional zone. Domain III corresponds to the area covered by the second species.

If \( a_1a_2 > 1 \), i.e., interspecific competition is stronger then intraspecific one, there is also a transition zone. The formation mechanism of such kind of structure in the parametric space is shown in Fig. 13.

\[
\varepsilon_2 = (1/a_2) \varepsilon_1 \\
\varepsilon_2 = a_1 \varepsilon_1
\]

**Fig. 13.** Case \( a_1a_2 < 1 \): movement in the parametric space \( \{\varepsilon_1, \varepsilon_2\} \), corresponding to the movement along the space axis \( s \).
However, inside this zone the continuous transition from one species to another is not feasible which is principally different from the case above. All non-trivial equilibriums, located on the $BC$ interval, are unstable, and either the first or the second species dominates in this spatial point, depending on the initial conditions. Under random perturbations that always occur in nature the transition zone will be a patchy pattern of either one or another species. Sometimes these patches combine a single patch with mixed composition. Such kind of transition zone is shown in Fig. 14. We call it "hard" border.

![Fig. 14. The "hard" transition zone. Biomasses of plants are expressed in percents. Black and grey correspond to the first and second species, respectively.](image)

In detail you can find all these results in my paper (Svirezhev, 2000).

9. "Migranon": the system of two populations bound by linear migration

When we studied physics in school and later on we knew that diffusion tends to smooth out all spatial non-homogeneities in a continuous medium, but (relatively) recently we have learned that diffusion can also create non-homogeneities and maintain them at some stable level. These are so-called Prigogine’s "dissipative structures". I would like to bring to your attention one – as it seems to me - simplest model of a dissipative structure: the system of two populations with an identical law of growth bounded by linear migration with the intensity $m$:

$$\frac{dx}{dt} = f(x) - m(x - y), \quad \frac{dy}{dt} = f(y) + m(x - y). \quad (18)$$

We can be rid of one parameter if we scale time: $mt \to t$, then $\tilde{f} = (1/m)f$, and $\tilde{x} = \tilde{f}(x) - (x - y), \quad \tilde{y} = \tilde{f}(y) + (x - y)$.

It is interesting that this system can be re-written in the following "gradient" form:

$$\frac{dx}{dt} = -\frac{\partial W}{\partial x}, \quad \frac{dy}{dt} = -\frac{\partial W}{\partial y}, \quad (19)$$
with the potential function:

\[ W = 2(x - y)^2 - \int_0^x \tilde{f}(\xi)d\xi - \int_y^\infty \tilde{f}(\xi)d\xi . \]  

(20)

Calculating the total time derivative for \( W \) we get

\[ \frac{dW}{dt} = \frac{\partial W}{\partial x} \frac{dx}{dt} + \frac{\partial W}{\partial y} \frac{dy}{dt} = -\left[ \left( \frac{\partial W}{\partial x} \right)^2 + \left( \frac{\partial W}{\partial y} \right)^2 \right] \leq 0 . \]  

(21)

Hence any trajectory of (18) is a trajectory of steepest descent for the function \( W(x, y) \) in the positive quadrant \( x, y \geq 0 \), and its stationary points \((x^*, y^*)\) are equilibria of system (18) – minima are stable, and maxima are unstable. These points are found from the equations:

\[ y^* = x^* - \tilde{f}(x^*); \quad y^* - \tilde{f}(y^*) = x^* , \]  

(22)

and their stability is defined by the eigenvalues of the Jacobi matrix:

\[ \begin{vmatrix} f_x'(x^*)-1 & 1 \\ 1 & f_y'(y^*)-1 \end{vmatrix} . \]  

(23)

Thus, these equilibriums are stable (nodes), if

\[ \sigma = f_x'(x^*) + f_y'(y^*) < 2, \quad \text{and} \quad \sigma < f_x'(x^*) \cdot f_y'(y^*) = \rho , \]  

(24)

and they are unstable, if \( \rho < \sigma , \quad \sigma < 2 \) (saddles), and \( \rho < \sigma , \quad \sigma > 2 \) (nodes).

It is obvious that there is a set of symmetric solutions to (23): \( x^* = y^* = 0 \), and the positive roots of the equation \( \tilde{F}(x^*) = 0 \) (where \( \tilde{f}(x) = x\tilde{F}(x) \)).

The analysis will be easier, if we change the variables: \( N = x + y \), \( \delta = x - y \) \((x = (N + \delta) / 2, \quad y = (N - \delta) / 2)\). Then we get instead of Eqs. (18):

\[ \frac{dN}{dt} = f(x) + \tilde{f}(y), \quad \frac{d\delta}{dt} = f(x) - \tilde{f}(y) - 2\delta , \]  

(25)

under a natural constraint: \( N \geq |\delta| \). Equilibriums, \( N^*, \delta^* \), are solutions to the equations

\[ f\left( \frac{N^* + \delta^*}{2} \right) + \tilde{F}\left( \frac{N^* - \delta^*}{2} \right) = 0, \quad f\left( \frac{N^* + \delta^*}{2} \right) - \tilde{F}\left( \frac{N^* - \delta^*}{2} \right) = 2\delta^* , \]  

(26)

It is obvious that the phase portrait of system (18) is symmetric with respect to the line \( y = x \) (or, for system (25) – to \( \delta = 0 \)).

The most popular form for the growth function is \( f(x) = \alpha x(1 - x / K) \), i.e., the right side of the logistic equation. It is easy to see that the function is a quadratic polynomial. The next function can be a cubic polynomial: \( f(x) = \alpha x(x/k - 1)(1 - x / K), \quad k < K \). It is the so-called population with a single critical threshold. It is obvious that for \( x_0 < k \), \( x(t) \rightarrow 0 \) at \( t \rightarrow \infty \), and for \( x_0 > k \), \( x(t) \rightarrow K \) at \( t \rightarrow \infty \). If in the first case an intrinsic growth rate is equal to \( f'(0) = \alpha_q \),
and in the second case this value is defined as \( f'(k) = \alpha_c \left[ 1 - (k / K) \right] \). Certainly, more exotic non-linearities in \( f(x) \) are possible, but we shall consider only the types above.

As it is easy to show, that if our non-linearity is quadratic (logistic model), then we can expect nothing except two symmetric equilibriums \( (x^* = y^* = 0 \text{ is unstable, and } x^* = y^* = K \text{ is stable}) \). This non-linearity is very weak to maintain a difference in population sizes, or, in other words, generate the simplest dissipative structure. The cubic non-linearity is more interesting. Now we have three symmetric equilibriums, one of them, the intermediate equilibrium \( x^* = y^* = k \) is always unstable, the other two \( (x^* = y^* = 0 \text{ and } x^* = y^* = K) \) are stable. So the system can generate asymmetric stable equilibria. Thus, two populations with a cubic law of growth, bound into one system by symmetric linear migration, can give birth to a dissipative structure! I shall call it a “migranon”.

In order to demonstrate the principal feasibility of such a structure, we simplify the original equations. It is obvious that without loss of generality we can set \( K = 1 \). We can also assume that \( k = 1/2 \); then \( \tilde{f}(x) = ax(1-x)(2x-1) \), where \( a = \alpha_c / m \). Since the intrinsic growth rate \( r \) is equal to \( f'(k) = \alpha_c \left[ 1 - (k / K) \right] = \alpha_c / 2 = \alpha_c / 2 \), then \( a = 2r / m \). After a simple but cumbersome analysis we get:

1. If \( r < 2m \) then the system has only three symmetric equilibriums – diffusion is rather large (in comparison to the intrinsic growth rate), it can homogenise the system.

2. If \( 2m < r < 3m \) then diffusion is quite low, two new asymmetric equilibriums appear (see Fig. 15), but they are unstable. As a result, the system remains homogenous as before.

![Fig. 15. Phase portrait of system (18) at \( 2m < r < 3m \). 1 – 5 are equilibriums, \( a \) and \( b \) are isoclines
\( y = x - \tilde{f}(x) \) and \( x = y - \tilde{f}(y) \), correspondingly.](image)
3. Finally, if \( r > 3m \) then diffusion becomes rather low (in comparison to the intrinsic growth rate). Six new asymmetric equilibriums result in bifurcation: two stable nodes and four unstable saddles (see Fig. 16). Although attraction domains of these stable points are relatively small, they do exist! An asymmetric structure, the migranon, arises in a completely symmetric environment.

10. Chaos in natural and mathematical populations

"Chaos had arisen in the Universe, before everything."

_Hesiod_

The existence of dynamic chaos in a single population with non-overlapping generations became one of the truisms in mathematical ecology (May, 1976). However, using differential (and difference) equations for the description of population dynamics, we implicitly use the hypothesis about unlimited divisibility of the biomass. On the other hand discreteness is natural for living organisms: biomass exists only as individuals. For instance, we can speak about the biomass of half-individual, but we cannot imagine that this half-individual is able of reproduction, for this we need a whole organism (or even a pair of them). As a rule we ignore this contradiction, while we still use the Newton - Leibnitz formalism of continuous description, created for classical mechanics. We get satisfactory results for population dynamics as well, if the number of individuals is large and slowly changing. Although these criteria are not sufficiently accurate, they allow us to use differential (and difference) equations in models of population dynamics in cases, when this dynamics is more or less regular. Without taking into account these general problems, we used these models to describe dynamic chaos in populations and communities. Intuitively, the models should work, but let us take a closer look.
As a matter of fact, for chaotic dynamics described by Ricker equation, $N_{t+1} = rN_t \exp(-\lambda N_t)$, where $N_t$ is either biomass or size of population, there are some intervals, within which the value of $N_t$ is close to zero, but after that due to exponential growth the value of $N_t$ becomes very large. After non-regular periods of time this situation repeats. But since the mapping, described by Ricker’s equation, is a continuous one then sooner or later the value of $N_t$ will be neither an integer number nor a number that is divisible by a biomass of one individual. The first is important when the state variable is the population number, the second when the state variable is the population biomass. This means that the standard Ricker model must be modified, since from the biological point of view a fractional number or biomass is nonsense. In this case, the modified Ricker's model can be presented as follows: $N_{t+1} = E\{rN_t \exp(-\lambda N_t)\}$, where $E\{x\}$ is the integer part of $x$. If the state variable is biomass then the latter must be scaled by the value of individual biomass. The question is: will the model manifest a chaotic behaviour or not? Since the chaos on a denumerable set is impossible, the modified Ricker model does not possess the chaotic dynamics. In other words, an introduction of natural discreteness into the model excludes any theoretical possibility of chaos. Moreover, while the elimination of the population is principally impossible in the classic Ricker model, it is possible in the modified model. Nevertheless, although the “pure” chaos is excluded in this model, it can still produce a “nearly” chaotic behaviour, i.e., a series of non-linear oscillations with a very large amplitude.

### 11. Chaos in trophic chains

Note that in mathematical ecology the dynamic chaos is rather the rule than an exotic exception; the problem is how to make a model to adequately describe it. Unfortunately, some authors get chaotic regimes in their models by violating conservation laws (matter and energy). These disturbances, although weak, are sufficient to produce a chaotic behaviour. I think that this way is not a good way to go; we better keep the conservation laws.

For instance, a closed, three-level trophic chain with non-linear trophic functions $V_i(N_i)$ can be considered, perhaps, as the simplest continuous model that generates dynamic chaos. We know that the conservation law of matter holds here. A model of this system can be represented as (Svirezhev, Logofet, 1978):

\[
\begin{align*}
\frac{dN_0}{dt} &= -V_0(N_0)N_1 + \sum_{i=1}^{n} N_i, \\
\frac{dN_1}{dt} &= N_1\left[-d_1 + V_0(N_0)\right] - V_1(N_1)N_2, \\
\frac{dN_2}{dt} &= N_2\left[-d_2 + V_1(N_1)\right] - V_2(N_2)N_3, \\
\frac{dN_3}{dt} &= N_3\left[-d_3 + V_2(N_2)\right], \\
V_0 &= \alpha_0N_0, \\
V_1(N_k) &= \alpha_kN_k/(K_k + N_k), & k &= 1,2. 
\end{align*}
\]  

(27)

We assume for simplicity that the trophic function $V_0(N_0)$ is linear.

An amount of free resource (the material found outside of consumers) is equal to $N_0$, it is consumed by the first species with biomass $N_1$, which in turn is consumed by the second species with biomass $N_2$, which is consumed by the third species with biomass $N_3$. The coefficients
$d_1$, $d_2$, $d_3$ are coefficients of natural mortality for these species. Since the trophic chain is closed the conservation law holds:

$$N_0 + \sum_{i=1}^{n} N_i = A = \text{const.} \quad \text{and} \quad N_0 = A - N_1 - N_2 - N_3. \quad (28)$$

Then Eqs. (27) are re-written as:

$$\frac{dN_1}{dt} = N_1\left(\alpha_0 A - d_1 - \alpha_0 (N_1 + N_2 + N_3) - W_1 N_2\right),$$

$$\frac{dN_2}{dt} = N_2\left[-d_2 + W_1 N_1 - W_2 N_3\right],$$

$$\frac{dN_3}{dt} = N_3\left[-d_3 + W_2 N_2\right] \quad W_k(N_k) = \alpha_k/(K_k + N_k), \quad k = 1,2. \quad (29)$$

This system, where $d_1 = 0.1; d_2 = d_3 = 0.2; \alpha_1 = \alpha_2 = 1; K_1 = K_2 = 5$, and $\alpha_0 = \alpha \in [0.30, 0.37]$, was studied numerically; the total amount of matter, $A$, and the per capita rate of resource consumption at the first trophic level, $\alpha$, were selected as bifurcation parameters. Two curves, $A_1(\alpha)$ and $A_\infty(\alpha)$, separate the domains with different dynamic behaviour in the plane $(A,\alpha)$ (Fig. 17). At the point $\alpha = 0.34$ $A_1(\alpha) = 36.25$ and $A_\infty(\alpha) = 36.24$.

Fig. 17. The domains of different dynamic behaviours: I – regular, II - stochastic, III - "pre-stochasticity" domain.

If we now move along the line $ab$ ($\alpha = 0.34$) increasing the parameter $A$, then the behaviour of the system changes, the cycles are doubled switching from a regular to a stochastic regime. The transition does not occur directly: there is the "pre-stochasticity" domain III, in which there are both regular and stochastic trajectories, and in parallel with the “strange attractor” that results in the doubling of cycles, there is a stable limit cycle. This regime, also called a “pre-turbulence” or “meta-stable chaos”, is characterised by the existence of both chaotic trajectories and regular ones, which are attracted to the stable cycle. The latter are very similar to chaotic trajectories; but
in spite of this actually they are regular. It is interesting that the pre-stochasticity regime is typical for Lorenz’s attractor, but in the latter the process of stochastisation differs from Feigenbaum’s mechanism of the doubling of cycles. Our “ecological strange attractor” occupies an intermediate position between Lorenz’s and Feigenbaum’s attractors. It is interesting that the phase volume of our system contracts; in other words, our system (like Lorenz’s) is dissipative in spite of the conservation of matter taking place within it.

By moving further along $ab$ we get into the domain of stochasticity, in which chaos arises. This is domain II, or more correctly, its lower bound, as its upper bound and its geometry are yet to be studied in detail. The chaotic trajectories are shown in Fig. 18.

![Fig. 18. An approach of the non-periodic trajectory of (29) to the strange attractor: $A = 36.5; \alpha = 0.34$.](image)

What kind of natural ecosystem may correspondent to our model? For instance, the ecosystem with the trophic chain

$phytoplankton \rightarrow zooplankton \rightarrow fish$,

where nutrients may be considered as a resource. As to the conservation law of matter, then it takes place either in closed water-bodies or in so-called “up-welling” ecosystems. A typical example of such a system is the Portugal shelf. On the one hand, a numerical study of (29) showed that chaos appears when we increase the mortality of zooplankton (with simultaneous increase in fish catches). On the other hand, we know that zooplankton is more sensitive to toxic pollution than phytoplankton. Thus, we meet a typical situation provoking the rise of chaos in
coastal fisheries of different countries with its main consequence, namely, principal unpredictability of the behaviour of the national fishery.

Let us try to answer the following question: would the property of dynamic stochasticity be conserved as chain length grows? It has been proven that the existence of a strange attractor for chains of arbitrary length (longer than 3) follows from the existence of the strange attractor for a closed trophic chain of a length of three (Svirezhev, 1983, 1987).

On the contrary, there are only regular trajectories (cycles) in open chains, in which a dead biomass is neither decomposed nor returned to the resource compartment. Naturally there is a constant inflow of an external resource, \( q \), which is equal to zero for the closed chain. Let now the chain be partly closed, i.e. suppose a certain part of matter contained in the dead biomass returns to the resource level. A model of such a system can be represented as follows:

\[
\frac{dN_0}{dt} = q - V(N_0)N_1 + \lambda \sum_{k=1}^{3} d_k N_k, \quad 0 < \lambda < 1, \tag{30}
\]

\[
\frac{dN_k}{dt} = -d_k N_k + V_{k-1} N_k - V_k N_{k+1}, \quad V_k = \frac{\alpha_k N_k}{K_k + N_k}, \quad k = 1,2,3.
\]

It would be interesting to find a domain \( \Omega^{\lambda}_q \) in the plane \( \{q, \lambda\} \), where \( \lambda \) is the “closure” parameter (\( \lambda = 0 \) for open system and \( \lambda = 1 \) for fully closed one), such that if \( q, \lambda \in \Omega^{\lambda}_q \) then the dynamic chaos arises in system (30).

Naturally, other formulations are also possible. We believe that models in mathematical ecology have much potential when looking for different strange attractors and dynamic stochastic behaviour corresponding to them, but it is necessary to remember about the biological adequacy of the models being used.

12. Conclusions

We have shown here that different non-linear effects (such as hysteresis, structural instability, dissipative structures, dynamic chaos, etc.) exist in models from mathematical ecology. Nevertheless, the problem how to detect these phenomena in real ecosystems is not yet solved. Of course, we can observe there a similar behaviour, but... the similarity is not a proof. Although from the methodological point of view, this similarity could speak in favour of applying the non-linear models as powerful tools to describe some real ecological processes.

One of the problem is how to detect the minimal necessary degree of non-linearity, which matches the ecological reality. Maybe a quadratic non-linearity in Volterra’s models is sufficient, and we are living in the Volterra world. This opinion is very popular among mathematical ecologists. However, I tried to show here, that the complexity of our real world is higher than the complexity of the Volterra one.

In general, the problem of selecting adequate mathematical formalizations is very urgent in ecology. Borrowed from other, more "mathematized" sciences, the current methods of description have largely exhausted their potential. It is necessary to look for new unconventional approaches that could still rely securely upon the mathematical concepts already known.
Cited and recommended literature:


