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Catastrophes of Ecosystems

By

Norio YAMAMURA

Department of Biophysics, University of Kyoto

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1. Introduction

A lot of theoretical ecologists (Volterra, Lotka, MacArthur, May, e.t.c.) have tried to represent temporal developments of various ecosystems in various cases by differential equations. Such formulations are next ones.

$$\frac{dN_i}{dt} = F_i(N_1, N_2, \cdots N_m, a_i^1, a_i^2, \cdots a_i^k) \qquad i = 1, 2, \cdots m$$

where N_i is the number of i-th species, and a_i^s $(s=1, 2, \cdots k)$ are coefficients in the function F_i. Then we must get solutions $N_i(t)$ of these equations as functions of a_i^k's and initial values $N_i(0)$'s. This is impossible except a few of very simple cases.

So, qualitative properties of these equations have been researched by using properties of the functions F_i's, also by various men.

Especially, behaviours when the time t becomes infinity, are most interesting. These final states, of course, change dependent on a_i^k. Recently topologists (Thom,[1] Zieman[2]) researched how properties of the solutions of dynamical systems changes when the parameters of the system change continuously. This is so called 'catastorophe theory'. In this paper, we look again at basic equations of mathematical ecology from this view-point.

2. Malthus Equation

If one individual produces e other individuals per unit time, the time variation of whole individuals N, is represented by next equation (Malthus[3]).

$$\frac{dN}{dt} = e\,N$$

The solution is

$$N = N(0) \exp (et) ,$$

where $N(0)$ is the value of N at the time $t=0$.

The behaviour of the solution at sufficiently large t, depends on the value e. Drawing the orbits and stationary points in a space $e \times N$, we can see this behaviour at one glance. (Fig. 1) The set of the stationary points $dN/dt=0$ in this space, is called a stationary manifold. Here, this is straight line $N=0$. The right half $(e>0)$ is a repellar, that is, any orbits starting from the neighborhood of this half line leave there. Conversely the left half $(e<0)$ is an attractor, that is, orbits approach to this. Thus, the stationary manifold is separated to two parts carrying different properties at a point (0, 0). Such a point is called a catastorophe point.

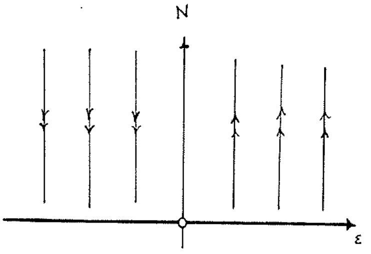

Fig. 1.

3. Saturation Level and Constant Flow

As we saw in the previous section, if $e>0$, N becomes infinity. Actually, intraspecies competitions occur when N becomes large, and N saturates to a value s. (Verhulst[4]) What matter happens if we add a constant flow furthermore? (the positive flow means immigrations and the negative flow means emigrations or captures) Such a situation is represented by next equation.

$$\frac{dN}{dt} = e\, N\, (s-N) + f$$

The stationary manifold in the space $N \times s \times f/e$, is a paraboloid $f/e = N^2 - sN$. (Fig. 2) The upper surface of the paraboloid is an attractor and lower surface is repellar. When $f>0$, all orbits starting from $N(0)>0$, approach to the attractor (stable states). But when f is negative (for example, fishery), there are two cases. One is stable one, and the other is the case having no equilibrium points. In the parameter space $s \times f/e$, the two regions are separated by a line $f/e = -s^2/4$ (Fig. 3). This is named 'fold catastorophe' by Thom.

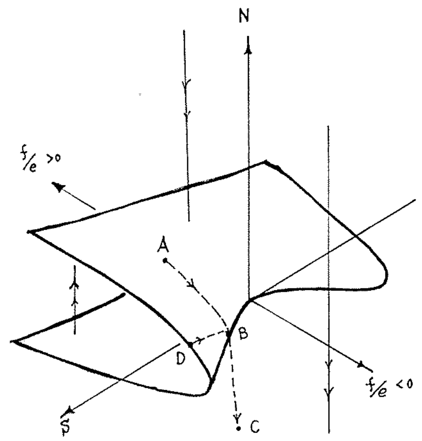

Fig. 2.

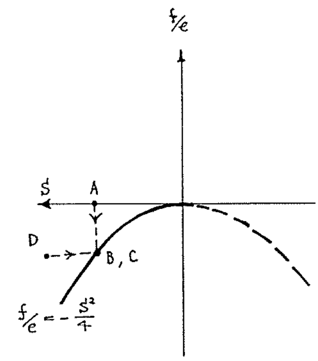

Fig. 3.

Starting from a point A ($s>0, f=0$) in Fig. 2 and Fig. 3, let us decrease f. At the moment the point reaches B on the catastorophe, the point falls down rapidly to $C(N=0)$. The same thing occurs if we decrease s, starting from D. In other words, the population may extinct rapidly, even if we increase a fish catch slowly or the saturation level decreases continuously because of changes of environments such as a pollution.

4. Competition

Next, we consider interactions berween two species. The growth rates e_1, e_2, of each species are functions of N_1, N_2. If two species compete one another for same food or habitat, e_i is decreasing function of N_j. We assume e_i is first order function of N_j, so that

$$e_1(N_1, N_2) = e_1^0 - a_{11}N_1 - a_{12}N_2$$
$$e_2(N_1, N_2) = e_2^0 - a_{21}N_1 - a_{22}N_2$$

where e_i^0, a_{ij} are all positive. Because we want to seek only qualitative properties of the solution, it is sufficient that we assume $e_1^0 = e_2^0 = 1$, $a_{11} = a_{12} = 1$, $a_{21} = 1/a$, $a_{22} = 1/b$.

$$\frac{dN_1}{dt} = (1 - N_1 - N_2)N_1$$

$$\frac{dN_2}{dt} = (1 - N_1/a - N_2/b)N_2$$

where $1/a$ represents how much species 1 disturbs species 2, and $1/b$ represents how much species 2 disturbs itself. The global situation is separated to next four cases (Fig. 4).

(i) $a>1$, $b>1$; extinction of species 1.

(ii) $a<1$, $b<1$; extinction of species 2.

(iii) $a<1$, $b>1$; extinction of either species 1 or species 2.

(iv) $a>1$, $b<1$; coexistence of both species.

The manifold $dN_1/dt=0$, $dN_2/dt=0$ in the four-dimentional space $N_1\times N_2\times a\times b$

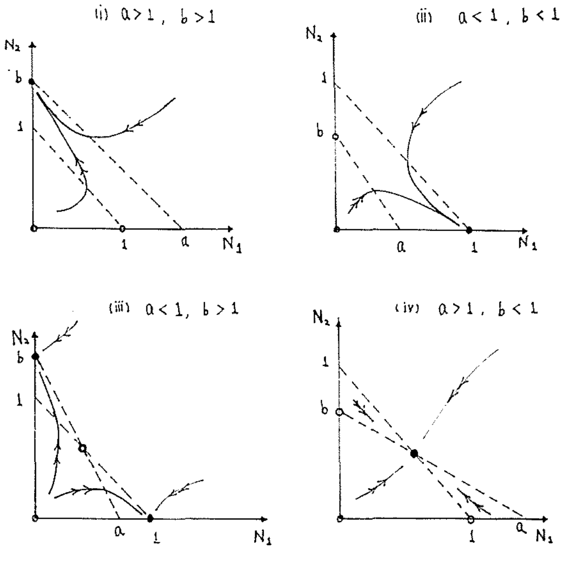

Fig. 4.

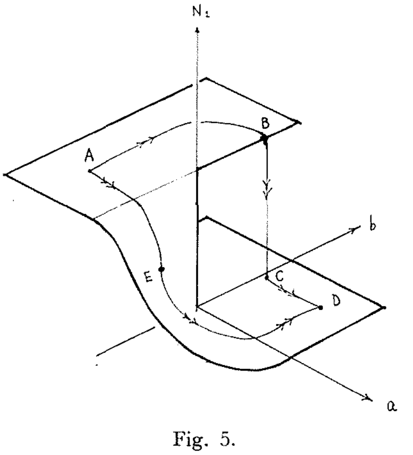

Fig. 5.

is two-dimentional surface. It is impossible to illustrate it on the two-dimentional paper. So, we project only attractor of the manifold on three-dimentional space $N_1 \times a \times b$ (Fig. 5). Mapping on parameter space $a \times b$ brings a cusp-like catastrophe at a point (1,1) (Fig. 5). If we project the attractor on another space $N_1 \times a \times b$, we get similar figure.

There are two types of processes for plant succession from one species to another species.[5] One is rapid substitution in a short interval. The other is slow change through coexistence states. These processes are reappeared on this model, by changing parameters a,b continuously through pathes ABCD and AED in Fig. 5 and 6.

5. Predation

We consider the case which species 2 captures and eats species 1. The reproduction rate of species 1 has a maximum at a suitable value of N_1, and decreases after then, so that we may write

$$\frac{dN_1}{dt} = (-N_1^2 + 2N_1)N_2 - aN_1N_2$$

$$\frac{dN_2}{dt} = -N_2 + aN_1N_2$$

There are three cases depending on the predation rate a. When it is small ($a < 1/2$), the predator extincts. As it becomes larger to some extent ($1/2 < a < 1$), the two species coexist with constant populations. When a is more larger ($a > 1$), the stable state is a sustained oscillation or a limite cycle. The attractor in space $N_1 \times N_2 \times a$ is illustrated in Fig. 7. At $a = 1$, we see a catastorophe which is a bifurcation point from the stable point to the periodic attractor.

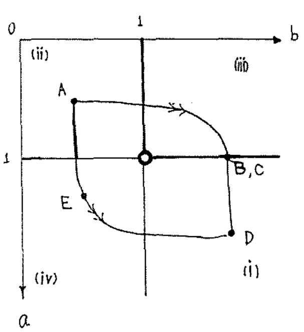

Fig. 6.

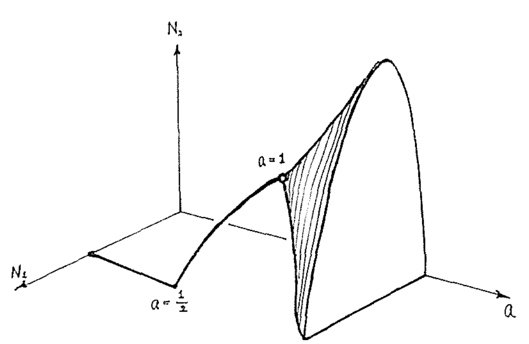

Fig. 7.

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