Extention of Kolmogorov-type Predation Equations to the Three Species Interactions

MEMOIRS OF THE FACULTY OF SCIENCE, KYOTO UNIVERSITY, SERIES OF BIOLOGY
Vol. VII, pp. 111–118, March 1976

Extention of Kolmogorov-type Predation Equations to the Three Species Interactions

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(Received March 10, 1975)

ABSTRACT Volterra's semi-linear equations are very popular as a mathematical representation of the interactions between species, but they have some defects. Kolmogorov improved them in the case of two species, and made qualitative considerations. In this paper, we give them simple concrete representations and consider its biological meanings. Moreover we extend them to all types of predation relations between three species and research their stabilities. The result is that linear-chain type and pyramid type are more stable than other types.

1. Volterra equations and Kolmogorov equations

D'Ancona[1] sought Volterra's advice about periodic change of the populations of the fish in the Adriatic. Volterra[2] proposed next equations.

$$\frac{dN_1}{dt} = e_1N_1 - a_1N_1N_2$$

$$\frac{dN_2}{dt} = -e_2N_2 + a_2N_1N_2$$

where N_1, N_2 represent numbers of species 1 and species 2. The solutions of these equations are periodic (Fig. 1). But the period and the amplitude change, depeding on initial values. And the equations are structurally unstable.
For improving these facts, Kolmogorov[3] proposed next equations.

$$\frac{dN_1}{dt} = K_1(N_1)N_1 - L(N_1)N_2$$

$$\frac{dN_2}{dt} = -gN_2 + K_2(N_1)N_2$$

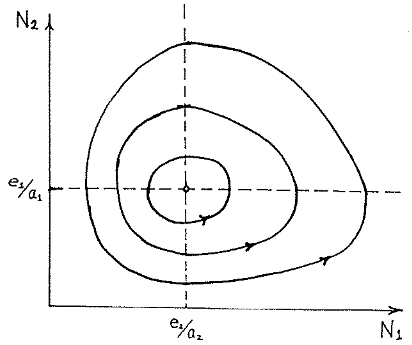

Fig. 1.

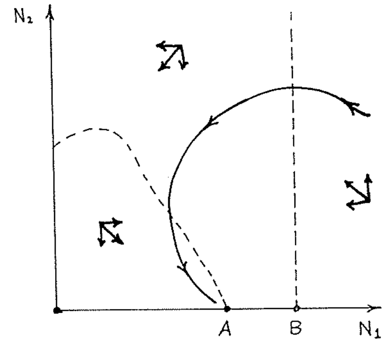

Fig. 2.

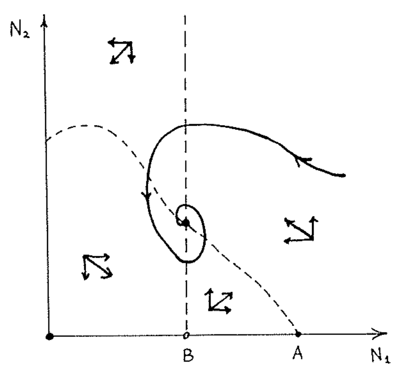

Fig. 3.

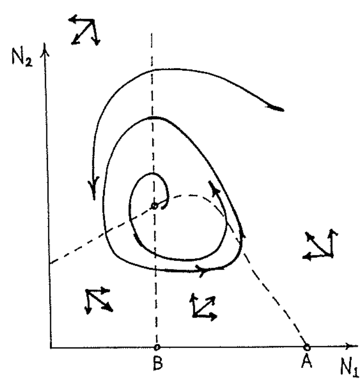

Fig. 4.

where $K_1'(N_1)<0$, $L(N_1)>0$, $K_2'(N_1)>0$, and there exist positive A and B such that

$$K_1(A) = 0\,, \quad K_2(B) = g\,.$$

We draw the isoclines, $\frac{dN_1}{dt}=0$ and $\frac{dN_2}{dt}=0$ on the phase plane $N_1 \times N_2$. The line $N_2=K_1(N_1)/L(N_1)$ runs from the positive part of N_2 axis to the positive part of N_2 axis $(A, 0)$. The line $K_2(N_1)=g$ is a straight line $N_1=B$ (Fig. 2, 3, 4). Writing arrows indicating directions of the vector field in each part separated by the isoclines, we get global properties of the solutions.

If $A<B$, $(A, 0)$ is a stable point (Fig. 2). If $A>B$, $(B, K_1(B)/L(B))$ is a stable point (Fig. 3), or unstable point (Fig. 4). Around the unstable point, there exist a limit cycle. After all, the solution of these equations approaches a stable point or a closed circle. Strictly, this can be proved, using Poincare-Bendixson[4] theorem.

2. Simplification of Kolmogorov equations

We propose next simple equations. Their isoclines are similar to Kolmogorov's, and therefore global behaviours of its solutions are also similar.

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

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

If $a<\frac{1}{2}$ (the predation rate is too small), its stable point is (2, 0) (Fig. 5). That is, the predator extincts. If $\frac{1}{2}<a<1$, (the rate is middle), its stable point is $\left(\frac{1}{a}, \frac{2a-1}{a^3}\right)$. That is, the two species coexist (Fig. 6). If $a>1$ (the rate is too large), $\left(\frac{1}{2}, \frac{2a-1}{a^3}\right)$ is an unstable critical point, and there exists a limit cycle around this point (Fig. 7). Of course, the period and the amplitude of this periodic solution

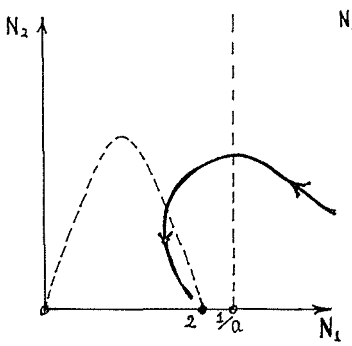

Fig. 5.

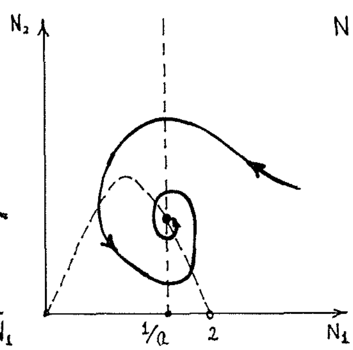

Fig. 6.

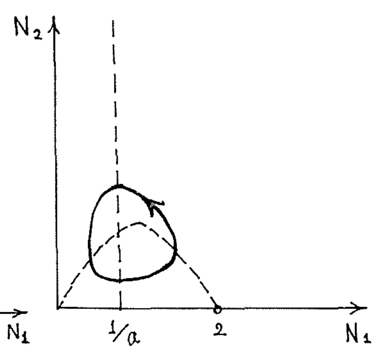

Fig. 7.

are determined by the value of a, independent of initial states. As the value of a becomes extremely large, the limit cycle also becomes large, and runs nearby N_1 axis and N_2 axis. Such a case is considered to be unstable (extinction probability is large).

3. Extention to three species interactions

If we consider animals either herbivore or carnivore, there are five types of predation relations between three species. Showing species by a number enclosed by

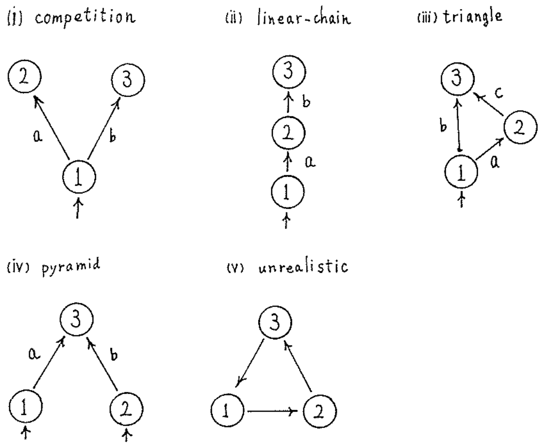

Fig. 8.

a circle, and the energy flow through them by an arrow, we can draw five graphs (Fig. 8). The fifth graph is constructed by only carnivores. It is unrealistic. Except this cases, we research stabilities of these graphs, using interactions used in the preveous section.

(i) species 2 and species 3 both eat species 1 (herbivore)

$$\frac{dN_1}{dt} = N_1(-N_1^2+2N_1)-aN_1N_2-bN_1N_3$$

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

$$\frac{dN_3}{dt} = -N_3+bN_1N_3$$

We draw isoplanes, $\frac{dN_1}{dt}=0$, $\frac{dN_2}{dt}=0$, $\frac{dN_3}{dt}=0$, in the phase space $N_1\times N_2\times N_3$ (Fig. 9). Cross points of these three planes are stationary points. If $\frac{1}{2}<a<b<1$, there are two stationary points; one $\left(\frac{1}{a}, \frac{2a-1}{a^3}, 0\right)$ is unstable, and the other $\left(\frac{1}{b}, 0, \frac{2b-1}{b^3}\right)$ is stable. Starting from any states, all orbits appraoch the latter point. If $a<b$, and $b>1$, all orbits approach a limit cycle on the plane $N_2=0$ though $\left(\frac{1}{b}, 0, \frac{2b-1}{b^3}\right)$ becomes unstable. So far as $a<b$ (species 3 is more excellent than species 2 in the capture ability), species 2 extincts after all. This competition principle so called 'one niche one species' is well known among ecologists (Gause[5]).

(ii) species 3 eats species 2 which eats species 1

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

$$\frac{dN_2}{dt} = -N_2+aN_1N_2-bN_2N_3$$

$$\frac{dN_3}{dt} = -N_3+bN_2N_3$$

We again draw isoplanes (Fig. 10). If $\frac{1}{2}<a<1$, $b>\frac{a^3}{2a-1}$, all orbits approach one stationary point $(N_1^*N_2^*N_3^*)$, where $\frac{1}{a}<N_1^*<2$, $0<N_2^*<\frac{2a-1}{a^3}$, $N_3^*=\frac{1}{b}>0$. In this case, three species coexist with their constant populations. Therefore, linear-chain type interaction is comparatively stable.

(iii) species 3 eats species 2 and species 1, and species 2 eats species 1

$$\frac{dN_1}{dt} = N_1(-N_1^2+2N_1)-a_1N_2N_1-bN_1N_3$$

$$\frac{dN_2}{dt} = -N_2+aN_1N_2-cN_2N_3$$

$$\frac{dN_3}{dt} = -N_3+bN_1N_3+cN_2N_3$$

If $a<b$, species 2 extincts. If $a>b$, $\frac{1}{2}<a<1$, $c>\frac{a^3}{2a-1}$ three species coexist as same as the case (ii). This case can be said to be more stable than the case (i), but less stable than the case (ii) (Fig. 11).

(iv) species 3 eats both species 1 and species 2

$$\frac{dN_1}{dt} = N_1(-N_1^2+2N_1)-aN_1N_3$$

$$\frac{dN_2}{dt} = N_2(-N_2^2+2N_2)-bN_2N_3$$

$$\frac{dN_3}{dt} = -N_3+aN_1N_3+bN_2N_3$$

If $a+b<\frac{1}{2}$, species 3 extincts, because only one stable point is (2, 2, 0). If $\frac{1}{2}<a+b<1-a\sqrt{\frac{b-a}{b}}$, $a<b$, or $\frac{1}{2}<a+b<1-b\sqrt{\frac{a-b}{a}}$, $a>b$, all orbits approach

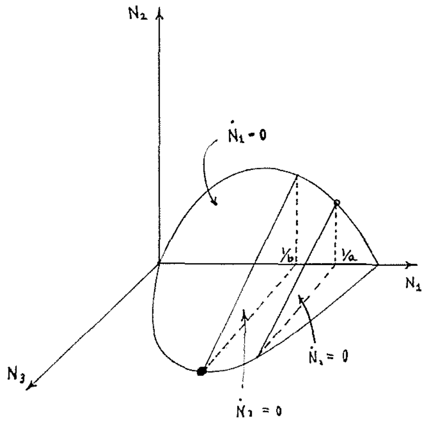

Fig. 9.

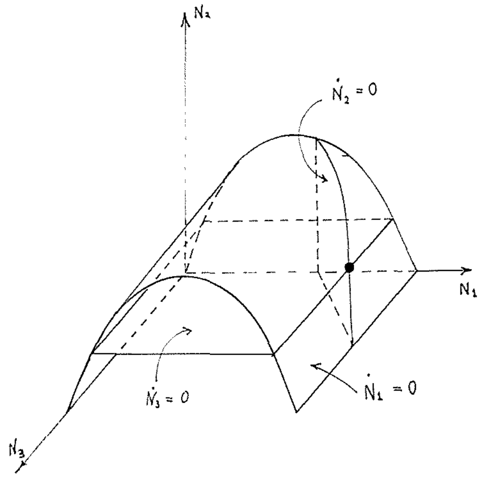

Fig. 10.

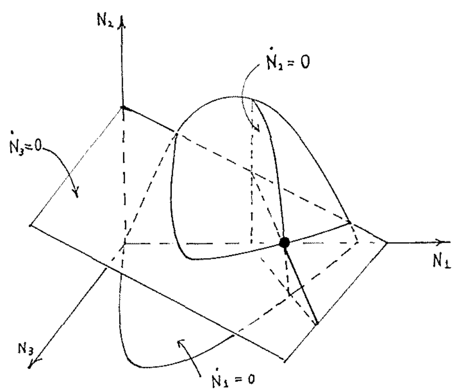

Fig. 11.

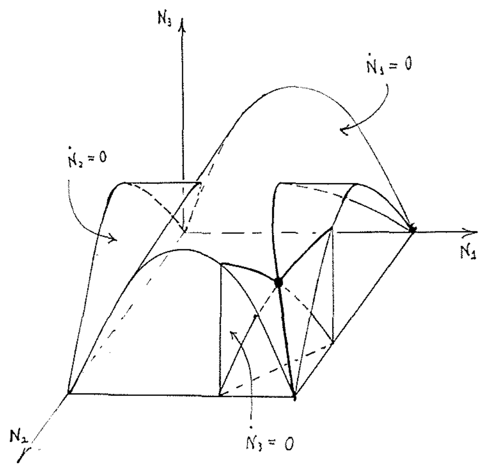

Fig. 12.

an stationary point ($N_1{}^*$, $N_2{}^*$, $N_3{}^*$), where $N_1{}^*$, $N_2{}^*$, $N_3{}^*$ are all positive.

This pyramid type interaction is stable different from antipyramid type of the case (i) (Fig. 12).

After all, linear-chain type and pyramid type are more stable than other types. Because of this fact, we think that general structures of food webs constructed by a lot of species are also inclined to be pyramidus.

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