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THE STRUGGLE FOR LIFE: I. TWO SPECIES

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The general equations are discussed describing two species in competition or in symbiosis or feeding one on the other.

Introduction. The simple ecological situation of two species living in the same environment can be represented by the equations

$$\begin{aligned}\frac{dN_1}{dt} &= N_1K_1(N_1, N_2),\\ \frac{dN_2}{dt} &= N_2K_2(N_1, N_2),\end{aligned} \tag{1}$$

where N_1 and N_2 are the number of individuals of the two species, and K_1 and K_2 are two given functions of N_1 and N_2. The hypotheses implicit in equations (1) are that the rate of increase or decrease of the populations does not depend on time and that the populations are so large as to be measurable with real numbers and not subject to random fluctuations. The explicit hypotheses we are making are that the initial values of N_1 and N_2, namely N_{10} and N_{20}, are positive and that K_1 and K_2, with their first derivatives, are defined and continuous for all non-negative values of N_1 and N_2. The particular ecological situation will dictate additional specific conditions on the two functions K_1 and K_2.

The interrelation between the two species may be of three main types: *a.* the first species is disadvantaged, the second is advantaged, by the presence of the other (predator–prey relationship), *b.* both species are disadvantaged by the presence of the other (competition), *c.* both species are advantaged by the presence of the other (symbiosis).

Predator and prey. This case has been studied by Volterra (1927) and later, under broader hypotheses, by Kolmogoroff (1936); the paper by Kolmogoroff is not widely known, so we think it useful to present here a summary of it together with our comments and extensions.

The prey is represented by N_1 and the predator by N_2.

To make the equations biologically plausible, the following properties are required of K_1:

a1. The multiplication of the prey is slowed by an increase in the number of predators; therefore, $\partial K_1/\partial K_2 < 0$.

a2. For a constant ratio N_1/N_2, the multiplication of the prey is slowed by an increase in the number of predators because the predator-prey encounters are more frequent; therefore, $dK_1/dS < 0$ where the derivative is taken along a vector starting at the origin.

a3. If both populations are very small, the prey multiply; therefore, $K_1(0, 0) > 0$.

a4. If there are too many predators, the prey cannot multiply; therefore, there exists an $A > 0$ such that $K_1(0, A) = 0$.

a5. If there are too many prey, they cannot multiply even in the absence of predators; therefore there exists a $B > 0$ such that $K_1(B, 0) = 0$.

The following properties are required of K_2:

b1. The multiplication of the predators decreases with their number; therefore $\partial K_2/\partial N_2 < 0$.

b2. For a constant ratio N_1/N_2, the multiplication of the predators is increased by an increase in the number of prey; therefore, $dK_2/dS > 0$.

b3. If there are not enough prey, the predators cannot multiply; therefore, there exists a $C > 0$ such that $K_2(C, 0) = 0$.

Now, if $B < C$ or $B = C$, the predators will disappear in a finite interval of time; and the populations will reach a point of equilibrium at $N_1 = B$ and $N_2 = 0$. A non-trivial solution can therefore be found only with the additional hypothesis:

c1. $B > C$.

It follows that the two curves $K_1 = 0$ *and* $K_2 = 0$ *cross at one point* Z and divide the positive quadrant of the plane (N_1, N_2) into four zones, I, II, III and IV (see Fig. 1). There are three singular points: 0, B, and Z. The only integral curves starting or ending at 0 are the two axes. B is a saddle point (Poincaré, 1881); the integral curve L (see Fig. 2) leaves this point with a direction normal to the N_1 axis. This integral curve and all other integral curves originating from the points at infinity go cyclically from zone to zone, i.e., from zone I to zone II, from zone II to III, from III to IV and from IV to I. These integral curves do not necessarily reach the point Z.

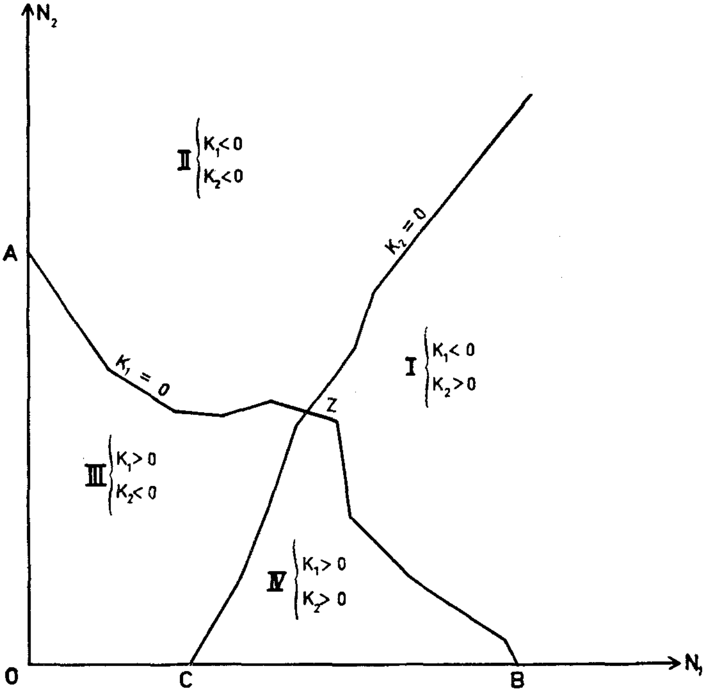

Figure 1.

There are three possibilities:

a. The integral curves reach Z with a definite direction; i.e., the two populations reach the point of equilibrium in a finite interval of time;

b. The integral curves approach Z asymptotically: i.e., the two populations approach the point of equilibrium with oscillations;

c. The integral curves go an infinite number of times through the zones I, II, III and IV, without approaching indefinitely the point Z; in this case, according to the second Theorem of Bendixson (1901), they approach asymptotically a closed line F containing Z; i.e., the two populations oscillate with period and amplitude approaching determined non-zero values. According to the same theorem, F itself is an integral curve of equations (1); i.e., if N_{10} and N_{20} correspond to a point of F, then the two populations oscillate with constant period and amplitude.

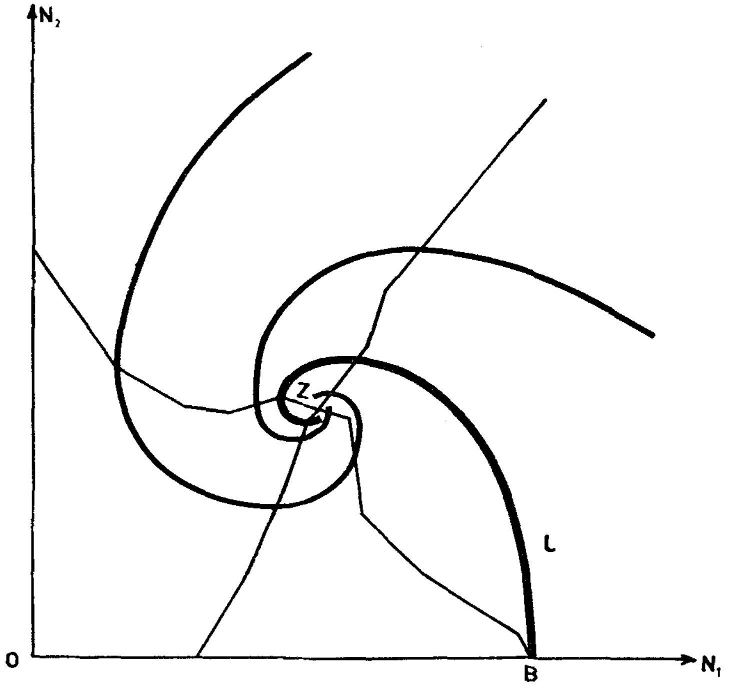

Figure 2.

For an integral curve passing through a point internal to F there are five possibilities:

c.a. It reaches Z with a definite direction;

c.b. It approaches Z asymptotically;

c.c. It approaches asymptotically, from the external side, a closed line contained in F and containing Z;

c.d. It is a closed line containing Z;

c.e. It asymptotically approaches F from its internal side or a closed line contained in F and containing Z.

These five cases are not mutually exclusive. If, for any positive number ε, we can find a number η such that in a circle centered at Z with radius η the absolute values of the derivatives of K_1 and K_2 are less than ε, then (Cauchy 1839, 1842) the behavior of the integral curves near Z is revealed by the equation

$$\begin{vmatrix} \left(N_1 \dfrac{\partial K_1}{\partial N_1}\right)_Z - X & \left(N_1 \dfrac{\partial K_1}{\partial N_2}\right)_Z \\ \left(N_2 \dfrac{\partial K_2}{\partial N_1}\right)_Z & \left(N_2 \dfrac{\partial K_2}{\partial N_2}\right)_Z - X \end{vmatrix} = 0. \tag{2}$$

If there are two real negative roots, then *a.* or *c.a.* is the case; if there are two complex roots with negative real part, then *b.* or *c.b.* is the case; if there are two real positive, or complex with positive real part, roots, then *c.e.* is the case. Equation (2) cannot have a positive and a negative root; in fact, calling z_1 and z_2 the coordinates of Z, for hypothesis *a2*, we have

$$\left(\frac{\partial K_1}{\partial N_1}\right)_Z < -\left(\frac{\partial K_1}{\partial N_2}\right)_Z \left(\frac{z_2}{z_1}\right),$$

and for hypothesis *b2*.

$$\left(\frac{\partial K_2}{\partial N_1}\right)_Z > -\left(\frac{\partial K_2}{\partial N_2}\right)_Z \left(\frac{z_2}{z_2}\right).$$

It follows that

$$\left(\frac{\partial K_1}{\partial N_2}\right)_Z \left(\frac{\partial K_2}{\partial N_1}\right)_Z < \left(\frac{\partial K_1}{\partial N_1}\right)_Z \left(\frac{\partial K_2}{\partial N_2}\right)_Z,$$

and by the rule of Descartes (1637; see also Gauss, 1828) equation (3) has an even number of positive roots.

We were unable to find a simple condition, necessary and sufficient, for the existence of periodic solutions; a sufficient, though not necessary, condition for the existence of a closed integral F is equation (2) having neither real negative, or complex with negative real part, roots.

Competitors. The case of two species competing for a single common niche was studied by Volterra (1927). Here we try to reach analogous conclusions starting from broader hypotheses.

The following properties are required of K_1 and K_2:

a. An increase in either of the two populations produces a decrease in the growth rate of both populations; therefore,

$$\frac{\partial K_1}{\partial N_1} < 0, \quad \frac{\partial K_1}{\partial N_2} < 0,$$

$$\frac{\partial K_2}{\partial N_1} < 0 \quad \text{and} \quad \frac{\partial K_2}{\partial N_2} < 0.$$

b. If both populations are very small, they both multiply; therefore, $K_1(0, 0) > 0$ and $K_2(0, 0) > 0$.

c. Each population, even if very small, cannot increase if the other reaches a certain size; therefore, there exist an A and a C such that $K_1(0, A) = K_2(C, 0) = 0$.

d. Each population cannot increase over a certain size even if the other population is very small; therefore, there exist a B and a D such that $K_1(B, 0) = K_2(0, D) = 0$.

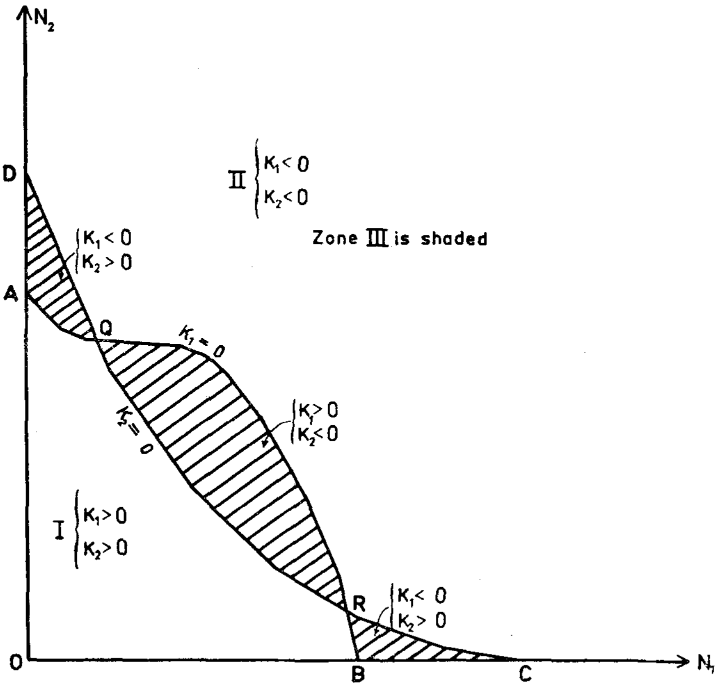

Figure 3.

In general, the two curves $K_1 = 0$ and $K_2 = 0$ can have any number of points in common. The positive quadrant of the plane (N_1, N_2) will be divided into three zones: zone I, where $K_1 > 0$, $K_2 > 0$; zone II, where $K_1 < 0$, $K_2 < 0$; and zone III, where $K_1K_2 \leq 0$. Such zones are shown diagrammatically in Figure 3. All integral curves originating in zones I and II eventually enter zone III. Zone III is formed by the curves $K_1 = 0$, $K_2 = 0$, by the points enclosed by them and by the segments AD and BC. Depending upon the explicit form of the functions K_1 and K_2, the points of this zone less the border points, may form one or more connected sets; each of these connected sets plus its border points, forms a sub-zone; all integral curves in a given sub-zone end at its point corresponding to N_1 = maximum, N_2 = minimum, or corresponding to N_1 = minimum, N_2 = maximum, according to whether for the internal points of the sub-zone it is $K_1 > 0$, $K_2 < 0$, or $K_1 < 0$, $K_2 > 0$. For instance, in the case of Figure 3, D is the point of equilibrium of a sub-zone and R the point of equilibrium of the other two sub-zones. It is possible, but improbable, that some points of zone III belong to no sub-group; this occurs when the curves $K_1 = 0$ and $K_2 = 0$ have an arc in common. In this case, the integral curves arriving from zones I and II reaching this arc stop.

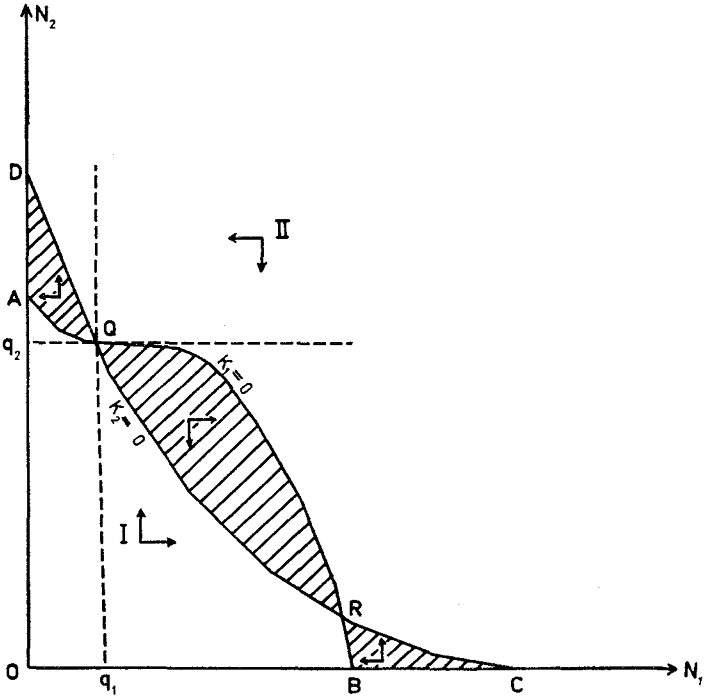

Figure 4.

A simple graphic device can often disclose a great deal of information about the limiting behavior of the integral curves. As an example, the curves of Figure 3 are reproduced in Figure 4; here the *signs* of the functions K_1 and K_2 are represented diagrammatically by two unit vectors parallel to the axes. In zone I, we have $K_1 > 0$ and $K_2 > 0$ and hence, with increasing time, the integral curves in this zone are limited to the quadrant defined by the two unit vectors as shown in Figure 4.

For the sake of illustration, consider the sub-zone limited by the points Q

and R; it is obvious from the vectors, that Q is a point of unstable equilibrium and that R is a point of stable equilibrium. Note also that any integral curve passing through the rectangular region $N_1q_1Q\infty$ must eventually terminate at the point R. Integral curves passing through the rectangular region $N_2q_2Q\infty$ will never reach R, but D. The behavior of the integral curves in the remaining regions of the phase plane must be determined by detailed analysis.

In conclusion, when the curves $K_1 = 0$ and $K_2 = 0$ do not intersect, one species will survive; namely, the first if $B > C$ or the second if $B < C$. When the curves $K_1 = 0$ and $K_2 = 0$ intersect at one point, then if $B > C$, either the first or the second species only will survive, depending upon the initial conditions; if $B < C$, both species will survive. When the curves $K_1 = 0$ and $K_2 = 0$ have many intersections, many fates are possible for the two species, depending upon the initial conditions. In general, the points of intersection where the curve $K_1 = 0$ has the same or a greater slope (in absolute value) than the curve $K_2 = 0$, are points of pacific coexistence.

Is the possibility of survival of both species in contradiction with the Competitive Exclusion Principle formulated by Volterra? In a mathematical sense, this question should not be posed; for, if two species interact according to the conditions of the Volterra model, then only one species survives. However, the Volterra model is the simplest possible, and as seen from the consideration of a more general form of the population growth equations, there is a great variety of modes for the development of two competing species. To be more specific, it is not difficult to find a model only slightly more elaborate than Volterra's which allows both species to survive.

We have shown (Rescigno and Richardson, 1965) that if one can put

$$\begin{aligned} K_1(N_1, N_2) &= \partial_{10} - \partial_{11}F_1(N_1, N_2) - \partial_{12}F_2(N_1, N_2), \\ K_2(N_1, N_2) &= \partial_{20} - \partial_{21}F_1(N_1, N_2) - \partial_{22}F_2(N_1, N_2), \end{aligned} \tag{3}$$

with the F's increasing with their arguments and the ∂'s positive constants such that

$$\begin{aligned} F_1(0, 0) &= F_2(0, 0) = 0, \\ \partial_{10}/\partial_{20} &\neq \partial_{11}/\partial_{21}, \\ \partial_{10}/\partial_{20} &= \partial_{12}/\partial_{22}, \\ \partial_{11}/\partial_{21} &= \partial_{12}/\partial_{22}, \end{aligned}$$

then one should speak in general of *two niches*; the functions $F_1(N_1, N_2)$ and $F_2(N_1, N_2)$ measure their filling or utilization.

For any particular ecological situation compatible with equations (3), the

∂'s satisfying the given conditions can be determined in infinitely many ways; for instance

$$\partial_{10} = K_1(0, 0); \qquad \partial_{11} = k > 0; \qquad \partial_{12} = 0;$$
$$\partial_{20} = K_2(0, 0); \qquad \partial_{21} = 0; \qquad \partial_{22} = 1;$$

which gives

$$F_1(N_1, N_2) = \frac{1}{k}[K_1(0, 0) - K_1(N_1, N_2)];$$
$$F_2(N_1, N_2) = K_2(0, 0) - K_2(N_1, N_2).$$

If, with a proper choice of k, F_1 and F_2 can be made identical; i.e., if K_1 is a linear function of K_2, then we have a single niche. If this is not the case, then we have two niches, but they may or may not be different enough to allow the survival of two species.

Symbiosis. Kostitzin (1934) studied a number of cases of symbiosis; here we are interested in the perfect symbiosis, i.e., the association of two species such that each species gets an absolute advantage from the other.

The following properties are required of K_1 and K_2:

a. The multiplication of one species is speeded by an increase in the number of individuals of the other species; therefore, $\partial K_1/\partial N_2 > 0$ and $\partial K_2/\partial N_1 > 0$.

b. For a constant ratio N_1/N_2, the multiplication of each species is slowed by an increase in the number of individuals of both species; therefore $dK_1/dS < \alpha$, and $dK_2/dS < \alpha$, where α is a negative number. At first it seems $\partial K_1/\partial N_1 < 0$ and $\partial K_2/\partial N_2 < 0$ could be sufficient conditions, but it is not so because the combined food supply of the two species is limited; for the same reason we cannot put $\alpha = 0$, or else we could have

$$\lim_{N_1 \to \infty} (dK_1/dS) = 0 \quad \text{and} \quad \lim_{N_2 \to \infty} (dK_2/dS) = 0,$$

which imply an unlimited supply of food.

c. If both populations are very small, each species can multiply; therefore $K_1(0, 0) > 0$ and $K_2(0, 0) > 0$.

d. In the absence of one species, the other cannot multiply over a certain size; therefore there exist a $B > 0$ and a $D > 0$ such that $K_1(B, 0) = K_2(0, D) = 0$.

It follows that the two curves $K_1 = 0$ and $K_2 = 0$ cross at one point Z and divide the positive quadrant of the plane (N_1, N_2) into four zones (see Fig. 5). No integral curve can cross the curves $K_1 = 0$ and $K_2 = 0$ more than once;

all integral curves reach point Z *in a finite interval of time;* this is a point of stable equilibrium.

Other biological situations can be thought of as intermediate cases between the ones here examined. With a little additional effort we could have made the problem look nicely more complicated; but, as Descartes said, we want to leave this pleasure to the reader.

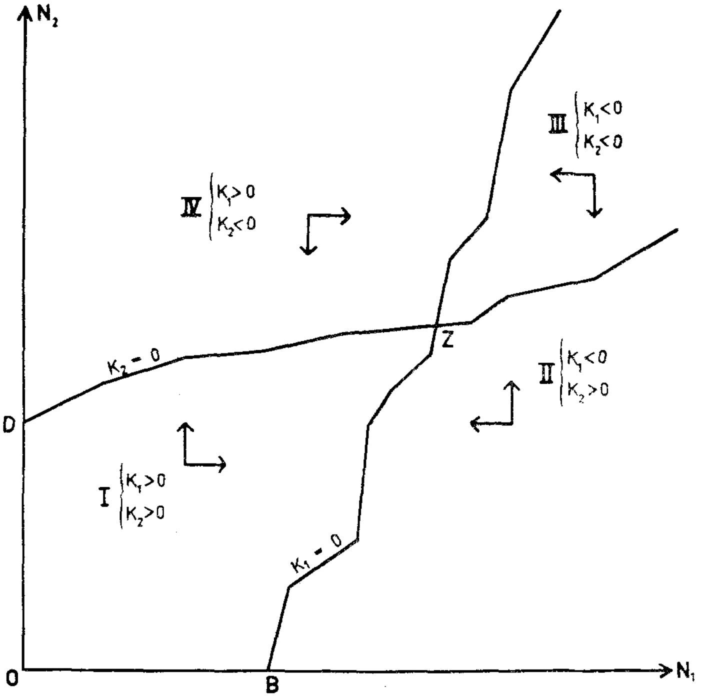

Figure 5.

Examples. For a comprehensive bibliography of the problem, we refer the reader to the book by D'Ancona (1954). Here we have chosen from the recent literature on the subject a few examples that can be considered as special cases of our equations (1).

Hutchinson (1947) has shown that, if the classical Volterra equations of two competing species are slightly modified to include "social phenomena," thus

$$dN_1/dt = b_1N_1(k_1 - N_1 - \gamma N_2^2)/k_1,$$

$$dN_2/dt = b_2N_2(k_2 - N_2 - \delta N_1^2)/k_2,$$

then for a large range of values of k_1, k_2, γ, δ, either species can survive according to the initial conditions. These equations actually represent two niches, but for no positive values of the coefficients can both species survive.

Cunningham (1955) examined the equations

$$dN_1/dt = a_1[k_1 - N_1 - F_1(N_2)]N_1,$$
$$dN_2/dt = a_2[k_2 - N_2 - F_2(N_1)]N_2,$$

which are a generalization of both Volterra's and Hutchinson's, and represent a case of predator and prey, competition, or symbiosis; he studied in detail all singular points but did not find a general condition for the existence of periodic solutions.

Utz and Waltman (1963) gave sufficient conditions for the existence of periodic solutions of the Cunningham equations. They also studied the equations

$$dN_1/dt = N_1F_1(N_2),$$
$$dN_2/dt = N_2F_2(N_1),$$

and gave sufficient conditions for the existence of periodic solutions; but these equations cannot describe a predator-prey situation, as function $F_1(N_2)$ cannot satisfy our conditions *a3* and *a5* at the same time.

Finally Waltman (1964) showed that equations (1), under certain conditions compatible with the conditions we have stated for the existence of a predator-prey relationship, have periodic solutions.

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