

#### 4.11 The principle of competitive exclusion in population biology

- (a) Show that the change of coordinates  $\beta_i y_i(t) = x_i(t/\alpha_i \beta_i)$  reduces this system of equations to

$$\dot{y}_1 = y_1(1 - y_1) + a_1 y_1 y_2, \quad \dot{y}_2 = y_2(1 - y_2) - a_2 y_1 y_2$$

where  $a_1 = \gamma_1 \beta_2 / \alpha_1 \beta_1$  and  $a_2 = \gamma_2 \beta_1 / \alpha_2 \beta_2$ .

- (b) What are the stable equilibrium populations when (i)  $0 < a_2 < 1$ , (ii)  $a_2 > 1$ ?
- (c) It is observed that  $a_1 = 3a_2$  ( $a_2$  is a measure of the aggressiveness of the predator). What is the value of  $a_2$  if the predator's instinct is to maximize its stable equilibrium population?
6. (a) Let  $x(t)$  be a solution of  $\dot{x} = ax - M\sqrt{x}$ , with  $M > a\sqrt{x(t_0)}$ . Show that
- $$a\sqrt{x} = M - (M - a\sqrt{x(t_0)})e^{a(t-t_0)/2}.$$
- (b) Conclude from (a) that  $x(t)$  approaches zero in finite time.
- (c) Let  $x(t), y(t)$  be a solution of (7), with  $by(t_0) > a\sqrt{x(t_0)}$ . Show that  $x(t)$  reaches zero in finite time. *Hint*: Observe that  $y(t)$  is increasing for  $t \geq t_0$ .
- (d) It can be shown that  $by(t)$  will eventually exceed  $a\sqrt{x(t)}$  for every solution  $x(t), y(t)$  of (7) with  $x(t_0)$  and  $y(t_0)$  positive. Conclude, therefore, that all solutions  $x(t), y(t)$  of (7) achieve  $x=0$  in finite time.

#### 4.11 The principle of competitive exclusion in population biology

It is often observed, in nature, that the struggle for existence between two similar species competing for the same limited food supply and living space nearly always ends in the complete extinction of one of the species. This phenomenon is known as the "principle of competitive exclusion." It was first enunciated, in a slightly different form, by Darwin in 1859. In his paper 'The origin of species by natural selection' he writes: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitutions and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera."

There is a very interesting biological explanation of the principle of competitive exclusion. The cornerstone of this theory is the idea of a "niche." A niche indicates what place a given species occupies in a community; i.e., what are its habits, food and mode of life. It has been observed that as a result of competition two similar species rarely occupy the same niche. Rather, each species takes possession of those kinds of food and modes of life in which it has an advantage over its competitor. If the two species tend to occupy the same niche then the struggle for existence between them will be very intense and result in the extinction of the weaker species.

An excellent illustration of this theory is the colony of terns inhabiting the island of Jorilgatch in the Black Sea. This colony consists of four different species of terns: sandwich-tern, common-tern, blackbeak-tern, and lit-

tle-tern. These four species band together to chase away predators from the colony. However, there is a sharp difference between them as regards the procuring of food. The sandwich-tern flies far out into the open sea to hunt certain species, while the blackbeak-tern feeds exclusively on land. On the other hand, common-tern and little-tern catch fish close to the shore. They sight the fish while flying and dive into the water after them. The little-tern seizes his fish in shallow swampy places, whereas the common-tern hunts somewhat further from shore. In this manner, these four similar species of tern living side by side upon a single small island differ sharply in all their modes of feeding and procuring food. Each has a niche in which it has a distinct advantage over its competitors.

In this section we present a rigorous mathematical proof of the law of competitive exclusion. This will be accomplished by deriving a system of differential equations which govern the interaction between two similar species, and then showing that every solution of the system approaches an equilibrium state in which one of the species is extinct.

In constructing a mathematical model of the struggle for existence between two competing species, it is instructive to look again at the logistic law of population growth

$$\frac{dN}{dt} = aN - bN^2. \quad (1)$$

This equation governs the growth of the population  $N(t)$  of a single species whose members compete among themselves for a limited amount of food and living space. Recall (see Section 1.5) that  $N(t)$  approaches the limiting population  $K = a/b$ , as  $t$  approaches infinity. This limiting population can be thought of as the maximum population of the species which the microcosm can support. In terms of  $K$ , the logistic law (1) can be rewritten in the form

$$\frac{dN}{dt} = aN \left( 1 - \frac{b}{a} N \right) = aN \left( 1 - \frac{N}{K} \right) = aN \left( \frac{K - N}{K} \right). \quad (2)$$

Equation (2) has the following interesting interpretation. When the population  $N$  is very low, it grows according to the Malthusian law  $dN/dt = aN$ . The term  $aN$  is called the “biotic potential” of the species. It is the potential rate of increase of the species under ideal conditions, and it is realized if there are no restrictions on food and living space, and if the individual members of the species do not excrete any toxic waste products. As the population increases though, the biotic potential is reduced by the factor  $(K - N)/K$ , which is the relative number of still vacant places in the microcosm. Ecologists call this factor the environmental resistance to growth.

Now, let  $N_1(t)$  and  $N_2(t)$  be the population at time  $t$  of species 1 and 2 respectively. Further, let  $K_1$  and  $K_2$  be the maximum population of species 1 and 2 which the microcosm can support, and let  $a_1N_1$  and  $a_2N_2$  be the biotic potentials of species 1 and 2. Then,  $N_1(t)$  and  $N_2(t)$  satisfy the sys-

tem of differential equations

$$\frac{dN_1}{dt} = a_1 N_1 \left( \frac{K_1 - N_1 - m_2}{K_1} \right), \quad \frac{dN_2}{dt} = a_2 N_2 \left( \frac{K_2 - N_2 - m_1}{K_2} \right), \quad (3)$$

where  $m_2$  is the total number of places of the first species which are taken up by members of the second species, and  $m_1$  is the total number of places of the second species which are taken up by members of the first species. At first glance it would appear that  $m_2 = N_2$  and  $m_1 = N_1$ . However, this is not generally the case, for it is highly unlikely that two species utilize the environment in identical ways. Equal numbers of individuals of species 1 and 2 do not, on the average, consume equal quantities of food, take up equal amounts of living space and excrete equal amounts of waste products of the same chemical composition. In general, we must set  $m_2 = \alpha N_2$  and  $m_1 = \beta N_1$ , for some constants  $\alpha$  and  $\beta$ . The constants  $\alpha$  and  $\beta$  indicate the degree of influence of one species upon the other. If the interests of the two species do not clash, and they occupy separate niches, then both  $\alpha$  and  $\beta$  are zero. If the two species lay claim to the same niche and are very similar, then  $\alpha$  and  $\beta$  are very close to one. On the other hand, if one of the species, say species 2, utilizes the environment very unproductively; i.e., it consumes a great deal of food or excretes very poisonous waste products, then one individual of species 2 takes up the place of many individuals of species 1. In this case, then, the coefficient  $\alpha$  is very large.

We restrict ourselves now to the case where the two species are nearly identical, and lay claim to the same niche. Then,  $\alpha = \beta = 1$ , and  $N_1(t)$  and  $N_2(t)$  satisfy the system of differential equations

$$\frac{dN_1}{dt} = a_1 N_1 \left( \frac{K_1 - N_1 - N_2}{K_1} \right), \quad \frac{dN_2}{dt} = a_2 N_2 \left( \frac{K_2 - N_1 - N_2}{K_2} \right). \quad (4)$$

In this instance, we expect the struggle for existence between species 1 and 2 to be very intense, and to result in the extinction of one of the species. This is indeed the case as we now show.

**Theorem 6** (Principle of competitive exclusion). *Suppose that  $K_1$  is greater than  $K_2$ . Then, every solution  $N_1(t)$ ,  $N_2(t)$  of (4) approaches the equilibrium solution  $N_1 = K_1$ ,  $N_2 = 0$  as  $t$  approaches infinity. In other words, if species 1 and 2 are very nearly identical, and the microcosm can support more members of species 1 than of species 2, then species 2 will ultimately become extinct.*

Our first step in proving Theorem 6 is to show that  $N_1(t)$  and  $N_2(t)$  can never become negative. To this end, recall from Section 1.5 that

$$N_1(t) = \frac{K_1 N_1(0)}{N_1(0) + (K_1 - N_1(0))e^{-a_1 t}}, \quad N_2(t) = 0$$

is a solution of (4) for any choice of  $N_1(0)$ . The orbit of this solution in the  $N_1$ - $N_2$  plane is the point  $(0,0)$  for  $N_1(0)=0$ ; the line  $0 < N_1 < K_1$ ,  $N_2=0$  for  $0 < N_1(0) < K_1$ ; the point  $(K_1,0)$  for  $N_1(0)=K_1$ ; and the line  $K_1 < N_1 < \infty$ ,  $N_2=0$  for  $N_1(0) > K_1$ . Thus, the  $N_1$  axis, for  $N_1 \geq 0$ , is the union of four distinct orbits. Similarly, the  $N_2$  axis, for  $N_2 \geq 0$ , is the union of four distinct orbits of (4). This implies that all solutions  $N_1(t)$ ,  $N_2(t)$  of (4) which start in the first quadrant ( $N_1 > 0, N_2 > 0$ ) of the  $N_1$ - $N_2$  plane must remain there for all future time.

Our second step in proving Theorem 6 is to split the first quadrant into regions in which both  $dN_1/dt$  and  $dN_2/dt$  have fixed signs. This is accomplished in the following manner. Let  $l_1$  and  $l_2$  be the lines  $K_1 - N_1 - N_2 = 0$  and  $K_2 - N_1 - N_2 = 0$ , respectively. Observe that  $dN_1/dt$  is negative if  $(N_1, N_2)$  lies above  $l_1$ , and positive if  $(N_1, N_2)$  lies below  $l_1$ . Similarly,  $dN_2/dt$  is negative if  $(N_1, N_2)$  lies above  $l_2$ , and positive if  $(N_1, N_2)$  lies below  $l_2$ . Thus, the two parallel lines  $l_1$  and  $l_2$  split the first quadrant of the  $N_1$ - $N_2$  plane into three regions (see Figure 1) in which both  $dN_1/dt$  and  $dN_2/dt$  have fixed signs. Both  $N_1(t)$  and  $N_2(t)$  increase with time (along any solution of (4)) in region I;  $N_1(t)$  increases, and  $N_2(t)$  decreases, with time in region II; and both  $N_1(t)$  and  $N_2(t)$  decrease with time in region III.

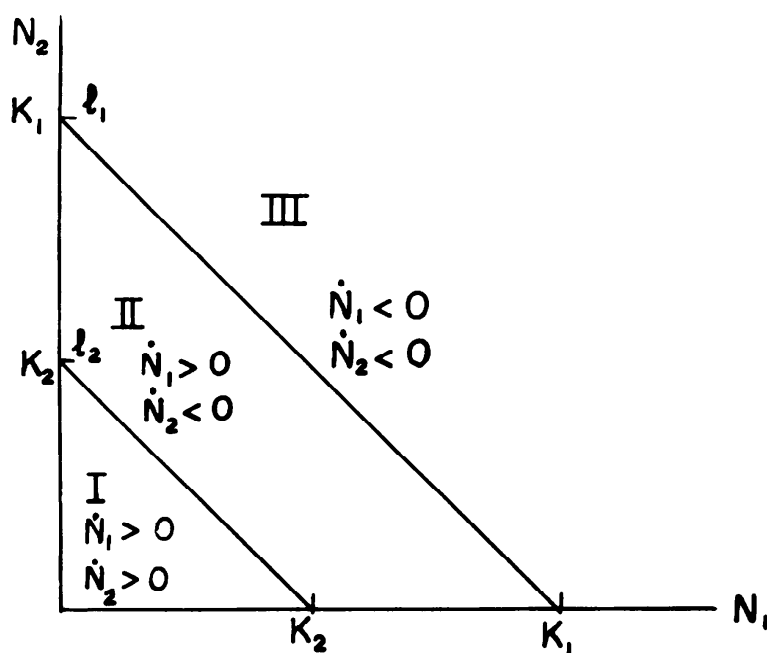


Figure 1

**Lemma 1.** Any solution  $N_1(t)$ ,  $N_2(t)$  of (4) which starts in region I at  $t = t_0$  must leave this region at some later time.

**PROOF.** Suppose that a solution  $N_1(t)$ ,  $N_2(t)$  of (4) remains in region I for all time  $t \geq t_0$ . This implies that both  $N_1(t)$  and  $N_2(t)$  are monotonic increasing functions of time for  $t \geq t_0$ , with  $N_1(t)$  and  $N_2(t)$  less than  $K_2$ . Consequently, by Lemma 1 of Section 4.8, both  $N_1(t)$  and  $N_2(t)$  have limits

$\xi, \eta$  respectively, as  $t$  approaches infinity. Lemma 2 of Section 4.8 implies that  $(\xi, \eta)$  is an equilibrium point of (4). Now, the only equilibrium points of (4) are  $(0, 0)$ ,  $(K_1, 0)$ , and  $(0, K_2)$ , and  $(\xi, \eta)$  obviously cannot equal any of these three points. We conclude therefore, that any solution  $N_1(t), N_2(t)$  of (4) which starts in region I must leave this region at a later time.  $\square$

**Lemma 2.** *Any solution  $N_1(t), N_2(t)$  of (4) which starts in region II at time  $t = t_0$  will remain in this region for all future time  $t \geq t_0$ , and ultimately approach the equilibrium solution  $N_1 = K_1, N_2 = 0$ .*

**PROOF.** Suppose that a solution  $N_1(t), N_2(t)$  of (4) leaves region II at time  $t = t^*$ . Then, either  $\dot{N}_1(t^*)$  or  $\dot{N}_2(t^*)$  is zero, since the only way a solution of (4) can leave region II is by crossing  $l_1$  or  $l_2$ . Assume that  $\dot{N}_1(t^*) = 0$ . Differentiating both sides of the first equation of (4) with respect to  $t$  and setting  $t = t^*$  gives

$$\frac{d^2 N_1(t^*)}{dt^2} = \frac{-a_1 N_1(t^*)}{K_1} \frac{dN_2(t^*)}{dt}.$$

This quantity is positive. Hence,  $N_1(t)$  has a minimum at  $t = t^*$ . But this is impossible, since  $N_1(t)$  is increasing whenever a solution  $N_1(t), N_2(t)$  of (4) is in region II. Similarly, if  $\dot{N}_2(t^*) = 0$ , then

$$\frac{d^2 N_2(t^*)}{dt^2} = \frac{-a_2 N_2(t^*)}{K_2} \frac{dN_1(t^*)}{dt}.$$

This quantity is negative, implying that  $N_2(t)$  has a maximum at  $t = t^*$ . But this is impossible, since  $N_2(t)$  is decreasing whenever a solution  $N_1(t), N_2(t)$  of (4) is in region II.

The previous argument shows that any solution  $N_1(t), N_2(t)$  of (4) which starts in region II at time  $t = t_0$  will remain in region II for all future time  $t \geq t_0$ . This implies that  $N_1(t)$  is monotonic increasing and  $N_2(t)$  is monotonic decreasing for  $t \geq t_0$ , with  $N_1(t) < K_1$  and  $N_2(t) > 0$ . Consequently, by Lemma 1 of Section 4.8, both  $N_1(t)$  and  $N_2(t)$  have limits  $\xi, \eta$  respectively, as  $t$  approaches infinity. Lemma 2 of Section 4.8 implies that  $(\xi, \eta)$  is an equilibrium point of (4). Now,  $(\xi, \eta)$  obviously cannot equal  $(0, 0)$  or  $(0, K_2)$ . Consequently,  $(\xi, \eta) = (K_1, 0)$ , and this proves Lemma 2.  $\square$

**Lemma 3.** *Any solution  $N_1(t), N_2(t)$  of (4) which starts in region III at time  $t = t_0$  and remains there for all future time must approach the equilibrium solution  $N_1(t) = K_1, N_2(t) = 0$  as  $t$  approaches infinity.*

**PROOF.** If a solution  $N_1(t), N_2(t)$  of (4) remains in region III for  $t \geq t_0$ , then both  $N_1(t)$  and  $N_2(t)$  are monotonic decreasing functions of time for  $t \geq t_0$ , with  $N_1(t) > 0$  and  $N_2(t) > 0$ . Consequently, by Lemma 1 of Section 4.8, both  $N_1(t)$  and  $N_2(t)$  have limits  $\xi, \eta$  respectively, as  $t$  approaches infinity. Lemma 2 of Section 4.8 implies that  $(\xi, \eta)$  is an equilibrium point of (4). Now,  $(\xi, \eta)$  obviously cannot equal  $(0, 0)$  or  $(0, K_2)$ . Consequently,  $(\xi, \eta) = (K_1, 0)$ .  $\square$

## 4 Qualitative theory of differential equations

**PROOF OF THEOREM 6.** Lemmas 1 and 2 above state that every solution  $N_1(t), N_2(t)$  of (4) which starts in regions I or II at time  $t = t_0$  must approach the equilibrium solution  $N_1 = K_1, N_2 = 0$  as  $t$  approaches infinity. Similarly, Lemma 3 shows that every solution  $N_1(t), N_2(t)$  of (4) which starts in region III at time  $t = t_0$  and remains there for all future time must also approach the equilibrium solution  $N_1 = K_1, N_2 = 0$ . Next, observe that any solution  $N_1(t), N_2(t)$  of (4) which starts on  $l_1$  or  $l_2$  must immediately afterwards enter region II. Finally, if a solution  $N_1(t), N_2(t)$  of (4) leaves region III, then it must cross the line  $l_1$  and immediately afterwards enter region II. Lemma 2 then forces this solution to approach the equilibrium solution  $N_1 = K_1, N_2 = 0$ .  $\square$

Theorem 6 deals with the case of identical species; i.e.,  $\alpha = \beta = 1$ . By a similar analysis (see Exercises 4–6) we can predict the outcome of the struggle for existence for all values of  $\alpha$  and  $\beta$ .

### Reference

Gause, G. F., 'The Struggle for Existence,' Dover Publications, New York, 1964.

### EXERCISES

1. Rewrite the system of equations (4) in the form

$$\frac{K_1}{a_1 N_1} \frac{dN_1}{dt} = K_1 - N_1 - N_2, \quad \frac{K_2}{a_2 N_2} \frac{dN_2}{dt} = K_2 - N_1 - N_2.$$

Then, subtract these two equations and integrate to obtain directly that  $N_2(t)$  approaches zero for all solutions  $N_1(t), N_2(t)$  of (4) with  $N_1(t_0) > 0$ .

2. The system of differential equations

$$\begin{aligned} \frac{dN_1}{dt} &= N_1 [-a_1 + c_1(1 - b_1 N_1 - b_2 N_2)] \\ \frac{dN_2}{dt} &= N_2 [-a_2 + c_2(1 - b_1 N_1 - b_2 N_2)] \end{aligned} \quad (*)$$

is a model of two species competing for the same limited resource. Suppose that  $c_1 > a_1$  and  $c_2 > a_2$ . Deduce from Theorem 6 that  $N_1(t)$  ultimately approaches zero if  $a_1 c_2 > a_2 c_1$ , and  $N_2(t)$  ultimately approaches zero if  $a_1 c_2 < a_2 c_1$ .

3. In 1926, Volterra presented the following model of two species competing for the same limited food supply:

$$\begin{aligned} \frac{dN_1}{dt} &= [b_1 - \lambda_1(h_1 N_1 + h_2 N_2)] N_1 \\ \frac{dN_2}{dt} &= [b_2 - \lambda_2(h_1 N_1 + h_2 N_2)] N_2. \end{aligned}$$

Suppose that  $b_1/\lambda_1 > b_2/\lambda_2$ . (The coefficient  $b_i/\lambda_i$  is called the susceptibility of species  $i$  to food shortages.) Prove that species 2 will ultimately become extinct if  $N_1(t_0) > 0$ .