7

Competition

What happens when two species are grown together? One of the first careful experiments of this kind was performed by Gause (1935). He grew two different species of *Paramecium* both separately and together under laboratory conditions. The results he obtained are graphed in Figure 7.1. As you might guess, the number of each species was lower when the two species were grown together than when each was grown individually. Similar experiments have been performed many times since.

We would like to understand this process of competition. Can we predict when the outcome will be the one obtained by Gause (1935) in which both species coexist? What would cause one species to eliminate the other instead? Can we predict, or understand, how much the equilibrium level of each species would be reduced by the other? In the experiment by Gause, the population of each species approached its equilibrium value more or less monotonically. Is this the expected result? To answer these and other questions about the dynamics of competition, we turn to a modeling approach.

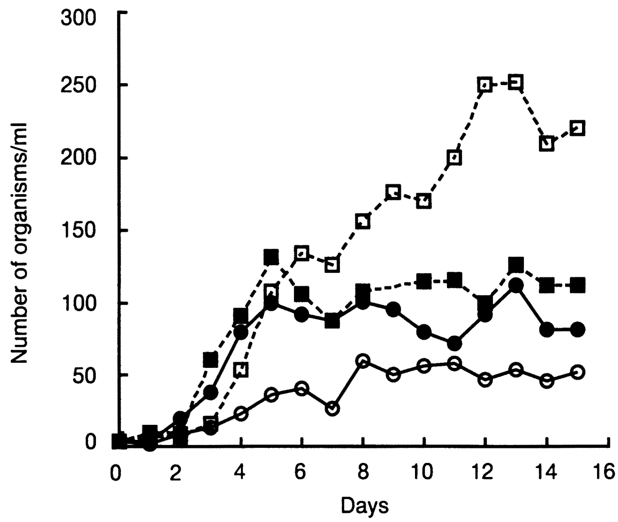


FIGURE 7.1. Competition between two laboratory species of *Paramecium*. The numbers of *P. bursaria* when grown alone are indicated by open boxes, and the numbers of *P. caudatum* when grown alone are indicated by closed boxes. The results of growing the two species together are also given, with the number of *P. bursaria* indicated by open circles, and the number of *P. caudatum* by closed circles. The numbers of both species are lower when they are grown together, and they reach an approximate equilibrium. The experimental protocol included removal of a fixed fraction of the individuals each day (data are from Gause 1935).

7.1 Lotka–Volterra models

Gause's work on competition was motivated by the Lotka–Volterra competition models, which can be viewed as the natural extension of the logistic model to two species. The logistic model can be written as

When initially presented by Lotka and Volterra, this model was justified phenomenologically, meaning that no underlying biological meaning was attached to the coefficients a_{ij}. There was no prescription for measuring these competition coefficients other than fitting the model to data. Since then, there have been some attempts to derive these competition coefficients from other models.

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \tag{7.1}$$

$$= rN(1 - a_1 N), \tag{7.2}$$

where $a_1 = 1/K$.

We now look at a system with two species, where we let N_i be the number of individuals in species i, r_i is the intrinsic growth rate of species i, and include four positive constants, a_{ij} which represent interspecific and intraspecific density dependence. Here we start with equation (7.2). For each species we replace the term a_1 by a_{ii} to represent the effect of each species on itself, and add a second term to each equation with the coefficient a_{ij} representing the effect of species j on species i. Extending the logistic model, we obtain

$$\frac{dN_1}{dt} = r_1N_1(1 - a_{11}N_1 - a_{12}N_2) \tag{7.3}$$

$$\frac{dN_2}{dt} = r_2N_2(1 - a_{21}N_1 - a_{22}N_2). \tag{7.4}$$

At times it is more useful to include explicitly the carrying capacity of each species, and write this pair of equations as

In this formulation, α_{12} gives the relative effect of species 2 on the population growth rate of species 1, as compared to the effect of species 1 on its own population growth rate.

$$\frac{dN_1}{dt} = \frac{r_1N_1}{K_1}(K_1 - N_1 - \alpha_{12}N_2) \tag{7.5}$$

$$\frac{dN_2}{dt} = \frac{r_2N_2}{K_2}(K_2 - \alpha_{21}N_1 - N_2). \tag{7.6}$$

We now look at the solutions of this model, trying to relate qualitatively different biological outcomes (different species surviving) to different assumptions about the species interactions (as reflected in the parameters of the model).

Graphical approach

One of the most powerful approaches for understanding the dynamics of two-species systems is the graphical approach. In this approach, we focus on a *phase plane* (Figure 7.2), where we draw the dynamics of species through time, but ignore the time axis, and look only at the species numbers.

The phase plane is the projection of a graph of the numbers of two species against time in three dimensions onto the two dimensions consisting of just the species numbers.

Why are we only interested in nonnegative values of N_1 and N_2?

The first step is to draw the isoclines (as they are known in ecology, although more properly called nullclines) for the model under consideration. Isoclines are the curves along which the rate of change of the population of a species is zero, i.e., $\frac{dN_i}{dt} = 0$ for $i = 1$ or 2. Thus, for example, the growth rate of species 1 is zero if

$$\frac{r_1N_1}{K_1}(K_1 - N_1 - \alpha_{12}N_2) = 0. \tag{7.7}$$

This isocline equation has two solutions:

$$N_1 = 0 \tag{7.8}$$

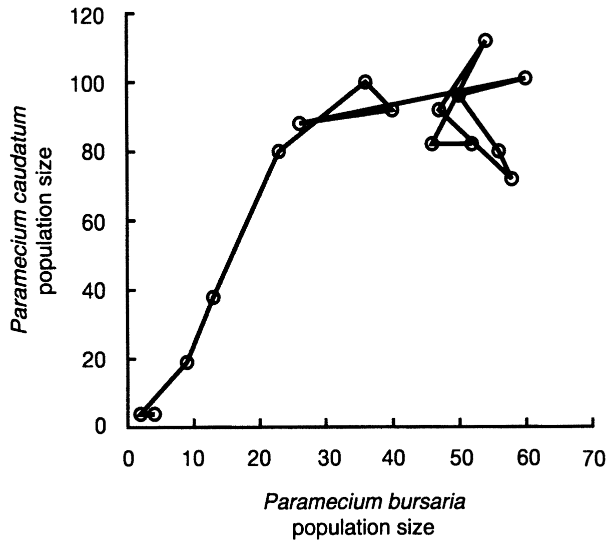


FIGURE 7.2. Phase plane depiction of competition between two laboratory species of *Paramecium*. The data from Figure 7.1 for the two species grown together are shown on a phase plane. The initial conditions are in the lower left, and the line joins circles which each represent numbers of the two species on a given day. As this is a phase plane, the time axis is implicit.

or

$$(K_1 - N_1 - \alpha_{12}N_2) = 0. \tag{7.9}$$

One point along (7.9) that is easy to find is $N_1 = 0, N_2 = K_1/\alpha_{12}$. What is the other?

The first solution lies along the axis, so we will focus on the solution (7.9). To graph this equation, notice first that it is the equation of a straight line. A straight line is specified by two points. What two points that lie on this line are easy to find on a graph?

How many equilibria are there in Figure 7.3?

We then graph the isocline for species two in a similar fashion, producing Figure 7.3. Equilibria occur at points where the isoclines for the two species cross, because these are the points where the growth rates of both species are zero. Equilibria also occur where an isocline for species 1 crosses the axis $N_2 = 0$, because the growth rate of species 2 is zero when $N_2 = 0$.

To proceed further we need an indication of how the species numbers change with time. Although time is not explicitly included in the phase plane as an axis, we indicate changes through time by vectors showing how the numbers in each species would change if the number of each species was given by the coordi-

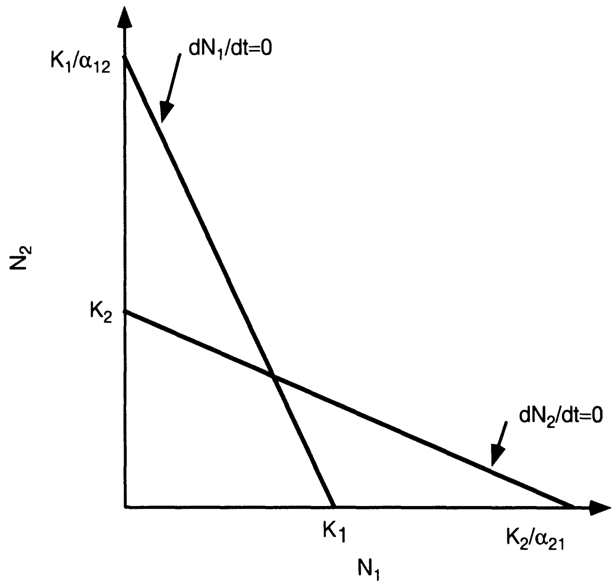


FIGURE 7.3. Isoclines in the phase plane of the Lotka–Volterra model for competition.

nates on the phase plane. From the equations, we see that increasing the numbers of either species reduces the per capita growth rate of both species. Thus, in the phase plane, in the upper-right portion the growth rate of both species is negative. We indicate this in Figure 7.4 both by labeling this portion and by drawing a vector showing that the change in numbers through time leads to a movement down and to the left.

We can then proceed in a similar fashion to label the other three portions of the phase plane to indicate the direction of change in species numbers. This is illustrated in Figure 7.5. In this case, we conclude from the phase plane that the species ultimately coexist, approaching the equilibrium at the center of the phase plane. Note that at this equilibrium each species is at a lower population level than it would be if it were by itself.

Figure 7.5 is just one possible placement of the isoclines. Try to think of others, leading to different outcomes of competition, before you go on.

In drawing Figure 7.5, the outcome depended on the relative positioning of the carrying capacities, K_i, and the relative effects of the species on each other, α_{12}, α_{21}. There are four different cases possible, with three of them qualitatively different. By 'different cases', we refer to the relative positions of the isoclines. We illustrate two other cases in Figure 7.6 and Figure 7.7.

There are two cases which are similar because one corresponds to the elimination of species 1 by species 2, while the other corresponds to the elimination of species 2 by species 1.

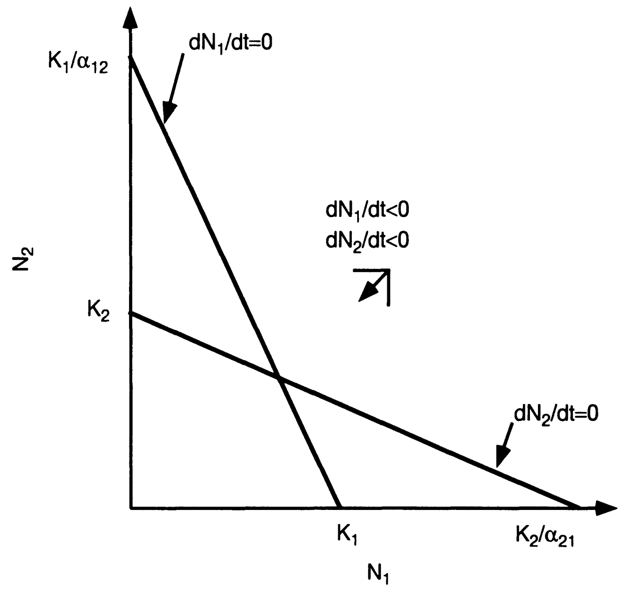


FIGURE 7.4. Phase plane for Lotka–Volterra competition. The next step in completing the phase plane in Figure 7.3 is drawing the direction of the change in species numbers. This is done for the upper right of the phase plane, where the numbers of both species are declining.

In Figure 7.6, from the directions of the arrows, we conclude that species 1 is eliminated and only species 2 remains. In Figure 7.7 we conclude that the stable outcome is the elimination of either species 1 or species 2, with the outcome depending on the initial conditions. The steps we have used in a general phase plane analysis are summarized in Box 7.1.

Another way to view the dynamics of competition is to solve the equations describing the dynamics on a computer and plot the numbers of each species through time. This is illustrated in Figures 7.11 through 7.14. The outcome in each case corresponds to what we would predict based on our phase plane analysis. Note that to solve the model by computer, we first have to pick specific parameter values.

The importance of our phase plane analysis, as opposed to just doing numerical solutions, is that the phase plane analysis can tell us the outcome of competition for all parameter values, while numerical solutions only tell us the outcome for each specific set of parameters for which we plot the solutions. Thus, even the pervasiveness of computers does not reduce the importance of the phase plane approach developed here.

From the phase portraits we conclude that the conditions for coexistence are those met in Figure 7.5, namely

$$K_1 < \frac{K_2}{\alpha_{21}} \qquad (7.10)$$

Box 7.1. Steps in phase plane analysis.

To do a phase plane analysis of a model of the form

$$\frac{dN_1}{dt} = N_1 f_1(N_1, N_2) \qquad \frac{dN_2}{dt} = N_2 f_2(N_1, N_2)$$

we have employed the following steps.

- Determine the isoclines. The nontrivial isocline for species 1 is given by the equation $f_1(N_1, N_2) = 0$. The nontrivial isocline for species 2 is given by the equation $f_1(N_1, N_2) = 0$. Plot the solutions of these two equations on the N_1, N_2 plane, focusing only on nonnegative population sizes N_1 and N_2. Label each isocline as in Figure 7.7.
- Find the equilibria. The equilibria are the points where the isoclines for the two species cross, or where the isocline for species 1 intersects the line $N_2 = 0$, or where the isocline for species 2 intersects the line $N_1 = 0$.
- Find the signs of the rates of change of population size in the different parts of the phase plane. The isoclines will have divided the phase plane into different regions. Using both the model equations and the knowledge that the rate of change of each species is zero along its isocline, determine the signs of the population change $\frac{dN_1}{dt}$ and $\frac{dN_2}{dt}$ in each region of the phase plane. Write these on the phase plane.
- Draw arrows indicating the direction of population changes on the phase plane. If $\frac{dN_1}{dt}$ is positive, the arrow points to the right; if it is negative the arrow points to the left. If $\frac{dN_2}{dt}$ is positive, the arrow points up; if it is negative the arrow points down. Combine this information to determine the direction of population change. Draw the arrows indicating the direction on the phase plane.

From the phase plane, you can often infer the fate of interacting populations.

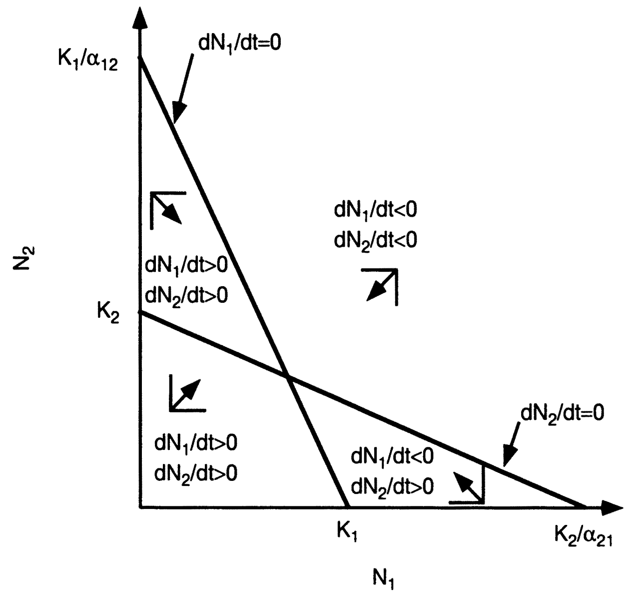


FIGURE 7.5. Phase plane for competition in which both species coexist. The phase plane in Figure 7.4 is completed by drawing in the direction of the change in species numbers in the four regions of the phase plane created by the isoclines. From the arrows indicating change in species numbers, one can see that the system ends up at the interior equilibrium.

$$K_2 < \frac{K_1}{\alpha_{12}}. \tag{7.11}$$

These conditions involve both the carrying capacities and the competition coefficients. From this pair we can derive a necessary (but not sufficient) condition for coexistence in terms of the competition coefficients alone. Rearrange the conditions for coexistence as

If the necessary condition for coexistence is violated, we know that one of the species will be eliminated.

$$\frac{K_1}{K_2} < \frac{1}{\alpha_{21}} \tag{7.12}$$

$$\alpha_{12} < \frac{K_1}{K_2}, \tag{7.13}$$

so the condition for coexistence becomes

$$\alpha_{12} < \frac{K_1}{K_2} < \frac{1}{\alpha_{21}}. \tag{7.14}$$

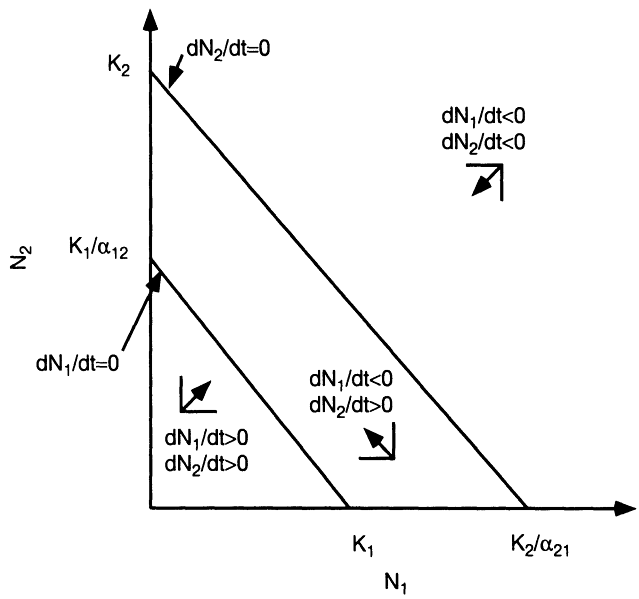


FIGURE 7.6. Phase plane for competition in which species 2 outcompetes species 1. The phase plane is changed from that in Figure 7.5 by changing the relative position of the isoclines.

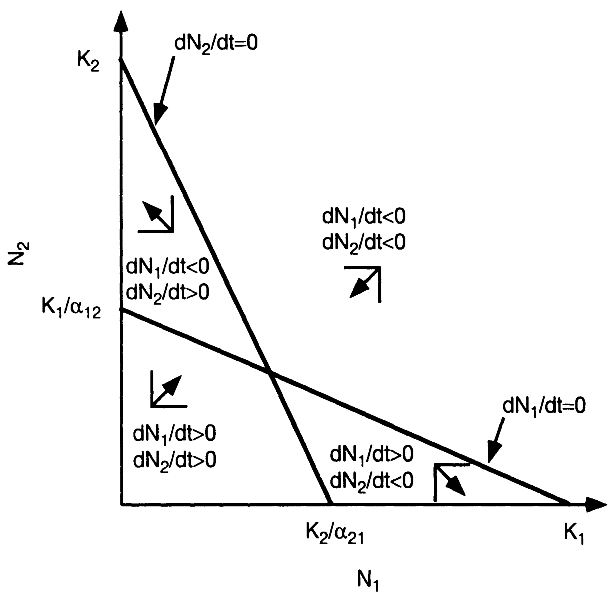


FIGURE 7.7. Phase plane for competition in which the outcome depends on the initial conditions – which species is eliminated depends on the initial conditions.

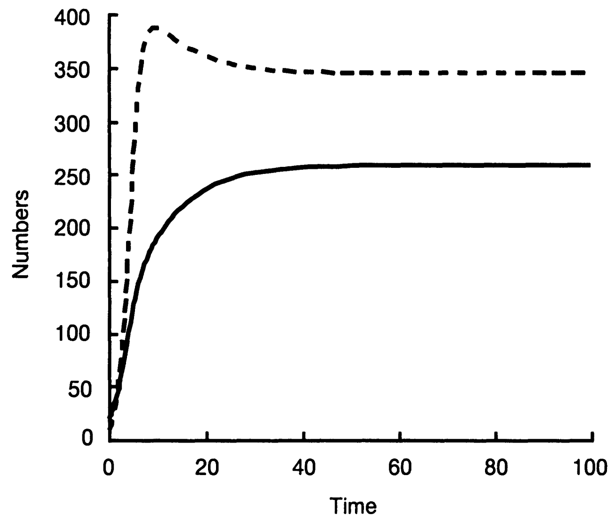


FIGURE 7.8. Dynamics of competition with coexistence. The curves represent a solution of the Lotka–Volterra competition model with parameter values $r_1 = 0.9$, $r_2 = 0.5$, $\alpha_{12} = 0.6$, $\alpha_{21} = 0.7$, and $K_1 = K_2 = 500$. Observe that the conditions for coexistence are satisfied, and that at the joint equilibrium the sum of the population sizes of the two species is greater than 500.

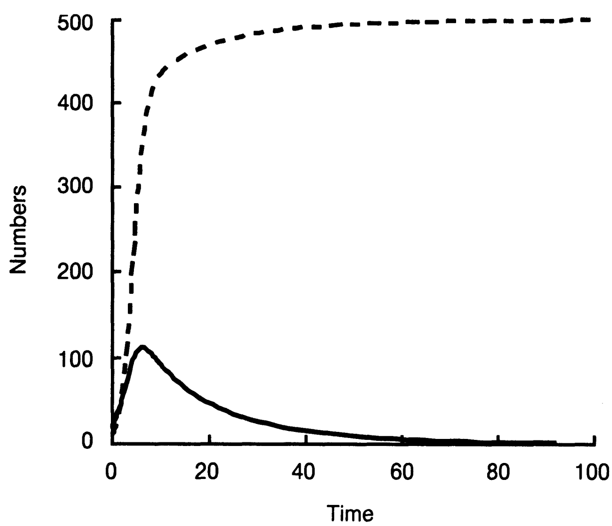
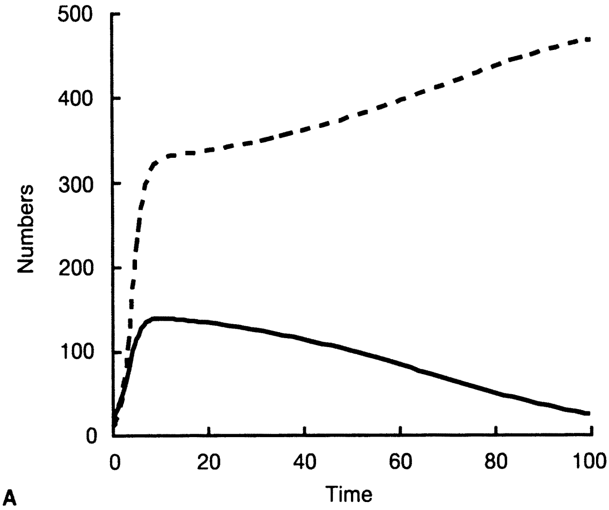


FIGURE 7.9. Dynamics of competition with one species outcompeting the other. The curves represent a solution of the Lotka–Volterra competition model with parameter values $r_1 = 0.9$, $r_2 = 0.5$, $\alpha_{12} = 0.6$, $\alpha_{21} = 1.1$, and $K_1 = K_2 = 500$.



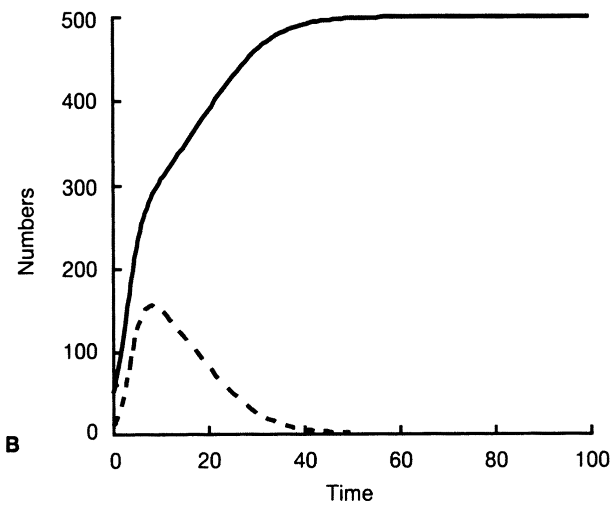


FIGURE 7.10. Dynamics of competition where the outcome depends on the initial conditions. The curves represent a solution of the Lotka–Volterra competition model with parameter values $r_1 = 0.9$, $r_2 = 0.5$, $\alpha_{12} = 1.2$, $\alpha_{21} = 1.1$, and $K_1 = K_2 = 500$. The only difference between the two figures is the initial condition. This is the case outlined in Figure 7.7.

For this condition to be satisfied, we must have

$$\alpha_{12} < \frac{1}{\alpha_{21}} \tag{7.15}$$

or, rearranging,

$$\alpha_{12}\alpha_{21} < 1. \tag{7.16}$$

The geometric mean of two numbers is the square root of their product.

We interpret this condition as saying that coexistence requires that the geometric mean effect of each species on the other must be less than the effect of each species on itself.

Recall that in the model the effect of each species on itself is 1.

If we assume that competition results from the exploitation of a common resource, such as food, then the competition coefficients α_{12} and α_{21} must be equal, so the condition for coexistence is then stated as the principle that each species must affect the other less than itself. This can be rephrased as Gause's *competitive exclusion principle*: to coexist, species must differ in their resource use.

Stability and equilibria

One of the most important outcomes of our graphical analysis of the competition model is that the long-term outcome is always an approach to a stable equilibrium and not to cycles. Thus, if we observe that the dynamics of two species do not eventually lead to a stable equilibrium, then competition between two species, of the form assumed in the Lotka–Volterra model, cannot explain the interaction.

What might lead to an outcome other than a stable equilibrium? One possibility is competition between three or more species. Think of other possible biological situations, or of features of two-species interactions that might lead to other outcomes.

Another approach to analyzing the models would be to solve for the equilibria analytically, and then to determine the stability of the resulting equilibria using the approach outlined in the previous chapter. The outcome is the same as for the graphical analysis. Because we will have to go through a stability analysis in the next chapter, this approach is left for the problems.

7.2 Extensions to Lotka–Volterra models

How can we 'test' the predictions of the Lotka–Volterra models? We observe, both in nature and the laboratory, all possible outcomes – coexistence or elimination of one species or the other – and parameters are difficult to measure. Are there ways to make other tests of the models?

One way to 'test' the Lotka–Volterra model is to take a fixed environment, such as a garden plot for plants or a bottle for *Dro-*

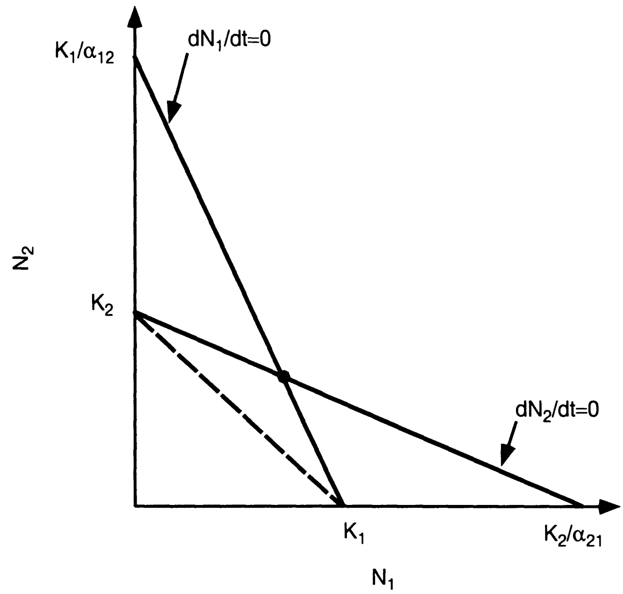


FIGURE 7.11. Relationship of coexistence equilibrium to equilibria of two species in isolation for Lotka–Volterra competition.

sophila, and grow each of two species in isolation and together. The Lotka–Volterra competition model makes a strong qualitative prediction about the relationship among population numbers in these three cases, if the species can coexist. This is illustrated in Figure 7.11. In isolation, species 1 will be at the population level K_1, while species 2 will be at the population level K_2. Note that if the species coexist, the dotted line joining these two points always lies below the coexistence equilibrium. The equation for the dotted line joining these two isolation equilibria is

To see that this is the right equation, look at the point where $N_2 = 0$ and at the point where $N_1 = 0$.

$$\frac{N_2}{K_2} + \frac{N_1}{K_1} = 1. \tag{7.17}$$

As the coexistence equilibrium lies above and to the right of the line 7.17, it must satisfy

$$\frac{N_2}{K_2} + \frac{N_1}{K_1} > 1. \tag{7.18}$$

This prediction, that the joint equilibrium lies above the line joining the two single-species equilibria, can be easily tested by first

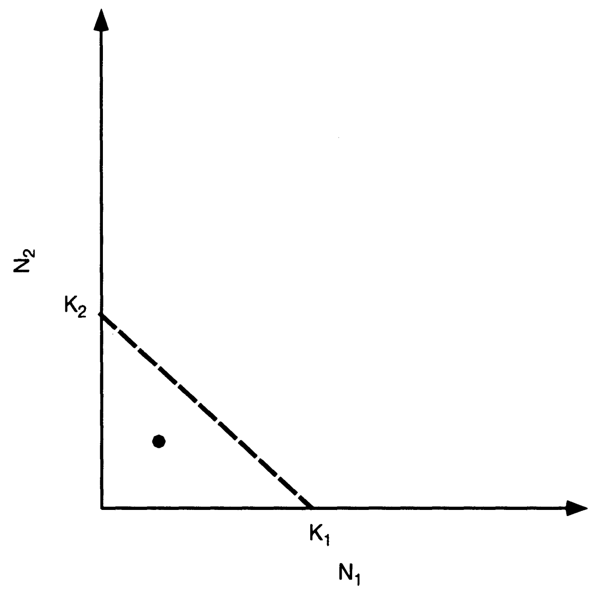


FIGURE 7.12. Relationship of coexistence equilibrium to equilibria of two species of *Drosophila* in isolation as examined by Ayala et al. (1973).

growing two species separately and then together. This was done by Ayala et al. (1973) for *Drosophila pseudoobscura* and *Drosophila serrata*, obtaining the result illustrated schematically in Figure 7.12.

A similar experiment had been performed almost 40 years earlier by Gause (1935) using two species of *Paramecium*, as illustrated in Figure 7.13. Here as well, the position in the phase plane of the coexistence equilibrium contradicts the Lotka–Volterra theory for one of the two experiments performed. The experiments differed in the food sources used for the *Paramecium*.

What is the explanation for the location of the coexistence equilibrium relative to the single-species equilibria? The explanation is that the isoclines must be curved, as illustrated in Figure 7.14. Thus we conclude that even in a system as simple as *Drosophila* or *Paramecium* in a bottle, the Lotka–Volterra model is inadequate.

What are the possible explanations for curved isoclines?

- Frequency-dependent competition, which is not included in the Lotka–Volterra equations, would make the isoclines curved.

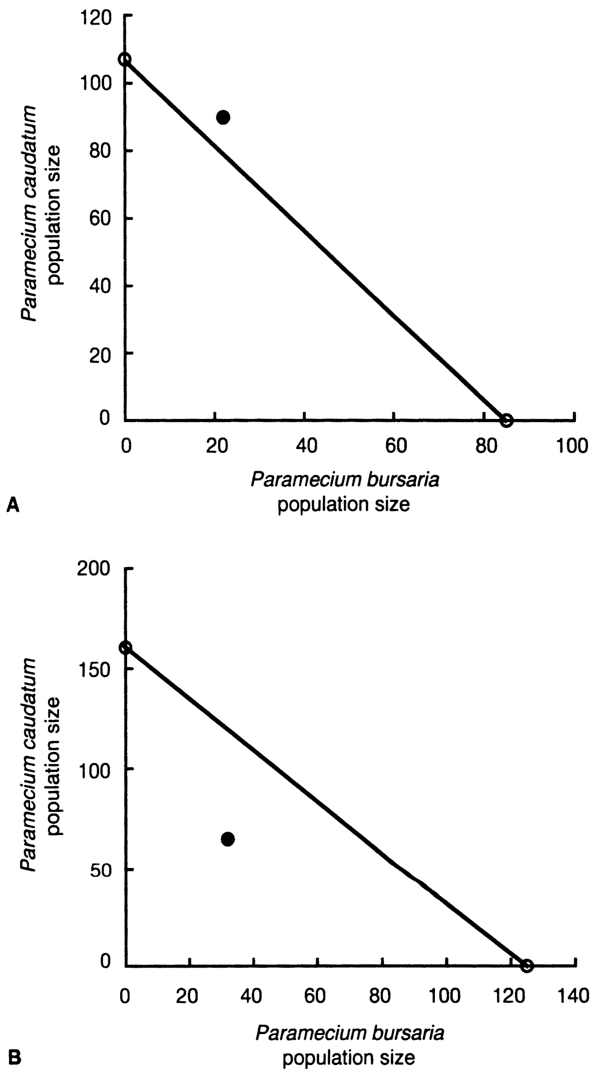


FIGURE 7.13. Outcome of competition between *Paramecium bursaria* and *P. caudatum* using data from Gause (1935). In each case the estimates of carrying capacities and joint equilibrium given by Gause (1935) are used. The open circles represent what are unstable equilibria in the two-species case; the number of each species in isolation. The closed circles represent the stable two-species equilibrium approached in the experiment. The two experiments differed in the strain of bacteria used as food. In the top experiment the joint equilibrium is above the line joining the one-species equilibria, as predicted by the Lotka–Volterra theory. However, in the bottom experiment the joint equilibrium is below the line joining the one-species equilibria, contradicting the Lotka–Volterra theory and showing that even in this simple case more complex theories are needed.

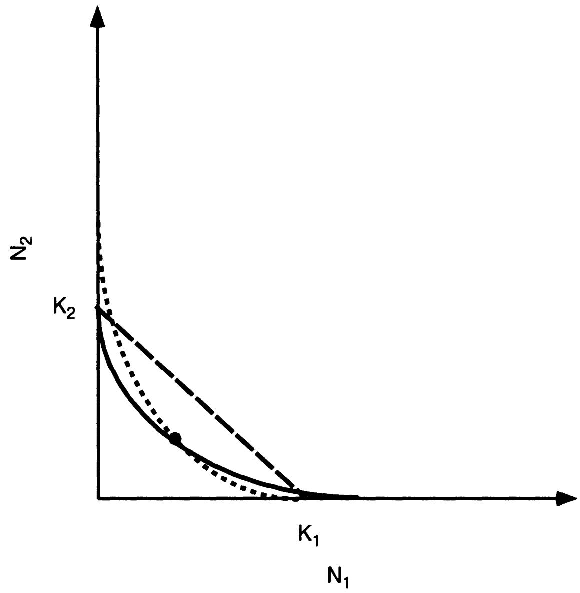


FIGURE 7.14. Curved isoclines in a competition model.

- Energetic considerations would lead to curved isoclines in mechanistic models (Schoener, 1974).
- Age dependence, where larval and adult competition are described by different models, each with linear isoclines, would lead to curved isoclines for the whole system.

We do not pursue these complications further here.

7.3 Competition in field experiments

Is competition an important force shaping natural communities? We have seen how competition can act in model systems, and in laboratory systems, but we have not seen whether competition can be detected in more complex systems. One can look for competition in specific systems, or ask how common competition is in general.

Two surveys, by Schoener (1983) and Connell (1983), both asked essentially the same question of how prevalent competition is in field experiments. Although the details of the two literature surveys are different, both authors concluded that competition was found quite often – more than half the time – in field experiments. Even though both found competition in many studies, the likelihood of finding competition as a function of trophic level was different in the two studies. Schoener did find support for the thesis advanced by HSS, but Connell did not. It is not obvious why the two reviews reached different conclusions.

The HSS hypothesis was discussed at the beginning of Chapter 6.

One illustrative example of an experiment testing competition in a specific system is that performed by Brown and his collaborators (Brown and Davidson, 1977; Brown et al., 1979) to look at competition between ants and rodents in the Arizona desert. In these experiments, if either kind of animal was removed, then the other species showed a dramatic increase in its density. This is strong evidence for competition. There was also a mechanism for competition: the animals all shared the same food source, seeds, in a habitat with limited food supplies.

7.4 Competition for space

Another approach to looking at competition is to consider competition for space. Alternatively, we can think of the effects of spatial structure in a patch model. We will look at the simple case of a competitive hierarchy, which is a simple extension of our metapopulation (patch) model for one species. The possible transitions at one location in the model are illustrated in Figure 7.15. We will assume that species 1 always outcompetes species 2, and that the time scale for this to take place is very short. Thus, species 2 does not change the dynamics of species 1. The dynamics of species 1 therefore are given by an equation which says that the rate of change of the fraction of habitat occupied by species 1 is given by the colonization rate of species 1 minus the extinction rate. The colonization rate of species 1 is proportional to the product of the fraction of patches not occupied by species 1 (those available for colonization) and the fraction of patches occupied by species 1 (and producing colonizers). The extinction rate is simply assumed to be proportional to the fraction of patches occupied by species 1. These assumptions lead to the model equation

The habitat sites occupied by subpopulations of a metapopulation can be called patches. An example of such a site is the host plant of an insect.

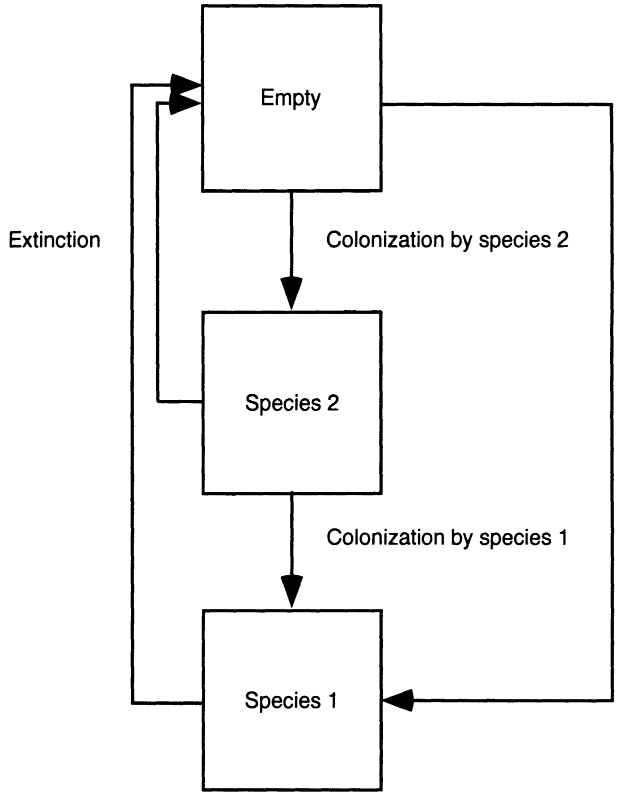


FIGURE 7.15. Transitions at one location in a simple model of competition for space, where species 1 always outcompetes species 2. In the model there is one term for each arrow leading to or from each box.

We do not need the equation for empty space or patches, because the proportion of empty space is just the space not occupied by either species.

$$\frac{dp_1}{dt} = m_1 p_1(1 - p_1) - e p_1, \tag{7.19}$$

where p_1 is the fraction of patches occupied by species 1, m_1 is a measure of the colonization rate of species 1, and e is the extinction rate.

The dynamics of species 2 are derived similarly, except that species 2 cannot colonize a patch occupied by species 1 and that some patches occupied by species 2 are lost as a result of colonization by species 1. Thus, those patches available for colonization are the empty patches, with frequency $1 - p_1 - p_2$. Also, we need to add a loss term accounting for the colonization by species 1 of patches occupied by species 2. This leads to an equation for the dynamics of species 2:

$$\frac{dp_2}{dt} = m_2p_2(1 - p_1 - p_2) - m_1p_1p_2 - ep_2. \qquad (7.20)$$

The analysis of this model is pursued further in the problems. The interesting feature is that the outcome can be coexistence, or species 1 eliminating species 2, or species 2 eliminating species 1. The competitive advantage of species 1 within a patch or at a single site can be offset by the superior dispersal capabilities assumed for species 2. This model has been used quite extensively to understand problems in conservation biology where the effects of habitat destruction are considered.

Summary

We have described three approaches for studying competition. Models can be used to show the kind of dynamics resulting from competition and the conditions that allow species to coexist, or possibly to be eliminated by competition. Cycles cannot occur in competition between two species. In the laboratory, one can show that the process of competition operates, and that even in this simplified setting the Lotka–Volterra competition models are not adequate descriptions. Studies of competition in the field show that competition does occur, but we have not shown that it is *the* force regulating populations.

Problems

1. This problem is based on ideas from Slobodkin (1961, 1964). Slobodkin looked at competition between a brown hydra, *Hydra littoralis*, and a green hydra, *Chlorohydra viridissima*, in laboratory experiments. In these experiments, he was able to achieve coexistence only by the process he called *rarefaction*, removing a fraction of the population of both species at regular intervals by removing part of the medium in which the animals were grown. Demonstrate how this works by adding the term $-mN_i$ to equations (7.3) and

(7.4), representing the effect of the experimenter. If, without the additional term, coexistence is impossible and one species always eliminates the other, show that it is possible to have coexistence with the additional term. Do this by starting with isoclines arranged so that coexistence is impossible, and showing that the additional term could produce equations with isoclines where coexistence is possible.

2. The model we presented of competition for space can be analyzed quite easily. One could analyze the model using phase plane techniques, but we take a different approach that yields additional insights.

   (a) First, find the nonzero equilibrium for the dominant competitor by setting the right-hand side of equation (7.19) equal to zero and solving for p_1. What conditions on the parameters are required for this equilibrium to be positive? Give an ecological interpretation.

   (b) Assuming that the dominant competitor can survive, determine the resulting nonzero equilibrium for species 2 by substituting the equilibrium value for p_1 into equation (7.20), equating the right-hand side to zero, and solving for p_2. What must be true about the colonization rate m_2, relative to the colonization rate m_1, for both species to survive? Does this make ecological sense?

   (c) Start with colonization rates and extinction rates that allow both species to survive. Which species would be eliminated first (at equilibrium) if the extinction rate was slowly increased? (For which species will the equilibrium become negative at the highest value of e?)

   (d) If both species have positive equilibrium levels, what happens to the equilibrium level of species 2, as the extinction rate is increased? Does this make sense?

3. We have not gone through the procedure outlined in Box 6.1 for analytically determining the equilibria and stability of equilibria in the Lotka–Volterra competition model. This is a relatively straightforward problem to solve. Find the equilib-

ria of the Lotka–Volterra competition model and determine their stability. Do the results agree with the phase plane analysis?

4. Discuss the possibilities and difficulties of detecting competition in the laboratory and the field. You will need to refer to some of the suggested reading to complete your answer.
   (a) Describe competition in the laboratory and the field using Lotka Volterra equations.
   (b) Discuss looking at numbers of two species grown together.
   (c) Discuss the approach of looking at overlap in resources used by putative competitors.
   (d) Discuss experimental field manipulations of populations.

Suggestions for further reading

The two surveys on competition in field experiments, by Connell (1983) and Schoener (1983), provide many more details on attempts to discover competition in the field. Two classic studies, Park (1948, 1954) and Connell (1961), are important to read. Park looked at competition in laboratory populations of the flour beetle, *Tribolium*; Connell demonstrated competition in the intertidal zone. Harper and McNaughton (1962) provide a classic example of a study of plant competition for which the Lotka–Volterra approach is not appropriate.

The model describing competition for space is a special case of one first developed in Hastings (1980). The model has been recently used to look at questions in conservation biology and competition for space in plants by Nee and May (1992) and by Tilman (1994).