

15

Multispecies Communities

GENERALIZED LOTKA–VOLTERRA EQUATIONS

In Chapter 14 we extended two-species competition models to three and more species. In the process, we showed that with matrix algebra the analysis was easily generalized. In this chapter we explore interactions among several species at multiple trophic levels. The method of solving for and evaluating the stability of equilibrium points for n interacting species, using matrix mathematics, is particularly straightforward for systems of equations called the generalized Lotka–Volterra equations. A **generalized Lotka–Volterra (GLV) system** is a community model in which the dynamics of the species can be described by equations with a linear *per capita* form, such as

$$\frac{dN_i}{N_i dt} = k_i + \sum_{j=1}^n a_{ij} N_j. \quad (15.1a)$$

Here k_i and a_{ij} are constants with different biological meanings for different trophic levels. Equation (15.1a) may be written in matrix form as

$$\frac{d\mathbf{N}}{\mathbf{N} dt} = \mathbf{k} + \mathbf{A} \mathbf{N}, \quad (15.1b)$$

where \mathbf{A} is a square matrix containing all the species interaction terms, a_{ij} . Matrix \mathbf{A} is sometimes called the interaction matrix or the **community matrix**.¹ Note, for example, that the two-species Lotka–Volterra competition equation for species 1 is typically cast as

$$\frac{dN_1}{N_1 dt} = \frac{r_1}{K_1} (K_1 - \alpha_{11} N_1 - \alpha_{12} N_2).$$

It may then be rearranged to match the form of Eq. (15.1a):

$$\frac{dN_1}{N_1 dt} = r_1 + \frac{-r_1 \alpha_{11} N_1}{K_1} + \frac{-r_1 \alpha_{12} N_2}{K_1}.$$

Similarly, for an arbitrary number of competitors, say, n , we could write

$$\frac{dN_i}{N_i dt} = r_i + \sum_{j=1}^n \frac{-r_i \alpha_{ij} N_j}{K_i} \quad \text{for } i = 1 \text{ to } n. \quad (15.2)$$

1. This terminology is not necessarily standard. Some ecologists call the Jacobian matrix, the “community matrix” (see e.g., Yodzis 1989). With this usage, the terms of the community matrix change, depending on the equilibrium point under consideration. In our usage, the “community matrix” is invariant, but is undefined except for GLV systems.

In this form the a_{ij} terms of Eq. (15.1a) are given by α_{ij} multiplied by $-r_i/K_i$, and the k_i of Eq. (15.1a) equals r_i . Thus an n -species Lotka–Volterra competition community can also be written in matrix form as

$\frac{d\mathbf{N}}{\mathbf{N} dt}$	$=$	$\mathbf{k} + \mathbf{A}\mathbf{N}$	
An $n \times 1$ vector with elements of the per capita growth rate of each species i	An $n \times 1$ vector with elements r_i	An $n \times n$ matrix with elements $-r_i\alpha_{ij}/K_i$. Since $\alpha_{ii} = 1$, the diagonal elements are $-r_i/K_i$.	An $n \times 1$ vector of the state variables N_i

At equilibrium, the per capita growth rate of each species is zero, so

$$\mathbf{A}\mathbf{N}^* = -\mathbf{k}.$$

The interior equilibrium point \mathbf{N}^* , an $n \times 1$ vector, can be solved as

$$\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{k}, \quad (15.3)$$

where \mathbf{A}^{-1} is the inverse of the $n \times n$ community matrix \mathbf{A} .

Problem: Show that Eq. (15.3), with $a_{ij} = -r_i\alpha_{ij}/K_i$ and $k_i = r_i$ is equivalent to the expression used in Chapter 14, $\mathbf{N}^* = \mathbf{A}^{-1}\mathbf{k}$, where now $a_{ij} = \alpha_{ij}$ and $k_i = K_i$.

Predator–prey systems with linear zero-isoclines also fit the form of the generalized Lotka–Volterra equations (see Chapters 12 and 13). Here are the coupled equations from Chapter 13 where the prey, V , grows logistically and the predator, P , has a type 1 functional response:

$$\frac{dV}{Vdt} = \frac{r}{K}(K - V) - aP \quad \text{and} \quad \frac{dP}{Pdt} = -d + kaV,$$

where a is the encounter rate with prey, d is the per capita death rate of the predator, and k is the predator's conversion efficiency. This model may be arranged into the generalized Lotka–Volterra matrix form as

$$\begin{bmatrix} \frac{dV}{Vdt} \\ \frac{dP}{Pdt} \end{bmatrix} = \begin{bmatrix} r \\ -d \end{bmatrix} + \begin{bmatrix} -r & -a \\ K & 0 \end{bmatrix} \begin{bmatrix} V \\ P \end{bmatrix}. \quad (15.4)$$

The community matrix \mathbf{A} is

$$\mathbf{A} = \begin{bmatrix} -r & -a \\ K & 0 \end{bmatrix}$$

and that the vector of constants \mathbf{k} is

$$\mathbf{k} = \begin{bmatrix} r \\ -d \end{bmatrix}.$$

Problem: Algebraically solve for the equilibrium values P^* and V^* in Eq. (15.4), using Cramer's rule (see Appendix 3).

A number of extensions are possible with this basic framework. The predator–prey system may be modified to allow for additional interspecific interactions. For example, if two prey species compete directly with one another, the terms become

$$\mathbf{A} = \begin{bmatrix} -r_1 & -r_1\alpha_{12} & -a_1 \\ \frac{-r_1}{K_1} & \frac{-r_1\alpha_{12}}{K_1} & -a_1 \\ \frac{-r_2\alpha_{21}}{K_2} & \frac{-r_2}{K_2} & -a_2 \\ kw_1a_1 & kw_2a_2 & 0 \end{bmatrix} \quad \text{and} \quad \mathbf{k} = \begin{bmatrix} r_1 \\ r_2 \\ -d \end{bmatrix}. \quad (15.5)$$

Direct interspecific competition between the two prey species is described by α_{12} and α_{21} . We also slipped a new parameter into Eq. (15.5): w_j , which weights the different prey according to their importance to predator growth. One prey may be bigger or more nutritious than another. An assumption here is that these weights depend only on prey type, not predators. At the end of this chapter, we explore some surprising dynamics that emerge from this simple two-prey, one-predator model.

The GLV description can be generalized further by using the machinery of matrix math to include n prey species and m different predators. The growth vector for each species can be partitioned into two subvectors, one for the prey species and one for the predator species.

$$\begin{bmatrix} \frac{dV_1}{V_1 dt} \\ \frac{dV_2}{V_2 dt} \\ \vdots \\ \frac{dV_n}{V_n dt} \\ \frac{dP_1}{P_1 dt} \\ \frac{dP_2}{P_2 dt} \\ \vdots \\ \frac{dP_m}{P_m dt} \end{bmatrix} = \begin{bmatrix} \frac{d\mathbf{V}}{\mathbf{V} dt} \\ \frac{d\mathbf{P}}{\mathbf{P} dt} \end{bmatrix}.$$

With this notation, we have

$$\begin{bmatrix} \frac{d\mathbf{V}}{\mathbf{V} dt} \\ \frac{d\mathbf{P}}{\mathbf{P} dt} \end{bmatrix} = \begin{bmatrix} \mathbf{r} \\ -\mathbf{d} \end{bmatrix} + \begin{bmatrix} -\mathbf{r}\alpha & -\mathbf{a} \\ \mathbf{K} & \mathbf{0} \end{bmatrix} \begin{bmatrix} \mathbf{V} \\ \mathbf{P} \end{bmatrix}, \quad (15.6)$$

where \mathbf{V} is an $n \times 1$ vector containing V_1, V_2, \dots, V_n and \mathbf{P} is an $m \times 1$ vector containing P_1, P_2, \dots, P_m . Similarly the vector \mathbf{k} is composed of two subvectors: \mathbf{r} is an $n \times 1$ vector holding the r_i term of each prey species, V_i , and $-\mathbf{d}$ is an $m \times 1$ vector

holding the death rates, d_i , for each predator, P_i . The entire community matrix \mathbf{A} has dimensions of $(n + m \times n + m)$. It has four blocks, of which the top-left block is

$$\frac{-\mathbf{r}\alpha}{\mathbf{K}} = \begin{bmatrix} \frac{-r_1}{K_1} & \frac{-r_1\alpha_{12}}{K_1} & \cdots & \frac{-r_1\alpha_{1n}}{K_1} \\ \frac{-r_2\alpha_{21}}{K_2} & \frac{-r_2}{K_2} & \vdots & \frac{-r_2\alpha_{2n}}{K_2} \\ \vdots & \vdots & \vdots & \vdots \\ \frac{-r_n\alpha_{n1}}{K_n} & \frac{-r_n\alpha_{n2}}{K_n} & \vdots & \frac{-r_n}{K_n} \end{bmatrix}.$$

This block describes the interactions among the n different prey. Therefore it is $n \times n$, and both subscripts refer to prey species. The top-right block is

$$-\mathbf{a} = \begin{bmatrix} -a_{11} & -a_{12} & \cdots & -a_{1m} \\ -a_{21} & -a_{22} & \vdots & -a_{2m} \\ \vdots & \vdots & \vdots & \vdots \\ -a_{n1} & -a_{n2} & \vdots & -a_{nm} \end{bmatrix}. \quad (15.7)$$

Block $-\mathbf{a}$ describes the effects of each of the m predators on each of the n prey species. This block has dimension $n \times m$, where the first subscript is a prey species and the second subscript is a predator. If any two columns of this block are identical or are simple multiples of one another (i.e., two consumers utilize the resources in exactly the same relative proportions) or if there are more predator species than prey species (i.e., $n < m$), then the community matrix \mathbf{A} will have a zero determinant and therefore the inverse \mathbf{A}^{-1} will not exist. In this case, there can be no stable feasible equilibrium involving all the species.

The lower-left block is

$$\mathbf{k}\mathbf{a}^T\mathbf{w} = \begin{bmatrix} k_1 & 0 & \cdots & 0 \\ 0 & k_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & 0 \\ 0 & 0 & \cdots & k_m \end{bmatrix} \begin{bmatrix} a_{11} & a_{21} & \cdots & a_{n1} \\ a_{12} & a_{22} & \vdots & a_{n2} \\ \vdots & \vdots & \vdots & \vdots \\ a_{1m} & a_{2m} & \vdots & a_{nm} \end{bmatrix} \begin{bmatrix} w_1 & 0 & \cdots & 0 \\ 0 & w_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & 0 \\ 0 & 0 & \cdots & w_n \end{bmatrix}, \quad (15.8)$$

and its dimensions are

$$m \times n = (m \times m) \times (m \times n) \times (n \times n).$$

The $\mathbf{k}\mathbf{a}^T\mathbf{w}$ block describes the effects of each of the n prey on each of the m predators' growth rate. As shown, it is the product of three matrices: the first matrix gives the conversion rates, k_i , for each predator, $m \times m$; and the second matrix gives the consumption rates of each prey by each predator, $m \times n$, and is simply the transpose of the $-\mathbf{a}$ matrix but in positive form, since prey benefit predators. The first subscript refers to a specific predator and the second subscript to a particular prey. The different weights for each resource are contained in the diagonal matrix \mathbf{w} on the right, $n \times n$. As usual with matrix arithmetic, the order of multiplication is important.

Problem: Verify that the matrix multiplication given by Eq. (15.8) produces a term for prey i and predator j that exactly matches that in Eq. (15.5), or $k_j w_i a_{ij}$.

The fourth and final submatrix lies in the bottom-right corner. It is an $m \times m$ matrix of zeros describing the direct interactions of predators on predators:

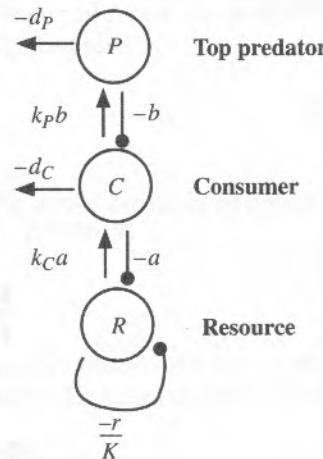
$$\mathbf{0} = \begin{bmatrix} 0 & 0 & \cdots & 0 \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 \end{bmatrix}. \quad (15.9)$$

Naturally, if predators directly interfered with each other, then this block would contain negative terms describing those interference rates, which we labeled f_i in Chapter 12. With such interference, the $\mathbf{0}$ submatrix would become an \mathbf{F} submatrix, where f_{ij} is the direct per capita effect of predator j on predator i 's per capita growth rate.

We discuss some results for a two-prey, one-predator version of Eq. (15.6) at the end of this chapter.

Three Trophic Levels

An extension of the generalized Lotka–Volterra equations to describe interactions among three species, each at a different trophic level, is described by the following diagram.



The dynamic equations are as follows.

$$\text{Predators: } \frac{dP}{P dt} = k_P b C - d_P.$$

$$\text{Consumers: } \frac{dC}{C dt} = k_C a R - d_C - b P.$$

$$\text{Resources: } \frac{dR}{R dt} = \frac{r}{K} (K - R) - a C.$$

Both consumers and predators experience some density independent mortality ($-d_C$ and $-d_P$), and resources and consumers have mortality due to consumption by a higher trophic level. These equations may be cast in matrix form as

$$\begin{bmatrix} \frac{dR}{R dt} \\ \frac{dC}{C dt} \\ \frac{dP}{P dt} \end{bmatrix} = \begin{bmatrix} r \\ -d_C \\ -d_P \end{bmatrix} + \begin{bmatrix} -\frac{r}{K} & -a & 0 \\ k_C a & 0 & -b \\ 0 & k_P b & 0 \end{bmatrix} \begin{bmatrix} R \\ C \\ P \end{bmatrix}. \quad (15.10)$$

The zero-isosurfaces for this system are shown in Figure 15.1.

Figure 15.1

The zero-isosurfaces for the three trophic level system of Eq. (15.10).

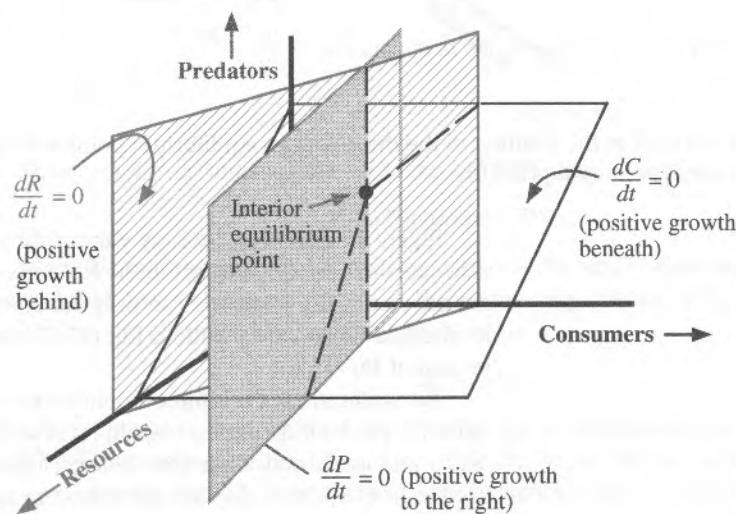
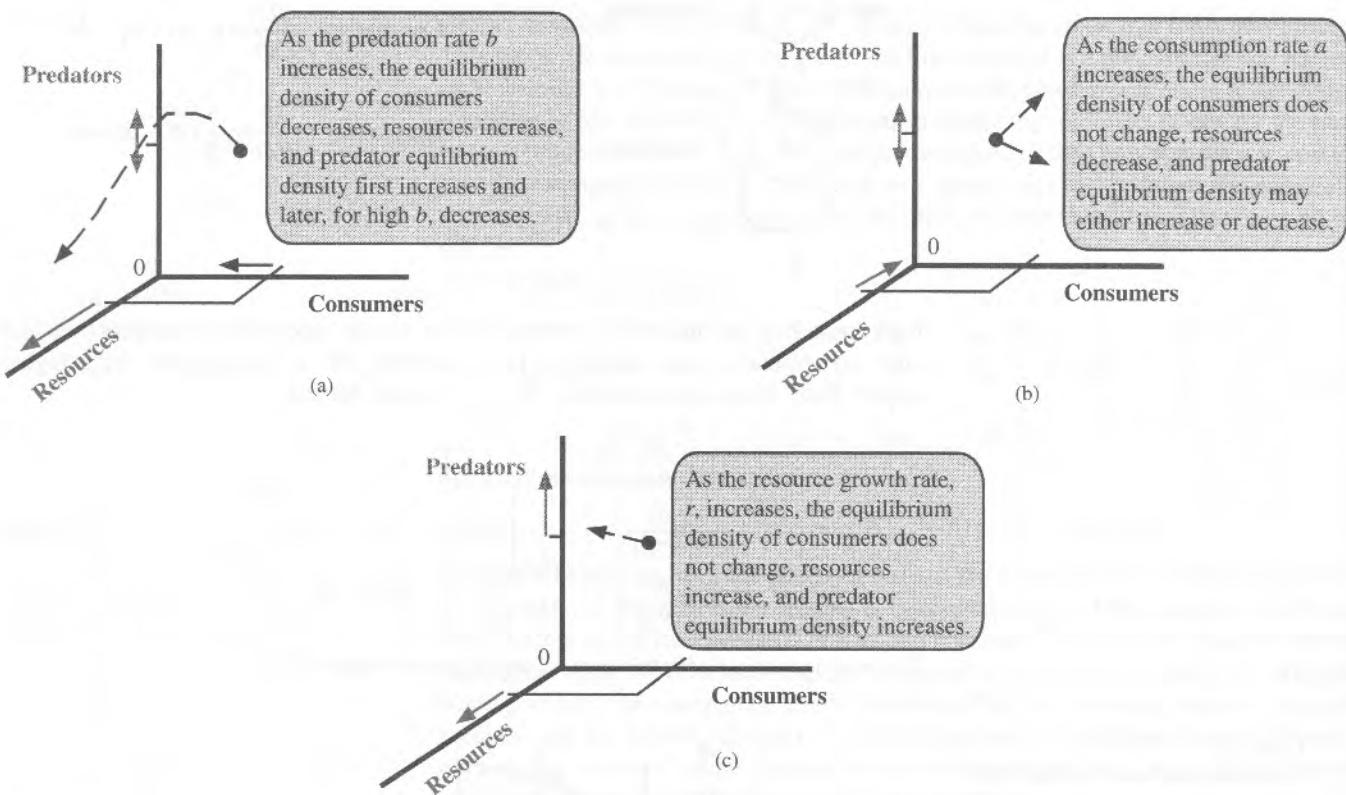
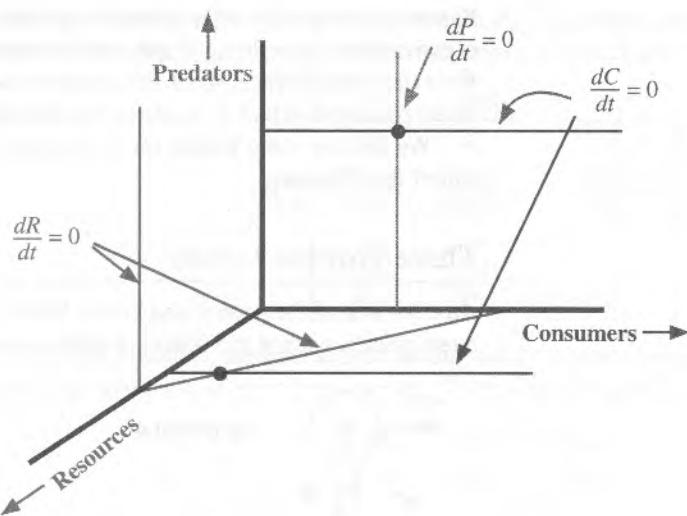


Figure 15.2

A cutaway view of Figure 15.1, showing the location of the boundary equilibria on each two-species phase plane.

**Figure 15.3**

The arrows indicate the shift in the position of the three-species equilibrium point with qualitative changes in some of the parameters of the model given by Eq (15.10).

Figure 15.2 shows a cutaway view of the various boundary equilibria. Note that the zero-isoclines do not intersect in the Resource–Predator orthant because predators cannot eat resources; predators can only eat consumers. Multiple species at each trophic level could be added by putting Eq. (15.10) into block form like the two-trophic-level system of Eq (15.6).

An exploration of this three-trophic-level system is shown in Figure 15.3. The addition of a predator as a third trophic level will always result in greater resource abundance and lower consumer abundance. However, more complicated models of three-trophic-level systems may not have these same features, depending on the presence of self-damping and interference at higher trophic levels (Rosenzweig 1973).

STABILITY EVALUATION (ADVANCED)

For any generalized Lotka–Volterra system, the interior equilibrium point is found by applying Eq. (15.3),

$$\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{k}.$$

Depending on the actual terms in \mathbf{A} and \mathbf{k} , this equilibrium point may not be feasible (i.e., $N_i^* < 0$ for some i), but assuming that it is feasible, the next step is to evaluate its local stability. The stability of this interior equilibrium is evaluated by forming the Jacobian matrix, \mathbf{J} (Chapters 13 and 14). The Jacobian matrix contains the partial derivatives of the growth equations with respect to each variable (species). The form of the Jacobian matrix for GLV systems is a straightforward extension of that developed in Chapter 14 for LV competition communities. From Eq. (15.1a), the growth equation for the i th species is

$$\frac{dN_i}{dt} = N_i \left(k_i + \sum_{j=1}^n a_{ij} N_j \right).$$

The partial derivative of dN_i/dt with respect to N_j (for $j \neq i$) is therefore just

$$\frac{\partial \frac{dN_i}{dt}}{\partial N_j} = a_{ij} N_i, \quad (15.11)$$

and this partial derivative evaluated at the equilibrium point \mathbf{N}^* is simply $a_{ij}N_i^*$. The partial derivative of dN_i/dt with respect to its own density, N_i , is

$$\frac{\partial \frac{dN_i}{dt}}{\partial N_i} = k_i + 2a_{ii}N_i + \sum_{\substack{j=1 \\ j \neq i}}^n a_{ij}N_j. \quad (15.12)$$

At equilibrium,

$$k_i = -\sum_{j=1}^n a_{ij}N_j^*. \quad (15.13)$$

When we substitute Eq. (15.13) into Eq. (15.12), we note that the sum on the right-hand side of Eq. (15.13) is over all species, including species i , but that the sum on the right-hand side of Eq. (15.12) excludes species i . Hence we can cancel k_i with the sum in Eq. (15.12) only if we also cancel an $a_{ii}N_i$ term. Thus Eq. (15.12) becomes

$$\begin{aligned} \frac{\partial \frac{dN_i}{dt}}{\partial N_i} &\quad (\text{evaluated at } \mathbf{N}^*) = (2a_{ii}N_i^* - a_{ii}N_i^*) \\ &= a_{ii}N_i^*. \end{aligned} \quad (15.14)$$

Thus for GLV systems we can write the Jacobian matrix, \mathbf{J} , as

$$\mathbf{J}(\text{interior}) = \mathbf{D}^*\mathbf{A}, \quad (15.15)$$

where \mathbf{D}^* is a square diagonal matrix containing the equilibrium densities on the diagonal and zeros elsewhere and \mathbf{A} is the community matrix of Eq. (15.1). From Eq. (15.15), the elements of \mathbf{J} will have the form

$$J_{ij} = N_i^* a_{ij}. \quad (15.16)$$

This is consistent with what we found earlier for the diagonal elements (Eqs. 15.11 and 15.14). For example, for LV competition the terms in the community matrix are $a_{ij} = -r_i \alpha_{ij}/K_i$ (Eq. 15.2), so the terms of $\mathbf{J}(\text{interior})$ are $J_{ij} = -N_i^* r_i \alpha_{ij}/K_i$. (Verify that this is the same result we reached in Chapter 14, using a somewhat different approach.)

The eigenvalues of $\mathbf{J}(\text{interior})$ are indicative of the local stability of the interior equilibrium point \mathbf{N}^* ; this equilibrium point is locally stable if and only if all the eigenvalues of $\mathbf{J}(\text{interior})$ have negative real parts.

Problem: Form the Jacobian matrix for the predator–prey system described by Eq. (15.4).

All that you learned about stability evaluation in Chapters 13 and 14, applies directly to any generalized Lotka–Volterra system. The elements of the community matrix, \mathbf{A} , may have different signs, depending on the type of direct interaction between each pair of species. If predator j eats prey species i , then $a_{ij} < 0$ and $a_{ji} > 0$. If the two species are mutualists, $a_{ij} > 0$ and $a_{ji} > 0$. Finally, two species that do not have any direct interactions will have $a_{ij} = a_{ji} = 0$.

Exercise: Can you think of any biologically realistic cases where $a_{ji} > 0$ but $a_{ij} = 0$? Can you think of any biologically realistic cases where $a_{ji} < 0$ but $a_{ij} = 0$?

Exercise: Show that, for Lotka–Volterra competition, Eq. (15.15) is equivalent to Eq. (14.13), that is, $\mathbf{J}(\text{interior}) = \mathbf{D} \alpha$.

Exercise: Form the Jacobian matrix to evaluate the stability of the interior equilibrium point for the three-trophic-level system of Eq (15.8). Algebraically solve for the equilibrium values of R , C , and P and use them to form the \mathbf{D}^* needed to evaluate the Jacobian matrix of Eq. (15.15).

NON-GLV SYSTEMS WILL BEHAVE AS GLV SYSTEMS IN A SMALL NEIGHBORHOOD AROUND AN EQUILIBRIUM

As we have demonstrated in Chapters 12 and 13, many predator–prey systems will not have linear zero-isoclines and thus cannot be cast in the framework of GLV. This is the case when predators have type 2 or 3 functional responses, when prey or predator recruitment comes, in part, from outside the system (open populations), or when species have Allee effects, refuges, or higher-order interference terms. For such systems, linear algebra cannot be used to solve for the equilibrium point. Some systems of nonlinear equations may still have analytical solutions for the equilibrium point, but others may not, typically forcing us to apply iterative numerical methods to find the equilibrium point(s).

Once an equilibrium point is found in a non-GLV system, its stability can be evaluated by making a linear approximation to the original dynamical equations using a Taylor's expansion (Chapters 5 and 13). In this way, a linear GLV system resembling Eq. (15.1) can still be formed, but these dynamics apply only to small perturbations in densities, n_i , around the focal equilibrium point, \mathbf{N}^* . These perturbations are given by $n_i = N_i - N_i^*$, and over time the perturbation amount n_i changes approximately as

$$\frac{dn_i}{dt} = \sum_{j=1}^n J_{ij} n_j,$$

or in matrix form as

$$\frac{d\mathbf{n}}{dt} = \mathbf{J} \mathbf{n}. \quad (15.17)$$

The J_{ij} are the partial derivative terms in the Jacobian matrix. As before, these partial derivatives are evaluated at the equilibrium point of interest, \mathbf{N}^* . The stability of the equilibrium point is assessed as before, by determining the sign of the real parts of the eigenvalues of \mathbf{J} . The only difference is that the Jacobian matrix for an interior equilibrium point in a GLV system had a particularly simple form given by Eq. (15.15) that did not require much mathematical manipulation to produce, whereas for non-GLV equations, it can be tedious indeed to find \mathbf{N}^* to calculate all the partial derivatives that go into \mathbf{J} and to evaluate them at \mathbf{N}^* . In the next section we illustrate a simple example, using a slightly new twist on the old predator-prey model introduced in Chapter 13.

One Prey with Two Age Groups and a Predator That Eats Only Young Prey

In Chapter 13 we introduced the classical Lotka–Volterra predator-prey equations in which neither the prey nor the predator population is self-damped. This model produces neutrally stable cycles around the interior equilibrium point. The amplitude and period of the cycles is determined, in part, by the initial conditions. The cycles become larger and longer as the system is initialized farther from the equilibrium point. Only if the predator and prey are initialized precisely at the equilibrium point does the cycling disappear. We now modify this model to incorporate a simple age structure in the prey population. This modification should reinforce the notion that the state variables in predator-prey systems need not always be restricted to “species.” Also we show that this simple modification drastically alters the nature of the dynamics. In this model, only the young of the prey are susceptible to predation. The model is shown in Figure 15.4.

Notice that this model cannot be put into the form of a GLV because the per capita equations for young and adults are nonlinear. Nevertheless, it is quite easy to

Figure 15.4

A predator-prey model with simple age structure in the prey.

The prey, P , are subdivided into young, Y , which are subject to predation, and adults, A , which are not

$\frac{dY}{dt} = bA - cPY - \gamma Y.$
The change in $=$ the births minus deaths minus losses due the number of from adults from predators to the aging young from adults with capture rate of young into adults.
$\frac{dA}{dt} = \gamma Y - d_A A.$
The change in $=$ the number minus the mortality of the number of young turning adults (not of adults into adults density dependent).

For the Predator, P ,

$$\frac{dP}{dt} = kcYP - dpP.$$

The change in the number of predators $=$ the birth rate of predators, which is proportional to the number of young prey eaten, minus a density independent mortality term.

solve algebraically for the equilibrium point. Setting all three equations equal to zero, from the predator equation we have

$$Y^* = \frac{d_P}{kc}. \quad (15.18)$$

Plugging this expression for Y^* into the growth equation for adults, we find that

$$A^* = \frac{\gamma d_P}{kcd_A}. \quad (15.19)$$

Finally, putting the solutions for A^* and Y^* into the equation for young gives the predators' equilibrium abundance as

$$P^* = \frac{\gamma}{c} \left(\frac{b}{d_A} - 1 \right). \quad (15.20)$$

The next step is to form the Jacobian matrix to explore the dynamics of perturbations around the equilibrium point. We use the lowercase symbols y , a , and p to denote the perturbation amounts from the interior equilibrium point (Y^*, A^*, P^*) . The first-order Taylor's expansion for the dynamics of these perturbation amounts is given by Eq. (15.17), which for this case is

$$\begin{bmatrix} \frac{dy}{dt} \\ \frac{da}{dt} \\ \frac{dp}{dt} \end{bmatrix} = \begin{bmatrix} \frac{\partial \left(\frac{dY}{dt} \right)}{\partial Y} & \frac{\partial \left(\frac{dY}{dt} \right)}{\partial A} & \frac{\partial \left(\frac{dY}{dt} \right)}{\partial P} \\ \frac{\partial \left(\frac{dA}{dt} \right)}{\partial Y} & \frac{\partial \left(\frac{dA}{dt} \right)}{\partial A} & \frac{\partial \left(\frac{dA}{dt} \right)}{\partial P} \\ \frac{\partial \left(\frac{dP}{dt} \right)}{\partial Y} & \frac{\partial \left(\frac{dP}{dt} \right)}{\partial A} & \frac{\partial \left(\frac{dP}{dt} \right)}{\partial P} \end{bmatrix} \begin{bmatrix} y \\ a \\ p \end{bmatrix}.$$

After evaluating these partial derivatives for the model shown in Figure 15.4, we reach

$$\mathbf{J} = \begin{bmatrix} -cP - \gamma & b & -cY \\ \gamma & -d_A & 0 \\ kcP & 0 & kcY - d_P \end{bmatrix}. \quad (15.21)$$

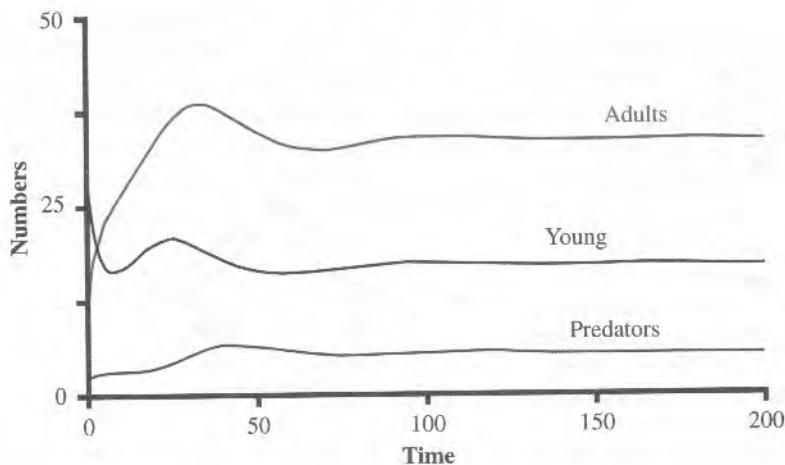
The next step is to evaluate these partial derivatives at the interior equilibrium point ($Y = Y^*$, $A = A^*$, $P = P^*$) as given by Eqs. (15.18)–(15.20). This gets a bit messy. However, even without going through the algebra, you can see that this matrix does not have zero elements on the diagonal as does the Jacobian of the classical LV predator-prey model. Although it is probably not immediately apparent, the eigenvalues of this Jacobian matrix always have negative real parts as long as the interior equilibrium is feasible.

Problem: Can you duplicate each of the partial derivatives in Eq. (15.21)?

In summary, the addition of a simple age structure to the prey population combined with differential vulnerability of these ages to predation causes the neutral stability of the classical Lotka–Volterra predation to be replaced by true stability. Fig 15.5 shows a typical time series.

Figure 15.5

The results of this predator-prey model when $b = 0.2$, $d_A = 0.1$, $\gamma = 0.2$, $d_P = 0.2$, $k = 0.3$, and $c = 0.04$. Any feasible interior equilibrium will be stable.



INDIRECT EFFECTS IN MULTISPECIES SYSTEMS

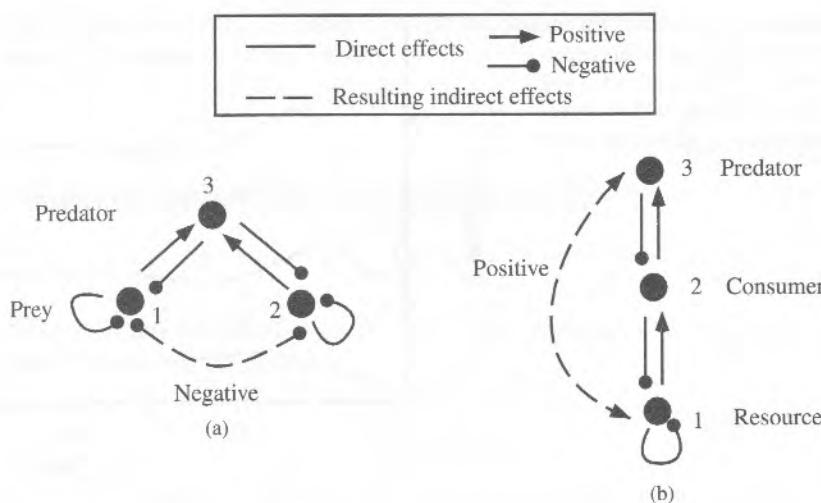
Note in the two-trophic-level model given by Eq. (15.6) that several consumer species are eating several different prey species. The **direct effects** between the predators, in the lower right-hand corner of \mathbf{A} , were set to zero. Nevertheless, these different predators are exploitative competitors with one another to the extent that they share these limiting resources. These predators negatively affect the growth of one another through their effects on resource levels. This represents a subtle shift in modeling compared to our previous exploration of the Lotka-Volterra competition equations. There we considered two consumer species as competitors when α_{ij} and α_{ji} were greater than 0. By explicitly considering resource dynamics, we can show that two consumers, i and j , can still be exploitative competitors even though $a_{ij} = a_{ji} = 0$; the exploitation competition emerges as an indirect effect through their mutual exploitation of the same resources. **Indirect effects** are effects between two species mediated wholly in terms of changing population densities of intermediary species (Holt 1977, Bender et al. 1984, Roughgarden and Diamond 1986, Schoener 1993). Indirect effects pass from one species to another via the density changes in one or more intermediary species in the food chain. A colorful example of an indirect effect was offered by Charles Darwin in the *Origin of Species*, where he wrote concerning humblebees (an old name for bumblebees):

Humblebees alone visit red clover (*Trifolium pratense*), as other bees cannot reach their nectar. . . . The number of humblebees in any district depends in a great degree on the number of field-mice, which destroy their combs and nests. . . . Now the number of field mice is largely dependent, as every one knows, on the number of cats. . . . Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!

Indirect effects are also referred to as **interaction chains** (Wootton 1992). Different interaction chains in communities can produce different types of indirect effects between species. Figure 15.6 illustrates these effects for some simple multispecies communities. In Figure 15.6(a), two species that share the same predator, but otherwise have no direct interaction, may nevertheless negatively affect each others' density. As one prey increases, the predator's numbers may, in turn, increase. This increase in the predator, in turn, causes a decline in the density of the other prey species, and vice-versa. This type of indirect interaction is called **apparent competition** to distinguish it from true competition where the prey directly affect each other or compete for shared resources (Holt 1977).

Figure 15.6

Two simple food webs, showing direct and indirect effects. (a) Apparent competition between two noninteracting prey that share a common predator (or parasite). (b) Species 1 and 3 are indirect mutualists. The arrows on the direct effects (solid lines) pointing to a consumer indicate a positive effect flowing to the consumer; a negative effect occurs in the opposite direction on the prey. The sign of the indirect effect between a species pair (dashed line) may be positive or negative. For these two examples, the sign is the same in both directions.



It is possible to evaluate the sign of an indirect interaction between two species by multiplying the elements of the community matrix connecting the species through an interaction chain. If this product is negative, the indirect effect between this species pair is negative; if it is positive, the two species are indirect mutualists, as shown in Figure 15.6(b). Apparent competition, as shown in Figure 15.6(a), has a community matrix with a sign structure as follows:

$$\begin{matrix} & V_1 & V_2 & P \\ V_1 & - & 0 & - \\ V_2 & 0 & - & - \\ P & + & + & 0 \end{matrix} \quad (15.22)$$

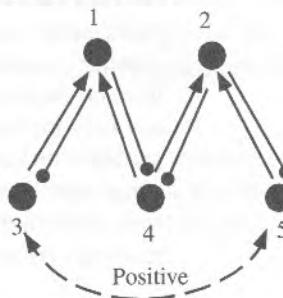
Here we read the direct effect of the species in the column headings on the species in each row; for example, the direct effect of the predator on prey 1 is given in the first row, third column, as negative. To determine the sign of the indirect effect of prey 1 on prey 2 through the predator, we multiply the effect of prey 1 on the predator times the effect of the predator on prey 2. This gives $(a_{P1})(a_{2P}) = (+)(-) = (-)$. Thus prey 1 indirectly harms prey 2 through its positive effect on predator numbers.

For the three-trophic-level system (Figure 15.6b), we have

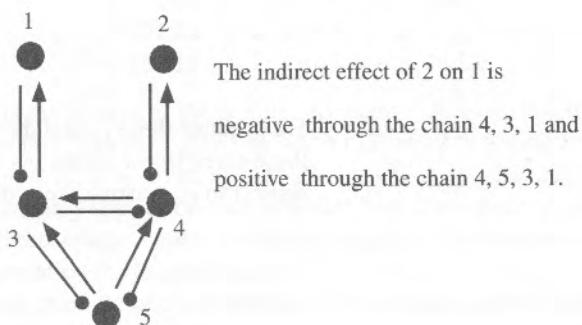
$$\begin{matrix} & 1 & 2 & 3 \\ 1 & - & - & 0 \\ 2 & + & 0 & - \\ 3 & 0 & + & 0 \end{matrix}$$

The indirect effect of species 1 on 3 through species 2 is $(a_{21})(a_{32}) = (+)(+) = (+)$. Thus species 1 indirectly benefits species 3 through its positive effect on species 2's numbers.

Exercise: Show for the following diagram that the indirect effect of species 3 on species 5 is positive and that the indirect effect of species 5 on species 3 is positive. Species 3 and 5 are indirect mutualists



For complicated food webs with more than three species, several different interaction chains may connect a given pair of species through different other species. We may calculate the indirect effect of each possible path (i.e., interaction chain) as before. The total effect across all possible paths may be undetermined unless more detailed quantitative information about the relative strength of interactions in the different chains is available. (We deal with this issue in the next section.) For example, consider the following food web.



The necessary information can be determined, however, from all the strengths of the pairwise interactions in the community matrix, \mathbf{A} , assuming, of course, that they are available.

The Inverse of the Community Matrix

The total effect of one species on another (direct plus indirect) can be measured by determining how that species responds to additions of the other. Consider this three-species example where the Press perturbation (see the next section) involves a continuous addition of species 2 at a rate I_2 . If this was a removal experiment, then I_2 would be a negative quantity:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1 \left(k_1 + \sum_{j=1}^n a_{1j} N_j \right); \\ \frac{dN_2}{dt} &= N_2 \left(k_2 + \sum_{j=1}^n a_{2j} N_j \right) + I_2; \\ \frac{dN_3}{dt} &= N_3 \left(k_3 + \sum_{j=1}^n a_{3j} N_j \right).\end{aligned}$$

This system will come to equilibrium with some new densities for all species. These equilibrium densities, N_i^* , will be functions of the experimental perturbation I_2 . At equilibrium, we may write

$$\begin{aligned}0 &= k_1 + \sum_{j=1}^n a_{1j} N_j^*(I_2); \\ 0 &= k_2 + \sum_{j=1}^n a_{2j} N_j^*(I_2) + I_2; \\ 0 &= k_3 + \sum_{j=1}^n a_{3j} N_j^*(I_2).\end{aligned}$$

Next, we differentiate these equations with respect to I_2 , which is a value manipulated by the experimenter:

$$0 = \sum_{j=1}^n a_{1j} \frac{\partial N_j^*(I_2)}{\partial I_2};$$

$$0 = \sum_{j=1}^n a_{2j} \frac{\partial N_j^*(I_2)}{\partial I_2} + 1;$$

$$0 = \sum_{j=1}^n a_{3j} \frac{\partial N_j^*(I_2)}{\partial I_2}.$$

We evaluate these partial derivatives at the equilibrium point (N_1^*, N_2^*, N_3^*) . We solve these three linear equations in the three unknowns—the three partial derivatives with respect to I_2 . Casting these three equations in matrix form, we get

$$-\begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix} = \mathbf{A} \begin{bmatrix} \frac{\partial N_1^*(I_2)}{\partial I_2} \\ \frac{\partial N_2^*(I_2)}{\partial I_2} \\ \frac{\partial N_3^*(I_2)}{\partial I_2} \end{bmatrix},$$

which means that

$$\begin{bmatrix} \frac{\partial N_1^*(I_2)}{\partial I_2} \\ \frac{\partial N_2^*(I_2)}{\partial I_2} \\ \frac{\partial N_3^*(I_2)}{\partial I_2} \end{bmatrix} = -\mathbf{A}^{-1} \begin{bmatrix} 0 \\ 1 \\ 0 \end{bmatrix}. \quad (15.23)$$

This assumes that matrix \mathbf{A} has a nonzero determinant; otherwise, the inverse of \mathbf{A} does not exist. If the new equilibrium point is stable, then \mathbf{A} must have an inverse. Equation (15.23) says that the effect of adding individuals of species 2 on species i 's new resulting equilibrium density is given by

$$\frac{\partial N_i^*(I_2)}{\partial I_2} = -(a_{i2})^{-1},$$

where $(a_{i2})^{-1}$ is the element in position $(i, 2)$ of the inverse of the interaction matrix \mathbf{A}^{-1} . (Note: This is not the same as $1/a_{i2}$.) More generally, we could perturb any species j and look at the resulting response on the equilibrium densities of any other species i :

$$\frac{\partial N_i^*(I_j)}{\partial I_j} = -(a_{ij})^{-1}. \quad (15.24)$$

In this way the elements of the inverse of the community matrix, *following a sign reversal*, give the total effect (direct plus indirect effect) of one species on another within the context of the entire community. In other words, if $(a_{ij})^{-1} > 0$, then $-(a_{ij})^{-1} < 0$, with the interpretation that the total effect of species j on species i is negative.

Let's now reexamine one of the examples presented earlier, namely, the case of apparent competition in Figure 15.6(a). We use Matlab® to enter a community matrix with the sign structure shown in Eq. (15.22). (Boldface type denotes our input, and the computer prints out the rest.)

```
EDU>> A = [-.2 0 -.3;
               0 -.2 -.4;
               .2 .3 0]
```

A =

$$\begin{matrix} -0.2000 & 0 & -0.3000 \\ 0 & -0.2000 & -0.4000 \\ 0.2000 & 0.3000 & 0 \end{matrix}$$

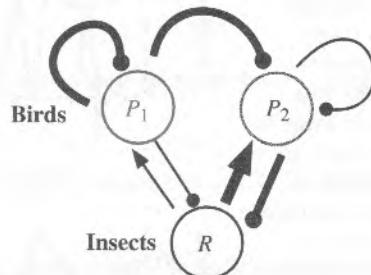
EDU>> inv(A)

ans =

$$\begin{matrix} -3.3333 & 2.5000 & 1.6667 \\ 2.2222 & -1.6667 & 2.2222 \\ -1.1111 & -1.6667 & -1.1111 \end{matrix}$$

This last matrix is the inverse of the community matrix, A. Note that the total effect of prey species 2 on prey species 1 given by $-A^{-1}(1, 2)$ is -2.5. Similarly, the total effect of species 1 on species 2 is given by $-A^{-1}(2, 1)$, which is -2.2222. Since the direct effects of these two prey species on each other are both zero, these total effects are simply due to the indirect effects—each of which is negative. This matches our earlier more qualitative interpretation for this community.

An interesting example of the importance of an indirect effect in pest control was provided by a study of birds feeding on larval insects on Eucalyptus trees in Australia (Loyn et al. 1983). One bird species, the bell miner, was extremely aggressive both intra- and interspecifically. It effectively kept many other birds from foraging in the trees. Since the bell miner spent so much time in territorial pursuits, its foraging rate on larval insects was lower than that of other less aggressive birds. The following diagram captures this situation (the thickness of the lines is roughly proportional to the strength of interaction). Here P_1 are the bell miners, P_2 are other insectivorous birds, and the larval insects are the resources, R .



A community matrix qualitatively consistent with this arrangement is

$$\begin{matrix} & R & P_1 & P_2 \\ R & \begin{bmatrix} 0 & -0.02 & -0.05 \\ 0.002 & -0.04 & 0 \\ 0.005 & -0.1 & -0.02 \end{bmatrix} \end{matrix} \quad (15.25)$$

Using Matlab® to take the inverse of this matrix, we get

EDU>> inv(A)

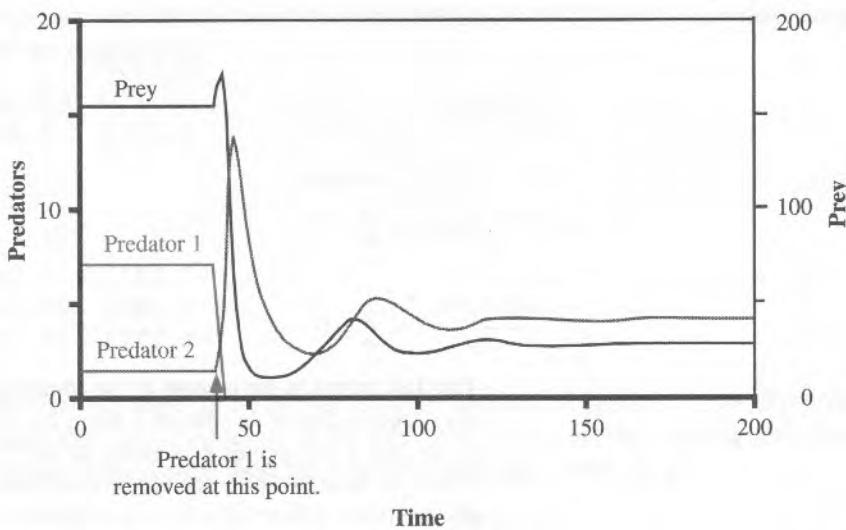
ans =

$$\begin{matrix} -1000.0 & -5750.0 & 2500.0 \\ -50.0 & -312.5 & 125.0 \\ 0000.0 & 125.0 & -50.0 \end{matrix}$$

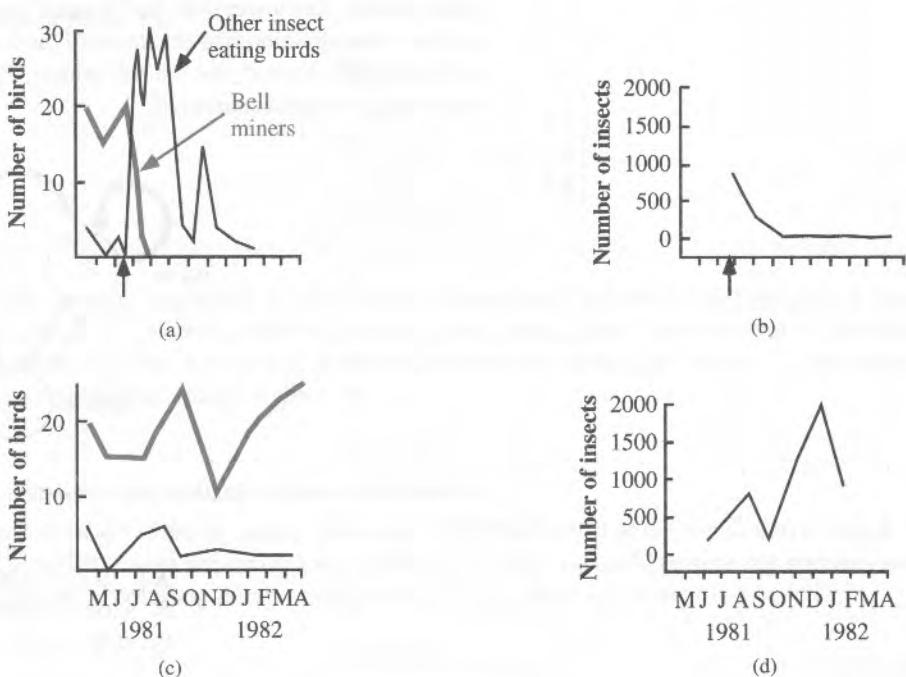
You can see that the total effect of the bell miners, P_1 , on insects, R , is positive, even though they eat these insects, since the $A^{-1}(1, 2)$ element of the inverse of A is negative (-5750). According to this model, the removal of bell miners should increase the number of other birds while decreasing the numbers of insects. A simulation of this model, shown in Figure 15.7, quantifies this prediction.

Figure 15.7

A simulation of the bird/insect model. Prior to removal of the highly aggressive predator 1 (bell miners), they outnumber predator 2 (other insectivorous birds), and prey numbers are relatively high at equilibrium. The removal of predator 1 at time 40 leads to an increase in the number of predator 2 and a decrease in the number of prey (insects) at the new equilibrium. Note, however, that the prey's initial trend was briefly upward, following the removal. This reflects the negative direct effect of predator 1 on prey. Later, this direct effect is overwhelmed by the indirect effect as predator 2 increases, causing insect numbers to collapse. This model is based on Eq. (15.6) with community matrix A given in Eq. 15.25; other parameters are $r = 0.2$, $d_1 = 0.03$, and $d_2 = 0.05$.

**Figure 15.8**

Birds and insects in two eucalyptus groves. (a) and (b) Bell miners were experimentally removed from the experimental plots on the date indicated by the arrows. (c) and (d) Control plots also with high insect numbers but no bell miner removal. The groves were about 3 ha in area. Insects were primarily leps (a stage of a homopteran life history), which were sampled in trays on the forest floor. Numbers represent the mean number of leps per tray and the number of birds per site. After Loyn et al. (1983).



Loyn et al. (1983), in fact, undertook an experimental removal of bell miners. The results were broadly consistent with the model's prediction, as shown in Figure 15.8. Following the bell miner's experimental removal, insect numbers in the trees decreased as other birds moved into the now vacant territories to feed on them. In control plots, the other birds stayed at low numbers while insect numbers remained high. Case et al. (1979) and Holt and Polis (1997) generalized this phenomenon of joint resource exploitation and interference by using multispecies predator-prey models. Interference competition among the dominant predators can keep resources from being effectively exploited, with the result that the total numbers of all predators (summed over species) is not as high as it would be if the those predators with the higher interference rates were removed.

Press Experiments

Often it will be difficult experimentally to maintain and measure the I_j terms of Eq. (15.23). However, it will be relatively easy to set the perturbed species at some new equilibrium level (say, zero) by constantly removing all individuals of species j or excluding their entry. This is the type of experiment that Loyn et al. (1983) did when they removed the bell miners. In it one species (or set of species) is held at a new reduced level, while all the other species are allowed to reach new equilibrium abundances. It is called a **Press experiment** (Bender et al. 1984) since the experimenter is pressing the system in a sustained way. We examine the response in equilibrium density of some nonperturbed species i while we hold some other species (usually just one) at a fixed density. The perturbed species' change in equilibrium density is simply its old equilibrium density, N_j^* , minus the new "equilibrium" density at which it is experimentally held. The latter is zero in the case of a complete removal of species j , so ΔN_j^* is simply N_j^* . The response of species i 's equilibrium density following the removal of all individuals of species j then is

$$\frac{\Delta N_i^*}{\Delta N_j^*} = \frac{\Delta N_i^*}{N_j^*} = \frac{(a_{ij})^{-1}}{(a_{jj})^{-1}}. \quad (15.26)$$

The switch to deltas (Δ) from infinitesimal partials (∂) is justified for any perturbation of a generalized Lotka–Volterra system (as long as no species other than the perturbed species become extinct). However, is it valid only in a narrow region around the old equilibrium if the equations are not GLV. If we knew the values of $(a_{ij})^{-1}$ and $(a_{jj})^{-1}$, we could simply rearrange Eq. (15.26) to solve for change in equilibrium density of species i :

$$\Delta N_i^* = \frac{(a_{ij})^{-1}}{(a_{jj})^{-1}} \Delta N_j^*. \quad (15.27)$$

Therefore for a complete removal of species j the new equilibrium density of unmanipulated species i is

$$\text{New } N_i^* = \text{old } N_i^* - \frac{(a_{ij})^{-1}}{(a_{jj})^{-1}} \text{ old } N_j^*.$$

Bender et al. (1984) made a slight modification to Eq. (15.26). They asked: What is the relationship between the change in equilibrium density of a species i relative to the change in another species j , following a press perturbation to a third species k ? The answer, in the form of the resulting equation, is

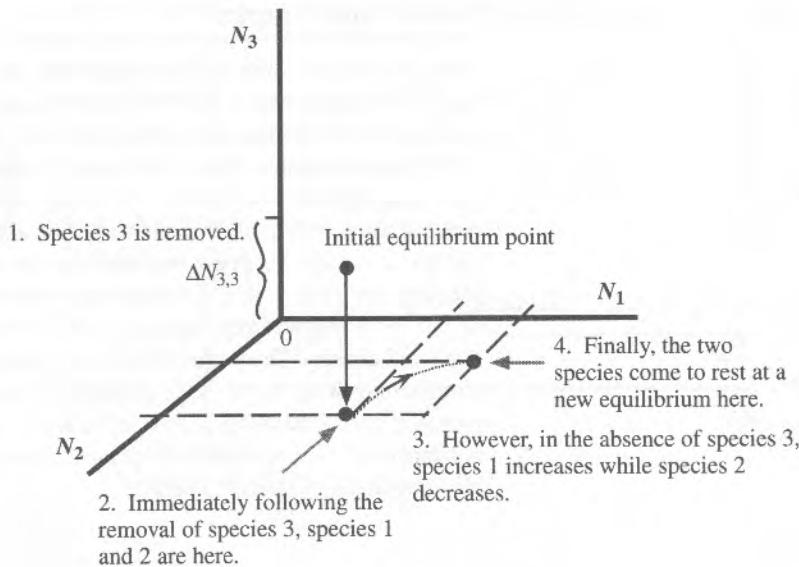
$$\frac{\Delta N_{i,k}^*}{\Delta N_{j,k}^*} = \frac{(a_{ik})^{-1}}{(a_{jk})^{-1}}, \quad (15.28)$$

where $\Delta N_{i,k}^*$ is the change in equilibrium density of species i following a perturbation in species k . Note the subscripts in Eq. (15.28). Figures 15.9 and 15.10 illustrate the application of this equation to a three-species system. The three species' initial interior equilibrium point is the black dot in the center of phase space. The perturbation is to press species 3's density to zero and maintain its numbers there, allowing all the other species to adjust in density until they reach a new equilibrium (shown in the N_1 – N_2 orthant).

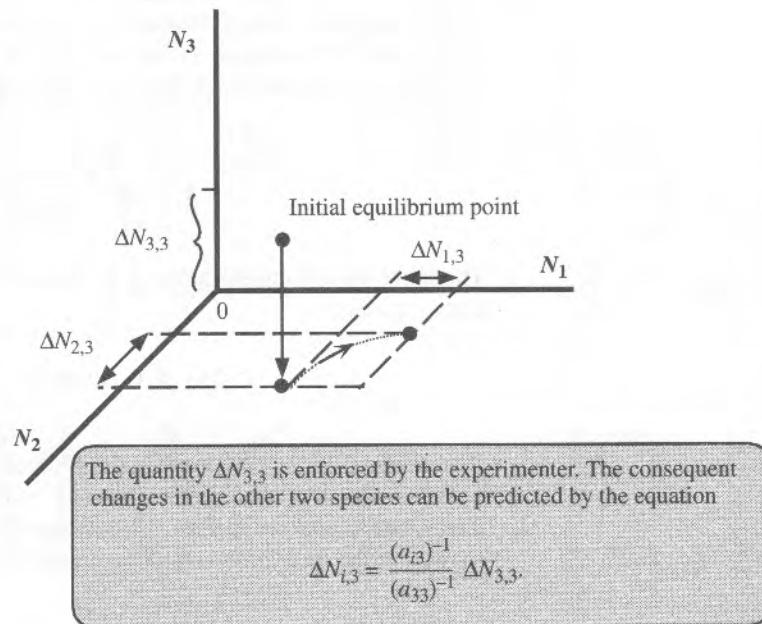
It is important to remember that the long-term numerical response of species j to the removal of species i , is directly proportional to the ij element in the sign-reversed inverse of the community matrix, not the ij element in the community matrix itself. Thus the long-term response depends not only on the direct interaction between species i and j , but also on the direct interactions of these species with other species in the community through all the interaction chains connecting the species pair.

Figure 15.9

A diagram showing a Press experiment for a three-species community and the resulting community response. Press perturbation of species 3 forces its density to zero, and the densities of species 1 and 2 adjust to this manipulation—eventually coming to a new equilibrium in the $N_1 - N_2$ orthant.

**Figure 15.10**

The experiment depicted in Figure 15.9. The community response following the Press perturbation of species 3 can be predicted from elements in the inverse of the community matrix, \mathbf{A} , using Eq. (15.27).

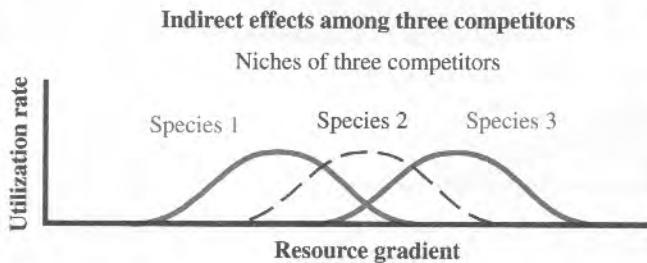


Because Press experiments integrate both direct and indirect effects, we can get some counterintuitive results (Yodzis 1988). One such example, involving three Lotka–Volterra competitors, is illustrated in Box 15.1.

Problem: Using the information provided in Box 15.1, calculate the equilibrium population size of species 2 following the removal of species 3.

Problem: Using the information provided in Box 15.1, calculate the $\Delta\mathbf{N}$ matrix based on the complete removal of each of the three competitors in three successive experiments. Use Eq. (15.28) to verify that you can use $\Delta\mathbf{N}$ to calculate the community matrix, \mathbf{A} .

Box 15.1 Indirect Effects among Three Competitors



In the diagram, the degree of overlap of the three species niches is indicative of the strength of pairwise competition. Species 1 and 2 and species 2 and 3 have strong competitive impacts on one another, but species 1 and 3 have weak competitive impacts on one another. An α matrix consistent with this diagram is

$$\alpha = \begin{bmatrix} 1 & 0.5 & 0.063 \\ 0.5 & 1 & 0.5 \\ 0.063 & 0.5 & 1 \end{bmatrix}.$$

If all three species have $K = 100$, then the equilibrium densities are $N_1^* = N_3^* = 88.81$ and $N_2^* = 11.19$. The community matrix is $A = D\alpha$, where D is a 3×3 diagonal matrix containing the terms $-r_i/K_i$ along the diagonal and zeros elsewhere. The inverse of A is

$$A^{-1} = (D\alpha)^{-1} = \alpha^{-1} D^{-1}$$

Note the reversal of multiplication order in this last step (see Appendix 3). Obtaining α^{-1} via Matlab®, we get

$$A^{-1} = \begin{bmatrix} 1.422 & -0.888 & 0.354 \\ -0.888 & 1.888 & -0.888 \\ 0.354 & -0.888 & 1.422 \end{bmatrix} D^{-1}$$

Since D is a diagonal matrix, its inverse is just the matrix with 1 over each diagonal element of D . These multiply each column of α^{-1} to yield

$$A^{-1} = \begin{bmatrix} \frac{-K_1}{r_1} 1.422 & \frac{K_2}{r_2} 0.888 & \frac{-K_3}{r_3} 0.354 \\ \frac{K_1}{r_1} 0.888 & \frac{-K_2}{r_2} 1.888 & \frac{K_3}{r_3} 0.888 \\ \frac{-K_1}{r_1} 0.354 & \frac{K_2}{r_2} 0.888 & \frac{-K_3}{r_3} 1.422 \end{bmatrix}.$$

Note that the total effect of species 1 on 3 is *positive*, since the (1, 3) element of the inverse matrix is $(-0.354K_3/r_3)$ is *negative* (see Eq. (15.24)). Although species 3 competes directly with species 1 ($\alpha_{13} = 0.0625$), it competes much more with species 2 ($\alpha_{23} = 0.5$), which, in turn, is a strong

competitor of species 1 ($\alpha_{12} = 0.5$) and depresses 1's density much more. Thus the indirect effect of species 1 on species 3 is beneficial through the depression of species 2—as in the saying, "My enemy's enemy is my ally."

The removal of species 3 will result in a decrease in species 1's new equilibrium density. The amount of this decrease can be quantified by applying Eq. (15.27):

$$\Delta N_{13}^* = \frac{(\alpha_{13})^{-1}}{(\alpha_{33})^{-1}} N_{33}^* \\ = \frac{-0.354 \frac{K_3}{r_3}}{-1.422 \frac{K_3}{r_3}} (-88.81) = -22.11. \quad (15.29)$$

The new equilibrium density of species 1, following removal of species 3, is $88.81 - 22.11 = 66.70$.

Note how the K_3/r_3 terms canceled out in Eq. (15.29). Because of this we could have gotten this same result by using just the inverse of the $-\alpha$ matrix instead of the A matrix to do the calculation with Eq. (15.29). The interaction matrix, A , of a GLV can sometimes be written as the product of a diagonal matrix, D , and a simpler matrix, A' (for example, for LV competition $A' = -\alpha$). Since the D terms factor out anyway in the application of Eq. (15.27), we can predict density changes more readily by using the simpler matrix, A' , and its inverse elements instead in Eq. (15.27).

The simulation depicted in Figure 15.11 verifies our predictions.

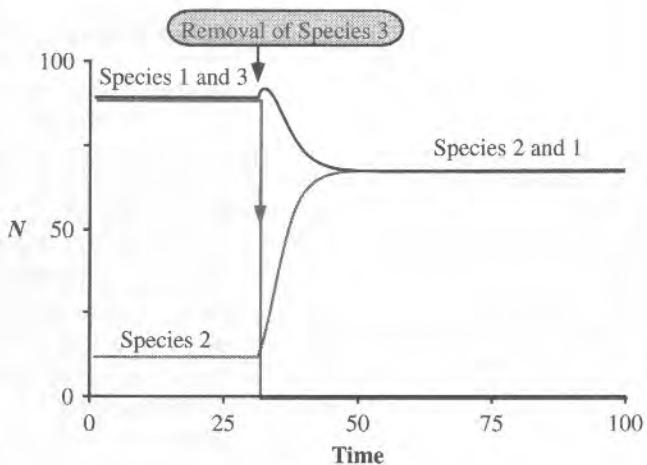
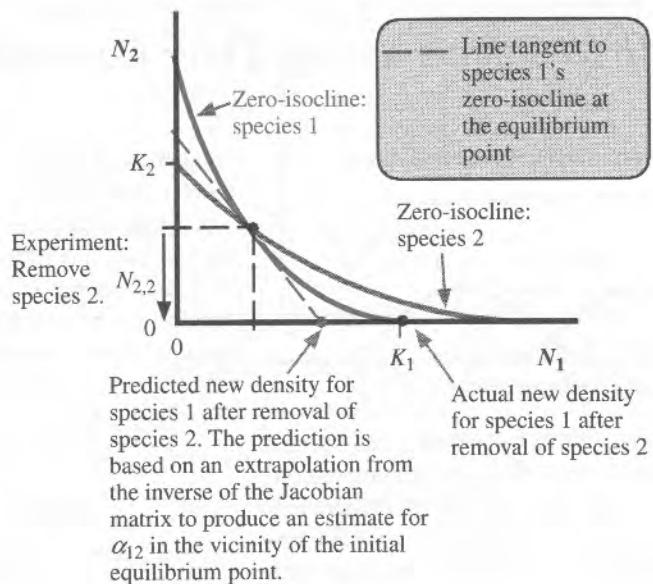


Figure 15.11

A simulation of the three-competitor model. Species 3 is removed at time 30. This results in a lower equilibrium density for species 1 (at 66.7) and a higher equilibrium density for species 2 (also at 66.7).

Figure 15.12

A Press experiment involving the removal of species 2 when the per capita dynamics is nonlinear (nonlinear zero-isoclines).



The other way to use Press experiments is to deduce the \mathbf{A} matrix from the density changes in each experiment. This requires n different species removals to get the \mathbf{A}^{-1} matrix for n interacting species (Bender et al. 1984). Then the experimentally derived \mathbf{A}^{-1} matrix may be inverted to form the community matrix, \mathbf{A} . If the species dynamics are not adequately described by GLV equations, we could still apply Press experiments and use the results to estimate the inverse, not of the community matrix, but of the Jacobian matrix evaluated at the initial equilibrium point. This Jacobian matrix could then be used to predict the response in species densities following more sustained manipulations. However, the perturbations must be kept relatively small for two reasons: first, the Jacobian matrix is a valid predictor of dN/dt only in a small neighborhood of the existing equilibrium; and second, if some species become extinct following the perturbation, then the analysis falls apart. The first sort of error is illustrated in Figure 15.12 for a simple two-species community whose zero-isoclines are like those of the *Drosophila* shown in Figure 14.25.

Pulse Experiments

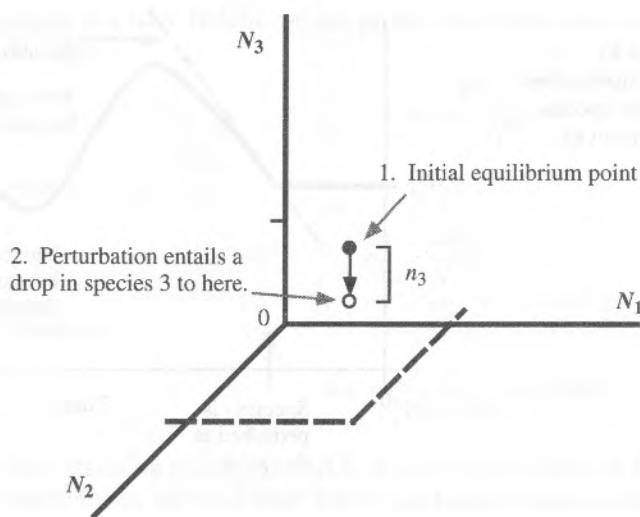
Another type of ecological experiment is called a **Pulse experiment** (Bender et al. 1984). Theoretically a pulse experiment involves a quick one-time change in the numbers of one or more species. Then all the species, *including* the perturbed species, dynamically adjust. Figures 15.13 and 15.14 illustrate a Pulse experiment involving a three-species community. In this experiment only species 3 is perturbed from N_3^* to a new density N_3 . The initial growth rate of each species is measured immediately following this perturbation. As before, we let $N_{i,j}$ represent the abundance of species i following a perturbation, n_j , to species j ($n_j = N_j^* - N_j$). We measure the change in $N_{i,j}$ over time, that is, $dN_{i,j}/dt$. In theory the terms in the community matrix can be calculated from these measurements of $dN_{i,j}/dt$, as illustrated in Figure 15.15.

By focusing on just the initial change in numbers—and if the perturbation is small—it is safe to assume that a linear differential equation model will approximate the true dynamics of the situation. (This is just the first-order Taylor's expansion again.) The immediate change in the numbers of species 1 following this Pulse perturbation to just species 3, then, is

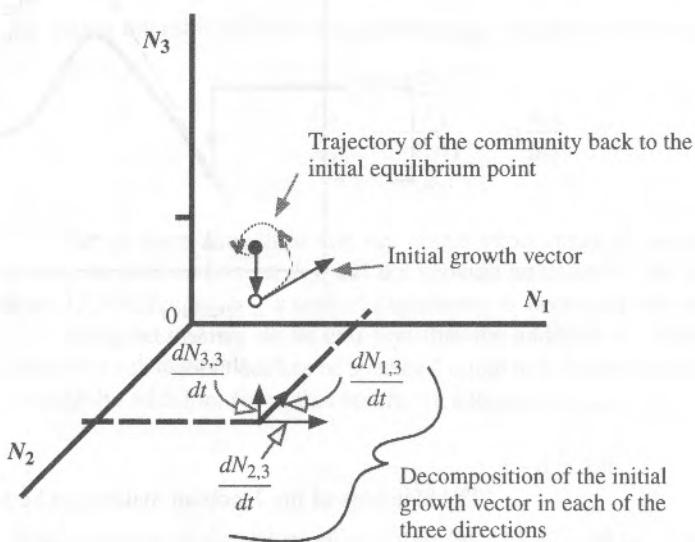
$$\frac{dN_{1,3}}{dt} = n_3 \left. \frac{\partial f_1}{\partial N_3} \right|_{N_1^*, N_2^*, N_3} \quad (15.30)$$

Figure 15.13

An illustration of a Pulse experiment, involving perturbation of species 3. Three interacting species exist at an equilibrium point prior to the removal of some number, n_3 , of species 3.

**Figure 15.14**

Measurement of the interaction terms of matrix A based on Figure 15.13 requires estimating the initial growth rate of each species following the perturbation of species 3.



where f_i is the growth equation for species 1 and n_3 is the perturbation amount. To keep things general, we assume that these f_i functions are *not necessarily GLV*. Also note where this partial derivative is evaluated—not at the original equilibrium point, (N_1^*, N_2^*, N_3^*) , but at the new perturbed position, (N_1^*, N_2^*, N_3) . The reason is that we are measuring the rates of change of each species from the perturbed position. For GLV equations the partial derivative in Eq. (15.30) is simply $N_1^* a_{13}$ (from Eq. 15.16), but for non-GLV it may be a more complicated function of the species densities. Similarly, the immediate growth rate of species 2 after the perturbation is

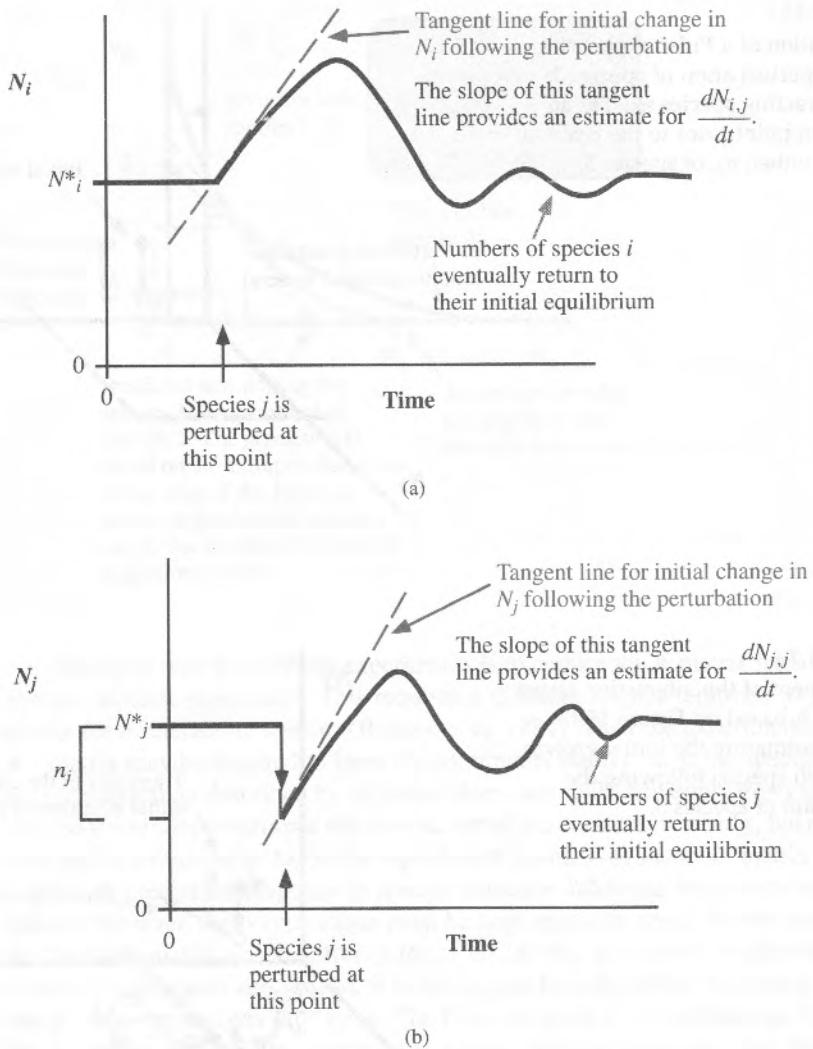
$$\frac{dN_{2,3}}{dt} = n_3 \frac{\partial f_2}{\partial N_3} \Big|_{N_1^*, N_2^*, N_3}$$

and for the perturbed species 3, we have

$$\frac{dN_{3,3}}{dt} = n_3 \frac{\partial f_3}{\partial N_3} \Big|_{N_1^*, N_2^*, N_3}$$

Figure 15.15

An example of the changes in population size of (a) an unperturbed species and (b) a perturbed species following a Pulse perturbation to species j .



The elements of the Jacobian matrix can be solved as

$$\begin{aligned}
 J_{i3} &= \frac{\partial f_i}{\partial N_3} \Big|_{N_1^*, N_2^*, N_3} \\
 &= \frac{\frac{dN_{i,3}}{dt}}{n_3}.
 \end{aligned} \tag{15.31}$$

The final term on the right-hand side of Eq. (15.31) contains two quantities, both measurable from the experiments.

As an example, suppose that we perturb a community of three competing species of *Paramecium*. Let's assume that all three species are at the same density of 100/ml. The perturbation is to add 20 individuals of species 3 so that $N_3 = 120$; thus, $n_3 = N_3 - N_3^* = 20$. We find that, immediately following this perturbation, species 1 decreases during the first few hours by 2 individuals/hour, species 2 decreases by 1.5 individuals/hour, and species 3 decreases at a rate of 3 individuals/hour. Then, with the growth equation for species 1, f_1 , also expressed in per hour units, J_{13} from Eq. (15.31) is

$$J_{1,3} = \frac{-2.0}{20} = -0.1.$$

If this is a GLV system, we can go one step further and rearrange Eq. (15.11) to solve for a_{13} :

$$a_{13} = \frac{J_{13}}{N_1^*}.$$

Hence

$$a_{13} = \frac{-0.1}{N_1^*} = -0.001. \quad (15.32)$$

Similarly,

$$a_{33} = \frac{-3}{(20)(120)} = -0.0015.$$

Still assuming that this is a GLV, we may find α_{13} but we require an additional experiment. To see this, first recall that for the Lotka–Volterra competition equations the Jacobian terms are

$$J_{13} = \frac{-r_1 \alpha_{13} N_1^*}{K_1} \quad \text{and} \quad J_{11} = \frac{-r_1 N_1^*}{K_1},$$

By taking the ratio of these two expressions, we can solve for α_{13} :

$$\frac{J_{13}}{J_{11}} = \frac{\frac{-r_1 \alpha_{13} N_1^*}{K_1}}{\frac{-r_1 N_1^*}{K_1}} = \frac{\alpha_{13}}{a_{11}} = \alpha_{13}. \quad (15.33)$$

The problem though is that our single experiment of perturbing species 3, while giving us information on J_{13} , did not provide an estimate for J_{11} , the denominator of Eq. (15.33). To get α_{13} , a second experiment is necessary: we must perturb species 1. Let's imagine that we do so and find that the addition of 20 individuals of species 1 leads to a subsequent decline of species 1 equal to 3.5 individuals/hour immediately following the addition. From this result, we calculate a_{11} as

$$a_{11} = \frac{-3.5}{(20)(120)} = -0.00146. \quad (15.34)$$

Now, plugging in the values of a_{13} from Eq. (15.32) and a_{11} from Eq. (15.34) into Eq. (15.33), we find that

$$\alpha_{13} = \frac{a_{13}}{a_{11}} = \frac{-0.001}{-0.00146} = 0.685.$$

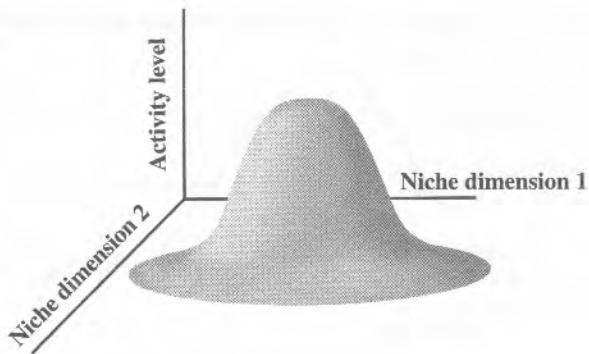
Solving for all the α 's will take three separate perturbation experiments involving the manipulation of each of the three species. Even to estimate a single α in a Pulse experiment, it takes at least two perturbation experiments. Another problem with Pulse experiments is that the perturbation must be kept small. Consequently, the responses of the species growth rates, dn_i/dt , will also be small and thus easily obscured by experimental error.

APPLICATIONS TO NICHE THEORY

A species **niche** is the sum of its activities and relationships in the community. It is a difficult concept to measure, just as phenotype and genotype are abstract and difficult to quantify. Nevertheless these concepts have heuristic value. Hutchinson (1957) described niches by plotting species in an n -dimensional space where the dimensions are important environmental features affecting the species and one axis

Figure 15.16

A diagram of a two-dimensional niche of a hypothetical species and its activity level for different values of these niche dimensions.



is the *activity level* of the species under those environmental conditions, as shown in Figure 15.16.

If a group of species compete for similar prey and if the only factor differentially influencing the competitors' success is the size of prey that they eat, then the relevant niche axis for these species would be prey size. Species that show greater diet overlap based on prey size, would be expected to compete more than species with less niche overlap in prey size. More typically several niche dimensions may influence population dynamics and competitive impacts since species may eat the same prey types but take them in different microhabitats or at different times.

The central tenet of niche theory is that niche overlap between two species, i and j, can be quantified into a metric α_{ij} such that the dynamic effects of competitors on one another, e.g. the α_{ij} terms, will be directly proportional to the degree of niche overlap between species pairs (i.e., $\alpha_{ij} \approx \alpha_{ji}$).

A corollary is that taxonomic relatedness will usually go hand in hand with morphological similarity and, in turn, niche overlap. Consequently interspecific competition is expected to be more severe among species in the same genus than in different genera or different families. For example, J. B. Steere (1894) investigating the biogeography of Philippine land birds wrote:

In 17 genera and 74 species each bird genus is represented in the Islands by several species, two or more of which may be found inhabiting the same island; but the species found together, with the same generic name, differ greatly in size, colouring or other characteristics and belong to different natural sections or subgenera. These sections or subgenera may each be represented in the archipelago by several species; but where this occurs each species is found isolated and separated for all the other species of the subgenus. . . . No two species structurally adapted to the same conditions will occupy the same area.

Perhaps the most common metric for quantifying ecological similarity is based on a resource utilization matrix. Each row of this matrix represents a consumer species, i , and the elements in the row are the rates of consumption for each resource, k , by that consumer, a_{ik} . However, typically the resource use is converted into a proportional use by dividing a_{ik} by the total resource use for that consumer. The proportion of resource k used by consumer i then is

$$P_{ik} = \frac{a_{ik}}{\text{total resource use by consumer } i = \sum_{q=1}^n a_{iq}}.$$

These proportional uses are then used to produce a **niche overlap formula**:

Summation is over all the n resources.

Proportion of resource k used by consumer i

$\sum_{k=1}^n P_{ik} P_{jk}$

$$o_{ij} = \frac{\sum_{k=1}^n P_{ik} P_{jk}}{\sum_{k=1}^n P_{ik}^2}$$
 Denominator species i 's "overlap" with itself.

With this definition, $o_{ii} = 1.0$.

(15.35)

Another way to view this formula is to note that a convenient definition of the niche width of consumer species i is

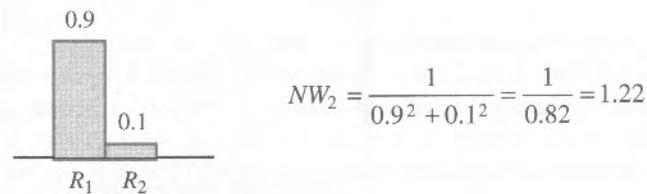
$$NW_i = \frac{1}{\sum_{k=1}^n P_{ik}^2}. \quad (15.36)$$

As an example, contrast one species that takes equal proportions of two resources and another species that consumes primarily resource 1.

Consumer 1 takes equal amounts of two resources, R_1 and R_2 :



Consumer 2 takes mostly R_1 :



Conclusion: By this formula the niche width of species 1 is larger than the niche width of species 2.

As it should, the niche width formula, Eq. (15.36), assigns a higher niche width to species 1. The magnitude of the niche width may be thought of as the number of "equally" consumed resources. Species 1 takes both resources equally; therefore NW_1 is 2. Species 2 takes the equivalent of 1.22 resources.

Now let's return to the niche overlap formula, Eq. (15.35). The o_{ij} term can be thought of as a measure of the shared niche space between species i and j multiplied by the niche width of species i , or

$$o_{ij} = NW_i \sum_{k=1}^n P_{ik} P_{jk}. \quad (15.37)$$

This formula does not necessarily produce a symmetric relationship (i.e., $o_{ij} \neq o_{ji}$) unless species i and j have the same niche width. Here's an example based on the two species depicted in the preceding box.

$$o_{12} = 2[(0.5)(0.9) + (0.5)(0.1)] = 2(0.5) = 1.0,$$

and

$$o_{21} = 1.22[(0.5)(0.9) + (0.5)(0.1)] = 1.22(0.5) = 0.61.$$

Conclusion: By Eq. (15.35), the niche overlap of species 1 (with the wider niche) on species 2, o_{21} , is less than the overlap of 2 on 1, o_{12} . Species with wider niches suffer more from competition by this formula than do narrower niche species. This is not a conclusion about the ecological world, however; it is only an assumption on which this particular formula is based. Some ecologists have argued that this particular aspect of the formula is unrealistic and have gone on to suggest alternative formulations. Ultimately this is an empirical question still to be settled by data.

Box 15.2 presents another example of the application of this niche overlap formula, showing that niche overlaps may be greater than one.

Extending these definitions to many competitors and many resources, we can rewrite the niche overlap formula, Eq (15.37), in matrix form as

$$\mathbf{O} = \mathbf{D} \mathbf{P} \mathbf{P}^T, \quad (15.38)$$

where \mathbf{P}^T is the transpose of matrix \mathbf{P} , which means that the matrix \mathbf{P} is flipped on its side by exchanging rows with columns. Since \mathbf{P} had dimension $m \times n$, \mathbf{P}^T has dimension $n \times m$ and the product $\mathbf{P} \mathbf{P}^T$ is $m \times m$. Matrix \mathbf{D} is a diagonal matrix with the niche widths, NW_{ii} , along the diagonal and zeros elsewhere. Thus matrix \mathbf{D} is a square matrix with dimensions $m \times m$.

Problem: Based on the example in Box 15.2, verify that the matrix in Eq. (15.38) gives the same values as calculated there.

Solution:

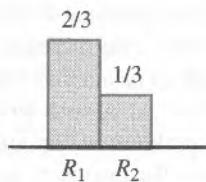
$$\begin{bmatrix} 1 & 6/5 \\ 2/3 & 1 \end{bmatrix} = \begin{bmatrix} 9/5 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 2/3 & 1/3 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} 2/3 & 1 \\ 1/3 & 0 \end{bmatrix} \\ = \begin{bmatrix} 9/5 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} 5/9 & 2/3 \\ 2/3 & 1 \end{bmatrix}$$

Finish this multiplication.

Strictly speaking, the overlap formula should not be based on proportional resource use, P_{ik} , since the central tenet of niche theory is that these overlap values are proportional to the dynamical effects that species have on one another. When we use proportions, the overlap of one species on another is independent of the total amount of resource consumption by those species. For example, if one species eats 10 times more resources per unit time than another species, then its impact on that species should be greater. But the formula in Eq. (15.35) does not capture this feature and therefore cannot be dynamically correct. MacArthur (1972) took up this issue and derived a niche theoretic formula for competitive impacts based on first principles. He used the predator-prey system of Eq. (15.6), without the resource-resource competition terms, to derive a formula for α_{ij} between consumer species. He assumed that, as consumer numbers changed, the resources adjusted to new equilibria instantaneously. With this assumption, MacArthur found that he could derive the consumer-consumer

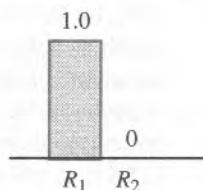
Box 15.2 Niche Width Calculations

Consumer 1:



$$NW_1 = \frac{1}{(2/3)^2 + (1/3)^2} = 1.8$$

Consumer 2 takes only R_1 :



$$NW_2 = \frac{1}{1^2 + 0^2} = 1$$

$$\alpha_{12} = 1.8[(2/3)(1) + 0] = 1.8(2/3) = 1.2$$

and

$$\alpha_{21} = 1[(2/3)(1) + 0] = 2/3$$

Conclusion: By this formula, the niche overlap of a narrow-niche species on a wide-niche species may exceed 1.

interactions in the form of the Lotka–Volterra competition equations where α_{ij} now had the form

$$\alpha_{ij} = \frac{\sum_{k=1}^n \frac{K_k w_k}{r_k} a_{ik} a_{jk}}{\sum_{k=1}^n \frac{K_k w_k}{r_k} a_{ik}^2}. \quad (15.39)$$

Equation (15.39) differs from the formula for α_{ij} based on niche overlap, Eq. (15.35), in two important ways. First Eq. (15.39) involves the use of raw consumption rates, a_{ij} , rather than proportional use of resources, p_{ij} . Second, it weights each resource, k , in terms of its importance to consumer–consumer impacts by a term $K_k w_k/r_k$. Resources that have very high r 's are less important to consumer competition because once these resources are consumed they are quickly replaced. Shared consumption of resources that are highly nutritious (w_k is large) are more important to consumer competition than shared resources that are less nutritious. Finally, resources that are relatively common in the environment (high K) will also be common in the diets of the consumers and thus will be more important to consumer competition compared to relatively rare and therefore infrequently consumed resources.

Equation (15.39) also suggests a more mechanistic formulation for niche width:

$$\tilde{NW}_{ij} = \frac{1}{\sum_{k=1}^n \frac{K_k w_k}{r_k} a_{ik}^2}. \quad (15.40)$$

The tilde is used to distinguish this measure of niche width from the earlier one of Eq. (15.36). It is nearly identical to the earlier formula. The exception is that it, too, is modified to include information about the relative importance of different resources to consumer growth rates. Finally MacArthur derived the consumer carrying capacities, \tilde{K}_i ,

based on these assumptions (the tilde over the K is added to distinguish the derived consumer carrying capacities from assumed resource carrying capacities):

$$\tilde{K}_i = \tilde{N}W_i \left(-\frac{d_i}{k_i} + \sum_{k=1}^n K_k w_k a_{ik} \right). \quad (15.41)$$

Thus by Eq. (15.41) a consumer's carrying capacity is directly proportional to its niche width as defined by Eq. (15.40), but becomes smaller as its death rate increases. The summation over resources in the parentheses can also be thought of as another measure of niche width, since it simply sums all the resource consumption rates, each weighted by an importance index for that resource ($K_k w_k$). One obvious problem in applying Eq. (15.41) to real communities is that it is difficult to enumerate all the resources used by consumers, let alone the r , K , and w for each.

Density Compensation

Support for some qualitative predictions made by niche theory comes from comparisons of island and mainland communities (MacArthur 1972, Cody 1974, Cox and Ricklefs 1977). Islands typically have only a subset of species that exist on comparable habitats on the mainland. If island habitats are perfectly matched to mainland habitats in other respects, the expected release from competition on an island can be predicted by using the framework developed for Press experiments.

The carrying capacities of competitors are very difficult to measure compared to their abundances. Carrying capacity is rarely observed, but abundances are measurable. If we assume that present abundances are at equilibrium, we could base estimates of K 's on an independently derived α matrix. This is where the overlap matrix comes in. The hope is that detailed studies of foraging method, prey types, and other niche dimensions can lead to the estimation of an overlap \mathbf{O} matrix that is proportional to α . For the moment, we make this very tenuous assumption and see where it leads us. Note, however, that niche overlap tells us nothing about how strong the interactions may be between these species and other trophic levels. Predators and parasites may be equally important in shaping patterns of abundance.

Let's work through a hypothetical example for a group of four competitors. We first estimate the 4×4 \mathbf{O} matrix, using the niche metrics presented earlier. The relative densities of the four species on typical mainland sites can also be directly measured. Using the Lotka–Volterra competition equations, we can solve for the carrying capacities of the species:

$$\mathbf{K} = \mathbf{O} \mathbf{N}^*.$$

This last step invokes the important assumption that the species dynamics are following these competition equations. Now let's suppose that an island exists where some set of the mainland species are absent—for example, species 1 and 2. The relative abundances of species 3 and 4, then, should be

$$\mathbf{N}_I^{*(1,2)} = (\mathbf{O}_M(1,2)^{-1} \mathbf{K}_M(1,2)), \quad (15.42)$$

where $\mathbf{N}_I^{*(1,2)}$ is the relative abundance vector on the island in the absence of species 1 and 2, $\mathbf{O}_M(1,2)$ is the overlap matrix estimated on the mainland with rows and columns 1 and 2 removed, and $\mathbf{K}_M(1,2)$ is the \mathbf{K} vector for the mainland with rows 1 and 2 removed. By measuring the relative abundances of species 3 and 4 on the island we can check to see whether their actual densities match the values predicted from Eq (15.42).

Yeaton (1974) studied the passerine birds of chaparral habitats in 7-acre sites in southern California. He found 17 species in mainland Santa Monica and 12 species on Santa Cruz Island. He then calculated niche overlaps between bird species from field studies in the Santa Monica Mountains. Table 15.1 compares predicted and actual abundances of the commoner bird species on Santa Cruz Island.

The loss of some species from Santa Cruz Island has led to a net increase in the density of several species that are present. This phenomenon is called **density compensation**.

Table 15.1 From Yeaton (1974).

Species	Mainland density (pairs/acre)	Island density expected, based on formulas like Eq.(15.42)	Actual island density
Scrub jab	0.27	1.00	1.11
Orange crowned warbler	0.07	0.50	0.55
Huttons vireo	0.14	0.60	0.55
Bewicks wren	0.61	1.28	1.27
Total bird density	5.52	—	5.39

pensation. When it is common, the net result is that the total bird density is nearly equal in the two places despite the lowered species number on the island.

Density compensation is often accompanied by an expansion of a species niche and its habitat use. Collectively, density compensation and **niche and habitat expansion** are referred to as **competitive release**. Again, this pattern is suggestive but not definitive proof that competition occurs among these species, since the islands and mainland sites may not be replicates in all respects except for the presence or absence of certain competitors.

Limiting Similarity

For over a century naturalists have noticed striking regularities in the abundance, niche positions, and distribution of similar species (Vandermeer 1972, Cody 1974, Schoener 1974, Pianka 1976). Several of these regularities seem consistent with expectations from niche theory, and entire books have been written on the subject. One common theme is that related species that are similar in morphology, especially body size, and thus have similar diets often occupy different habitats or occur in different geographic regions (i.e., in allopatry). In contrast, closely related species that are sympatric and occur in the same habitat (i.e., syntopic) frequently have niches that segregate strongly in body size or other directions related to foraging mode. These observations spawned an analysis of how similar species niches can be, before they can no longer coexist.

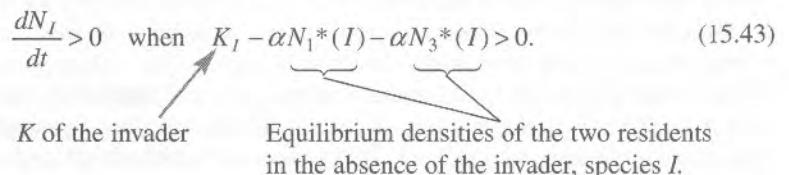
We will work through one theoretical approach to this problem (MacArthur and Levins 1967). It assumes a single niche dimension and normal distributions for the niche of each species. Figure 15.17 presents a graphical description of the situation.

For the invasion to be successful, the invader's population must be able to increase when it is rare and in the presence of the two residents at their equilibrium densities with each other, that is, we require

$$\frac{dN_I}{dt} > 0.$$

We use niche theory to convert the static picture presented in Figure 15.17 to Lotka–Volterra dynamics. We then solve for the invader's growth rate when its population is rare:

$$\frac{dN_I}{dt} > 0 \quad \text{when} \quad K_I - \alpha N_1^*(I) - \alpha N_3^*(I) > 0. \quad (15.43)$$



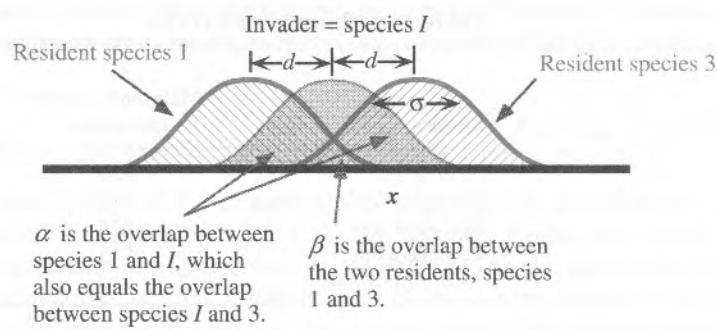
 K of the invader Equilibrium densities of the two residents
 in the absence of the invader, species I.

We solve for the equilibrium densities of the two residents in the absence of the invader by applying Cramer's rule (see Appendix 3):

$$N_1^*(I) = \frac{\begin{vmatrix} K & \beta \\ K & 1 \end{vmatrix}}{\begin{vmatrix} 1 & \beta \\ \beta & 1 \end{vmatrix}} = \frac{K(1-\beta)}{1-\beta^2} = \frac{K(1-\beta)}{(1-\beta)(1+\beta)} = \frac{K}{1+\beta}.$$

Figure 15.17

A graphical depiction of the classical limiting similarity problem. Can an invading species insert itself between the niches of two resident species? All the niches have the same standard deviation, σ , and total area, A . Each species has the same carrying capacity, K , and the niches are evenly spaced d units apart, the distance between the peaks (means) of adjacent niches.



From the symmetry of the niches depicted in Figure 15.17, the equilibrium density of species 3 in the absence of species 2 must be identical to that of species 1, or

$$N_1^*(I) = N_3^*(I) = \frac{K}{1 + \beta}. \quad (15.44)$$

We substitute Eq. (15.44) into the inequality of Eq. (15.43) to reach

$$K_I - \frac{2\alpha K}{1 + \beta} > 0. \quad (15.45)$$

Next, we want to find an expression for niche overlap as a continuous function of niche separation, d . We apply the continuous version of the niche overlap function, Eq. (15.35):

$$\beta = \frac{\int_{-\infty}^{\infty} p_1(x)p_2(x)dx}{\int_{-\infty}^{\infty} p_1(x)^2 dx}. \quad (15.46)$$

The niches p_1 and p_2 can be described by the gaussian curves with means $-d$ and d , standard deviation, σ , and area, A :

$$p_1(x) = \frac{A}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(-d-x)^2}{2\sigma^2}\right) \quad (15.47a)$$

and

$$p_2(x) = \frac{A}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(d-x)^2}{2\sigma^2}\right) \quad (15.47b)$$

We substitute Eqs. (15.47a) and (15.47b) into Eq. (15.46) and evaluate the integrals of Eq. (15.46) to reach the much simpler expression,

$$\beta = \exp\left(\frac{-s^2}{(2\sigma)^2}\right), \quad (15.48)$$

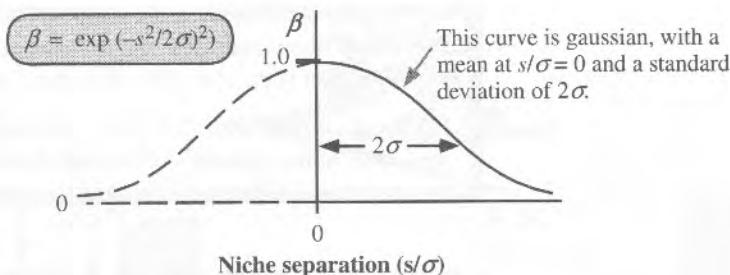
where s = niche separation—in our case $s = 2d$ for the two outer species, 1 and 3. Equation (15.48) describes a gaussian curve with standard deviation of 2σ . When niche separation $s = 0$, niche overlap $\beta = 1$. β depends only on the ratio of s/σ . As s/σ increases, niche overlap decreases according to a gaussian curve, as shown in Figure 15.18.

Since in our case $s = 2d$ for species 1 and 3 and $s = d$ for species 1 and 2, as well as species 2 and 3, we have

$$\beta = \exp\left(\frac{-(2d)^2}{(2\sigma)^2}\right) \quad \text{and} \quad \alpha = \exp\left(\frac{-d^2}{(2\sigma)^2}\right).$$

Figure 15.18

Niche overlap, β , as a function of niche separation s/σ between two gaussian niches (as defined by Eq. 15.48); s is the distance between the two means, and σ is the standard deviation of the niche. Since negative niche separation is not defined, the dashed portion of the overlap curve is not observed.



Thus $\beta = \alpha^4$ and the inequality, Eq. (15.45), can be rewritten as

$$K_I - 2\alpha \left(\frac{K}{1 + \alpha^4} \right) > 0. \quad (15.49)$$

We can rearrange Eq. (15.49) to get

$$K_I > \frac{2\alpha K}{1 + \alpha^4}. \quad (15.50)$$

If the invader has the same carrying capacity as the residents, then Eq. (15.50) simplifies further to

$$1 > \frac{2\alpha}{1 + \alpha^4}.$$

Hence the critical α_c for invader success is obtained by solving

$$1 = \frac{2\alpha}{1 + \alpha^4} \quad (15.51)$$

for α . There will be four roots, or solutions, for α_c from Eq. (15.51). Two are nonnegative real numbers:

1. $\alpha_c = 1.0$, which implies that $d/\sigma = 0$; and
2. $\alpha_c = 0.544$, which implies that $d/\sigma = 1.56$.

The second root is the most interesting. The invader will be successful if α , here defined as its niche overlap with the residents, is less than 0.544. Moreover, for this case of equal K 's, if the invader can grow when rare, it will reach a positive equilibrium density with both residents present. The invader will not displace either resident. This limiting similarity paradigm may be extended in several directions. The K 's may be made unequal, the number of resident species may be increased from two to several, the shape of the niche can be altered from gaussian to some other form, and the growth rate may include stochastic terms. Abrams (1975) and Roughgarden (1979) provide a review of some of these modifications.

Given enough time and a large species pool, we might expect communities to accumulate species until they become competitively saturated: any niche gaps will be invaded by new species, and competition-driven extinctions will eliminate species whose niches are too close. Thus **species-assortment** based on niche position may be one reason why some co-occurring competitors display a regularity in their niche positions or body sizes (Cody 1974, Schoener 1974). Another complementary explanation is that species may genetically coevolve over time to minimize competitive impacts with one another: This is generally referred to as **character displacement** when a pair of species is more divergent morphologically in sympatry than in allopatry. More complicated models combine these two processes to represent the long-term evolution of competition communities through species assortment and coevolution (see, e.g., Taper and Case 1992).

Problem: Show that for a single-resident species, there is no limiting similarity for an invader (i.e., $\alpha_c = 1.0$) when the K 's are equal.

Problem: Prove that, for two residents (and equal K 's for residents and invaders), both residents will be able to coexist with a successful invader.

LIMITING SIMILARITY AND PREDATION

How might a predator alter the limiting similarity of its prey? The answer depends on the way that the predator acts (Abrams 1977). If the predator indiscriminately eats prey in such a way that the carrying capacity, K , of each prey species is reduced by the same amount, then the predator has no impact on the limiting similarity of these prey species. Such a predator will not prevent the competitive exclusion of one prey by another if that would occur in the absence of predation. (Note that, when K 's were equal, K canceled out of Eq. 15.50). As an example, mosquito larvae that filter-feed indiscriminately on protozoans living in rainwater collected in pitcher plants do not enhance the diversity of protozoan prey species in these communities. Addicott (1974) experimentally added varying numbers of mosquito larvae to pitcher plants and measured the impact to prey numbers and prey species diversity. Both measures decreased with increasing mosquito larvae.

Recall, however, that in Chapter 11 we introduced the situation where “switching” predators may take disproportionate numbers of prey that are relatively common. This situation was modeled by Roughgarden and Feldman (1975) in the context of the limiting similarity paradigm. They imagined that the invading prey, at very low numbers, would experience much less predation on a per capita basis than the resident prey. This would be the case, for example, if the predator had a type 3 functional response for all prey. In the limit when the invader experiences no predation, its growth when rare and thus the condition for it to invade, is from Eq. (15.49)

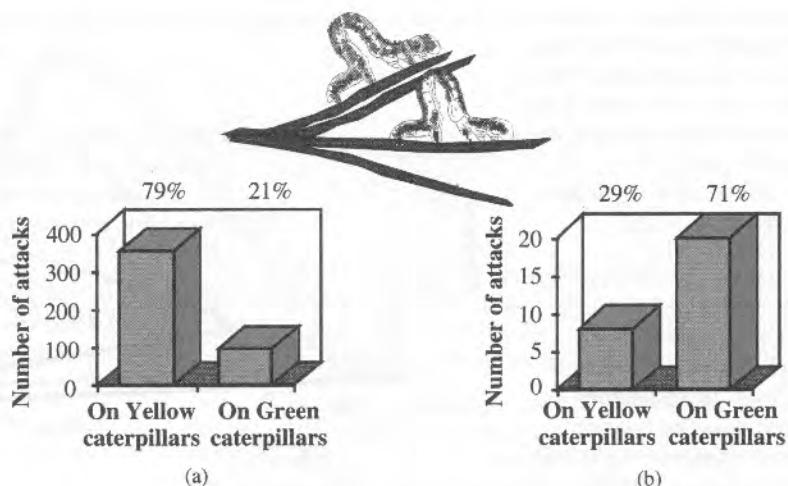
$$K_I - 2\alpha N^*(I) > 0,$$

where $N^*(I)$ is again the equilibrium density of the residents in the absence of the invader but now in the presence of the predator. As predation increases, $N^*(I)$ will become lower and thus it will be easier for the invader to insert itself in the community. In the absence of the predator, $N^*(I)$ was given by Eq. (15.44) as $K/(1 + \alpha^4)$, but with such a predator it will be a value less than this. Consequently, the critical limiting similarity, α_c , will be greater. In this way, a predator that feeds disproportionately on common prey items can enhance the coexistence of its several competing prey.

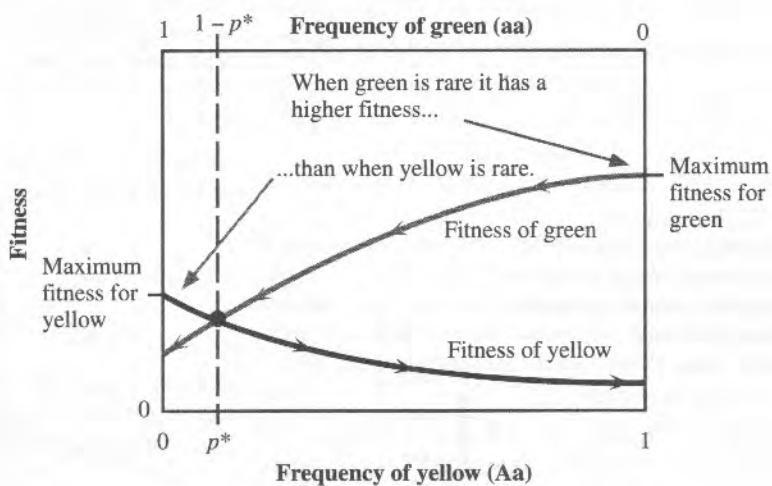
An example of a low-frequency advantage is seen in birds feeding on pine looper caterpillars. The older caterpillars exhibit a color polymorphism caused by a single genetic locus. The wild type aa genotypes are green and quite cryptic on their normal background of pine needles. The heterozygote genotypes Aa are yellow. The other homozygote AA is lethal and never found in nature. The color polymorphism is not expressed in adult moths or the youngest stages of the caterpillars. The typical frequency of the heterozygote yellow morphs in the wild is about 0.06 to 2.5%, which is rare but much higher than would be expected if only new mutations each generation were responsible for producing these yellow morphs. Boer (1971) could find no differences between adult moths from green and from yellow caterpillars with respect to mating preferences, mating success, fecundity, egg hatching, and larval growth rate. This caused Boer to look for factors that might favor the survival of heterozygote caterpillars in the wild. He placed caterpillars on green pine needles in an aviary and then introduced birds (great tits and coal tits) without previous exposure to either color morph. As expected yellow caterpillars are attacked much more frequently than green, as depicted in Figure 15.19(a).

Figure 15.19

Attacks by birds on equal numbers of both color morphs of pine looper caterpillars. (a) Naive birds. (b) Birds trained on green caterpillars.

**Figure 15.20**

As the yellow morph increases in frequency from 0 to 1, the green morph must decrease in frequency since the frequency of both morphs always sums to 1. As yellow increases in frequency, its fitness declines. As green increases in frequency, its fitness declines. When the fitness of both types is equal, which occurs where the two fitness lines intersect, they will be at equilibrium. The equilibrium frequency of yellow, p^* , is less than that of green, $1 - p^*$, since green has a higher maximum fitness than yellow.



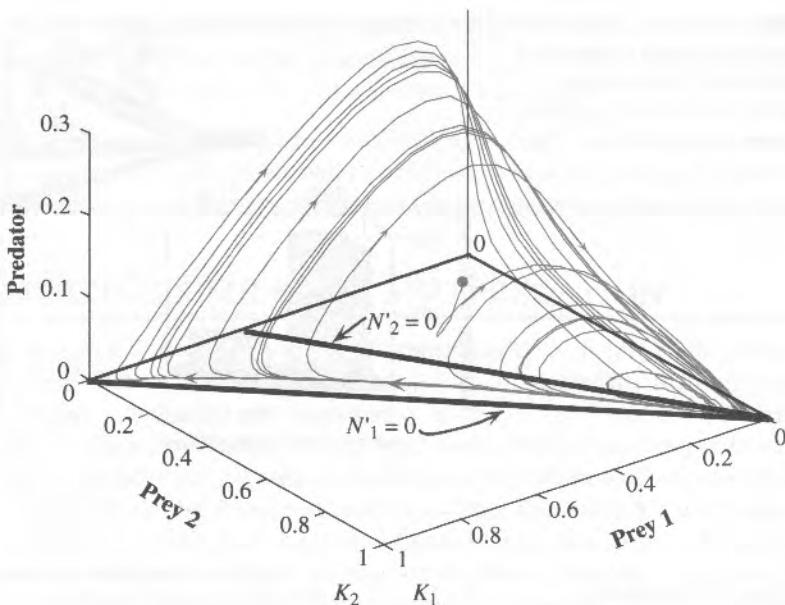
But, once birds have been exposed to the green caterpillars, they learn how to detect and find them, and they perfect a search image for these cryptic green morphs. If these experienced birds are now offered equal numbers of both color morphs in an aviary, the results are quite different, as shown in Figure 15.19(b): the green caterpillars are eaten more frequently than the yellow.

These results suggest that in nature both color morphs have a relative advantage when rare, since birds would not gain experience with them or be able to develop a search image. Yet, since the green morph is more cryptic than yellow on the normal green pine needle background, green's advantage when rare is greater than that of yellow when it is equally rare. Figure 15.20 puts these considerations together to explain the stable polymorphism and the relatively rare but persistent frequency of yellow in the population.

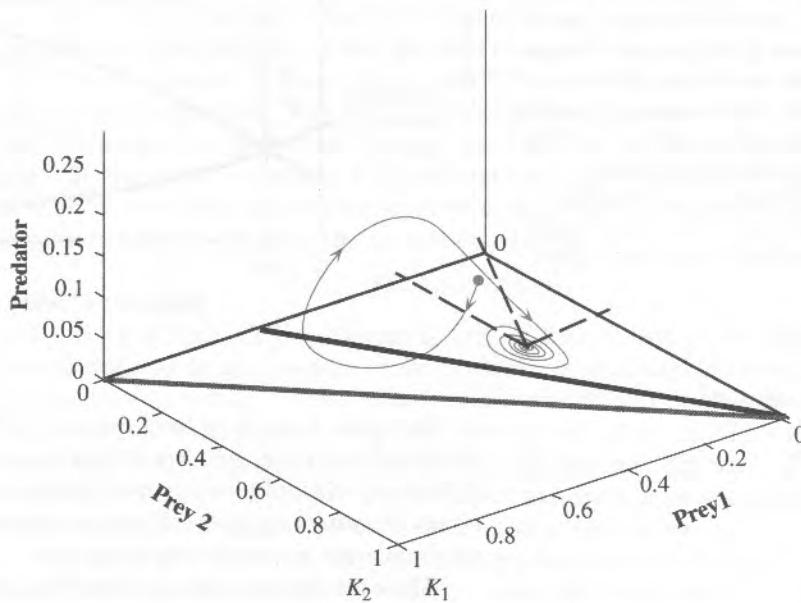
Another way that a predator can enhance the coexistence of competing prey types is by preferring to eat prey that happen to be competitively dominant, regardless of this prey's relative frequency. As an example, consider a situation with a single predator and two competing prey. The predator has a simple type 1 functional response for each prey, so there is no switching here. Let's imagine a case where the two prey also directly compete, as modeled by Eq. (15.5). Let's further suppose that, in the absence of the predator, prey 1 competitively excludes prey 2 (which means that $K_1 > K_2/\alpha_{21}$ and $K_2 < K_1/\alpha_{12}$, from Chapter 14). If the predator prefers to eat species 1, it may rescue species 2 from competitive exclusion. Moreover, if $\alpha_{12}\alpha_{21} > 1$, then a feasible

Figure 15.21

An example of spiral chaos involving two prey and a single predator. Prey 1 is competitively superior to prey 2, but the predator has a higher capture rate for prey 1 than for prey 2. The equations governing these dynamics are given by Eq. (15.5), with $r_1 = r_2 = d = k = K_1 = K_2 = 1$, $w_1 = w_2 = 0.5$, $\alpha_{12} = 1$, $\alpha_{21} = 1.5$, $a_1 = 10$, and $a_2 = 1$. The zero-isoclines for the two competing prey species are shown in the prey 1-prey 2 plane as thick straight lines. The trajectory begins at the red dot. The interior equilibrium point is at prey 1 = 0.1184, prey 2 = 0.8158, predator = 0.0066.

**Figure 15.22**

As in Figure 15.21, but now the predation rate on the competitively superior prey is lowered from $a_1 = 10$ to 5. All three species coexist at a stable equilibrium point. All other parameters are the same. The equilibrium point here is at prey 1 = 0.2963, prey 2 = 0.5185, predator = 0.0370.



three-species equilibrium point may exist, which may be stable or unstable, depending on the other parameters. If it is unstable, all three species may still coexist via a limit cycle or on a chaotic attractor with the spiral shape illustrated in Figures 15.21 and 15.22 (Gilpin 1979). The trajectory never settles down, but continually roams around the spiral “horn.”

Problem: Form the Jacobian matrix for the interior equilibrium point shown in the captions of Figures 15.21 and 15.22 and evaluate the eigenvalues. Verify that the interior equilibrium point is unstable in Figure 15.21 but is stable in Figure 15.22. This will require a computer and matrix software.

PROBLEMS

1. Suppose that you have a single-resident Lotka–Volterra competitor species with $K = 100$. Another competitor, also with $K = 100$, attempts to invade. The niches of the two competing species are gaussian with separation d/σ . How small can d/σ be for this invasion to still be successful?

2. Using Matlab® for the community matrix of Eq. (15.25) and the vector \mathbf{k} given in the caption to Figure 15.7, verify that the equilibrium densities for this two-predator, one-prey model are:

$$\text{Prey} = 152.5000$$

$$\text{Predator 1} = 6.8750$$

$$\text{Predator 2} = 1.2500$$

Using the inverse of the community matrix in Eq. (15.25), follow the procedure in Box 15.1 to calculate the expected change in numbers of predator 2 following the removal of predator 1. Check your result with the simulation results of Figure 15.7. What would happen to the density of predator 1 if predator 2 was removed?

3. Using the niche overlap formula of Eq. (15.35), calculate the niche overlap for these two consumers for the proportionate use of the three resources shown.

	R_1	R_2	R_3
Consumer 1	0.5	0.5	0
Consumer 2	0	0.5	0.5

If the carrying capacities of the two competing consumer species are both $K = 100$ —and assuming that these overlaps reflect α 's in the Lotka–Volterra competition equations—what are the predicted equilibrium densities of the two consumers?

4. Suppose that the community matrix for a three species GLV community is

$$\mathbf{A} = \begin{bmatrix} -1 & 0 & -0.5 \\ -0.5 & -1 & -0.5 \\ 1.5 & 1 & 0 \end{bmatrix} \quad \text{with} \quad \mathbf{k} = \begin{bmatrix} 1 \\ 1 \\ -0.1 \end{bmatrix}.$$

Draw a food chain for these three species. What are the equilibrium densities of the three species? Suppose that species 3 is missing from an island, but everything else is equivalent. Then what are the predicted equilibrium densities for species 1 and 2 on the island?

5. Imagine a situation for three competitors like that shown in Figure 15.17, except that the outer tails of the niches of the two residents loop around in a circle so that they overlap to degree α . Let the niche separation between the means of adjacent niches be d for all three adjacent pairs on this ring. Form the α matrix for this community and determine the limiting similarity for these three species.

6. In desert scrub habitats on a mainland you determine that the niche overlap matrix for three lizard species is

$$\mathbf{O} = \begin{bmatrix} 1 & 0.3 & 0.5 \\ 0.4 & 1 & 0.2 \\ 0.6 & 0.2 & 1 \end{bmatrix}.$$

The population densities you observe per acre are $N_1 = 10$, $N_2 = 20$, and $N_3 = 15$. Given the usual assumptions for niche theory (i.e., these overlaps represent competitive impacts, the community is at equilibrium, the Lotka–Volterra competition equations are valid, etc.), what are the carrying capacities for each of the three species on the mainland?

On some islands you find that species 2 is absent. What are the expected equilibrium densities of species 1 and 3 in the same desert scrub habitats on these islands (assuming all other conditions on the islands are the same)?