Recall that we linearize (look only at linear terms) because at equilibrium, $n_i = 0$, and near equilibrium $n_i \ll n_i^2$. Since linearizing only works near equilibrium, this is where our assumption of small perturbations is used.

We approximate equation (6.2) by linearizing near equilibrium. The deviation from equilibrium for each species is $n_i = N_i - \hat{N}_i$. We approximate the dynamics near the equilibrium by a linear model. We then use the theory of eigenvectors and eigenvalues developed in Chapter 2 to look at age-structured growth, to compute the growth rates of perturbations away from equilibrium. If all perturbations shrink to zero, the equilibrium is stable. If any perturbation grows, the equilibrium is unstable. The matrix that we use in linearizing the model (Box 6.1) is the *community matrix*, the matrix describing the effects of species on their own growth rate and the growth rate of interacting species. The entire procedure for determining stability is summarized in Box 6.1.

6.4 Qualitative behavior of the community matrix

We can gain some insight into the dynamics of two-species systems by considering the qualitative nature of the community matrix in two-species models. First, let us determine the signs of the entries, when they can be determined, in the community matrix for two species. In a competition model we assume that all the entries are negative. In a predator–prey model, we would assume that the effect of the prey on the predator is positive, while the effect of the predator on the prey is negative.

This information is useful because of the following facts, which can lead to some simple stability conditions:

These facts about the relationship between the trace and determinant and eigenvalues of a matrix hold for larger matrices, except the determinant of an $n \times n$ matrix equals $(-1)^n$ times the product of the eigenvalues. These relationships can help to understand qualitative features of stability of more complex systems.

- The *trace* of a matrix (the sum of its diagonal elements) is equal to the sum of its eigenvalues.
- The determinant of a matrix is equal to the product of its eigenvalues.

Thus, we see that if both eigenvalues are negative, the determinant is positive and the trace is negative. If one eigenvalue is positive and one is negative, the determinant is negative. If both eigenvalues are positive, the trace must be positive. From this we can determine simple stability conditions, as summarized in Box 6.2.

Box 6.1. Computing equilibria and stability in a two-species model.

Begin with a model of the form

$$\frac{dN_1}{dt} = N_1 f_1(N_1, N_2) \equiv F_1(N_1, N_2)$$
$$\frac{dN_2}{dt} = N_2 f_2(N_1, N_2) \equiv F_2(N_1, N_2),$$

so we have defined both per capita growth rates f_i and total growth rates F_i.

- Determine equilibria by setting F_i to be 0 and solving for $\hat{N}_1$ and $\hat{N}_2$. (Note that if $F_i = 0$, then either $N_i = 0$ or $f_i = 0$.) You must solve both equilibrium equations simultaneously, which may not be easy and in fact may be impossible. There will typically be more than one equilibrium; one will be the trivial one with both species absent ($\hat{N}_1 = \hat{N}_2 = 0$). There can be equilibria with one species absent ($\hat{N}_1 = 0, f_2(0, \hat{N}_2) = 0$ or $\hat{N}_2 = 0, f_1(\hat{N}_1, 0) = 0$). There may also be nontrivial equilibria with both species present, so $f_1(\hat{N}_1, \hat{N}_2) = 0$ and $f_1(\hat{N}_1, \hat{N}_2) = 0$.
- Linearize the model about each equilibrium. Describe the rate of change of the deviation from equilibrium, $n_i = N_i - \hat{N}_i$, near equilibrium by the equation

$$\begin{pmatrix} \frac{dn_1}{dt} \\ \frac{dn_2}{dt} \end{pmatrix} = \begin{pmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix},$$

  which in matrix form is

$$\frac{d\vec{n}}{dt} = A\vec{n},$$

  where $\vec{n}$ is the vector of population sizes.
- Compute the elements of the community matrix A as for one species, using the formula

$$\alpha_{ij} = \frac{\partial F_i}{\partial N_j},$$

Box 6.1(cont.)

where the partial derivatives are evaluated at the equilibrium for which we are trying to determine stability.

- Determine stability by computing the eigenvalues λ of the matrix A as the solutions of the equation

$$(\alpha_{11} - \lambda)(\alpha_{22} - \lambda) - \alpha_{12}\alpha_{21} = 0.$$

- If the real part of both solutions λ is negative, the equilibrium is stable. If the real part of either solution λ is positive, the equilibrium is unstable.

(We will discuss complex numbers when we discuss predator–prey models. This will explain our use of the term 'real part'.)

Box 6.2. Stability conditions for a 2×2 matrix.

Both eigenvalues of the 2×2 matrix

$$\begin{pmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{pmatrix}$$

have a negative real part if and only if

$$\alpha_{11} + \alpha_{22} < 0$$

and

$$\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0.$$

If either of the inequalities is violated, then the equilibrium is unstable.

Summary

Our goal is to understand what regulates populations. If regulation results from interactions with other species, the process could be competition or predation. The concept of stability will play a central role in our investigation of interactions between species. We have presented both a way to compute stability for two-species models and a discussion of the rationale for using stability as a central theme. It is important to recognize the limitations of using stability as the means to understand the dynamics of species in nature – there are both biological and mathematical problems. In the following chapters, we will use approaches based on stability and additional ways of understanding the dynamics of interacting species.

Problems

1. Discuss why concepts of stability of mathematical models are likely (or are not likely) to be useful approaches when trying to understand why we observe the communities we see in nature. If you see difficulties with the concept of stability, can you suggest alternative concepts?
2. In this chapter we emphasize the role of two-species interactions for studying the dynamics of interacting species. Explain both the advantages and potential pitfalls of focusing on the interactions between two species, as opposed to looking at more than two species. (You need to indicate which species is 'species 1' and which is 'species 2'.)
3. Later, when we actually analyze models of interacting species, the following will be important: classify models as predator-prey, competition, or mutualist by determining the signs of $\frac{\partial f_1}{\partial N_2}$ and $\frac{\partial f_2}{\partial N_1}$, the change in per capita growth, as the numbers of the other species are changed.

Suggestions for further reading

The classic paper by Hairston, Smith and Slobodkin (1960) sets the stage for any discussion of population regulation. For more recent work on this subject see the edited books by Carpenter and Kitchell (1993) and Polis and Winemiller (1996).

Concepts of stability in an ecological context are discussed in Lewontin (1969) and Holling (1973).

The survey paper of Connell and Sousa (1983) provides important data on stability, with the paper of Hanski (1990) giving an update on this important topic. Issues related to chaos and stability are discussed in Hastings et al. (1993).

The approach to modeling two-species interactions presented here began with the classic work of Lotka (1926, 1932) and Volterra (1926, 1931). May (1975) presents a more modern, in-depth treatment of this topic.