6

Interactions Between Species

In this chapter we begin our examination of interactions between species. For two reasons, we will focus only on the interactions between two species.

- There are some natural systems that come close to being two species systems, such as the predator–prey interaction between wolves and large ungulates or the interaction between hosts and parasitoids.
- Before we can hope to understand systems with more than two species, we will need to understand systems with two species. Two-species models are simpler both biologically and mathematically.

We start by outlining the different kinds of interactions possible between pairs of species. If both species use a common resource, or inhibit each other, each will have a negative effect on the other. We call this kind of interaction *competition*.

A second kind of interaction involves the consumption of one species by another. We will call this a *predator–prey* system, where the predator eats the prey. The interaction is predation. A similar situation would be one where an animal eats a plant, so more generally we can speak of *exploiter–victim* interactions.

A third kind of interaction, which we do not discuss in detail here, is one in which each species benefits the other. One example is the relationship between a plant species and a pollinator whereby the plant benefits by having its seeds pollinated and the pollinator benefits by collecting nectar (a food source). This is called *mutualism*. These three classes do not encompass all possible interactions, but are a useful categorization.

How would you classify the interaction between humans and a potentially fatal disease?
Where do decomposers fit into this classification?

The paper by Hairston, Smith, and Slobodkin (1960) has had such an impact that it is often referred to by their initials, HSS.

As already noted, a long-standing question in ecology is what actually regulates populations in nature. This question was expressed quite forcefully by Hairston, Smith, and Slobodkin (1960), who suggested that since the earth is 'green' – live plant material is abundant – then predation, not food limitation or competition, must act to regulate the populations of herbivores (consumers of plant material). This appealing argument may be correct, or it may be that much of the green and apparently edible plant material is in fact not easily consumed because it is protected by either physical or chemical means. HSS goes on to state that the consumers of herbivores are themselves limited by their food supply; they are regulated by competition. The ultimate goal of our study of population interactions is to shed light on this question of what regulates populations: to examine the consequences of different kinds of regulation and elucidate ways to determine which form of regulation is occurring.

In this chapter, we set up the overall approach we will use to examine population interactions that could serve to regulate populations in nature. We will consider both the intuitive concept of stability and a precise definition of stability. We also look at specific steps we will use in analysis and computation of the stability of equilibria.

6.1 Two-species models

Before turning to models of the specific interactions we have defined, we explore some general features of two-species models, as well as some issues central to our attempts to understand the interactions between two species. The general form of the models we will examine in succeeding chapters is the natural extension of the one-species models we have examined earlier. Let N_i be the number of individuals in species i. In a continuous time model, we will assume that

How would the different kinds of interactions between species be reflected in the per capita growth rates f_i?

$$\frac{dN_1}{dt} = N_1 f_1(N_1, N_2) \tag{6.1}$$

$$\frac{dN_2}{dt} = N_2 f_2(N_1, N_2), \tag{6.2}$$

where f_i is the per capita growth rate of species i as a function of the numbers of species 1 and 2. This framework can be used to examine the different interactions of competition, predation, mutualism, and even diseases. We will use an analogous discrete time model later. Before we can focus on the consequences and causes of competition, predation, and diseases, we need to focus on the tools we will use to explore these models.

Concept of stability

Underlying all our investigations of two-species systems is the concept of *stability*. We have used this concept in our one-species models, and will define it precisely in the next section. One rationale underlying the use of stability is the claim that the systems we see in nature correspond to stable solutions of the models we use to describe these systems. This claim is controversial for both biological and mathematical reasons.

The biological controversy over stability is essentially the question of how stable natural systems really are. Connell and Sousa (1983) attempted to provide an empirical answer to this question. Their data, given in Figure 6.1, show that variability in natural populations often is quite high. What has remained a subject of controversy is the cause of the variability that is observed – is it the result of ecological processes at the level of the population, or is it a reflection of environmental variability?

The mathematical controversy will become clearer when we give our definition of stability, but the problem is that our notion of stability, as we have seen earlier, strictly relates only to behavior near equilibrium. Our ultimate goal is to understand the dynamics of two-species systems, and not just their behavior near equilibrium. However, there still is a rationale for beginning with stability

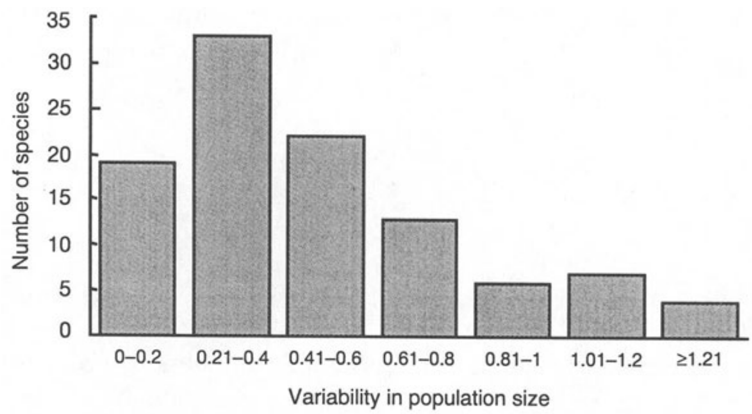

FIGURE 6.1. Population size variability (from Connell and Sousa 1983). This is a plot of the number of species exhibiting different levels of population stability, defined as the standard deviation of the logarithm of population sizes for the species. The original data on population sizes were obtained from a literature survey.

analysis. The first step toward understanding the dynamics of a system is to understand its possible equilibrium behavior, because complete solutions are almost always impossible. In contrast to one-species models, there are virtually no two-species models for which we can write down an explicit solution.

6.2 Definition of stability

We will first precisely define stability in the context of equilibrium behavior. The intuitive concept is that an equilibrium is *stable* if the system returns to the equilibrium when perturbed. To make this definition more precise we need to define carefully the notion of return to equilibrium and perturbation. A system is *locally stable* if for some sizes of perturbation – which might be arbitrarily small – away from the equilibrium, the system stays near the equilibrium. If in addition, the system approaches the equilibrium through time, it is said to be *locally asymptotically stable*. This notion is biologically suspect because we do not expect arbitrarily small perturbations, but the concept is mathematically convenient. When we use this notion in our biological reasoning we are as-

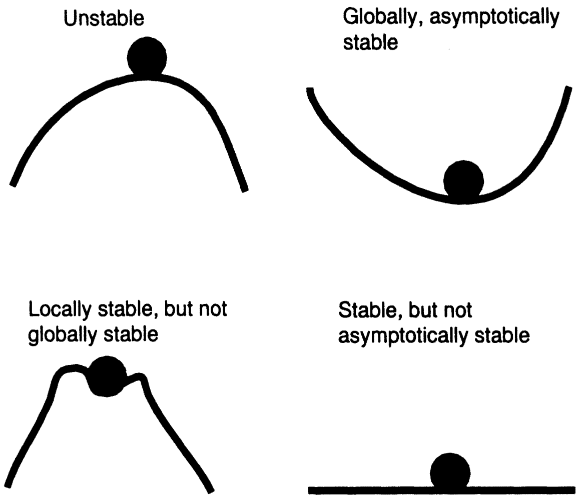

FIGURE 6.2. Concepts of stability used in analyzing ecological models. The ball 'rolls downhill'.

suming that the system can, in fact, withstand perturbations that are not arbitrarily small.

We can also define *global stability*, where we allow perturbations of arbitrary size within the confines of a particular model. The notion of global stability can be used when we do not want to restrict attention to arbitrarily small perturbations, but we must remember that we are still working within the confines of a particular model. Examples of biological circumstances that would cause a system to leave the confines of a particular model could be the addition of a species not included in the model, or the complete removal of a species.

Large perturbations might be fire, or a hurricane.

We use perturbation for temporary effects. Long term changes, like global climate change, are systematic changes in a model.

6.3 Community matrix approach

We will develop the general approach used to determine local asymptotic stability, which depends on the mathematical tools we introduced to study age-structured models. Because we are focusing on local asymptotic stability, we need only consider arbitrarily small perturbations. Thus, we only need to consider the dynamics of the model near equilibrium, as we did for the one-species model.