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Long-Term Dynamics or Equilibrium

The previous chapters in this unit focused on how a biological process that can be in one of a few states (such as disease states of susceptible, exposed, infected, and immune) can be modeled to project what fraction of a population changes states over short periods of time. Our objective in this chapter is to extend these ideas to long time periods. In the landscape change case, we may want to know the long-term implications of disturbances, such as fire, storms, and insect outbreaks, on the vegetation across the landscape. We essentially want to take the matrix multiplication approach we developed earlier and apply it over many time periods. An important question in landscape ecology is whether, overall, the fraction of the landscape in each class is always changing or whether the landscape stabilizes. That is, does the landscape and then stays near these values?

You can certainly think of simple cases in which a landscape has been completely urbanized so that there is no longer any forest or in which a region is dammed so that area that was forest is now underwater in a lake. In these cases, it is easy to intuit what happens in the long term, but in many real-world situations, such as recurring fires, it is not easy to tell what happens if fires don't occur too often, particularly from the perspective of the whole landscape. For example, about 10% of the land area of the nonpolar regions of the planet are maintained in savannas (a grassy or herbaceous layer with a thin overstory canopy of trees) because of disturbances, such as fire and foraging by herbivores. So our objective in this chapter is to point out that matrix methods can be used to determine the long-term structure of a landscape. Furthermore, we can determine whether this long-term structure is stable in the face of perturbations, such as a short period of changed environmental conditions that lead to higher fire frequencies and thus a changed landscape or a period of harvesting in which forest is removed. A biological system that stays mostly unchanged over time is said to be at equilibrium, and it is stable if it returns to this equilibrium following a small change in the system. This is closely related to the idea of homeostasis in physiology, which we will discuss later in the text.

8.1 Notion of an Equilibrium

Recall the succession models of Section 6.3. After a long enough time period, if you make some additional calculations, you will see that the fraction of the landscape in each class (submerged, saturated, and dry) will approach some constant. In the simplest model (Example 6.3), all the land will move to the "climax" state, in this case, the dry state. Thus, the vector that describes the landscape would eventually become very close to

 $\begin{vmatrix} 0\\0\\1\end{vmatrix}$.

However, when we add more complexity to the system (as in Example 6.6), each class of the system will eventually approach some fixed fraction. What we want to do now is define a mathematical method to find these "final" states: the jargon for this is that we are finding an "eigenvector" for the system. In the models presented in this chapter, the *eigenvector* is a vector whose elements tell us what fraction of the system each class will have after a long time. This is also called the *long-term equilibrium state* of the system.

8.2 Eigenvectors

Suppose that we are modeling a nonfatal disease for which either an individual is susceptible to acquiring the disease (S), is infected with the disease (I), or has recovered from the disease and is susceptible again (we built such a model in Example 6.6 for a common cold spreading among a dormitory population). Suppose that in this model, each day 10% of the susceptibles become infected and 20% of the infected recover and become susceptible again. Then, the transfer matrix T that models the daily change in this population is

$$\mathbf{T} = \begin{bmatrix} 0.9 & 0.2\\ 0.1 & 0.8 \end{bmatrix}.$$

(Review Example 6.6 for how such a matrix is constructed.) Suppose that at time t = 0, we have 297 susceptible individuals and three infected individuals, and we assume that no new individuals enter the population and no one in the population dies or leaves. Thus, the population size remains at a constant size of 300 individuals. Then, the vector

$$\mathbf{x}(0) = \begin{bmatrix} 297\\3 \end{bmatrix}$$

describes the structure of the population at time t = 0.

What do we expect to happen over time? How many individuals do we expect to be infected after 50 days? 100 days? 365 days?

Recall that to get the population structure after 1 day, t = 1, we would multiply

$$\mathbf{x}(1) = \mathbf{T}\mathbf{x}(0).$$

If we then wanted to know the population structure after 2 days, t = 2, we would multiply again:

$$\mathbf{x}(2) = \mathbf{T}\mathbf{x}(1) = \mathbf{T}(\mathbf{T}\mathbf{x}(0)) = \mathbf{T}^2\mathbf{x}(0).$$

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In general, we have

$$\mathbf{x}(1) = \mathbf{T}\mathbf{x}(0) = \begin{bmatrix} 267.9\\ 32.1 \end{bmatrix}$$
$$\mathbf{x}(2) = \mathbf{T}\mathbf{x}(1) = \mathbf{T}^{2}\mathbf{x}(0) = \begin{bmatrix} 247.5\\ 52.5 \end{bmatrix}$$
$$\mathbf{x}(3) = \mathbf{T}\mathbf{x}(2) = \mathbf{T}^{3}\mathbf{x}(0) = \begin{bmatrix} 233.3\\ 66.7 \end{bmatrix}$$
$$\vdots$$
$$\mathbf{x}(t) = \mathbf{T}\mathbf{x}(t-1) = \mathbf{T}^{t}\mathbf{x}(0),$$

 $\mathbf{x}(50) = \begin{bmatrix} 0.9 & 0.2\\ 0.1 & 0.8 \end{bmatrix}^{50} \begin{bmatrix} 297\\ 3 \end{bmatrix} = \begin{bmatrix} 200\\ 100 \end{bmatrix},$

$$\mathbf{x}(51) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^{51} \begin{bmatrix} 297 \\ 3 \end{bmatrix} = \begin{bmatrix} 200 \\ 100 \end{bmatrix}.$$

It appears that after 50 days, the proportion of the population in each class (or compartment) is no longer changing. We will refer to this characteristic as the *equilibrium*, that is, the situation in which the proportion or number in each class remains constant after some period of time. The vector representing the proportion or number in each class at equilibrium is known as an *eigenvector*. In the disease model we just considered,

 $\begin{bmatrix} 200\\ 100 \end{bmatrix}$

is an eigenvector. Now, just because the population structure is at equilibrium does not mean that individuals are no longer moving between the susceptible and infected classes. There is still movement between the classes; however, the movement is such that the proportion in each class remains constant.

We would like to develop a mathematical method for determining the eigenvector without having to take large powers of matrices. Notice that at equilibrium, $\mathbf{x}(t) = \mathbf{x}(t-1)$. Thus,

$$\mathbf{x}(t) = \mathbf{T}\mathbf{x}(t-1)$$

= $\mathbf{T}\mathbf{x}(t)$
$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}.$$
 (8.1)

Recall from Chapter 6 that a matrix multiplication equation such as this can be written as the system of equations

$$x_1 = 0.9x_1 + 0.2x_2. \tag{8.2}$$

$$x_2 = 0.1x_1 + 0.8x_2. \tag{8.3}$$

Notice that we can rewrite Equation (8.2) as

$$0 = -0.1x_1 + 0.2x_2 \tag{8.4}$$

and that we can rewrite Equation (8.3) as

$$0 = 0.1x_1 - 0.2x_2. \tag{8.5}$$

This shows that the Equations (8.2) and (8.3) are equivalent (since Equations (8.4) and (8.5)are multiples of each other). Since the two equations are equivalent, we essentially have one equation and two unknowns; therefore, we will not be able to uniquely determine both values (only one in terms of the other). Thus, we will use one of the equations to solve for x_1 in terms of x_2 and then choose a value for x_2 .

If we solve Equation (8.2) for x_1 in terms of x_2 , we get

$$0.1x_1 = 0.2x_2 x_1 = 2x_2.$$
(8.6)

Let us choose $x_2 = 1$; then $x_1 = 2x_2 = 2$. So, an eigenvector is

At this point, you should be thinking, "Doesn't this mean an eigenvector is dependent on what value I choose for x_2 ?" Indeed, it does. If we had instead chosen $x_2 = 50$, then $x_1 = 2x_2 = 100$, and the eigenvector would be

 $\begin{bmatrix} 2\\1 \end{bmatrix}$.

An eigenvector for this system is any point (x_1, x_2) on the line $0 = -0.1x_1 + 0.2x_2$. Since the eigenvector is not unique, we will express the eigenvector in a normalized form (a form that is unique). To *normalize* any vector, sum the values of each element of the vector and then divide each element of the vector by that sum. So, if normalizing

the sum of the elements is 3, and the normalized eigenvector is

If normalizing

the sum of the elements is 150, and the normalized eigenvector is

$$\begin{bmatrix} 100/150\\ 50/150 \end{bmatrix} = \begin{bmatrix} 2/3\\ 1/3 \end{bmatrix}.$$

Notice that no matter what value we choose for x_2 , the normalized eigenvector will always be the same.

[10	0]
50	
_	

$\lceil 2 \rceil$	
[1]	,

 $\begin{bmatrix} 2/3\\ 1/3 \end{bmatrix}.$

 $\begin{bmatrix} 100\\50 \end{bmatrix}$,

Now, recall that our population of susceptible and infected individuals was originally comprised of 300 individuals. So at equilibrium, how many individuals are susceptible, and how many are infected? To answer this question, we simply multiply the normalized eigenvector by the total population size, 300:

$$300\begin{bmatrix} 2/3\\1/3\end{bmatrix} = \begin{bmatrix} 200\\100\end{bmatrix}.$$

This is what we expected on the basis of our earlier investigations.

Now, let us apply this method to find the normalized eigenvalue to the ecological succession model that we constructed and investigated in Examples 6.5 and 7.5.

Example 8.1 (Ecological Succession Equilibrium)

Recall that in Examples 6.5 and 7.5, we developed a model for wetland ecological succession consisting of three class: submerged wetlands, saturated but nonsubmerged land, and dry land. The model was defined by the matrix equation

$$\mathbf{v}(t+1) = \begin{bmatrix} 0.94 & 0.02 & 0.01 \\ 0.05 & 0.86 & 0.06 \\ 0.01 & 0.12 & 0.93 \end{bmatrix} \mathbf{v}(t).$$

Find the eigenvector that describes the composition of the wetlands at equilibrium.

Solution: We need to find *u*, *s*, and *d* at equilibrium when

$$\begin{bmatrix} u \\ s \\ d \end{bmatrix} = \begin{bmatrix} 0.94 & 0.02 & 0.01 \\ 0.05 & 0.86 & 0.06 \\ 0.01 & 0.12 & 0.93 \end{bmatrix} \begin{bmatrix} u \\ s \\ d \end{bmatrix},$$
(8.7)

where u is the submerged class, s is the saturated by nonsubmerged class, and d is the dry class. We can represent Equation (8.7) as a system of equations:

$$u = \frac{47}{50}u + \frac{1}{50}s + \frac{1}{100}d.$$
(8.8)

$$s = \frac{1}{20}u + \frac{43}{50}s + \frac{3}{50}d.$$
(8.9)

$$d = \frac{1}{100}u + \frac{3}{25}s + \frac{93}{100}d.$$
(8.10)

Here, each of the coefficients has been rewritten as a fraction (to simplify the algebra). Notice that the sum of Equations (8.8) and (8.9) gives an equation that is the same as multiplying Equation (8.10) by -1. Since the third equation can be written as a sum of the first two, we gain no additional information from the third equation. This means that, we essentially have two equations and three variables. Thus, we must write two of the variables in terms of the third variable and then pick a value for the third variable. Here, we will write u and s in terms of d.

(Continued)

First, we solve Equation (8.8) for u in terms of s and d:

$$\frac{3}{50}u = \frac{1}{50}s + \frac{1}{100}d$$
$$u = \frac{1}{3}s + \frac{1}{6}d.$$
(8.11)

Next, we substitute Equation (8.11) into Equation (8.9):

$$s = \frac{1}{20} \left(\frac{1}{3}s + \frac{1}{6}d \right) + \frac{43}{50}s + \frac{3}{50}d$$

$$= \frac{1}{60}s + \frac{1}{120}d + \frac{43}{50}s + \frac{3}{50}d$$

$$= \frac{263}{300}s + \frac{41}{600}d$$

$$\frac{37}{300}s = \frac{41}{600}d$$

$$s = \frac{41}{74}d.$$
 (8.12)

Now we can substitute Equation (8.12) into Equation (8.11) to get an equation for u in terms of only d:

$$u = \frac{1}{3} \left(\frac{41}{74} d \right) + \frac{1}{6} d$$

= $\frac{41}{222} d + \frac{1}{6} d$
= $\frac{13}{37} d.$ (8.13)

Let us choose d = 74; then

$$u = \frac{13}{37} \cdot 74 = 26$$
, and $s = \frac{41}{74} \cdot 74 = 41$.

Thus, we have the eigenvector

that, when normalized, is

$$\begin{bmatrix} 26/141\\ 41/141\\ 74/141 \end{bmatrix} \approx \begin{bmatrix} 0.184\\ 0.291\\ 0.525 \end{bmatrix}.$$

8.3 Stability

In this section, we ask what would happen if we started with a different initial condition, a different $\mathbf{v}(0)$.

Consider the model that we developed for the spread of a nonfatal disease with two classes S and I described by Equation (8.1) at equilibrium. We saw that if there was an initial population of 300 individuals with only 3 that were infected, at equilibrium there were 200 susceptible individuals and 100 infected individuals. That is, an eigenvector for the system is

 $\begin{bmatrix} 200\\ 100 \end{bmatrix}.$

What would happen if we started with a different ratio of susceptible to infected individuals? Would we still reach the same equilibrium?

Consider starting with

$$\mathbf{x}(0) = \begin{bmatrix} 10\\290 \end{bmatrix},$$

that is, starting with most of the population infected. Then

$$\mathbf{x}(1) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix} \begin{bmatrix} 10 \\ 290 \end{bmatrix} = \begin{bmatrix} 67.0 \\ 233.0 \end{bmatrix}$$
$$\mathbf{x}(2) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^2 \begin{bmatrix} 10 \\ 290 \end{bmatrix} = \begin{bmatrix} 106.9 \\ 193.1 \end{bmatrix}$$
$$\mathbf{x}(3) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^3 \begin{bmatrix} 10 \\ 290 \end{bmatrix} = \begin{bmatrix} 134.8 \\ 165.2 \end{bmatrix}$$
$$\vdots$$
$$\mathbf{x}(10) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^{10} \begin{bmatrix} 10 \\ 290 \end{bmatrix} = \begin{bmatrix} 194.6 \\ 105.4 \end{bmatrix}$$
$$\vdots$$
$$\mathbf{x}(20) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^{20} \begin{bmatrix} 10 \\ 290 \end{bmatrix} = \begin{bmatrix} 199.8 \\ 100.2 \end{bmatrix}$$
$$\vdots$$
$$\mathbf{x}(70) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^{70} \begin{bmatrix} 10 \\ 290 \end{bmatrix} = \begin{bmatrix} 200 \\ 100 \end{bmatrix}.$$

Thus, we can see that, with a very different initial condition, we still approach the same equilibrium.

What if we started with a different population size? What do you expect would happen? For example, say that we started with a population of 30 individuals with only 1 infected at the initial time:

$$\mathbf{x}(1) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix} \begin{bmatrix} 29 \\ 1 \end{bmatrix} = \begin{bmatrix} 26.3 \\ 3.7 \end{bmatrix}$$
$$\mathbf{x}(2) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^2 \begin{bmatrix} 29 \\ 1 \end{bmatrix} = \begin{bmatrix} 24.4 \\ 5.6 \end{bmatrix}$$
$$\mathbf{x}(3) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^3 \begin{bmatrix} 29 \\ 1 \end{bmatrix} = \begin{bmatrix} 23.1 \\ 6.9 \end{bmatrix}$$
$$\vdots$$
$$\mathbf{x}(10) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^{10} \begin{bmatrix} 29 \\ 1 \end{bmatrix} = \begin{bmatrix} 20.3 \\ 9.7 \end{bmatrix}$$
$$\vdots$$
$$\mathbf{x}(20) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^{20} \begin{bmatrix} 29 \\ 1 \end{bmatrix} = \begin{bmatrix} 20.0 \\ 10.0 \end{bmatrix}$$
$$\vdots$$
$$\mathbf{x}(70) = \begin{bmatrix} 0.9 & 0.2 \\ 0.1 & 0.8 \end{bmatrix}^{70} \begin{bmatrix} 29 \\ 1 \end{bmatrix} = \begin{bmatrix} 20.0 \\ 10.0 \end{bmatrix}$$

After enough time has passed, the proportion in each class is the same in both cases: $\frac{2}{3}$ in the susceptible class and $\frac{1}{3}$ in the infected class.

Why does this happen? Recall that when we were solving for the eigenvector, we never utilized the initial condition information. The eigenvector depends only on the model, not on the initial condition. Thus, it does not matter what initial condition we start with: we will always approach the same equilibrium.

If the eigenvector depends only on the model, then we should expect that if we change one of the values in the transfer matrix, it will change the model's normalized eigenvalue.

Example 8.2 (Changing Transfer Rates)

Consider the model that we developed for the spread of a nonfatal disease with two classes S and I described by Equation (8.1) at equilibrium. Suppose now that each day, 30% of the infected individuals recover and become susceptible again (instead of the 20% we had before). Now the model at equilibrium becomes

$$\begin{bmatrix} x_1 \\ x_2 \end{bmatrix} = \begin{bmatrix} 0.9 & 0.3 \\ 0.1 & 0.7 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}.$$

Find the normalized eigenvalue for this model. How does changing the recovery rate of the infected class change the normalized eigenvalue? Does it make biological sense?

(Continued)

Solution: Our model can be written as the system of equations:

$$x_1 = 0.9x_1 + 0.3x_2. \tag{8.14}$$

$$x_2 = 0.1x_1 + 0.7x_2. \tag{8.15}$$

Notice that we can rewrite Equations (8.14) and (8.15) as

$$0 = -0.1x_1 + 0.3x_2. \tag{8.16}$$

$$0 = 0.1x_1 - 0.3x_2. \tag{8.17}$$

Since Equation (8.16) can be written as -1 times Equation (8.17), the two equations are equivalent. Thus, we will use one of the equations to solve for x_1 in terms of x_2 and then choose the value of x_2 . If we solve Equation (8.14) for x_1 in terms of x_2 , we get

 $x_1 = 3x_2$.

Let us choose $x_2 = 1$; then $x_1 = 3$. Thus, an eigenvector of this model is

The normalized eigenvector for this system is

Thus, we see that when we increase the recovery rate of the infected class, the normalized eigenvector has a smaller proportion in the infected class. This does indeed make biological sense and you should guess what happens to the equilibrium structure of the population as the recovery rate continues to increase.

8.4 Matlab Skills

In Matlab, we use the function eig to find eigenvalues (which we will discuss in the following chapter) and eigenvectors. Since the output of this function will not be completely understood until the material of the next chapter is covered, we postpone demonstrating how to find eigenvectors in Matlab until the end of the next chapter.

8.5 Exercises

8.1 Could the matrix below represent a transfer matrix? Why or why not?

$$\begin{bmatrix} 0.7 & 0.2 \\ 0.3 & 0.6 \end{bmatrix}$$

$$\begin{bmatrix} 3/4 \\ 1/4 \end{bmatrix}.$$

 $\begin{bmatrix} 3 \\ 1 \end{bmatrix}$.

- 8.2 Write a matrix of size 3×3 that is a transfer matrix with two of its entries being 0.
- 8.3 Suppose that an eigenvector of a transfer matrix is

 $\begin{bmatrix} 20\\10 \end{bmatrix}.$

Write the normalized eigenvector for this matrix.

8.4 Suppose that an eigenvector of a transfer matrix is

 $\begin{bmatrix} 0.2\\ 0.3 \end{bmatrix}.$

Write the normalized eigenvector for this matrix.

8.5 Suppose that the normalized eigenvector of a transfer matrix in a population model with 2 classes is

 $\begin{bmatrix} 0.4 \\ 0.6 \end{bmatrix}.$

Explain the meaning of that vector in terms of the equilibrium structure of the population after a long time.

For each transfer matrix in Exercises 8.6 and 8.7, find the normalized eigenvector that would describe the equilibrium structure of the system (using that matrix).

- $8.6 \quad \begin{bmatrix} 0.7 & 0.9 \\ 0.3 & 0.1 \end{bmatrix}$
- 8.7 $\begin{bmatrix} 0.7 & 0.4 \\ 0.3 & 0.6 \end{bmatrix}$
- 8.8 Suppose that you are modeling a nonfatal infectious disease. You assume the people within the population that you are modeling are either susceptible to infection or infected. The following flow diagram shows the rates at which individuals flow from one category to the other.



We formed a transfer matrix for this system in Exercise 6.5a.

- (a) Find the normalized eigenvector that describes the system's equilibrium structure.
- (b) Suppose that the rate of infection increases from 0.35/week to 0.50/week. How does this change the equilibrium structure?
- (c) Suppose that the rate of infection decreases from 0.35/week to 0.25/week. How does this change the equilibrium structure?
- **8.9** (From [16]) Strontium-90 is deposited into pastureland by rainfall. To study how this material is cycled through the ecosystem, we divide the system into four compartments and

consider how much Strontium-90 is in each compartment: grasses (G), soil (S), streams (W), and dead organic matter (O). Suppose that the time step is 1 month. A flow diagram displaying the transfer rates of Strontium-90 between compartments is shown below.



We formed a transfer matrix for this system in Exercise 6.5c.

- (a) Find the normalized eigenvector that describes the system's equilibrium structure.
- (b) Using Matlab, find approximately how many months pass before the system reaches its equilibrium structure if 100% of the strontium-90 starts in the grass.
- (c) Using Matlab, find approximately how many months pass before the system reaches its equilibrium structure if 100% of the strontium-90 starts in the streams.
- (d) Using Matlab, find approximately how many months pass before the system reaches its equilibrium structure if 100% of the strontium-90 starts in the dead organic matter.
- (From [16]) Radioisotopes (such as phosphorus-32 and carbon-14) have been used 8.10 to study the transfer of nutrients in food chains. The flow diagram below shows a compartmental representation of a simple aquatic food chain with phytoplankton (P), zooplankton (Z), and water (W) and the transfer rates of nutrients between these compartments.



0.05/hr (excretion)

One hundred units (e.g., microcuries) of tracer are dissolved in the water of an aquarium containing a species of phytoplankton and a species of zooplankton.

- (a) Construct the transfer matrix that represents the above flow diagram.
- (b) Predict the state of the system over the next 6 hours.
- (c) Find the normalized eigenvector that describes the system's equilibrium structure.