28 SUCCESSION

Objectives

- Understand the concept of succession and several theories of successional mechanisms.
- Set up a spreadsheet matrix model of succession.
- Use the model to explore predictions of various theories of succession.

INTRODUCTION

Succession is change in community composition at one site over time-scales longer than a year and shorter than millenia. We exclude shorter time-spans because we want to exclude cyclic seasonal changes in abundance, and longer time-scales because we want to exclude evolutionary changes and responses to climate changes.

Succession may occur on newly exposed substrate, such as glacial till or fresh lava, in which case it is called **primary succession**. Succession may also occur on previously vegetated soil, from which much or all of the biota has been removed by some disturbance, such as fire or clear-cutting. In this case, we call it **secondary succession**.

A Markov Chain Model of Succession

Primary and secondary succession often differ in the sequence of organisms that appear at a site and in the mechanisms that determine that sequence. However, we can describe either kind of succession in purely phenomenological terms by specifying transition probabilities from one state of the community to another. The technical term for such a model is a **Markov chain** or **Markov process**. A Markov chain is a sequence of states of a system in which each successive state depends only on the previous state and the transition probabilities between possible states.

To make the concept a bit more concrete, consider algal succession on rock in the intertidal zone of an ocean shore. A storm roils the surf, shifting boulders, and scraping some clean. Let us focus on the surface of one such boulder. After the waters calm, propagules of species A may settle out and begin to grow. Soon thereafter, propagules of species B may settle out on the same rock, compete with species A, and eventually take over the rock. Somewhat later, species C may similarly displace species B. In short, we have a successional sequence of species A → B → C.

The system here is the community (consisting in this case of a single species) occupying the rock surface. The states of the system are "Occupied by bare rock," "Occupied by species A," "Occupied by species B," and "Occupied by species C." Whatever state the system is in at any given time, there is some probability that it will be in each of the other states one time unit later. These probabilities are the transition probabilities.

We can conveniently represent the states of the system, and the transition probabilities between states, in matrix form (Table 1). By convention, the top row of the matrix lists all possible current states of the system (species occupying the rock) at some time t; the left column lists all possible succeeding states of the system one arbitrary time unit later. The entries in the body of the matrix represent the probabilities of each possible transition from one state to another state or the same state over that time period.

Table 1. Matrix of hypothetical transition probabilities between successional states on a rock in the intertidal zone.

		Species occupying the rock at time t			
		Bare Rock	A	B	C
Species occupying the rock at time $t + 1$	Bare Rock	0.10	0.10	0.10	0.10
	A	0.80	0.75	0.02	0.01
	B	0.06	0.10	0.80	0.04
	C	0.04	0.05	0.08	0.85

According to this matrix, bare rock is unlikely ($p = 0.10$) to remain bare from time t to time $t + 1$. The probability that a bare rock will be colonized by species A in that time is 0.80; that it will be colonized by species B is 0.06; and by species C, 0.04. A patch of rock already occupied by species A is likely to remain so ($p = 0.75$), but there is a 10% chance that it will succeed to species B and a 5% chance that it will succeed to species C. There is also a 10% chance that a new disturbance will remove whatever species currently occupies the rock (note the values of 0.10 in the three right-hand cells of the top row).

Notice that each column of the transition matrix adds to 1. This has to be, because we must account for the fate of all patches that began the interval from t to $t + 1$ in each state.

To apply the transition matrix, we must begin with the number of rocks currently in each stage of succession (i.e., bare rock or occupied by species A, B, or C). These numbers are arranged in a **state vector**, which describes the current state of the system. For example, if we examined our intertidal area at some time and found 70% of the rocks were bare, 20% occupied by species A, 5% occupied by species B, and 5% occupied by species C, we could write that as a state vector $\mathbf{s}_t$

$$\mathbf{s}_t = \begin{bmatrix} 0.70 \\ 0.20 \\ 0.05 \\ 0.05 \end{bmatrix}$$

To predict the number of rocks occupied by each species (or bare) in the future, we multiply the state vector by the transition matrix $\boldsymbol{A}$:

$$\mathbf{A} = \begin{bmatrix} 0.10 & 0.10 & 0.10 & 0.10 \\ 0.80 & 0.75 & 0.02 & 0.01 \\ 0.06 & 0.10 & 0.80 & 0.04 \\ 0.04 & 0.05 & 0.08 & 0.85 \end{bmatrix}$$

That is,

$$\mathbf{s}_{t+1} = \mathbf{A} \times \mathbf{s}_t$$

or in our example,

$$\mathbf{s}_{t+1} = \begin{bmatrix} 0.10 & 0.10 & 0.10 & 0.10 \\ 0.80 & 0.75 & 0.02 & 0.01 \\ 0.06 & 0.10 & 0.80 & 0.04 \\ 0.04 & 0.05 & 0.08 & 0.85 \end{bmatrix} \times \begin{bmatrix} 0.70 \\ 0.20 \\ 0.05 \\ 0.05 \end{bmatrix}$$

We can carry our predictions as far into the future as we wish by iterating this matrix multiplication:

$$\mathbf{s}_{t+1} = \mathbf{A} \times \mathbf{s}_t$$

$$\mathbf{s}_{t+2} = \mathbf{A} \times \mathbf{s}_{t+1}$$

$$\mathbf{s}_{t+3} = \mathbf{A} \times \mathbf{s}_{t+2}$$

$$\mathbf{s}_{t+4} = \mathbf{A} \times \mathbf{s}_{t+3}$$

and so on. (If you are unfamiliar with matrix multiplication, or have forgotten the details, consult the Appendix at the end of this exercise.)

We can ask a variety of interesting questions about long-term model predictions. For example, will the system eventually come to equilibrium? If so, will the equilibrium consist of a single species (a **climax**), or will it consist of a stable mixture of species? If the latter, what will be the proportion of each species? Does the eventual state of the system depend on the initial state vector, or only on the transition probabilities?

It may be tempting to conceive of successional changes not from one species to another but of entire communities. This presupposes that communities in a successional sequence are discrete entities, corresponding to the discrete states of a Markov chain. However, the evidence from field ecology shows that communities are not discrete entities, and that succession is not a change from one discrete community to another, but rather individualistic, species-by-species changes in abundance, presence, and absence. Therefore, to model successional change accurately at the community level requires a species-level model.

We can use a Markov chain model, however, if we keep in mind that we are modeling a continuous process as if it proceeded in discrete steps. That is, we may choose to look at community composition at, say, 50-year intervals. With that much time, community composition may have changed enough to permit us to regard communities as discretely different, despite our knowledge that change over the intervening years was individualistic and continuous.

Whether we think of our model as representing species-by-species replacement or whole-community replacement, the mathematics is the same, only our interpretation changes. Indeed, the model is mathematically identical to a Leslie matrix model of a size-structured or stage-structured population.

PROCEDURES

Connell and Slatyer (1977) described three fundamentally different ways in which succession might proceed. Early-arriving individuals ("pioneers") may change the environment in ways that favor other species at the expense of their own offspring, as for example by casting shade or adding organic matter and other substances to the soil. Connell and Slatyer call this the **facilitation model**. Alternatively, early-arriving individuals may simply hold onto their sites, and the only way other individuals can enter the community is if disturbance removes the site-holders. Connell and Slatyer call this the **inhibition model**. Finally, it is logically conceivable that existing individuals may have no significant influence, either positive or negative, on the establishment of others. Connell and Slatyer call this the **tolerance model**. You can examine the outcome of each of these models with the Markov chain model set up in this exercise.

As always, save your work frequently to disk.

INSTRUCTIONS / ANNOTATION

A. Markov chain model of succession.

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 1

The text items are all literals, so just select the appropriate cells and type them in. The transition probabilities correspond to Table 1.

	A	B	C	D	E
1	***Succession***				
2	A Markov-chain model of community change over time.				
3	Example: Table 1 from Introduction				
4		Transition matrix: A			
5		Bare rock	Species A	Species B	Species C
6	Bare rock	0.10	0.10	0.10	0.10
7	Species A	0.80	0.75	0.02	0.01
8	Species B	0.06	0.10	0.80	0.04
9	Species C	0.04	0.05	0.08	0.85
10	Sum	1.00	1.00	1.00	1.00

Figure 1

2. Enter formulae to sum up each column of transition probabilities.

In cell B10 enter the formula **=SUM(B6:B9)**. Copy this formula into cells C10–E10. You will use these sums to check your transition probabilities when you change them later in the exercise. Remember that each column of the transition matrix must add up to 1.

3. Enter column and row headings shown in Figure 2. Continue the sequence of time values to the right until you reach $t = 20$ in column AB.

	G	H	I	J	K	L
4		State vectors: *s* (*t*)				
5	Time (*t*)	0	1	2	3	4
6	Bare rock	0.70				
7	Species A	0.20				
8	Species B	0.05				
9	Species C	0.05				
10	Sum	1.00				

Figure 2

4. Enter the initial state vector.

Enter the values shown in cells H6 through H9.

5. Enter a formula to total the frequencies in the initial state vector.

In cell H10 enter the formula **=SUM(H6:H9)**.
This is another check on your model. State vectors must also add up to 1.

6. Enter a formula to calculate the state vector at time 1.

In cell I6 enter the formula **=$B6*H$6+$C6*H$7+$D6*H$8+$E6*H$9**.
Be careful to use absolute and relative addresses exactly as shown. This allows you to copy the formula into other cells and get correct results. Any deviation from the formula will produce erroneous results.

7. Copy the formula from cell I6 into cells I7 through I9.

8. Copy cells I6 through I9 into cells J6 through AB9

9 Your spreadsheet is complete. Save your work.

10. Graph the proportion of rock surfaces occupied by each species (or bare rock) against time.

Select cells G5 through AB9. Make an XY (Scatterplot) Chart. Edit your graph for readability. It should resemble Figure 3.

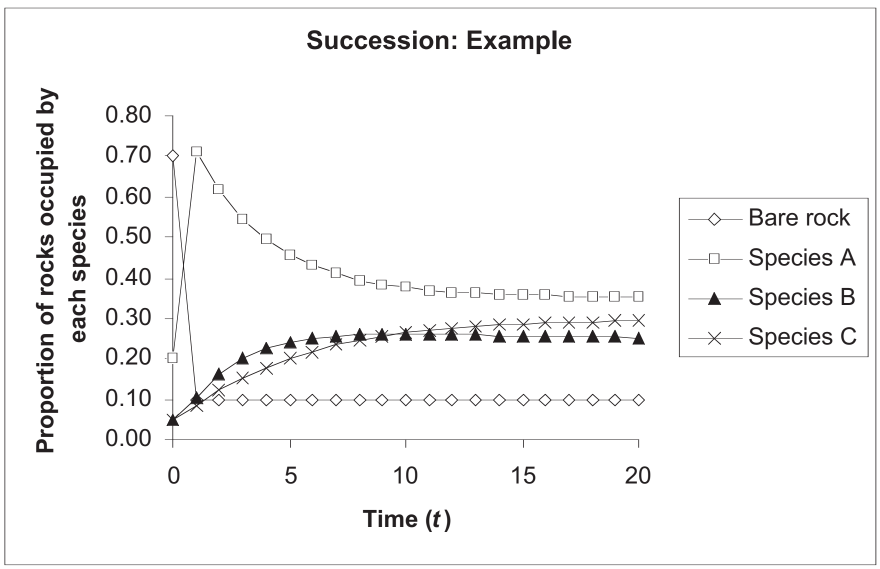

Figure 3

B. Facilitation model.

1. To see the predictions of Connell and Slatyer's (1977) facilitation model of succession, change the transition probabilities in your spreadsheet to those given in Table 2.

These probabilities indicate that bare rock is frequently replaced by species A, species A by species B, and species B by species C. All these species are equally likely to be replaced by bare rock. Species C is unique in that it is almost always replaced by itself, only rarely by bare rock, and never by other species.

Table 2. Transition matrix for the Connell and Slatyer (1977) facilitation model.

	Transition Matrix: Facilitation			
	Bare Rock	Species A	Species B	Species C
Bare Rock	0.10	0.10	0.10	0.01
Species A	0.90	0.10	0.00	0.00
Species B	0.00	0.80	0.10	0.00
Species C	0.00	0.00	0.80	0.99
Sum	1.00	1.00	1.00	1.00

2. Change the initial state vector so that the initial frequency of Bare Rock is 1.00, and all other species have frequencies of 0.00. Graph the results.

Your graph should resemble Figure 4.

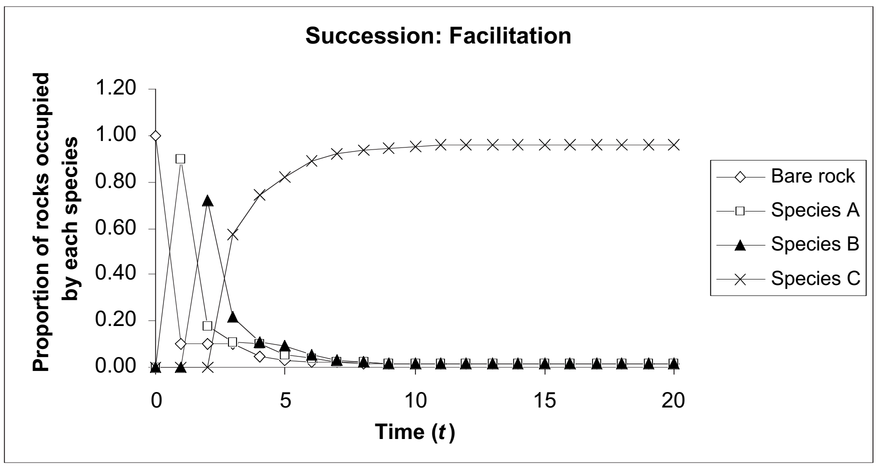

Figure 4

C. Inhibition model.

1. To see the predictions of Connell and Slatyer's inhibition model, enter the transition probabilities given in Table 3 in your spreadsheet.

These probabilities indicate that each species is equally likely to colonize bare rock, and all species are equally susceptible to disturbance. The transition probabilities between species are all 0.00, indicating that each species holds its site and inhibits occupancy by al others. Replacement occurs only by disturbance.

Table 3. Transition matrix for the Connell and Slatyer (1977) inhibition model.

	Transition Matrix: Inhibition			
	Bare Rock	Species A	Species B	Species C
Bare Rock	0.10	0.10	0.10	0.10
Species A	0.30	0.90	0.00	0.00
Species B	0.30	0.00	0.90	0.00
Species C	0.30	0.00	0.00	0.90
Sum	1.00	1.00	1.00	1.00

2. Keep the initial state vector set with the initial frequency of bare rock at 1.00 and all other frequencies at 0.00. Graph the results

Your graph should now resemble Figure 5.

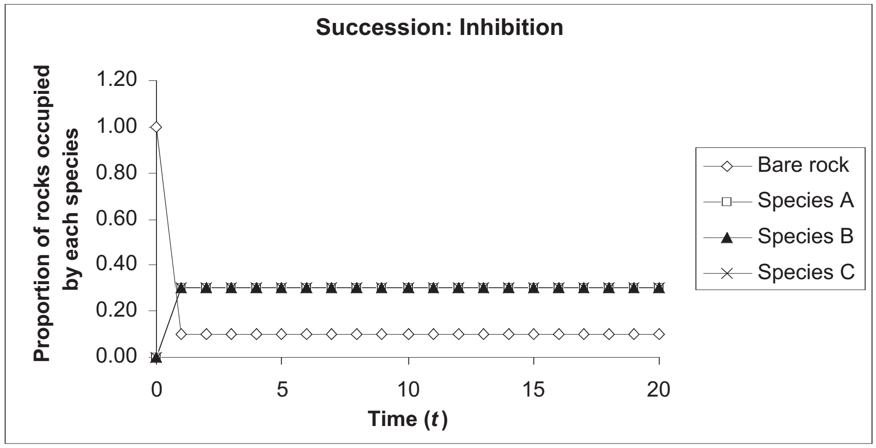

Figure 5

D. Tolerance model.

1. To see the predictions of Connell and Slatyer's tolerance model, enter the transition probabilities given in Table 4.

As you can see, all the transition probabilities are equal. This indicates that any species is equally likely to replace any other, and equally susceptible to disturbance.

Table 4. Transition matrix for the Connell and Slatyer (1977) tolerance model.

	Transition Matrix: Tolerance			
	Bare Rock	Species A	Species B	Species C
Bare Rock	0.25	0.25	0.25	0.25
Species A	0.25	0.25	0.25	0.25
Species B	0.25	0.25	0.25	0.25
Species C	0.25	0.25	0.25	0.25
Sum	1.00	1.00	1.00	1.00

2. Keep the initial state vector set with the initial frequency of bare rock at 1.00 and all other frequencies at 0.00. Graph the results.

Your graph should now resemble Figure 6.

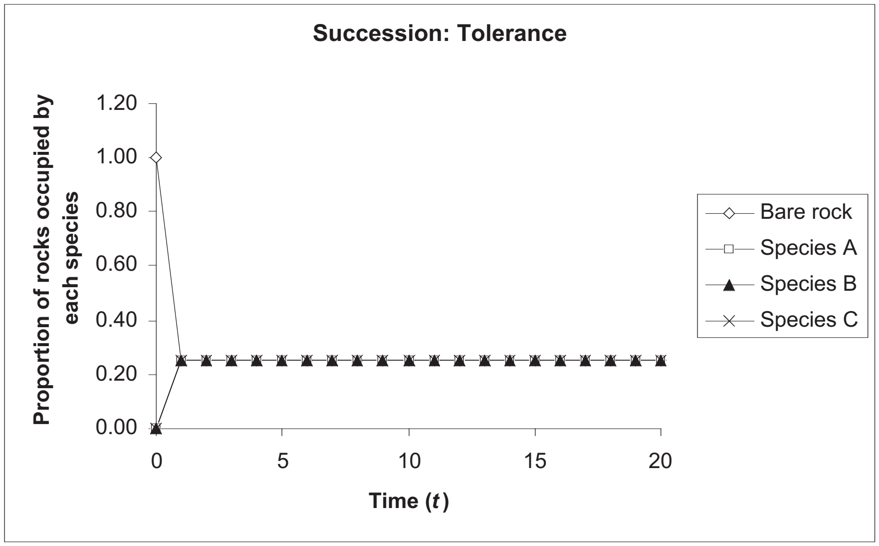

Figure 6

QUESTIONS

1. Will the system eventually come to equilibrium? That is, will the frequencies of rocks occupied by three species and bare rock stop changing?
2. Does the equilibrium consist of a single species occupying all rocks, or is there a stable mixture of species?
3. Are the equilibrium frequencies determined by the initial frequencies (initial state vector), by the transition probabilities, or both?
4. Will any valid transition matrix (valid meaning that the columns each add to 1) result in equilibrium? Or are there valid transition matrices that do not lead to an equilibrium?
5. Describe each of Connell and Slatyer's (1977) models of succession, based on the information in the graphs you produced in Sections B–D of this exercise.

(A) Facilitation model (Figure 4)
(B) Inhibition model (Figure 5)
(C) Tolerance model (Figure 6)

LITERATURE CITED

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 119–144.

Appendix: MATRIX MULTIPLICATION

A matrix is a rectangular array of numbers characterized by the number of its rows and columns. Matrix **A** below is a 2×3 matrix. A matrix with one row or one column is called a vector. Vector **B** is a 3×1 vector.

$$\mathbf{A} = \begin{bmatrix} 31 & 7 & 23 \\ 11 & 5 & 17 \end{bmatrix} \qquad \mathbf{B} = \begin{bmatrix} 2 \\ 4 \\ 6 \end{bmatrix}$$

Matrices and vectors can only be multiplied by other matrices or vectors if the number columns of the first equals the number of rows of the second. Thus, matrix **A** could be multiplied by vector **B**; that is, $\mathbf{A} \times \mathbf{B}$ is a valid matrix multiplication.

Matrix multiplication is not commutative: that is, $\mathbf{A} \times \mathbf{B} \neq \mathbf{B} \times \mathbf{A}$. Indeed, $\mathbf{B} \times \mathbf{A}$ cannot be done, since the number of columns in **B** does not equal the number of rows in **A**.

Finally, here is how to do $\mathbf{A} \times \mathbf{B}$:

$$\begin{bmatrix} 31 & 7 & 23 \\ 11 & 5 & 17 \end{bmatrix} \times \begin{bmatrix} 2 \\ 4 \\ 6 \end{bmatrix} = \begin{bmatrix} 31 \times 2 + 7 \times 4 + 23 \times 6 \\ 11 \times 2 + 5 \times 4 + 17 \times 6 \end{bmatrix} = \begin{bmatrix} 228 \\ 144 \end{bmatrix}$$

Notice that the resulting matrix (vector in this case) has the same number of rows as the first matrix and the same number of columns as the second.