Answers to Exercise 28

Succession

1. You can see from your graph that the system does come to equilibrium with the given values of the transition matrix and initial state vector. The proportion of bare rock goes to its equilibrium value of 0.10 in one time step. The other frequencies continue to change, but by $t = 10$, they are approaching equilibrium at $f(A) = 0.35$, $f(B) = 0.25$, and $f(C) = 0.29$.

   Note that this equilibrium is **dynamic**. That is, the species occupying any given rock continues to change over time (according to the transition probabilities), but the overall mix remains the same.

2. You can also see that the equilibrium in this case consists of a stable mixture of all three species and bare rock. No one species excludes the others.

3. You can determine whether the equilibrium state is determined by the transition matrix, by the initial state vector, or both by systematically changing the values in your spreadsheet.

   A good place to start is by changing the initial state vector. Enter different values into cells H6 through H9, making sure that the vector adds to 1. You should find that changing the initial state vector does not change the equilibrium state, although it may change how long it takes the system to reach equilibrium. This property of some systems to reach the same end point regardless of starting state is called **ergodicity**.

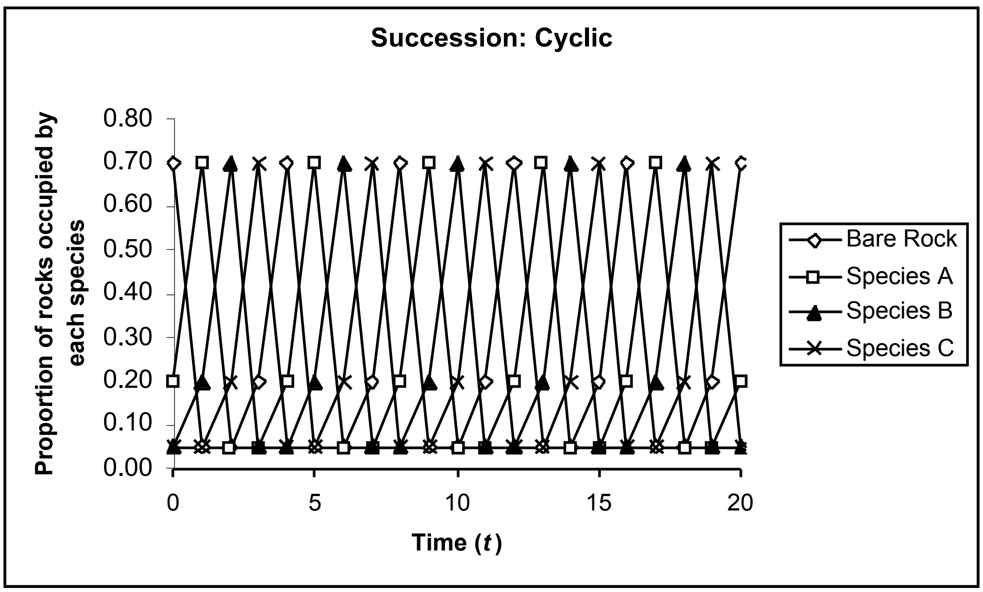
   Next try changing the transition probabilities. Enter different values into cells B6 through E9, making sure that each column of the resulting matrix adds to 1. You should find that changing the transition frequencies changes the equilibrium state. You may find transition probabilities that do not lead to equilibrium.

   Ergodicity and the fact that the transition matrix alone determines equilibrium are important properties of Markov chains. They imply that you may be able to determine the end point of the chain directly from the transition matrix, without iteratively calculating all the intermediate stages, as you do in your spreadsheet model. Such solutions are, however, beyond the scope of this exercise.

4. As you were changing your transition matrix to answer Question 3, you may have found matrices that did not lead to equilibrium. In any case, try the values given in the table and graph on the following page.

Example: A transition matrix that does not lead to equilibrium.

	Transition Matrix: Nonequilibrium			
	Bare Rock	Species A	Species B	Species C
Bare Rock	0.00	0.00	0.00	1.00
Species A	1.00	0.00	0.00	0.00
Species B	0.00	1.00	0.00	0.00
Species C	0.00	0.00	1.00	0.00
Sum	1.00	1.00	1.00	1.00



The figure above shows no trend toward equilibrium. Careful examination reveals cyclic replacement: Bare Rock → Species A → Species B → Species C → Bare Rock. This cycle repeats indefinitely. Such cyclic replacement has been proposed to occur among some plant species. Whether cyclic succession actually occurs or not, this example shows that not all valid transition matrices lead to equilibrium.

5A. The facilitation model graphed in Figure 4 shows that the system reaches an equilibrium dominated by species C, with very small frequencies of the other species and bare rock. These small residual frequencies are maintained by infrequent disturbance (low transition probabilities from all other states to bare rock; top row of transition matrix). You can confirm this by changing the probability of the transition species C → bare rock to 0.00 and the probability of species C → species C to 1.00. With these values, the frequency of species C eventually reaches 1.00 and all others go to 0.00.

This is the classic relay floristics model of succession, first proposed by F. E. Clements early in the twentieth century. According to this concept, each species (or community) changes the environment in ways that favor later successional species. This results in an orderly replacement of species or communities over time, eventually leading to a self-perpetuating climax (species C in this case).

5B. The inhibition model graphed in Figure 5 shows that the system goes to equilibrium in one time step, with the frequency of bare rock dropping to 10%, and the frequencies of the three species rising to 30% each. In a sense, there is no succession here—that is, there is no orderly sequence of species replacements. The equilibrium is still dynamic, because individuals continue to be removed by disturbance and replaced randomly.

All three species have equal equilibrium frequencies because their turnover rates are equal. You can confirm this by giving one species a lower probability of transition to bare rock. The equilibrium frequency of that species will increase. This models a succession in which progressively longer-lived species replace shorter-lived ones. “Climax” in such a succession would consist of the longest-lived species.

5C. The tolerance model graphed in Figure 6 shows that the system goes to equilibrium in one time step, with the frequency of all system states equal at 25%. As in the inhibition model, there is no orderly sequence of species replacements. The equilibrium is still dynamic, because individuals continue to be removed by disturbance and replaced randomly.

In contrast to the inhibition model, the tolerance model predicts equal frequencies of all species even if one is less susceptible to disturbance. To see this, lower the transition probability to bare rock for any one species. The equilibrium frequency of bare rock will decline, and the equilibrium frequencies of all three species will increase equally.