20 METAPOPULATION DYNAMICS

Objectives

- Determine how extinction and colonization parameters influence metapopulation dynamics.
- Determine how the number of patches in a system affects the probability of local extinction and probability of regional extinction.
- Compare “propagule rain” versus “internal colonization” metapopulation dynamics.
- Evaluate how the “rescue effect” affects metapopulation dynamics.

INTRODUCTION

Can you think of any species where the entire population is situated within one patch, where all individuals potentially interact with each other? You will probably be hard pressed to come up with more than a few examples. Most species have distributions that are discontinuous at some spatial scale. In some species, subdivided populations may be linked to each other when individuals disperse from one location to another. For example, butterflies may progress from egg to larvae to pupa to adult on one patch, then disperse to other patches in search of mates, linking the population on one patch to a population on another. This “population of populations” is often called a **metapopulation**, and in this exercise we will explore the dynamics of such interacting systems.

Metapopulation theory was first formalized by Richard Levins in 1969 (Levins 1969, 1970). In Levins’ model, a metapopulation exists in a network of habitat patches, some occupied and some unoccupied by subpopulations of individuals. The dynamics of metapopulations can be explored by examining patch occupancy patterns over time. In the left-hand side of Figure 1, the 100 squares represent 100 patches in a metapopulation at time t. The right-hand side of the figure shows the pattern of patch occupancy at time $t + 1$.

In the traditional metapopulation model (Levins 1970), each subpopulation has a finite lifetime and each subpopulation has the same probability of extinction. Additionally, all unoccupied patches have the same probability of being colonized. At equilibrium, the proportion of patches that are occupied remains constant, although the pattern of occupancy continually shifts as some subpopulations suffer extinction

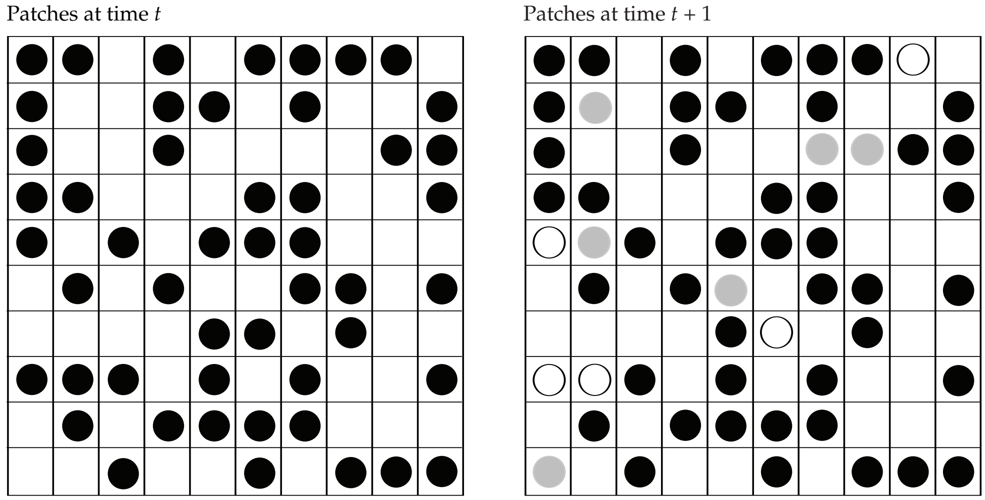

Figure 1 At time t, occupied habitat patches are represented with filled circles; empty squares represent currently unoccupied patches. At time t + 1, some of the patches that were occupied in time t are vacant (open circles), some patches that were vacant at time t are now occupied (gray circles), and some patches maintain their "occupancy status" from time t to time t + 1 (filled circles).

followed by recolonization. This is sometimes referred to as the "winking" nature of metapopulations, as newly colonized patches "wink in" and extirpated patches "wink out." Thus, the classic metapopulation model (sensu Levins 1970) is a "presence-absence" model that examines whether a population is present or absent on a given patch over time, how presence and absence changes over time, and how the entire metapopulation system can persist. In other words, metapopulation models explain and predict the distribution of occupied and unoccupied habitat patches, factors that affect dispersal between patches, and the persistence of the greater metapopulation (Hanski and Gilpin 1997).

Metapopulation Dynamics: Colonization and Extinction

Let's begin our exploration of metapopulation dynamics by defining extinction and colonization mathematically. Patches that are currently occupied in the system have a probability of going extinct, p_e, and a probability of persistence, $1 - p_e$. Patches that are currently empty in the system have a probability of being recolonized, p_i, and a probability of remaining vacant, $1 - p_i$. Since both p_e and p_i are probabilities, their values range between 0 and 1.

Metapopulation dynamics focus on the occupancy patterns of patches over time. We can think about the fate of a given patch over the course of time, and additionally we can consider the fate of the entire metapopulation over the course of time. For a given patch, the probability that a patch will persist for n years in a row is simply the probability of persistence, raised to the number of years in consideration (Gotelli 2001).

$$P_n = (1 - p_e)^n \qquad \text{Equation 1}$$

For example, if a patch has a probability of persistence = 0.8, and we are interested in computing the probability of that patch remaining occupied for 3 consecutive years, $P_3 = 0.8^3 = 0.512$. In other words, if we had 100 occupied patches in a metapopulation, approximately 51.2% of the patches would persist over a 3-year period; 48.8% would likely go extinct within that time period.

If we want to consider the fate of the *entire* metapopulation over time, we need to know the extinction probabilities of each patch, and the number of patches in the system. Given this information, we could compute the probability that all patches would go extinct simultaneously, leading to extinction of the entire metapopulation. Assuming that all patches have the same probability of extinction, the probability that the entire metapopulation will go extinct is simply the p_e raised to the number of patches in the system. Thus, when $p_e = 0.5$ and there are 6 patches in the system, the probability that all 6 patches will go extinct simultaneously is $0.5^6 = 0.0156$. Thus there is about a 1.5% chance that the system will go extinct. Similarly, we can compute the probability of metapopulation persistence as the probability of persistence raised to the power of the number of patches in the system.

$$P_x = 1 - (p_e)^x \qquad \text{Equation 2}$$

Now that we know a little bit about extinction and colonization of patches, let's focus on the dynamics of a metapopulation system, or how patch occupancy patterns change over time. The basic metapopulation model has the form

$$\frac{df}{dt} = I - E \qquad \text{Equation 3}$$

where f is the fraction of patches occupied in the system. For example, if our system contained 25 patches, and 5 of them are occupied, $f = 5/25 = 0.2$. By definition, 20/25 patches are vacant. Equation 3 simply states that the (instantaneous) *change* in the fraction of patches that are occupied depends on the rates of immigration (I) to empty sites and the rates of extinction (E) of occupied sites (Gotelli 2001). If you have completed the exercise on exponential growth, this equation has a form that might be familiar to you, but instead of births and deaths (B and D in the exponential growth model), we are now concerned with I and E. Two critical pieces of information determine I, the rate at which empty patches are recolonized: the number of patches that are currently empty and available for recolonization, and p_i, the probability that an empty patch will actually be recolonized. If f is the fraction of patches that are occupied, then $1 - f$ is the fraction of patches that are currently empty, and we can compute I as

$$I = p_i(1 - f)$$

Now let's focus on E, the rate at which currently occupied patches go extinct. E depends on the number of patches that are currently occupied and available for extinction, as well as p_e, the probability that an occupied patch will go extinct. If f is the fraction of patches that are currently occupied, we can compute E as

$$E = p_e f$$

Substituting the above two values for I and E into Equation 3, we now have a general model of metapopulation dynamics:

$$\frac{df}{dt} = p_i(1-f) - p_e f \qquad \text{Equation 4}$$

This model is called a **propagule rain model** or an **island-mainland model**, because the colonization rate does not depend on patch occupancy patterns—it is assumed that colonists are available to populate an empty patch and that these colonists can originate from either currently occupied patches or from patches outside the metapopulation system. At equilibrium, the fraction of patches remains constant over time, although patches continually "wink in" and "wink out" of existence. How do we solve for this equilibrium?

To solve for the equilibrium fraction of patches, set the left-hand side of Equation 4 to 0 (which indicates that the system is not changing, and the fraction of patches is therefore constant) and solve for f:

$$0 = p_i - p_i f - p_e f$$

$$f = \frac{p_i}{p_i + p_e} \qquad \text{Equation 5}$$

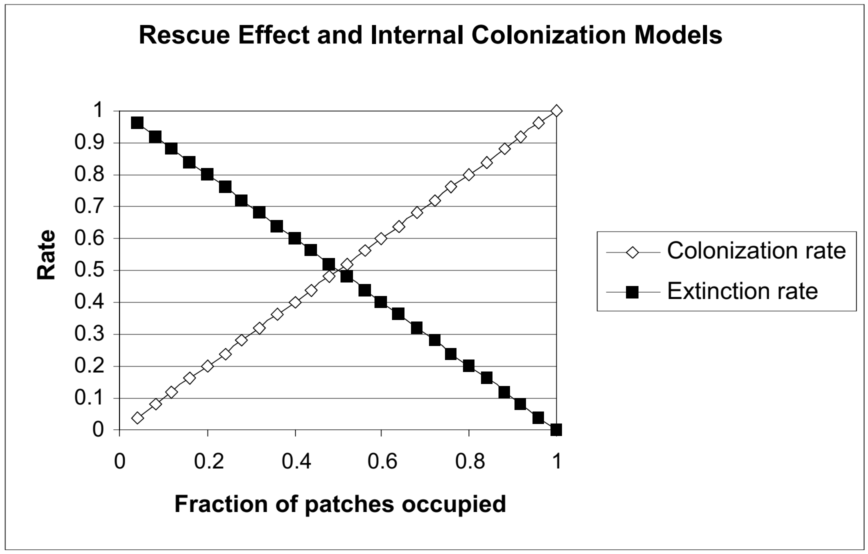

Figure 2 The colonization rate rises as a greater fraction of habitat patches are occupied (the internal coloniation model), whereas extinction rates are higher when fewer habitat patches are occupied (the rescue effect model).

As with all models, the metapopulation model has several assumptions, the most important being that all patches are created equal: p_e and p_i are constant over time and apply to patches regardless of their population size, habitat quality, or other factors. Additionally, this basic model assumes that the explicit location of any patch in relation to other patches is not an important factor in p_e or p_i (Gotelli 2001).

Clearly, some of these assumptions are violated in natural populations, where p_e and p_i are not independent of *f*, the fraction of patches in the metapopulation that are occupied. For example, colonization of an empty patch may be more likely when *f* is high than when *f* is low. When *f* is high, potentially more colonists are available to recolonize a vacant site. When *f* is low, colonists arise from only a few patches and may not be able to colonize empty patches efficiently. This kind of metapopulation model is often called an **internal colonization model** because colonization rates depend on current status (*f*) of the metapopulation system.

Similarly, extinction of a patch may depend on the fraction of patches occupied in the metapopulation system. When *f* is high, there are many potential colonists available to keep a patch from going extinct; when *f* is low, there are fewer potential colonists, and risk of extinction increases. This kind of metapopulation model is often called a **rescue effect model** because extinction rates depend on the current status (*f*) of the metapopulation system. Graphically, the "adjusted" colonization and extinction rates may be proportionally related to the fraction of patches occupied (Figure 2), although the exact relationship between rates and fraction of patches can take a variety of forms.

PROCEDURES

The metapopulation concept has become an important paradigm in conservation biology in recent years, and it is worth exploring some of its assumptions and predictions. In this exercise, you will develop a spreadsheet model of metapopulation dynamics. We will expand the model and explore the internal colonization and rescue effect models in the Questions section. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Set up the model.

1. Open a new spreadsheet file and fill in column and row headings as shown in Figure 3.

	A	B	C	D	E
1	***Introduction to Metapopulation Dynamics***				
2					
3	**Model parameters:**				
4	**x = number of patches in system**				25
5	**n = number of years under consideration**				10
6	**p_e = probability of local extinction**				0.3
7	**1 - p_e = probability of local persistence**				
8	**p_n = probability of continued local persistence**				
9	**p_i = probability of local colonization**				0.9
10	**P_x = probability of regional extinction**				
11	**1 - P_x = probability of regional persistence**				
12	**f = equilibrium number of patches occupied**				

Figure 3

2. Set up a scenario in which there are 25 habitat patches.

Enter the value 25 in cell E4. (The term *metapopulation* implies that there must be at least 2 habitat patches in the system. To begin, we will consider a system in which there are 25 patches.)

3. Consider what will happen to our metapopulation in the next 10 years.

Enter the value 10 in cell E5.

4. In cell E6, set p_e equal to 0.3.

Enter 0.3 in cell E6. Remember that p_e is the probability of local extinction—that is, the probability that any currently occupied patch in the system will go extinct. The value $p_e = 0.3$ means that any occupied patch has a 30% probability of going extinct. (This cell has been shaded to indicate that its value can be manipulated in the spreadsheet.)

5. In cell E7, enter a formula to caculcate the probability that any given occupied patch will persist.

The probability that any occupied patch will persist (i.e., *not* go extinct) is 1 – E6. Thus you can enter the formula **=1-E6** in cell E7.

6. In cell E8, enter a formula to calculate the probability that a patch will be occupied for 10 straight years.

This is simply E7 raised to the tenth power. For a population to persist 10 years in a row, we multiply the probability of persistence by itself for the number of years we are interested in projecting to the future. Recall that you entered the the value 10 in cell E5; thus the formula in cell E8 can be **=E7^E5**, where the ^ symbol indicates the power to which the value in cell E7 is raised.

7. In cell E9, set p_i equal to 0.9.

Enter 0.9 in cell E9. This is the colonization parameter, p_i—the probability that an unoccupied site will become colonized through immigration to that site. (This cell has been shaded to indicate that its value can be manipulated in the spreadsheet.)

8. In cells E10 and E11, enter formulae to calculate the probability of regional extinction and the probability of regional persistence, respectively.

Since you know the probability that each patch will go extinct, and you know how many patches there are in the system, the probability that all of the patches will simultaneously go extinct is simply the probability of local extinction raised to the number of patches in the system. Enter **=E6^E4** in cell E10.

The probably of persistence is simply 1 – E10; thus enter **=1-E10** in cell E11.

9. In cell E12, enter a formula to calculate *f*, the equibrium fraction of patches occupied.

Enter the formula **=E9/(E9+E6)**. This corresponds to Equation 5, $f = p_i/(p_i + p_e)$. Review your work to this point and interpret your results before proceeding.

10. Save your work.

B. Simulate the metapopulation dynamics from Year 0 to Year 1.

Now we are ready to simulate how metapopulations work. You should make sure that your calculation key is set to "Automatic" at this time. Go to Tools | Options | Calculation and select the Automatic button.

1. Set up new column headings as shown in Figure 4.

We'll start with a hypothetical system that consists of 25 patches, where each cell in A14–E18 represents a patch. The first block of cells in the figure below indicates the pattern of patch occupancy in Year 0. The second block of cells (A22–E26) indicates the patch occupancy pattern in Year 1.

	A	B	C	D	E
13	**Initial patch occupancy, year 0**				
14	0	1	1	1	1
15	1	0	0	1	1
16	0	0	1	1	1
17	0	1	0	0	0
18	0	1	1	0	0
19				***f*** **=**	**0.52**
20					
21	**Landscape occupancy, year 1**				
22					
23					
24					
25					
26					
27				***f*** **=**	

Figure 4

2. Enter 0s and 1s as shown in cells A14–E18.

Cells A14–E18 will represent the initial patch occupancy of the 25 patches in the metapopulation system (Year 0). Cell A14 is the upper-left patch in the system; cell C16 is the middle patch in the system, and so on. We let 0 indicate that the patch is currently unoccupied and 1 indicate that the patch is occupied.

3. Format cells A14–E18 so that occupied patches are a different color than the unoccupied patches.

To format the cells, select cells A14–E18 with your mouse, then select Format | Conditional Formatting. The dialog box similar to Figure 5 will appear. Follow the prompts to format your cells. For Condition 1, set the cell value to equal to 1, then click on the Format button, select the Patterns tab, and format the pattern of the cell to be shaded one color. Click OK. Then select the Add >> button to add a new Condition and format cells that are equal to 0 as a different color. When you are finished, click OK and continue to the next step.

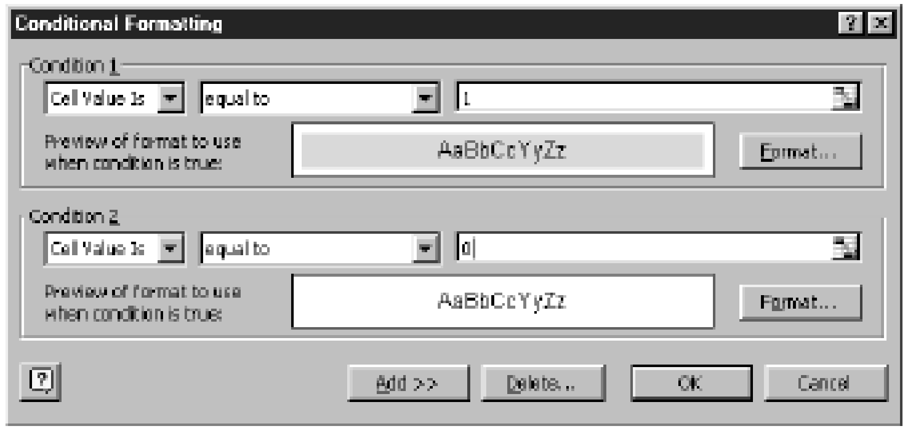

Figure 5

4. In cell E19, enter a formula to calculate the fraction of patches that are occupied, *f*.

We used the formula **=ROUND(SUM(A14:E18)/25,2)**. This formula nests two functions, **SUM** and **ROUND.** Remember that the formula within parentheses will be computed first. Thus the spreadsheet first sums the number of patches occupied and divides this number by the total number of patches in the system (25). The result is then rounded to 2 decimal places with the **ROUND** function.

5. In cell A22, enter a formula to simulate the fate of the upper-left patch (cell A14) in year 1, given its current status and extinction and colonization probabilities. Copy this formula across the 25 patch landscapes (cells A22–E26).

The upper-left patch (A14) in our initial (Year 0) landscape is currently unoccupied. Thus we need a formula that tells the spreadsheet to evaluate whether cell A14 is 0 (unoccupied) or 1 (occupied). If it's 0, then let the patch be colonized according to the colonization probability in cell **E9**. If it's 1, then let it go extinct according to the extinction probability in cell **E6**. We entered the following formula in cell A22:

=IF(A14=0,IF(RAND()<E9,1,0),**IF(RAND()<E6,0,1))**

There are three **IF** formulae here, nested within each other; boldface type has been applied in a way that separates the three formulae. Let's walk through them carefully. Remember that the **IF** formula returns one value if a condition you specify is TRUE, and another value if the condition you specify is FALSE.

The overall structure of the formula in cell A20 tells the spreadshet to examine cell A14. If A14 is 0, then carry out the second IF statement (in light type); otherwise, carry out the third **IF** statement. Since cell A14 is 0 (unoccupied in year 0), the spreadsheet will carry out the second **IF** statement.

The second IF statement, IF(RAND()<E9,1,0), tells the program to draw a random number between 0 and 1 (the RAND() portion of the formula). If this random number is less than the colonization rate given in cell E9, then let the patch be colonized (i.e., assign it the value 1); otherwise, keep it uncolonized by assigning it the value 0.

If cell A14 had been occupied (=1), the spreadsheet would have computed the third **IF** statement, **IF(RAND()<E6,0,1)**. This portion of the formula tells the spreadsheet to draw a random number between 0 and 1. If this random number is less than the extinction rate given in cell **E6**, then let the patch go extinct (assign it the value of 0); otherwise, let it persist by assigning the cell the value 1.

Copy this formula across the landscape to see how patch occupancy changed from year 0 to year 1.

6. Conditionally format cells A22–E26 to add shading.

See Step 3 and Figure 5.

7. In cell E27, enter a formula to calculate the fraction of patches occupied in Year 1.

We entered the formula **=ROUND(SUM(A22:E26)/25,2)**. Your spreadsheet should now look something like Figure 6, although your landscape occupancy pattern for year 1 will likely differ from ours due the nature of the random number function in determining patch occupancy.

In Figure 6, Patch A14 was empty in year 0, but was colonized in year 1 (cell A22). Patch B14 was occupied in year 0 and remained occupied in year 1. Patch C14 was occupied in year 0 but went extinct in year 1.

	A	B	C	D	E
13	**Initial patch occupancy, year 0**				
14	0	1	1	1	1
15	1	0	0	1	1
16	0	0	1	1	1
17	0	1	0	0	0
18	0	1	1	0	0
19				***f*** **=**	**0.52**
20					
21	**Landscape occupancy, year 1**				
22	1	1	0	1	1
23	1	0	1	1	1
24	0	0	0	1	1
25	0	1	0	1	1
26	0	0	0	1	0
27				***f*** **=**	**0.56**

Figure 6

8. Press F9, the Calculate key, several times to simulate changes in patch occupancy from Year 0 to Year 1.

9. Save your work.

Each time you press F9 the spreadsheet generates a new set of random numbers, which in turn affects whether patches become colonized or go extinct. When you press F9, you should see under various scenarios how the fraction of patches in the landscape changes from year 0 to year 1. You should also see the "winking" nature of metapopulations: Patches "wink in" when they become colonized and "wink out" as they go extinct. Given a configuration of occupied patches in year 1, our next step is to determine what the occupancy pattern will be in year 2 and into the future. We will do this in the next step.

C. Simulate metapopulation dynamics over time.

Now we'll track "winking" over time, and determine the fraction of patches that remain occupied over time. When the *fraction occupied* no longer changes across generations, but the *pattern of occupancy* continually shifts, the metapopulation has reached an equilibrium state.

1. Set up new column headings as shown in Figure 7.

	A	B	C	D	E
29	**Landscape occupancy, year *t***				
30					
31					
32					
33					
34					
35				***f*** =	
36					
37	**Landscape occupancy, year *t* + 1**				
38					
39					
40					
41					
42					
43				***f*** =	

Figure 7

2. Copy cells A22–E26, and then go to Edit | Paste Special | Paste Values into cells A30–E34. Do not copy and paste the formulae.

We will now let the pattern of patch occupancy in year 1 be labeled *year t***.** We want to predict what will happen in year *t* + 1—that is to say, in year 2. To continue simulating the metapopulation dynamics over time, the occupancy pattern in year 2 will then be pasted into year *t*, and year 3 will be year *t* + 1. After year 3 is calculated, year 3 will become year *t*, and year 4 will become year *t* + 1 (and so on). You can ignore the cells labeled "Landscape Occupancy, year 0" (cells A14–E18) and "year 1" (cells A22–E26) from this point forward.

3. In cell E35, enter a formula to calculate the fraction of patches that are occupied in year *t*.

We entered the formula **=ROUND(SUM(A30:E34)/25,2).**

4. In cell A38, enter a formula to determine the fate of the upper-left patch in the system (cell A30) for year *t* + 1 (refer to the formula entered in cell A22). Copy this formula across the landscape.

To predict the pattern of occupancy for year *t* + 1, we need to write a formula based on the occupancy patterns in year *t*. We used the formula **=IF(A30=0,IF(RAND()<E9,1,0),IF(RAND()<E6,0,1))**.

5. Calculate the fraction of patches that are occupied in cell E43.

Enter the formula **=ROUND(SUM(A38:E42)/25,2)**.

6. Set up new column headings as shown in Figure 8.

	G	H
2		**Fraction**
3	**Year**	**occupied**
4	0	
5	1	
6	2	
7	3	
8	4	
9	5	
10	6	
11	7	
12	8	
13	9	
14	10	

Figure 8

7. Enter **=E35** in cell H4.

This designates the occupancy rate in the initial landscape.

8. Write a macro to simulate patch occupancy over 10 years.

Under Tools | Options | Calculation, set your caculation key to Manual. Then record a macro to track *f* across years (see Excercise 2, "Spreadsheet Functions and Macros"). Once your macro is in the "Record" mode, do the following:

- Press F9, the calculate key, to determine the pattern of occupancy for Year *t* + 1 (cells A38–A42).
- Select cell E43, the new proportion of the landscape occupied, and select Edit | Copy.
- Select cell H4, then go to Edit | Find. Leave Find What *completely blank*, searching by columns, and select Find Next and then Close (Figure 9).

Figure 9

- Select Edit | Paste Special, and paste in the values, which are the proportion of the landscape that is occupied for that year.
- Use your mouse to highlight cells A38–E42 and select Edit | Copy.
- Now select cell A30, then select Edit | Paste Special and paste in the values. This is your new metapopulation configuration for the following year.
- Select Tools | Macro | Stop Recording.

Now when you press the shortcut key you assigned, the macro automatically determines the proportion of patches that are occupied and enters this value into the appropriate generation. Run your macro until you have tracked your metapopulation over 10 years.

9. Save your work.

D. Create graphs.

1. Graph the fraction of patches occupied over time. Use the line graph option and label your axes fully. Save your work.

Your graph should resemble Figure 10, although the exact fraction of patches will vary due to the random number function used to determine the fate of a given patch.

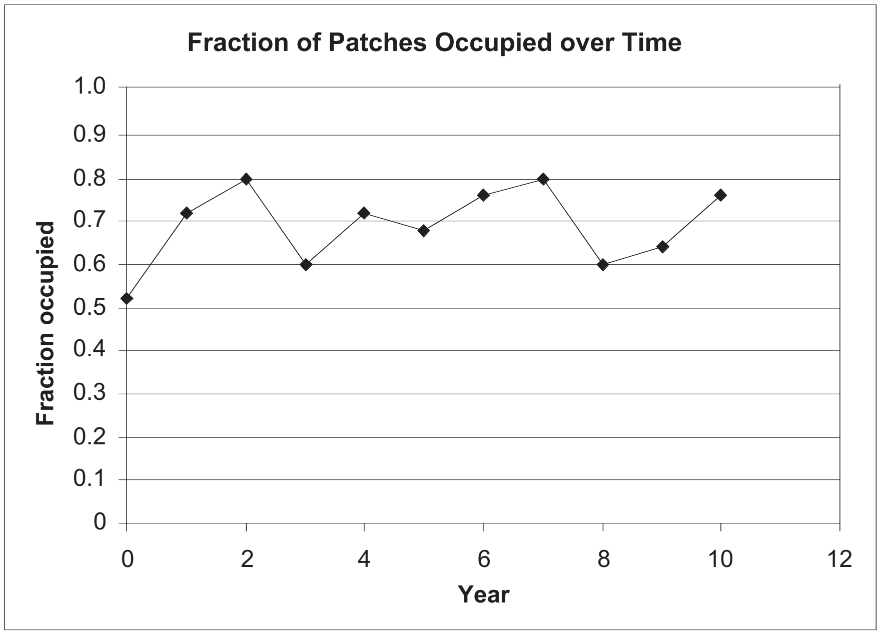

Figure 10

E. Explore the model.

1. Explore your model by changing the probability of extinction and the probability of colonization.

Choose any (reasonable) values you'd like. Run your macro again for 10 years to simulate the new conditions. Remember that as long as the calculation is set to manual, you will always have to press the F9 key to complete any calculations.

In your explorations, don't forget that you'll have to "reset" the cells labeled "Landscape occupancy, year *t*" (cells A30–E34) to reflect the initial conditions you desire. You will also want to clear the simulation results in cells H5–H14 before you run your new macro.

QUESTIONS

1. Compute *f*, the equilibrium number of patches occupied in the metapopulation system. (Refer to Equation 5.) Examine the graph of the metapopulation simulation. Has the population reached an equilibrium value, where the number of patches stays constant over time although the occupancy of each patch changes over time? Why or why not? Extend years in column G to 100. Run your macro until 100 simulations are completed. Is the system in equilibrium by year 100? Why or why not?

2. How does number of patches in a metapopulation system affect the probability of regional persistence (P_x) under a fixed level of local colonization but various scenarios of local extinction? Enter model parameters as shown. To address this question, change cells E4 and E6 according to the table below (cells J8–N15), then record the value in cell E11 in the appropriate cell.

	A	B	C	D	E
3	**Model parameters:**				
4	***x*** **= number of patches in system**				1
5	***n*** **= number of years under consideration**				1
6	p_e **= probability of local extinction**				0.2
7	**1 -** p_e **= probability of local persistence**				0.8
8	p_n **= probability of continued local persistence**				0.8
9	p_i **= probability of local colonization**				0.5
10	P_x **= probability of regional extinction**				0.2
11	**1 -** P_x **= probability of regional persistence**				0.8

Set up column headings as shown, and record $1 - P_x$ (the probability of regional persistence) in the appropriate cell. We have filled in the $1 - P_x$ values for $P_e = 0$ and $P_e = 0.2$ as an example. Fill in the remaining cells. Then select cells K10–N15 and graph your results using the line graph option. Interpret your graph.

	J	K	L	M	N
8		**Number of patches**			
9	***Pe***	**1**	**2**	**4**	**8**
10	0	1	1	1	1
11	0.2	0.8	0.96	0.998	0.999
12	0.4				
13	0.6				
14	0.8				
15	1				

3. How does *f*, the equilibrium fraction of patches occupied, change as function of p_e and p_i? Set up spreadsheet columns as shown:

	J	K	L	M	N	O	P
18		P_i					
19	P_e	$p_i = 0$	$p_i = 0.2$	$p_i = 0.4$	$p_i = 0.6$	$p_i = 0.8$	$p_i = 1$
20	0	0	1	1	1	1	1
21	0.2						
22	0.4						
23	0.6						
24	0.8						
25	1						

For each combination of p_i and p_e, enter f in the appropriate cell. For example, in cell L21 enter f (computed in cell E12) when $p_i = 0.2$ and $p_e = 0.2$. Graph and interpret your results. Use the line graph option and select the data series in columns option.

4. Set cell E6 to 1, and cell E9 to 0.9. This will make the probability of extinction, p_e, equal to 1, and the probability of colonization, p_i, equal to 0.9. Clear your old macro results and run a new simulation. Why has the population persisted, considering that all patches are doomed to extinction?
5. Set cell E6 to 0.3, and enter 1s and 0s in cells A30–E34 such that $f = 0.6$. Assume that p_i is now a function of the number of patches occupied (instead of the propagule rain model in question 4). As more patches are occupied, the colonization rate increases because a greater number of colonists will likely locate an empty patch. Write an equation in cell E9 to modify the model into an internal colonization model and re-run your simulation. How do your results differ from those of question 4?
6. Return cell E9 to 0.6 (propagule rain model), and enter 1s and 0s in cells A30–E34 such that $f = 0.6$. Assume now that p_e is now a function of the number of patches occupied. As more patches are occupied, the extinction rate decreases because more colonists are available to "rescue" the patch from extinction. The fewer patches that are occupied, the more likely a patch will go extinct because colonists are less available to "rescue" a patch from extinction. This metapopulation model is called the *rescue effect model* (Gotelli 2001), where the extinction rate *depends* on how many patches are currently occupied. Write an equation in cell E6 to modify your model into a rescue effect model, and re-run your simulation. How do your results compare to questions 4 (propagule rain model) and 5 (internal colonization model)?
7. *Advanced. How does number of patches in the system affect the "stochastic" behavior of a metapopulation? Set up a new system in which the number of patches is 10,000 (100 × 100 cells), and compare the two models.

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