35 | *NEUTRAL LANDSCAPE THEORY AND CONNECTIVITY*

Objectives

- Develop a spreadsheet model of neutral landscapes.
- Determine how the spatial characteristics of landscapes change as the percentage of forest changes.
- Evaluate "thresholds" in connectivity for landscapes that vary in composition.
- Evaluate "thresholds" in edge characteristics for landscapes that vary in composition.

Prerequisite Exercise: VBA Programming

INTRODUCTION

Imagine that you've been given 10 square kilometers of land and can "design" it in any way you'd like. You might like a few ponds scattered among forests, and perhaps a few streams. Or you might like a stretch of unbroken prairie habitat. If people are a part of your landscape, you might include some farms, and a few houses or towns. Or maybe you'd like to turn your land into a bustling city. Now think about *where* the different elements (farm, stream, houses, roads, etc.) should go on the land. Will they be randomly positioned across the landscape, or will there be some sort of structure to the layout?

Although we may not conscientiously plan them, landscapes often don't appear to be random at all. It's no accident, for example, that major cities in the midwestern United States are located on the shores of the Great Lakes (Chicago, Milwaukee, Cleveland) or on the banks of the Mississippi River (St. Louis, Minneapolis, New Orleans). And it's no accident that large-scale food production occurs on the most productive soils that are accessible to harvesting. Indeed, it would be hard to imagine how a landscape that has been arranged at random might function for humans. **Random models** (also called **null models** or **neutral models**), however, are an essential part of ecological studies. They are useful because they reveal how something of interest "works" when other biological or physical phenomena are excluded from the puzzle. For example, you might be interested in knowing whether a local plant and animal community is a random assortment of species, or if the assortment of species present is the result of interspecific competition. Just as the null or neutral model of Hardy-Weinberg equilibrium (Exercise 21) reveals the genetic make-up of a population in the absence of evolutionary forces such
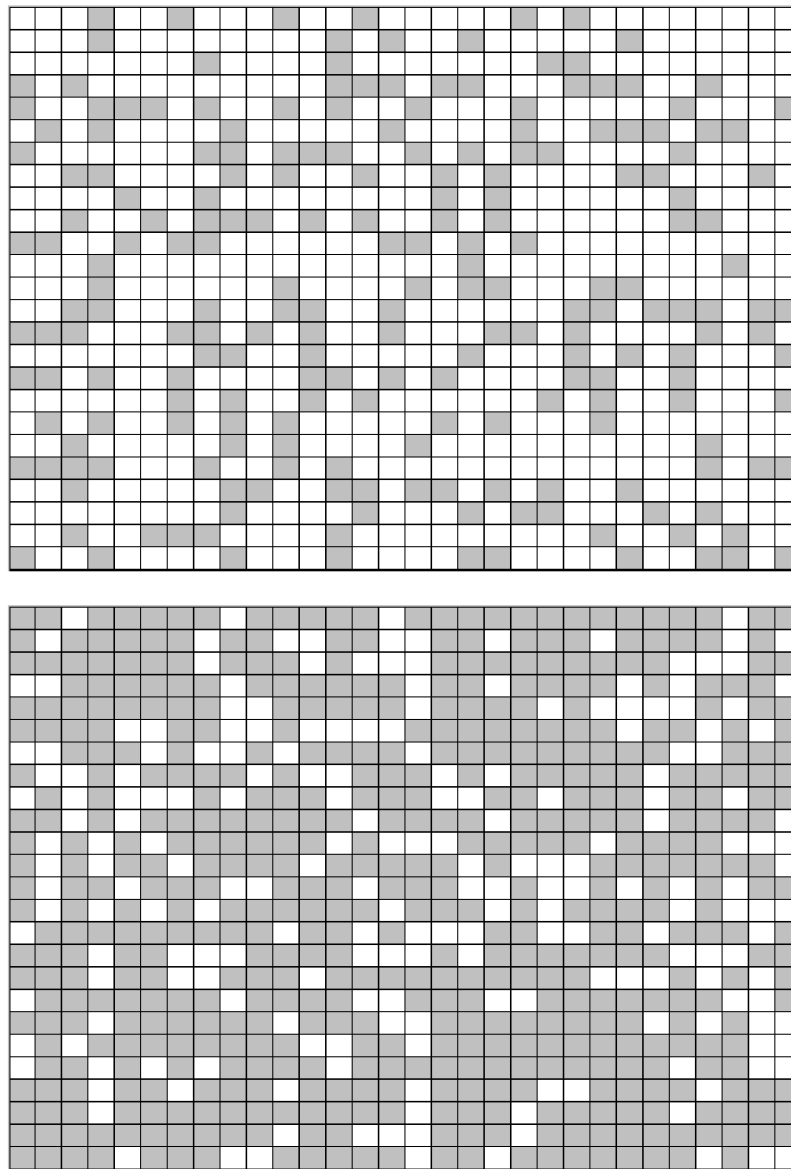
Figure 1 The top landscape was generated by assigning a random number between 0 and 1 to each cell, then assigning a habitat type to the random numbers. Numbers less than 0.3 were shaded gray, while numbers greater than 0.3 were left white. The bottom landscape was also generated with random numbers, except that random numbers less than 0.7 were shaded gray and those above 0.7 were left white.

as natural selection, mutation, or drift, neutral models in ecology can be used to determine how plant and animal communities are structured in the absence of biological factors such as interspecific competition. Such models give us a basis for determining if the patterns we observe in the local habitat patch deviate from a random pattern or not. If the deviation is strong, we might plan some experiments to test the hypothesis that interspecific competition (or some other ecological force) is driving the pattern.

Landscape ecologists also use neutral models in their studies. A **neutral landscape** is one that is neutral in structure and composition relative to other kinds of ecological or geographical factors. These models generate spatial patterns randomly, and hence remove the effects of land use or other nonrandom properties (Gardner et al. 1987). Figure 1 shows two **neutral landscapes**, or **random maps**.

Randomly generated landscapes have properties that are of interest to landscape ecologists. **Percolation thresholds** are one such property. The word *percolate* means to trickle or filter through a permeable substance. A landscape composed of two habitat types, "suitable" and "unsuitable," percolates if an organism can successfully navigate from one end of the landscape to the other by traversing suitable habitat patches. Thus, if you can navigate a hypothetical organism across the landscape by moving only to adjacent, suitable cells, the landscape percolates. Assuming that the suitable habitat patches in Figure 1 are the ones shaded in gray, the top landscape does not percolate because an organism on any patch cannot move across the landscape without dispersing into nonhabitat. In contrast, the landscape at the bottom of Figure 1 percolates because there are many ways in which an organism can traverse from one end of the landscape to the other without leaving suitable habitat. When a landscape percolates, the **percolating cluster** is defined as the cluster that connects the habitats across the landscape, and is the largest patch on the landscape.

In random landscapes, percolation theory suggests that landscapes should percolate as long as there is over 58% cover (Gardner et al. 1987), or **connectivity**. If you evaluate a number of landscape metrics for neutral landscapes that vary in the proportion of habitat, you will notice that some metrics suddenly change in value around this proportion. This is because as habitat is lost incrementally, the percolating cluster suddenly loses its structural integrity. This happens when a few, key cells are converted from one habitat type to the next. This point is called a **percolation threshold**, because the landscape is on the brink of being either "connected" or "disconnected" at this point. Other thresholds also appear in neutral models (Figure 2). We will explore landscape metrics under a variety of landscape conditions in this exercise, and we will search for such thresholds.

How can ecologists and conservation biologists use neutral models? Conservation biologists may use percolation theory in designing reserves because a percolating landscape, in theory, provides enough suitable habitat for organisms to successfully disperse from one location to another. Ecologists also may want to know how quickly a pest or disease may spread, which may in turn depend on the connectivity of a landscape.
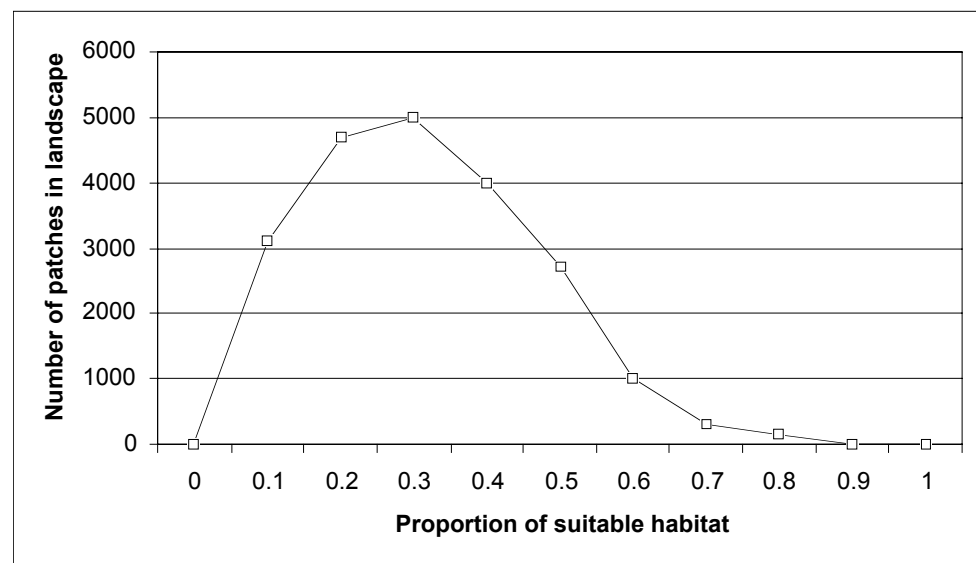
Figure 2   The number of patches in neutral landscapes peaks when the landscape consists of 20–40% habitat, then suddenly drops off as the proportion of habitat increases. (After Gardner et al. 1987.)

Kimberly With (1997) has outlined several other ways in which neutral models can be applied in conservation biology. These include

- Incorporation of complex spatial pattern in population models
- Identification of species' perception of landscape structure
- Determination of landscape connectivity (e.g., when is a landscape "fragmented")
- Evaluation of the consequences of habitat fragmentation for population subdivision
- Identification of the domain (scale) of metapopulation dynamics
- Prediction of the occurrence of extinction thresholds
- Determination of the genetic consequences of habitat fragmentation
- Reserve design and ecosystem management.

Landscape ecologists have recently begun to test predictions from percolation theory, including how organisms respond to the amount of habitat as well as its arrangement on the landscape (e.g., Andren 1994, Fahrig 1997). At the present time theory far outweighs the number of empirical studies testing it, and much exciting work remains to be done in the field.

PROCEDURES

In this exercise, you'll build on the spreadsheet and macro you developed in the previous exercise, "VBA Programming," to develop a neutral landscape model. You will consider just two kinds of habitat on the landscape, suitable and nonsuitable (In the exercise, we've used forest and nonforest as habitats, but these habitats were chosen arbitrarily.) You will generate random maps that vary in the amount of suitable habitat, and then examine the properties of your neutral landscapes. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Set up the spreadsheet.

1. Open the spreadsheet you used in Exercise 34, "VBA Programming." Save the spreadsheet as **"Connectivity."**

2. Modify the column headings so that cell A1 reads **"Neutral Landscapes and Connectivity"**

3. Add the heading **"Proportion of forest habitat"** in cell C21 as shown in Figure 3, and enter 0.5 in cell K21.

	A	B	C	D	E	F	G	H	I	J	K	L
1	*Neutral Landscapes and Connectivity*											
2												
3												
4												
5												
6												
7												
8			**Analyzed data (Plot_Range)**									
9												
10												
11												
12												
13												
14												
15												
16												
17												
18												
19												
20												
21			**Proportion of forest habitat =**									
22												
23			**Raw data (Raw_Range)**									
24												
25												
26												
27												
28												
29												
30												
31												
32												
33												
34												

Figure 3

4. Conditionally format cells C10–L19 (the Patch Plot landscape), so that the cells not equal to "h" are shaded green. The letter "h" will designate hostile habitat, and the letter "f" will designate forest habitat.

Select cells C10–L19, then go to Format | Conditional Format. The dialog box in Figure 4 will appear. Set Condition 1 as Cell Value Not Equal to h, then select the Format button, then the Pattern tab, and select the color green. Press OK. Now when you run your analysis, the forested cells (f) in the Patch Plot landscape will be shaded green, and the non-forested cells (h) will remain white.

Figure 4

B. Develop the neutral landscape.

1. In the Patch Raw Data landscape (cells C25–L34), enter a formula to randomly generate a landscape with 50% forest cover.

Enter the formula **=IF(RAND()<$K$21,"f","h")** in cell C25 and copy the formula across cells C25–L34.

About 50 of our 100 cells in the Patch Raw Data landscape will consist of forest, and will be designated by the letter "f." The remaining habitat will consist of neutral or hostile habitat, which will be designated by the letter "h." The formula in cell C25 tells the spreadsheet to draw a random number between 0 and 1 (the **RAND()** portion of the formula). If that random number is less that the value given in cell K21 (the proportion of forest), the program will return the letter "f" to the cell. Otherwise, it will return the letter "h" to the cell. In this way, you will generate a map that is approximately 50% forested, but which cells are forested and which are nonforested is completely random.

2. Press F9 several times to generate several, different neutral landscapes.

Each time you press F9, the calculate key, the spreadsheet will generate a new set of random numbers, which in turn will generate a new Patch Raw Data plot.

3. Run the macro **AnalyzePatch**, (shortcut key <Control><a>) that you generated in Exercise 34 to generate patch and landscape statistics for one of your neutral landscapes.

When you run your macro, a new landscape is generated in the raw data landscape (cells C25–L34), while the analyzed data landscape now contains an image of the previous landscape. This happens because the word "Calculate" is incorporated into the AnalyzePatch macro, which is necessary to update the landscape statistics generated by the macro. The Calculate command generates new random numbers, which changes the landscape configuration in the raw data. Don't worry about this; just keep in mind that the landscape statistics being generated are associated with the analyzed data landscape. If you run your macro again, it will analyze the new raw data landscape, but as soon as the new data is analyzed, yet another new random landscape will be generated.

4. Adjust formula in cell AA10 to read **=COUNTIF($C$10:$L$19,"h")*100/AA7.**

Enter the formula **=COUNTIF($C$10:$L$19,"h")/AA7** in cell AA10. This small adjustment will allow you to compute the proportion of nonforest habitat by counting the number of hostile habitat cells out of the total cells.

5. Save your work.

C. Assess the neutral landscapes.

1. Set up new spreadsheet headings as shown in Figure 5.

	AC	AD	AE	AF	AG	AH
6	**Neutral Landscape Analysis**					
7	**Trial**	**Prop**	**# patches**	**Max patch**	**Total edge**	**Prop. core**
8	1	1	1	10000	400	0.64
9	1	0.9				
10	2	0.9				
11	3	0.9				
12	4	0.9				
13	5	0.9				
14	6	0.9				
15	7	0.9				
16	8	0.9				
17	9	0.9				
18	10	0.9				
19	1	0.8				
20	2	0.8				
21	3	0.8				
22	4	0.8				
23	5	0.8				
24	6	0.8				
25	7	0.8				
26	8	0.8				
27	9	0.8				
28	10	0.8				
29	1	0.7	↓↓↓↓↓	↓↓↓↓↓	↓↓↓↓↓	↓↓↓↓↓

Figure 5

2. Evaluate the landscape statistics for 10 neutral landscapes that vary in proportion of forest, in increments of 0.1.

For each level of forest cover, run 10 trials and record the landscape stats for each trial. Extend your chart down to Row 98 for 10 trials when the proportion of forest is 0.1. Row 99 should contain a single trial (when the proportion of forest = 1, there will be no variation in the landscape statistics so only one trial is needed.)

3. Set cell K21 to 1 and run the AnalyzePatch macro.

Record the results in cells AD8–AH8 as shown in Figure 5.

4. Set cell K21 to 0.9, and run the Analze Patch macro. Record the pertinent results in cells AD9–AH9. Repeat until 10 trials have been filled in.

You can complete Step 4 more efficiently by writing a macro to perform the tasks for you. Set cell K21 to 0.9, open Record New Macro, assign a shortcut key, and enter the following steps:
- Press the shortcut key to run your AnalyzePatch macro.
- Select cell AA16 (the number of patches) and go to Edit | Copy.
- Use your mouse and select cell AE7.
- **Go to Edit | Find. A dialog box will appear. Leave the space under Find What blank and select the Search By Columns option. Select the Find Next button, then select Close. Your cursor should move down to the next blank cell.**
- **Go to Edit | Paste Special, and select Paste Values. Select OK.**
- Select cell AA17 (the maximum patch size) and go to Edit | Copy.
- Use your mouse and select cell AF7.
- **Repeat the two steps in boldface above.**
- Select cell AA11 (the total edge) and go to Edit | Copy.
- Use your mouse and select cell AG7.
- **Repeat the two steps in boldface above.**

- Select cell AA9 (the proportion of core habitat) and go to Edit | Copy.
- Use your mouse and select cell AH7.
- **Repeat the two steps in boldface above.**

Go to Tools | Macro | Stop Recording.

When you press your shortcut key for the above macro, the AnalyzePatch macro will be run for a given trial, and the pertinent statistics will be filled into your chart. Repeat the macro until 10 trials have been filled in.

After 10 trials, change the proportion of forest habitat cell K21, press the calculate key (F9), and simply run the macro another 10 times. Repeat until the proportion of forest cover is 0. You will need to press F9, the calculate key, each time you change the value in cell K21 so that the Analyze Patch macro analyzes a landscape with the new proportion of forest cover.

5. Adjust cell K21 to 0.8 and run 10 trials, then 0.7, etc. until your chart is filled.

6. Save your work.

D. Summarize the trial results.

1. Set up headings as shown in Figure 6.

	AJ	AK	AL	AM	AN
6	**Average Results**				
7	**Proportion**	**# patches**	**Max patch**	**Total edge**	**Prop. core**
8	1	1	10000	400	0.64
9	0.9				
10	0.8				
11	0.7				
12	0.6				
13	0.5				
14	0.4				
15	0.3				
16	0.2				
17	0.1				
18	0	0	0	0	0

Figure 6

2. Use the **AVERAGE** function to enter the average of the 10 trials in the appropriate cells.

For example, we used the formula **=AVERAGE(AG79:AG88)** in cell AM16 to generate the average total edge for landscapes with 20% forest cover.

3. Save your work.

E. Create graphs.

1. Graph average number of patches as a function of proportion of forest habitat. Your graph should resemble Figure 7.

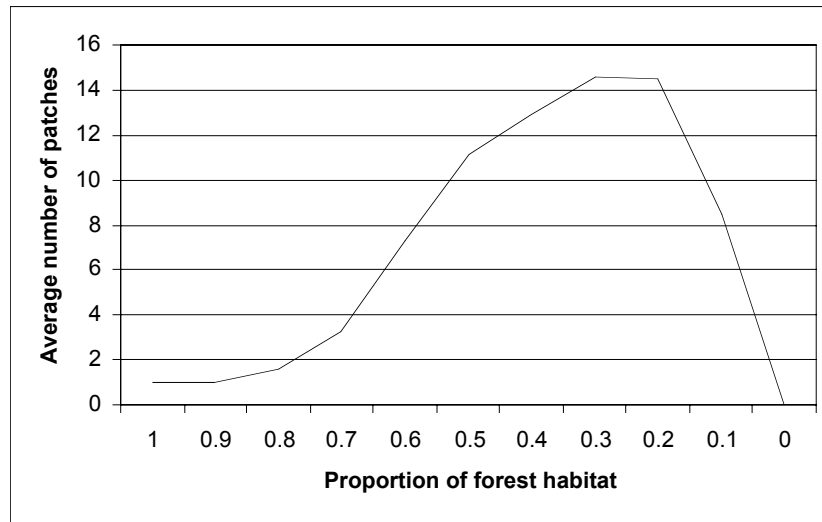Use the line graph option and label your axes fully.

Figure 7

2. Graph total edge as a function of proportion of forest habitat. Your graph should resemble Figure 8.
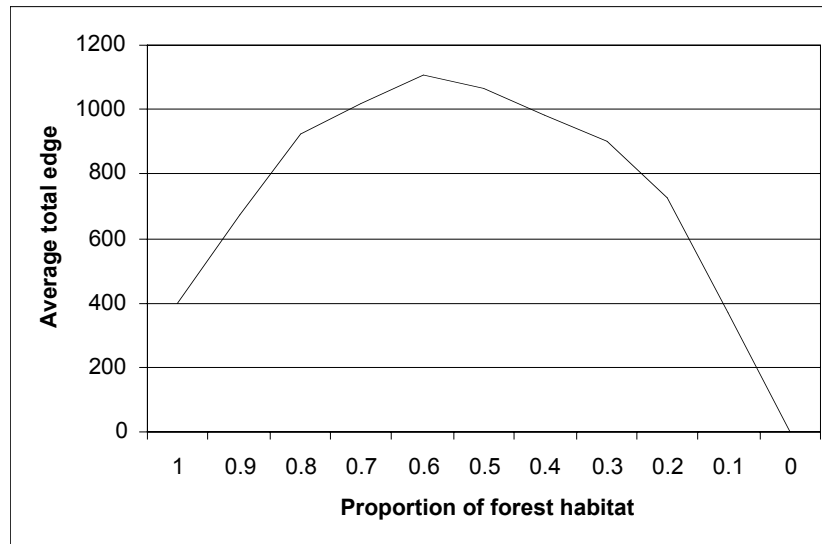
Figure 8

3. Graph maximum patch size as a function of proportion of forest habitat. Your graph should resemble Figure 9.
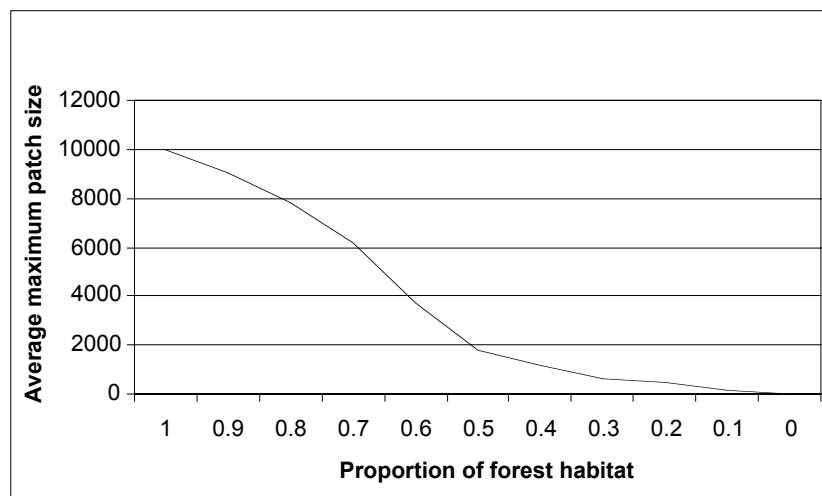
4. Graph the proportion of core habitat as a function of proportion of forest habitat. Your graph should resemble Figure 10.
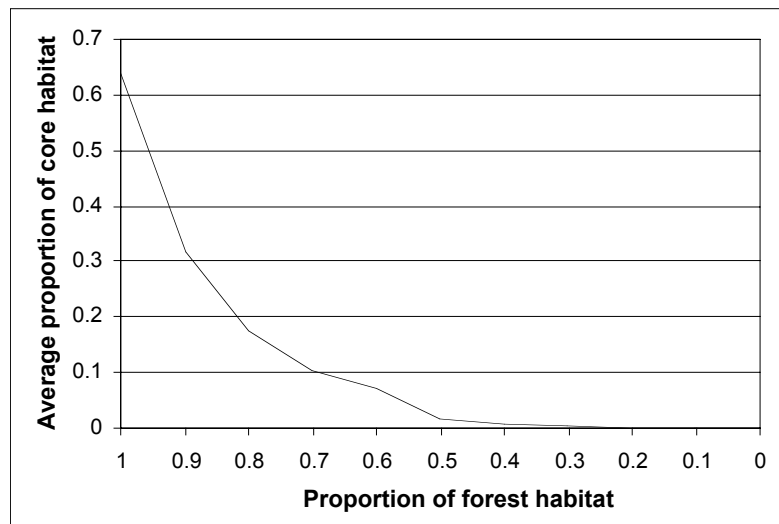
5. Save your work.

Figure 9

Figure 10

QUESTIONS

1. Two of your graphs (average number of patches and amount of edge) take on maximum values when the landscape is 40–60% forest cover. Why do these indices "behave" as they do?

2. Examine the results of your neutral models carefully. When a landscape is 100% forest cover, it obviously is not fragmented. Similarly, when a landscape is 0% forest cover, it is not fragmented. As you changed the proportion of forest cover from 1 to 0, at what point does it appear that the landscape becomes fragmented? In other words, does there appear to be a percolation threshold?

3. Why is the proportion of core habitat only 0.64 when the landscape is 100% forest habitat? Does the relatively small map size bias the percolation threshold? If so, how?

4. Compare the summary of your neutral landscape results to a real map. Choose a topographic map of an area near your home, and calculate the proportion of forest habitat. Then choose a metric, such as total edge, and devise a way to estimate the amount of edge on the map. How does the amount of edge in your real map compare to the amount predicted in your neutral model?

5. Find a map that is approximately 40–60% forest cover. Does it appear that 58% habitat connectivity is an indication of percolation across a map? Why or why not?

LITERATURE CITED

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Gardener, R. H., B. T. Milne, M. G. Turner and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape patterns. *Landscape Ecology* 1: 1–19.

With, K. A. 1997. The application of neutral landscape models in conservation biology. *Conservation Biology* 11: 1069–1080.