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15 Effective Exercises in Teaching Landscape Ecology

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The development of landscape ecology and its many applications to land management created a need for courses that address both the conceptual and practical sides of the discipline. Graduate seminars and full-fledged courses in landscape ecology are now featured at many colleges and universities; undergraduate ecology courses may include an introduction to principles of landscape ecology. Because landscape ecology involves the study of spatially explicit ecological patterns and processes along with much larger regions than ecologists have typically studied, landscape ecologists often employ a variety of new quantitative analysis techniques in their work. In particular, metrics are used to quantify spatial patterns, and the importance of spatial heterogeneity for ecological processes is evaluated. Modeling also plays an important role in landscape ecology because it is logistically impossible to conduct truly replicated experiments across entire landscapes. Students of landscape ecology, even at the undergraduate level, need some familiarity with the tools of the discipline to gain confidence in the practice of landscape ecology and to develop a critical understanding of the strengths and weaknesses of these techniques.

This chapter contains six exercises created to teach concepts in landscape ecology. All three authors currently teach ecology at the undergraduate and/or graduate levels and incorporate landscape ecology principles in their specialized and general courses. The text of each exercise is written for general use in a class; notes specifically to the instructor and recommended readings are included in the appendices.

This collection of exercises stresses three main aspects of landscape ecology. Exercises I and II emphasize the quantification of landscape pattern. The first exercise is designed to familiarize students with straightforward techniques for quantifying the similarities and differences between landscapes. The second demonstrates the important influence of spatial scale (both grain and extent) and classification scheme on landscape metrics. Exercises III and IV address the interpretation of landscape patterns. The third exercise allows students to quantify changes through time in a landscape, challenging them to consider where and why these changes occur.

The fourth exercise has students interpret a landscape from the perspective of four nonhuman species which vary in their vulnerability to human influences. This exercise demonstrates how the same landscape can functionally be quite different for various species. Exercises V and VI foster understanding dynamic landscapes and lead students through the process of generating working hypotheses about drivers and mechanisms of landscape change (i.e., landscape models). These last two exercises help students bridge the intellectual gap between quantifying pattern and understanding the processes underlying landscape pattern and change.

Exercise I: Neutral Models and Landscape Connectivity

Background

This exercise is about modeling and spatial heterogeneity, with particular reference to landscape ecology. Landscape ecology is defined by two characteristics: (1) landscape ecology often studies ecological processes over very large areas (such as the upper midwest, or all of Yellowstone National Park, or the southern Appalachian Mountains) that include a variety of different ecosystems or habitats, rather than focusing only one type of ecosystem; and (2) landscape ecology explicitly studies the effects of spatial patterning—heterogeneity—on ecological processes (such as the movement or dispersal of organisms or the spread of natural disturbances). Therefore, landscape ecological studies may involve studying the amount and spatial distribution of a particular habitat type over a large geographic area and understanding the effects of different habitat arrangements on particular species or ecological processes. For example, the study of how the amount and spatial arrangement of old-growth habitat affects population dynamics of the northern spotted owl in the Pacific Northwest is an example of a landscape study.

To understand the relationship between spatial pattern and an ecological process, ecologists need to know how to quantify spatial patterns and also have some "yardstick" against which the effects of particular spatial patterns can be measured. Considerable effort has gone into developing pattern metrics that can be compared across different landscapes or monitored through time. These include intuitive attributes like number of patches of a habitat type, the size distribution and mean size of the patches, and the ratio of edge to area for the habitats. It is important to be able to tease apart the effects of the total amount of the habitat from the effect of its spatial arrangement. Students will examine these effects in this exercise using a neutral model. The neutral model serves as the yardstick for comparison with actual landscapes.

Purpose

This lab will introduce you to a neutral landscape model based on percolation theory (Gardner et al. 1987; Gardner and O'Neill 1991). Percolation theory was developed in the physical sciences to explain and predict the processes that lead to connectivity across a two-dimensional space (Stauffer 1985). Its development was motivated by questions such as, How much metal must be plated across a surface so that electricity can flow across it? A physicist would want to have just enough gold to maintain conductivity, but perhaps not extra because of the cost. Percolation theory studies the properties of clusters, or patches as ecologists would say, across a two-dimensional space. Ecologists also are interested in questions that deal with connectivity or conductivity across two-dimensional space. For example, How much habitat must be present for a red-backed vole to move across a given landscape? How much flammable forest must there be for a fire to spread (or stop spreading) across a landscape? Because of the similarity in the questions and the well-developed theory in the physical sciences, percolation theory has been applied in ecology to develop neutral models for landscape patterns (e.g., Gardner et al. 1987; Turner et al. 1989; Andren 1994; With et al. 1997).

Why develop neutral models? One approach to modeling is to develop very simple models to compare with empirical data to see how well they fit. If the predictions of a very simple neutral model fit satisfactorily with the data, it may not be necessary to develop more complex approaches. However, it is often more informative and interesting if there is a relevant difference between the model predictions and the empirical data. Then it is possible to expand the neutral model and learn what additional features must be included to achieve agreement with the data—that is, What other parameters are important?

The exercise contains two parts. In the first part, students will develop percolation maps (that is, the neutral model of a landscape) and observe how the spatial characteristics on these maps change with the abundance of a particular habitat type. The set of characteristics describing the pattern will be plotted (on the Y axis) against the proportion of the map occupied by the habitat (on the X axis), and the shapes of the curves will be examined. In the second part, students will quantify the spatial patterns of land and water from different portions of the Wisconsin landscape by using topographic maps provided. To illustrate an important concept—that the scales at which we conduct our studies influences our answers, something true for science as a whole—these patterns will be quantified at two spatial resolutions on each topographic map. Results from the whole class will be synthesized to make two comparisons: (1) How different or similar are random (i.e., the neutral model) maps and actual landscapes, and (2) How different or similar are the spatial patterns of land and water in Wisconsin when quantified at different scales from the same maps?

Procedure

Read the instructions for the exercise in advance. The Introduction and Discussion sections from Gardner et al. (1987) should be included with the handout as background material.

Random Maps

Percolation theory provides a framework for examining landscapes as two-dimensional grids, usually square grids of size $m \times m$ containing m^2 unique sites or cells. Gardner in chapter 13 uses computers to create random two-dimensional maps of various sizes ranging from 50×50 to 500×500 cells. Here, you will use pencil and papers to generate smaller 10×10 grids containing 100 unique sites or cells.

Consider the probability, p, that any of the 100 cells is occupied by a particular habitat type (e.g., forest or grassland). In an empty (homogeneous) 10×10 grid, $p = 0$. If you choose two random coordinates (x,y) and fill in that cell on the grid, then $p = 0.01$. If $p = 0.10$, then 10 cells are occupied; when $p = 1.0$, all 100 cells are occupied. When the grid contains some cells of the habitat of interest, several properties about its spatial arrangement can be measured. For example, we can measure the number of habitat patches or clusters, their sizes, and the amount of edge surrounding the habitat patches. On our hypothetical 10×10 landscape where $p = 0.01$, we observe:

C = number of clusters = 1
L = size of largest cluster = 1 cell
O = number of outer edges = 4
I = number of inner edges = 0

In this exercise, the following definitions and rules for describing the spatial patterns will be followed. These calculations are illustrated for the simple maps shown in Figure 15.1.

1. An edge is a surface of an occupied cluster adjacent to an unoccupied area.
2. Outer edges lie along the outside of a cluster.
3. In contrast, inner edges are adjacent to unoccupied areas completely enclosed by a cluster, like the holes in Swiss cheese.
4. Two clusters only merge into one when they share an horizontal or vertical edge; a diagonal does not connect clusters.
5. When it falls on the edges of the grid, the outside-most edge of the patch should always be included in your count of outside edges, but not for your count of inside edges.

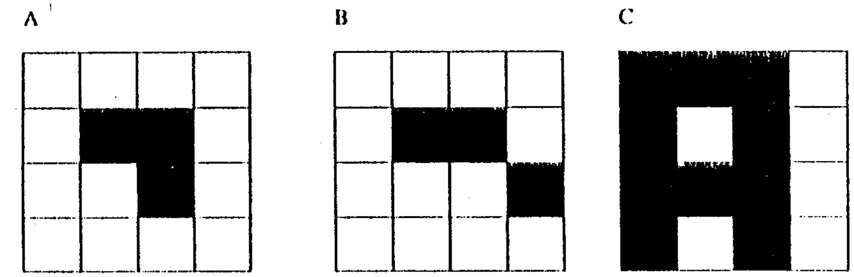

FIGURE 15.1. Simple 4×4 grids illustrating the rules for identifying habitat clusters and quantifying their inner and outer edges. (A) one cluster, with 8 outer edges and 0 inner edges; (B) two clusters with a total of 10 outer edges and 0 inner edges; and (C) one cluster with 4 inner edges (not 7) and 16 outside edges (not 7).

To be sure that you understand how to count clusters and outer and inner edges, consider the following example (Fig. 15.2), where $p = 0.45$. (Answers are at the end of this portion of the exercise.)

What is C? ——— L? ——— O? ——— I? ——— $O + I$ ———

To further check your understanding, consider a completely filled grid ($p = 1.0$):

What is C? ——— L? ——— O? ——— I? ——— $O + I$ ———

Look back at Figure 15.2, where $p = 0.45$, and note that although the grid is almost half full, it is not possible to "travel" from one edge of the grid to the other edge on occupied (filled) clusters. (Remember that a diagonal does not connect clusters; travel across a diagonal is disallowed). When the habitat is not connected, we say that the grid does not percolate. From percolation theory, we know that on a random map with the rules defined above, habitat will suddenly become connected at $p = 0.5928$ (Stauffer 1985). This value is called the critical threshold for percolation, or p_c. In the exercise explained below, students should begin to watch for percolation at approximately $p = 0.50$.

Work in groups of five or six to generate random maps with p ranging from 0.0 to 1.0 and tracking the habitat patterns as follows. One or two students will draw random x, y coordinates and fill in the habitat on the grid using an erasable marker. As the grid is filled in, three students should track the pattern, quantifying C, L, O, I and $O + I$. The first can count the number of clusters and the largest cluster size and watch for percolation when $p > 0.50$. The value of p at which percolation is observed should be recorded. The second student should count the total number of outer edges, and the third student can count the total number of inner edges. Be particularly attentive to these edge calculations, since filling in "holes" or creating

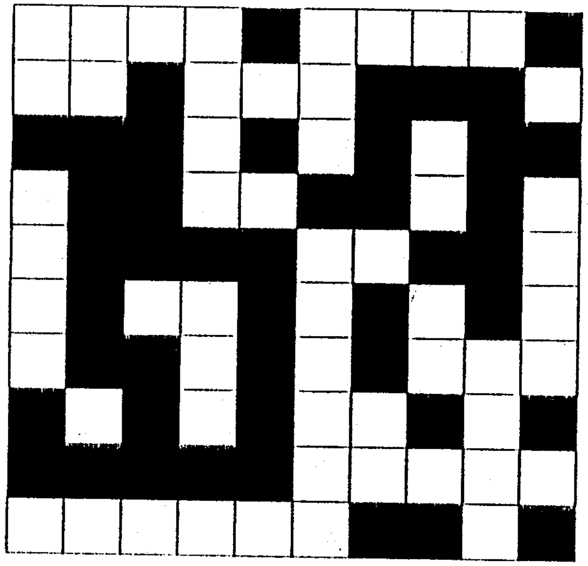

FIGURE 15.2. A simple random 10 × 10 map for which $P = 0.45$.

clusters can dramatically change the number of edges on the map. Another student should record the data for all 100 "moves" from $p = 0.0$ to $p = 1.0$. (Data sheets and write-on, wipe-off 10 × 10 grids should be provided by the instructor.) You should always work all the way through the exercise (not just stopping when "percolation" is reached). Ideally, your class should have several groups of students do this exercise twice, then compile all the results. Results should be plotted as a function of the p value of the map.

"Real" Maps at Different Scales

This part of the exercise asks whether the characteristics of "real" landscapes are similar to the characteristics of landscapes produced by the random neutral model. In addition, the exercise examines how the quantification of the landscape pattern may differ with spatial resolution. A series of topographic maps is provided along with transparent 10 × 10 transparent grids of two different sizes that will be superimposed on the topographic maps. Grids will be overlaid on the maps beginning in the top left corner and working along to the bottom right on each map. Twelve large grids are indicated by pins on the maps; four small grids fit within each of the large grids (48 small grids per map).

On each grid, estimate five characteristics: (1) p, the proportion of land covered by lakes; (2) the size of the largest lake in the grid; (3) the number of lakes in the grid; (4) whether it is possible to traverse the grid horizontally; and (5) whether it is possible to traverse the grid vertically. Data should be recorded (see Fig. 15.3) for at least one fourth of the map with the smaller grid, or the entire map should be used with the larger grid. (In a larger class, each laboratory section can analyze a different map.) The size of the largest lake, number of lakes detected, and the presence or absence of percolation (both horizontal and vertical) should be plotted against p for each topographic map and compared with the neutral models. In your plots,

DATA SHEET - FINER SCALE

MAP LAYOUT: **MAP NAME:**

Note that 12 larger grids fit across the 7.5′ topo map, and 4 smaller grids fit within each larger grid.

A1a	A1b	A2a	A2b	A3a	A3b
A1c	A1c	A2c	A2d	A3c	A3d
B1a	B1b	B2a	B2b	B3a	B3b
B1c	A1c	B2c	B2d	B3c	B3d
C1a	C1b	C2a	C2b	C3a	C3b
C1c	C1c	C2c	C2d	C3c	C3d
D1a	D1b	D2a	D2b	D3a	D3b
D1c	D1c	D2c	D2d	D3c	D3d

GRID	Lakes (P)	# of Lakes	Size of Largest	Trav. Vert?	Trav. Hor?	GRID	Lakes (P)	# of Lakes	Size of Largest	Trav. Vert?	Trav. Hor?
A1a						C1a					
A1b						C1b					
A1c						C1c					
A1d						C1d					
A2a						C2a					
A2b						C2b					
A2c						C2c					
A2d						C2d					
A3a						C3a					
A3b						C3b					
A3c						C3c					
A3d						C3d					
B1a						D1a					
B1b						D1b					
B1c						D1c					
B1d						D1d					
B2a						D2a					
B2b						D2b					
B2c						D2c					
B2d						D2d					
B3a						D3a					
B3b						D3b					
B3c						D3c					
B3d						D3d					

FIGURE 15.3. Example of data sheet indicating the position of both large and small grids to be positioned across a 7.5′ topographic map and the format for recording data on the spatial pattern of land and water on for each of the small grids.

use an open circle if the data came from the large grids and a solid dot if the data came from the small grids. Should plots from the random and "real" map data look the same? Does the scale of the sampling affect the results for each map?

Summary and Discussion

Answers to Sample Exercises

$p = 0.45$, C = 10, L = 23, I = 10; $p = 1.00$, C = 1, L = 100, O = 40, I = 0.

Questions for Discussion

1. Why might percolation be observed at values other than the critical threshold, $p_{crit} = 0.5928$?
2. Why should real landscapes differ (or not differ) from random maps? How might these differences relate to the forces, both natural and anthropogenic, that create the pattern?
3. What kinds of ecological processes might be affected by thresholds of connectivity, and how might you detect their responses?
4. Why should the manager of a wilderness preserve or a regional planner be concerned about critical thresholds of habitat connectivity?
5. Can ecologists compare data collected at different scales? Why or why not, and under what conditions?

Exercise II: Constraints on Landscape Pattern Analysis

Purpose

The objectives of this exercise are (1) to gain hands-on experience with the analysis of landscape structure on digitized maps by using some standard (representative) landscape metrics; (2) to explore the implications of changes in grain and extent of the landscape data on the results of the analyses; and (3) to explore the effects of altering the classification scheme on the results of the analyses.

Procedure

Work in groups of four. The analyses can be conducted on raster data that you already have, such as from individual research projects, or 100 × 100 cell subsets of larger GIS data bases provided in class. Landscape metrics can be computed by using (1) stand-alone code provided by the instructors, such as SPAN (Turner 1990); (2) FRAGSTATS (McGarigal and Marks 1995); (3) r.le (Baker and Cai 1992), if you have access to this interface with the GRASS geographic information system; or (4) other code to which the students have access. The instructor should provide detailed instructions on

accessing the data set and for running the analysis program to be used. For illustration, the following text assumes the use of a 100 × 100 landscape to be analyzed with SPAN.

Effects of Changing Grain and Extent on Landscape Metrics

Two sets of analyses are to be completed here. Copy the initial data file to a new file name, then edit the new file to change its grain size. (If you are good at programming and can write a quick code to do this, it can be done on the computer; however, editing the file manually is fine, and actually makes the point well).

First, the map will be reduced from 100 × 100 to a 50 × 50 by taking each 2 × 2 "window" and replacing the four grid cells in the window with a single value. The replacement will be by majority rule, that is, the dominant cover type "wins"; if there is no dominant, roll a die or do some other random assignment. For example, the following 2 × 6 array would be reduced to a 1 × 3 with the following composition:

```
223456    236
233343
```

where the 2 and 3 are obtained from the majority rule, and the 6 is a random assignment. This can be done manually in a word processor (make sure you save the file as text only!). Note that the number of rows and columns must be adjusted in the spatial analysis program. students follow the same procedure for a 4 × 4 window and a 5 × 5 window (which give you matrices of 25 × 25 and 20 × 20, respectively. The original and each of the new maps should be analyzed with SPAN, and selected metrics (students' choice) plotted as a function of grain size to show how they change with this component of scale. NOTE: For the interested, you can also experiment with alternative assignment rules to see how the mode of aggregation influences results (for ideas, see Gardner and O'Neill 1991).

Second, leave the original grain size alone but successively reduce the size of the landscape array by units of 10 rows and 10 columns. Run SPAN on each new map from the 100 × 100, 90 × 90, 80 × 80, ..., 10 × 10. Again, plot the metrics as a function of extent of the map to determine how the results are influenced by spatial extent.

Effects of Classification Scheme on Landscape Metrics

In this part of the exercise, the grain and extent will be left alone (e.g., the matrix will remain 100 × 100 in size), but the categories of land cover used for the analyses will be reclassified. You should explore the effects of at least two alternative ways of aggregating the data; for our purposes, students will always be reducing rather than increasing the number of categories. The aggregations can be done by lumping like categories into a single category. For example, with data on forest composition and age, one might aggregate by species (i.e., lumping age classes) or by age classes (i.e., lumping species). Landscape metrics should then be presented in a table by the classification scheme employed; results for the original landscape map should be included for comparison.

Summary and Discussion

Products

Results should be submitted as group reports. Reports should contain three parts: (1) a description of what was actually done for each problem, (2) graphs depicting the results, and (3) a thoughtful interpretation/discussion of the implications of changes in grain and extent and of sensitivity to the classification scheme for landscape analyses. Pay particular attention to part (3). Your interpretation is one of the most important efforts for this exercise. Be sure to cite the appropriate literature.

Questions for Discussion

1. How important is the selection of categories used in an analysis of landscape pattern? What are the implications of different classification schemes for the comparison of different landscapes or changes through time in a given landscape?
2. What are the advantages and limitations of various metrics of landscape pattern with regard to their sensitivity (or lack thereof) to changes in grain, extent and classification?
3. One metric alone is not sufficient to describe a landscape adequately, but how many are needed and why?
4. Can the results of a landscape pattern analysis be extrapolated to other scales? How?

Exercise III: Quantifying Land-Cover Change

Background

Landscapes change through time because of natural processes (e.g., disturbance, succession) and human use (e.g., urban growth). The type and rates of these changes can be quantified from remotely sensed data taken at different times. This lab exercise is designed to familiarize the student with a technique for quantifying land-cover change from a time series of land-cover maps. The land-cover maps used in this exercise show change around Franklin, North Carolina. The maps were developed from Multi-spectral Scanner (MSS) images taken in 1975 and 1986 and show the distribution of forest, grassy/brushy, and unvegetated/urban land covers. The

dimensions of both maps are 210 rows × 180 columns; pixel size is 90 × 90 m.

Purpose

This exercise will address the following research questions:

1. For a given land-cover type, what is the probability of change during the period 1975 to 1986?
2. Which land-cover type is the most stable through time? Which one is the most unstable?
3. Given its 1975 land cover, what is the projected land-cover for the same location in 1986?

Procedure

These questions will be answered by constructing a transition probability matrix by sampling random locations on the two land-cover maps.

Sampling the Maps

1. Use a random number table to select 50 points from the sampling-grid transparency provided with this exercise. (For example, number the rows and columns of the grid. Then, draw a series of two-digit, random numbers. Use each number to designate the row or column address of a sampling point (if the random number exceeds the number of rows or columns, just take the next number).)
2. Place the sampling-grid transparency over the 1975 map (Fig. 15.4). Use a pen to mark the corners of the map on the transparency so it can be placed on top of the 1986 map (Fig. 15.5) in the same manner. Use paper clips to secure the transparency to the map. Working from the top left toward the bottom right, record the land-cover class for each point in Table 15.1. Number the points on the transparency with your pen as you record each one.
3. Place the transparency on the 1986 map (Fig. 15.5). Line up the corners of the map with the marks on the transparency. Record the land-cover class for each point, working through the same sequence of points used for the 1975 map.

Calculating the Transition Probabilities

4. Using the data in Table 15.1, tally the number of occurrences for each of 1975 to 1986 land-cover combinations.
5. Total each row and column of Table 15.2. Divide the row and column totals by the number of sampling points to estimate the frequencies of

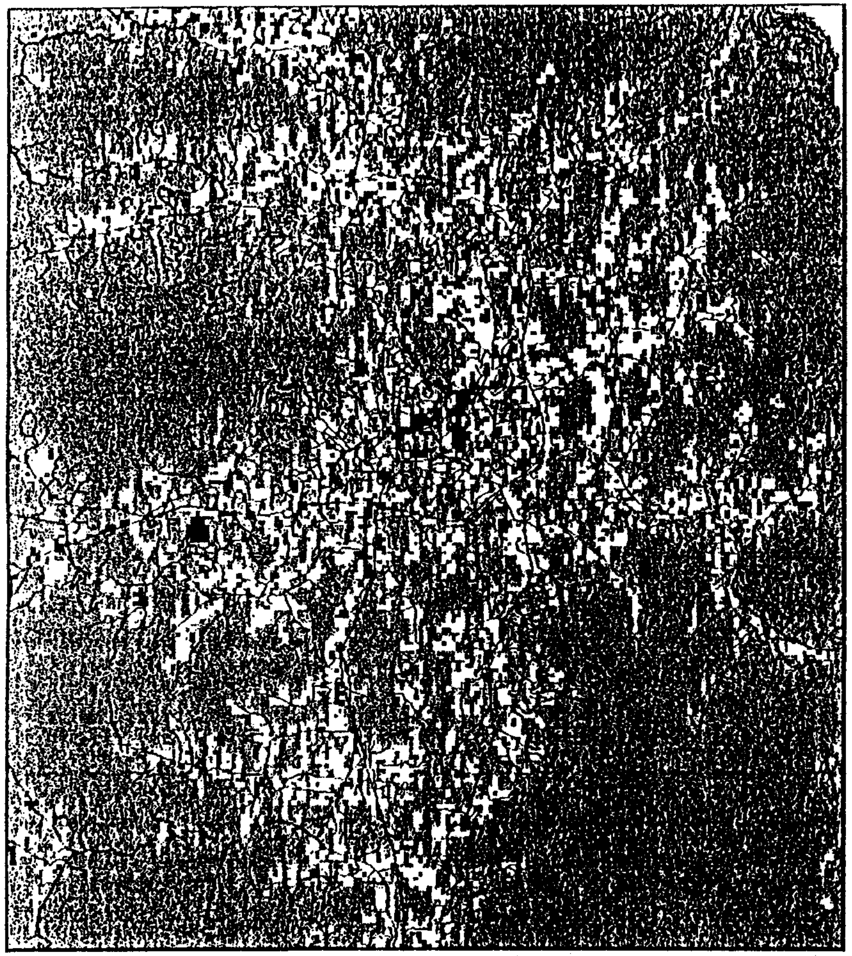

FIGURE 15.4. Land cover around Franklin, NC, in 1975. This land-cover map was developed from a MSS image. The land-cover classes are as follows: forested (gray), grassy/brushy (white), and unvegetated/urban (black). Roads are shown as black lines.

each land-cover type for each year. Did the frequencies change across time?

6. Calculate the transition probabilities for each 1975 land-cover (row in Table 15.2) by dividing the number in each cell by the row total. Record the result in Table 15.3. This conditional probability estimates the likelihood of the 1986 land cover, given a particular 1975 land cover at a location.

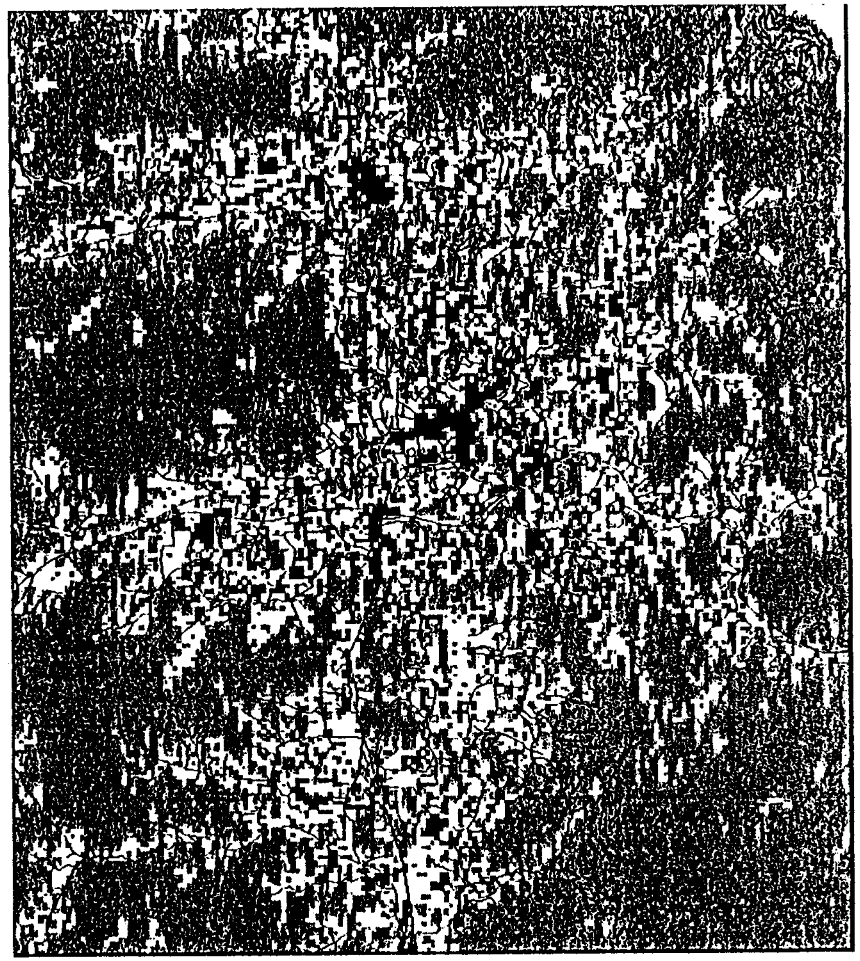

FIGURE 15.5. Land cover around Franklin, NC, in 1986. This land-cover map was developed from a MSS image. The land-cover classes are as follows: forested (gray), grassy/brushy (white), and unvegetated/urban (black). Roads are shown as black lines.

Summary and Discussion

1. Did the frequency of land-cover types change across time? Which cover types showed increases/decreases?
2. Given a site was in forest during 1975, what is the probability it remains in forest in 1986? What is the probability it becomes grassy or unvegetated?

Table 15.1. Land-cover at each sample point for the 1975 and 1986 maps.

Point	1975	1986	Point	1975	1986
1			26		
2			27		
3			28		
4			29		
5			30		
6			31		
7			32		
8			33		
9			34		
10			35		
11			36		
12			37		
13			38		
14			39		
15			40		
16			41		
17			42		
18			43		
19			44		
20			45		
21			46		
22			47		
23			48		
24			49		
25			50		

Table 15.2. Land-cover change frequencies.

1975 Land cover	1986 Land cover			1975 Totals
	Forest	Grassy	Unvegetated	
Forest				
Grassy				
Unvegetated				
1986 Totals				

Table 15.3. Transition probability matrix.

1975 Land cover	1986 Land cover		
	Forest	Grassy	Unvegetated
Forest			
Grassy			
Unvegetated			

3. Which land cover class was most stable (cover type is likely to remain unchanged) through time? Which one was most unstable? Speculate about the reasons some cover types are more stable than others.
4. This analysis assumes that the processes affecting land-cover change in this map are homogeneous across space. Is this assumption valid?

Exercise IV: Organism-Based Views of the Landscape

Background

One of the challenges of ecosystem management is understanding the effects of landscape-level changes on biological diversity. Depending on their habitat requirements and life-history attributes, species may respond quite differently to landscape changes. Changes that favor one species may reduce the habitat for others. The abundance and spatial pattern of habitat in a landscape can vary between species because species have different habitat requirements (e.g., preferences for late versus early successional stages). Moreover, life-history attributes, such as area requirements and vagility, can interact with the spatial pattern of habitat (i.e., fragmented vs. connected) to affect population dynamics on a landscape. Therefore, an organism-based perspective (e.g., Wiens 1989; Pearson et al. 1996) is needed to estimate the effects of landscape pattern on nonhuman species.

Purpose

The goal of this laboratory exercise is to illustrate how landscape patterns, recorded on land-cover maps, can be interpreted from the perspective of different species. Habitat maps will be produced for four species: mountain dusky salamander (*Desmognathus ochrophaeus*, a native amphibian), princess tree (*Paulownia tomentosa*, an exotic tree), showy orchis (*Orchis spectabilis*, a native herb), and wood thrush (*Hylocichla mustelina*, a forest-interior breeding bird). The following research questions will be addressed:

1. Is the abundance and spatial pattern of habitat similar for both native and exotic species?
2. Does the area requirement of native species affect the suitability of landscapes?

Procedure

The land-cover map used for this exercise was produced from a 1986 Multispectral Scanner (MSS) image of a region northeast of Franklin, North Carolina (Fig. 15.6). The land-cover types include: mixed forest, mesic forest, unvegetated, and grassy/brushy (see map legend). Landscape metrics for these land covers are listed in Table 15.4. The forests of this area are mostly deciduous interspersed with occasional pines. Mesic forests (cove forests) are found on slopes and ravines with north-facing aspects.

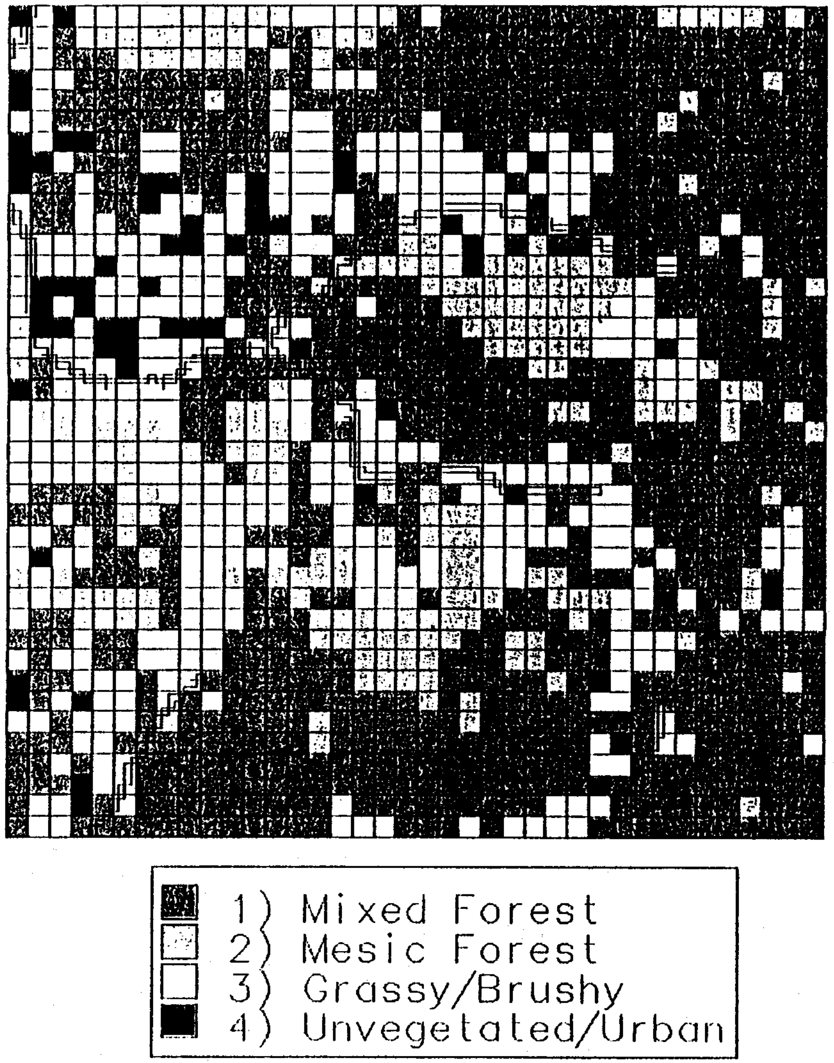

FIGURE 15.6. Land-cover map of region east of Franklin, NC. Pixel size is 90 × 90 m.

The elevation ranges from 638 to 900 m above sea level. This map can be used to produce habitat maps for each species by applying a habitat recipe based on requirements (Table 15.5).

Making Habitat Maps

Obtain four copies of the land-cover map; use one copy for each species. Secure a piece of mylar over the map using paper clips. Use a marking pen

TABLE 15.4. Landscape metrics for land-cover map. Units are in cells. Each cell is 0.81 ha.

Land cover	Total area in cells	Number of patches	Mean patch size	Area of largest patch
Mixed forest	839	5	167.8	792
Mesic forest	219	40	5.5	48
Grassy/brushy	400	27	14.8	169
Unvegetated/urban	62	28	2.2	13

to color in all map cells that are suitable for the species of interest. Make a map for each species; be sure to label the mylar sheets with the species names.

Quantify Habitat Abundance and Pattern

A *patch* of suitable habitat is defined as a group of contiguous cells. For each patch, record its size by counting the number of cells. Record the patch number and sizes in Table 15.6. Calculate the total area of habitat (in cells) and mean patch size, and note the size of the largest patch for each species.

Summary and Discussion

1. Compare the abundance of habitat among the species. Which species has the most habitat in this landscape? Which one has the least?
2. The fragmentation of species' habitats can be compared by examining the mean patch size, number of patches, and size of largest patch. For which species is its habitat most connected?—most fragmented?
3. The wood thrush can use both types of forest in this landscape; however, it is restricted to forest-interior cells. Compare the total number of cells of thrush habitat to the total number of forested cells (Table 15.4). What percentage of the forest cells are unsuitable for the thrush because of edge effects?

TABLE 15.5. Habitat requirements and mapping recipes for species.

Species	Habitat required	Mapping recipe
Mountain dusky salamander	Forests with streams	Forest cells crossed by or adjacent to streams.
Princess tree	Open habitats, disturbed sites	Unvegetated and grassy cells
Showy orchis	Rich woods and stream banks	Mesic forest cells and mixed-forest cells adjacent to streams
Wood thrush	Forest-interior sites	Forest cells at least two cells away from unvegetated and grassy cells

Requirements taken from Wofford (1989), Hamel (1992), and Robinson et al. (1995).

TABLE 15.6. Patch-based statistics for each species' habitat map. Record patch sizes in number of cells.

Species	List of patch sizes	Total cells	Number of patches	Mean patch size	Area of Largest patch

4. Suppose that we evaluate the landscape from a perspective of another species, such as a broad-winged hawk (*Buteo platypterus*), that requires the same habitat as the wood thrush but has a minimum area requirement (e.g., territory size) of 50 cells (40.5 ha). What proportion of the patches would be too small? What proportion of the forested cells would therefore be unsuitable? What effect would an expansion of nonforest land covers have on this species?
5. Limitations in dispersal ability may prevent some species from recolonizing patches that have experienced local extinctions. Lungless salamanders are such species because they can seldom cross dry, open land covers. If we assume that mountain dusky salamanders cannot cross more than two cells of unsuitable habitat, how many of the existing patches of salamander habitat are isolated with respect to potential colonists from other patches?
6. If urban expansion in this landscapes increases the extent of grassy and unvegetated land-covers, how will each of these species be affected? Will these effects depend on the spatial pattern (where and how much) of urban expansion?
7. Given a scenario of future urban growth and the potential to regulate the location of that growth, what portions of the landscape would you protect? Which species would influence your strategy?

Exercise V: Agents of Landscape Pattern

Background

The agents of pattern formation on landscapes include the physical template (abiotic gradients such as temperature and precipitation as influenced by elevation; edaphic heterogeneity), biological processes (demographic processes such as: establishment, growth, and mortality; competition; dispersal), and disturbance (natural as well as anthropogenic regimes). Inferences about the relative importance of these agents in shaping any particular landscape are confounded by interrelationships among the agents (e.g., fire regimes that are conditioned by forest pattern and by topography), and also by the sheer logistical difficulties of collecting data at landscape scales. The central problem in this issue is to devise analysis strategies that can partition the relative importance of pattern-generating agents most efficiently, that is, to provide the most information for the least amount of hard-bought data.

Purpose

The objective of the exercise is to develop a logical framework for quantitative analysis of landscape pattern, partitioning the relative importance of the physical template, biotic processes, and disturbances in governing the distribution of vegetation types or focal species.

Procedure

Approach

The strategy for landscape analysis focuses on an additive regression model, such as forward-selection stepwise regression or regression trees (see below). The approach is to add explanatory variables into the analysis sequentially, choosing the variables and the sequence according to a priori hypotheses (choosing the most likely predictors first) and also according to logistical considerations (specifying the necessary data strategically). In general, this approach amounts to choosing a likely predictor variable, specifying how and where it should "fail" (misclassify) under given circumstances, and then adding predictions about these residuals as the next stage of the analysis. This process is iterative, with additional layers added until no further improvements can be anticipated. This approach is also consistent with a "levels of activity" program funded at varying levels and thus with varying capacity for fieldwork and analysis. For example, one might propose to perform only a few iterations of this process under a low level of funding (i.e., few personnel and little time), but pursue the analysis to additional levels if more funding (personnel, time) was available.

Preparation

The key concepts related to this exercise are concerned with methods for characterizing the physical template (e.g., terrain analysis, geometric models of solar radiation, methods for interpolating climate over complex landscapes); the action of demographic processes, competition, and dispersal in generating or amplifying pattern; and the role of disturbance acting alone and disturbance as it interacts with other agents.

The multiple regression methods tend to be most helpful in this area (e.g., a forward-selection, stepwise model). Classification and regression trees (CART; e.g., Michaelsen et al. 1987; Venables and Ripley 1994; MacNally 1996) are especially appealing because the "flowchart" or tree structure of these methods are a natural fit for this approach. Consequently, CART will seem natural even if you have no prior experience with this analytical technique. Some familiarity with GIS (overlays, buffering) will also be helpful.

Protocol

For this exercise, you will read a paper describing the distribution of some species or land cover type, and then outline an analysis to explain the observed distribution. You should work in a small group of students—three to six participants, with one student acting as moderator—to develop these analyses. Specifically, your group should:

1. Outline the sequence of steps in the analysis in terms of which variable would be entered, how it would be quantified from field or map data (i.e., what data would be required), and the form and direction of the expected relationship.
2. Detail the field or map data needed to verify the predictive model (this data collection effort could include a combination of pilot studies, the main field campaign, and any follow-up studies implied by the analysis). Emphasize *where* these data would be collected.
3. Explain how the results of the analysis would be interpreted, with particular attention to model failures (predictive residuals or misclassifications). It is the residuals or misclassifications that serve as the point of departure for the next stage of the analysis.
4. Summarize the analysis in terms of a flowchart that illustrates the logical flow of the analysis, with key decision points (branches of the tree) explained.

Example 1: Live Oaks in California Foothills

One example of this approach can be reconstructed by embellishing an analysis conducted by Davis and Goetz (1990) (with sincere apologies to the authors for willful recasting of their study to meet this need). The problem is concerned with predicting the distribution of live oaks in the foothills of California. The facts relevant to this contrived example are these. The oaks tend to be found on more mesic sites, which are defined by topographic moisture as driven by solar radiation (a function of slope and aspect), drainage (a function of slope and upslope contributing area), and soil water-holding capacity (estimated from parent material). Thus, the physical template is derived via terrain analysis and a geology map. But oaks occur frequently on sites not predicted to be oak habitat, and also fail to occur on sites predicted to support oaks. The second step of the analysis is to add variables to explain these misclassifications, and so on. The analysis might produce a regression tree and flowchart that looks like Figure 15.7.

In this example, the logic is that some oaks might occur on "non-oak" sites if there was a sufficient dispersal rain to support them in habitats that are demographic sinks (Fig. 15.7). On the other hand, oaks might fail to occur on mesic sites if there was some natural (fire) or anthropogenic disturbance (development, firewood harvesting) operating on those otherwise appropriate sites. In each of the second-tier stages, the approach might involve buffering the maps to focus on particularly informative locations (zones within the presumed dispersal range of sites supporting dense oaks; zones within a specified distance of roads or urban areas).

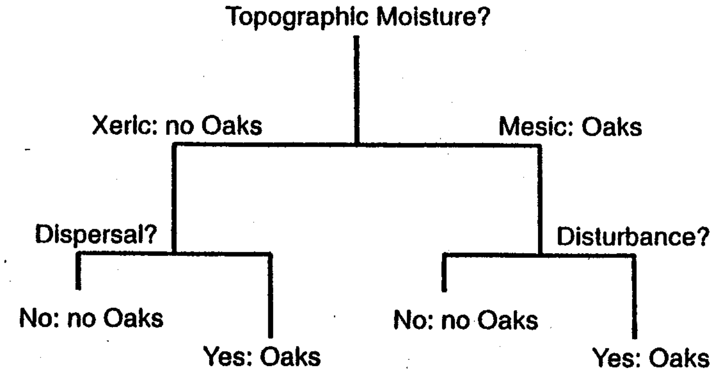

FIGURE 15.7. Flow chart of logic used to relate moisture, dispersal, and disturbance conditions for oaks.

Your summary of the analysis would include the flowchart as well as a more detailed explanation of the logic and interpretation of the analysis.

Example 2: Relic Populations of the Rare *Fusilli puttanesca*

Fusilli puttanesca is a rare herb found on limestone bluffs and outcrops in the Shawnee Hills of southern Illinois. Its current distribution is very patchy. Human disturbance does not seem to be an issue, as these sites are too rugged for agriculture or development. Conservationists would like to be able to predict its occurrence so that they can locate potential sites for reserves. A key concern is to maintain connectedness among relic populations, which are presumed to operate as a classical metapopulation.

Assume that you have or can obtain reasonable data (a DEM, an accurate map of the plant's current distribution, etc.). Devise an approach to explain (predict) the distribution of the species across these landscapes. Outline the approach as a sequence of steps, being specific about your hypotheses and how you would test and interpret them. Summarize the analysis as a flowchart.

Exercise VI: Modeling Landscape Dynamics

Background

Much of landscape ecology is concerned with predicting how landscape pattern might change under various future scenarios including natural succession, alternative management, or anthropogenic climatic change. As many of these future scenarios are without historical precedent, this goal implies an emphasis on models that incorporate at least some level of landscape-scale processes and forcings. Even for ecologists with no plans to actually build and use models, an appreciation of landscape models is crucial because of the increasingly widespread use of models in the discipline.

Purpose

The objective of this exercise is to acquaint you with the basic stages of model building, and also to introduce you to the variety of modeling approaches currently being used in landscape ecology. The objective is not so much to convert you to modelers, but rather to give you a more sophisticated appreciation for how models are developed and applied in landscape ecology.

Procedure

Model Building Basics

This exercise follows an overview of the model-building process, which itself recognizes discrete stages of model development: *conceptualization* (a narrative model), *formulation* (choosing state variables, key processes, and the equations that describe these), *parameterization* (assigning empirical estimates to the state equations and auxiliary functions), and *verification* (initial tests to ensure that the model can adequately reproduce the data used to build it). Subsequent stages of model analysis (sensitivity, uncertainty) and validation (tests against independent data) are discussed in lecture but not addressed in this exercise.

In preparation for this lab, review your lecture notes on the types of models commonly applied in landscape ecology: Markov models, cellular automata, and patch transition simulators. Look in recent journal articles for examples of studies using these models. Also, review your notes on the use of Forrester diagrams or similar notations. This diagrams are used to provide "box and arrow" representations of models.

Protocol

Select one of the papers provided that describe factors affecting change in a particular landscape. These papers were selected to illustrate key issues in landscape dynamics. You should work in a small group of students. The group should follow the steps below. Your group should evaluate alternative conceptual models or opinions about what needs to be included in the model. However, in the end the group should reach consensus on formulation to be used. The steps in the model-building exercise are:

1. State the general goal of building the model, and a small number of specific objectives for initial applications (these may be dictated by the instructor, simply to provide a common focus for the class). Objectives should be few and specific, and should define the spatial scale, resolution, and information content required of predictions, as well as the time scale over which these predictions will be made.
2. Write a concise narrative description of the conceptual model—one paragraph at most.
3. Outline the conceptual model schematically, using Forrester or similar conventions (see below). In this diagram, include the state variables, the key interactions (fluxes, transitions), and auxiliary variables that influence these states or processes.
4. In a companion table, itemize the parameters of the model, specifying their units and their nominal values (if known), or identify the data needed to estimate the parameter. In most cases, the values will not be known and a short explanation of how the data could be collected to parameterize that part of the model will be required. This step is one of the more sobering stages of model building, as landscape-scale models are often more data intensive than is logistically practical.
5. Specify how the model could be verified, by itemizing the comparisons between model output and empirical measurements that would corroborate its behavior, and also specify the criteria by which you would accept or reject the model's predictions. If data are already available, describe the test; if test data are not already available, describe data that could be collected to verify the model.

Example

Figure 15.8 shows an example of conventions for diagramming models. Here, cover type *X1* (a state variable) undergoes a transition to cover type *X2*, as modified by the auxiliary parameter *b1* (e.g., elevation or soil type). The influence of *b1* might be specified as a scaling function (e.g., linear or

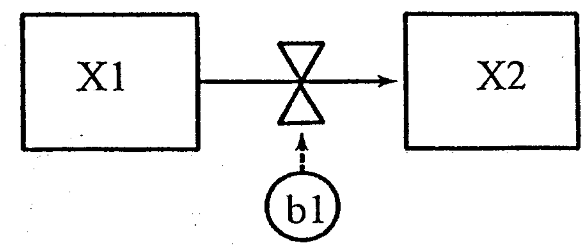

FIGURE 15.8. Conceptual model for relating the transition of a parcel of land from one cover type (*X1*) to another (*X2*).

some other form) or as a conditional probability, depending on the model. In a spatial model, *b1* might be the proportion of the neighborhood already occupied by cover type *X2*. It is at this level of implementation that most of the crucial decision in model building take place, and this stage is the focus of this exercise.

Appendix I. Origin and Acknowledgments for Exercises

Exercise I

This exercise is currently used in the undergraduate General Ecology course at the University of Wisconsin-Madison. The exercise was initially developed by Dr. Timothy F.H. Allen and graduate teaching assistant Hillary Callahan. Dr. Monica G. Turner subsequently modified the lab, and laboratory coordinator Dr. Susan Will-Wolf has supervised its implementation.

Exercise II

This exercise is currently used in the graduate Landscape Ecology course at the University of Wisconsin-Madison which is jointly taught by Monica G. Turner and David J. Mladenoff.

Exercise III

This exercise is being used in introductory and advanced courses in ecology for undergraduates at Mars Hill College, Mars Hill, North Carolina. It was prepared by Dr. Scott Pearson. The exercise is designed to demonstrate a straightforward technique for quantifying the frequency of land-cover types in complex landscapes. After the students complete this exercise, they are introduced to geographic information systems (GIS) explaining that computers provide means to conduct the same types of measurements with greater speed and accuracy. See Brewer and McCann (1982) for another simple exercise that uses aerial photographs.

Exercise IV

This exercise is being used in an introductory course in ecology for undergraduates at Mars Hill College, Mars Hill, North Carolina. It was created by Dr. Scott Pearson. The exercise is designed to demonstrate that species respond to landscape-level changes in different ways. Ideas for this exercise came from collaborations with R.H. Gardner, R.V. O'Neill, and V.H. Dale at Oak Ridge National Laboratory. The data for the maps has been provided and research related to Exercises III and IV has been supported by the Temperate Ecosystems Program of the U.S. Man-and-the-Biosphere Program, U.S. Department of State, and by a grant from the National Science Foundation DEB 9416803.

Exercise V

This exercise was produced by Dean Urban for his Landscape Ecology course. This survey course is intended for beginning graduate students at the Nicholas School of the Environment at Duke University. The School confers a professional degree, a Master's in Environmental Management (MEM), and these students comprise the bulk of the class roster (the remainder being Ph.D. students and an occasional advanced undergraduate). The MEM program emphasizes environmental problem solving and tries to instill in students a proficiency in the logic and tools of environmental analysis.

The Landscape Ecology course typically fills up with about 35 students. The format is a combination of lectures and student-moderated small-group discussions. In lieu of a formal laboratory session in a computer lab, the strategies and technical methods for problem solving are developed in "dry lab" exercises in which students work on the initial set-up and design of landscape analyses—that is, they outline the approach, specify how the analysis would proceed, and how the results would be interpreted. A combination of real examples from published analyses and hypothetical examples are contrived to illustrate specific points.

The example exercises outlined here (Exercises V and VI) are the capstone exercises for two units of the course and are concerned with (1) inferring the relative importance of various agents of pattern formation on landscapes, and (2) building models of landscape dynamics. The full course syllabus and a guided survey of key concepts and literature in landscape ecology are currently being made available over the Internet via http://www.env.duke.edu/lel.

Exercise VI

This exercise was prepared by Dean Urban for his landscape ecology course at the School of the Environment at Duke University.

Appendix II. Recommended Readings and Notes to Instructors

Exercise I

Recommended Reading

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366. (The author reviews the main results from percolation theory and asks whether empirical studies of birds and mammals are in agreement with the results.)

Turner, M.G., R.H. Gardner, V.H. Dale, and R.V. O'Neill. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55:121–129. (This paper links a neutral model of spatial pattern with the spread of disturbance and identifies different disturbance dynamics related to the threshold of connectivity.)

Notes to Instructors

This exercise assumes at least one prior lecture on elementary concepts and approaches to landscape ecology. Students should be familiar with what constitutes a landscape; why we study the effects of landscape heterogeneity; the use of models as a component of scientific inquiry; and notions of habitat connectivity and why it would be important for processes like the movement of organisms or spread of a disturbance.

An advantage of the lab is that it is clearly "low tech." That is, even though much of the landscape literature is replete with elegant computer-based explorations of various types of real and artificial maps, this exercise is pencil-and-paper based, requiring no computer resources, and the results are readily interpretable and intuitive. Also, the students work in groups of approximately five providing an excellent opportunity for interaction.

The instructor should assemble the following materials in advance: (1) A handout describing the lab and including a practice sheet on which students make sure they understand what is meant by defining patches, counting edges, and so on. The text provided in this chapter can serve as a foundation for an exercise based on local landscapes. (2) A random number table or generator from which to draw (x, y) coordinates ranging from 1 to 10. (3) Either many copies of 10×10 blank grids or erasable 10×10 grids for generating the random maps. (4) A set of topographic maps (USGS 7.5′ quads work just fine) or other mapped source of data from real landscapes. For Wisconsin, we use topographic maps and have students look at the spatial distribution of land and water in different regions of the state. For other regions, however, one might choose other categories, such as forest versus nonforest, or developed versus undeveloped land. (5) A set of acetate 10×10 grids at two spatial scales that will be overlain on the real landscape maps.

Exercise II

Recommended Reading

Gardner, R.H., and R.V. O'Neill. 1991. Pattern, process, and predictability: the use of neutral models for landscape analysis. In: Quantitative Methods in Landscape Ecology, pp. 289–307. M.G. Turner and R.H. Gardner (eds.). Springer-Verlag, New York.

Moody, A., and C.E. Woodcock. 1995. The influence of scale and the spatial characteristics of landscapes on land-cover mapping using remote sensing: Landscape Ecology 10:363–379.

Turner, M.G., R.V. O'Neill, R.H. Gardner, and B.T. Milne. 1989. Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecology 3:153–162.

Wickham, J.D., and D.J. Norton. 1994. Mapping and analyzing landscape patterns. Landscape Ecology 9:7–23.

Woodcock, C.E., and A.H. Strahler. 1987. The factor of scale in remote sensing. Remote Sensing Environment 21:311–332.

Notes to Instructors

Prior to implementing this exercise, students should have had an in-depth introduction to the quantification of spatial pattern and a basic introduction to scale issues. The following topics would be appropriate to cover in advance: definition of grain and extent; why scale is important; why quantify pattern; data used in landscape analyses; metrics of landscape pattern; temporal change in landscape patterns; and neutral models of landscape patterns.

Prior to the exercise, the instructor should assemble the following materials: (1) A data set or sets for the class to analyze. These should not be too large (100×100 is plenty) and should be in a format that is ready to go. (2) A source and executable code for conducting spatial pattern analyses OR a set of very simple but sensitive metrics that can be applied by pencil and paper. Ideally, a set of computers available for the class would be loaded with the data and programs. (3) Visualizations of the original data file (hard copy, overhead, or slide). (4) Detailed handout of instructions, and a readiness to deal with computer problems! (5) Group assignments. Students enjoy doing this lab collaboratively. However, the instructor should form the groups, recognizing that the computer/GIS expertise within a class of graduate students is extremely variable! Make sure that a computer-experienced student is in each group. Four students is an optimal group size.

As presented here, completing this exercise requires between 50 and 60 person hours, or about 15 hours per student. Rescaling the data set—either by writing an algorithm or by doing it manually in a word processor—was very time consuming. To reduce the amount of time required by the students, a program to do this could be supplied or the data could be distributed initially at the various scales.

Some students prefer to receive more explicit instructions on what metrics to use and compare, and how to go about this. Leaving the exercise open-ended may be unsettling, yet in the "real world" one must make choices about what to consider and learn about how sensitive the metrics may be to various manipulations of the data. However, the instructor should decide what will be most effective for his or her students.

Exercise III

Recommended Reading

Baskent, E.Z., and G.A. Jordan. 1995. Characterizing spatial structure of forest landscapes. Canadian Journal of Forest. Research 25:1830–1849.

Gustafson, E.J., and G.R. Parker. 1992. Relationship between landcover proportion and indices of spatial pattern. Landscape Ecology 7:101–110.
Jelinski, D.E., and J. Wu. 1996. The modifiable aerial unit problem and implications for landscape ecology. Landscape Ecology 11:129–140.
Kienast, F. 1993. Analysis of historic landscape patterns with a Geographical Information System—a methodological outline. Landscape Ecology 8:103 118.
O'Neill, R.V., J.R. Krummel, R.H. Gardner, G. Sugihara, B. Jackson, M.G. Turner, B. Zygmunt, S.W. Christensen, V.H. Dale, and R.L. Graham. 1988. Indices of landscape pattern. Landscape Ecology 1:153–162.
Pastor, J., and M. Broschart. 1990. The spatial pattern of a northern conifer-hardwood landscape. Landscape Ecology 4:55–68.
Turner, M.G., and R.H. Gardner. (eds.), 1991. Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York.

Notes to Instructors

Sampling grid: The sampling-grid transparency is a piece of mylar or transparency film with a grid of points. The rows and columns of this grid may be numbered ahead of time, or the students can do the numbering as part of the exercise.

Question (1): Students can perform a goodness-of-fit test to test the statistical significance of the change in land-cover frequencies recorded in Table 15.2. Given a null hypothesis of no change, we can expect the 1986 row totals (observed) to closely match the 1975 column totals (expected). Plug the totals for each land-cover type into the following equation:

$$X^2 = \sum\left[(\text{total}_{1986} - \text{total}_{1975})^2 / \text{total}_{1975}\right] \quad \text{d.f.} = 2$$

Reject the null hypothesis of no significant change if $X^2 > 5.991$ ($p \leq 0.05$). See a statistics text such as Bailey (1995) for more information.

Question (4): The mechanisms of land-cover change for this area are not homogeneous. Wear and Flamm (1993), Turner et al. (1996), and Wear et al. (1996) demonstrate that a number of site characteristics, including sociological and economic qualities, influence the frequency and trajectory of land-cover changes in this study area. Students may notice that most of the conversion of forest to non-forest covers occurs along the existing road network. Therefore, the rate and pattern of change along roadsides was different than the rate and pattern of changes away from roads. Students could test this hypothesis by repeating the analysis to compare the results from a set of random points near roads to a set of points some maximum distance away from roads.

Exercise IV

Recommended Reading

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

Blake, J.G., and J.R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724–1734.
Flather, C.H., S.J. Brady, and D.B. Inkley. 1992. Regional habitat appraisals of wildlife communities: a landscape-level evaluation of a resource planning model using avian distribution data. Landscape Ecology 7:137–147.
Hansen, A.J., and D.L. Urban. 1992. Avian response to landscape pattern: the role of species' life histories. Landscape Ecology 7:163–180.
Hansson, L., and P. Angelstam. 1991. Landscape ecology as a theoretical basis for nature conservation. Landscape Ecology 5:191–201.
Kadmon, R. 1993. Population dynamic consequences of habitat heterogeneity: an experimental study. Ecology 74:816–825.
Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.
Pearson, S.M., J.M. Walsh, and J. Pickering. 1992. Wood stork use of wetland habitats around Cumberland Island, Georgia. Colonial Waterbirds 15:33–42.
Price, M.V, P.A. Kelly, and R.L. Goldingay. 1994. Distance moved by Stephen's kangaroo rate (*Dipodomys stephensi* Merriam) and implications for conservation. Journal of Mammalogy 75:929–939.
Robinson, S.K., F.R. Thompson III, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

Notes to Instructors

Rather than using the mylar template for making the habitat maps, you can provide students with extra photocopies of the land-cover map. They can use ink markers or grease pencils (red or orange) to color in the cells that meet the habitat criteria for a given species. Students need one additional map for each species.

Having each student make a map for each species is time consuming. You can divide the students into small groups (two–four students each) and assign one or two species to each student. When they finish making the maps, have them compare maps within and between groups.

The questions listed above can be used for group discussions or to from the basis of a lab report to be prepared for each group or individual student. Instructors are encouraged to use alternative land-cover maps and/or develop mapping recipes for species native to their geographic region.

Exercise V

Recommended Reading

Davis, F.W., and S. Goetz. 1990. Modeling vegetation pattern using digital terrain data. Landscape Ecology 4:69–80.
Gardner, R.H., B.T. Milne, M.G. Turner, and R.V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology 1:19–28.

Notes to Instructors

The key issue to underscore in this exercise is that data at the landscape scale are logistically expensive and by focusing the analysis as much as possible we can derive the most information from minimal data, carefully selected. If nothing else, the students should appreciate that all data are not created equal, that some data are more informative and hence more valuable than others.

The example concerned with oaks in California foothills also illustrates the utility of CART analysis in analyses like this. CART is a recursive procedure which, for categorical response variables, executes a logistic regression at each "branch" of the regression tree, yielding a split between, say, mesic "oak sites" and more xeric "non-oak sites" (Fig. 15.7). Importantly, the analysis also provides a summary of how many sites classified as "oak sites" were not observed to support oaks, and reciprocally, how many "non-oak sites" actually had oaks on them. The next step in the analysis would be to refine these branches, that is, to distinguish the misclassified sites on either branch, improving the model's classification accuracy recursively. As a tree diagram, this procedure highlights the take-home message that information about dispersal limitations is best expressed on sites that are potential habitat but are not occupied by oaks. Reciprocally, it is impossible to gain any information about dispersal limitations from sites that do not qualify as potentially usable habitat in the first place. Thus, the regression tree can graphically enforce the notion that landscape analysis often requires highly selective subsets of site conditions to provide useful answers to questions about agents of landscape pattern. (The instructor should note that there are analysis scenarios that can be sufficiently complicated that CART still works as an analysis but may fail miserably as a heuristic device!)

Given real data and adequate computing facilities, this exercise could be expanded into a "live" analysis. In this, students actually would analyze data using either partial regression or regression trees. (This is how it's done in the more advanced, second-year classes in Duke's MEM curriculum.)

Exercise VI

Recommended Reading

Baker, W.L. 1989. A review of models of landscape change. Landscape Ecology 2:111–133.

Sklar, F.H., and R. Costanza. 1991. The development of dynamic spatial models for landscape ecology: a review and prognosis. In: Quantitative Methods in Landscape Ecology, pp. 239–288. M.G. Turner and R.H. Gardner (eds.). Springer-Verlag, New York.

Usher, M.B. 1992. Statistical models of succession. In: Plant Succession: Theory and Prediction, pp. 215–248. D.C. Glenn-Lewin, R.K. Peet, and T.T. Veblen (eds.). Chapman & Hall, London.

Weinstein, D.A., and H.H. Shugart. 1983. Ecological modeling of landscape dynamics. In: Disturbance and Ecosystems, pp. 29–45. H.A. Mooney and M. Godron (eds.). Springer-Verlag, New York.

Notes to Instructors

The challenge in teaching landscape modeling, of course, is that few students will have the technical skills needed to actually build a model (for example, programming language, algorithms), and the empirical effort in parameterizing and testing a model are even more intimidating. Commercial software packages that make simple models easy (for example, STELLA)©, can be quite useful for labs such as this, but the initial investment in getting students acquainted with the package might require more time than is available for a single lab exercise (Duke's Masters in Environmental Management program defers STELLA© to a separate course, Principles of Ecological Modeling).

In this exercise, students build models by concentrating on the conceptual stages of model development, but stopping short of actual coding. This approach argues that the conceptual stages are the most crucial steps in model building, and also presumes that an appreciation of models at this level might be adequate for many students' needs. Models are developed from purely empirical, descriptive papers that document particular landscapes.

Because this exercise requires a prior familiarity with some landscape, it is difficult to provide a facile example of this exercise that can be explored in just a short time. Some example landscapes that might provide useful tutorials: First, Foster (1992) provides a nice reconstruction of the history of landscape change in New England. This paper underscores an important point, that the rules that drive landscape change vary over time. New England has undergone a shift from deforestation to reforestation during the past century. Implemented as a simple Markov model, this would imply nonstationary transition probabilities; to circumvent this problem, a model must either become more than first-order (i.e., transitions depend on past states as well as current states), or multiple transition matrices could be used (one for each time period of interest). Second, gradient studies (there are countless examples) provide easy empirical patterns for use in building models in which transitions among cover types or vegetation zones are conditioned by environmental variables such as those derived from digital elevation models. Finally, in more complicated scenarios, transitions might include disturbances (pest outbreaks, fires) that include feedbacks to vegetation status or environmental variables. (This level of complexity matches many current landscape models.)

The exercise of building a model prototype in a small-group setting nicely illustrates the trade-offs between realism and simplicity in model construction. A further benefit of doing this exercise in multiple small groups is that the groups can compare models in a follow-up discussion session. Different groups invariably will devise different models, and it is especially fruitful to force groups to justify the approach they adopted over other alternatives.

The emphasis on the initial, largely conceptual aspects of modeling allows students with limited math and computer skills to participate equally with their more technically advanced peers.

The next level of activity beyond this exercise would be to actually use models. There are two approaches to this. The easier would be to provide students with simple models that they could use to perform various demonstration runs or model experiments. This approach would require a well-documented model and adequate computer facilities, and would also require a minimal level of computer familiarity of the students. A more in-depth approach would be to have students build and encode a model themselves. This is clearly beyond the scope of most introductory courses.

As an example of the former approach, that of using an existing model, we have had quite good experiences by providing the students with a simple Markov model of succession in a forested landscape. Usher (1992) provides an excellent overview of the construction and analysis of Markov models such as this. The example is drawn from a Pacific Northwestern landscape that has been classified from Landsat Thematic Mapper imagery into discrete age classes (see http://www.env.duke.edu/lel for similar lab exercises on landscape change). Students are given an array of cell values that indicates the age class of the cell in each of the three time periods; these data are provided for 200 cells randomly sampled from the images. Students then build the transition tally matrix from these data, summarizing the number (ultimately, the proportion) of cells that changed from type (age) i to type j during each time interval. Students then normalize these transitions to an annual timestep, and construct the transition matrix $\boldsymbol{P}$, which gives the probability of a cell (equivalently, the proportion of cells) that change from type i to j in each timestep.

$$P = \begin{bmatrix} p_{11} & p_{12} & p_{13} & \cdots \\ p_{21} & p_{22} & p_{23} & \cdots \\ p_{31} & p_{32} & p_{33} & \cdots \\ \cdots & \cdots & \cdots & \cdots \end{bmatrix}$$

The students also tally the initial state vector $\boldsymbol{x}$, which is the proportion of cells in each type (age class) for the first time period. For model testing, they also tally the state vectors for the second and third time steps.

The solution of a Markov model is given by:

$$x_{(t+1)} = x_{(t)}P$$

where $x(t)$ is the initial state vector. Similarly,

$$x_{(t+2)} = x_{(t+1)}P = x_{(t+1)}P^2$$

and, in general,

$$x_{(t+k)} = x_{(t)}P^k$$

for k timesteps after the initial condition. The steady-state solution can be solved by eigenanalysis, that is, by finding the vector x^* such that $\boldsymbol{x^* = x^*P}$.

For our purposes, students are provided with a simple Fortran program that iterates the model and provides output in a format suitable for graphics packages. They initialize the model with data from the first time period, verify it against the second time period (which works nicely), and then validate the model using data from the third time period (it does not validate because the timber harvest rates have increased). They are then asked to find the steady state, and to speculate on how the model might be extended to address landscape-scale issues such as stationarity (they see the lack of this when they attempt to validate the model with data from the third time period) and spatial contingencies in forest harvest or other land use change.

This exercise is especially effective because it allows students to parameterize a model, test it to discover its weaknesses, and then to speculate on how they would improve the model. Still, the exercise does not require any special skills such as programming. It should be noted that commercial packages such as STELLA© (High Performance Systems Inc., Hanover, NH) could also be used in this exercise; STELLA© would solve the model as a system of differential equations as compared to a Markov model, but the parameters and the solution are equivalent.

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Part VI
Synthesis