CHAPTER 11

LANDSCAPE DISTURBANCE

LOCATION, PATTERN, AND DYNAMICS

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OBJECTIVES

The causes, patterns, dynamics, and consequences of disturbances are major research topics in ecology and particularly landscape ecology (Romme and Knight, 1982; Risser et al., 1984; Pickett and White, 1985; Turner, 1987; Turner et al., 1989; Baker, 1989; Turner et al., 1997; Turner and Dale, 1998). Disturbances are also of tremendous importance in land and resource management, both for managing human activities (e.g., Hunter, 1993; Parsons et al., 1999) and for conserving resources and biodiversity in landscapes influenced by disturbance (e.g., Dale et al., 1998). In this lab, students will

1. use analyses of point data to compare spatial patterns of disturbance and examine multiple drivers of disturbance-generated landscape pattern;
2. compare and contrast the landscape mosaic created by a natural and a human-induced disturbance regime and explore the "historic range of variability" concept; and
3. consider the concept of equilibrium on a disturbance-prone landscape and its sensitivity to spatial and temporal scale.

Students will use a combination of hand calculations, analysis of spreadsheet data, and graphical analyses to understand several different aspects of the interaction between disturbance and landscape pattern. First, students will

examine the influence of landscape position on susceptibility to disturbance, using fire initiation patterns in Alaska, USA, as an example. In Part 2, students will examine differences in pattern created by crown fire and harvesting activities in a coniferous landscape in the Rocky Mountains. Finally, students will examine the effects of spatial and temporal scale as they influence inferences about the stability of a landscape.

INTRODUCTION

Disturbance has long been recognized as an important driver of landscape heterogeneity (Watt, 1947), which is integral to understanding landscape dynamics. A **disturbance** is defined as a relatively discrete event that disrupts the structure of an ecosystem, community, or population and changes resource availability or the physical environment (White and Pickett, 1985). Disturbances are interesting in that they both create and respond to spatial heterogeneity in the landscape, and this is one reason disturbance has received such attention in landscape ecology. Landscape ecological studies of disturbance focus on several aspects of these relationships.

A variety of attributes are used to characterize a disturbance regime. Included among these are the spatial location of the disturbance, the size and shape of disturbed patches, and the spatial extent and frequency of disturbance. In addition, because disturbed landscapes fluctuate through time as succession occurs, the temporal pattern of variation in the landscape is important. Observations of this variation through time in different landscapes have influenced perceptions of how stable a landscape is and whether a particular event results in departures from typical levels of variation.

EXERCISES

Part 1. Landscape Position and Susceptibility to Disturbance

Are various spatial locations in the landscape differentially susceptible to disturbance? If so, can we predict which areas are more or less susceptible to particular types of disturbance? Can locational differences be used to suggest driving factors for particular disturbances? Do the spatial patterns of disturbance locations differ for natural and human-caused disturbances? Susceptibility to disturbance of sites located at particular landscape positions is evaluated by comparing the probability or frequency of occurrence of a particular disturbance at many places in a landscape. A variety of studies have demonstrated that particular locations in a landscape may be more or less sensitive to a given kind of disturbance. For example, Foster (1988a, 1988b) examined a natural disturbance regime characterized by frequent, local events, such as windstorms, pathogens, and lightning strikes, and occasional broad-scale damage by hurricanes and winds in New England. Susceptibility of a site in New

England to disturbance was controlled by slope position and aspect. In landscapes subject to fire, the probability of ignition may vary spatially (e.g., Burgan and Hartford, 1988; Chou et al., 1993). For example, there is a high frequency of lightning ignitions on ridgelines and south-facing slopes in Glacier National Park, Montana (Habeck and Mutch, 1973).

Whereas topographic position does influence fire ignitions, human influences in the landscape may also produce spatial variability in fires. In the Upper Midwestern United States, Cardille et al. (2001) investigated the relationship between wildfire origin locations and environmental and social factors for over 18,000 fires between 1985 and 1995. Results revealed that fires were more likely to occur in locations having higher human population density and less likely to occur in interior forests.

In this exercise, a simple analysis of the spatial distribution of natural and human-caused fire ignitions in Alaska will be used to illustrate the influence of proximity to roads on the spatial pattern of fire and the differences in spatial aggregation of natural and human-caused fires.

Study Site

Natural fires in Alaska occur primarily in the middle third of the state, between the Brooks Range to the north and the Alaska Range to the south (Figure 11.1a). In this interior portion of the state are extensive stands of highly flammable black spruce forests and a continental climate supporting hot, dry summers. Lightning is the major natural source of ignition, with as many as 4000 lightning strikes per day. North of the Brooks Range and along the western coast, lightning strikes are rare and the vegetation is dominated by tundra, whose surface organic mat is normally too wet to burn. South of the Alaska Range, relatively few convective storms generate lightning strikes, and the vegetation is dominated by deciduous forests and deciduous shrub understory, which is also typically too wet to burn. Alaska has relatively few roads, and the majority of the state's population is concentrated in a few towns and cities or dispersed along these roads. Human ignitions account for 85% of the number of fires; however, lightning-caused fires account for more than 90% of the area burned.

EXERCISE 1.1

First, examine the location of natural and human-caused fires in Alaska from the period 1957 to 1975 (Figure 11.1; Gabriel and Tande, 1983). From visual inspection, natural fires seem to be distributed randomly, but the human-caused fires are not. Visually, the human-caused fires appear to be related to the distribution of cities and major roads. To test this relationship, a *t*-test will be used to compare the distances to roads from 20 randomly selected natural fires and 20 randomly selected human-caused fires using a subset of the landscape (Figure 11.2). The hypothesis is that

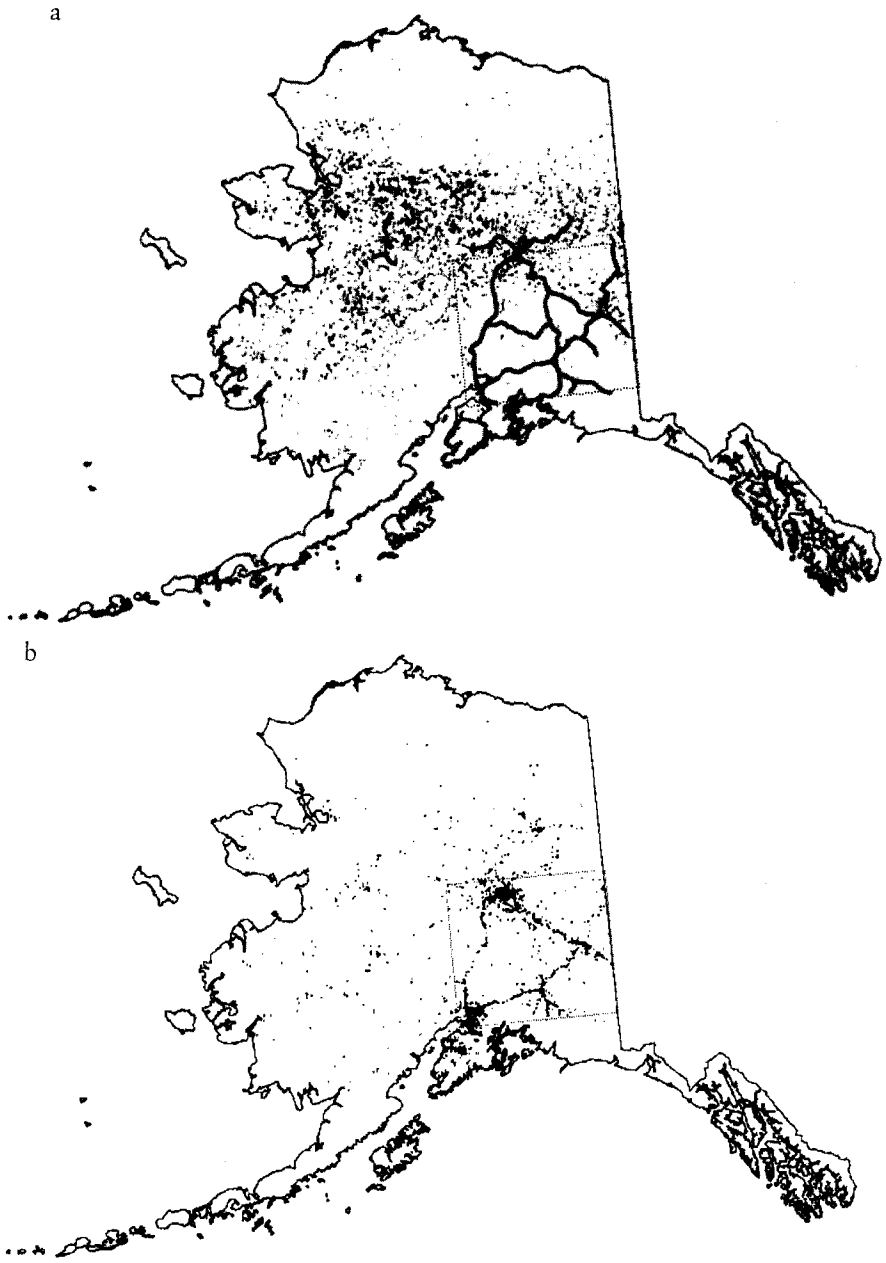

FIGURE 11.1
Maps showing locations of (a) natural fires and (b) human-caused fires in Alaska from 1957 to 1975. The dotted line represents the study landscape used for this exercise and is approximately 250,000 km^2 in extent (see Figure 11.2a, b). The roads have been removed from Figure 11.1b to better show the locations of human-caused fires.

mean distance to roads will be greater for the natural fires than for those of human origin.

1. Print Figure 11.2a from the CD. Use a calculator or other random number generator to select 20 points of fire initiation from the map of natural fires (Figure 11.2a) as follows:
   (a) For the first randomly selected fire, select a random number between 0 and 135 (the length, in mm, of the x-axis of Figure 11.2a).
   (b) Next, select a random number between 0 and 119 (the length, in mm, of the y-axis of Figures 11.2a and b).
   (c) Plot these two numbers (in mm) as an x–y coordinate on Figure 11.2a and select the fire nearest the x–y coordinate.
   (d) Repeat this until 20 fire locations have been chosen.

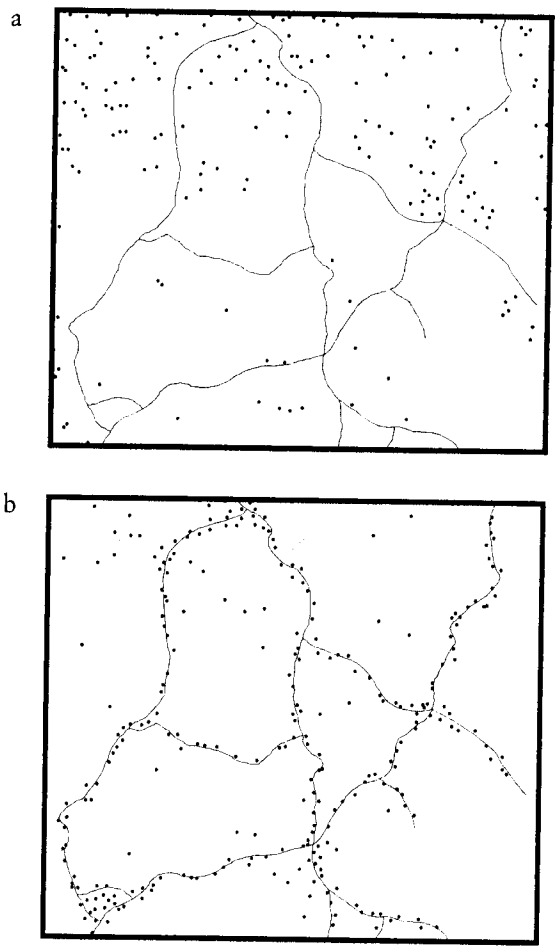

FIGURE 11.2
Maps representing the 250,000-km^2 study landscapes used for this exercise, showing locations of (a) natural fires and (b) human-caused fires in Alaska. Each point represents a single fire, and solid lines represent roads. Be sure to base your calculations on the printed versions from the CD.

2. Use a ruler to measure the distance (in mm) between each randomly chosen fire and
   (a) the nearest major road
   (b) the nearest fire ("nearest neighbor")
3. Record the distance between each fire and the nearest road in Table 11.1 (which can be printed from the CD), under the column labeled "Distance (mm) on map to nearest road—Natural fire."
4. Record the distance between each fire and its nearest neighbor in Table 11.1, under the column heading "Distance (mm) on map to nearest neighbor—Natural fire."
5. Repeat the analysis (steps 1–3) for the printed map of human-caused fire (Figure 11.1b). Record your results in Table 11.1 under the column "Human-caused fire" for both roads and the nearest neighboring fire.

To test the hypothesis that the mean distance to roads will be greater for natural fires than for human-caused fires, conduct a *t*-test using data from Table 11.1 and Microsoft Excel.

1. Enter the data for the distance to nearest road for both natural and human-caused fires (the first and second columns of data in Table 11.1) into a worksheet in Excel, including the column headings.
2. Under the **Tools** menu, select **Data Analysis.** In the **Analysis Tools** window, scroll down to **"t-test: Two-Sample Assuming Unequal Variances."** (*NOTE:* If Data Analysis does not appear under the **Tools** menu, Select **Add-Ins,** and add the **Analysis Tool Pak.**)
3. Enter the distance to nearest road data from the natural fire and human-caused fire columns into the variable 1 and variable 2 range boxes by highlighting the data in the worksheet using the mouse.
4. Under the **Output Options** box, select the circle next to **Output Range,** and enter a destination cell or range of cells for the *t*-test output in the worksheet, usually a cell a few columns away from your data.
5. Click **OK,** and the *t*-test will be computed.

If the absolute value of the *t*-statistic computed for your data is greater than the *t*-critical value provided in the output, this rejects the null hypothesis, but supports the alternative hypothesis that the mean distance to roads is greater for natural fires than for human-caused fires.

EXERCISE 1.2

To determine whether the spatial dispersion patterns (e.g., random, clumped, or uniform) for natural and human-caused fires are similar or different, you will use a modified Clark and Evans (1954) method of nearest-neighbor analysis. For each fire type, the **expected** mean distance between

fires is the density of all fires (number of fires/km^2, or number of fires/mm^2 in map units) within the entire study area. The **observed,** or measured, mean distance between fires is determined using your nearest-neighbor measurements. The ratio of the observed mean distance of fires to the expected mean distance represents a measure of the degree of randomness of the spatial patterns of fire distribution: If the ratio is 1, the fires have a random distribution; if the ratio is 0, the fires are completely aggregated; and a ratio of 2.1419 reflects a completely uniform distribution of the fires.

1. Using either Microsoft Excel or a pocket calculator, calculate the mean distance to the nearest neighbor for natural and human-caused fires (the third and fourth columns of data in Table 11.1). The **expected mean distance between natural fires,** given a density of 180 fires/250,000 km^2, is 18.1 km in the real world, or **4.7 mm** in map units for the purposes of this exercise. The **expected mean distance for human-caused fires,** given a density of 1020 fires/250,000 km^2 is 7.8 km in the real world, or **1.9 mm** in map units for the purposes of this lab.
2. Compute the ratios of the mean observed-to-expected distances for each fire type by dividing the observed value by the expected value.

Question 1.1. Based on your computations, is the spatial pattern of human-caused fires different from the spatial pattern of naturally occurring fires in Alaska? Why or why not?

Question 1.2. In this example, only a single extrinsic variable (distance to roads) was used for the comparison of fire ignition patterns. However, often multiple factors influence the susceptibility of a site to disturbance. If you were to model the ignition of fires across a landscape, what other independent variables might you consider? How might you test for the effects of multiple factors on disturbance initiation and spread? Would these variables be likely to change as the scale of analysis changes from a few hectares to a region, then to continental or global scales? How would they change?

Question 1.3. More generally, under what conditions would you expect landscape position to increase the susceptibility of a site to disturbance? Are there conditions in which landscape position would not be important?

Part 2. Disturbance-Generated Landscape Patterns and the Natural Range of Variability

Disturbances create complex heterogeneous patterns across the landscape because the disturbance may affect some areas but not others, and severity of the disturbance often varies considerably within the affected area. These resulting mosaics may show considerable persistence through time. The spatial patterns created by a variety of natural disturbances have been described (e.g., Foster et al., 1998), and the landscape patterns in human-influenced land-

scapes have been compared with those subjected to natural disturbances only (e.g., Krummel et al., 1987; Mladenoff et al., 1993). In particular, the landscape patterns resulting from forest harvesting strategies have received considerable attention (e.g., Franklin and Forman, 1987; Li et al., 1993; Gustafson and Crow, 1996), and a number of comparative studies have examined the differences in the landscape mosaic resulting from wildfire and forest harvesting. For example, Delong and Tanner (1996) compared the spatial characteristics of landscapes in British Columbia subjected to regularly dispersed 60- to 100-hectare clearcuts with the historic patterns generated by wildfire. They found that wildfires created a more complex landscape mosaic that included a greater range of patch sizes and more complex disturbance boundaries. In addition, individual wildfires were often greater than 500 hectares in size, but unburned forest patches remained within the perimeters of the fire (Delong and Tanner, 1996).

There has been considerable discussion about the use of natural spatial patterns as a model for the pattern and timing of human disturbances (e.g., clearcutting) (Hunter, 1993; Attiwill, 1994; Holling and Meffe, 1996), with the implicit assumption that ecological processes will be better maintained in this way. For example, Runkle (1991) suggested that temperate deciduous forest should be harvested in a pattern that mimics small treefall gaps, whereas Hunter (1993) recognized that boreal forests would require very large clearcuts if they were to imitate the size and arrangement of boreal fires. Improved understanding is needed of the nature and dynamics of disturbance-generated mosaics in a wide variety of landscapes and how these differ from human-generated patterns. Although this idea is intuitively appealing, it is difficult to define and mimic natural patterns objectively. Meeting such an objective also requires understanding the dynamics of the natural disturbance regime in a given landscape and the range of variation to be expected in its spatial pattern.

The use of historical patterns and processes as reference conditions for informed land management has emerged as an increasingly recognized and debated concept in ecosystem management (Parsons et al., 1999). **Natural variability** is defined as the spatial and temporal variation in ecological conditions that are relatively unaffected by people within a period of time and geographic area appropriate to an expressed goal (Landres et al., 1999). The concepts considered under the rubric of "range of natural variation" or "natural variability" include (1) that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems, and (2) that past conditions and processes provide context and guidance for managing ecological systems today (Landres et al., 1999). Using these concepts in ecosystem management requires understanding the history of a given landscape and knowing its disturbance regime.

This exercise will involve comparing the differences in landscape pattern that are produced by two different disturbances—naturally occurring wildfire and forest harvesting—and assessing whether the forest harvesting moves the landscape mosaic out of a 300-yr range of natural variation. Both landscapes are coniferous forests dominated by lodgepole pine and located in the Rocky

Mountain region in Wyoming (USA). Large, infrequent crown fires are the dominant natural disturbance (Turner and Romme, 1994), but the region has been subject to intensive timber management since the early part of the 20th century.

Study Site

The reference landscape is a 14.7 × 16.3-kilometer section of Yellowstone National Park (YNP). The landscape mosaic for the past 250 years has been reconstructed based on dendrochronology and fire history at approximately 100-year intervals based on Tinker et al. (in review) (Figure 11.3). The human-influenced landscape is a 14.7 × 16.3-kilometer section of the Medicine

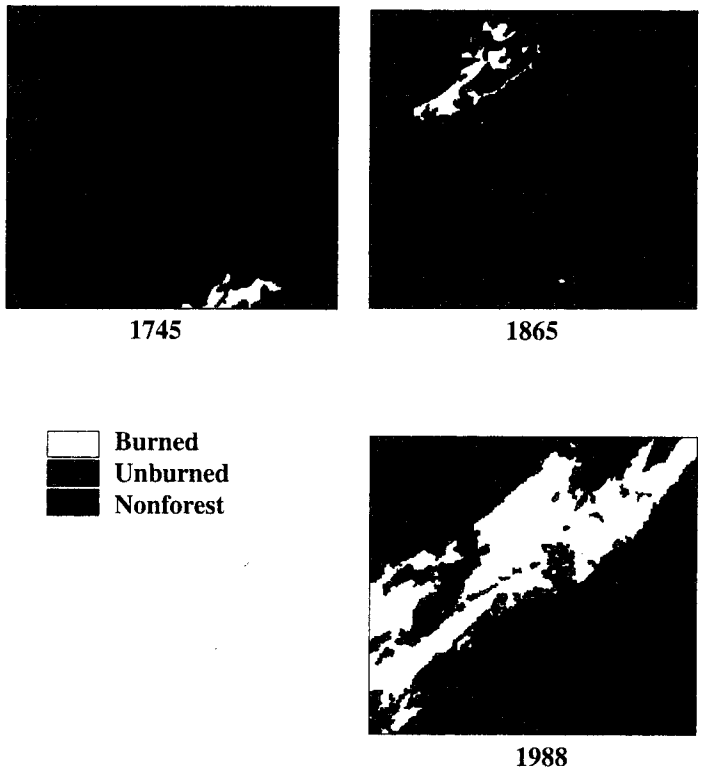

FIGURE 11.3
Digital maps of three of the nine landscape mosaics for Yellowstone National Park, Wyoming, used in the FRAGSTATS analyses of landscape metrics. All maps depict the same ~240-km^2 region. The 1745 map represents a period of few fires; the 1765 map represents a period during which a moderate amount of the landscape was burned; and the 1988 map represents the landscape following the widespread, intense fires of 1988.

Bow National Forest (MBNF), which is similar to the YNP landscape but has undergone extensive forest harvesting (Figure 11.4). Two alternative cutting patterns are depicted: (1) the historical harvest (Figure 11.4a and b), in which large clearcuts were separated by long, narrow buffer strips of uncut forest, and (2) the more recent harvest pattern (Figure 11.4c and d), designed to better reflect natural patterns.

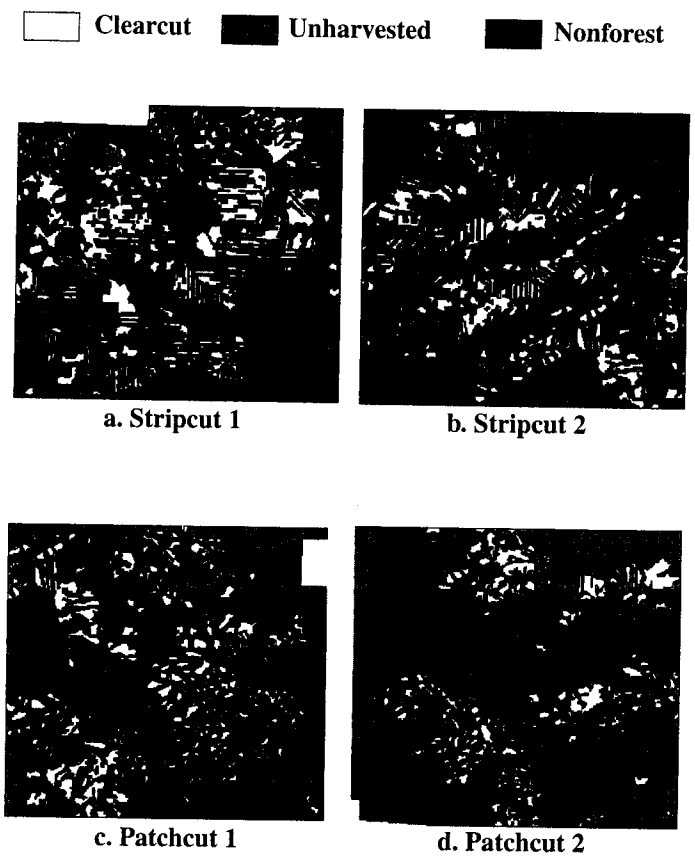

FIGURE 11.4
Digital maps of the Medicine Bow National Forest, Wyoming, used in the FRAGSTATS analyses of landscape metrics. All maps depict the same ~240-km² region. The upper two maps, stripcut 1(a) and stripcut 2(b), represent clear-cut harvesting patterns practiced during the 1960s and 1970s, when long, linear patches of forest were harvested, leaving narrow strips of uncut forest ~50–100 m wide between. The lower two maps, patchcut 1(c) and patchcut 2(d), represent clearcut harvesting patterns practiced during the 1980s and 1990s. The shape and allocation of these clearcuts have been designed to better reflect natural patterns.

EXERCISE 2.1

Spatial analyses were conducted on each of these study landscapes using Fragstats (McGarigal and Marks, 1995). The output from the spatial analyses can be found in a spreadsheet data file (**cut_burn.xls**) on the CD, under the directory for this lab.

1. After the **cut_burn.xls** file has been opened, use the **Save As** command in Excel to copy the file to a location on the hard drive or a floppy disc. This is done so that modifications to the file may be made.
2. Under **Tools** and **Data Analysis** in Excel, calculate **Descriptive Statistics** for each of the YNP landscape metrics—use the **Fire-generated landscape** section of the spreadsheet. After selecting a column of data to analyze (the input range), you must also choose an output range and be sure that "Summary statistics" is checked. For example, generate descriptive statistics for the number of burned patches in YNP from 1705 to 1988. Among the statistics generated by Excel will be (a) the mean, and (b) the standard deviation for each column of data.
3. Calculate the coefficient of variation (CV) for each of the YNP metrics using the formula:

   $$CV = 100 \times \text{standard deviation} / \text{mean}$$

   The CV is a relative measure of the variation in the data, independent of the unit of measure of the original data, expressed as a percentage of the sample mean. Compare the mean and CV values for each metric in the YNP landscape ($n = 9$) to the corresponding values for each metric for the MBNF landscape ($n = 4$) listed in the cut_burn.xls file.
4. Using the functions within Excel, generate the following plots (metric vs. year) for YNP:
   (a) Number of patches
   (b) Mean patch size
   (c) Percent of landscape (occupied by each patch type)
   (d) Edge density (edge length in meters per unit area of the landscape)
   (e) Total core area index (percentage of burned or unburned core area in the landscape)

   Plot burned and unburned patches separately (total of 9 plots – total core area index data only for unburned patches). For example, use the nine map years (e.g., 1705, 1745, etc.) as the x-axis values, and the number of patches for the y-axis values. Label each axis and provide a title describing the metric that was plotted.
5. After plotting the YNP data on each graph, double-click on the **Y-axis**—this will show the **Format Axis** dialog box. Click on the **Scale**

tab and ensure that the **Maximum Value (Y) Axis Scale** is at least as large as the largest corresponding value from the MBNF data. This is necessary because the MBNF data will be added to the graph by hand in a later step. You may need to change the minimum value as well to accomodate the MBNF data.

6. Print out hard copies of each of the nine plots of YNP Metrics. Draw two dotted lines on each graph. One line should pass through the maximum value and the other line should pass through the minimum value. The range of values **between** the two dotted lines may be thought to represent an historic range of variability, or reference landscape for naturally developing forests in the central Rocky Mountains.
7. Using a pencil, add data points representing corresponding values for the four MBNF landscapes (patchcuts 1 and 2; stripcuts 1 and 2) to the appropriate YNP plot. Add clearcut values to plots containing burned values from YNP, and add uncut values to plots containing unburned values from YNP. These plots will be used to answer the questions below.

Question 2.1. Describe the range of natural variability for the spatial pattern of forests in the YNP (reference) landscape. Use the full set of metrics and their variability (CV as well as the plots showing their temporal trends) to develop your description.

Question 2.2. Describe the spatial patterns of forests in the National Forest (managed) landscape. Again, use the full set of metrics that were computed.

Question 2.3. Compare the spatial patterns in the reference and managed landscapes. Which aspects of spatial pattern are similar? Which are different?

Question 2.4. Based on the quantitative assessment, does the landscape produced by the *historic* pattern of clearcutting fall within the range of natural variability of the reference landscape?

Question 2.5. Based on the quantitative assessment, does the landscape produced by the *recent* pattern of harvesting fall within the range of natural variability of the reference landscape?

Question 2.6. Do your interpretations of similarity or difference between reference and managed landscapes change depending on what metric you consider? What recommendations might you make to managers regarding how many metrics and which ones should be considered when evaluating dynamics of a disturbance-prone landscape?

Question 2.7. If a goal of landscape management is to have human disturbances mimic natural disturbances, what factors must be considered in addition to the spatial pattern and timing of the disturbance events?

Part 3. Disturbance and Landscape Equilibrium

The natural range of variability concepts emerged from the recognition that landscapes are constantly changing, and that many ecological systems cannot be described as equilibrial (Wu and Loucks, 1995). Watt (1947) first proposed the notion of a dynamic spatial mosaic that produces a stable distribution of successional stages at the landscape level. Over the years, questions of whether equilibrium can be detected on landscapes subject to disturbance, and how large a landscape must be to incorporate a given disturbance regimes, have been important themes in landscape ecology (e.g., Shugart and West, 1981; Romme, 1982; Baker, 1989; Turner and Romme, 1994). Much of the disagreement surrounding equilibrium versus nonequilibrium, and stability versus instability, can be attributed to several factors: the ambiguity in various definitions, different views of spatial heterogeneity and its effects, the lack of explicit specification of scales, and differences in theoretical foundations (Turner et al., 1993). Landscapes can exhibit a variety of behaviors under different disturbance regimes, and the same landscape may shift among different regions of behavior.

This exercise examines the temporal dynamics that may be observed in a landscape by using a simplified version of the model used by Turner et al. (1993) to explore landscape equilibrium. The landscape will be assumed to contain three potential seral stages: a pioneer, mid-, and late-successional class. A disturbance that affects a grid cell will return that cell to the pioneer stage, which persists until the next time step. The midsuccessional class also persists for one time step. The late-successional stage persists until a disturbance event resets it to the pioneer stage.

The landscape is represented as a grid of cells. Disturbance events occur at a prescribed frequency and size. Two integrated parameters relate the size of the disturbance to the size of the landscape, and the frequency of the disturbance to the recovery time of the vegetation. The **spatial parameter** S equals the disturbance size/landscape size. The parameter S varies between 0 and 1 and is easily interpreted as the proportion of the landscape disturbed per event. For example, if a disturbance affects 10 hectares of a 100-hectare landscape, then $S = 0.10$. In this exercise, the disturbance size and the landscape size will both be varied. The **temporal parameter,** T, equals disturbance return interval/recovery time. If disturbances occur every ten years and a disturbed site recovers to the mature successional stage in five years, then $T = 10/5 = 2$. The parameter T has three qualitatively different states that are useful to understand. When $T = 1$, then the disturbance interval is equal to the recovery time, and there is adequate time for a disturbed cell to reach the mature stage before again being disturbed. When $T < 1$, the disturbance will recur before full recovery has been achieved. Thus, if the disturbance is also large, the landscape can be effectively maintained in an early pioneer stage. When $T > 1$, the disturbed sites recover fully and persist in the mature state for some time before the next disturbance event occurs. In this exercise, the recovery time will always be set to three time steps, but the interval between disturbances will be varied.

EXERCISE 3.1

Consider how the model operates by first describing the changes that would occur in one cell (thus $S = 1.0$), just to assure that the basic operation of the model is clear. Examine and print out Figure 11.5 on the CD, which provides appropriately sized landscape grids for use in the next several exercises.

1. Consider a disturbance that occurs every 5 years (i.e., $T = 5/3 = 1.67$). Enter a 3 in the first cell in Figure 11.5a, then have the disturbance set the cell back to a 1 during the next time step (each cell represents the landscape at a different time step). Continue writing the number in the cell at each time step to describe the successional stage of the cell (1 = pioneer, 2 = mid, 3 = late).
2. Using either a pencil and paper or Excel, plot the proportion of the landscape occupied by each successional stage at each of the 12 time steps. The y-axis will be scaled from 0 to 1, and the x-axis will extend from 1 to 12. The plot will contain three lines, one for each successional stage.

Question 3.1. Next, assume that the disturbance occurs each year. What would happen to the relative abundances of successional stages present on that landscape? Which ones would be lost, and why?

EXERCISE 3.2

Next, you consider disturbances of two different sizes: one cell (in Exercise 3.2) and four cells (in Exercise 3.3) on a landscape that contains nine cells. The return interval of the disturbance is set to 1 year ($T = 0.33$).

1. On Figure 11.5b, begin by penciling a 3 in each of the open grid cells of the 3 × 3 landscape to represent the initial landscape.
2. For the second time interval, simulate a one-cell disturbance. Select a cell to be disturbed at random, and reset that cell to the pioneer stage by entering a 1. As the remaining cells were not disturbed, enter a 3 in each remaining cell.
3. At the third time step, another cell is disturbed at random. Choose a cell and enter a 1 in that cell. The pioneer cell that was disturbed at the last time step makes the transition to midsuccessional stage, so record a 2 in the cell. Note that the same cell might be disturbed in two successive time steps; if that occurs, then the cell will remain at stage 1.
4. Continue with this procedure, penciling in the successional stages on the landscape for each of the 12 time steps, assuming a one-cell disturbance.

5. Compute the proportion of the landscape occupied by each successional stage at each time step and plot this; you will have one graph with three lines (one for each stage).

EXERCISE 3.3

Now, the size of the disturbance will be increased to four cells (a 2 × 2 square), and the disturbance will still occur each year.

1. Repeat the procedure that you used in Exercise 3.2, keeping the disturbance frequency the same but imposing the larger disturbance on the landscape (use Figure 11.5c).
2. As you did earlier, plot the proportion of the landscape occupied by each successional stage under each of these two scenarios for 12 time steps.
3. Compute the spatial parameter, S, for each of the disturbance sizes in Exercises 3.2 and 3.3.

Question 3.2. Compare the plots for the two landscapes in Exercises 3.2 and 3.3. How do the landscapes differ in terms of their relative abundances of the pioneer and mature successional stages? Do the landscapes show similar or different levels of fluctuation through time?

EXERCISE 3.4

1. Repeat the preceding procedure for the four-cell disturbance but change the disturbance return interval to 5 years (Figure 11.5d). Compute the proportions occupied by each successional stage through time, and plot these for each of the 12 time steps.
2. Compute the spatial parameter, S, and temporal parameter, T.

Question 3.3. When the return interval of the disturbance was increased, did the fluctuations in the proportions of the landscape occupied by each successional stage change? Do you interpret this as moving toward more or less stable conditions? How do you weight the relative proportions of the successional stages and their relative fluctuations?

Question 3.4. If the spatial extent of the landscape was increased to 36 cells (a 6 × 6 grid, see Figure 11.5e), what would happen to the changes through time in the proportions of successional stages 1, 2, and 3? (*NOTE:* you can compute this easily by changing the denominator that you used to compute the proportions in the preceding example from 9 to 36 for stages 1 and 2; note that the number of cells for stage 3 will fluctuate). If the landscape was reduced in size to four cells, what would happen to the changes through time? Does the landscape appear more or less stable with these changes in spatial extent?

Results from many computer-based simulations using a similar simple model were used to generate a state space describing the variation in a landscape for disturbance regimes characterized by different values of T and S (Turner et al., 1993, Figure 11.6). When disturbances are small relative to the landscape, and the return interval is long relative to the recovery time, the landscape will be dominated by the mature successional stage and will fluctuate little through time. When the disturbances are very large relative to the size of the landscape, the proportions of each successional stage will fluctuate widely on the landscape.

Question 3.5. From your calculations and from considering the state-space diagram, describe the perceived stability of a landscape under the following disturbance regimes:

(a) Small, frequent disturbances
(b) Small, infrequent disturbances
(c) Large, frequent disturbances
(d) Large, infrequent disturbances

Question 3.6. What are the advantages and disadvantages of using such a simple model to represent a disturbance regime on a landscape? Should other factors also be included in such a conceptualization? Why or why not?

Question 3.7. How does the state space defined by S and T relate to the concept of the natural range of variability addressed in Part 2? Can this conceptualization aid landscape managers? Why or why not?

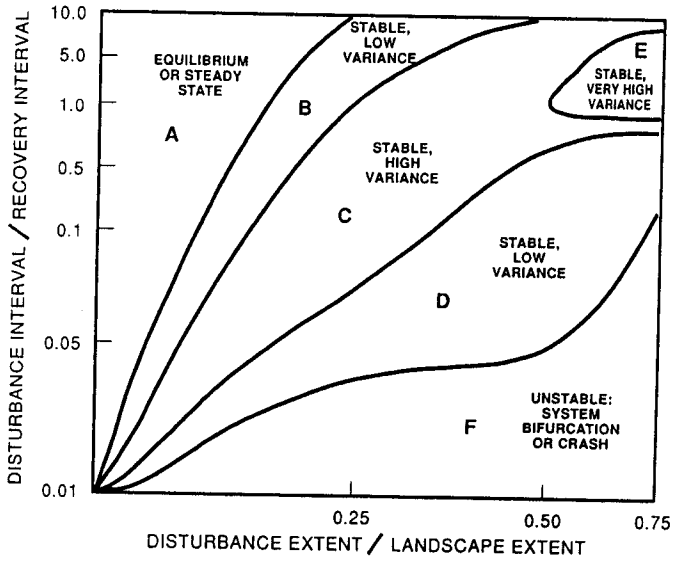

FIGURE 11.6
Landscape disturbance state space. Adapted from Turner et al. (1993).

CONCLUSIONS

The preceding exercises have demonstrated how the initiation of disturbance can be affected by landscape position, how disturbances create pattern and dynamics on landscapes, and how spatial and temporal scale influences whether a landscape is equilibrial. You've also seen the wide range of variability in natural disturbance regimes and the difficulty in setting reference conditions for a disturbance. Either explicitly or implicitly, each of these examples also illustrates the potential importance of humans in governing disturbance dynamics. The first example showed how the use of the landscape for purposes seemingly unrelated to the disturbance in question can influence the pattern of disturbance (e.g., roads influencing the initiation of fires). Direct use of the landscape for forest harvest can also substantially alter landscape patterns. In the last example, the parameters S and T were used to estimate how human-induced changes in a disturbance regime (e.g., alteration of disturbance size or frequency) might push the landscape into regions of different behavior. Humans might alter the size of the disturbance relative to the size of the landscape (S) by either altering the extent of fire or by altering the extent of the landscape itself (through land conversion and fragmentation). Furthermore, humans could alter landscape disturbance by burning or cutting areas larger than might otherwise be disturbed. The recovery time of the disturbance relative to the recovery time of the vegetation (T) can also be altered by humans—by initiating disturbance more frequently through altering the frequency of fires or frequency of harvests. Thus, humans can influence the spatial and temporal dynamics of disturbance, creating another layer of complexity in addition to the natural variability in disturbance dynamics, which should not be ignored.

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Note. An asterisk preceding the entry indicates that it is a suggested reading.

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