CHAPTER 17

Feedbacks between Organisms and Ecosystem Processes

Linda L. Wallace and Steve T. Gray

OBJECTIVES

The fact that the structure of the environment affects organisms within a system is so well known as to be an axiom of ecology. However, precisely *how* system structure does this is less well understood. Further, organism behavior may have strong feedbacks onto system structure and function. This exercise presents an examination of models and field data to explore interactions between organisms and ecosystem structure at several spatial scales, particularly the landscape scale. This is a critical first step in understanding how any given landscape may function and how perturbations (either human-induced or "natural") may influence the functioning of that landscape and the ecosystems contained within it. The primary objectives in this exercise are to help students

1. understand how ecosystem processes and landscape structure influence organisms at landscape scales, and how organisms influence ecosystem dynamics at equally broad scales;
2. appreciate how the interaction between organisms and their landscapes creates and maintains landscape heterogeneity;
3. understand and discriminate between positive and negative feedbacks; and
4. gain exposure to a diversity of approaches to analyzing the interactions between organisms and ecosystems or landscapes.

Part 3. An Analysis of Landscape Usage Patterns by the Fall Webworm

Fall webworms (Hyphantria cunea), a generalist lepidopteran herbivore (mem-ber of the butterfly and moth group), provide another example of insects whose outbreaks interact with landscape structure. The larvae of the Hy-phantria moth form silk tents over the foliage of deciduous trees, which they consume until reaching maturity. Work with similar lepidopteran herbivores ...
has shown that many species choose locations in full sun over those in shaded environments (Louda and Rodman, 1996). Also, the severity of tent-forming caterpillar outbreaks is known to increase with forest fragmentation (Roland, 1993).

In the summer and fall of 1996, central Oklahoma experienced a severe outbreak of the fall webworm. During this time Wallace et al. (in prep) performed a study to determine how forest structure influenced webworm distributions on the landscape shown in the aerial photograph in Figure 17.1. The locations of webworm-infested trees are identified with white circles. Edges of the forested areas and forested openings appear as lighter and gray while forested areas are darker gray and have a more "textured" appearance. You will conduct two different spatial analyses using the data collected in that study.

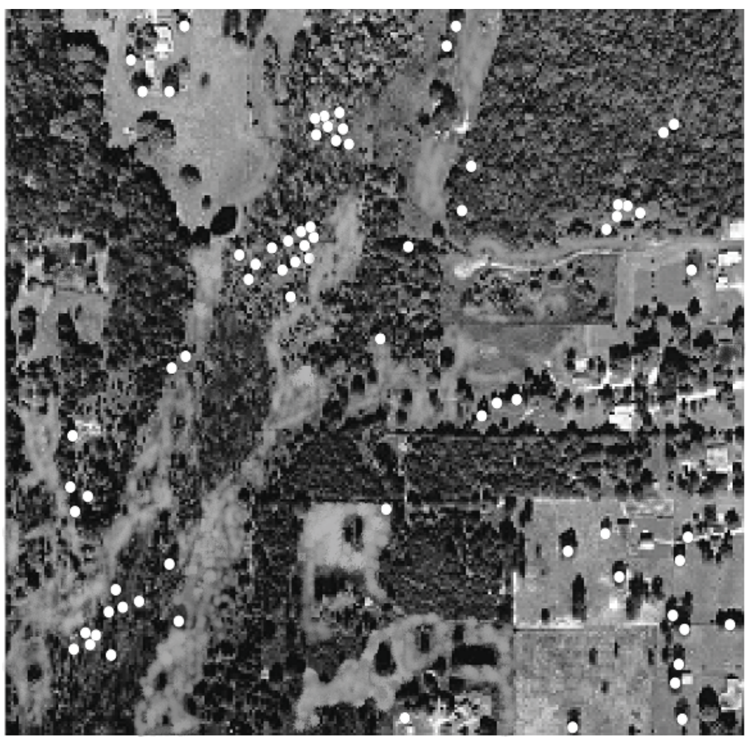

FIGURE 17.1
Black-and-white aerial photograph showing fall webworm distributions in a grassland–forest mosaic in Oklahoma. Forested areas are dark, and open, nonforested areas are lighter gray. Trees in which webworms were present are marked with white circles. This image has also been included on the CD-ROM under the directory for this lab and is entitled **webs.pdf.** The file can be viewed and then printed using Adobe Acrobat Reader.

EXERCISE 3.1
Do Webworms Preferentially Choose Forest Edge Trees?

Here you will conduct a *t*-test to determine if infested trees are closer to edges and openings than would be expected by chance. You will compare the mean distance from a random point to the nearest infested tree to the mean distance between and infested tree and a forest edge or opening.

1. First, use a ruler to demarcate axes for an *x*-*y*-coordinate system along the two edges of Figure 17.1.
2. Use a random numbers table (or a calculator with a random number generator) to locate a random point in the photograph: generate a random number for the *x*-coordinate, and then another random number for the *y*-coordinate. Record your *x*- and *y*-coordinates in Table 17.5 which can be printed from the CD.
3. Using the ruler and the *x*- and *y*-coordinates, locate your first random point on the photograph.
4. Determine the distance to the nearest infested tree from this random point. Mark this infected tree on the image and enter the distance in Table 17.5.
5. Next, record the distance from the nearest infested tree to the nearest forest edge or opening.
6. Repeat steps 2–5 until you have 15 observations.

Next, you'll conduct a *t*-test (identical to the tests you did in Part 1 of Chapter 11, Landscape Disturbance: Location, Pattern, and Dynamics).

1. Enter the two columns of distance data from Table 17.5 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 infested tree" and "distance to nearest forest edge" columns into the variable 1 and variable 2 range boxes by highlighting the data in the worksheet using the mouse.
4. In 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, you will reject the null hypothesis, but accept the alternative hypothesis that the mean distance between infested trees and edge is less than or greater than would be expected by chance.

EXERCISE 3.2
Are Webworm-Infested Trees Clumped Throughout the Landscape?

A second analysis can be made using the aerial photograph to determine whether fall webworm-infested trees exhibit a clumped distribution. This can be determined using the T-square index of spatial pattern, termed C (Ludwig and Reynolds, 1988).

1. From the randomly selected points used in the previous analysis, determine the distance from that point to the nearest infested tree (x_i). (You should already have this number from your previous *t*-test analysis.)
2. From that tree (x_i), determine the distance to the nearest infested neighbor (y_i).
3. Use the following formula to calculate C where n = the total number of sample points.

$$C = \frac{\sum \dfrac{x_i^2}{(x_i^2 + \frac{1}{2} y_i^2)}}{n}$$

4. Determine the value of C. C is approximately 0.5 for random patterns, significantly less than 0.5 for uniform patterns, and significantly greater than 0.5 for clumped patterns.
5. To determine if the value of C is significantly different from 0.5, use the following z-test:

$$z = \frac{C - 0.5}{[1/(12n)]^{0.5}}$$

If z is greater than or equal to 1.96, then C is significantly different from half, or in other words, the webworm-infested trees are nonrandomly distributed on the landscape.

Question 3.1. Although tree mortality from webworm infestation is rare, indirect influences on host health such as increased disease susceptibility may be important for long-term host survival. Paying particular attention to forest fragmentation, discuss the possible interactions between webworm distribution and landscape structure. How might this interaction affect ecosystem processes? (HINT: see Turner et al., 1989.)

Question 3.2. Webworm outbreaks may cause widespread damage to trees and mast crops (fruits and nuts). White-tailed deer (*Oidocoileus virginianus*) populations in central Oklahoma depend heavily on mast production for winter forage. How might patterns of webworm damage influence patterns of deer survival? Draw a conceptual model of this interaction.

Question 3.3. Unlike pine bark beetles, fall webworms are known to use a large array of host species (Nothnagle and Schultz, 1987). However, some species, such as pecan (*Carya illinoensis*) and sweetgum (*Liquidambar styraciflua*), are chosen preferentially as hosts. In addition, some unpalatable tree species such as red cedar (*Juniperus virginiana*) are seldom (if ever) used by fall webworms. If individual trees of the preferred species were protected from webworm infestation when located in the midst of unpalatable species, how might this so-called "plant defense guild" (Atsatt and O'Dowd, 1976) influence landscape patterns of webworm infestation? How could you test this hypothesis?

CONCLUSIONS

In this lab you have seen and used different techniques for analyses of the effects of landscape structure and ecosystem function on organisms as well as the feedbacks that organisms have on the structure and function of ecosystems and landscapes. Both modeling and direct observation of organism distribution and landscape structure and function are important tools in this endeavor. There are numerous other examples in the literature; however, most work of this sort is conducted in the field (or in a model parameterized with field data) rather than in the laboratory. Nevertheless, laboratory data can also be useful to understand some of the finer-scale mechanisms that may be driving a particular system. While it may seem intuitively obvious that organisms can influence ecosystem processes and landscape structure, much work is still needed to understand the mechanisms behind these effects.

BIBLIOGRAPHY

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

*Atsatt, P. R., and D. J. O'Dowd. 1976. Plant defense guilds. *Science* 193:24–29. This benchmark paper in ecology, the first to describe a potentially mutualistic interaction among plants involving interaction with a separate trophic level, represents one of the finest early studies of spatial ecology, as well.

Christensen, N. L., J. K. Agree, P, F. Brussard, J. Hughes, D. H. Knight, G. W. Minshall, J. M. Peek, S. J. Pyne, F. J. Swanson, J. W. Thomas, S. Wells, S. E. Williams, and H. A. Wright. 1989. Interpreting the Yellowstone fires of 1988. *BioScience* 39:678–685.

Despain, D. 1990. *Yellowstone Vegetation*. Roberts Reinhart, Boulder, Colorado.

Edwards, P. J., and S. D. Wratten. 1980. *Ecology of Insect-Plant Interactions*. Edward Arnold, London.

Houston, D. G. 1982. *The Northern Yellowstone Elk*. MacMillan, New York.

*Jones, C. G., and J. H. Lawton. 1995. *Linking Species and Ecosystems*. Chapman and Hall, New York. This seminal volume on linking processes across scales includes chapters on linkages between species-level processes and landscape and ecology levels with examples of population structure and function, evolution, and trophic-level interactions.

JONES, C. G., J. H. LAWTON, AND M. SHACHAK. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.

KNIGHT, D. H. 1987. Parasites, lightning and vegetation mosaic in wilderness landscapes. In M. G. Turner, ed. *Landscape Heterogeneity and Disturbance*. Springer-Verlag, New York, pp. 59–83.

LOUDA, S. M., AND J. E. RODMAN. 1996. Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, bittercress). *Journal of Ecology* 84:299–237.

LUDWIG, J. A., AND J. F. REYNOLDS. 1988. *Statistical Ecology: A Primer on Methods and Computing*. John Wiley and Sons, New York.

MCNAUGHTON, S. J. 1984. Grazing lawns: Animals in herds, plant form and coevolution. *American Naturalist* 124:863–886.

MEAGHER, M. M. 1973. The bison of Yellowstone National Park. National Park Service Scientific Monographs, No. 1.

NOTHNAGLE, P. J., AND J. C. SCHULTZ. 1987. What is a forest pest? In P. Barbosa and J. C. Schultz, eds. *Insect Outbreaks*. Academic Press, New York, pp. 59–80.

PASTOR, J., A. DOWNING, H. E. ERICKSON. 1996. Species-area curves and diversity-productivity relationships in beaver meadows of Voyageurs National Park, Minnesota, USA. Oikos 77:399–406.

PEARSON, S. M., M. G. TURNER, L. L. WALLACE, AND W. H. ROMME. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. *Ecological Applications* 5:744–755

ROLAND, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* 93:25–30.

RYKIEL, E. J., R. N. COULSON, P. J. H. SHARPE, T. F. H. ALLEN, AND R. O. FLAMM. 1988. Disturbance propagation by bark beetles as an episodic landscape phenomenon. *Landscape Ecology*. 1:129–139.

*SENFT, R. L., M. B. COUGHENOUR, D. W. BAILEY, L. R. RITTENHOUSE, O. E. SALA, AND D. M. SWIFT. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799. This paper will also be a benchmark paper in ecology because of its efforts to link foraging processes across scales. Although few people now use the concept of overmatching as described in the paper, many use the conceptual processes developed here.

THATCHER, R. D., J. L. SEARCHY, J. E. COSTER, AND G. D. HERTEL. 1982. The southern pine beetle. USDA Forest Service Technical Bulletin 1631.

*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 describes, in both mathematical and ecological terms, how heterogeneity should influence the spread of disturbances, populations, matter, and information across a landscape. It also describes a null-model approach for testing the effects of heterogeneity on these flows.

TURNER, M. G., Y. WU, W. H. ROMME, AND L. L. WALLACE. 1993. A landscape simulation model of winter foraging by large ungulates. *Ecological Modeling* 69:163–184.

TURNER, M. G., Y. WU, L. L. WALLACE, W. H. ROMME, AND A. BRENKERT. 1994. Simulating interactions among ungulates, vegetation, and fire in northern Yellowstone park during winter. *Ecological Applications* 4:472–496.

WALLACE, L. L., AND S. T. GRAY. In Prep. Impact of a fall webworm (Hyphantria cunea) outbreak on prairie woodlands.

WALLACE, L. L., M. G. TURNER, W. H. ROMME, R. V. O'NEILL, AND Y. WU. 1993. Scale of heterogeneity of forage production and winter foraging by elk and bison. *Landscape Ecology* 10:75–83.

WHICKER, A. D., AND J. K. DETLING. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.