A Spatial Simulation Model of Land Use Changes in a Piedmont County in Georgia

Monica Goigel Turner*

Institute of Ecology
University of Georgia
Athens, Georgia

ABSTRACT

A spatial simulation model was developed to predict temporal changes in land use patterns in a piedmont county in Georgia. Five land use categories were included: urban, crop, abandoned cropland, pasture, and forest. Land use data were obtained from historical aerial photography and digitized into a matrix based on a 1 ha grid cell format. Transitions of cells from one state to another were dependent on temporal transition probabilities and neighborhood, or spatial, influences. To compare the simulated and actual land use patterns, three spatial pattern descriptors were used: (1) nearest neighbor probabilities, (2) amount of edge between land uses, and (3) the number of patches by size class and land use. The model simulated land use area and patch sizes fairly well, but did not adequately capture the complexity of the shapes of some land uses. Several possible modifications of model structure are proposed. The modeling approach presented here is a potentially general one for simulating human-influenced landscapes.

INTRODUCTION

Many landscapes are influenced by the pattern of human land use. Landscape pattern in such areas includes a mixture of natural and human-managed patches that vary in size, shape, and arrangement (e.g. [4, 7, 8, 14]). The ecological importance of the spatial pattern of landscapes has been recently acknowledged [8, 20, 23]. Land use patterns can influence many ecological and environmental phenomena, such as animal dispersal (e.g. [28]), water runoff and erosion (e.g. [19, 29]), or species diversity (e.g. [9, 18]), and

*Present address: Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830.

52 Vanderbilt Ave., New York, NY 10017 0096-3003/88/$03.50

are thus important in the study of landscape level phenomena [25]. Land use pattern might be a common denominator for seemingly unrelated phenomena within the same landscape [25].

Human land use reflects natural [2] as well as economic and social constraints. Thus, changes in land use pattern may be more complex and difficult to predict than changes in natural vegetation. Transition models have frequently been used to predict changes in vegetation [6, 16, 26, 27] or land use [5, 11, 12] through time. However, most models have not simulated spatial dynamics. Spatial pattern must be explicitly included in simulation models to gain an understanding of landscape level phenomena, and at least one recent dynamic simulation model has successfully done so [21, 22]. This paper describes the development of a spatial-temporal transition model that simulates changes in land use patterns in Georgia. A series of statistical descriptors of the spatial pattern are also described, allowing the simulated and actual land use patterns to be compared.

METHODS

Study Area and Data Collection

Georgia encompasses three major physiographic regions, each of which has undergone substantial changes in land use during the past two centuries [3, 10, 17]. These regions include the mountains (1,470,310 ha), piedmont (4,606,139 ha), and coastal plain (8,971,206 ha). The piedmont region has undergone the most dramatic land use changes during the past 50 years [24]. For development of the simulation model, a piedmont county (Oglethorpe) was selected as the study area. Data and simulations from Oglethorpe County will be used in the remainder of this paper to demonstrate the model. Ultimately, several counties will serve as samples of the land use patterns observed in each physiographic region of the state.

Net rates of land use transitions in Oglethorpe County were obtained from published statistics including the Census of Agriculture and Forest Service Surveys. Data on the spatial patterns of land use were obtained from historical black and white aerial photography for each of three time periods (1942, 1955, 1980), beginning with the earliest available photography. Photos from 1942 and 1955 were at the 1:20,000 scale, and photos from 1980 were at the 1:40,000 scale. Six sample areas were studied, each encompassing a 2116 ha square (4.6 km on each side), the area of a single photograph at the 1:20,000 scale. These six samples were contiguous, and the total sample area of 12,698 ha represented approximately 12% of the county.

Five land uses were identified on the photographs: (1) urban, (2) cropland, (3) abandoned cropland, (4) pasture, and (5) forest. Patches (contiguous areas of the same type) of each land use were delineated; then a square grid representing 1 ha cells was overlaid on the pattern. Cells were considered to be wholly in one or another of the discrete land uses, and land use patterns were digitized to form a land use matrix. The descriptors of spatial pattern were calculated for each matrix, and the landscape patterns in 1942 on each of the six sample areas served as initial conditions for simulations.

Model Development

The ultimate utility of the simulation model is to predict the landscape pattern under different hypothetical conditions. There are particular challenges in simulating changes in land use patterns. First, land use changes are not strictly Markovian; that is, the change of state of a cell is not simply a function of its current state, but is influenced by surrounding cells. For example, a patch of abandoned land adjacent to an urban area is more likely to become urban than a similar patch which is further away. In other words, there are spatial neighborhood effects. Second, the rates of transition are not constant through time. The rate of cropland abandonment in Georgia, for example, has decreased substantially since the early part of the century [13, 24]. Thus, dynamic transition probabilities are required. Third, the causation of land use transition may be largely economic rather than natural [1, 5], and the use of empirical transition rates masks this causality.

Given these constraints, I developed a simulation model using empirically estimated transition probabilities with spatial influences to simulate land use changes. The transition of a particular cell in the land use matrix was a function of two factors: the transition probabilities $p_{i,j}$ and the state of the nearest eight neighbors of the cell. The simulation algorithm involves several steps:

First, the number of cells for which state changes will occur is determined by multiplying the temporal transition probability $p_{i,j}$ by the number of cells of type i, N_i. For example, if there are 200 cells of land use type 2, and the probability of transition from state 2 to state 3 is 0.30, then 60 cells must change from state 2 to state 3. These values are stored in an array and used to force the correct amount of land to undergo transition.

To determine which cells in the landscape make the transition from i to j, the model incorporates the effects of the surrounding neighborhood to generate a transition index for each cell in the matrix. Adjacent and diagonal neighbors are given equal weight. For example, let us consider a land use matrix that contains nine cells and three possible land use states, given as

$$\begin{bmatrix} 1 & 1 & 2 \\ 1 & 2 & 3 \\ 1 & 1 & 2 \end{bmatrix}$$

and suppose the transition probabilities $p_{i,j}$ of changing from i to j during an interval are given as

$$\text{From:}\quad \begin{array}{c} \\ 1 \\ 2 \\ 3 \end{array}\!\!\begin{array}{c} \text{To:} \\ \begin{array}{ccc} 1 & 2 & 3 \end{array} \\ \begin{bmatrix} 0.9 & 0.1 & 0.0 \\ 0.0 & 0.3 & 0.7 \\ 0.5 & 0.0 & 0.5 \end{bmatrix} \end{array}.$$

The most likely state to which the central cell of the land use matrix (presently in state 2) will change is determined as follows: A transition index is calculated for the (2,2) cell in the matrix by finding the maximum value of $p_{i,j}N_j$, where N_j is the number of neighboring cells of state j. In the above example, then, we determine

$$p_{2,1}N_1 = 0.0\times 5 = 0, \tag{1}$$

$$p_{2,2}N_2 = 0.3\times 2 = 0.6, \tag{2}$$

$$p_{2,3}N_3 = 0.7\times 1 = 0.7. \tag{3}$$

Since 0.7 is the maximum value, the transition index is 0.7 and the (2,2) cell is most likely to change to state 3. A transition index is determined in the same way for each cell in the land use matrix, and the indices are stored in a buffer matrix. This buffer is then searched to find the maximum transition index, and the equivalent cell in the land use matrix is changed to the new state. This procedure is then repeated: the transition indices for the land use matrix are recalculated to identify the next cell that will be changed. The number of $i \to j$ transitions is counted and compared with the allowable number, which was calculated initially. These steps are repeated until all allowable transitions have been made. If there are no neighbors of type j to effect a particular i, j transition, cells of type i are selected at random and changed to j. This may occur, for example, when urban land appears for the first time.

During a simulation interval, a cell is changed only once. However, it may subsequently influence the transitions of surrounding cells, since the transition indices are recalculated each time a single cell is changed. This allows patches to grow or shrink through time, since a single iteration will generally represent a multiyear interval. When the number of transitions reaches the allowable number, the new land use matrix is output and the spatial pattern is analyzed.

TABLE 1

TEMPORAL TRANSITION PROBABILITIES USED IN THE SIMULATION OF LAND USE CHANGES IN OGLETHORPE COUNTY, GEORGIA

First time period (1942 to 1955)					
From	To: Urban	Crop	Trans.	Pasture	Forest
Urban	1.00				
Crop		0.80	0.19	0.01	
Trans.	0.01		0.77		0.22
Pasture				1.00	
Forest					1.00
Second time period (1955 to 1980)					
From	To: Urban	Crop	Trans.	Pasture	Forest
Urban	1.00				
Crop		0.430	0.570		
Trans.	0.008		0.212		0.780
Pasture				1.00	
Forest					1.00

Simulations

Simulations of Oglethorpe County were begun with the land use patterns from the 1942 photographs. Land use changes were simulated for two iterations, representing the 1942–1955 period and the 1955–1980 period. Each 2116 ha sample area was simulated separately ($n = 6$). Transition probabilities for each interval (Table 1) were derived empirically from net changes in land use for the county from sources other than the aerial photos, such as the Census of Agriculture and Forest Service Surveys. Transition probabilities were established such that urban, pasture, and forest lands were sinks (the probability of changing from one of these states to any other was zero), all gains to urban and forest land came from abandoned land, and cropland could be abandoned or converted to pasture; thus, transition probabilities only represent net changes. The same probabilities were used in each of the six simulations.

Descriptors of Landscape Pattern

The area and frequency of each land use type were calculated to determine the net changes in land use regardless of the spatial arrangements. Three major descriptors of spatial pattern were then used to assess changes in spatial pattern and to compare the simulated and actual landscapes:

(1) Nearest neighbor probabilities $f_{i,j}$ [15] were estimated from nearest neighbor frequencies for all pairs of adjacent cells. These represent the

probability of cells of land use i being adjacent to cells of land use j [where $j = 1, \ldots, (\text{no. of states})$]. Probabilities were calculated both vertically and horizontally so that directionality in the land use pattern might be identified. The general formula was

$$f_{i,j} = n_{i,j}/N_i, \tag{4}$$

where

$f_{i,j}$ = nearest neighbor probability of cells of land use type i next to j;
$n_{i,j}$ = number of cells of type i adjacent to type j;
N_i = number of cells of type i.

Nearest neighbor probabilities indicate the degree of fragmentation in the landscape and the complexity of patch boundaries. For example, a landscape with very large patches of type i will have a relatively high $f_{i,i}$, whereas if the same area is allocated across a large number of smaller patches, the $f_{i,i}$ will be low. Note that these probabilities have no temporal component and are used only to describe the spatial pattern.

(2) The amount of edge, or boundary, between all land uses was determined, providing an index of the dissection of the landscape and the proximity of land uses to one another. This was calculated by summing both horizontal and vertical edges and then multiplying by 100 m, the length of the side of a cell.

(3) The number of patches by land use type and size class was determined. Every patch in the land use matrix was located, and adjacent and diagonal cells of the same type were considered to be within the same patch.

Notes on the Computer Program

The computer code was written in standard FORTRAN, and the program can run on a personal computer using small land use matrices. However, the simulation is time-intensive, requiring 10 hours on a PC to simulate a 50×50 matrix through two iterations. The same simulation requires only 160 seconds on a Cyber 205 supercomputer. To simulate transitions using large land use matrices, such as the 138×92 matrix of the six photos combined, a supercomputer is necessary, as several equally large buffer matrices are required in the simulation and spatial analysis sections of the program. The model has been run using the automatic vectorization capability of the Cyber 205 compiler, but the code has not been manually vectorized. Although this would undoubtedly increase the efficiency of the computation, substantial effort would be required to translate the numerous conditional statements into vector format, and one would then be left with machine-dependent code.

TABLE 2

PROPORTION OF LAND AREA BY LAND USE IN OGLETHORPE COUNTY, GEORGIA

	Proportion[a]				
	1942	1955		1980	
Land use	Actual	Actual	Simulated	Actual	Simulated
Urban	.00 (.30)	.00 (.01)	.01 (.00)	.01 (.02)	.01 (.00)
Cropland	.44 (.09)	.35 (.11)	.34(.07)	.15(.07)	.15 (.03)
Abandoned cropland	.43 (.06)	.41 (.10)	.42 (.03)	.28 (.07)	.28 (.04)
Pasture	.00 (.00)	.01 (.01)	.01 (.00)	.01 (.01)	.01 (.00)
Forest	.13 (.05)	.22 (.05)	.21 (.05)	.54 (.05)	.55 (.07)

[a] Mean (standard deviation); $n = 6$ sample areas.

RESULTS

Changes in land use area were apparent between 1942 and 1980 in the actual and simulated landscapes (Table 2). In the real landscape, urban and pasture area each increased from 0 to 1%, forests increased from 13 to 54%, and cropland declined from 44 to 15%. There was close agreement between the simulated and actual landscapes with regard to the proportion of area in each land use. Thus, given that area per land use was adequately simulated, were the spatial arrangements similar?

Changes in the nearest neighbor probabilities were observed (Table 3). In the actual landscape, there was a marked increase in the forest-forest adjacency and a decrease in the crop-crop adjacency between 1942 and 1980. This suggests that forest patches increased in size and coalesced, whereas cropland patches became somewhat more fragmented. The abandoned cropland–abandoned cropland probability did not change. The nearest neighbor probabilities of different land uses (the nondiagonal elements in Table 3) also indicate changes in the spatial pattern. In 1942, a hectare of cropland had a 0.22 probability of being adjacent to transitional land and a 0.06 probability of being adjacent to forest. In 1982, this trend was reversed, with the probability of crop-forest being 0.21 and that of crop-transitional only 0.12. A similar reversal was also seen for the proximity of transitional land to cropland (higher probability in 1942) and forest (higher probability in 1980).

The $f_{i,j}$'s that included cropland in the simulated landscape were quite close to those of the actual landscape (Table 3). Thus, the spatial arrangement of cropland in the simulated landscape appeared to be similar to that of the actual landscape. However, the transitional-forest probabilities show discrepancies between simulated and actual. The transitional-transitional and

TABLE 3
NEAREST NEIGHBOR PROBABILITIES[a] FOR THE THREE DOMINATE LAND USES, OGLETHORPE COUNTY, GEORGIA

1942

From:	Actual To: Crop	Aband.	Forest
Crop	.72	.22	.06
Aband.	.22	.67	.11
Forest	.18	.40	.42

1955

	Actual Crop	Aband.	Forest	Simulated Crop	Aband.	Forest
Crop	.70	.19	.10	.74	.16	.08
Aband.	.18	.67	.15	.14	.78	.08
Forest	.13	.29	.58	.11	.16	.72

1980

	Actual Crop	Aband.	Forest	Simulated Crop	Aband.	Forest
Crop	.64	.12	.21	.65	.07	.25
Aband.	.06	.71	.21	.04	.85	.09
Forest	.06	.11	.82	.06	.05	.88

[a] Differences between the vertical and horizontal spatial transition probabilities never exceeded 0.03, indicating there was no directionality in the land use patterns. Horizontal and vertical probabilities were thus averaged to determine net first order spatial transition frequencies.

forest-forest probabilities were greater in the simulated than in the actual landscape, suggesting that forest and transitional patches coalesced too quickly in the simulation.

There was close agreement between simulated and actual edge between crop and forest land (Table 4). The edge between crop and transitional land was slightly lower in the simulated than in the actual landscape, by 15% in 1955 and 36% in 1980. The forest-transitional edge was underestimated in the simulation by 44% in 1955 and 52% in 1980. This indicates that the simulated forest and transitional patches were too highly coalesced, and that the boundary between them was not as complex as in the real landscape. It is also interesting to note that the total length of edge between major land uses decreased substantially in the actual landscape between 1942 and 1980. This

TABLE 4

EDGE (KILOMETERS) BETWEEN THE THREE MAJOR LAND USES IN A 2116 HA AREA IN OGLETHORPE COUNTY, GEORGIA

Land uses	Edge[a]			
	1942			
Crop-abandoned	77.7	(7.3)		
Crop-forest	19.0	(5.5)		
Abandoned-forest	39.3	(12.2)		
Total	136.0			
	1955			
	Actual		Simulated	
Crop-abandoned	54.1	(11.6)	46.1	(3.48)
Crop-forest	25.8	(10.5)	21.0	(3.35)
Abandoned-forest	51.5	(16.9)	28.6	(7.80)
Total	131.4		95.7	
	1980			
	Actual		Simulated	
Crop-abandoned	13.9	(3.8)	8.9	(3.22)
Crop-forest	27.6	(11.4)	29.1	(2.55)
Abandoned-forest	48.1	(5.2)	22.9	(3.09)
Total	89.6		60.9	

[a] Mean (standard deviation); $n = 6$ sample areas.

large reduction in landscape boundaries could have important implications for flows across the landscape (e.g. [30]).

The distribution of patches by size class has changed through time (Table 5). In 1942, the number of forest patches in the two smallest size classes was quite high, whereas by 1980 there were few small fragments of forest. The actual and simulated landscapes show similar distributions of patches by size class, with the exception of transitional land in 1980. The simulation created fewer small patches and more large patches of transitional land. However, the overall agreement in the frequency distribution of patches suggests that it is the shapes rather than sizes of the patches that are not realistically simulated.

DISCUSSION

These results suggest that simulation modeling of land use patterns is feasible. Some modifications to the model might improve the prediction of

TABLE 5

NUMBERS OF PATCHES IN MAJOR LAND USES IN A 2116 HA AREA IN OGLETHORPE COUNTY, GEORGIA

Year[a]	Number[b]					
	Size class (ha): 1	2–10	11–50	51–100	101–1000	> 1000
			Cropland			
1942	6 (3)	8 (2)	3 (3)	1 (1)	2 (1)	0 (0)
1955-A	8 (3)	11 (2)	4 (3)	2 (1)	2 (1)	0 (0)
1955-S	3 (2)	6 (2)	4 (2)	1 (1)	2 (1)	0 (0)
1980-A	4 (1)	8 (3)	4 (2)	1 (1)	1 (1)	0 (0)
1980-S	6 (4)	10 (3)	5 (2)	1 (1)	0 (0)	0 (0)
			Abandoned cropland			
1942	8 (4)	15 (11)	5 (2)	1 (1)	1 (1)	0 (0)
1955-A	9 (5)	16 (5)	6 (4)	1 (1)	1 (1)	0 (0)
1955-S	6 (3)	14 (5)	5 (1)	1 (1)	2 (1)	0 (0)
1980-A	7 (3)	13 (6)	6 (4)	1 (1)	1 (1)	0 (0)
1980-S	5 (1)	5 (2)	2 (2)	1 (1)	2 (1)	0 (0)
			Forest land			
1942	25 (8)	23 (5)	4 (1)	1 (1)	0 (0)	0 (0)
1955-A	14 (8)	18 (5)	5 (2)	1 (1)	1 (1)	0 (0)
1955-S	20 (6)	15 (4)	5 (5)	1 (2)	1 (0)	0 (0)
1980-A	4 (2)	6 (2)	2 (1)	1 (1)	1 (1)	1 (1)
1980-S	7 (2)	5 (2)	1 (0)	0 (0)	1 (1)	1 (0)

[a]A = actual, S = simulated.
[b]Mean (standard deviation), $n = 6$ sample areas.

spatial patterns. The model simulates the clustering of certain land uses, such as cropland, reasonably well. However, for other land uses, the simulated arrangement is not as complex as the actual landscape. There are several possible explanations for this, which suggest alternative model modifications.

First, the simulated neighborhood effects may just be too strong. This might be countered by several different modifications. First, a stochastic element could be incorporated into the simulation. For example, the search sequence could be randomized so as not to bias the results toward a particular section of the matrix. Second, the form of the neighborhood influence might also be changed by including only the four nearest neighbors or by weighting adjacent and diagonal neighbors differently. This might generate a suitably complex and realistic pattern without implying a specific underlying mechanism. Third, more detail could be incorporated into the model. Transitions could be conditional on additional characteristics, such as edaphic conditions, proximity to roads, or patterns of land ownership.

Alternatively, the scale of the land use transitions may differ by land use. For example, urban area may increase on a hectare by hectare basis, whereas cropland may be abandoned in parcels of several hectares. Or there may be different scales affecting managed and natural patches [14] since a primary influence of humans is to rescale patterns in time and space [25]. Variable scales for land use transitions could be incorporated into the model.

Adequate transition probabilities are required for each simulation interval. While these can be difficult even to obtain empirically, dynamically generated transition rates would be preferable. To be predictive in a real, human-dominated landscape, the economic or social mechanisms driving land use transition rates should be incorporated in the model. This might also allow for greater "back and forth movement" between land uses.

The model described in this paper offers a potentially general approach for simulating spatial and temporal changes in human-influenced landscapes. By simulating the spatial land use pattern, such a model can also provide the basis for simulating flows across boundaries in such landscapes. Flows might include dispersal of organisms, movement of water and dissolved chemicals, or the spread of disturbance. With the availability of more powerful computers, realistic simulation of spatial patterns across landscapes is feasible and offers potential for modeling spatially distributed ecological processes.

I am grateful to T. H. Richardson for her invaluable computer assistance and programming advice, and to C. L. Ruscher for interpreting the aerial photography. The comments and suggestions of R. Costanza, V. H. Dale, V. H. Ferreira, F. B. Golley, H. R. Pulliam, and D. L. Urban on an earlier version of the manuscript are greatly appreciated. This work was part of a broader study of the state of Georgia and was funded by a grant from the Kellogg Foundation to the University of Georgia. Computer time on the Cyber 205 at Colorado State University was funded by NSF grant No. BSR-8607611 to D. A. Jameson.

REFERENCES

1 R. J. Alig, Econometric analysis of the factors influencing forest acreage trends in the southeast, *Forest Sci.* 32:119–134 (1986).

2 G. W. Bowen and R. L. Burgess, A Quantitative Analysis of Forest Island Pattern in Selected Ohio Landscapes, ORNL/TM-7759, Oak Ridge National Lab., Oak Ridge, Tenn., 1981.

3 E. V. Brender, Impact of past land use on the lower Piedmont forest. *J. For.* 72:34–36 (1974).
4 R. L. Burgess and D. M. Sharpe, *Forest Island Dynamics in Man-Dominated Landscapes*, Springer, New York, 1981.
5 B. O. Burnham, Markov intertemporal land use simulation model, *Souther J. Agric. Econom.* 5:253–258 (1973).
6 M. Debussche, M. Godron, J. Lepart, and F. Romane, An account of the use of a transition matrix, *Agro-Ecosystems* 3:81–92 (1977).
7 R. T. T. Forman and M. Godron, Patches and structural components for a landscape ecology, *BioScience* 31:733–740 (1981).
8 R. T. T. Forman and M. Godron, *Landscape Ecology*, Wiley, New York, 1986.
9 K. E. Freemark and H. G. Merriam, Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments, *Biol. Conserv.* 36:115–141 (1986).
10 R. G. Healy, *Competition for Land in the American South*, Conservation Foundation, Washington, 1985.
11 J. Hett, Land Use Changes in East Tennessee and a Simulation Model Which Describes These Changes for 3 Counties, ORNL-IBP-71-8, Oak Ridge National Lab., Oak Ridge, Tenn., 1971.
12 W. C. Johnson, A mathematical model of forest succession and land use for the North Carolina piedmont, *Bull. Torrey Bot. Soc.* 104:334–346 (1977).
13 W. C. Johnson and D. M. Sharpe, An analysis of forest dynamics in the north Georgia piedmont, *For. Sci.* 22:307–322 (1976).
14 J. R. Krummel, R. H. Gardner, G. Sugihara, and R. V. O'Neill, Landscape patterns in a disturbed environment, *Oikos*, 48:321–324 (1987).
15 C. Lin and J. W. Harbaugh, *Graphic Display of Two- and Three-Dimensional Markov Computer Models in Geology*, Van Nostrand Reinhold, New York, 1984.
16 E. Lippe, J. T. de Smidt, and D. C. Glenn-Lewin, Markov models and succession: A test from a heathland in the Netherlands, *J. Ecology* 73:775–791 (1985).
17 T. C. Nelson, The original forests of the Georgia piedmont, *Ecology* 38:390–396 (1957).
18 R. F. Noss, A regional landscape approach to maintain diversity, *BioScience* 33:700–706 (1983).
19 W. T. Peterjohn and D. L. Correll, Nutrient dynamics in an agriculatrual watershed: Observations on the role of a riparian forest, *Ecology* 65:1466–1475 (1984).
20 P. G. Risser, J. R. Karr, and R. T. T. Forman, Landscape Ecology: Directions and Approaches. Illinois Natural History Survey Spec. Publ. No. 2, Champaign, Ill., 1984.
21 F. H. Sklar, R. Costanza, and J. W. Day, Jr., Dynamic spatial simulation modeling of coastal wetland habitat succession, *Ecol. Modelling* 29:261–281 (1985).
22 F. H. Sklar and R. Costanza, A spatial simulation of ecosystem succession in a Louisiana coastal landscape, in *Proceedings of the 1986 Summer Computer Simulation Conference* (R. Crosbie and P. Luker, Eds.), Soc. for Computer Simulation, 1986.

23 M. G. Turner (Ed.), *Landscape Heterogeneity and Disturbance*, Springer, New York, 1987.
24 M. G. Turner, Land use changes and net primary production in the Georgia landscape: 1935–82, *Environ. Management* 11(2):237–247 (1987).
25 D. L. Urban, R. V. O'Neill, and H. H. Shugart, Landscape ecology, a hierarchical perspective, *BioScience* 37:119–127 (1987).
26 M. B. Usher, Modelling ecological succession, with particular reference to Markovian models, *Vegetatio* 46:11–18 (1981).
27 R. Van Hulst, On the dynamics of vegetation: Markov chains as models of succession, *Vegetatio* 40:3–14 (1979).
28 J. Wegner and G. Merriam, Movements by birds and small mammals between a wood and adjoining farmland habitats, *J. Appl. Ecol.* 16:349–357 (1979).
29 F. C. White, J. R. Hairston, W. N. Musser, H. F. Perkins, and J. F. Reed, Relationship between increased crop acreage and nonpoint-source pollution: A Georgia case study, *J. Soil Water Conserv.* 36:172–177 (1981).
30 J. A. Wiens, C. S. Crawford, and J. R. Gosz, Boundary dynamics: A conceptual framework for studying landscape ecosystems, *Oikos* 45:421–427 (1985).