Ralph E. J. Boerner, Michael N. DeMers
John W. Simpson, Francisco J. Artigas
Alejandra Silva, and Leslie A. Berns

Markov Models of Inertia and Dynamism on Two Contiguous Ohio Landscapes

This study examined landcover change during 1940–1988 in two contiguous landscapes of approximately 12,400 hectares in central Ohio, USA: an inertial till plain area and a more dynamic moraine area. Agriculture dominated both landscapes throughout, however, the cover of natural vegetation and urban-suburban development increased over time on the moraine while natural vegetation decreased and agriculture increased on the till plain. Markov process models for landcover change were constructed for three 14–17-year time intervals and for the entire forty-eight-year study period. Probabilities of self-replacement for agricultural lands (0.91–0.97) were higher and those for forests (0.54–0.65) lower than those reported for other landscapes. Predictions of landcover percentages for fifty years in the future were made using Markov process models derived from actual cover changes in 1940–1957, 1971–1988, and 1940–1988. All three models produced similar predictions for the inertial till plain area. In contrast, the three models' predictions differed considerably for the moraine area. Only the 1971–1988 transition matrix was sensitive to increases in urbanization and reforestation which began on the moraine in the 1970s. These results indicate that reliance on lengthy study intervals and net rates of change can obscure spatial and temporal patterns of landcover change that are caused by natural and socioeconomic factors operating on shorter time scales.

INTRODUCTION

Studies of patterns of change in landcover in agricultural and postagricultural landscapes generally present rates of change in terms of percentages of land
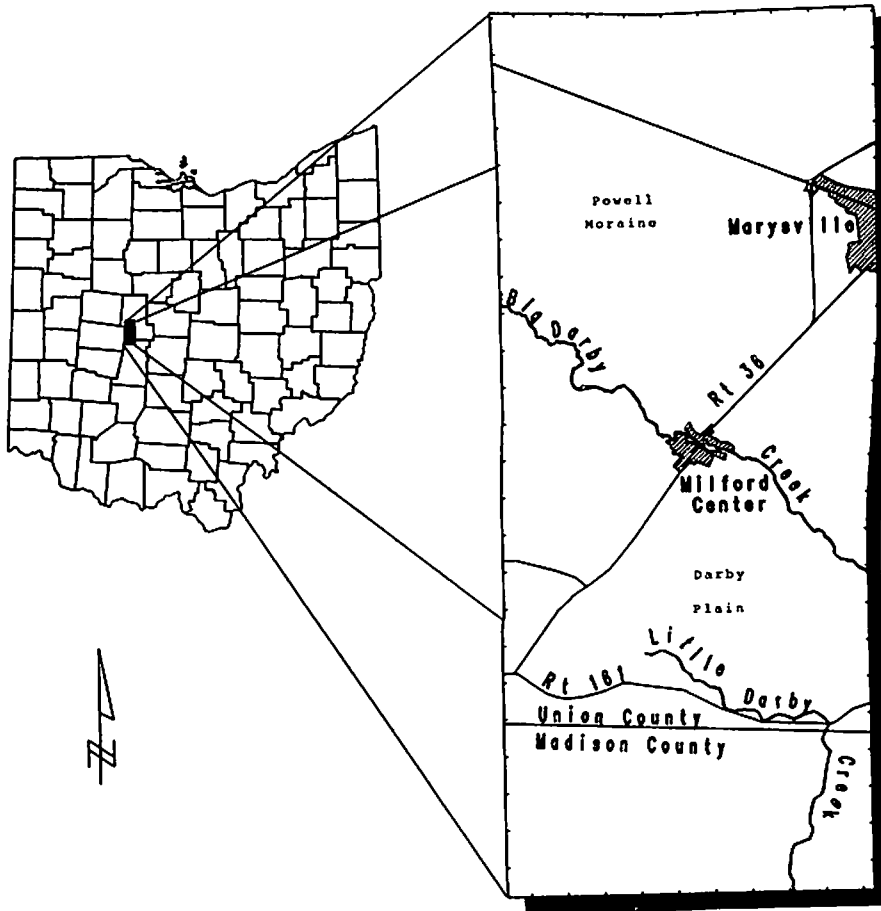
FIG 1. Location of the 242 square kilometer Study Area in Central Ohio

patterns of change in landcover during the three individual time intervals and for the entire study period, (2) model landcover change utilizing Markov process models, and (3) evaluate the importance of within-interval versus among-interval changes in transition probabilities in these two landscapes.

METHODS

Study Area

The study area was located west of Marysville, Ohio (1990 population 9,656), in the Till Plains physiographic province of central and western Ohio, an area comprised of mosaics of ground moraine till plains and undulating moraines (Figure 1). We divided the study area into two distinct landscapes of approximately 12,400 hectares each: an undulating northern half defined by the Powell Moraine, and a flat, somewhat featureless southern half defined by the Darby Till Plain.

At the time of Euro-American settlement in the early 1800s, the moraine landscape was covered by relatively unbroken deciduous forest, ranging from beech-maple (*Fagus-Acer*) on mesic slopes to oak-hickory (*Quercus-Carya*)

area or absolute area that changed over some discrete time period (for example, Curtis 1956; Foster 1993; Simpson et al. 1994). Although such methods do enhance our understanding of the gross temporal patterns of landscape change, they are subject to two complicating factors which may lead to faulty inferences concerning the forces generating that change (Muller and Middleton 1994). First, the time period over which proportional change in landcover is calculated may not fit well the time frames over which landcover typically changes in that landscape. If the study interval is too long, the cover and/or use of a parcel of land may change more than once during the study period, but not be detected in the analysis. In such a situation, a dynamic landscape may appear quite inertial if the study period is long in relation to the turnover time of the average parcel.

Second, landcover change is not a random process. Because of differences in geomorphology and prior land use, a given pattern of change in landcover or use may be much more likely on one land parcel than another. Because the probability of certain changes in cover occurring on a given parcel of land is, to a great extent, dependent on the existing land use or cover at the beginning of the study period, patterns of landcover change can be modeled more effectively as Markov processes than as random processes (Muller and Middleton 1994). In general, Markov processes are stochastic processes in which the transitions among the various states occur with some characteristic probabilities or probabilities which depend only on the current state of the system (Kemeny and Snell 1960). Models based on Markov processes have proven in the past to be useful in understanding and predicting patterns of change at the ecological community (Waggoner and Stephens 1970; Cho and Boerner 1991), landscape (Turner 1987), neighborhood (Bourne 1969; Gilbert 1972), and regional (Drewet 1969; Bell 1974) levels. In modeling successional changes in forests, the system states are the various community compositions/structures that might occur in some discrete area at some point in time, and the transition probabilities the likelihood that a tree of a given species will replace an existing canopy tree. Similarly, in a landscape context, the current state is the mosaic of landcover types existing on that landscape today, and the transition probabilities describe the likelihood that a landscape patch or GIS polygon will change from one landcover type to another over time.

Regular or stationary Markov processes are those that settle into a behavior pattern in which the transition probabilities among states become more or less constant. Such stationary Markov processes do exist for some forested landscapes (for example, Waggoner and Stephens 1970; Horn 1975). They may not, however, exist for landscapes with significant human activity. In addition to changes that occur on time scales shorter than those used for the historical reconstruction, socioeconomic forces unique to a specific landscape may result in changes over time in the "rules" for landcover change based in that landscape. Thus, from the point of view of Markov modeling, changes in policy, legislation, or attitudes concerning landcover changes may result in a failure of the matrix of transition probabilities to remain stationary over time.

In this study, we examined changes in landcover over a forty-eight-year period (1940–1988) in two contiguous landscapes in central Ohio: a relatively inertial till plain and a more dynamic moraine landscape (Simpson et al. 1994). To gain insight into the nonrandom aspects of landcover change on these two landscapes, and to evaluate the degree to which the forces driving landcover change varied over time, we assembled Markov models of landcover change for these two landscapes for four time intervals: three shorter intervals of 14–17 years (1940–1957, 1957–1971, 1971–1988) and an overall forty-eight-year interval (1940–1988). Our specific objectives were to (1) determine overall

cover map for the beginning of that time period to determine what landcover type had existed on the area bounded by that polygon at the beginning of that time interval. In instances where a polygon of a given landcover type present at the beginning of a given interval was split and developed into two or more polygons with different landcover types, each of the final polygons was considered separately in the calculation of the transition matrix. This process produced eight transition matrices that expressed change in landcover (or the lack thereof) as transition probabilities.

For purposes of evaluating the relative change in human-induced landcovers versus natural vegetation, the patterns of landcover change were pooled into two groups: (1) human-induced changes, that is, conversion of natural vegetation to urban, industrial, or agricultural uses, and (2) natural successional changes, that is, conversion of land formerly in human landcovers to early successional or forested land. Areas not falling into either of those categories (for example, agricultural land that remained in production over the time interval) were considered to be inertial over that time period.

To determine what the patterns of change might imply for long-term changes in these landscapes, we then generated a series of predictions for the landscape composition in A.D. 2036–2039 using three of the transition matrices for each of the two landscapes (the 1940–57 matrix, the 1971–88 matrix, and the overall 1940–1988 matrix) and the 1988 landcover percentages. This approach was designed to contrast the predictions for long-term change in the two landscapes given the transition probabilities of (1) the "Old Rules," based on the patterns of landcover change during 1940–1957, (2) the "New Rules," based on the landcover changes during 1971–1988, and (3) the "General Rules," based on the net changes in landcover over the entire forty-eight-year study period, 1940–1988. To arrive at predictions for the period 2036–2039, we iterated the General Rules model once for a forty-eight-year generation, and the Old Rules model and New Rules model three times each (seventeen years per generation) for a three-generation total of fifty-one years.

RESULTS

Change in Landcover, 1940–1988

Both landscapes were dominated by agriculture throughout the study period, with an average of 78 percent of the moraine and 93 percent of the till plain devoted to agriculture (Table 1). Over the forty-eight-year study period, however, agricultural landcover decreased by 5.0 percent on the moraine while it increased by 3.6 percent on the till plain. The rate at which nonagricultural land was brought into agricultural production was greater during the first two time intervals than during 1971–1988, whereas the rate of urban/suburban development increased over time on the moraine (Table 2). Over the full study period, there was a net gain of 15.8 hectares yr^{-1} of agricultural land on the till plain and a net loss of 2.9 hectares yr^{-1} of agricultural land on the moraine.

The area covered by closed canopy upland forest and transitional, young forest was greater on the moraine than on the till plain throughout the study period, by an average factor of approximately 6.0× for upland forest and 3.2× for young woodland. The cover of upland forest on the moraine increased from 1940 through 1971, but remained relatively constant on the till plain throughout the study period. Riparian forest was approximately 3× as abundant on the moraine than on the till plain, and the area covered by riparian forest increased throughout the study period in both landscapes (Table 1). The area covered by

forest on morainal ridges (Dobbins 1937; Howe 1857; King 1981; Sears 1925). The riparian forests along the major drainages were dominated by combinations of elm, ash, and maple (*Ulmus, Fraxinus,* and *Acer*). In contrast, the till plain was a mosaic of tall-grass (*Andropogon-Sorghastrum*) prairie, bur oak (*Quercus macrocarpa*) savanna, and oak-hickory forest (Dobbins 1937; Howe 1857; King 1981; Sears 1925).

Euro-American settlement and subsequent development through the 1800s removed the Native American community from these landscapes, cleared much of the primary forest, and created a low-density agricultural landscape composed of small farms and communities scattered across a matrix of secondary forest (Durant 1883; Howe 1857). By the 1850s, the population density was approximately 7.7 people per square kilometer (Howe 1857). Agriculture began earlier on the moraine and the areas of the till plain that had originally been the forests and oak savannas than on the poorly drained flats and prairies of the till plain. This patchwork landscape of farms, prairies, towns, and secondary forest changed little through the nineteenth century.

The second period of significant landscape change began in the early 1900s as the result of widespread agricultural drainage. This brought the poorly drained soils on the till plain into cultivation, thus increasing the amount of agricultural land and decreasing the area of moist forest and wet prairie (J. Rush, U.S.D.A. District Conservationist for Union County, Ohio, personal communication). Thus, even though the soils of the till plain have agricultural capabilities 14–59 percent greater than those of the moraine (depending on crop), portions of the better-drained moraine were converted to agriculture earlier than was the till plain (Waters and Matanzo 1975).

The typical farm of the early 1900s was small and family run. A closely knit German-Lutheran community developed along the southern edge of the moraine in the eastern portion of the study area during this period. This community remains intact today and greatly influences current agricultural practices (Rush, personal communication).

GIS Database

Landcover mosaics for these two landscapes were interpreted from aerial photographs taken in 1940, 1957, 1971, and 1988, and incorporated into an ARC/INFO GIS database. Each polygon in the photomosaics was classified as upland, closed canopy forest, young (transitional) woodland, oak savanna/parkland, riparian forest, agriculture, suburban/urban, or industry (including borrow pits from gravel mining). Following manual photo interpretation of unrectified aerial photo mosaics and ground-truthing of the 1988 landcover patterns, we transferred the interpreted classes to mylar overlays for digital input and co-registration into an ARC/INFO GIS data base.

Each landcover data layer was subdivided into virtually equal north and south portions to represent the moraine and till plain physiographic types (landscapes), respectively. We then produced landcover maps for each date, and used the capabilities of the GIS software to generate descriptive statistics for the entire study area and separately for each landscape. The attributes of the GIS database are given in more detail by Simpson et al. (1994).

Markov Modeling

Transition matrices were assembled for the two landscape segments over each of the three shorter time intervals (1940–1957, 1957–1971, 1971–1988) and over the entire study period (1940–1988) by determining the landcover for each polygon at the end of each time interval, then backtracking to the land-

TABLE 1

Proportion of Land Area Occupied by Seven Landcover Types in Two Central Ohio Landscapes of Approximately 12,400 Hectares Each in Four Different Years

	1940		1957	
Landcover	Moraine	Till Plain	Moraine	Till Plain
Agriculture	79.7	90.8	78.3	91.4
Upland Forest	6.3	1.4	7.8	1.4
Young Woodland	6.1	3.0	4.2	1.9
Oak Savanna	3.8	4.2	4.1	3.6
Riparian Forest	3.0	0.6	3.9	1.5
Urban/Suburban	1.1	0.0	1.5	<0.1
Industrial	<0.1	0.0	<0.1	0.0

	1971		1988	
	Moraine	Till Plain	Moraine	Till Plain
Agriculture	78.2	93.6	74.7	94.4
Upland Forest	9.0	1.4	8.6	1.1
Young Woodland	2.6	0.2	5.9	0.7
Oak Savanna	3.0	2.7	1.3	1.6
Riparian Forest	4.5	1.8	4.7	1.7
Urban/Suburban	2.5	0.0	3.7	0.3
Industrial	2.3	<0.1	2.2	<0.1

TABLE 2

Changes in Landcover Types in Ha.Yr^{-1} in Two Central Ohio Landscapes.

	Moraine				Till Plain			
	1940–1957	1957–1971	1971–1988	Net 1940–1988	1940–1957	1955–1971	1971–1988	Net 1940–1988
Natural Vegetation	16.2	12.2	(1.9)	9.5	6.2	0.5	(2.8)	(0.4)
Agriculture	45.0	48.9	30.3	13.3	33.6	32.4	17.1	16.2
Urban/Suburban	4.0	8.5	10.5	6.7	0	0	0	0

Losses are indicated by (). Natural vegetation is the sum of upland forest, riparian forest, young transitional woodland, and oak savanna. Increases in industrial landcover are included under urbanization.

open parkland/oak savanna differed little between landscapes or among years. In both landscapes, there was a net increase in natural vegetation (upland forest + riparian forest + young woodland + oak savanna) during both 1940–1957 and 1957–1971, but a net loss of natural vegetation during 1971–1988 (Table 2). On the moraine, these losses of natural vegetation were to urban/suburban development whereas on the till plain they were to increased agricultural production. Over the entire study period there was a net gain of natural vegetation cover on the moraine and a small net loss on the till plain (Table 2).

There was no significant urban, suburban, or industrial development on the till plain at any time during 1940–1988. In contrast, on the moraine there was steady growth in urban/suburban landcover throughout the study period and growth in industrial landcover from 1957–1971 (Table 1), with 78 percent of the area converted to urban/suburban landcover and 90 percent of the area converted to industrial cover coming from agricultural land.

Transition Probabilities

The tendency for a polygon of land to remain in the same landcover over our study period was measured by the self-replacement probabilities in the transition matrices (Table 3). The probability of agricultural land remaining over fourteen to seventeen years averaged 0.91 on the moraine and 0.97 on the till

TABLE 3
Self-replacement Probabilities for Landcover Types in Two Central Ohio Landscapes

	Moraine				Till Plain			
	1940–1957	1957–1971	1971–1988	1940–1988	1940–1957	1957–1971	1971–1988	1940–1988
Upland Forest	.57	.76	.62	.50	.54	.54	.55	.31
Riparian Forest	.54	.68	.69	.65	.43	.56	.57	.48
Agriculture	.90	.93	.90	.85	.96	.98	.98	.97
Young Woodland	.17	.23	.24	.17	.11	.02	.16	.03

plain. This persistence of agricultural landcover was the primary force generating landcover inertia in these two landscapes. The probability that a polygon of upland or riparian forest would remain unchanged in landcover over a given time period was lower: moraine, 0.65 and 0.64, respectively; till plain, 0.54 and 0.52, respectively. Young woodlands (including early successional sites) had the lowest persistence in these two landscapes. The average self-replacement probabilities for young woodlands averaged 0.21 on the moraine and 0.10 on the till plain.

These two landscapes differed in the relative importance of succession to closed canopy forest versus reconversion to agriculture in producing the low persistence of young woodland. On the moraine, the average probability of conversion of early successional sites to closed canopy woodland over the three time periods (0.35) was approximately the same as the average probability of reconversion of early successional sites to agriculture (0.30). Furthermore, these probabilities differed little among the three time periods studied. In contrast, on the till plain, the average probability of conversion to agriculture (0.57) exceeded the probability of succession to closed forest (0.15) by a factor of 3.8. Furthermore, the probability of conversion to forest was greater (0.33), and the probability of reconversion to agriculture (0.43), was lesser during 1971–1988 than during the two previous time periods.

Markov Chain Models of Temporal Change

On the moraine, the Markov process model based on the New Rules (that is, 1971–1988 transition matrix) predicted that natural vegetation and urban/suburban/industrial landcover would increase (by 14 percent and 53 percent relative to 1988, respectively) and agriculture would decrease (by 6 percent relative to 1988) (Figure 2). In contrast, the Markov models for the moraine based on the Old or General Rules (that is, 1940–1957 and 1940–1988 matrices, respectively) predicted just the reverse: an increase in agriculture and decreases in natural vegetation and urban/suburban land.

Only the General Rules model for the moraine predicted a substantial increase in riparian forest. The current conservation focus of both governmental agencies and nongovernmental organizations (especially The Nature Conservancy) in the region is on the Darby Creek ecosystem (one of The Nature Conservancy's twelve "Last Great Places") and its riparian zone, which bisects our study area from northwest to southeast. Despite increased awareness in the region of biodiversity issues, this model result suggested that the factors driving landcover change during 1971–1988 were no more likely to result in an increase in riparian woodland than were those of 1940–1957.

For the till plain, all three transition matrix models predicted modest increases in agricultural land over the prediction period, ranging from 0.8 percent relative to 1988 under the New Rules to 2.9 percent under the General Rules (Figure 2). None of the three models predicted appreciable growth in
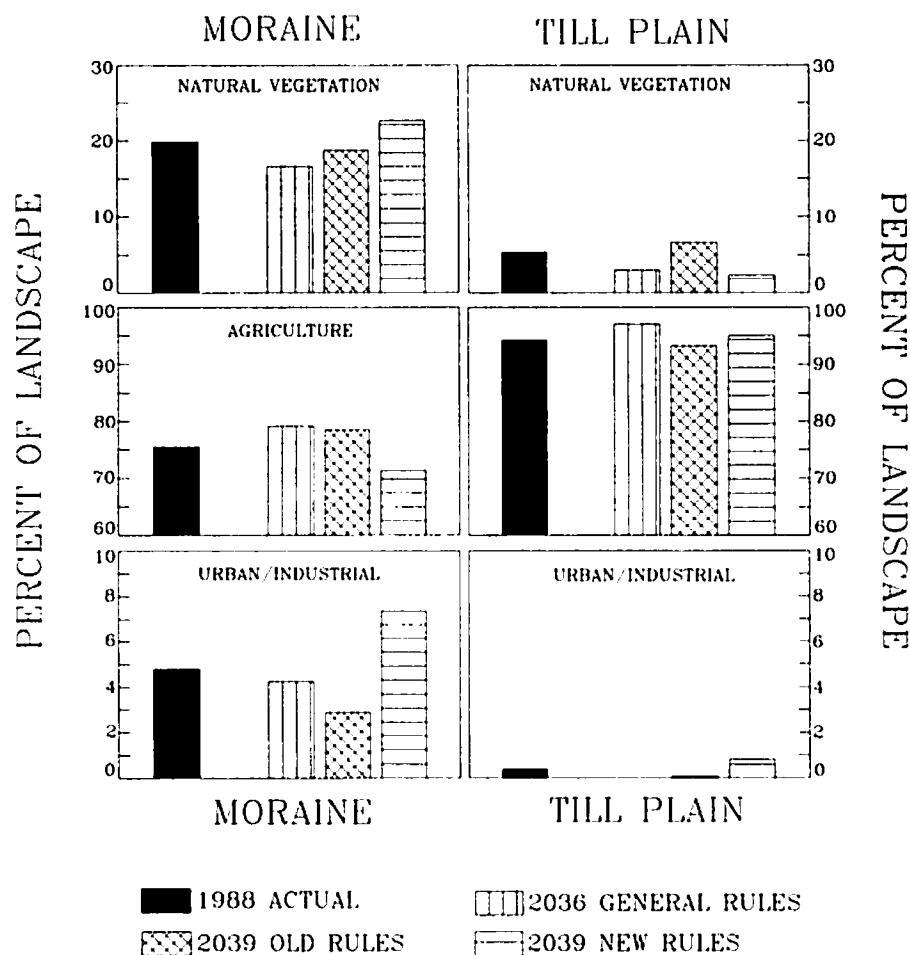
Fic 2. Predictions of Three Markov Process Models for Changes in Major Landcover Groupings over Approximately Fifty Years. The General Rules model was based on actual landcover changes during 1940–1988, the Old Rules model on changes during 1940–1957, and the New Rules model on changes during 1971–1988. Actual 1988 landcover percentages are given for reference.

suburban/urban/industrial land. However, the predictions of the change in natural vegetation on the till plain did disagree among the three models, with the Markov model based on the Old Rules predicting an increase in natural vegetation while the General Rules and New Rules models predicted decreases in natural vegetation. However, the actual magnitude of the differences was small, ranging only from an increase of 1.3 percent under the Old Rules to decreases of 2.0 percent and 2.3 percent under the General Rules and New Rules, respectively.

DISCUSSION

From the perspective of the net rate of change in landcover over our forty-eight-year study period, these two Ohio landscapes appear quite static when compared to other landscapes in the eastern third of North America. Studies of landscape change in New England (Foster 1992, 1993), Georgia (Turner

and Ruscher 1988), and the unglaciated hill country of southeastern Ohio (Artigas 1993) have all reported rates of reversion of agricultural land to natural vegetation much greater than those we observed in our two study sites. In part, the persistence of agricultural dominance in our study sites, Illinois (Iverson 1988) and southern Ontario (Muller and Middleton 1994) may be a function of the relatively high fertility of the soils of these areas compared to the less fertile soils of New England (Foster 1993) and southeastern Ohio (Artigas 1993) and the intensive cropping history of the piedmont of Georgia (Waters and Matanzo 1975).

Such a broad-brush approach may, however, obscure patterns of change occurring at finer spatial scales and over shorter time periods. For example, in our two Ohio landscapes, the probability that a given patch of forest would persist through a 14–17-year period averaged only 0.65 on the moraine and 0.53 on the till plain. In contrast, the self-replacement transition probabilities for forest patches on the piedmont of Georgia through two 23–25-year periods approached 1.00 (Turner 1987) and ranged from 0.71 to 0.85 during 5–16-year periods on the Niagara Peninsula of Ontario, Canada (Muller and Middleton 1994). Thus, although the net rate of change in forested area over forty-eight years in our study sites was relatively low, there was considerable turnover in forested land at shorter time scales.

Although the spatial dynamics of patches of natural vegetation may have been more dynamic over these shorter time frames than in other landscapes, agricultural landcover may have been more persistent than elsewhere. The probability that a given patch of agricultural land would persist as such through our 14–17-year study periods averaged 0.91 for the moraine and 0.97 for the till plain. This was consistent with the self-replacement transition probability for agricultural land in Ontario of 0.93 (Muller and Middleton 1994), but considerably greater than the averages of 0.80 for 1942–1955 and 0.43 for 1955–1980 in Georgia (Turner 1987). Thus, in our two Ohio landscapes, the agricultural matrix tended to be persistent and inertial while the patches of other landcover embedded within that matrix supplied what dynamism existed in the area.

If all of the natural and socioeconomic forces that drive landcover change remained constant and consistent from 1940 through 1988, then the probabilities of any given landcover type to any other would remain constant. Thus, the transition matrices for the three shorter time periods we studied would all be identical to the overall forty-eight-year matrix. In such a case, the model would be stationary and the predictions of the landcover mosaic for any time period into the future would be the same, no matter which of the matrices one used. This was clearly not the case here.

For the moraine landscape, the Markov process model based on the New Rules (that is, the 1971–1988 matrix) predicted increases in natural vegetation and urbanization and a decrease in agricultural landcover; the models based on the Old Rules (that is, the 1940–1957 matrix) and the General Rules (that is, the overall forty-eight-year matrix) predicted the reverse. During the 1960s and early 1970s some of the family farms on the less fertile parts of the moraine landscape became unprofitable because of combinations of increasing farm commodity surpluses, the oil embargo of 1973, and the rise in interest rates (Simpson et al. 1994). This resulted in the conversion of some of these family farms to country estates for gentleman farmers. As these newer land owners were not as dependant on farm income as their predecessors, they were more likely to participate in conservation reserve programs or simply to allow their land to return to natural vegetation. Construction of a major automobile assembly plant outside of Marysville in the early 1980s then triggered

suburban-urban development in what is the northeast corner of our study areas. Thus, the Markov process model based on the New Rules generated predictions opposite in direction from those of the General Rules and Old Rules models because socioeconomic events that occurred during the 1971–1988 period changed the mix of factors driving landscape change.

For the till plain landscape, in contrast, the three Markov process models produced predictions that varied relatively little. All predicted modest increases in agricultural landcover, a continuing lack of suburban/urban and industrial development, and small changes in natural vegetative cover. From the 1940s through the 1960s, there continued to be expansion of agriculture on the till plain because there were still areas of potentially productive soils that remained to be tiled and drained. In addition, because of the expansion of the operations of the German-Lutheran community farming operations in the southern part of the till plain and the integration of smaller family farms into larger, single-crop operations (Rush, personal communication), agriculture could continue to grow in a profitable manner throughout our study period. Thus, the relatively stationary nature of the Markov process models for the till plain reflect the inherent inertia in that landscape over this forty-eight-year period.

These analyses have demonstrated an inherent problem in using Markov process models to understand landscape change in dynamic landscapes. As those natural and socioeconomic processes that drive landcover change themselves change, the transition probabilities among landcover types must also change. Unfortunately, predicting how the transition probabilities will change is not often straightforward. Gilbert (1972), in a Markov model of changes in neighborhood housing patterns, recommended using temporally nonhomogeneous (nonstationary) Markov process models that applied weighting factors to each transition probability for each time period. Although those weighting factors were to be based on the socioeconomic processes considered most important during each time period (for example, changing racial attitudes, mortgage availability), Gilbert presented no empirical framework for estimating the weighting functions robustly. Thus, in an inertial landscape, Markov process models can be used to predict future landscape configurations with some precision. In dynamic landscapes, however, the utility of Markov process models will be limited to the time frame during which the socioeconomic drivers which operated at the beginning of one's study period continue relatively unchanged.

LITERATURE CITED

Artigas, F. J. (1993). "The Effect of Landscape Structure and Change on Fluxes of Materials and Water between Patches of Different Ecosystem Types in the Hocking Hills of Ohio." Ph.D. thesis, Ohio State University, Ohio.

Bell, E. J. (1974). "Markov Analysis of Land Use Change—An Application of Stochastic Processes to Remotely Sensed Data." *Journal of Socioeconomic Planning Science* 8, 311–16.

Bourne, L. S. (1969). "Forecasting Land Occupancy Changes through Markovian Probability Matrices: A Central City Example." Research Report 14, Centre for Urban and Community Studies, University of Toronto.

Cho, D. S., and R.E.J. Boerner (1991). "Structure, Dynamics, and Composition of Sears Woods and Carmean Woods State Nature Preserves, Northcentral Ohio." *Castanea* 56, 77–89.

Curtis, J. T. (1956). "The Modification of Mid-latitude Grasslands and Forests by Man." In *Man's Role in Changing the Face of the Earth*, edited by W. L. Thomas, pp. 721–36. Chicago: University of Chicago Press.

Dobbins, R. A. (1937). "Vegetation of the Northern "Virginia Military Lands" of Ohio." Ph.D. thesis, Ohio State University, Columbus.

Drewet, J. R. (1969). "A Stochastic Model of the Land Conversion Process—An Interim Report." *Regional Studies* 3, 269–80.

Durant, P. A. (1883). *The History of Union County, Ohio.* Chicago, Il.: W.H. Beers Publishers.

Foster, D. R. (1992). "Land-use and Vegetation Dynamics in Central New England: An Historical Perspective." *Journal of Ecology* 80, 753–72.

——— (1993). "Land-use History and Forest Transformations in Central New England." In *Humans as Components of Ecosystems,* edited by M. J. McDonnell and S. T. A. Pickett, pp. 91–110. New York: Springer-Verlag.

Gilbert, G. (1972). "Two Markov Models of Neighborhood Housing Turnover." *Environment and Planning* 4, 133–46.

Horn, H. S. (1975). "Markovian Processes of Forest Succession." In *Ecology and Evolution of Communities,* edited by M. L. Cody, and J. M. Diamond, pp. 196–213. Cambridge, Mass.: Belknap Press.

Howe, H. (1857). *Historical Collections of Ohio.* Cincinnati, Oh.: E. Morgan.

Iverson, L. R. (1988). "Land-use Change in Illinois, USA: The Influence of Landscape Attributes on Current and Historic Land Use." *Landscape Ecology* 2, 45–62.

Kemeny, J. G., and J. L. Snell (1960). *Finite Markov Chains.* New York: Van Nostrand.

King, C. C. (1981). "Prairies of the Darby Plains of West-central Ohio." In *The Prairie Peninsula—In the Shadow of Transeau.* Proceedings of the Sixth North American Prairie Conference, edited by R. L. Stuckey and K. J. Reese, pp. 108–27. Columbus, Oh.: Ohio Biological Survey.

Muller, M. R., and J. Middleton (1994). "A Markov Model of Land-use Change Dynamics in the Niagara Region, Ontario, Canada." *Landscape Ecology* 9, 151–57.

Nilon, C. H., Jr. (1986). "Quantifying Small Mammal Habitats along an Urbanization Gradient." Ph.D. thesis, S.U.N.Y. College of Environmental Science and Forestry, Syracuse. 148 pp.

Sears, P. B. (1925). "The Natural Vegetation of Ohio. I. A Map of the Virgin Forest." *Ohio Journal of Science* 25, 139–49.

Simpson, J. W., R.E.J. Boerner, M. N. DeMers, L. Berns, F. J. Artigas, and A. Silva (1994). "Forty-eight Years of Landscape Change on Two Contiguous Ohio Landscapes." *Landscape Ecology* 9(3), 261–70.

Turner, M. G. (1987). "Spatial Simulation of Landscape Changes in Georgia: A Comparison of Three Transition Models." *Landscape Ecology* 1, 29–36.

Turner, M. G., and C. L. Ruscher (1988). "Changes in Landscape Patterns in Georgia, USA." *Landscape Ecology* 1, 241–52.

Waggoner, P. E., and G. R. Stephens (1970). "Transition Probabilities for a Forest." *Nature* (London) 225, 1160–61.

Waters, D. D., and F. Matanzo (1975). *Soil Survey of Union County, OH.* Washington, D.C.: U.S. Soil Conservation Service.