Landscape Ecology vol. 2 no. 2 pp 111-133 (1989)
SPB Academic Publishing, The Hague

A review of models of landscape change

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Keywords: Models, landscape change, review

Abstract

Models of landscape change may serve a variety of purposes, from exploring the interaction of natural processes to evaluating proposed management treatments. These models can be categorized as either whole landscape models, distributional landscape models, or spatial landscape models, depending on the amount of detail included in the models. Distributional models, while widely used, exclude spatial detail important for most landscape ecological research. Spatial models require substantial data, now more readily available, via remote sensing, and more easily manipulated, in geographical information systems. In spite of these technical advances, spatial modelling is poorly developed, largely because landscape change itself is poorly understood.

To facilitate further development of landscape models I suggest (1) empirical multivariate studies of landscape change, (2) modelling of individual landscape processes, (3) explicit study of the effect of model scale on model behavior, and (4) 'scaling-up' results of studies, on smaller land areas, that have landscape relevance.

Introduction

Landscape structure and composition may change dramatically over time in a variety of landscapes. In managed landscapes, for example, changes in the size and spatial configuration of remnant forest patches may have important ramifications for species that utilize these patches (Burgess and Sharpe 1981; Harris 1984). In more natural landscapes, disturbances, such as fires, insect attacks, and windstorms may alter the age, size, and spatial structure of patches (Pickett and White 1985).

Empirical studies of the landscape change process are invaluable, but for some research questions there is also a need for models. For example, studies using experimental manipulations of landscapes may be impractical, due to the large land area required and the long time needed to recover from a single experiment. As another example, global climatic change or other environmental changes may affect landscape structure indirectly, through changes in disturbance regimes, and directly, through effects on the growth and survival of particular species (e.g., Emanuel *et al.* 1985). To anticipate these changes, landscape models that are sensitive to environmental fluctuation are needed.

Models of landscape change have been reviewed previously (Shugart and West 1980; Loucks *et al.* 1981; Weinstein and Shugart 1983; Shugart 1984; Risser *et al.* 1984; Shugart and Seagle 1985). My purpose here is (1) to review the assumptions, limitations, and possible applications of a broad spec-

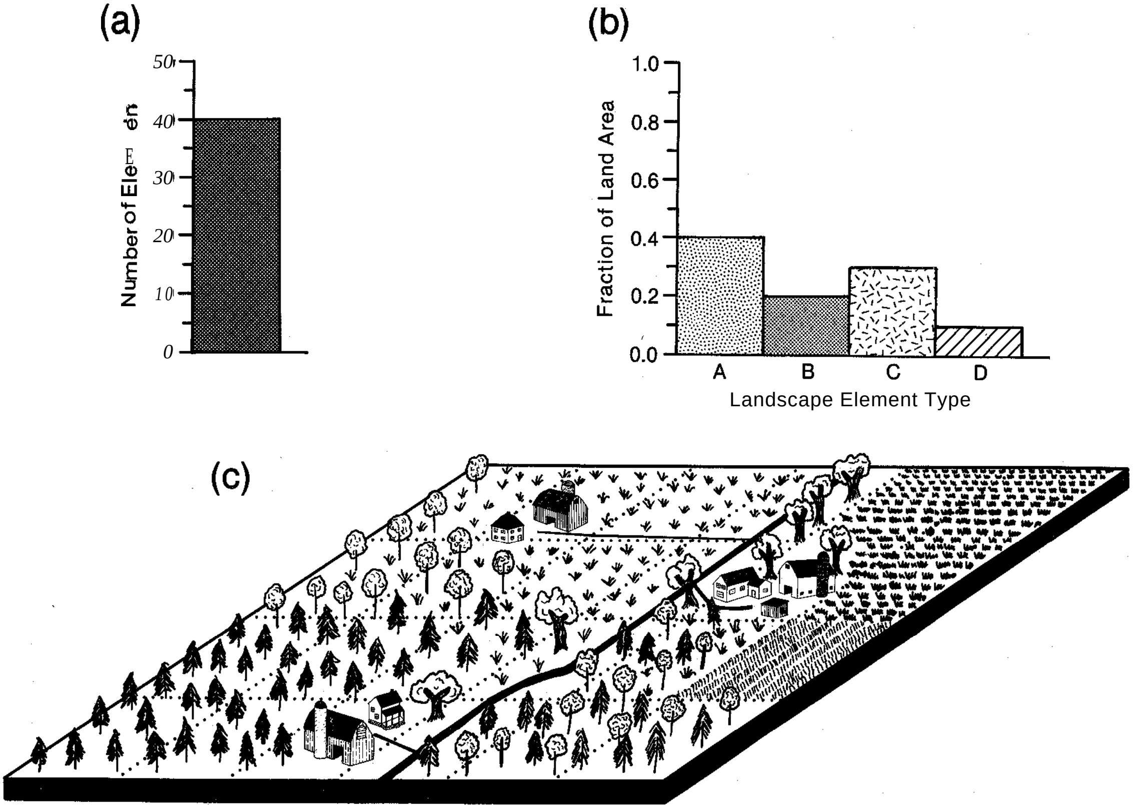

Fig. 1. Data monitored by three kinds of models of landscape change, distinguished by their level of data aggregation. Landscape elements or states may be defined by aggregating similar grid cells. Models may, then, be: (a) whole landscape models, (b) distributional landscape models, or (c) spatial landscape models, depending on the level of aggregation. Models may also be univariate, or include more than one variable.

trum of models of landscape change, (2) to classify the kinds of models, and (3) to suggest possible extensions of these models, based on models developed in other fields. Such cross-disciplinary review, while by no means comprehensive, may suggest new approaches. I will particularly draw on plant and animal population models, and on a variety of geographical models, as these models have particular relevance to certain aspects of landscape change.

As this is a review of models useful for landscape ecological research (*cf.* Risser ***et al.*** 1984; Naveh and Lieberman 1984; Former and Godron 1986; Risser 1987), I will focus on models of processes on the landscape scale. There is no absolute lower physical limit to this scale, but, generally, the landscape scale is one that contains a few interacting ecosystems, and thus is on the scale of kilometers, rather than meters or hundreds of meters (Forman and Godron 1986).

A taxonomy of models of landscape change

A variety of criteria could be used to distinguish models of landscape change. Perhaps the most important are: (1) the level of aggregation, and (2) the use of continuous or discrete mathematics. Models could also be distinguished by the kind of data source, the method of defining states, the kind of output, and a number of other criteria.

The level of aggregation criterion refers to the level of detail with which the landscape change process is modelled. A convenient way to think about modelling landscape change is to imagine that the landscape consists of a variety of spatially arranged ‘landscape elements’ (Forman and Godron 1988, p. 12) underlain by a system of grid lines, so that there are boxes or ‘grid cells’ formed by the grid lines (Fig. lc). These grid cells are analogous to the pixels in a digital satellite image (Lillesand and Kiefer 1979) or the grid cells in a raster-based geographical information system (Burrough 1986).

A distinguish three kinds of models, based on the level of aggregation criterion (Fig. 1). First, are *whole landscape models* (Fig. la), in which the value of a variable in some landscape area is modelled. One might, for example, model the number of landscape elements in a particular township over time. Second, are *distributional landscape models* (Fig. lb), in which the distribution of values of a variable in some landscape area is modelled. One might, for example, model the distribution of land area among the landscape elements in a particular township over time. Finally, and most detailed, are *spatial landscape models* (Fig. lc), where the fate of individual subareas of the landscape, and their configuration is modelled, using a set of either whole landscape models or distributional landscape models as submodels. In such spatial models, for example, the number of landscape elements in a configuration of townships could be modelled, using a set of whole landscape submodels. Similarly, the distribution of land area among landscape elements in a configuration of townships could be modelled, using a set of distributional landscape submodels.

This three-part classification differs from other classifications of ecological models (e.g., DeAngelis *et al.* 1985; DeAngelis and Waterhouse 1987). First, these authors referred to some models, that I have classified as distributional models (e.g., Levin 1976), as spatial models. But, here I require that spatial models explicitly make use of the location and configuration of landscape subareas. The models of Levin and others are thus, in my classification, non-spatial, because the patch dynamics are modelled without location and configuration. This distinction is important, now that geographical information systems (Burrough 1986), which will facilitate spatial modelling, are becoming widely available. Second, DeAngelis *et al.* distinguish equilibrium and non-equilibrium models, a useful distinction for their purposes, but the literature commonly follows lines of development related to the kind of mathematical treatment, and review is facilitated by following these lines.

Table 1. Kinds of models of landscape change.

Whole landscape models: Models of landscape phenomena, in aggregate, for the landscape as a whole (e.g., total number of landscape elements in a township)

Distributional landscape models: Models of the distribution of land area among classes of landscape phenomena (e.g., distribution of land area among five landscape elements in a township)

- ***Differential equation models:*** Continuous time models
  - Continuous state space models
  - Discrete state space models
- ***Difference equation models:*** Discrete time models
  - Markov chain models
  - Semi-Markov models
  - Projection models

Spatial landscape models: Models of the spatial location and configuration of landscape phenomena (e.g., spatial location and configuration of five landscape elements in a township)

- ***Mosaic models:*** Models composed of a spatial mosaic of subareas, each having its own submodel.
  - Whole mosaic models
  - Distributional mosaic models
- ***Element models:*** Models composed of a configuration of landscape elements, each having its own submodel.

Models may use either continuous mathematics or discrete mathematics, in two ways. First, time may be a continuous or discrete variable. Second, the state space of the models may be either continuous or discrete. I distinguish models (Table 1), within each of the three main types (above), first using the treatment of time and then the treatment of the state space.

Model components

The basic components of all models of landscape change are: (1) an initial configuration, (2) birth, death, and change functions, and (3) an output configuration. The initial configuration is simply a starting value in whole landscape models, a starting distribution of land area among states in distributional landscape models, and a complete raster of grid cell values in a spatial landscape model. These initial configurations may be derived from a variety of sources, including published land use data, permanent plots or monitoring data, or remotely-sensed data.

Birth, death, and change functions are the most important parts of the models. Birth functions add land area to, and death functions remove land area from the landscape being modelled. Since many landscape change processes are modelled on a fixed land area, birth and death functions are often absent. The change function modifies the output of a whole landscape model, changes the distribution of land area in a distributional landscape model, and alters the subarea values in a spatial landscape model. The change function may be as simple as a single linear differential or difference equation, but could also be a set of complex nonlinear equations with interactions.

Outputs from whole landscape models are nothing more than a value for each variable. Output from distributional landscape models may include summary values for variables, as in whole landscape models, but the more important output is a univariate or multivariate distribution of land area. Spatial landscape models can output whole landscape summary statistics, distributional landscape data, or individual subarea values. One can aggregate data, in other words, in more detailed models, and produce several kinds of output. Spatial models, in this sense, are the most flexible.

Whole landscape models

Whole landscape models focus on the value of a variable or several variables in a particular land area as a whole. Values of variables can be output directly (continuous state space) or can be classified into states (discrete state space). The time dimension in these models can be formulated using continuous or discrete mathematics. The basic differential equation, in the case of continuous mathematics, is

$$dX/dt = f(X) \qquad (1)$$

where X is some landscape variable of interest, f(X) is some function of X, and t is time. The basic difference equation, using discrete mathematics, is

$$X_{t+1} = f(X_t) \qquad (2)$$

where X, t, and $f(X_t)$ are as in equation 1. The function, f(X), may have a variety of forms, allowing for changes in the value of X to be some function of X itself, or other endogenous or exogenous variables. Comparable models have been applied in a variety of other fields (e.g., Freedman 1980; Nisbet and Gurney 1982; Edelstein-Keshet 1988) too, numerous to review here.

Whole landscape models have received no use, so far as I am aware, except as submodels in spatial models, and they are mentioned here only for completeness and to set the stage for discussion of spatial models. Nonetheless, changes in landscape attributes, such as diversity and connectivity (Forman and Godron 1986) could certainly be modelled over time as a function of various endogenous and exogenous variables in a whole landscape modelling framework. The completely general equations (1 and 2) undoubtedly will be refined if such models are developed.

Distributional landscape models

Distributional landscape models all focus on changes in the distribution of land area among values of a variable or variables. Although the state-space can be continuous, more typically the state-space is discrete. Discrete states might include a variety of landscape elements or types such as forest types, land-use types, age-classes, or successional states. Distributional models do not provide information on the actual location or configuration of states in the landscape, and thus are less-detailed, but also simpler to develop and use, than are spatial models.

There are several ways to determine the states used in a distributional model. The states may be defined *a priori,* and somewhat subjectively, using information in the literature (Shugart *et al.* 1973; Sharpe *et al.* 1981). The number and kinds of states may also be constrained or determined by the data source. Only a certain number and kind of states, for example, can currently be distinguished in remotely-rensed data (Hall *et al.* 1987), and available land-use records may also restrict state definition (Shugart *et al.* 1973). Where fewer restrictions apply, a variety of multivariate quantitative methods can be used to more objectively classify states (Johnson and Sharpe 1976; Noordwijk-Puijk *et al.* 1979; Austin and Belbin 1981; Usher 1981; Kachi *et al.* 1986), though these methods do not objectively determine the number of states. Vandermeer (1978) suggested that the optimum number of states can be determined by a method that minimizes the tradeoff between a 'sample error', that increases as the narrowness of states (and the number of states) increases, and an 'error of distribution', that increases as the narrowness of states (and the number of states) decreases. As the number of states increases, the computational burden and data requirements for these models increase exponentially.

Both continuous and discrete mathematics have been used for the time dimension in these models, but there may be little difference in the utility of these two approaches. For example, the average response of a stationary Markov chain can be matched by a corresponding linear, constant-coefficient differential equation (Shugart *et al.* 1973). Differences in the development of the supporting literature may influence the choice between these two approaches, but differential equations may no longer be a better framework for the use of nonstationary transitions (Johnson and Sharpe 1976), and computational advantages (Shugart *et al.* 1973) may be less important now, due to recent computer developments. The matrix approach may still provide an easier framework for modelling changes in variance along with changes in mean (Shugart *et al.* 1973). In most cases, empirically-based models of landscape change use estimates of change determined by resampling the landscape at discrete intervals. In this case, discrete mathematics may be more congruent with the modelling approach, but in more theoretically-based models, either approach may be appropriate.

Differential equation models

Continuous state space models:

In the simplest univariate case, these models can be formulated as a single partial differential equation. Where the distribution variable is age, the equation may be a derivative of the McKendrick-Von Foerster equation (McKendrick 1926; Von Foerster 1959) used to model biological populations:

$$\frac{\partial N(a,\ t)}{\partial a} + \frac{\partial N(a,\ t)}{\partial t} = -\ \mu(a,\ t)*N(a,t) \qquad (3)$$

where N(a, t) is a function describing the age distribution of individuals (or land area, in a landscape model), $\mu(a,\ t)$ is a mortality function describing the loss of individuals (or land area) by age, a is age, and t is time. This equation has been generalized for modelling size distributions of populations (DeAngelis and Mattice 1979). The McKendrick-Von Foerster equation is quite general, and does not, for example, require constant coefficients. The $\mu(a,\ t)$ function could also be a time-varying function of endogenous or exogenous variables affecting landscape change. Reviews of extensions of these models, in population research, are available (e.g., Gurtin and MacCamy 1979; Nisbet and Gurney 1982; Gyllenberg 1984).

Continuous state space differential equation models may also be multivariate. Multivariate versions were developed for modelling joint age-size distributions of animal populations (e.g., Sinko and Streifer 1967, 1969; Streifer 1974; Oster and Takahashi 1974). The equation in this case is

$$\frac{\partial N(t,a,m)}{\partial t} + \frac{\partial N(t,a,m)}{\partial a} + \frac{\partial N(t,a,m)}{\partial m}*[g(t,a,m)*$$

$$N(t,a,m)] = -\ \mu(t,a,m)*N(t,a,m) \qquad (4)$$

where N(t,a,m) is a function describing the age-size distribution of individuals at time t, g(t,a,m) is the average rate of growth for an animal of age a and mass m at time t, and $\mu(t,a,m)$ is the death rate for animals of age a and mass m at time t.

The multivariate version of these models can also be applied to landscape change. The model in this case describes the changing age-size distribution of patches, where the patches in the original conception (Levin and Paine 1974; Levin 1976) may be of any size, including those on the landscape scale. The equation, then, is identical to equation 4, but N(t,a,m) is the age-size distribution of patches at time t, g(t,a,m) is the average rate of growth for a patch of age a and size m at time t, while $\mu(t,a,m)$ is the death rate for patches of age a and size m at time t. The model has been applied, not on the landscape scale, to the dynamics of small patches (< 40 m^2) in intertidal mussel beds along the Washington coast (Paine and Levin **1981)**, but could equally well be used to model multivariate dynamics of disturbance patches in landscapes.

Discrete state space models:
These models all consist of a system of ordinary differential equations. In the univariate case, the models contain one equation for each state. The system may thus have the form

$$\begin{aligned} dX_1/dt &= f_1(X_1, \ldots X,) \\ dX_2/dt &= f_2(X_1, \ldots X,) \\ &\vdots \\ dX_n/dt &= f_n(X_1, \ldots X_n) \qquad (5) \end{aligned}$$

where X_i is the ith of n states.

Such systems of equations have been used to model interspecific competition for space in a patchy environment (Horn and MacArthur 1972; **Slatkin** 1974; Hastings **1980)**, as well as the dynamics of multispecies tree populations (Turnbull 1983; Lynch and Moser 1986). Both applications included endogenous effects, but neither **modelled** the influence of exogenous variables.

A single univariate study (Johnson and Sharpe 1976) has been conducted at the landscape scale. These authors developed a compartment model of succession among 10 forest types in the northern Piedmont of Georgia. They used the rates of change between types found in 928 ‘Continuous Forest Inventory’ plots sampled by the U.S. Forest Service in 1961 and 1972. Although the plots were rather small, they were regional in extent, so that Johnson and Sharpe felt that the model represented regional dynamics of change. But, such an extrapolative approach may miss potentially important interactions between contiguous land areas.

The mathematics of these models have been extended to the multivariate case (Slobodkin 1953). Multivariate extensions of Horn and MacArthur’s (1972) model have been developed for competitive and predator-prey interactions in patchy environments (Levin 1974, 1976).

A well-developed group of multivariate differential equation, discrete state space models are the JABOWA (Botkin ***et al.*** 1972) and FORET (Shugart and West 1977) models and their derivatives. These models have been used widely in modelling forests, and could be used as submodels in spatial landscape models (discussed later), and thus are worthy of brief review (cf. Shugart 1984 for more thorough review). The JABOWA/FORET models contain a set of differential equations for diameter growth of individual trees by species (the discrete states). Additional variables (e.g., leaf area index, biomass, and basal area on the plot as a whole) are derived from these primary variables. The models contain explicit natality and mortality functions, and tree growth is dependent on exogenous (temperature and moisture), and endogenous (the shade-related height profile of trees on the plot) conditions. This means that the models are responsive to climatic changes, spatial variation in environment, and shading effects within the plot. The models can also be modified to incorporate natural or anthropogenic disturbances. Although these models contain numerous desirable features, they were designed to model species composition on rather small plots (typically 0.1 ha), and would require modification to be useful at the landscape scale.

Multivariate models have been designed for modelling change at the landscape scale. Shugart ***et al.*** (1973) developed a compartment model of succession among 15 forest types in the western Great Lakes region. The model is bivariate in that each of the 15 forest types is divided into 3 size-classes, so that the total system contains 45 ordinary differential equations. These authors used published data on the percentage of forest land of each type, in Michigan in 1966, to initialize the model and estimate rate coefficients. The accuracy of the model’s coefficients and initial conditions, and model validity were challenged (Hahn and Leary 1974), but the model still illustrated a new modelling approach (Shugart *et al.* 1974). A comparable model was applied to succession among 11 forest types with 3 size-classes in the North Carolina piedmont (Johnson 1977), but Johnson also simulated the effects of harvesting and natural disturbances (e.g., wind, insects). Johnson's model has since been modified and coupled directly with a model of gypsy moth infestation (Byrne *et al.* 1987). All three modelling efforts required substantial estimation, as direct estimates of transfer coefficients were unavailable. Moreover, these models did not include the effect of exogenous variables, though such variables could be incorporated in the equations. Nonetheless, these models represent a potentially useful approach to modelling landscapescale change in a non-spatial format.

Difference equation models

There are no landscape models that use difference equations and a continuous state space. All difference equation, distributional models, using discrete state spaces, can be expressed in their simplest form, in matrix notation, as:

$$\mathbf{n}_{t+1} = \mathbf{P}\mathbf{n}_t \qquad (6)$$

where $\mathbf{n}_t$ is a column vector, n = $(n_1 \ldots n,)$, whose elements are the fraction of land area in each of m states at time t, and P is an m X m matrix, whose elements, p_{ij}, incorporate the birth, death, and change rates of each state during the time interval (or 'time-step') from t to t + 1. All the models thus project an initial distribution of land area among states forward to an output distribution by means of a projection, or 'transition', matrix.

Three kinds of difference equation distributional models, relevant to landscape modelling, can be distinguished, based upon model assumptions. First, are Markov chain models, which are stochastic models with fixed sojourn times (explained below). Second, are semi-Markov models, which are also stochastic models, but with variable sojourn times. Third, is a general group of models, that are deterministic, and that can be called projection models.

Markov chain models:

Markov chain models have several assumptions and limitations. I have derived the following discussion from texts in applied mathematics (Kemeny and Snell 1960; Feller 1968; Bhat 1984) and review articles in several fields (Collins *et al.* 1974; Collins 1975; Hulst 1979; Pickles 1980). First, these models are stochastic, as opposed to deterministic, because model output, which is the distribution among states, is based on the probability of transition, p_{ij}, between states i and j. Since the transitions are probabilities, it follows that

$$\sum_{j=1}^{m} p_{ij} = 1 \qquad i = 1, 2, \ldots m \qquad (7)$$

The transition probabilities are usually derived from a sample of transitions occurring during some time interval. Maximum likelihood estimates of the transition probabilities (Anderson and Goodman 1957) are, then:

$$\hat{p}_{ij} = n_{ij} \Big/ \sum_{j=1}^{n} n_{ij} \qquad (8)$$

where p_{ij} is as in equation 7 and n_{ij} is the number of transitions from state i to state j. Second, it often is assumed that the Markov chain is a first-order process, which means that the probability of a particular set of outcomes depends only on the current distribution among states and the transition probabilities, so that history has no effect. An explicit test of this assumption, and tests to determine the order in general, require transition estimates from two or more time intervals (Anderson and Goodman 1957; Robinson 1978). Third, is the assumption of stationarity of transition probabilities over time. A test of this assumption also requires estimates from two or more time intervals (Anderson and Goodman 1957). Markov chain models can still be used when these assumptions are not met, as I will discuss below.

Simple first-order stationary Markov chains have been used in a variety of fields. They have been used, for example, to model changes in animal populations (Usher and Parr 1977), succession as a plant-plant replacement process (Anderson 1966; Horn 1975), changes in diameter distributions of forest trees (e.g., Roberts and Hruska 1986), and migration of people (e.g., Brown 1970). But, although the methods employed in these studies are comparable, more relevant to landscape modelling are applications in modelling changes in vegetation types and land use.

Markov chains have been used to model changes in vegetation types on a variety of spatial scales. Changes on small areas of less than a few hectares (Austin 1980; Austin and Belbin 1981; Kachi *et al.* 1986) or on a single small plot (Lough *et al.* 1987) have been modelled. There are also many studies of changes in vegetation on areas of less than a few hundred hectares, based upon changes in scattered plots or transects within the area (e.g., Williams *et al.* 1969; Stephens and Waggoner 1970; Noordwijk-Puijk *et al.* 1979; Hobbs 1983; Gibson *et al.* 1983; Lippe *et al.* 1985; Rejmanek *et al.* 1987). Some of these were conducted on areas approaching the landscape scale, but even when very large areas are considered, using small plots to estimate regional changes (e.g., Bellefleur 1981) obscures interactions between contiguous land areas that are an important aspect of the landscape ecological approach.

Explicit consideration of landscape-scale changes is common in studies of changes in land use in human-modified land areas, and changes in landscapes in more ‘natural’ areas. The literature on these two subjects is often separated in spite of similarities in method and approach. Changes in a wide variety of landscapes, from predominantly urban (e.g., Bourne 1971) to wilderness landscapes (e.g., Marsden 1983; Hall *et al.* 1987; Baker, in press) have been modelled (Table 2). All of these models are first-order Markov chain models, though the order of the chain has only been formally tested in a few instances (Bell 1974; Robinson 1978). Stationarity has usually also been assumed, but in the few instances where it has been tested (Bourne 1971; Bell 1974; Bell and Hinojosa 1977) the transitions were not, in fact, stationary. Nonstationary transitions have also been found for Markov chain models of vegetation dynamics on smaller land areas (Binkley 1980; Austin and Belbin 1981; Gibson *et al.* 1983; Lippe *et al.* 1985; Rejmanek *et al.* 1987). But, even if transitions are in reality nonstationary, stationarity can be assumed as a heuristic device, to provide answers to ‘what if’ kinds of questions (Baker, in press). Moreover, nonstationarity alone does not preclude the use of a Markov chain approach.

Table 2. Markov chain models of change in land use and change in natural landscapes.

Author	States	Location
Land use		
Drewett 1969	10 levels of urbanization	Reading
Bourne 1971	10 levels of urban land use	Toronto
Bell 1974	6 land-use types	San Juan Is.
Bell and Hinojosa 1977	6 land-use types	San Juan Is.
Robinson 1978	4 urban-fringe land-use types	Akron, Ohio
Finn 1985	13 land-use types	Massachusetts
Jahan 1986	5 urban-fringe land-use types	Ontario cities
Natural landscapes		
Henderson and Wilkins 1975; Wilkins 1977	12 vegetation succession stages	Tasmania
Marsden 1983	650 forest age-classes and fires	Montana
Rejmanek *et al.* 1987	5 levels of marsh open water	Louisiana
Hall *et al.* 1987	5 vegetation succession stages	N. Minnesota
Jenkins and Wright 1987	6 vegetation succession stages	Montana river
Baker, in press	7 forest age classes	N. Minnesota

Markov chain models are often thoughtto have limited utility because they cannot accommodate higher-order effects, the influence of exogenous or endogenous variables, spatial effects, or heterogeneity (e.g., Barringer and Robinson 1981; Alig 1985). In fact, all of these can be, and have been modelled using Markov chains in other fields, and all could be incorporated into Markov chain models of landscape dynamics.

Higher-order effects can be modelled by redefining the state space so that the new states are defined by both present and preceding states (Massy *et al.* 1970). A second-order model would thus include m^2 states instead of the m states in a first-order model. Estimating the transitions for such a model would require substantial data, derived from observations during at least two time intervals following the initial observation.

The contribution of exogenous or endogenous variables to the transitions, and thus nonstationary transitions, can be modelled using two approaches. In the first approach, equation 6 is modified to be:

$$\mathbf{n}_{t+1} = \mathbf{P}[f(t)]\mathbf{n}_t \qquad (9)$$

so that

$$p_{ij} = b_1X_1 + b_2X_2 + \ldots + b_sX_s \qquad (10)$$

where p_{ij} is an element of matrix P, and $b_1, \ldots b_s$ are parameters relating the p_{ij} to the variables $X_1, \ldots X_s$. The variables $X_1, \ldots X_s$ may be exogenous variables (Ginsberg 1972b) or endogenous variables (Conlisk 1976). Such an approach has been taken in modelling the effects of temperature and density on mite population dynamics (Woolhouse and Harmsen 1987). In the case of landscape models, exogenous variables, such as socioeconomic factors or climatic conditions, and endogenous variables, such as landscape age-class structure or composition might be included. A variety of linear and nonlinear functions can be derived for equation 10. Such functions can be either theoretical or empirical. In two applications of this approach in landscape modelling (Henderson and Wilkins 1975; Marsden 1983), transitions between successional stages following fires were made a function of the fire frequency associated with each stage. Marsden (1983) also incorporated an exogenous variable, the probability of insect attack. Another approach to modelling nonstationarity is to switch between different stationary transition matrices (Harary *et al.* 1970; Horn 1975; Rejmanek *et al.* 1987). But, in this case, the process driving the switch must still be modelled.

It has been widely noted that transitions have a spatial dependence that is not accounted for in simple constant-transition Markov chains (Bell and Hinojosa 1977; Austin 1980; Austin and Belbin 1981; Usher 1981; Lippe *et al.* 1985). Models that explicitly account for this spatial dependence have been developed, and are discussed with other spatial models later in the paper.

Landscapes may be heterogenous, so that transitions of individual pixels in a particular state may vary, depending on the location of the pixel. It is impossible to correctly specify the order of a Markov chain for an aggregate of heterogenous pixels or, in the human realm, heterogenous individuals (Massy *et al.* 1970). Two remedies to this problem have been proposed, based on research on human migrations. The first is to disaggregate the population (or land area, in the case of landscape models) into homogenous subunits, with each subunit then having its own transition matrix (Ginsberg 1973). Ultimately, the population could be disaggregated to the level of individuals (pixels or grid cells in the landscape case) and individual transition matrices determined (Spilerman 1972). This approach will be discussed further in the spatial modelling section. The second approach is to explicitly model how the aggregate population (land area) is distributed over the transition values (Ginsberg 1973). One method of doing this is to assume the heterogeneity has a particular distribution, such as a beta distribution (Massy *et al.* 1970). Another method is to attempt to recover the underlying form of the distribution by using the behavior of the transition matrix over time to estimate the moments of the distribution, from which its form may be derived (Ginsberg 1973).

I have suggested here some possible extensions of simple first-order Markov chain models that might be used in landscape modelling. There are many other extensions. The interested reader may wish to explore further the literature in fields with long histories of applied Markov chain modelling. Modelling of migration (e.g., Pickles 1980) and buying behavior (e.g., Massy *et al.* 1970) are two areas with such histories.

Semi-Markov models:

There are a variety of landscape-scale phenomena for which the probability of transition from state i to state j during the time interval from t to t + 1 depends not only on i and j, but also how long the landscape feature (or pixel) has been in state i. Such phenomena are thus non-Markovian, and Markov chain models may be inappropriate. Examples of such phenomena might include forests whose fire probability increases with time since fire and urban structures more likely to be either torn down or, alternatively, preserved as historical features, as their age increases.

The effect of this varying 'duration-of-stay' or 'sojourn time' can be dealt with in two ways. The first way is to redefine the state space so that each previous "state includes several duration classes (e.g., McGinnis 1968). The resulting model may then be Markovian.'The second way (Ginsberg 1971, 1972a) is to use a semi-Markov model. In such a model movements among states are governed by a constant-transition Markov chain, with transition matrix $P = \{p_{ij}\}$, while sojourn times have distribution $F_{ij}(t)$, which depend only on i and j. In a Markov chain the sojourn times are constant, while in the semi-Markov model the distribution $F_{ij}(t)$ may take any form. The matrix $Q = p_{ij}*F_{ij}(t)$ is, then, a matrix of transition distributions for the semi-Markov process. Transition probabilities for the process and the expected distribution among states at any time t can be derived from the Q matrix (Ginsberg 1971; see Gilbert 1972 for a worked example). The p_{ij} of matrix P can be made functions of exogenous or endogenous variables, just as in Markov chain models (Ginsberg 1972b). Additional details of semi-Markov models are in these references and in most texts on stochastic processes (e.g., Bhat 1984).

Semi-Markov models have received little use in biogeography. A semi-Markov model of tropical forest succession has been developed (Acevedo 1981). I believe that the only application of semi-Markov models to landscape change is a model of the effects of fires on the Tasmanian landscape (Henderson and Wilkins 1975; Wilkins 1977). These authors experimented with two Gamma distributions for $F_{ij}(t)$, but found that the most realistic of the two did not produce results much different from those obtained by using a simpler Markov chain model. Nonetheless, semi-Markov models my have potential for improved modelling of certain landscape change processes.

Projection models:
An extensive literature has arisen in the modelling of biological populations using deterministic projection models (e.g., Leslie 1945; Lefkovitch 1965; Usher 1966), and derivatives of such models have been used in landscape modelling. These deterministic projection models again have the general form of equation 6, but the P matrix may be different from that used in Markov chain models.

Researchers in many fields have preferred deterministic projection models over stochastic models, such as Markov chains, in part because the transition rates being modelled may not always be true probabilities (Rees 1986). Moreover, there are few advantages and some disadvantages in meeting the more stringent assumptions of the Markov framework. The mathematics of fully-developed projection models may require the skills of an accountant (Rees and Wilson 1977), but are simpler conceptually than are corresponding stochastic models. In a utilitarian sense, there may be little real difference in projection results using the two approaches, as nearly equivalent models can be, and have been developed. This is particularly true, since many of the limitations thought to be inherent in the Markov chain framework have been overcome, as was discussed earlier in the paper. The choice between the two modelling frameworks appears to be based in part on the tradition in a particular discipline.

The Leslie model and its derivatives, as well as more generic projection models, have long been used to model plant and animal, as well as human population dynamics. While the Leslie models have explicit birth functions designed for biological populations, it is a simple matter to adapt extensions of these models and other projection models for landscape use. Developments in deterministic projection modelling are too extensive to review in detail here (see Rees and Wilson 1977; Usher 1972, 1981; Rees 1986). But, there are few limits in these models in incorporating higher-order effects (Leslie 1959), nonstationary transitions and effects of endogenous or exogenous variables (e.g., Pennycuick *et al.* 1968; Solbrig *et al.* 1988), harvesting (Doubleday 1975), spatial effects (Rees and Wilson 1977), and heterogeneity. Fully elaborated models may bear little resemblance to the original Leslie model (e.g., Ek 1974). As an example of how extensive these models can become, the Census Bureau uses a model with '142 economic equations for 51 geographic units, or over 7000 endogenous equations with over 10,000 endogenous and exogenous variables, . . . 26,000 migration flows, and . . . over 500 age-sex groups' (Long and McMillen 1987, p. 170).

Projection models for land use and landscape change are, by comparison, much less developed. Simple first-order stationary projection models with no exogenous or endogenous variables, or other effects, have been used to model the dynamics of vegetation types and the effects of human land uses in the mountains of France (Godron and Lepart 1975; Debussche *et al.* 1977). A similar model has been applied to project the percentages of land in five different forest types on industrial forest land in the southeastern United States (Alig 1985; Alig and Wyant 1985).

Spatial landscape models

In'many senses spatial models embody the essence of the landscape ecological approach. In contrast to distributional models, spatial models use the location and configuration of landscape elements in projecting change, and can thus explicitly output maps of these changing spatial configurations. In developing a spatial model one must choose (1) raster or vector format; (2) variables to include in the model; (3) pixel size in raster-based models or resolution in vector-based models, and (4) the change algorithm.

Data storage and representation can be in either a raster or vector format. Many spatial models use a two-dimensional raster-format of grid cells or pixels (Fig. lc) like that in many geographical information systems, although a vector-based model can also be used (Burrough 1986). In raster-format models, each pixel represents a rectangular location in space, while in vector-based models the locations of entities (e.g., landscape elements) are specified by x and y coordinates of points, lines, and polygons outlining the entity. Models may be univariate, which can be conceptualized as a single plane of pixels (vectors) or multivariate, with multiple planes of pixels (vectors). Pixel values in a single or several planes can be classified into states, and thus distributional output can be derived from a single or several planes of pixel values. In vector-based models, landscape elements are the states, and these must be defined *a priori.* One advantage of a pixel-based spatial model is that states need not be defined at all, or can be defined as needed.

Because landscape elements have characteristic sizes, choice of variables and choice of pixel size are linked. Errors that arise in 'rasterizing' a landscape may be substantial (Burrough 1986), particularly if pixels are larger than the landscape elements of interest. Clearly, small pixel sizes provide more accurate representations of boundaries and areas of landscape elements, but using small pixels also increases the data-handling requirements. Similarly, polygon outlines can be digitized as a series of vectors, with the number of vectors determining the accuracy of the outline. Again, a large number of vectors means greater accuracy, but also greater data-handling requirements.

Two basic kinds of spatial models are (1) mosaic models, in which change in a mosaic of individual subareas in modelled and (2) element models, in which change in individual landscape elements is modelled.

Mosaic models

In many cases it is convenient to divide the landscape into (1) a two-dimensional grid or raster of equal-area square or rectangular pixels or grid-cells, or (2) a mosaic of equal- or unequal-area polygonal subareas. I will refer to the subareas in either case by the generic term 'cells' and the collection of cells by the generic term 'mosaic', recognizing that in practice most mosaic models will use a raster of grid-cells, and can be called 'grid-cell' models, a subset of 'mosaic' models. In the simplest univariate case, with a single plane of cells, each cell has a single value (continuous state space) or is in a single state (discrete state space). Multivariate models, with multiple planes of cells, are also possible. In any event, the location, configuration, shape, and size of landscape elements are not modelled explicitly, but are built up from the configuration of cells of the same value, or in the same state, on the output map.

The models can thus be conceptualized as a mosaic of submodels (Fig. 2), with each submodel a whole landscape model or distributional landscape model in itself. Although the submodels illustrated in Fig. 2 are grid-cell models using discrete mathematics, other submodels could be used, including differential equation or matrix models of a variety of forms (e.g., equations 1–6, 8 and 9). The models are thus flexible enough to allow incorporation of higher-order effects, effects of endogenous or exogenous variables, variable sojourn times, and a variety of other effects.

Spatial models, such as these, are obviously particularly appropriate for modelling spatial dependence, which is a common feature of many landscapes. Landsat data, for example, which are now an important source of data for landscape change modelling, tend to have spatial autocorrelations that can be described by a (1 ,0,1) autoregressive-integrated-moving average process (Craig and Labovitz 1980). This autocorrelation is derived from both equipment sources and geophysical variation, and this latter source may vary both temporally and spatially in remotely sensed data. The spatial dependence may thus be complex, but if it could be specified, then transitions could be modelled as endogenous functions, using equations 9 and 10, with the function specified for some fixed or perhaps varying 'window' around each grid cell or pixel. Turner (1987) experimented with this approach, and found that four-neighbor windows did better than eight-neighbor windows at replicating actual land-use transitions. Additional research is needed on the patterns of spatial dependence in landscapes, as well as on functional relationships with transitions. Ideas for indices of spatial dependence in landscapes could be borrowed from comparable, but smaller-scale indices designed to measure the growth-dependence of individual plants on the configuration of surrounding plants (reviewed by Johnson 1973 and Alemdag 1978).

Spatial models obviously also may explicitly account for spatial heterogeneity in the landscape. One approach to this problem might be to disaggregate the landscape into homogenous subareas, and then model changes on these individual polygonal subareas. The overall response of the landscape would then be the sum of the responses in the subareas. This approach has not been used in landscape modelling, but a comparable disaggregation approach has been suggested as one means to deal with heterogeneity in human populations (Ginsberg 1973).

Two kinds of mosaic models can be distinguished. In whole mosaic models, the submodel in each cell is a whole landscape model. In distributional mosaic models, the submodel in each cell is a distributional landscape model.

Whole mosaic models:

While the submodel in each cell of a whole mosaic model is a whole landscape model, the essential distinguishing feature of these models is that each cell has only one value (continuous state-space) or is in only one state (discrete state-space). The landscape as a whole may contain cells in several states. Often, these models are simple two-state 'checkerboard' models (e.g., occupied-not occupied, land-water, forest-clearcut), which, because of their conceptual simplicity, have substantial utility in certain kinds of simulation study.

Whole mosaic models are not very developed, perhaps because distributional mosaic models are nearly as easy to develop and use. In what was apparently the first application, Browder et al. (1985) simulated, using a grid-cell model, the spatial configuration of land and water, and the length of the land-water interface in disintegrating marshes in Louisiana. The disintegration function in the model included the effect of surrounding pixels and the configuration of the marsh in relation to exogenous environment. Franklin and Forman (1987) developed hypothetical grid-cell models of changes in the proportion of forest and clearcut patches under several levels of cutting and several types of cutting system. Turner (1987) used a grid-cell algorithm incorporating four- and eight-neighbor influences to simulate changes in five land-use types in a piedmont county in Georiga. Wilkie and Finn (1988) used a 2,000 cell grid-cell model to simulate land-clearing and secondary forest succession for four

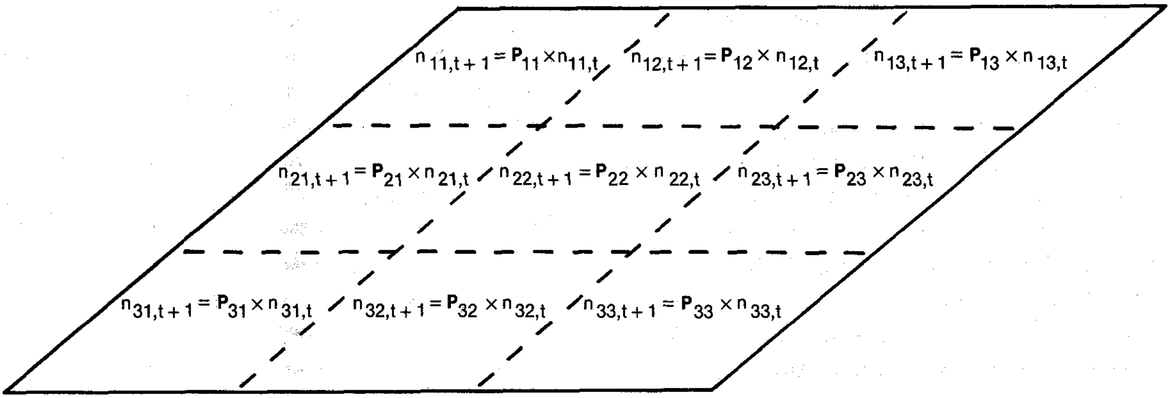

Fig. 2. Example of a mosaic model for a 3 *x* 3 grid. Change in each cell is modelled by separate equations, $n_{ij,\,t+1} = P_{ij} * n_{ij,\,t}$, where $n_{ij,\,t}$ is a column vector, $n = (n_1 \ldots n_m)$ whose elements are the fraction of land area in each of m states at time t in the grid cell in row i and column j, and P_{ij} is an m X m matrix, whose elements, p_{ij}, incorporate the birth, death, and change rates of each state in the grid cell in row i and column j during the time interval from t to t + 1.

‘shifting horticulturalist’ villages in the rain forests of Zaire. These authors explored the effects of population growth and changes in land-tenure on landscape pattern.

A special type of whole mosaic model has been proposed as a ‘neutral’ model for landscape pattern studies (Gardner *et al.* 1987). The neutral models are randomly-generated mosaics of occupied or not-occupied cells, whose generation and analysis is based upon percolation theory (Stauffer 1985). The random patterns can be used as ‘null’ models to test hypotheses about landscape pattern, but Turner *et al.* (1988) also used them to simulate the effects of landscape pattern on the spread of disturbance.

Distributional mosaic models:

In these models each cell has a distributional landscape submodel, which can be univariate or multivariate, use continuous or discrete mathematics, and include a variety of processes and effects. Any of the distributional landscape models discussed in this paper could serve as a submodel in a mosaic model, but all would benefit from some modification to incorporate interactions between cells, which is facilitated by the spatial modelling framework.

Certainly among the most complex mosaic models are the general circulation models of the atmosphere (Simmons and Bengtsson 1984). These models use a continuous state-space for as many as two dozen variables, a series of differential equations, and a global grid of points, generally 2-5” of latitude or longitude apart. These models often have explicit links to exogenous variables, including ocean conditions and terrestrial surface conditions, such as topography and albedo. An increasing appreciation of the importance of land-surface conditions (e.g., Mintz 1984) has resulted in further development of models of biosphere-atmosphere interactions (Sellers *et al.* 1986, Wilson *et al.* 1987), though currently these models are non-interactive, including only the effect of biosphere on the atmosphere, and not the reverse. Moreover, the biosphere submodels lack direct integration of landscape-level processes, and are driven instead by static or periodically-updated archival data on land cover (Thomas and Henderson-Sellers 1987). But, accurate projections of future land-surface conditions will require direct modelling of landscape processes, particularly in view of the apparent dependence of many landscape-altering disturbance regimes (e.g., fires, floods, wind) on climatic conditions (e.g., Hubbard 1980). This atmosphere-biosphere link at the landscape scale is a particularly fertile area for future landscape modelling research.

Aside from these very complex differential equation models, deterministic projection models are also well-developed, and take a variety of forms. The most extensive literature and most elaborate models of this type are in the area of multi-regional human population projection models (Rogers 1975, 1985; Rees and Wilson 1977; Woods and Rees 1986; Long and McMillen 1987). Fully developed population models may incorporate thousands of endogenous and exogenous variables in tens of geographic units (e.g., Long and McMillen 1987). Comparable, but much less complex spatial projection models have been applied in modelling other animal and plant populations (e.g., Usher and Williamson 1970; Cuff and Hardman 1980; Hobbs and Hobbs 1987) at small spatial scales. As will be discussed below, these spatial population models can also be applied at the landscape scale.

Building on multi-regional population models there is also a very extensive spatial modelling literature relating to urban systems (reviewed by Bertuglia *et al.* 1987). Based in large part on urban 'spatial interaction' models pioneered by Lowry (1964) and Wilson (1974), these models now typically include submodels for population growth, residential location, workplace location, the development of infrastructure and transport systems, job location, location of services, and economic development (e.g.,, Wilson 1987). Models such as these, modified for rural settings, could help in understanding how landscape structure develops in human-modified landscapes.

A major impetus for the development of landscape-level models of natural systems came from the realization that spatial environmental heterogeneity results in spatial variation in the population dynamics of plants and animals (e.g., Smith 1980). Some authors (Shugart and Noble 1981; Dale and Gardner 1987), for example, have used differential equation distributional models, modified from the original JABOWA model (Botkin *et al.* 1972), to simulate landscape-level spatial variation in forest growth and disturbance effects. But, the JABOWA model and its derivatives were designed for small plots (typically 0.1 ha), and the landscape-level simulations involve simply altering the boundary conditions to replicate spatial variation in the environment at distinct locations over a region. Pearlstine *et al.* (1985) used this approach on a smaller land area, but even on small areas such approaches omit plot-to-plot (cell-to-cell) interactions that are fundamental to landscape ecological research.

Models like the JABOWA model could be used as submodels in a spatially contiguous mosaic, but even at a minimum landscape scale (at least a few km^2), several hundred to several thousand JABOWA submodels would need to be linked, and the models modified to incorporate spatial interactions. This linkage has been proposed, but not implemented (Botkin *et al.* 1985), but although it would be possible, the amount of detail in each submodel means that substantial computer time would be needed to run such models. For larger-scale landscape processes, such as fires in northern temperate forests, which may affect hundreds of km”, the cell size of these models may be much too small for practical use. Nonetheless, the JABOWA model and its derivatives do incorporate the influence of exogenous and endogenous variables, natural disturbances, and species-specific responses to environmental change-all desirable features for many landscape modelling questions.

Several models have been applied at the landscape scale, utilizing larger cell sizes, simpler submodels, and with explicit treatment of cell-to-cell interactions. A set of distributional projection submodels has been linked in a mosaic model of the changing age-structure of small mammals in adjoining woodlots in an agricultural landscape (Fahrig *et al.* 1983; Lefkovitch and Fahrig 1985; Fahrig and Merriam 1985). This model is comparable to the multi-regional human population projection models discussed above. Similarly, but on a larger spatial scale, the distribution of forest patches of different ages in a fire-prone forest region has been modelled using a mosaic of Markov chain submodels (Baker, in press). Both of these matrix models incorporated non-constant transitions by linking a temporal series of different matrices, but neither explicitly developed a functional link with exogenous or endogenous variables.

In one of the most interesting landscape-modelling approaches to date, Sklar *et al.* (1985) modelled multivariate changes in the environment and expected changes in habitat conditions in a Louisiana coastal marsh, using a mosaic model containing differential equation submodels. These authors used a grid of 1 km^2 cells, and allowed for external forcing by river and tidal flows, as well as cell-to-cell exchanges of water and materials. Changes in water volume, salinity, and sediments were used to predict changes in marsh habitats. Sklar and Constanza (1986) then tested their modelling approach by predicting 1978 habitat distributions over a mosaic of 2479 cells from 1956 distributions and weekly data on changes in environment.

Similarly comprehensive mosaic models of landscape change have been developed, for terrestrial landscapes, by Kessell and his coworkers (Kessell 1976, 1977, 1979a, 1979b; Kessell and Cattelino 1978; Potter *et al.* 1979; Potter and Kessell 1980; Kessell *et al.* 1984). These models have been applied in the coniferous forests of Glacier National Park, Montana (Kesselll976, 1977, 1979a), in the chaparral of southern California (Kessell and Cattelino 1978), and in a variety of ecosystems in Australian parks and nature reserves (Kessell and Good 1982; Kessell *et al.* 1984). A very general version of the models, called FORPLAN, has also been developed and applied (Potter *et al.* 1979; Potter and Kessell 1980).

All of Kessell *et al.* 's models operate from a grid-cell based resource inventory, stored and manipulated, in the most recent versions (Kessell *et al.* 1984), as part of a geographical information system (GIS). Vegetation and fuels data are estimated for each grid-cell from its environmental location by using gradient models that relate species composition and fuel levels to environment location. A major strength of Kessell *et al.* 's models is their explicit modelling of fire behavior and post-fire succession on the landscape in relation to the landscape data in the GIS. The fire behavior model has usually been Rothermel's (1972), and it has been linked explicitly, in some cases, with a weather model (e.g., Kessell 1979a). The post-fire succession models have been deterministic models, based on habitat types (Kessell 1979a) or life-history traits of each species (e.g., Cattelino *et al.* 1979). Separate models have also been developed, on a more limited basis, for predicting the response of large and small mammals to changes in landscape structure (Kessell 1979a; Potter and Kessell 1980; Kessell *et al.* 1984).

In some senses the strength of Kessell *et al.*'s models is the simplicity of the submodels, which allows very large arrays of small cells (as small as 0.01 ha in the Glacier National Park model) to be modelled with reasonable computer time. Kessell (1979a, 1979b) has some useful comments on the tradeoffs between resolution, usefulness, and cost. Useful additions to these models would be explicit modelling of plant dispersal (Kessell 1979a), the effects of other kinds of disturbances (e.g., insect attacks), and species-specific response to climate change. Certainly, there are an almost unlimited number of other subroutines that would be desirable for specific modelling purposes, but, inevitably, models of this complexity are limited by fiscal constraints, computer capabilities, available data, and scientific knowledge. Kessell *et al.*'s models are exemplary in incorporating real-world environmental and vegetational data with explicit modelling of landscape-scale natural disturbances in a GIS framework useful for resource managers.

Finally, a relatively unexplored modelling area, in terms of landscape dynamics is the possibility of using space-time autoregressive integrated moving-average (STARIMA) models (e.g., Pfeifer and Deutsch 1980). Such models have been applied in hydrologic forecasting (Deutsch and Ramos 1986), and have been suggested for use in, but not applied to landscape modelling (Barringer and Robinson 1981). One difficulty of such models may be that they do not allow direct incorporation of exogenous variables. But, STARIMA models may be valuable when coupled with other models. For example, a STARIMA model could be built for the autoregressive-moving average process in a temporal series of remotely-sensed images, with the residuals from this model subsequently used in a mosaic model.

Element models

Beginning in the 1960's and 1970's with forest trees (e.g., Bella 1971), a number of models have been developed that focus on the response of individual organisms to the spatial configuration, character, and density of neighbors. Such models, using a grid-cell or vector data base of mapped organism locations, often use spatial-influence, or competition-indices to quantify neighborhood effects (Bella 1971; Pacala and Silander 1985) and may also include dispersal functions (e.g., Weiner and Conte 1981) and a mechanism for lateral growth (e.g., Tongeren and Prentice 1986). Models of this type have been developed for trees (e.g., Bella 1971), annual plants (Weiner and Conte 1981; Pacala and Silander 1985), shrubs (Tongeren and Prentice 1986), and sessile marine organisms (Maguire and Porter 1977; Karlson.1981; Eston *et al.* 1986).

Such individual organism models are not landscape models, but they may have some relevance to modelling landscape change. First, it is possible that analogous individual landscape 'element' models could be developed, particularly in landscapes where ecosystem-to-ecosystem interactions are significant, or disturbance patches are the major landscape elements (Forman and Godron 1986). Although individual organism models have focused on the growth of the organism, individual landscape elements, which are landscape analogs of individual organisms, may not grow, or their growth may be of less interest than changes in other properties, such as their composition, age, or physical characteristics. It is unclear, however, just how such element models might be constructed and whether they would have advantages over mosaic models. In contrast, in landscapes with disturbance patches, individual patch models can be developed that describe the birth, growth, and mortality of patches. Such disturbance-patch models have been developed for fires in urban landscapes (Hirabayashi and Kasahara 1987) and in forested landscapes (Kessell 1979a), and for the oak-wilt disease in midwestern forests (Menges and Loucks 1984). Second, the overall character of ecosystems, which constitute most landscape elements in natural landscapes, is determined in part by organism-to-organism interactions within the ecosystem. The deciduous forest landscape element in eastern United States landscapes, for example, was changed dramatically by the decline of the chestnut (Mackey and Sivec 1973). As another example, the spread of patch-creating insect attacks and diseases may depend upon tree-to-tree spatial relations that can be modelled (e.g., Menges and Loucks 1984). Where biotic interactions strongly control the character of landscape elements or create patches, spatial individual organism or individual patch models may be appropriate as submodels in a mosaic model. Obviously, such models may require immense quantities of data and substantial computer resources, and could, as a result, be impractical for many landscapes.

Discussion

There is no perfect landscape change model, but models have been developed to serve a variety of purposes. Whole landscape models, which focus on aggregate phenomena of the landscape as a whole, have not been developed, perhaps because distributional and spatial data are usually desired. Certainly the most widely used models of landscape change have been distributional models, which are models whose output is the percentage of land area in a set of classes or element types. Distributional models are popular largely because of their simplicity and utility, in addition to a well-established history of use. Spatial models, models that focus on the location and configuration of landscape elements, have not been widely developed and used, in spite of the necessity of spatial data for answering many landscape ecological questions. This lack of development is probably because the data and computational requirements have, in the past, been prohibitive.

Data and computational limits are becoming less significant, at least for some purposes, due to advances in remote sensing for change detection (e.g., Price 1986) and in the incorporation of remotely-sensed data and auxiliary data into geographical information systems (Burrough 1986). But, although there are substantial data on how much and what kind of landscape change has occurred, remote sensing change-detection studies seldom include explicit modelling of change processes. Similarly, for modelling important landscape ecological processes, the GIS data management framework is increasingly essential, and is receiving substantial research attention, but spatial models of landscape processes using a GIS have only been developed in a few cases. It appears, then, that the rate of development of remote sensing and GIS technology greatly exceeds the rate of development of models of landscape change.

The most important present limit to the development of better models of landscape change may be a lack of knowledge of how and why the landscape changes, and how to incorporate such knowledge in useful models, rather than a lack of technology to develop and operate models of landscape change. I suggest four possible approaches to alleviate this problem.

First, multivariate analyses of possible exogenous and endogenous contributions to empirically-derived (perhaps from historical sequences of aerial photographs) rates of landscape change may help to refine our understanding of the causes of landscape change (e.g., Alig 1986). This may be particularly true if such studies employ carefully designed 'natural experiments' (Diamond 1986) to limit possible outcomes. Nonetheless, multivariate analysis is no panacea, and has its own limits (e.g., Green 1979). Modelling itself is another route to identification of key variables controlling landscape processes.

Second, modelling of individual , landscape change processes could lead to general modules that could be exchanged among models. A good example of this is Rothermal's (1972) model of fire spread. Some kinds of landscape change process, such as those driven by certain natural disturbances, are more amenable to a modular approach than others. Nonetheless, even such processes as economically-driven changes in farm woodlot sizes could conceivably be modelled in this way.

Third, careful attention to the scale of the models may be important. Landscape processes operate on a variety of spatial and temporal scales (Meentemeyer and Box 1987; Baker, in press), but spatial models typically use a single grid-cell size or vector resolution. Models, like plot samples, thus have a limited ability to capture multiscale processes, so that modelling results need to be explicitly interpreted in view of model scale. Complicating the matter is the presence of many processes operating at different scales in the same landscape. Explicit study of the effects of scale on model behavior may help (e.g., Baker, in press).

Finally, a variety of processes, that have been studied on small areas, have important ramifications on the landscape scale that have not been well-studied. A good example of this is the dieback process in certain forests (Mueller-Dombois 1987). Whether such dieback is due to anthropogenic causes, such as air pollution and the introduction of exotic pathogens, or 'cohort senescence' (Mueller-Dombois 1987), large-scale diebacks alter many aspects of the landscape, including its diversity, age-class structure and patch structure. These alterations, while important in themselves, also have important ramifications for the spread of subsequent disturbances. Thus, some increase in understanding landscape processes might come from 'scaling-up' from more detailed studies that have already been completed on smaller land areas.

Landscape change modelling *is* also partly limited by available data. Aerial photography is available for many parts of the world only from the 1930's and 1940's, and satellite data are limited to the period since the 1970's (Lillesand and Kiefer 1979). These data sources thus are of little value for studying longer-term landscape change processes. Longer-term studies may require use of a variety of historical data sources (e.g., Vale 1982), including maps, historical accounts, and original land survey records, among others. A good example of this multi-source approach is Iverson and Risser's (1987) combined analysis, using a GIS, of original land survey records, U.S. Forest Service inventory data, and Landsat data. Very long-term studies of landscape change may be facilitated by analysis of pollen or macrofossils in a network of close proximity sites (e.g., Dodson et al. 1986).

Finally, temporal data limits are, in some cases, less important than the limited availability of unaltered landscapes needed for some kinds of contemporary process studies. The important link between climatic change and changes in disturbance regimes in natural landscapes, for example, is becoming increasingly difficult to study in many areas as forested landscapes are fragmented, and as their disturbance regimes come under increasing human control. Moreover, many large nature reserves were not designed to perpetuate landscape-level processes and structures (Baker, in press), or retain effects of previously-altered disturbance regimes, and thus have limited value for some kinds of studies. I have argued in this paper that models of landscape change may be the only means we have to understand some landscape processes, but useful models cannot be developed without appropriate empirical data. An important prerequisite to developing useful models of landscape change is that landscape processes be perpetuated in some of the remaining relatively unaltered landscapes, and that these processes be studied over time.

Acknowledgments

This work was supported in part by a grant from the National Science Foundation (SES-8601079). I thank the Department of Geography at the University of Hawaii at Manoa for providing office space and assistance during the writing. Some of the ideas in this paper were formulated while I was a research assistant with Robert K. Peet at the University of North Carolina.

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