State and transition models for rangelands.
5. The use of state and transition models for predicting vegetation change in rangelands

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Abstract

State and transition models are similar in nature to Markov models which have been applied in the field of ecology since the 1960s. Variations to true Markov processes that have been used in ecology include second-order, discrete Markov and semi-Markov processes and continuous-time Markov processes.

The uses of discrete-time and continuous-time Markov models are discussed. Three examples of how vegetation dynamics can be simulated by Markov models are presented. The way in which altered climate may alter the course of vegetation change is described for *Prosopis* savanna in south Texas (USA). Chemical control strategies for *Acacia nilotica* management in north-western Queensland were compared by incorporating a Markov model into a simulation model which included the effect of woody vegetation on pasture growth, as well as prediction of liveweight gain of cattle. The impact of altering grazing pressure on pasture composition change is presented using a continuous-time Markov model of pastures in tropical woodlands of northern Australia.

These examples indicate how state and transition models can be used. State and transition models may be used for prediction and analysis in addition to aiding communication. The integration of Markov models into process models shows promise for devising complex management models for rangelands.

Introduction

State and transition models are similar in structure to models based on Markov processes (named after the work of A.A. Markov in the early 1900s). The use of Markov models in biology has dated from the 1960s (Anderson 1966), their appeal being that they are the most tractable form of stochastic mathematical models. However, Hill (1982) dismissed the use of Markov models in ecology because "the world is not that neat". The inherent problems of transition matrix models are well known (see van Hulst 1979; Usher 1979). Nevertheless, this approach has provided insight into vegetation dynamics when other approaches were not possible (Enright and Ogden 1979; Lippe *et al.* 1985). Thus, the use of Markov models can be justified, especially when enhancements to the simple Markov process are included to address the situations where the assumptions of Markov processes are violated.

There are 2 forms of Markov models — one is based on discrete-time and the other on continuous-time theories. Two related mathematical models are Leslie matrix models and semi-Markov models. All variants will be considered in this paper, together with examples of the use of Markov models to describe woody plant dynamics and management, and pasture dynamics in tropical woodlands.

Model types

Markov models — general characteristics

A simple Markov model has 3 requirements: (1) a finite number of discrete, identifiable states; (2) the transition probabilities; and (3) the initial conditions. From these, the state of the system at any future time can be determined.

A Markov chain describes a system which moves from one state to another in a stochastic manner. The transition probabilities depend only

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on the immediately preceding state and not on any other state of the system. This system can be expressed in matrix notation as:

$$X_{t+1} = P. X_t \qquad \text{Eq 1}$$

where X_{t+1} and X_t are vectors whose elements are proportions of the system in that state, and P is a square matrix of transition probabilities i.e. probability of moving from each state to all other states during one time period.

Two major assumptions of Markov models are that: (1) the transition probabilities between states are constant over time (stationarity); and (2) the transition probabilities depend on the preceding state only and are independent of previous transitions (the Markov property holds). This definition means that Markov processes are first-order processes; however, higher-order processes are sometimes referred to as Markov processes.

Markov models — discrete-time

The transition matrix is composed of probabilities of moving to state i from state j (p_{ij}). In models of vegetation change, these probabilities represent the proportion of the area in state i changing to state j during one time step.

First-order, linear, stationary processes (Equation 1) reach a steady state vector after a large number of time steps. This state vector is independent of the starting conditions provided the sum of the column elements in the matrix P sum to 1. A vector X_{stable} exists such that:

$$X_{stable} = P. X_{stable} \qquad \text{Eq 2}$$

In relation to ecological succession, X_{stable} has been interpreted as the composition of the climax community. Mathematically, this vector is the right eigenvector of P. The largest eigenvalue of the matrix is 1, indicating that there is no net change to the sum of the state vector.

The assumption of stationarity is seldom valid in ecological studies because climate and disturbance are essentially stochastic processes (Usher 1979; Lippe *et al.* 1985). To model non-stationary systems, several transition matrices may be used in a model, with each matrix being appropriate for a particular set of environmental conditions (e.g. periods of contrasting annual rainfall as used by Burrows *et al.* (1985)). Another approach is to observe the system for a number of time steps and develop a "mean" transition matrix (Huenneke and Marks 1987). As in any averaging method, there is a loss of information whenever this method is used. The use of multiple transition

matrices makes it impossible to obtain an analytical solution for the composition of the stable state vector. Simulation modelling can be used to estimate the state vector for any particular scenario. Finding the mean of many simulations can give a pseudo-stable state vector.

The Markov property does not hold when past history influences future changes. Such a case may exist in shrub invasion of grasslands. The probability of transition from a grassland to a shrub-covered state may be influenced by whether or not that area had been covered by shrubs at any previous stage. Soil seed reserves and possible soil modifications caused by the presence of shrubs may influence the probability of shrubs recolonising the grassland. These cases are sometimes referred to as higher-order Markov processes.

Higher-order Markov models can simulate situations where previous conditions influence rates of transition, but there are often insufficient data on which to set model parameters and to validate a model. Conceptually, this is done by increasing the number of states. Thus, the states mentioned above would be grassland-grassland and shrubland-grassland — in both cases the present state is grassland but the previous state was different.

Spatial autocorrelations also violate the assumptions of Markov models because not all entities within one state have equal probability of moving between states. For example, an area of grassland would have a higher probability of becoming covered in woody plants if the area was surrounded by woodland than if it was surrounded by grassland. Thus, a model of vegetation change in patchy systems should take account of this spatial variability. Conceptually, the way this could be handled is similar to the case of higher-order Markov processes — new states would have to be defined (e.g. grassland surrounded by grassland; grassland surrounded by woodland), each with a different probability of transition. Separate simulations would be run for each different condition or situation.

In a true Markov process, the probability of each transition remains constant over time. However, there are many cases where the probabilities change according to the level of some resource or environmental characteristic, e.g. the probability that a grassland area will become covered by shrubs may be a function of the number of seeds produced within the management unit, giving a positive feedback — more trees produce more

seeds which in turn increases the number of trees. To allow for this, it is possible to make each transition a function rather than a constant. No stable state vector exists if this is done.

Markov model — continuous-time

An essential assumption of the discrete-time theory is that transitions occur at the end of a discrete, predefined time interval (the model time step). The transition probabilities are the likelihood of a one-step change i.e. change from one state through another to a third is not allowed. By contrast, continuous-time theory allows transitions at any instant in time. Instead of the transition being a probability of a one-step change, the value is a mean transition rate (i.e. number of transitions per unit time). Each transition has associated with it a mean transition rate (average number of transitions from state i to state j per unit time, given that the system was in state i).

As with the discrete-time theory, the system is assumed to exist in a number of defined states. Each state has a set of characteristics that differentiate that state from all others.

There are 4 basic assumptions for continuous-time Markov models (derived from Phillips *et al.* 1976):

(1) The system is first-order, i.e. the future state depends upon the current state of the system, and not on any previous state. This is the same as for the discrete-time version.

(2) The transition rates are constant over time (stationarity). This is the same as for the discrete-time version.

(3) The probability of transition from state i to state j occurring in time interval $\triangle t$ is proportional to $\triangle t$.

(4) The number of transitions in $\triangle t$ is either 1 or 0. As $\triangle t$ approaches zero, assumptions 3 and 4 become justified.

Some biological phenomena are continuous (e.g. photosynthesis and respiration) and so a continuous-time technique appears preferable to discrete-time approaches for modelling plant growth (Olson *et al.* 1985).

Semi-Markov processes

One of the major deficiencies of Markov models in vegetation change is that changes associated with plant aging and competitive interactions cannot be simulated because of the first-order nature of Markov chains (i.e. that any change to a

new state is affected only by the present state and not by any previous state). The semi-Markov process overcomes this difficulty.

The difference between a Markov process and a semi-Markov process is that, in the latter, transitions need not occur at all time steps. Rather there is a waiting time before a transition may occur, and this waiting time can be selected from a distribution that is specific to that state. At the end of the waiting time, the state may undergo a transition. Thus, the probabilities depend on initial and destination states as well as on the waiting time.

This process is discussed by Howard (1971), and an ecological example is given by Moore (1990). The mathematics are more complex than for simple Markov models, but have similar characteristics.

Leslie matrices

A Leslie matrix is a special case of a transition matrix. The first row contains the number of offspring from each parent in that class (usually an age or size class). The primary subdiagonal (the line immediately below the main diagonal) contains the probability of moving from one class to the next highest. If this matrix is multiplied by a vector containing the number of individuals in each class, then the resultant vector is the new class distribution (Leslie 1945). In animal populations, the rate of population increase can be determined from properties of the matrix. The rate of population growth is the largest positive eigenvalue of the matrix. There is usually not a stable state vector as the simulated population will be increasing or decreasing. However, a stable proportion of age/size classes is achieved after a large number of time steps and the composition is independent of the starting conditions. Leslie matrix models are usually applied to animal populations but the approach has been used to predict stable age class distributions in forests (Usher 1972).

It can be argued that the use of Leslie matrices is preferable to using differential equations as reproduction is pulsed, rather than continuous as implied by differential equations (e.g. Malanson 1984). The time step used can be chosen to match the required feature of the data. For animals, it could be the inter-generational time span; for annual plants the time between germination events; and for trees the time to establishment of juveniles.

Case studies

In the following section, 3 examples of analysing situations that are presented as state and transition models are presented. The first 2 cases have no system diagrams to represent them, as all transitions between all states are possible in both systems. Both of these cases contain discrete-time Markov models. The third case is a continuous-time model representing pasture composition change in northern Australian woodlands.

Case 1 — Predicting changes in Prosopis cover in south Texas grassland

Introduction. The plains of southern Texas potentially support an *Andropogon-Setaria-Prosopis-Acacia* savanna. However, the region is now dominated by a complex vegetation association of thorny shrubs. The change in community structure from grassland to thorn woodland began in the mid-1800s and has been described by Archer *et al.* (1988) and Scanlan and Archer (1991).

Probabilities of vegetation transition were used to explore the extent of changes in future landscape composition given a range of climatic scenarios. The probability of change between various herbaceous and woody vegetation states was determined from aerial photographs bracketing two periods of contrasting annual rainfall. The resulting transition matrices were then used to project future vegetation states under various annual rainfall regimes.

Method. Vegetation states were defined on the basis of work done by Archer *et al.* (1988) and are shown in Table 1. Probabilities of transition from one vegetation state to another were determined from grids superimposed on aerial photographs taken in 1941, 1960 and 1983. A grid of cells (each cell representing 400m^2) was superimposed on 1941 photographs and the dominant class of vegetation noted for each cell. The same grids were then placed on 1960 and 1983 photographs to coincide with placement on 1941 photographs and states of each cell reassessed. From these data, the proportion of each vegetation class that changed to another class was calculated. This was done for each period (1941-1960 and 1960-1983). The 1941 landscape consisted of herbaceous zones (6% of cells), woodland (50% of cells) and savanna parkland (44% of cells with grass–woody plant mixtures).

During 1941–1960 there were several years of severe drought, whereas rainfall between 1960 and 1983 was generally normal to above-normal. The transition matrices developed for the 1941–1960 and 1960–1983 periods are subsequently referred to as DRY and WET, respectively. The matrices for the 2 periods were significantly different ($X^2 = 697$; $P<0.001$) according to the method of Anderson and Goodman (1957).

Transition matrix models were developed to simulate changes in frequency distribution of the 7 vegetation classes described in Table 1. The models can be described as non-stationary Markov chains (Boyer 1979):

$$X_{t+1} = P_n \cdot X_t \qquad \text{Eq 3}$$

where X_t was the state vector at time t; P_n was one of the two 7 X 7 matrices (WET or DRY — see Table 2) of transition probabilities. The time step was 20 years. At each time step, a DRY or a WET transition matrix was chosen randomly.

Table 1. Vegetation classes used to define states in the south Texas *Prosopis* savanna (from Scanlan and Archer 1991).

State	Code	Characteristics
Herbaceous	H	Grasses *(Chloris cucullata, Bouteloua rigidiseta)* and forbs.
Pioneer clusters	P	Cluster area < 30m^2. *Prosopis* plant basal diameter < 10cm with 4–6 woody species in understorey.
Mature clusters	M	Cluster area 30–300m^2; typically 7–12 woody species; *Prosopis* basal diameter 10–30cm.
Coalesced clusters	C	Areas of extensive coalescence; discrete clusters not evident. Up to 15 woody species; numerous *Prosopis* plants with basal diameters >40cm.
	Cm	Coalesced cluster margins. This category was assigned where coalesced clusters (C) did not fully occupy a cell.
Woodland	W	Closed-canopy woodland; 19 woody species.
	Wm	Woodland margins. This category accounted for situations where woodlands (W) did not fully occupy a cell.

Table 2. Probabilities of vegetation change obtained from 3 sites over consecutive 20-year periods with contrasting patterns of precipitation (1941–1960=DRY; 1960–1983=WET; see Figure 2). Vegetation states are defined in Table 1 (from Scanlan and Archer 1991).

	DRY transitions, 1941–1960						
	W	Wm	C	Cm	M	P	H
W	0.873[1]	0.232	0.000	0.012	0.000	0.019	0.000
Wm	0.075	0.561	0.030	0.040	0.029	0.058	0.029
C	0.007	0.006	0.515	0.121	0.115	0.019	0.029
Cm	0.007	0.079	0.242	0.489	0.164	0.112	0.108
M	0.000	0.006	0.061	0.035	0.212	0.032	0.010
P	0.035	0.110	0.152	0.224	0.260	0.575	0.471
H	0.003	0.006	0.000	0.081	0.221	0.184	0.353
	WET transitions, 1960–1983						
	W	Wm	C	Cm	M	P	H
W	0.970[1]	0.497	0.373	0.132	0.044	0.088	0.019
Wm	0.027	0.429	0.090	0.126	0.065	0.121	0.086
C	0.003	0.000	0.328	0.137	0.196	0.036	0.019
Cm	0.000	0.042	0.119	0.432	0.522	0.170	0.216
M	0.000	0.000	0.030	0.058	0.109	0.104	0.111
P	0.000	0.011	0.060	0.095	0.065	0.447	0.475
H	0.000	0.021	0.000	0.021	0.000	0.036	0.074

[1] Probability of transition (p_{ij}) from state j (column) to state i (row) in the 20-year time step from time t to t+1.

Historical records indicated that the long-term P_{WET} was about 0.3–0.4 in the region.

A series of different precipitation scenarios was simulated such that the probability of using the WET transition matrix (P_{WET}) at each time step ranged from 0.0 (DRY always chosen) to 1.0 (WET always chosen). Data presented are means for 30 replicate simulations which yielded standard errors of ≤2% for the proportion of the landscape cells occupied by each vegetation class. No consistent changes in the proportion of the landscape occupied by vegetation classes were observed after 50 time steps and these proportions were used as the final (stable) state vector. As mentioned previously, there is no analytical solution possible to determine the stable state vector given this form of the model.

Results and Discussion. Simulations suggest the proportion of this landscape inhabited by woodlands will continue to increase provided $P_{WET} > 0.20$ (Table 3, Figure 1). The development of woodlands would occur at the expense of other vegetation classes, with only pioneer and coalesced cluster classes making sizeable (about 10%) contributions (Table 3 for $P_{WET} \leq 0.5$). Most of the predicted changes occurred within 200 years (10 time steps). At $P_{WET} = 0.20$, the predicted landscape vegetation composition was very similar to the present-day situation (data not shown).

The rate of succession to states of greater woody cover increased as P_{WET} increased. Simulations based on $P_{WET} > 0.2$ suggest the present landscape is unstable and will develop into a closed-canopy woodland within the next 180 years, assuming the processes operating between 1941–1983 continue (e.g. grazing by cattle and lack of fire).

Sensitivity analysis and simulations of vegetation changes prior to 1941 are presented in Scanlan and Archer (1991).

Conclusion. This analysis provides an example of how the lack of stationarity can be overcome. In this case, 2 matrices were chosen with differing probabilities. Any number of matrices could be used, provided there were sufficient data to develop them.

Case 2 — Comparing alternative management options

Introduction. Prickly acacia (*Acacia nilotica*) is a serious exotic weed of northern Australia, particularly the mitchell (*Astrebla* spp.) grasslands of Queensland. This shrub has spread rapidly since the 1970s with a combination of high rainfall years and a change from mainly sheep grazing to mixed sheep and cattle. About 7 million ha of mitchell grasslands now support at least some prickly acacia plants (Carter *et al.* 1989).
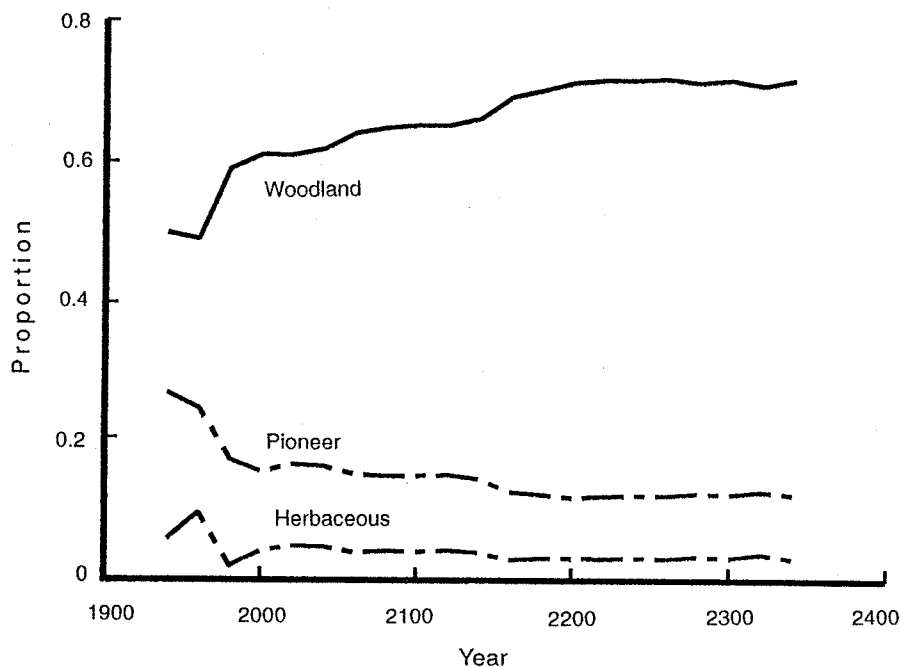
Figure 1. Mean predicted changes in the proportion of selected vegetation states (Table 1) in a *Prosopis* savanna parkland in southern Texas based on $P_{WET} = 0.4$. Data represent the mean of 30 simulations, with actual data plotted for 1941, 1960 and 1983. (Adapted from Scanlan and Archer 1991).

Table 3. Initial landscape status and predicted final state vectors (% after 50 time steps) for simulations under a series of rainfall regimes. State vectors represent the percentage of cells on the landscape dominated by each vegetation class (adapted from Scanlan and Archer 1991).

Vegetation state	Initial	P_{WET}[1]			
		0.00	0.33	0.50	1.0
Woodland	50[2]	37	69	77	98
Coalesced clusters	17	21	13	10	1
Mature clusters	5	3	2	1	0
Pioneer clusters	17	29	13	10	1
Herbaceous	2	11	3	3	0

[1] During simulations, the probability of selecting the WET transition was set to mimic different rainfall regimes.
[2] Initial condition was the 1983 state vector.

Many control methods exist. This study compared 2 possible control strategies in terms of long-term, accumulated cash flow from cattle grazing on prickly acacia-infested grasslands.

Method. Plant dynamics were monitored in permanent transects at 3 different sites in north Queensland (2 at Hughenden and 1 at Charters Towers). At each site, individual plants were allocated to one of 4 height classes: <0.5m, 0.5–1.5m, 1.5–4.0m and >4.0m at the first sampling time. The proportion of individuals remaining in their class, moving to another class or dying was calculated for the 3-year sampling period. These data sets were pooled to give a matrix of transition probabilities between height classes (Table 4).

A simulation model incorporating a Markov model of change in plant number and size and including recruitment and mortality data was used to evaluate 3 management scenarios: (1) no control practices; (2) control of plants greater than 4m every 12 years; and (3) control of plants greater than 0.5m every 12 years.

Changes in plant numbers (plants/ha) were simulated over 23 time steps (one step equals 3 years), starting with an original population of 40 plants/ha in each of the 4 size classes. Where chemical control was simulated, a modified

Table 4. State transition matrices over a 3-year period for prickly acacia height classes for: (a) no control; (b) control all plants; and (c) large plants only controlled (after Mooy *et al.* 1992).

		Height class (m)			
		<0.5	0.5–1.5	1.5–4.0	>4.0
(a)	<0.5	0.256	0.013	0.000	0
	0.5–1.5	0.147[1]	0.492	0.104	0
	1.5–4.0	0.021	0.234	0.709	0.100
	>4.0	0.000	0.000	0.036	0.825
	Dead	0.576	0.261	0.151	0.075
(b)	<0.5	0.256	0.0	0.0	0.0
	0.5–1.5	0.147	0.0	0.0	0.0
	1.5–4.0	0.021	0.0	0.0	0.0
	>4.0	0.000	0.0	0.0	0.0
	Dead	0.576	1.0	1.0	1.0
(c)	<0.5	0.256	0.013	0.000	0.0
	0.5–1.5	0.147	0.492	0.104	0.0
	1.5–4.0	0.021	0.234	0.709	0.0
	>4.0	0.000	0.000	0.036	0.0
	Dead	0.576	0.261	0.151	1.0

[1] Percentage of plants <0.5m tall that will move into 0.5–1.5m class over the 3-year time step.

matrix was used which simulated the effects of killing plants (Table 4). This was done by making all transitions for the particular size class under consideration zero, except for the transition to dead plants, which had a probability of 1.

At each time step, prickly acacia basal area (m²/ha) was calculated from the simulated plant number and the mean basal area for each height class. Pasture production was estimated from the equation of Carter *et al.* (1991):

$$Production = -350 + 2100*e^{(-0.23*Basal\ area)} \quad Eq\ 4$$

where production was in kg/ha/yr and tree basal area in m²/ha.

A safe stocking rate for cattle was estimated by assuming that consumption of 40% annual pasture production was sustainable and that this would produce 120 kg/hd/yr of liveweight gain, valued at \$1.20/kg. Thus, a value of production per hectare could be calculated based on methods in Scanlan and McKeon (1990).

Some simple assumptions were also made: climatic conditions experienced during the experimental period continued for the simulated period; chemical treatment had no impact on seedling recruitment; and chemical control was 100% effective on the targeted size class. The usual assumptions of Markov models were accepted as valid for this situation.

Treatments were compared by accumulating the annual gross profit (value of beef production minus chemical costs). The return (\$/ha) for the control (no treatment) was subtracted from both chemical treatments to give a net benefit of chemical control.

Results and Discussion. The net benefit of the management scenarios is shown in Figure 2. In the short to mid-term (first 25 years), chemical control of all plants taller than 0.5m resulted in lower accumulated cash than applying no treatment for the situation simulated (160 plants/ha). The removal of large plants alone gave increased benefits over the same period. The reason for this is that removal of large plants alone gave large increases in pasture growth. Control of smaller plants as well gave only a small additional increase in pasture growth whereas costs were increased markedly. However, both chemical control treatments were superior to no treatment by the end of the simulation (70 years), and the total-control treatment gave a 40% higher net benefit than controlling large plants only. Thus, the choice of appropriate control method depends on the chosen time frame. Further details can be found in Mooy *et al.* (1992).

Conclusion. This study shows how the transition matrix can be modified to represent some form of management. It also shows how a Markov model (of woody plant growth) can be integrated into a larger model to evaluate the economic impact of alternative management options.
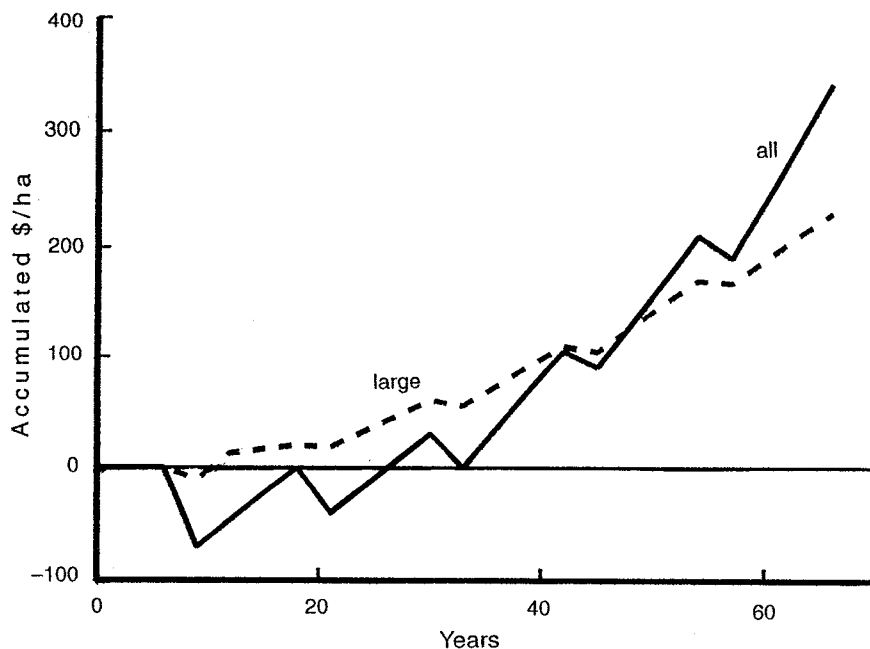
Figure 2. The accumulated cash benefit of controlling all or only large prickly acacia *(Acacia nilotica)* every 12 years, over and above the returns from no chemical treatment (after Mooy *et al.* 1992).

Case 3 — Pasture composition changes in tropical woodlands

Introduction. The tropical savanna woodlands of northern Australia have a variable pasture composition, containing a large number of perennial and annual grasses. Grazing pressures have varied greatly over the last 25 years, due to use of Brahman-infused cattle, supplementary feeding, the beef slump of the mid-1970s and the droughts of the 1980s. As a result, significant changes in pasture composition have been observed (Gardener *et al.* 1990). The naturalisation of the introduced, stoloniferous grass *Bothriochloa pertusa* is of particular importance. McIvor and Scanlan (1994) present a state and transition model of this system.

Method. A model of the pasture system in tropical woodlands is presented in Figure 3 (simplified from McIvor and Scanlan 1994). This shows the states (S_i) within the system and also the mean transition rates (k_i). States 1–4 represent perennial grass-dominated pasture, mixed perennial and annual grass pasture, annual grass-dominated pasture and naturalised, stoloniferous grass pasture, respectively.

This system is modelled as a continuous-time Markov process. The effect of different grazing pressures on the landscape composition of the 4 states was analysed by altering the transition rates.

To estimate the steady-state probabilities for each state, a set of equations has to be solved. These equations are derived from Figure 3 by equating the inflows with outflows as would occur under a steady-state system. In this model, the flows represent change of state rather than matter actually moving between compartments.

$$0 = S_1.k_6 - S_2.k_1 - S_4.k_5$$
$$0 = S_2.(k_7 + k_1 + k_4) - S_3.k_2 - S_1.k_6$$
$$0 = S_3.k_2 - S_2.k_7 - S_4.k_3 \qquad \text{Eqs 5}$$
$$0 = S_4.(k_3 + k_5) - S_2.k_4$$
$$1 = S_1 + S_2 + S_3 + S_4$$

Through solving these simultaneous equations, the following equation was derived:

$$\text{Eq 6}$$

$$S_2.\left[\frac{\frac{k_4.k_5}{(k_3 + k_5)} + k_1}{k_6} + 1 + \frac{\frac{k_3.k_4}{(k_3 + k_5)} + k_7}{k_2} + \frac{k_4}{(k_3 + k_5)}\right] = 1$$

After solving this for S_2, the proportions in other states can be calculated from the above set

of equations, for any combination of rates that is chosen.

Transition rates appropriate to a range of stocking pressures from very heavy to very light were estimated (Table 5). As grazing pressure increases, k_1, k_2 and k_5 become less frequent and k_3, k_4, k_6 and k_7 become more frequent. Transition rates that may apply for a range of grazing pressures were estimated (Table 5). For each combination of k values, Equation 6 and then Equations 5 were solved to obtain the steady-state composition. Though the vegetation states and the rates of transition were selected examples only, they are adequate for illustrative purposes.

Results. As the level of grazing pressure decreased from very high to very low, the proportion of area covered by perennial grasses increased from 5% to 72% while the proportion dominated by annual grasses decreased from 68% to 4% (Figure 4). The proportions of the other 2 states varied over a much narrower range with both having maximum proportions under normal grazing conditions (Table 5).

Discussion. This simple representation of pasture communities in tropical woodlands is in accord with general observations. Evaluating the composition of states given certain rates of transition is a simple process, not requiring a computer. Also, estimating the parameters as frequency of occurrence is more intuitive than estimating proportions of a state that may undergo a transition in a time interval, as is the case for discrete-time models.

Major disadvantages of this model are that rates of transition may be difficult to quantify experimentally and rates may not be constant over time.

These deficiencies could be overcome through the use of other simulation modelling approaches. The following points are relevant:
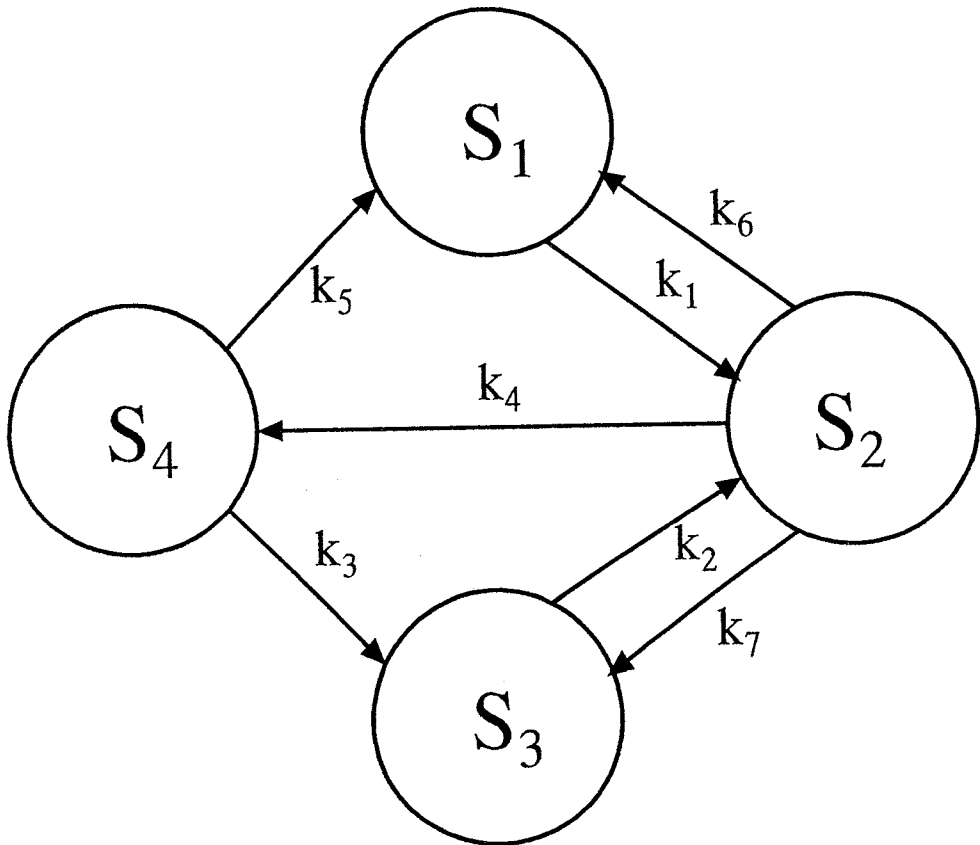
Figure 3. System diagram for continuous-time Markov model of tropical savanna woodlands in north Queensland. State 1 = perennial native grass; State 2 = unstable perennial and annual grass; State 3 = annual grass; State 4 = naturalised perennial grass. The k values are transition rates for changing from one state to another.
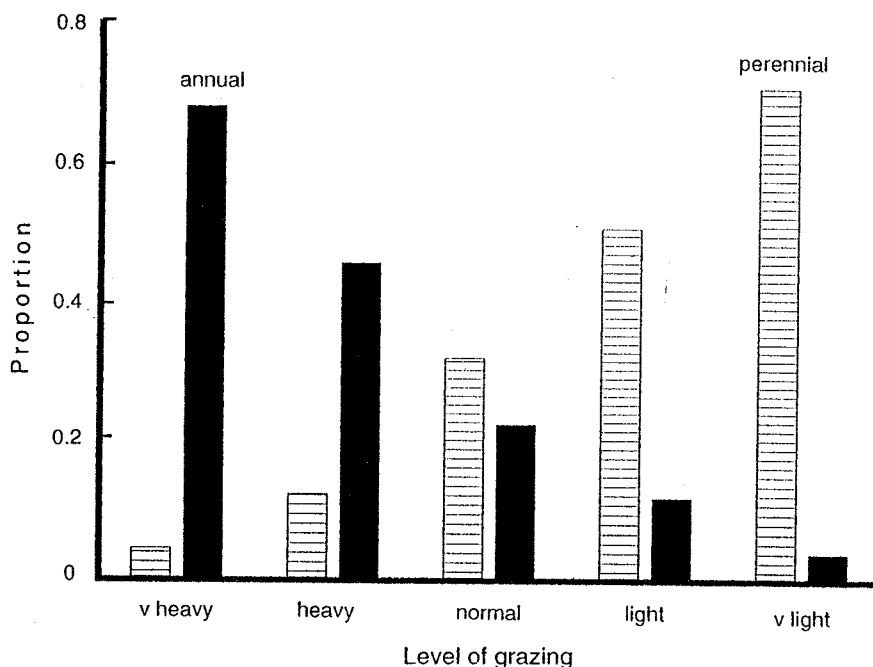
Figure 4. The proportion of a tropical woodland pasture dominated by perennial grasses and annual grasses at a range of stocking pressures. (See Figure 3 and Table 5 for description of the model and the parameters.)

Table 5. Transition rates (number of transitions per decade) for the continuous-time Markov model shown in Figure 3, together with the predicted stable composition (% of area) of community types for each set of transition rates.

Transition rate	Very heavy grazing	Heavy grazing	Normal grazing	Light grazing	Very light grazing
k1	1	1.5	2	2.5	3
k2	1	1.5	2	2.5	3
k3	2.5	1.75	1	0.75	0.5
k4	1.5	1.25	1	0.75	0.5
k5	0.5	1	1.5	2.0	2.5
k6	5	3.75	2.5	1.75	1
k7	2.5	1.75	1	0.75	0.5
State 1	5	14	33	51	72
State 2	18	27	32	30	21
State 3	68	46	22	11	4
State 4	9	13	13	8	3

(1) The first requirement is that the conditions under which transitions will occur are definable. A major effort is being placed on this area of research in collaborative projects among Department of Primary Industries/CSIRO/Department of Lands under the North Australia Program (NAP2) of the Meat Research Corporation.

(2) The continuous change of parameter values can be addressed conceptually by dividing the time period into shorter and shorter intervals, within which it can be assumed that the parameter values are constant. Thus, the continuously varying system can be approximated as a series of steps during which time the parameter values remain constant.

The sensitivity of the final composition of states to changes in any transition rate is easily determined, and this may indicate those areas which require the most detailed study. In a simple 4-compartment model as illustrated here, the

effect of changes to one transition rate is easy to visualise. When the number of compartments increases and the number of transitions altered increases, the results of changes become impossible to estimate without evaluating the analytical solutions (as in Equation 6).

The combination of empirical models of pasture composition in grazing systems with process models to determine rates of transition appears to offer great potential for evaluating research results, for projecting impacts of changes to management and for developing research strategies. A concerted effort will be made to do such a modelling project for the tropical woodlands of northern Australia.

From studies like those mentioned above, we can use process models of grazing systems (e.g. GRASP — McKeon *et al.* 1990) to run long-term simulation experiments to determine the frequency of conditions that lead to transitions. This would enable the parameters in Table 5 to be determined on a sound basis.

Conclusion. This case demonstrates the analysis of a continuous-time Markov model. For this model, the analytical solution is simple. One disadvantage not shown is that there is no capacity to determine how long it will take for the system to become stable in terms of the proportions in the 4 states.

A major appeal of this type of model is that the values of k can be determined by running process models to determine the frequency of conditions required to bring about each of the transitions. This contrasts with the previous example where the Markov model was used to predict woody plant change within a larger model. Here the detailed process model could be used to determine parameters of the continuous-time Markov model.

General conclusion

Discrete-time and continuous-time Markov models can be used in ecological studies to describe state and transition models as described by Westoby *et al.* (1989). Discrete-time models can be used to project changes in composition of vegetation states although the assumptions of the Markov process are rarely met. In the analysis of *Prosopis* spread into south Texas grasslands, the failure of assumptions was overcome by using matrices which represent transitions for different weather conditions. The same approach was used to simulate management changes in a mitchell grassland containing *Acacia nilotica*, with one matrix for non-control periods and others for periods in which control of *A. nilotica* was performed.

Continuous-time models have been used to a much smaller extent for ecological studies than have discrete-time models. The main advantage of this approach is that most biological processes are continuous by nature rather than occurring in particular time steps. The example of pasture change in tropical woodlands shows the simplicity of this modelling approach. Another advantage is that rates are easier to conceptualise by non-technical people than are the proportions that may experience a transition during a fixed time period.

The mathematics of Markov models are conceptually simple. Analytical solutions are available for models in which Markov process assumptions are valid. Simulation solutions can be obtained for those cases where the assumptions are not appropriate. The approaches presented here should be considered in any project which involves the use of state and transition models.

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