The Application of Markov Models in Recovery and Restoration

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ABSTRACT

The application of Markov models in recovery and restoration is a natural extension to their success in modelling ecological succession and disturbance. Due to the continual shifting of ecosystem function during the restoration, however, and the immigration and extinction of local species, the model must be reconsidered in terms of its ecological analogues. Modelling groups of species, classified by functional groups, is suggested. An extended Markov model, the hidden Markov model, is introduced as a method of linking the structure and function of the ecosystem in the modelling construct.

Key Words: Community, Forest, Succession, Prediction, Stationary Markov model, Hidden Markov model.

INTRODUCTION

Modelling tools can aid in dealing with the uncertainty inherent in ecological recovery and restoration and in evaluating the success of the efforts (Anand and Desrochers 2004, Kentula 2000). Often, the restoration effort will begin with the removal of some limiting factor (for example, toxic heavy metals, acidic conditions, noxious species) and the initialization of a recovery process on the site with a trajectory headed toward a system of reference (SER 2002). This might occur by liming (Winterhalder 2000), seeding and/or planting (Winterhalder 2000, McLachlan and Bazely 2003), harvesting and thinning (Asefa et al. 2003) or substrate deposition (Weinstein and Weishe 2002). Often these measures will introduce species that are representative of the target system composition. Recovery, however, is a kind of succession process (McIntosh 1980), and thus can be modelled in much the same way. Models of succession, then, are natural candidates for use as predictive tools in recovery and restoration efforts. One such model that has been used in ecology is the Markov model, and this paper focuses on its potential to shed light on the restoration process.


The most commonly used type of Markov model in use is the stationary Markov model (SMM). This is a relatively simple model in which the probability distribution of model states stabilizes after a given number of model steps. This property made the model ideal for modelling classic Clementsian succession (Clements 1928) towards a "climax" state. In these applications, the distribution of model states typically represents relative species abundance in the community. The SMM is limited, however, in terms of its ability to describe non-monotonic species dynamics in space or time. These have been observed in recovery and succession trajectories (Childress et al. 1998). Thus, while the SMM may be useful for modelling some recovery and succession processes (Horn 1975, Orlovi et al. 1993), extensions or adaptations to the model are desirable in order to deal with nonlinear responses.

The SMM modelling efforts to date have focused on the dynamics of the species in the community as evaluated on some abundance scale. This is sufficient to represent the change in community structure during succession. In restoration, however, the goal is to alter ecosystem function in order to promote and sustain the restoration of the ecosystem structure (i.e., species composition). Modelling restoration enhanced recovery requires making provision for the difference between a 'natural' succession pathway and a manipulated path-
way. Ecosystem restoration, as defined by Bradshaw (1996), is the return of an ecosystem to its original, pristine state. The restoration of an ecosystem is dependent on the return of both ecosystem structure, such as biodiversity, and ecosystem function, such as biomass and nutrient content cycling (Bradshaw 1987, Bradshaw 1996, Bradshaw 1997). There is little doubt that biodiversity and ecosystem function are inherently intertwined, although there is still debate regarding the degree to which they influence each other (Loreau et al. 2001). Nevertheless, it is well known in restoration ecology that, in order to be successful, the restoration must address ecosystem function prior to, and alongside, ecosystem structure (Bradshaw 1996). Required system processes must be available for the restored structural components in order for them to persist.

The models must be flexible enough to allow for increasing or decreasing dimensionality of the system as species and processes enter and leave the system throughout the restoration. Because processes can simultaneously affect multiple ecosystem components, restoration efforts must be multifaceted in their approach instead of focussing on a single characteristic of the system (Parker and Pickett 1997). Modelling efforts must reflect this, both by allowing for the multi-dimensionality of the restoration problem and providing for mechanisms to increase or decrease the dimensionality as the restoration effort continues. Past methods of applying the Markov model are problematic as all components of the system must be present in the initial conditions of the model. Modelling efforts must include provisions for the introduction of species and provide a link between ecosystem function and structure. Simple models of species abundance may not be sufficient, as large variability in species populations need not imply similar trends in underlying ecological processes (Tilman 1999, Pimm 1984).

Developing models for restoration activities can be daunting because of the diversity of degradation and restoration scenarios and the feeling that every project is unique, requiring equally unique modelling tools. Bradshaw (1996), however, points out that an increased understanding of general principles in ecology has allowed for general restoration concepts that are transferable between seemingly different restoration projects. An example is the application of forest restoration principles to coral reef restoration (Epstein et al. 2003). They discuss the use of silvicultural principles traditionally used in forest management for coral reef restoration and point to focussing on the structural components of the reef ("gardening" the corals) as a means of maintaining diversity. Weinstein et al. (2001) have developed "Restoration Principles" based on their experience in restoring wetlands with the intention they be used for other restoration projects. However, Zedler (2000) illustrates how ecological principles are still sometimes ignored in restoration efforts. Nevertheless, it is clear that general principles in ecology can be applied in restoration efforts. The modelling solutions, then, should also strive to reflect this generality and incorporate general principles into their constructs, which indirectly requires that the models are relatively simple in nature.

Parker and Pickett (1997) point out there is no ideal reference state for any type of ecosystem because of the complexity of interdependencies between ecosystem functions and that a range of possible references should be considered. Aronson et al. (1995) argue, however, that there must be some attempt at choosing an ecosystem of reference a priori in order to evaluate the success of the restoration. Both Parker and Pickett (1997) and Aronson et al. (1995) agree on the need to consider multiple 'steady states' as endpoints of many possible ecosystem trajectories. And and Desrochers (2004) discuss how recovery and restoration trajectories may be complex with non-linear behaviour or multiple attractors. This can further complicate the evaluation of the recovery and restoration because of the possibility of multiple stable states and recovery trajectories that are impossible to predict. The consideration of "community states" in restoration, whether multiple stable states, a single reference state, or a series of relatively distinct states during the recovery process, is an important requirement of modelling of recovery and restoration.

This paper serves as a review of Markov models used in ecology with concentration on adapting the model for application to specific restoration problems. It will discuss the use of stationary and non-stationary Markov models, as well as introduce the use of an extended Markov model in ecological modelling to further link ecosystem structure and function.

**THE SMM IN BRIEF**

A Markov model is composed of variables that can be in one of N states at any time t. At each discrete model step, the variables move to a new state according to the probabilistic function of their present state. Ecological analogues must be developed for these model states and their transition probabilities in order to provide a meaningful and realistic implementation of the model.

The simplest process to consider is the stationary, or homogeneous, Markov model. A SMM, of N states, is completely defined by $X_t$, the initial distribution of states at $t=1$, and $A$, the state transition probability matrix having elements $a_{ij}$ that represent transitions
between the states \( i, j \), where \( 1 \leq i, j \leq N \). The state distribution, \( X_t \), for model steps \( t + 1; t + 2, ..., T \) is generated by:

\[ X_t = X_{t-1} \times A. \]  

(1)

The problem that must be considered prior to application of SMMs, however, is the estimation of the parameters \( X_1 \) and \( A \). Often \( X_1 \), the initial state distribution, is determined by the point at which observation of the system being modelled begins (for example, the initial species abundances in a community at the beginning of the restoration). Although \( A \) can be parameterised using fine-scale observations of species transitions (Woottton 2001b), species transitions are often difficult to observe in many ecological systems (Hulst 1979). The problem of estimating the transitions of \( A \) indirectly from multivariate ecological time series was dealt with by Orłoci et al. (1993). The gain or loss in species abundances (to other species or bare ground) over each time step are recorded in a transition matrix unique to that time, \( t \). The average transition matrix over time represents the overall observation sequence (and thus remains stationary).

Reliable implementation of the estimated model requires some method of testing the Markov process against the observed vegetation dynamics. Binkley (1980) used chi-square to evaluate the stationary nature of the model put forth by Waggoner and Stephens (1970) while Balzter (2000) applied mean square error, Spearman’s rank correlation coefficient and Wilcoxon’s signed-rank test. Orłoci et al. (1993), however, utilised a method of evaluation based on randomisation testing of the null hypothesis that transitions at each model step are undirected (random).

The primary use of Markov models in ecology has been for modelling succession in plant communities. Lippe et al. (1985) describe and discuss shortcomings of past applications of the Markov model of succession that take two general approaches: (1) the modelling of the replacement of one individual by another and (2) the replacement of vegetation types. The former approach is that of Waggoner and Stephens (1970), Horn (1975), Enright and Ogden (1979), and Culver (1981) who use Markov models as forest models of tree-by-tree replacements. The latter approach is that of Legg (1980), Usher (1981), Orłoci et al. (1993), and Tucker and Anand (2003) who use Markov chains as models of the dynamics of vegetation types in a site. Balzter (2000) further illustrates the model’s utility by applying it to grassland communities using various sampling techniques, data types and vegetation parameters.

Those using the Markov model as a model of restored and recovering systems can rely on a wealth of work focused on applying the SMM to community succession. Waggoner and Stephens (1970) was first to use the Markov model in ecology to model stand development in a mixed hardwood forest. They used decadal enumeration of tree stems over 40 years to classify sampling plots into forest types defined by the dominant species, which were then used as the model states. They found that stand development can be described by the SMM. Later, Binkley (1980) found the transition matrix of Waggoner and Stephens (1970) to be non-stationary and speculated that, as Lippe et al. (1985) had found with heathland data, the non-stationary behaviour was the result of insect infestations. Horn (1975) also modelled forest succession as a tree-by-tree replacement process where, for each tree in the forest, there was an estimated probability for its replacement by another tree of the same or different species. Horn’s model also considered the lifespans of different species and seed rain proportional to local abundance. Culver (1981) applied the approach of Horn (1975) to a spruce-fir forest. McAuliffe (1988) modelled the dynamics of a 3-state desert system (open ground, Larrea, and Ambrosia) and found the stationary Markov model to perform well in predicting the proportions of barren ground, Larrea, and Ambrosia. Transition probabilities between the three states were estimated using recruitment and mortality rates of the two species on an annual basis. Due to its effectiveness in modelling community succession, the SMM may prove useful in modelling recovery, should the recovery process behave as that of a natural succession.

DEFINING THE MODEL STATES - FROM IDENTITY TO FUNCTION

A limitation of the SMM that is particularly important to restoration, is that it does not make provisions for the addition of new species in later stages of succession. The species in the community must be known a priori, which is not realistic in a system under restoration where species immigration is often one of the primary goals of the effort. The model can be modified to allow for immigration and extinction of species, however, by grouping species into functional groups (for example, Raunkier life forms, growth form, dispersal method, life history) and modelling the collective abundances of the group through time. The method of Usher (1981), using cluster analysis to form groups characterised by frequencies of the dominant higher plants, is related to this but requires that all species be present in the early stages of community development. Samuels and Lockwood (2002) partly address this problem by using
the broad classes annual and perennial in their introduction to Markov-set chains but do not discuss the possibility of using other classifications in the model. This approach is similar to Asefa et al. (2003) who use a state-and-transition model to assess biodiversity restoration of grazing lands in Ethiopia where vegetation states are based on plant life forms. Shifting dominance of the functional groups would indicate changes in the underlying ecological functions of the system and provide insight into possible trajectories of the recovery pathway.

There has been increased focus on the importance of functional groups on ecosystem processes (Diaz and Cabido 2001). Froys and Allen (2002) found that, despite large changes in species composition during extinctions and invasions in the Everglades, functional group richness and redundancy of ecological functions remain stable. Barbaro et al. (2001) suggest that assessment of restoration, in the case of biodiversity restoration of grasslands, should be based on dispersal abilities and functional roles of species rather than species richness. Médail et al. (1998) defined floral functional groups from 9 of 71 attributes and found that functional diversity does not always follow species diversity, particularly at forest edges in a fragmented landscape where, despite having higher species richness, they have lower functional diversity than do forest cores. Lavorel et al. (1998) examine functional groups characteristic of pasture disturbance and found functional diversity to be the key to community resilience to disturbance. Pausas (1999) models plant functional groups based on responses to disturbances. The dynamics of functional groups can also provide insight into the success of the community (Bonet 2004). An example from the smelter impacted forests of Sudbury, ON, Canada will further illustrate how alternate community groupings of species can provide different assessments of ecological state than individual species abundances. Figure 1 shows the relative abundance of understory (less than 1.5 m) vascular plants in quadrats from five sites, each with two transects, in un-restored, restored and reference forests. The species have been categorized by growth form according to Gleason and Cronquist (1991). The un-restored transects are characterised by relatively high relative abundances of tree species and low abundances of herbaceous species. The restored and reference transects, however, are characterised by relatively high abundances of understory herbs. The transects of restored and reference forests are remarkably similar when species are grouped into these simple categories. The reference forest and restored forests, however, are remarkably different in terms of species composition, as a correspondence analysis (CA) on the actual mean species abundance matrix for the 10 transects illustrates (Figure 2).

Figure 3 illustrates a generic 2-state stationary Markov model that has been adapted to consider plant functional groups instead of species abundance. It captures change in terms of dominant functional groups during a restoration induced succession. The arrows represent the gain and loss of cover abundance between two community groups, one that is characteristic of an

![Figure 1](image)

**Figure 1.** Mean relative cover abundance of herb, shrub, and tree species as measured in the understory level (less than 1.5 m tall) in 1 m contiguous square quadrats along 2 transects at each of five sites. Two sites (1 and 2) represent un-restored forest after devastation by SO2 fumigation and heavy metal deposition, two sites (3 and 4) have been restored by liming, seeding and planting, and one site (5) represents reference forest. Transects at site 4 are 50 m long while all others are 100 m long.
early-restoration community (grasses and weeds) and one that is characteristic of a late-restoration community (shrubs, perennials and trees). This model is fully specified by the initial state vector (2), which describes the initial relative cover abundance of the two functional groups (the early restoration community initially occupies all available space), and the transition matrix (3), which describes the amount of cover gained or lost from each group to the other.

\[
X_1 = \begin{pmatrix} 1.0 & 0.0 \end{pmatrix}
\]

\[
A = \begin{pmatrix} 0.9 & 0.1 \\ 0.0 & 1.0 \end{pmatrix}
\]

During the course of the restoration there is a high probability of new species entering the community (either by planting and seeding as per the restoration plan or by unaided immigration) and of some species already present at the site becoming locally extinct as ecosystem functions evolve. The use of the categorical organisation of the community provides for fluctuating species composition as the restoration continues.

**INCORPORATING SPATIAL INTERACTIONS AND GRADIENTS**

There have been few attempts at the application of the SMM to spatial dynamics. Lippe et al. (1985) argues that the dynamics of individual plants will be influ-
enced by their neighbours and that it is possible to use the Markov model only when changes in the transition probabilities resulting from spatial effects are relatively small or the abundance and patch structure are constant. Kenkel (1993), however, applied Markov models to the spatial pattern of *Aralia nudicaulis* and Li (1995) modelled vegetation patterns in a Texas savannah. Balzer et al. (1998) consider the addition of a spatial dimension to a discrete-time Markov chain and show how it results in a cellular automata called a spatio-temporal Markov chain. They examine the dynamics of a lawn with three species. Wootton (2001a, 2001b) found the SMM to perform as well as spatially explicit, cellular automata models in intertidal communities were spatial interactions are known to occur, indicating that the transition matrix of the Markov model may in fact incorporate spatial interactions. Wootton (2001a) also found that transitions among species may be the net result of many possible direct and indirect effects. Herein lies the power of this simple model because the transitions between states (gain or loss in cover abundance) need not reflect only direct mechanistic processes (for example, physical competition) but indirect processes as well. Yemshanov and Perera (2002) developed a simulation model of large-scale forest cover transitions in the North American boreal forest using a Markov chain where discrete states are defined by dominant forest species. Their models provided spatially explicit predictions of the temporal nature of disturbance cycles, forest cover composition, and canopy age. Tucker and Anand (2003) used a SMM to examine small scale, topographically induced vegetation gradients and large scale, pollution induced gradients. The models of understory vegetation used species cover abundance in quadrats but the models of overstory vegetation, however, relied upon a novel combination of abundance of overstory species weighted by tree height to capture the effect of both density and structure in overstory vegetation. The use of the model along spatial gradients is particularly helpful in restoration and recovery efforts because environmental perturbation often manifests itself along spatial gradients. Spatial models of gradients can therefore be used to draw conclusions about the properties of the gradient itself or make predictions on future gradient characteristics by simulating changes in community dynamics at points along the gradient.

**NON-STATIONARITY**

One requirement of a simple, stationary Markov chain, however, is that the state transitions are derived by a stationary transition matrix. It has been found that in some natural systems the Markov chain tends to be non-stationary (Lippe et al. 1985). This resulted in the application of non-stationary, non-homogeneous, or fuzzy Markov chains in ecology (Li 1995, Anand and Orlović 1997, Korotkov et al. 2001, and Yoon and Korvin 2001).

Lippe et al. (1985) applied SMMs to 19 years of *Empetrum nigrum* heathland data in Holland and found that transition probabilities were not stationary because the transition matrix was affected by climate and insect impacts, directional changes of the transition probabilities with time, and spatial influences. Years following major environmental perturbations accounted for a large portion of the non-stationary behaviour. Orlović et al. (1993), however, found that, using a different method of estimating transition matrices, a stationary Markov model could fit the heathland data well. Benabdellah et al. (2003) have used stationary Markov models and non-stationary Markov models in the Erzgebirge, Germany. The former was used as a hypothetical model of regional forest succession while the latter application was applied to an area devastated by sulphur dioxide emissions and harvesting. They illustrate the importance of the SMM as a successional model and the need to use a non-stationary model when examining “non-successional” influences (for example, atmospheric pollution). Woolhouse and Harnsen (1987a, 1987b) developed a non-homogeneous Markov chain model that described the dynamics of a one-prey-two-predators acrid complex inhabiting apple foliage.

Non-stationary transitions are a particularly important consideration while restoration efforts are ongoing. If alterations are made to the system in an effort to maintain the recovery trajectory fixed on the target system the adjustments will disrupt the state transitions, effectively resetting the system to a new initial condition from which the successions process will begin anew. This might occur by thinning, seeding and/or planting, harvesting and thinning, or substrate deposition. In order to deal with these impacts, as well as unplanned, natural events, such as drought or insect infestations, the transition matrix of the model can be made to vary with time.

**MODEL ADAPTATIONS**

Despite the shortcomings of the Markov model, it is clear that there are a wide range of possible applications to problems in restoration ecology. However, under highly variable conditions it is difficult to estimate parameters for the model, resulting in poor performance. For example, Childress et al. (1998) examined the performance of four Markov models, ranging from
stationary to semi-stationary, in their ability to reflect changes in species composition over time in the primary successional plant community at Mount St. Helens, Washington. They found that the models performed poorly due to high annual species turnover that resulted in high variation in annual transitions among classes. Such problems call for reevaluation and the development of extensions to the Markov model. Samuels and Lockwood (2002) have addressed this with the introduction of Markov-set chains (Hartfiel 1991), an extension to stationary Markov models, for application in restoration activities. Markov-set chains allow for increased incorporation of variability into succession models by using probabilities to predict the extreme outcomes of community succession. These models use the observed minimum and maximum probabilities that one plant will replace another to predict community composition intervals. Instead of each state having a specific probability of occurrence, as in the Markov model, the states of the Markov-set chain can occur within an interval of probabilities. The width of the interval is an indication of variability of the model state and provides an upper and lower bound within which ecological observations are predicted to occur. This method, however, does not link the observations to the underlying ecological processes. Although it is possible to infer ecosystem function by models of functional group dynamics that are relevant to the system (as in Figure 3), it is possible to extend the model in such a way that it can represent both the observations made on the system (for example, species or functional group abundances) and the underlying functional states of the ecosystem that influence those observations (for example, successional or recovery stage).

The hidden Markov model (see Baum and Petrie (1966), Baum and Egon (1967), Baum and Sell (1968), Baum et al. (1970) and Baum (1972) for the theory as well as Rabiner (1989) for a tutorial) is an extension to the Markov model. Ecological applications of HMMs include modelling seasonal vegetation cycles (Viovy and Saint 1994), detecting edges in grasslands (Hoef and Cressie 1997), and examining the underlying processes of a coastal wetland to evaluate the impact of funnelling (Dale et al. 2002).

If there is sufficient reason to assume that the underlying process of observed vegetation change is Markov, then it is reasonable to ask what other processes are active when observations show that the vegetation change is not pure Markov. The main advantage of the HMM is the capacity to incorporate the specifications of another process that is supposed to overlay the pure Markov process. An HMM models a sequence of observational data that is assumed to be the result of a stochastic process overlying a sequence of hidden states. The hidden states are generated by a

![Figure 4. A 4-state hidden Markov model that models the restoration of barren land to forest. The hidden component of the model changes through 4 states. After restoration begins, the community goes through 3 hidden states, each with a dominant vegetation type (state 2 - grass, state 3 - shrubs, state 4 - trees). These hidden states are responsible for the generation of the observed community states, which for simplicity have been partitioned into 4 broad categories (barren ground, grass, shrubs, trees). While in any 1 of the 4 hidden states, any community state may be observed with a probability specific to that state (for example, Barren ground is highly probable (p=0.9) in restoration state 1 (un-restored), but it may also be observed in other restoration states (p=0.1 in state 2, p=0.05 in state 3 and p=0.05 in state 4)).]
SMM and, at each hidden state, an observation state is emitted according to a probability distribution for that hidden state. Observations on ecological systems are likely to be the result of underlying ecological effects that are not easily quantified and whose dynamics may not be clear from the ecological observations, but on average directly influence them. For example, ecological processes (for example, ecological recovery) that are not easily observed directly may be changing in time or space and their dynamics can be inferred from observations on the community states they influence (for example, community composition). The HMM is designed to reveal such underlying processes, and therefore handles more complex dynamics (for example, non-monotonic responses) in plant ecological processes and provides a direct link between the structure and function of the ecosystem.

Continuing with Markov modelling of functional groups, a hidden Markov model is expected to provide a similar, but more powerful, service. Figure 4 shows a simple scheme as it may be used to model the restoration and recovery of barren land. The hidden states represent abstract or holistic “states of restoration” and the observations are the observed state of the site as measured by the abundance of plant growth forms. Before restoration activities begin, the ecosystem is in “restoration state 1”, a naturally recovering system with mostly barren ground. After restoration activities begin, however, a succession process is initiated which causes the system to evolve through a series of three recovery states, each with a dominant type of vegetation (grasses, shrubs and trees). As the recovery states change, there is a systematic change in the vegetation types from colonisation of grasses, to invasion of shrubs and development of forest. This addresses the need to link structure and function into a realistic model. The model can deal with variability in observations because transitions between states are stochastic. It also provides a method of directly modelling the inferred state of restoration and recovery based on ecological observations.

CONCLUSIONS

The application of the stationary and non-stationary Markov model in ecological succession can be transferred in practical and effective manners to restoration ecology. By grouping ecosystem components in a meaningful way, the formerly restrictive Markov model becomes an attractive proposition for modelling restoration. Extensions of the Markov model, such as Markov-set chains and the HMM should not replace the SMM, but serve as substitutes for the simpler model as required by the ecological data. Markov-set chains provide a range of possible community compositions during recovery. The HMM provides increased interpretive capabilities in revealing hidden processes by the underlying states and providing a link between the ecological observations and the underlying ecosystem function.

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