A Diffusion Model of Forest Succession

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Received 15 December 1982

ABSTRACT

Based on a tree by tree replacement mechanism, a diffusion model of forest stand canopy composition is formulated and analyzed. The model is used to explore composition dichotomies by estimating coefficients from forest stand data and interpreting the results in terms of mechanisms for succession. The model yields a concrete characterization of the succession phenomenon known as the climax state.

INTRODUCTION

Secondary forest succession refers to the changes observed in a particular forest habitat following a perturbation that opens up a large enough space. It appears that in some forest habitats the latter stages of secondary succession tend to approach a quasisteady state in which the annual ecosystem respiration approximately equals the gross primary productivity. The idealized concept of this slowly changing state as a terminal state is called the climax stage of succession. The concept has generated some discussion in the literature about the best way to characterize it [1], [4].

In this paper we describe a mathematical model of the evolution of a forest site canopy during the intermediate to late stages of secondary succession. The model allows succession to occur through a tree by tree replacement process in which openings in the canopy are caused by endogenous disturbances. Catastrophic exogenous disturbances such as severe fires or hurricanes are not incorporated into the model. Parameters in the model are determined from data. This allows one to make order of magnitude predictions on state transition times. Finally, the model yields a mathematical characterization of the climax state.


$^0$Elsevier Science Publishing Co., Inc., 1984
$^2$Vanderbilt Ave., New York, NY 10017

0025-5564/84/$03.00
THE TREE REPLACEMENT MODEL

We describe a mathematical model of the evolution of a forest site consisting of two kinds of trees, designated type A and type B. While the classification may be according to species in a two-species stand, we admit any dichotomy which makes sense, such as A = shade tolerant, B = shade intolerant, or A = hickories and oaks, B = other species, etc. The state variable of the system is a stochastic process, $X(t)$, which represents the proportion of type A trees occupying the canopy of the community plot. The model is based on the following primary assumptions:

(i) the total number of trees in the plot canopy is a constant, $N$;
(ii) type A (B) trees leave the canopy at an average proportional rate $\lambda$ ($\nu$), with the time intervals between departures being independent random variables with identical exponential distributions;
(iii) given that $X(t) = x$ and that a type A tree left the canopy, the probability of $\text{A} \rightarrow \text{B}$ (a tree of type A in the canopy being replaced by a tree of type B) is $r(x)$;
(iv) given that $X(t) = x$ and that a type B tree left the canopy, the probability of $\text{B} \rightarrow \text{A}$ is $s(x)$.

Assume that $X(t) = x$, and let $p = \lambda r(x) \Delta t$ and $q = \nu s(x) \Delta t$. During the time interval $[t, t + \Delta t)$ four possible tree replacements occur with the probabilities denoted below:

<table>
<thead>
<tr>
<th>Transition</th>
<th>Probability of occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A \rightarrow A$</td>
<td>$1 - p$</td>
</tr>
<tr>
<td>$A \rightarrow B$</td>
<td>$p$</td>
</tr>
<tr>
<td>$B \rightarrow B$</td>
<td>$1 - q$</td>
</tr>
<tr>
<td>$B \rightarrow A$</td>
<td>$q$</td>
</tr>
</tbody>
</table>

For example, the probability of $A \rightarrow A$ during $[t, t + \Delta t)$ is the probability of $A$ not leaving the canopy, $1 - \lambda \Delta t$, plus the probability of $A$ leaving the canopy times the probability of an $A$ being replaced by an $A$ given that an $A$ left the canopy, $\lambda \Delta t [1 - r(x)]$:

$$1 - \lambda \Delta t + \lambda \Delta t [1 - r(x)] = 1 - \lambda r(x) \Delta t.$$

THE DIFFUSION APPROXIMATION

Define

$$Z = Z(x) = \text{number of type A trees that get replaced by type A trees during } [t, t + \Delta t),$$

and

$$W = W(x) = \text{number of type B trees that get replaced by type B trees during } [t, t + \Delta t).$$

The random variable $Z$ is the binomially distributed number of successes in $Nz$ Bernoulli trials with probability of success $1 - p$. Similarly, $W$ is the binomially distributed number of successes in $N(1 - x)$ Bernoulli trials with probability of success $1 - q$. Given that $X(t) = x$,

$$X(t + \Delta t) - X(t) = [Z + N(1 - x) - W - Nx] \Delta t, \quad (1)$$

so our knowledge of the distributions of $Z$ and $W$ yields

$$E \{ X(t + \Delta t) - X(t) | X(t) = x \} = [-\lambda x r(x) + \nu (1 - x) s(x)] \Delta t \quad (2)$$

and

$$E \{ [X(t + \Delta t) - X(t)]^2 | X(t) = x \} = [\lambda x r(x) + \nu (1 - x) s(x)] \Delta t + O((\Delta t)^2). \quad (3)$$

If $N \gg 1$ and $x$ is not close to 0 and 1, $X(t + \Delta t) - X(t)$ is well approximated by a normal distribution. This suggests that it is not unreasonable to postulate a diffusion model with drift

$$a_1(x) = -\lambda x r(x) + \nu (1 - x) s(x) \quad (4)$$

and dispersion

$$a_2(x) = \frac{1}{N} [\lambda x r(x) + \nu (1 - x) s(x)]. \quad (5)$$

Incremental moments of order higher than $N^{-1}$ have been discarded. While in general this is not good practice, for processes which approach a stationary state the resulting diffusion model provides a useful approximation of dynamics in the neighborhood of equilibrium. We are primarily interested in a simple model of forest succession, and the diffusion model we select is motivated by the continuous parameter Markov chain. The resulting diffusion model is then

$$\frac{\partial p(x,t)}{\partial t} = \frac{1}{2N} \frac{\partial^2}{\partial x^2} [a_2(x)p(x,t)] - \frac{\partial}{\partial x} [a_1(x)p(x,t)], \quad (6)$$
where \(0 < x < 1\) and \(t > 0\). If we define
\[
J(x, t) = a_1(x)p(x, t) - \frac{1}{2N} \frac{\partial}{\partial x} [a_2(x)p(x, t)],
\]
then the simplest reasonable boundary conditions that can be imposed are
\[
J(0, t) = J(1, t) = 0
\]
provided \(r(1) > 0\) and \(s(0) > 0\). This boundary condition does not allow for the possibility of a stand becoming purely \(A\) or purely \(B\), but can still provide reasonable representations of such situations. If either \(r(1) = 0\) or \(s(0) = 0\), Equation (6) is singular and there is the possibility of permanent fixation of \(X(t)\) at \(x = 1\) or \(x = 0\).

**INTERPRETING THE MODEL**

The state dependent transition probabilities \(r(x)\) and \(s(x)\) embody the natural selective pressures governing the tree by tree replacement process. They are to be determined by a combination of hypotheses and observations. We show in this article how to estimate \(r(x)\) and \(s(x)\) from the data.

For interpretive purposes it is convenient to think of \(X(t) = X_N(t, \omega)\) as the state of a plot \(\omega\) consisting of \(N\) trees, where \(\omega\) is an element of an ensemble \(\Omega\) of \(k\) independent plots each containing \(N\) trees (Figure 1). \(\Omega\) is some selected set of plots of a forest community. A particular sample trajectory, \(X_N(\cdot, \omega)\), may then be identified as the evolution in time of a small portion of the canopy of a forest community. If \(k \gg 1\), then \(p(x, t) \Delta x\) is interpreted to be the fraction of \(k\) plots with proportion of type \(A\) trees in \((x, x + \Delta x)\) at time \(t\).

This interpretation suggests a method for determining \(r(x)\) and \(s(x)\) from observational data taken on the plots. The method is based on the assumptions that (i) \(\Omega\) is representative of the forest community at or near its climax state (for example, \(\Omega\) may consist of only plots containing a high level of biomass); and (ii) in the climax state one observes on a local scale the several various stages of late secondary succession [1]. In the case that \(s(0) > 0\), \(r(1) > 0\), and \(J(0, t) = J(1, t) = 0\), the fact that \(X(t)\) is a time homogeneous process yields a steady state solution \(p^{\infty}(x) = p(x, \infty)\) to Equation (5). The basic idea is to assume a functional form for \(r(x)\) and \(s(x)\) which depends on unknown parameters and then to estimate these parameters by requiring the moments of \(p^{\infty}(x)\) be equal to the sample moments calculated from the ensemble \(\Omega\). The procedure is illustrated in the examples below.

Before proceeding to the example, it is of interest to discuss briefly the qualitative behavior of \(p^{\infty}(x)\) for a few special cases. Since \(s(0) > 0\) and \(r(1) > 0\), we see that the drift coefficient must satisfy \(a_1(0) > 0\) and \(a_1(1) < 0\), so \(a_1(x)\) can have only an odd number of zeros in \((0,1)\). Thus, if \(r(x)\) and \(s(x)\) are either constant or affine functions, \(a_1(x)\) will have exactly one zero in the interval \((0,1)\). In any case where \(a_1(x)\) has only one zero, say \(\bar{x}\), in \((0,1)\), we find that for \(N \gg 1\)
\[
p^{\infty}(x) \sim \left[\frac{-Na_1(\bar{x})}{2\pi a_2(\bar{x})}\right]^{1/2} \exp \left[\frac{Na_1(\bar{x})(x - \bar{x})^2}{2a_2(\bar{x})}\right].
\]
Hence, the proportion of type \(A\) trees in the plot canopy tends to be normally distributed about \(x = \bar{x}\) with variance \(-a_1(\bar{x})/Na_1(\bar{x})\) when \(N\) is large.

In order for \(a_1(x)\) to have three zeros in \((0,1)\), it must be at least cubic, so \(r(x)\) and/or \(s(x)\) must at least be quadratic in \(x\). For large \(N\), this will correspond to a concentration in probability about the two outside zeros, stable equilibrium points of the deterministic equation
\[
\frac{dx}{dt} = a_1(x).
\]
It is expected that cases where \(a_1(x)\) has three or more zeros will be rare. Such cases would be very interesting, since they might be interpreted as a...
macroscopic indeterminacy in the evolution of a forest community. The fact that it would require a large amount of data (which is usually not available) to establish confidence in the higher empirical moments and the fact that the equation is defined for \( x \in (0,1) \) suggests that choosing \( r(x) \) and \( s(x) \) to be first or second degree polynomials will suffice in most cases for capturing the essential qualitative features of the empirical distributions in \( p^\infty(x) \).

THE SIGNIFICANCE OF THE MODEL

The diffusion model is related to the continuous parameter Markov chain model of Horn \[2\]. If \( Y(t) \) presents the proportion of type \( B \), then by the methodology of Horn's approach we write

\[
\frac{dX}{dt} = -\lambda X + \lambda [1 - r(X)] X + \nu s(X) Y, \tag{11}
\]

\[
\frac{dY}{dt} = -\nu Y + \nu [1 - S(X)] Y + \lambda r(X) X. \tag{12}
\]

Since \( X(t) + Y(t) = 1 \), Equation (12) may be disregarded and Equation (11) reduces to

\[
\frac{dx}{dt} = -\lambda X r(X) + \nu (1 - X) S(X). \tag{13}
\]

This is to be compared to the Ito stochastic differential equation associated with Equation (6):

\[
dX(t) = \left[ -\lambda X r(X) + \nu (1 - X) s(X) \right] dt
+ \frac{1}{\sqrt{N}} \left[ \lambda X r(X) + \nu (1 - X) S(X) \right]^{1/2} dW(t) \tag{14}
\]

Equation (14) reduces to Equation (10) as \( N \to \infty \). The Markov chain model is the deterministic limit of the diffusion model.

What is the significance of the parameter \( N \) in forest succession? Since \( N \) is proportional to the area of each plot, it is convenient to think of \( N \) as a measure of the size of the plot. Let us first discuss the meaning and role of \( N \) in the model. In the model, fluctuations in the number of each species of tree (in the canopy) arise through departures from the plot canopy at random points in time. The mechanism giving rise to these departures is taken to be endogenous disturbances to the forest site. From Equation (14) we see that the magnitude of fluctuations in the proportion of type \( A \) trees is inversely proportional to the square root of the size of the plot. When the forest community is viewed on a local scale (corresponding to \( N \) not being extremely large), the model implies there will be a good deal of variation in the relative species composition of the plot canopies. When the forest community is viewed on a large scale (corresponding to \( N \) being large), the model implies that there will be very little variation in relative species composition between large plot canopies. The inference to be made is that while the forest community as a whole appears to be evolving in a deterministic fashion, on a local scale one is likely to observe the several various stages of succession, though there may be a more or less predominant composition. The climax state, corresponding to \( p^\infty(x) = p(x, \infty) \) in the model, will also contain the various stages of succession on a local scale. Hence, succession can occur through endogenous disturbances and is a continuing, ever-present phenomenon that is closely tied to the size of the stand under observation.

The process \( X(t) \) associated with Equations (6) and (8) is also ergodic, that is,

\[
\lim_{t \to \infty} \frac{1}{T} \int_0^T f(X(t)) \, dt = \int_0^1 f(y) p^\infty(y) \, dy
\]

with probability 1 \[3\]. In particular, if \( f(x) = I_{\Gamma}(x) \), the indicator function for \( \Gamma \subset (0,1) \), the interpretation is that the average proportion of time a plot maintains its canopy composition in a certain interval is equivalent to the proportion of plots in the climax ensemble with canopy composition in that same interval.

The implications of the model compare very well with the shifting-mosaic characterization of a northern hardwood forest steady state as proposed by Borman and Likens \[1\]. We turn now to the problem of estimating the parameters of the model from observations.

THE COWEETA DATA SET

A grid of permanent tree census plots with about 500 lattice points was laid out in the mid 1930s covering the Coweeta Hydrologic Laboratory near Franklin, North Carolina. A sample plot of size \( \frac{1}{4} \) acre was established at each lattice point and the following information recorded: the line and plot numbers, the elevation, the aspect (which we interpret to be the compass direction of the downhill slope), the slope, and the position. The position of a plot is either upper, mid, or lower slope, ridge, valley, cover, or creek bed. A survey of trees growing on each plot was made at roughly ten-year intervals beginning in 1934. The data set we have access to contains the 1934 survey and a survey which was made between 1969 and 1972. The number of plots was reduced to 403 in the years between 1934 and 1969.

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The surveys are conducted as follows: The trees and shrubs are partitioned into DBH classes starting at one inch and proceeding in increments of one inch. (DBH stands for diameter at breast height.) The number of
individuals of each species in a DBH class is recorded. There are 42 species and an "other" class in the survey.

STEADY STATE AND THE METHOD OF MOMENTS

In order to use the assumption that the highest mass plots are at or near steady state, we select the highest mass plots by choosing those with total basal area (stem cross section area at breast height) of at least 5000 sq. in. Thus we select 43 of the 403 plots in the 1970 survey. Call this subcollection \( Q \), and label the elements of \( Q \) as 1, 2, ..., 43.

For \( j = 1, 2, ..., 43 \), let \( N_j(A) \) denote the number of type \( A \) trees in the canopy of plot \( j \), and \( N_j(B) \) the number of type \( B \) trees. We take

\[
\begin{align*}
    m_j &= N_j(A)/(N_j(A) + N_j(B)) \\
    \alpha_j &= N_j(A)/(N_j(A) + N_j(B))
\end{align*}
\]

for \( j = 1, 2, ..., 43 \).

Then the empirical moments for the steady state distribution of \( X \) are formed as \( \mu_i = \sum_j \left( \frac{N_j(A)}{N_j(A) + N_j(B)} + \frac{N_j(B)}{N_j(A) + N_j(B)} \right) \mu_i \).

In addition to the biological assumption that \( Q \) is representative of the forest community near steady state, we must make some modeling assumptions about \( r(x) \) and \( s(x) \). A reasonable assumption is that \( r(x) \) and \( s(x) \) are low degree polynomials, i.e., of degree 1 or 2. If we assume the affine case, then the estimation procedure we will outline requires three moments, and the quadratic case requires six moments. We will concentrate on the affine case.

Assuming \( r(x) = r_0 + r_1 x \) and \( s(x) = s_0 + s_1 x \), the steady state probability density \( p^\infty \) of \( X \) must solve [from Equations (6) and (8)]

\[
\begin{align*}
    \frac{1}{2N} \frac{\partial}{\partial x} \left\{ \left[ \lambda x (r_0 + r_1 x) + \nu (1 - x) (s_0 + s_1 x) \right] p^\infty (x) \right\} & - \lambda x (r_0 + r_1 x) + \nu (1 - x) (s_0 + s_1 x) \right\} p^\infty (x) = 0.
\end{align*}
\]

Factoring out \( \lambda r_0 \), the equation becomes

\[
\begin{align*}
    \frac{1}{2N} \frac{\partial}{\partial x} \left\{ \left[ x (1 + \alpha_1 x) + (1 - x) (\alpha_2 + \alpha_3 x) \right] p^\infty (x) \right\} & - \lambda x (r_0 + r_1 x) + \nu (1 - x) (s_0 + s_1 x) \right\} p^\infty (x) = 0, \quad (15)
\end{align*}
\]

where \( \alpha_1 = r_1 / r_0 \), \( \alpha_2 = \nu s_0 / (\lambda r_0) \), and \( \alpha_3 = \nu s_1 / (\lambda r_0) \).

Let \( \tilde{\alpha}_1(x) = -x (1 + \alpha_1 x) + (1 - x) (\alpha_2 + \alpha_3 x) \) and \( \tilde{\alpha}_2(x) = x (1 + \alpha_1 x) + (1 - x) (\alpha_2 + \alpha_3 x) \). The steady state probability density is then given by

\[
p^\infty (x) = \frac{1}{k \tilde{\alpha}_2(x)} \exp \left( 2N \int_0^x \frac{\tilde{\alpha}_1(t)}{\tilde{\alpha}_2(t)} dt \right).
\]

DIFFUSION MODEL OF FOREST SUCCESSION

where

\[
k = \int_0^1 \left[ \frac{1}{\tilde{\alpha}_2(x)} \exp \left( 2N \int_0^x \frac{\tilde{\alpha}_1(t)}{\tilde{\alpha}_2(t)} dt \right) \right] dx.
\]

By requiring the model moments to equal the empirical moments we find conditions that the \( \alpha_i \)'s must satisfy. Requiring \( \tilde{\alpha}_1(m_1) = 0 \) forces the probability density to converge to a \( \delta \)-function at \( x = m_1 \) as \( N \to \infty \). This gives the first necessary condition:

\[
-m_1 \alpha_1 + (1 - m_1) \alpha_2 + (1 - m_1) m_1 \alpha_3 = m_1.
\]

Integrating (15) from 0 to 1 and setting \( m_i = \int_0^x x p^\infty (x) dx, \ i = 1, 2 \), yields the second condition:

\[
m_2 \alpha_1 - (1 - m_1) \alpha_2 - (m_1 - m_2) \alpha_3 = \frac{a_1 (0) p^\infty (0) - a_1 (1) p^\infty (1)}{2N} - m_1.
\]

Remember \( a_1 \) and \( p^\infty \) both depend on the \( \alpha \)'s. Multiplying (15) by \( x \), integrating from 0 to 1, and setting \( m_i = \int_0^x x^i p^\infty (x) dx \) for \( i = 1, 2, 3 \) yields the third condition:

\[
\begin{align*}
    m_2 \alpha_1 - (1 - m_1) \alpha_2 - (m_1 - m_2) \alpha_3 & = \frac{a_1 (0) p^\infty (0) - a_1 (1) p^\infty (1)}{2N} - m_1, \\
    m_3 - m_2 & = m_1 - a_1 (1) p^\infty (1).
\end{align*}
\]

Let \( \alpha = (\alpha_1, \alpha_2, \alpha_3)^T \). Then the necessary conditions can be written as \( A \alpha = F(\alpha) \), where \( F \) is a nonlinear vector function of \( \alpha \). We can sometimes solve for \( \alpha \) by iterating as follows: if \( \alpha_0 \) is an initial guess, then \( \alpha_{n+1} = A^{-1} F(\alpha_n) \) for \( n = 0, 1, 2, \ldots \).

SAMPLE CALCULATIONS I

There are 43 census plots in the 1970 survey with basal area of at least 5000 sq. in. Considering this subcollection \( Q \) as representative of the forest at steady state, we find the sample mean for the number of trees in the canopy of a census plot to be \( N = 14.837 \). (The canopy is composed of trees with DBH at least 10 inches.)

We have partitioned the canopy species into two classes, shade tolerant and intolerant, in Table 1.

The computed states \( X \) of members of \( Q \) are shown in Table 2. The first three moments for \( X \) are \( m_1 = 0.7545 \), \( m_2 = 0.61064 \), and \( m_3 = 0.5124 \). With starting values \( \alpha_1 = -0.9 \), \( \alpha_2 = 0.1 \), and \( \alpha_3 = 0.8 \), the iteration procedure
Fig. 2. A comparison of the theoretical probability density \( \phi \) (smooth curve) with the ensemble histogram (crosses).

TABLE 2

<table>
<thead>
<tr>
<th>( x )</th>
<th>( 0)</th>
<th>( 0.1 )</th>
<th>( 0.2 )</th>
<th>( 0.3 )</th>
<th>( 0.4 )</th>
<th>( 0.5 )</th>
<th>( 0.6 )</th>
<th>( 0.7 )</th>
<th>( 0.8 )</th>
<th>( 0.9 )</th>
<th>( 1.0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>60.0</td>
<td>61.9</td>
<td>63.8</td>
<td>65.7</td>
<td>67.6</td>
<td>69.5</td>
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<td>73.3</td>
<td>75.2</td>
<td>77.1</td>
<td>79.0</td>
</tr>
<tr>
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<td>81.9</td>
<td>83.8</td>
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<td>87.6</td>
<td>89.5</td>
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</tr>
<tr>
<td>0.5</td>
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<td>107.6</td>
<td>109.5</td>
<td>111.4</td>
<td>113.3</td>
<td>115.2</td>
<td>117.1</td>
<td>119.0</td>
</tr>
</tbody>
</table>

Now take a random sample of 100 and lump them together, so we have

SCANNING THE MODEL WITH RESPECT TO TIME

...
This nonlinear equation can be solved, and we have
\[ \int_{n_0}^{n_1} \frac{dX}{a_1(X)} = \lambda r_0 (t_1 - t_0), \]
or
\[ \lambda r_0 = \frac{1}{t_1 - t_0} \int_{n_0}^{n_1} \frac{dX}{a_1(X)}. \]

Applying this procedure to the Coweeta data set, we aggregated all of the census plots in the 1934 survey on which the chestnut blight would have a minimal influence, i.e., plots which had no chestnuts of DBH greater than 7 inches. For the second point in time, we used this same collection of census plots from the 1970 survey. For the affine case, we have
\[ \frac{\lambda r_0}{\alpha_1 + \alpha_3} \left( \frac{n_0 - X_1}{n_0 - X_0} \right) \ln \left( \frac{n_0 - X_1}{n_0 - X_0} \right) \]
where \( X_0 < X_1 \) are the roots of \( \hat{a}_1(X) = 0 \). (If \( X_0 = X_1 \), the form of the equation changes.) Recall that we have constrained the problem so that \( m_1 \) is one of the roots. If type A trees are the dominant species, we would expect \( n_0 \) and \( n_1 \) to be smaller than \( m_1 \).

**SAMPLE CALCULATIONS II**

Out of the 403 census plots there are 57 on which the chestnut blight had only a minimal influence. Ideally, we would choose a subset of these plots at random from the larger set, but because of the small number available we will use all of them. Aggregating these plots, the canopy contained 376 trees in the 1934 survey and 606 in 1970. Thus we are dealing with a large enough portion of the forest to assume the deterministic model is appropriate. The proportions of the canopy which were shade tolerant in 1934 and 1970 are \( n_0 = 0.42287 \) and \( n_1 = 0.47195 \), respectively. Each survey took several years to complete, so we have approximated \( t_1 - t_0 \) as 35 years.

The roots of \( \hat{a}_1(X) = 0 \) are \( X_0 = m_1 = 0.7545 \) and \( X_1 = 2.0225 \). Since \( n_0 < n_1 < x_0 \), we would conclude that even in 1970 these plots are a long way from steady state. Finally, upon substituting we find \( \lambda r_0 = 0.01865 \).

We have found all of the model parameters that we can find using the Coweeta data set. However, there are some bounds that \( \lambda \) and \( \nu \) must satisfy. Since \( 0 < r, s < 1 \), we have \( \lambda > 0.01865 \) and \( \nu > 0.01945 \).

**NUMERICAL ASPECTS OF ESTIMATION PROBLEMS**

In solving the nonlinear vector equation \( A\alpha = F(\alpha) \) for \( \alpha \), where \( A \) is a square matrix and \( F \) is a nonlinear vector valued function, our hope is that
near the solution $F(a)$ doesn’t change rapidly compared to $\alpha a$. When this happens we can sometimes find a solution as a fixed point, i.e., $a = A^{-1}F(a)$, by iterating. If $a_0$ is the initial guess, then $a_{n+1} = A^{-1}F(a_n)$ for $n = 0, 1, 2, \ldots$. We are usually satisfied with this method if it converges after a few steps, maybe no more than a dozen.

However, convergence is sensitive to the initial guess. For some starting values one might not get convergence, while for others one might. We obtained convergence for all of the cases with which we worked. If we had not, there are other methods available based on gradients that could have been used.

EXPECTED STATE TRANSITION TIMES

With the parameters that have been estimated, it is possible to address the problem of finding the expected time for a census plot in state $x$ to first reach a state $y$, assuming $x < y$. This is a first passage time problem, which, as is well known, can be solved by solving the boundary value problem

$$\frac{1}{2N} \dddot{a}_1(x) u'' + \ddot{a}_2(x) u' = 1,$$

$$u'(0) = 0, \quad u(m_i) = 0.$$

The solution to this problem is presented in Figures 3 and 4 for two different values of $N$. In order to find the expected time for the plot to go from $x$ to $y$, difference the ordinates of points on the graph with the abscissas $x$ and $y$.

SUMMARY AND DISCUSSION

In this paper we employ a diffusion approximation of a Markov chain model of secondary forest succession which allows canopy composition to evolve through a tree by tree replacement process. The driving mechanism for the process is assumed to be due only to noncatastrophic endogenous disturbances which cause trees to depart from plot canopies; following departure, the resulting holes in the canopy are filled by trees from the understory. The state variable of the process is $X(t)$, the proportion of the plot canopy of a distinguished tree type, designated type $A$. $X(t)$ is a function of the constant average proportional departure rates, $\lambda$ and $\nu$; the state dependent tree type replacement probabilities, $r(x)$ and $s(x)$; and the constant number of trees per plot, $N$. All but one parameter group in the model can be estimated by a method of moments applied to the steady state density $p^\infty(x)$ of $X$. Sample values of the (ergodic) process $X(t)$ are selected from an ensemble of plots representative of the forest community at or near climax state. The time scale of the process is then estimated by lumping plots.
undisturbed by catastrophic events in addition to not being representative of the climax state. By computing the change in proportion of the distinguished tree type over a 35 year interval, the parameter group representing the time scale of the process may be estimated in the resulting deterministic model. A dynamic variable, the expected state transition time, can then be determined by solving the first passage time problem.

By using $\frac{1}{2}$ acre plots, a constraint imposed by the data, $N$ was restricted to be equal to 14.8 during the parameter estimation. For plots this small, however, it should be pointed out that the total basal area of a late successional plot may drop below the cutoff point of 5000 sq. in. per plot. Hence, some plots that should be used in the parameter estimation were left out. This possibly results in biased estimates. As discussed previously, the variance of the steady state distribution depends on $N$, and when $N$ becomes large the proportion of type $A$ trees in the plot canopy tends to be normally distributed about the mean of $X$, namely $m$. Once parameters in the model have been estimated, we are free to vary $N$ as we please in the model. This would correspond physically to combining adjacent plots into larger plots. The results of this are indicated in the two graphs of $p^\infty$ generated for $N = 50$ and $N = 100$ (Figures 5 and 6). This feature of the model has implications for our understanding of forest succession. For instance, for a large scale description of two types of trees a single number might suffice, the proportion of type $A$ trees. For a small scale description, one would have to give the probability density function $p^\infty$. In the mathematics literature, the type of stability possessed by $X(t)$ is called weak stochastic stability. Roughly, this means $p(x,t) \rightarrow p^\infty(x)$ as $t \rightarrow \infty$. What is stable is the steady state density $p^\infty(x)$. But its variance is a monotone decreasing function of the geographic scale size ($N$) of the subsystems (plots). In the small scale, there may be no obviously apparent stable canopy composition behavior. In characterizing climax states as stable, perhaps this is the type of stability we should have in mind.

The geographic scale size also plays a role in expected state transition times as indicated in Figures 3 and 4. It takes longer on the average for a larger plot to go from few shade tolerant trees in the canopy to 75% than for a smaller plot. Mathematically, this phenomenon is due to the reduction of the stochastic element of the model, and this seems to fit our intuition that in a smaller plot the removal of a canopy tree has a larger impact on the state of the canopy.

One advantage of the model is the ability to select plots according to the ideal forest community we are trying to model. In the present case, we were interested in succession through noncatastrophic exogeneous disturbances; hence we discarded plots on which the chestnut blight was likely to have had large influence. This selection in turn determines the infinitesimal parameters of the model and thus the expected state transition times. One way this plot
selection feature may be used is to compare results of totally undisturbed sites with results of those mildly disturbed by the presence of certain diseases, insects, or acid precipitation. Another possibility is to compare ensembles of sites with different topographic positions and/or soils.

Finally, we note that without a method of determining $\lambda$ and $\nu$ independently of the model, we have to be cautious in interpreting $r(x)$ and $s(x)$. Since $\lambda, \nu > 0$, and $\lambda r_0 > 0$, it follows that $r_1 < 0$ and $s_1 > 0$. Thus the slope of $r(x)$ is negative while the slope of $s(x)$ is positive. As the proportion of type $A$ ($B$) trees in the canopy increases, the probability of an $A$ ($B$) being replaced by a $B$ ($A$) from the understory upon departure of an $A$ ($B$) from the canopy decreases. This indicates a cooperative effect amongst the shade tolerant trees as well as a cooperative effect amongst the shade intolerant trees. There are several mechanisms which could give rise to the cooperative effect, the most obvious being that the trees in the understory may likely be of the same type as those in the canopy if the canopy is primarily one type [2].

The authors wish to thank Dr. Wayne Swank at the Southeastern Forest Experiment Station, Coweeta Hydrologic Laboratory, Otto, N. C., for use of the dataset used in the parameter estimation procedure in this paper. In addition, the authors wish to thank the referees for several helpful and provocative comments.

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