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NUMERICAL SOLUTIONS OF ECOSYSTEM MODELS

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NUMERICAL SOLUTIONS OF ECOSYSTEM MODELS

ABSTRACT

Deterministic and stochastic ecosystem models are described in detail and examples of simple population dynamic models are explored. Such models are usually nonlinear, stiff, and time delayed. Numerical techniques, in particular the method of Nordsieck and Gear, can be used to solve complex deterministic systems. Similary Monte Carlo techniques can be used to simulate extremely complex stochastic systems.

INTRODUCTION

This attempt to describe ecosystem models has two purposes. The first purpose is to examine the possible relationships between biological systems and their mathematical models or counterparts. The second purpose is to examine possible solutions of complex mathematical systems.

Biological systems are, for the most part, extremely complex, and it is naive to assume that a solution of their mathematical counterparts can be found by the use of simple mathematical techniques. This is not to imply that simple techniques are useless; the use of simplifying assumptions and elementary methods of solution as exploratory tools is extremely valuable in understanding the basic dynamics of any system. On the other hand, there is no guarantee that a given model will be solved just because powerful mathematical and numerical techniques are available. Hence a compromise must be reached - simplifications must be made to make models tractable, yet a model must not be so simple that all connection with reality is lost.

The possibility of using different mathematical and numerical techniques to analyze different parts of a given ecosystem model should be considered seriously. Such techniques have been successively used in reactor calculations. Neutron transport phenomena have been calculated using Monte Carlo techniques, while depletion rates of reactor fuels were

handled with numerical iterations or finite-difference techniques. A similar system might be possible in an ecosystem model. For instance, suppose the ecosystem under investigation is a mixed conifer forest, which is influenced by Western Pine Beetle (*Dendroctonus Brevicomis*), *Fomes Annosus* Root Rot, and certain abiotic factors. It is obvious that no single model can fully describe the system; however, a combination of models might describe such a system satisfactorily. The evolution of the conifer forest might be described by a numerical iteration technique, in which the effects of the Western Pine Beetle are described by Monte Carlo techniques. However, Monte Carlo techniques are not appropriate in all submodels. For example, the progression of Root Rot is extremely slow when compared to Western Pine Beetle dynamics, but fast when compared to the aging process of the forest, hence a "diffusion" approach could possibly describe the progression of Root Rot, which is a function not only of time but also of position. In essence a sequence of submodels could be used to describe a biological system. A particular submodel is chosen so that it best represents the biological process in question. The biological system is itself described by the biological processes which occur in it, but these processes are described by associated mathematical submodels. There is, therefore, no single defined model for a biological system. The model is simply a sequence of submodels which describes the biological processes in that system. We shall use the term "model" and submodel" interchangeably.

Two distinct classes of models are outlined and representative equations described. Deterministic models are inherently easier to solve, but may not be fully representative of ecosystem dynamics. Stochastic models may describe ecosystem dynamics more realistically, but they yield systems of nonlinear differential-difference equations which are extremely difficult to solve. Time delayed effects which occur in both classes of models are also discussed.

The examples used in this study have been directed towards a population-dynamics approach to ecosystems. Energy- and mass-dynamics models yield the same type of differential equations as does a population dynamics model; however, the parameters which describe the interactions and relations in either an energy- or mass-dynamics system are entirely different. The problem becomes one of describing an energy- or mass-dynamics system in a consistent way. Once the system of ordinary differential equations which describe the system has been derived, the method of numerically solving the equations will be similar.

The second purpose of this report is to discuss two numerical techniques (Runge-Kutta and Gear) for solving systems of ordinary differential equations. Gear's method is extremely powerful and efficient for handling nonlinear systems which are stiff, and would be a valuable tool in solving complex ecosystem models (ordinary differential equations are said to be stiff if the magnitudes of their eigenvalues vary greatly). Also, a method for solving stochastic type models is outlined, that is, the possibility of using a Monte Carlo simulator is examined. The Monte Carlo technique is extremely powerful and could be used effectively for certain stochastic models.

A number of statistical techniques such as regression, time-series analysis, and classification techniques are also discussed. Although these techniques do not solve systems of ordinary differential equations, they may be invaluable tools in the analysis and parameterization of such equations.

We do not discuss analytic solutions to ordinary differential equations. Complex systems require so many simplifying assumptions that the analytic solutions become academic. We also ignore finite-difference techniques which could prove to be important in certain cases.

The models we describe are temporal in nature. We have made no attempt to look at spatial dependence. Such considerations would further

compound the difficulties. However, in any realistic model, such spatial dependence must be considered.

Though time-delayed terms are described in the general ecosystem equation no solutions of systems of ordinary differential equations including such time delays have been considered here. Such solutions are extremely difficult to obtain.

BACKGROUND

The following four sections present a general mathematical form for describing an ecosystem. This form is consistent with the state of the art of ecosystem analysis as presented in Refs. 1-6. A number of assumptions concerning the functional forms to be used in the ecosystem equations are implicit in the equations presented below.

Let S_i be some state function or "vector" for species i ; then

$$\frac{dS_i}{dt} = f(S_i, S_j, t, t') , \quad (1)$$

where f is some general nonlinear expression and $t' = t - \tau$ where τ represents a delay or lag time. Let f be decomposed as follows:

$$f(S_i, S_j, t, t') = A_i(S_i, t, t') + B_{ij}(S_i, S_j, t, t') , \quad (2)$$

where A_i are the "abiotic" or physical effects acting on state S_i , and B_{ij} are the "biotic" or biological effects acting on S_i due to the existence of another species S_j . Let A_i and B_{ij} be defined as

$$A_i(S_i, t, t') = a_i(t, t') S_i \quad (3)$$

and

$$B_{ij}(S_i, S_j, t, t') = b_{ij}(S_j, t, t') S_i , \quad (4)$$

where a_i and b_{ij} are rate coefficients. Then Eq. (1) has the functional form

$$\frac{dS_i}{dt} = [a_i(t, t') + b_{ij}(S_j, t, t')] S_i, \quad (5)$$

where $i \neq j$. This form of the equation does not consider crowding, competition for space or symbiotic factors explicitly. The above system of equations is inherently nonlinear and dependent on both the current time and retarded time. If we, for the moment, ignore the retarded times, i.e.,

$$a_i(t, t') \rightarrow a_i(t)$$

and

$$b_{ij}(t, t') \rightarrow b_{ij}(S_j, t), \quad (6)$$

then

$$\frac{dS_i}{dt} = [a_i(t) + b_{ij}(S_j, t)] S_i = f(S_i, S_j, t). \quad (7)$$

This equation can be solved by using various techniques. One possible technique is the standard Runge-Kutta⁷ technique; however, if Eq. (7) is stiff, then the methods of Gear⁸ and Nordsieck⁹ seem most promising.

CONSTRUCTION OF MODELS

State Functions

In the previous section we referred to S_i as being some state function or "vector" which defines the state of some biological system. The definition of S_i is completely arbitrary in the sense that it can refer to energy E_i , mass M_i , or the population N_i of species. Once S_i is

defined, then the definitions of a_i and b_{ij} must be in compatible units.

For the moment let us consider the population of a given species N_i , where N_i is in S_i . N_i can be characterized by various factors such as age (ℓ) and Health class (h). The length of the vector N_i will just be $n_\ell \times n_h$, where n_ℓ is the number of age classes and n_h is the number of health classes for the i^{th} state. For example, let us assume that we are given only the number of living species for a particular system. Then both n_ℓ and $n_h = 1$ since all species occupy the same age and health class, and therefore N_i represents the number of alive items. Thus a_i and b_{ij} are simple mortality rates. If, however, N_i is more complicated, then a_i and b_{ij} will represent morbidity rates, and N_i will have the functional form $N_i(\ell, h)$. The description of such a system is given in the Appendix.

If E_i or M_i are the state functions considered, then these functions are continuous functions of time, initial energy, and/or initial mass for the i^{th} state; hence the length of the state function is (n_i) .

The length of the state function for a population ecosystem model is $(n_i \times n_\ell \times n_h)$.

Biotic and Abiotic Factors

An abiotic factor or coefficient describes the effect the physical environment has on a given species. Oxidant concentrations, availability of sunlight, and climatic and/or meteorological parameters are some abiotic factors that affect the age, health, ability to reproduce, and ability to convert energy of a species. The coefficient $a_i(t, t')$ given in Eq. (3) represents such effects and is defined by experimental observations.

Biotic coefficients represent the dynamical effects one species has on another. Such effects can represent predator-prey relationships between species or symbiotic relations between species. In Eq. (5), $b_{ij}(S_j, t, t')$ represents such biotic factors. A decomposition of $b_{ij}(S_j, t, t')$ is possible and has the form

$$b_{ij}(S_j, t, t') = \beta_{ij}(t, t') g(S_j), \quad (8)$$

where $\beta_{ij}(t, t')$ represents the intrinsic biotic rate coefficient and $g(S_j)$ represents some function of state S_j for species j . If S_j is assumed to represent some specification of population $N_j(\ell, h)$, then a further decomposition is possible,

$$b_{ij}(S_j, t, t') = \beta_{ij}(t, t') [N_j(\ell, h)]^m, \quad (9)$$

where m is some arbitrary power. For models which are deterministic, $m = 1$; however, for stochastic models, m can assume other values. The actual functional form of b_{ij} must be determined by biological data.

In Eqs. (2), (3), (4), (8), and (9) we have made the tacit assumption that the state function and rate coefficients are separable. The assumption is an extension of the Malthusian principle but must be justified biologically. The biological justification of mathematical assumptions is, therefore, a critical task. The application of sensitivity analysis and statistical analysis to both the biological input and the model's results is a necessary part of the validation of an ecosystem model.

The General Ecosystem Equations

In the previous sections, we attempted to define a system of non-linear differential equations in their full generality and to partially decompose the important terms. In this section we shall write the general forms of the equation for both a population ecosystem model and a mass or energy ecosystem model.

If S_i represents either the mass M_i or the energy E_i of some species i , then the dynamic equations are

$$\frac{dE_i}{dt} = f(E_i, E_j, t, t') \quad (10)$$

or

$$\frac{dM_i}{dt} = f(M_i, M_j, t, t'). \quad (11)$$

It is not clear whether further decomposition is possible, since both E_i and M_i could have as yet undefined functional dependences.

If S_i represents the population N_i of a species i with health class h and age ℓ , then the dynamic equations are

$$\frac{dN_i(\ell, h)}{dt} = [a_i(t, t') + \beta_{ij}(t, t')(N_j)^m] N_i(\ell, h). \quad (12)$$

Equations (10), (11), and (12) are systems of first order, nonlinear, stiff differential equations which are retarded and dependent upon past history. The solution of such systems is difficult - if not impossible. Since the intrinsic rate terms β_{ij} and a_i are nonlinear and time delayed, there seems to be no simple approach to understanding these terms.

An Example of a Simple Population Dynamics Model*

For simplicity let $S_i \rightarrow N_i$ represent the population of a given species i where N_i is independent of age and health classes. We shall also assume that a_i and b_{ij} are independent of any intrinsic time delay factors, so that $t' \rightarrow t$. The development given here is analogous to our previous development; however, the affects of crowding and competition are explored. From Eq. (1) it follows that

$$\frac{dN_i}{dt} = f(N_i, N_j, t), \quad (13)$$

where f is some general nonlinear function. Assuming the Malthusian principle for the change in population size, Eq. (13) can be rewritten as

*This exposition follows the technique of Lassiter and Hayne.¹

$$\frac{dN_i}{dt} = r_i(t, N_j) N_i, \quad (14)$$

where $r_i = b_i - d_i$ is the difference between the instantaneous birth and death rates for species i . The instantaneous birth rate can be written as

$$b_i = \bar{b}_i \prod_{m=1}^M \phi_{im}(t, N_j), \quad (15)$$

where $\bar{b}_i$ is the maximum possible rate of population increase and ϕ_{im} is the m^{th} modifying factor for species i such that $0 < \phi_{im} < 1$. Similarly the death rate can be written as

$$d_i = \sum_{k=1}^K \delta_{ik}, \quad (16)$$

where δ_{ik} is the k^{th} mortality factor for the i^{th} species. Note that if r_i is constant the simple exponential growth curve is the analytic solution.

A Simple Population Dynamics Model of Crowding, Competition, Symbiosis, and Predation

The notion of crowding implies that some resource such as space or energy is in short supply. Crowding also implies some sort of density dependent factor. The effect of limited space or energy is reflected in a change in both the instantaneous birth rate and the instantaneous death rate. One would expect an increase in the death rate and a decrease in the instantaneous birth rate. The death rate is not necessarily a function of the size of the population, but it is a function of competition for food.

Suppose a certain amount of space is available as a resource. If the space is not infinite, then there is competition for the available

space. Assume that there are m species of organisms. An individual of the j^{th} species takes up a space c_{ij} that an individual of the i^{th} species cannot simultaneously use. Therefore a matrix C with dimension m^2 can be constructed, and this matrix describes the spatial requirements of an ecosystem. For some species j , the modifying factor for the birth rate due to crowding by the other species can be written as

$$\phi_{cj} = \begin{cases} (K_j - \sum_{i=1}^m c_{ij} N_i) K_j^{-1} & \text{for } \left| \sum_{i=1}^m c_{ij} N_i \right| < K_j \\ 0 & \text{Otherwise} \end{cases} \quad (17)$$

where K_j is the maximum population for the j^{th} species and ϕ_{cj} represents a decay term which effectively shuts off the birth rate as the system becomes crowded. Note that the sign of c_{ij} is assumed negative in this expression.

In the above description we described a space coefficient c_{ij} which is inherently zero or negative; and this implies that the effect of competition is a limiting effect. There are situations where the presence of one species may be beneficial to another species. Such a situation is called a symbiotic relationship. The amount of resources available to some species i would be increased due to a symbiotic partner j . Hence the modifying factor to the birth rate due to symbiosis would be

$$\phi_{ij} = \left(K_j + \sum_{L=1}^m c_{ij} N_i \right) K_j'^{-1}, \quad (18)$$

where K_j' is defined such that

$$c_{ij}' = c_{ij} > 0$$

and

$$K_j' = K_j + \sum_{L=1}^m c_{ij}' N_i$$

Predation has a dual meaning since it is beneficial to the predator but is usually fatal to the prey. The mortality rate describes this process, but it is basically an interaction between two species. A matrix P with dimensionality m^2 can be developed in which the element P_{ij} represents the predation rate of predator species i on prey species j . The predation rate P_{ij} is specific to a given time interval and to a predefined area. Predation rates provide an operational measure of the relative vulnerability of a prey species to a predator species. The effective predation on each species is defined to be the effective rate of predation for each predator multiplied by the number of predators, i.e., $P_{ij} N_j$. We can now separate the predation factor from the instantaneous death rate:

$$d_i(t) = \sum_{k=1}^m \delta_{ik} = \sum_{k=1}^{m-1} \delta_{ik} + P_{ij} N_j, \quad (19)$$

where the sum is now over all other death rates. To adequately handle the predation problem, some knowledge of satiation levels is necessary. Such data must be obtained experimentally.

A Simple Population Dynamics Model - Abiotic Factors

Abiotic factors were briefly discussed in the Background section. Now we will discuss abiotic factors in the context of the simple population dynamics model. It is assumed that a biological species will have some prescribed response to a condition which is at an optimum level (in some optimum zone). As the condition changes and the species approaches its limit of tolerance, its response changes. Such response changes will be reflected in modifications of d_i and b_i .

Modification of the birth rate by abiotic conditions can be represented by changing the values of the modifier ϕ_{im} . The modifier has a range from 0 to 1. Hence, under optimum conditions the modifier should have no effect, but as the abiotic conditions become intolerable, the

effect of the modifier should become critical. For simplicity, it is assumed that the modifier is linear. The modification of ϕ_i for the x^{th} abiotic factor is

$$\phi_{ix} = \begin{cases} 1 & : \text{at optimum levels} \\ 1 - v_{ix}(0_{ix} - F_x) & : \text{at tolerance levels} \\ 0 & : \text{at intolerable levels,} \end{cases} \quad (20)$$

where 0_{ix} represents the bounds of the optimum zone, v_{ix} represents the rates of increase or decrease as the optimum zone is approached or left, and F_x is the current value of the abiotic factor.

For example consider oxidant impact upon a number of trees. For oxidant concentration between zero and some value 0_{q1} , the trees will

feel no adverse effects. Then from 0_{q1} to 0_{q2} the birth rate will decrease with some slope v_{ix} until the trees succumb. Beyond 0_{q2} life is untenable.

The instantaneous death rate, on the other hand, is expected to increase as the abiotic factor deviates from optimum. The corresponding instantaneous rate of death is assumed to be the natural logarithm of the rate of survival, however, survival must be greater than zero. Therefore

$$\delta_{ix} = \begin{cases} 0 & : \text{at optimum levels} \\ -\ln_e [1 - \lambda_{ix} (0_{ix} - F_x)] & : \text{at tolerance levels} \\ \text{constant} & : \text{elsewhere ,} \end{cases} \quad (21)$$

where δ_{ix} is the instantaneous mortality rate due to abiotic factor x for species i , λ_{ix} are the rates of increase (decrease) as x deviates from the optimum, and F_x is the current value of the abiotic factor x . Note that, if for some reason the abiotic factor goes beyond the tolerance regions, it is possible to have complete extinction of a given species.

In the preceding sections we gave the general formulation of the equations which describe an ecosystem, and we described a simple population model with its various factors. As one proceeds to more complex

systems, the relationship becomes harder to define; however, the system becomes more representative of an actual situation. Whether a particular ecosystem model represents faithfully an actual biological situation depends upon how well each of the rate factors and state functions are defined. Therefore, knowledge of the rate functions with all their nonlinearities and time delays is crucial to the success of any model.

Stochastic Models

In the previous sections we discussed the form the differential equations would assume for various types of state vectors. An example of a population dynamics model was given with a description of how various terms might be related. The differential equations which were discussed have one property in common - they are deterministic in nature. Given the state of some system at time $t = t_{n-1}$ and knowing the various rate coefficients and their time delay properties, it is possible to calculate uniquely the state of the system at $t = t_n$. This implies that a certain number of births and deaths or that certain energy or mass changes will occur. One finds, however, that even if all the requirements are satisfied, the model will not represent a physical situation because random events occurring in the environment can cause major modifications to the environment. Such random events cannot be handled by a deterministic system.

Since biological processes are not inherently deterministic, equations which represent the stochastic qualities of biological systems must be considered. There has been much work done on stochastic models by Bartlett,² Pielou,³ Leslie⁴ and others.⁵ In this section the appropriate forward stochastic equation will be given and we will assume a birth rate coefficient, a death rate coefficient, and an emmigration rate.

At some time t_0 it is assumed that $X_i(t_0)$ individuals of species i exist. Further let b_i , d_i , and τ_i be the birth, death and emmigration

rates for the species in question, and let σ and θ be the predation rate and symbiotic birth rate due to the presence of other species. Let δt be some small but finite element of time.

The transition probabilities P for a transition from a state (X_i, X_j) to the states $(X_i + 1, X_j)$, $(X_i - 1, X_j)$, $(X_i, X_j + 1)$ and $(X_i, X_j - 1)$ in some time interval $(t, t + \delta t)$ are

$$P(X_i + 1, X_j \mid X_i, X_j) = [\tau_i + (b_i + \theta X_j) X_i] \delta t + O(\delta t)^2 \quad (22)$$

$$P(X_i, X_j + 1 \mid X_i, X_j) = [\tau_j + b_j X_j] \delta t + O(\delta t)^2 \quad (23)$$

$$P(X_i - 1, X_j \mid X_i, X_j) = d_i X_i \delta t + O(\delta t)^2 \quad (24)$$

$$P(X_i X_j - 1 \mid X_i, X_j) = [d_j + \sigma X_i] X_j \delta t + O(\delta t)^2 \quad (25)$$

where $O(\delta t)^2$ implies that terms of order $(\delta t)^2$ are ignored. Equation (22) implies that the presence of species j has a beneficial effect on species i and Eq. (25) implies that species i preys on species j . If $p_{x_i x_j}(t)$ denotes the probability that, at time t , there are x_i individuals of species i and x_j individuals of species j in the environment, then the forward stochastic equations become

$$\begin{aligned} p_{x_i x_j}(t) = & [\tau_i + (b_i + \theta x_j)(x_i - 1)] p_{x_i-1, x_j} + [\tau_j + b_j(x_j - 1)] p_{x_i x_j-1} \\ & + [\tau_i + \tau_j + b_i x_i + \theta x_j x_i + b_j x_j + d_i x_i + d_j x_j + \sigma x_i x_j] p_{x_i x_j} \\ & + d_i(x_i + 1) p_{x_i+1, x_j} + (d_j + \sigma x_i)(x_j + 1) p_{x_i x_j+1}. \end{aligned} \quad (26)$$

Now the generating function

$$F_n(t, z) = \sum_{x_i=0}^{\infty} \sum_{x_j=0}^{\infty} x_i^{(n)} z^{x_j} p_{x_i x_j}(t) \quad (27)$$

yields the differential-difference equation

$$\begin{aligned} \frac{\partial F_n}{\partial t} &= [b_j z^2 - (b_j + d + n\sigma - n\theta) z + d_j] \frac{\partial F_n}{\partial z} \\ &= [\tau_j z + nb_i - nd_i - \tau_i] F_n + [n(n-1)b_i + \tau_i] F_{n-1} \\ &\quad - n(n-1) \beta z \frac{\partial F_{n-1}}{\partial z} \end{aligned} \quad (28)$$

with boundary conditions $F_n(0, z) = m_i^{(n)} z^{m_j}$. In Eq. (28), $m^{(n)}$ denotes the product $m(m-1) \dots (m-n+1)$, where m_i is the initial number of species i at time $t = t_0$. The system of ordinary differential equations corresponding to the left hand side of Eq. (28) contains a form of the Riccati equation:

$$\frac{dz}{dt} = b_j z^2 - [b_j + d_j + n(\sigma - \theta)] z + d_j, \quad (29)$$

which is solvable by numerical means.

The solution of Eq. (28) is extremely difficult, if not impossible. There have been some attempts to solve such mixed systems⁶ for special cases, but no generally accepted techniques have been developed. It might be possible to use numerical integration techniques on Eq. (29) and finite difference techniques on Eq. (28), but such solutions for a complex system would be suspicious.

In considering more realistic models, those for stochastic processes, the system of differential equations is enormously more complex than those which consider only biotic factors. The effect of abiotic factors was not explicitly discussed. They would modify the birth, death, and emmigration rate coefficients.

In the previous sections we have discussed the form the differential equations assume in describing an ecological system. The equations are inherently nonlinear and time-delayed ordinary differential equations which are difficult to solve. Stochastic differential equations are differential-difference equations which are very difficult to solve. In the next two sections numerical techniques for solving ordinary differential equations will be investigated, and Monte Carlo techniques will be discussed.

SOLUTIONS TO ECOSYSTEM MODELS

Numerical Solutions

Runga-Kutta Techniques

The standard Runga-Kutta technique is well known and well documented and is included for completeness.

Consider, for example, the single equation

$$\dot{y} = f(y, t), \quad (30)$$

and suppose that the initial value of y is known (that is $y(0) = y_0$). If y_0 is known, then $y_0 = f(y_0, t_0)$ can be calculated. If one uses the Taylor series expansion to first order with step size h , then

$$y(h) \cong y_0 + h \dot{y}_0 \quad (31)$$

and an approximation of y at h is possible. If $y(t_1)$ is defined as the solution to Eq. (31) at time $t = t_1$ then Eq. (31) can be written as

$$y_1 = y_0 + h f(y_0, t_0) \quad (32)$$

or, in general,

$$y_{n+1} = y_n + h f(y_n, t_n), \quad (33)$$

where

$$t_n = nh. \quad (34)$$

Suppose the following approximation is made:

$$y_h(t_n + h) = y_n + h f(y_n, t_n), \quad (35)$$

where

$$q_1 = y_{n/2}(t_n + h/2) = y_n + \frac{h}{2} f(y_n, t_n) \quad (36)$$

and

$$y_{h/2}(t_n + h/2) = q_1 + \frac{h}{2} f(q_1, t_n + h/2) \quad (37)$$

with two steps of size $h/2$. Then

$$y(t_n + h) = 2y_{h/2}(t_n + h) - y_n(t_n + h) + O(h^2) \quad (38)$$

or

$$y(t_n + h) = 2q_1 + hf(q_1, t_n + \frac{h}{2}) - y_n - hf(y_n, t_n) + O(h^2), \quad (39)$$

where the actual calculations involved are just

$$q_1 = y_n + \frac{h}{2} f(y_n, t_n) \quad (40)$$

and

$$y_{n+1} = y_n + hf(q_1, t_n + h/2). \quad (41)$$

In general, a class of second order explicit methods can be written in the following way:

$$q_1 = y_n + \alpha hf(y_n, t_n)$$

and

(42)

$$y_{n+1} = y_n + \beta hf(y_n, t_n) + \gamma hf(q_1, t_n + \eta h).$$

Now

$$\begin{aligned} y_{n+1} = y_n &+ \beta h \dot{y}_n + \gamma h \dot{y}_n + \gamma \alpha h^2 f_y \dot{y}_n + \gamma \eta h^2 f_t \\ &+ \frac{\alpha^2}{2} \gamma h^3 f_{yy} (\dot{y}_n)^2 + \alpha \gamma \eta h^3 f_{yt} \dot{y}_n + \frac{\gamma}{2} \eta^2 h^3 f_{tt} + O(h^4), \end{aligned}$$

where $f_{yy} = \frac{\partial^2 f}{\partial y^2}$, $f_{yt} = \frac{\partial^2 f}{\partial y \partial t}$, and $f_{tt} = \frac{\partial^2 f}{\partial t^2}$. Matching Taylor series about $t = t_n$, one finds that

$$(\beta + \gamma) h \dot{y}_n = h \dot{y}_n$$

and

$$\gamma (\alpha f_y \dot{y}_n + \eta f_t) h^2 = \frac{h^2}{2} \ddot{y}_n = \frac{h^2}{2} (f_y \dot{y}_n + f_t);$$

hence

$$\beta = 1 - \gamma$$

and

$$\alpha = \eta = \frac{1}{2\gamma} . \quad (43)$$

The methods in Eqs. (42) and (43) constitute the second order Runge-Kutta method.

Runge-Kutta methods have been studied extensively and are well documented in such texts as Householder,¹⁰ Hildebrand,⁷ Lapidus and Seinfeld,¹¹ and Gear.⁸ Such methods can be made as accurately as is desired; however, the amount of time required to do numerical calculation is prohibitively long.

Multivalued-Multistep Methods

Given an approximation of y at some value t_n , a technique exists for the computation, by Runge-Kutta or some similar method, of Y at time t_{n+1} . These methods are all single-step methods because they require only the previous value to compute the new value. Once a series of points, say at time t_{n-4} , t_{n-3} , t_{n-2} , t_{n-1} , have been calculated, they can aid in the computation of later points. Pieces of information concerning the solution of a differential equation at $t = t_{n-1}$ can be stored and used to compute equivalent information at $t = t_n$, and such methods are called multivalued methods. Such methods use values for the dependent variable and its derivatives at different mesh points and are commonly referred to as multistep methods.

Suppose there exists some system which has been approximated at k points, i.e., t_{n-k} , t_{n-k+1} , ..., t_{n-1} . There exists a history y_{n-k} , y_{n-k+1} , ..., y_{n-1} , and $h\dot{y}_{n-k}$, $h\dot{y}_{n-k+1}$, ..., and $h\dot{y}_{n-1}$. This information or some subset of it can be used to approximate y_n and $h\dot{y}_n = hf(y_n)$. Define a column vector $\bar{y}_{n-1}$ such that

$$\bar{y}_{n-1} = \begin{pmatrix} y_{n-1} \\ \cdot \\ \cdot \\ y_{n-k+1} \\ y_{n-k} \end{pmatrix} \quad (44)$$

The objective of a multivalue technique is to obtain a value for $\bar{y}_n$ from the initial vector $\bar{y}_{n-1}$ and the differential equation $y = f(y)$. Note we have simplified the differential equation, but the extensions are obvious. The vector $\bar{y}_n$ has the components

$$\bar{y}_n = \begin{pmatrix} y_n \\ y_{n-1} \\ \cdot \\ \cdot \\ y_{n-k+1} \\ \cdot \\ h\dot{y}_{n-1} \\ \cdot \\ \cdot \\ h\dot{y}_{n-k-1} \end{pmatrix} \quad (45)$$

The process that is described is repetitive; that is $\bar{y}_1, \bar{y}_2, \bar{y}_3, \dots, \bar{y}_n$ can successively be calculated once $\bar{y}_0$ is known. The method of finding $\bar{y}_0$ can be difficult, but methods are available.¹²

A multivalued method can be divided into two steps. In the first step, a prediction of y_n is made; that is, an approximation of $\bar{y}_n$ is computed from y_{n-1} by linear extrapolation. This approximation is labeled $\bar{y}_{n(0)}$ and is given by

$$\bar{y}_{n(0)} = B\bar{y}_{n-1}, \quad (46)$$

where B is some suitable matrix, with constants $\alpha_i, \beta_i, \gamma_i$ and δ_i , such that

$$\sum_{i=1}^k (\alpha_i y_{n-1} + \beta_i h \dot{y}_{n-i}) \quad (47)$$

is an approximation to y_n and

$$\sum_{i=1}^k (\gamma_i y_{n-i} + \delta_i h \dot{y}_{n-i}) \quad (48)$$

is an approximation to $h \dot{y}_n$.

The second step of the process is the correction step. The prediction step made no use of the differential equation; the correction step uses the differential equation to correct $\bar{y}_{n(0)}$ at t_n if $\bar{y}_{n(0)}$ does not satisfy the differential equation. The differential equation is written as

$$0 = G(\bar{y}_n) = -(\bar{y}_n)_k + hf[y_{n(0)}], \quad (49)$$

where $(\bar{y}_n)_k$ represents the k^{th} component of $\bar{y}$. The amount by which $\bar{y}_{n(0)}$ does not satisfy the differential equation is $G[\bar{y}_{n(0)}]$. A vector multiple of this scalar is added to $y_{n(0)}$ to correct it by the process

$$y_{n(1)} = y_{n(0)} + \bar{c}G[y_{n(0)}]. \quad (50)$$

The corrector process can be repeated m times until either convergence is obtained or m is some fixed value, i.e.,

$$y_{n(m+1)} = y_{n(m)} + \bar{c}G[y_{n(m)}], \quad (51)$$

where m is defined as the number of corrector iterations.

Many methods have been developed to implement the multipoint method above, and such methods are well documented.⁷ The method we shall investigate is called Gear's method.

Method of Gear and Nordsieck

In ecosystem models we are interested in solving systems of ordinary differential equations (ODEs) which have the form

$$y_i(t) = f_i[y_1(t) \dots y_n(t), n]. \quad (52)$$

It is assumed that the initial value of y is known, that is

$$y(t_0) = y_0.$$

The method developed by Gear⁸ and improved by Hindmarsh¹² computes a numerical solution for Eq. (52) for values of t in the interval (t_0, t_f) . Gear's method is a multistep, predictor-corrector method of the type outlined in the last section, but with some important improvements. The method has the remarkable ability to handle systems of ODEs which are stiff.

A system of differential equations is considered to be stiff if they contain both rapidly varying and slowly varying terms. Consider, for a moment the Jacobian

$$J = \frac{\partial f}{\partial y} = \left(\frac{\partial f_i}{\partial y_j} \right)_{i,j=1}^n.$$

If the eigenvalues λ_i of J all have negative real parts, but the time constants

$$\tau_i = \frac{1}{|\operatorname{Re}(\lambda_i)|}$$

are rapidly varying, then the system is defined as being stiff. The possibility of such stiff systems occurring in any ecosystem model is obvious. The property of stiffness is a local property, that is, a problem may be stiff in some regimes and not in others. The difficulty

with stiff systems is that one is necessarily forced to solve the system of incremental values of t which are commensurate with the minimum time constant, while the range of the problem is dependent on the maximum time constant. From a practical standpoint, this limitation means that the system would take a prohibitively long time to solve.

We can rewrite Eq. (47) of the previous section into the following form:

$$y_n = \sum_{j=1}^{k_1} \alpha_j y_{n-j} + h \sum_{j=0}^{k_2} \beta_j \dot{y}_{n-j}, \quad (53)$$

where h is again a constant time step: $h = t_{k+1} - t_k$. For Gear's method of order q : $k_1 = q$ and $k_2 = 0$. The requirement that $\beta_0 \neq 0$ means that Eq. (53) is an implicit equation for y_n and is a nonlinear system which must be solved at every step. Since the method is of order q , y_n will differ from the exact solution of Eq. (52) by a truncation error of $O(h^{q+1})$ for small h . If Eq. (53) is rewritten as

$$G(y_n) = y_n - h \beta_0 f(y_n, t_n) - \sum_{j=1}^{k_1} \alpha_j y_{n-1} - h \sum_{j=1}^{k_2} \beta_j \dot{y}_{n-j}, \quad (54)$$

then the nonlinear system $G(y_n) = 0$ may in principle be solved. Probably the most powerful method for obtaining a solution is Newton's predictor method

$$y_{n(m+1)} = y_{n(m)} - P_{n(m)}^{-1} G[y_{n(m)}], \quad (55)$$

where the matrix $P_{n(m)}$ is defined as

$$P_{n(m)} = \left. \frac{\partial G}{\partial y} \right|_{y_{n(m)}} = I - h \beta_0 \left. \frac{\partial f}{\partial y} \right|_{y_{n(m)}}. \quad (56)$$

Newton's method requires that the matrix $P_{n(m)}$ be inverted and this is usually a costly operation. The chord method and the functional iteration

method¹² describe two less expensive methods of obtaining $y_{n(m+1)}$.

In the previous section the vector $\bar{y}_n$ was described by Eq. (45). However, Nordsieck⁹ has transformed Eq. (45) into the following form:

$$\bar{z}_n = \begin{bmatrix} y_n \\ h\dot{y}_n \\ h^2 y_{n/2} \\ \vdots \\ h^q y^{(q)} / q! \end{bmatrix}, \quad (57)$$

which is an $n \times \ell$ array of scaled derivatives of y and t_n up to order q . The derivatives are defined by reference to a unique vector valued polynomial of order $\leq q$ defined by the $q + 1$ vectors in Eq. (45). The array $\bar{z}_n$ is the array of scaled variables of the polynomial at $t = t_n$. With this choice of history, the prediction of y_n from $\bar{z}_{n-1}$ is extremely simple and is given by

$$\bar{z}_{n(o)} = \bar{z}_{n-1} A, \quad (58)$$

where A is an $\ell \times \ell$ Pascal triangle matrix. Gear observed that the matrix multiplication can be done with addition only. The complete algorithm for the one iteration of Z , i.e., going from $\bar{z}_{n-1}$ to $\bar{z}_n$ has been given by Gear¹³ as:

$$\bar{z}_{n(o)} = \bar{z}_{n-1} A$$

$$Y_{n(m+1)} = Y_{n(m)} + \ell_o P_m^{-1} F_m$$

$$F_{(m)} = hf(Y_{n(m)}, t) - h\dot{y}_{n(m)}$$

$$Y_n = Y_{n(m)} = Y_{n(o)} + \ell_o E_n$$

$$E_n = \sum_{m=0}^{m=1} P_n^{-1} F_{(m)}$$

$$\bar{Z}_n = \bar{Z}_{n(0)} + E_n \bar{X}_0,$$

where M is the number of iterations performed and $\bar{X} = (\ell_i)_0^q$ is a row vector of constants satisfying $\ell_0 = \beta_0$ and $\ell_1 = 1$. The vector E_n is proportional to the estimated truncation error committed on the next step.

Monte Carlo Techniques

Monte Carlo techniques have been used for a number of years in physics, medicine, biology, and economics. The application of Monte Carlo techniques to ecosystem models has been carried out by Harris and Beyer¹⁴ at Los Alamos. The technique consists of making random selections in order to predict the development of a certain state of a process. Such techniques can be applied to a stochastic process in order to simulate that process. When a large number of states of the system are followed with the same initial conditions an average development of the stochastic process is predicted.

The technique developed by Harris and Beyer is called the event-consequence technique. In this technique one not only obtains the average development of the stochastic process, but departures from the average are found to be significant and can be related to observation. The Monte Carlo techniques as described in this section have been used for a population dynamics model of the Isle Royale Biome.¹⁵

Suppose there exists a population-dynamics system with properties that can be described by the time development of j random variables $X_1, X_2, \dots, X_j$. At a particular time, t_0 , the system can be described by a state vector $\bar{X}$ which is composed of the particular values of $\bar{X} = \{X_1(t_0), \dots, X_j(t_0)\}$. The populations obviously are not static but change as the

results of events $E_1, E_2, \dots, E_k$ which will modify $\bar{X}$. The rate R_k of events of type k at time t is a function of the state $\bar{X}$ of the system at time t and is also a function $\bar{f} = \{f_1(t), f_2(t), \dots, f_{\hat{n}}(t)\}$ where f is independent of the state of the system. Hence

$$R_{kt} = R_k(\bar{X}; \bar{f}; t) = R_k(X_1, X_2, X_3, \dots, X_{\hat{n}}; f_1(t), \dots, f_{\hat{n}}(t); t), \quad (59)$$

where $k = 1, 2, \dots, \hat{k}$. The total rate R of events at time t is simply the sum over k , i.e.,

$$R_t = \sum_{k=1}^{\hat{k}} R_{kt}. \quad (60)$$

The rate will either remain constant, or change as a function of $f_n(t)$, where $n = 1, 2, \dots, \hat{n}$. This change will continue until the next event and its related consequence occurs.

The probability that no event occurs between t and t' is just

$$e^{-\int_t^{t'} d\tau R_\tau}, \quad (61)$$

so the probability that $P(t')dt'$ of the next event occurring in the time interval $(t', t' + dt')$ is,

$$P(t') dt = e^{-\int_t^{t'} d\tau R_\tau} dt' R_{t'}. \quad (62)$$

The time that the next event will occur is selected by a Monte Carlo sampling of Eq. (62). Once the time t' of the event is known, the type of event is again selected by a Monte Carlo sampling of the set of probabilities R_{kt}/R_t , that the event occurring at time t' will be of type k .

Once an event occurs the consequence of that event must be determined. An event of type k can cause a number of different consequences $C_{k1}, C_{k2},$

..., C_{km} , each of which can alter the system $\bar{X}$ in different ways. The probability that the event of type k at time t' will have a consequence is defined as $P_{kmt'}$, and may also be a function of the state $\bar{X}$ and the deterministic quantities f at time t' :

$$P_{kmt'} = P_{km}(\bar{X}; f; t'). \quad (63)$$

The particular consequence is again selected by a Monte Carlo sampling of

$C_{kmt'}/C_{kt'}$, where $C_{kt'} = \sum_{m=1}^m C_{cmt'}$. Once the appropriate consequence is

selected, the state $\bar{X} = X_1, X_2, \dots, X_j$ is changed to reflect that consequence, and an iterative cycle is complete. One then returns to Eq. (62) to determine what time the next event will occur.

The above system is a simple, brute force method of simulating stochastic processes; however, the simulation is extremely dependent on the reliability of the input data.¹⁶ The implementation of a Monte Carlo calculation would require efficient computers to perform the needed samplings effectively. Such Monte Carlo techniques should be considered very seriously.

Statistical Methods

The techniques discussed in the main body of this report are primarily process oriented. A dynamic, ecosystem simulation model is presented as an attempt to abstract the significant features of the physical processes of the ecosystem. This approach is based upon having some degree of understanding of the physical and biological processes of the ecosystem.

The formulation and calibration of such a model proceeds with informed scientists making hypotheses concerning the essential characteristics of each ecosubsystem and its interactions with other subsystems. In the analysis of complex, poorly observed systems these hypotheses are

often based upon an elusive combination of intuition and experiment. There exists, however, a large body of knowledge which may be applied to problems of this type.

Following is a brief discussion of several techniques which appear to have substantial merit with regard to providing assistance in the formulation of complex ecosystem models. These techniques are primarily empirical and are best applied to testing a specific hypothesis concerning the operation of an ecosubsystem. Testing a variety of functional forms with respect to their value as descriptors of a particular interaction or determining the parameter values associated with a particular functional form are possible applications of the techniques presented below. For each case the mathematical details have been omitted. The appropriate references have been included.

Least-Squares Methods

Least squares analysis allows one to describe the variation of a dependent variable, called a predictand, as an arbitrary function of a number of other variables, sometimes called predictive variables. This technique is a generalization of regression analysis which includes methods to deal with nonlinear functions and dependent variables. The relation can be expressed as follows:

$$y = f(x_1, x_2, x_3, x_4, \dots, x_n),$$

where y is the predictand, $x_{i=1,n}$ are the predictors, and f is an arbitrary differentiable function.

If a hypothesis is made concerning the identity of a functional form describing a process for which data exists, the hypothesis can be tested by fitting the proposed function to the data using least squares methods and examining the residual variance, a measure of the goodness

of fit. The least squares analysis simultaneously calculates the best estimates of the parameters of the function (according to the least squares criterion) which can then be used in the dynamic tool.

Although this method is an extremely valuable tool it must be used with caution. The results of this type of analysis do not imply a cause and effect relationship between the predictand and the predictive variables. The analysis shows only how the variables vary together from a purely empirical standpoint. One must also beware of using least squares analysis on a system which has been only partially observed due to the danger of completely ignoring an important variable and thus generating spurious predictions. These considerations are the basis for using this type of analysis as a tool for testing hypotheses generated from other, less empirical, motivations. These methods have been extensively investigated,¹⁷⁻¹⁹ and "canned" computer codes appropriate for typical applications exist.

Time-Series Techniques

A logical extension of the least-squares technique is to include time as a variable. This modification can be viewed as changing the time origin of one or more of the predictive variables. This time lag ideally represents some physical delay in the ecosystem, for example the relationship between the number of seeds one year and seedlings the next.

Mathematically speaking we are looking at each of the predictive variables as a time series and we may, in principle, "slide" each such series until an optimal time lag for each, with respect to minimizing the least squares error of the values of the predictand, has been found. Note that time lags calculated in this way may be used in the calibration of dynamic simulators if the lag is determined to have some physical meaning.

This type of time-series analysis may be considered closely akin to least-squares analysis from the point of view of the ecosystem modeler who should view it as a tool to be used in the formulation of dynamic model subject to the same caveats as discussed above for least-squares methods.

Time-series analysis also is useful in estimating the frequency and magnitude of periodicities in the data. This information may be useful in testing hypotheses concerning the duration of biological cycles within the ecosystem, and perhaps for making simple predictions where deemed appropriate. Time series analysis has also been the subject of extensive investigation¹⁹⁻²¹ and "canned" computer programs are available.

Classification Techniques

There are a number of individual mathematical methods which are useful in identifying patterns in observations of a complex system. They include multiple discriminant analysis, factor analysis, cluster analysis, and various heuristic pattern recognition and classification schemes. The object here is to outline the capabilities and applicability of each without presenting the mathematical details.

Multiple Discriminant Analysis (MDA) is a statistical technique for classifying sets of observations into discrete categories. For example, if one were to attempt to classify a number of stands* into a set of pre-existing categories by determining the similarity of the attributes of each stand to the attributes of each category, MDA would be an appropriate tool. It compares the respective attributes quantitatively and develops classification functions called discriminant functions to perform the classification and calculate the probability of error in the classification.²²

Factor analysis refers to a group of procedures which analyze the intercorrelation between a set of variables. One technique, called

* A stand is a group of trees which can be viewed as homogeneous in their relevant characteristics.

principal-components analysis, is used to produce a composite scale from a group of variables by determining the principal axis of the ellipsoid of the correlogram. Using another technique, a set of m variables can be reduced to a set of n orthogonal factors which sacrifice the minimum amount of information possible, where n is arbitrary and smaller than m . This technique is especially valuable where the original variables are highly intercorrelated. A slightly more sophisticated technique is used to identify fundamental dimensions in a multivariate domain by first identifying the principal components of the domain and then transforming them so that the factors have the simplest physical interpretation possible.²³

The factor analysis techniques can be used in the classification of stands, the development of an objective standard for tree health, the description of complex interactions by simplified variables, and other applications where it is desirable to reduce the number of variables under consideration, or develop improved metrics for describing system variables.

Cluster analysis is a technique ordinarily considered under the rubric of graph theory. Given a set of points in an n dimensional space and an arbitrary but fixed number m of desired clusters, this technique will classify the points into m categories such that the distance between points within each cluster is minimized while the distance between points between clusters is maximized according to some specified criterion. This method can be applied to the classification of tree-types by plotting their attributes in n -dimensional space (age, health, location, etc. as axes) and performing a cluster analysis. This would aggregate neighboring trees in state space into a fixed number of categories.²⁴

The number of possible heuristic techniques is infinite. The basis of one such technique is to predict the evolution of a stand in a particular situation with respect to its own characteristics and those of its

environment by searching the data base for the occurrence of a similar situation in the past and examining the evidence concerning the evolution of the stand represented in the data base. We then assume that the stand for which we are making predictions will behave over a short interval of time as did the one in the historical record. These predictions may then be used to enter the data base again looking for a stand or a group of stands (if the original homogeneous group of trees has diverged in some characteristic) which are similar to the predictions. In this way an iterative look is created which allows predictions based only on the previous behavior of some element of the forest. Should such elements not exist in our data base we may "create" them by interpolating and/or extrapolating from other points in the data base to fill the gaps. This technique has several attributes of interest. First, it assumes no knowledge of the nature of the interaction of the various ecosystem components. It is strictly data limited with respect to the situations and events predicted. However it is straightforward, very simple to apply, and has a high probability of making useful estimates in situations for which data is available. It is potentially a valuable tool therefore, in validating a more complex ecosystem simulator.

SUMMARY

In the previous sections we have looked at particular forms an ecosystem model might assume, and we have investigated numerical techniques for solving such equations. There are, of course, many techniques for solving equations, each with their own advantages and drawbacks. Many of the techniques which are commonly used in physics, chemistry, and biology are only now becoming fashionable in ecology; we have looked at several such techniques.

Since ecosystems are extremely complex and highly varied, a combination of various mathematical techniques might be used to model them.

Such a method might use Monte Carlo and other statistical techniques to handle highly stochastic processes and discrete numerical techniques to solve the more deterministic processes.

APPENDIX

In this section, we discuss a further decomposition of the abiotic and biotic factors. The decomposition allows us to rewrite Eq. (12) in a different form.

Suppose that the abiotic functions can be decomposed as follows:

$$a_i(t, t') = a_{1i}(t, t') + a_{2i}(t, t') = a_{1i} + a_{2i}. \quad (A-1)$$

Here a_{1i} represents the abiotic coefficient which takes us from any other state of species i ; $N_i(\bar{\ell}, \bar{h})$ to the present state of species i ; $N_i(\ell, h)$.

Thus

$$a_{1i} N_i(\bar{\ell}, \bar{h}) \rightarrow N_i(\ell, h). \quad (A-2)$$

Similarly, a_{2i} represents the abiotic coefficient which projects out of the present state $N_i(\ell, h)$ of species i to any other state $N_i(\bar{\ell}, \bar{h})$ of species i , that is,

$$a_{2i} N_i(\ell, h) \rightarrow N_i(\bar{\ell}, \bar{h}). \quad (A-3)$$

A similar decomposition can be applied to the biotic coefficients

$$\beta_{ij}(t, t') = \beta_{1ij}(t, t') + \beta_{2ij}(t, t') = \beta_{1ij} + \beta_{2ij}, \quad (A-4)$$

where

$$\beta_{1ij} N_j N_i(\bar{\ell}, \bar{h}) \rightarrow N_i(\ell, h) \quad (A-5)$$

and

$$\beta_{2ij} N_j N_i(\ell, h) \rightarrow N_i(\bar{\ell}, \bar{h}). \quad (\text{A-6})$$

Here N_j represents the effect of another species N_j which may or may not have its own particular health class. Note that m has been arbitrarily set equal to one (see Eq. (9)). If such decompositions are possible, then Eq. (12) can be rewritten as:

$$\begin{aligned} \frac{dN_i(\ell, h)}{dt} = & [a_{2i} + \beta_{2ij} N_j] N_i(\ell, h) \\ & + \sum_{\bar{\ell}, \bar{h}} [a_{1i} + \beta_{1ij} N_j] N_i(\bar{\ell}, \bar{h}), \end{aligned} \quad (\text{A-7})$$

where the sum is over the other age and health classes (ℓ, h) . The first term on the right hand side of (A-7) represents a "depletion" of $N_i(\ell, h)$ due to both biotic and abiotic factors, while the second term represents an "addition" to $N_i(\ell, h)$ due to biotic and abiotic factors.

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