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The Ecosystem Modeling Approach in the Coniferous Forest Biome*

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I. Introduction

This chapter outlines the approach taken by the author and associates in development of a total system model for the Coniferous Forest Biome, summarizes the current state of development of the model form and modeling capacity, and identifies several currently recognized problem areas.

No attempt is made to report the "process modeling" activities of the Biome, even though it is recognized that such activities contribute to the development of subsystem models in the total system model. Process

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modeling is typically oriented to traditional disciplines and constrained by traditional boundaries and modes of thought. If the principles of general systems can contribute to the development of ecosystem theory through the development of explicit ecosystem models and model forms, then it is likely that some, or most, of the traditional boundaries and constraints must be abandoned.

The general orientation of the investigation here reported follows the view that modeling is the imposition of form and structure on knowledge, that scientific theory is a perceived order in a real world system, and hence that models are explicit expressions of theory. It follows that an attempt to develop a general model form for an ecosystem is an attempt to develop a conceptual structure for ecosystem theory, and that a proposed paradigm for an ecosystem model is a proposed component of the general paradigm of ecosystems.

II. Development of the General Requirements for an Ecosystem Model

The approach taken in development of a paradigm for ecosystem models was to choose a general system theory that apparently filled the needs of ecosystem modeling and adapt this into a general ecosystem paradigm. To implement this, we attempted to specify the general properties that such a paradigm should possess and identify a general system theory that readily accommodates these properties. To focus on the needed properties, we tried to analyze the problem from the *system point of view*.

A simple statement of the general system point of view is as follows: The system has properties, some of which are not recognizable as properties of its parts, but which result from the system structure. Further, the properties and behavior of a part cannot be studied *only* in isolation, but rather must be characterized in the context of couplings with the rest of the system.

In this view, it is not sufficient to model the behavior of parts, and couple the submodels together to obtain a model of the whole. Rather, it is necessary also to study and model the system as a whole so as to capture those properties which are not apparent from study of the parts.

It will be recognized that this view is not universal, that some investigators dismiss the holistic argument, holding that properly modeled parts, coupled together, will yield a properly modeled system. This difference in views is possibly semantic, because the holistic properties derive from the nature of couplings. However, it is difficult to see how couplings can be properly modeled in the absence of an explicitly prescribed holistic system behavior which the system model is constructed to reproduce.

Here it would be useful to illustrate the point with some nice ecosystem examples. Unfortunately, none have been verbalized at the ecosystem level so far as I know, and this may be interpreted as refutation of my position. However, it is my argument that the situation is due to the newness of the system study of ecosystems—we have few concepts of ecosystem behavior. The undeveloped state of general systems theory and analysis may also have a part; we have little to guide us in the search for holistic behavior. Nevertheless, we are supported in this view of system behavior by much current literature, as for example, von Bertalanffy (1968), Koestler (1967), and Simon (1973).

Our perception of the ecosystem as an entity—as an object—is based in part on our perception that ecosystems are self-organizing and resilient assemblages of interacting organisms and that they exhibit homeostasis, at least under some conditions. It is one objective, then, of ecosystem research to elaborate the concept of holistic behavior of ecosystems and to construct a theory of this behavior. One approach in constructing such a theory is to begin with a *general theory* (e.g., *general system theory*) and to explicate this as a *general ecosystem theory*. To implement this, we shall specify the general properties that such a theory should possess, and identify a general system theory which can accommodate these properties.

The ecosystems which are studied will exist, for the most part, in stable environments, and the systems themselves will generally exhibit a high degree of homeostasis. Our first models will describe the systems in such a state. To complete the description of the holistic behavior of these systems, it will be necessary to define the bounds of homeostasis—the limits of environmental perturbation or physical disturbance beyond which the homeostatic mechanisms break down and the system assumes another form. (This is made quite complex by the evolutionary or successional nature of the systems in question, which requires distinction between another point on the same successional trajectory vs a point on another successional trajectory.) The direct experimental study of these phenomena will either be impossible, as in the case of general climatic regimes, or destructive. It is here that mechanistic models are needed. The investigative approach must be of the general form (after elaboration of the holistic model): (i) construct mechanistic models which explicate *how* the system works according to the best current theory, (ii) analyze the mechanistic model(s) to *predict* the limits of homeostasis, (iii) determine by *sensitivity analysis* the model components to which the predictions are sensitive, and (iv) if necessary, construct *field experiments* to study these critical model components.

These thoughts led to the first organizational constraint for an ecosystem modeling effort. Each system will be conceptualized, characterized, and modeled in two ways: (i) holistically, in terms of the behavior of the system

as an object, and (ii) mechanistically, in terms of the coupled relations of explicit subsystems, each of which is modeled in terms of its holistic behavior.

Given that the system is to be studied and modeled both holistically and mechanistically, one must then ask the degree of fineness which can be allowed in the mechanistic model. That is, what will be the identity of the elements of this model? Will they be populations, trophic levels, or communities? How much *detail* can be accommodated in the mechanistic model? Hypothetically, there is no limit. If an arbitrarily large set of quantities is identified and the relations between them specified, then hypothetically it is possible to "run" the system, and this is the perspective that many people seemed to have in the early days of IBP.

However, there are very severe *practical* limits to system "size." Conceptualization, assembly, communication, verification, validation, analysis, and study of behavior are all greatly limited by the dimension of the system. Consider, for example, a small model with ten parameters. If one wishes to examine the response surface of this model with five points in each dimension, then $5^{10} = 9{,}765{,}625$ computer runs are required. If the model is so structured that one can study it in two *parts*, say with six parameters each, then $2 \times 5^6 = 31{,}250$ runs are needed. If one desires only two points in each dimension, the above procedure reduces the number of runs from 1024 to 128.

Now even 128 computer runs, for a 10-parameter model, seems high, particularly when we are used to thinking about ecosystem models with 200 parameters. Obviously something *else* needs to be done to reduce the number of runs necessary in studying behavior, but the above example demonstrates that the device of constructing *subsystems* is clearly of great advantage. That is, if large complex systems can be modeled in terms of subsystems, each of which can be studied in isolation by virtue of the specific coupling structure that has been provided, then the dimensionality problem can be greatly reduced.

This point recalls Herbert Simon's (1962) parable of the two watchmakers, the lesson of which is relevant not only to our view of evolution of stable natural ecosystems, but also to a properly verified assembly of computer models. The conclusion is inescapable. Large complex ecosystem models should be hierarchically modular, first because there is good reason to believe that this is the most useful conceptual structure for ecosystem theory, and second because this is the only practical way in which to assemble a large complex model. This requires the identification of several echelons of *subsystems* from *ecosystem* to *population* and, perhaps, *individual*, as the finest subsystem. In a purely speculative vein, it is proposed that each echelon consist of no more than five to eight subsystems with no more than ten to twenty state variables.

These thoughts lead to a second organizational constraint for ecosystem modeling. Each system, or subsystem, will be considered a *holon*, in the terminology of Arthur Koestler (1967); that is, it will be (potentially) a subsystem of a greater system and, simultaneously, a coupled collection of lesser subsystems. This leads to the elaboration of the two definitions (holistic and mechanistic) over a hierarchical model structure.

A few other relatively minor points regarding orientation of our modeling effort are relevant. A clear distinction is made between modeling and programming. Although some programming may be done by modelers, and some modeling by programmers, the two activities are separated as much as possible in order to maintain the distinction. It is easy for programming to dominate the activity pattern of persons engaged in both activities.

The use of a general model processor (which will be described later) contributes to this goal, and also serves other purposes. With a general processor available, programming becomes a secondary concern, and the modeler can get on with the business of modeling. There is some loss of flexibility, but this is more than compensated by reduction in debugging time and ease of communication. Anyone familiar with a general convention can quickly read and comprehend a strange model written in that convention. This also allows for general ease of critical review, which is an increasingly vital aspect of Coniferous Biome activity. An additional virtue of a general processor, which we did not anticipate, is that it discourages "brute force" modeling, and encourages some degree of modeling finesse, with obvious benefit to the goal of ecosystem theory elaboration.

In summary, the identified constraints on model structure and modeling activity are (i) the system model will be hierarchical, with perhaps five to eight subsystems and ten to twenty state variables per echelon, (ii) each "system" will be modeled at two levels, holistic and mechanistic, and (iii) a general processor will be developed which will accommodate this structure and so eliminate as far as possible special purpose programming.

In addition, these theoretical considerations have given recognition to several nonassembly research needs. First, the need to conceptualize meaningful subsystems of ecosystems is apparent, as is the need to identify holistic properties and behavior of ecosystems and subecosystems. These are areas in which modelers and models can contribute, but which are central problems in the development of ecosystem theory.

III. Development of a General Paradigm for an Ecosystem Model

The general system theory of George Klir seems to satisfy the requirements and provide the structure specified by our theoretical appraisal of

the ecosystem modeling problem. This theory is elaborated by Klir (1969) and by Orchard (in Klir, 1972), the latter of whom has suggested an additional structure to accommodate evolutionary systems. This is an appealing feature if we are looking forward to models which will exhibit successional behavior. However, our current efforts do not include evolutionary processes and, in any event, it is not apparent, at least to me, that Klir's original theory will not adequately accommodate evolutionary processes. The present treatment involves only Klir's original theory. The paper by Overton (1972) describes in some detail the development of a general ecosystem model structure according to Klir's general theory.

Of Klir's five alternate definitions of systems, two are relevant to our effort. The system may be defined:

(1) According to its permanent behavior. That is, by a time invariant relation between the *output quantities*, on the one hand, and the rest of the *principal quantities*, on the other.

(2) According to its universe–coupling (U-C) structure. That is, as a set of elements (subsystems), each defined according to its permanent behavior, and a set of directed couplings between the elements and between the elements and the environment.

The concept of *principal quantities* is essential to these definitions. First define the *external quantities* as the system *outputs* Y and *inputs* Z, and imagine, at time t, the instantaneous values of the external quantities, in the array of instantaneous values at all prior and subsequent times (Fig. 1). Now choose a *mask*, which blocks out most, but exposes some of these values. When oriented to time t, this mask identifies the value of the *principal quantities* for time t. These will typically include all of the output quantities at time t, and the *behavior* is defined as the time invariant relation between these instantaneous *output quantities* and the rest of the *principal quantities*.

The directed couplings between two systems S_i and S_j will be designated as C_{ij} and C_{ji}, where C_{ij} is the set of output variables of S_i which are inputs of S_j, $C_{ij} = Y_i \cap Z_j$, and similarly $C_{ji} = Y_j \cap Z_i$.

In restricting this general theory to form our current version of an ecosystem model, we have explicated the time invariant relation as a difference equation. We do not identify the principal quantities, per se, but rather maintain the identity of input (Z) and output (Y) quantities, with the additional specification of memory variables (M), which can include past values of input or *state* variables (the latter of which are not specified in Klir's theory). *State* variables are defined for structural economy and convenience; they are often identical to output variables. Note that this use of *state variables* is different from the usual state variable convention in

External Quantities	----	t-3	t-2	t-1	t	t+1	t+2	----
Z_1	----	$Z_{1,t-3}$	$Z_{1,t-2}$	$Z_{1,t-1}$	$Z_{1,t}$	$Z_{1,t+1}$	$Z_{1,t+2}$	----
Z_2	----	$Z_{2,t-3}$	$Z_{2,t-2}$	$Z_{2,t-1}$	$Z_{2,t}$	$Z_{2,t+1}$	$Z_{2,t+2}$	----
Y_1	----	$Y_{1,t-3}$	$Y_{1,t-2}$	$Y_{1,t-1}$	$Y_{1,t}$	$Y_{1,t+1}$	$Y_{1,t+2}$	----
Y_2	----	$Y_{2,t-3}$	$Y_{2,t-2}$	$Y_{2,t-1}$	$Y_{2,t}$	$Y_{2,t+1}$	$Y_{2,t+2}$	----
Y_3	----	$Y_{3,t-3}$	$Y_{3,t-2}$	$Y_{3,t-1}$	$Y_{3,t}$	$Y_{3,t+1}$	$Y_{3,t+2}$	----

(a)

External Quantities	----	t-3	t-2	t-1	t	t+1	t+2	----
Z_1				$P_{2,t}$	$P_{1,t}$			
Z_2			$P_{5,t}$	$P_{4,t}$	$P_{3,t}$			
Y_1					$P_{6,t}$			
Y_2				$P_{8,t}$	$P_{7,t}$			
Y_3				$P_{10,t}$	$P_{9,t}$			

(b)

FIG. 1. (a) The system activity, the external quantities at the instant of time t and all past and future instants. (b) The principal quantities of time t are identified as those visible when the *mask* is imposed on the system activity at time t [after Klir (1969)].

that memory quantities are not included in this classification in our usage.

These restrictions are incorporated into a *paradigm* for a general *behavioral* model structure, called FLEX ,which is currently implemented by the program, FLEX1. The influence of Freeman (1965) is noted. The FLEX paradigm is summarized as follows:

$$\mathbf{x}(k+1) = \mathbf{x}(k) + \boldsymbol{\Delta}(k),$$

$$\mathbf{y}(k) = \mathbf{h}[\mathbf{x}(k)],$$

where the lth element of $\boldsymbol{\Delta}(k)$ is defined as

$$\Delta_l(k) = \sum_{i=1}^{n} f_{il}(k) - \sum_{\substack{j=1 \\ j \neq l}}^{n} f_{lj}(k).$$

Here, the flux from element i to element j is

$$f_{ij}(k) = f_{ij}\{\mathbf{x}(k), \mathbf{z}(k), \mathbf{M}(k), \mathbf{b}, \mathbf{r}, \mathbf{g}(k), \mathbf{s}(k), k\},$$

where $\mathbf{b}$ and $\mathbf{r}$ are vectors of constants (parameters); $\mathbf{g}(k)$ is a vector of intermediate functions of the form of the f functions, with the restriction that $g_i(k)$ cannot be a function of $g_j(k)$ if $j > i$; $\mathbf{h}[\mathbf{x}(k)]$ is a vector of functions of the vector $\mathbf{x}$; and $\mathbf{s}(k)$ is a vector of "special functions" which may also use the argument set of the f functions.

FLEX1* (Overton *et al.*, 1973) is a model processor for a model written in the FLEX paradigm and representing either the whole system or a terminal subsystem in a hierarchical structure. Operation is teletype oriented, with provision for teletype monitoring during a run. Output is normally line printed and stored on a dump file, and a series of satellite programs have been written for examination of the stored output.

This system is operational with 20 system models implemented as of May 1, 1973. Several of these have been translated from other computer program documentation into the FLEX structure, so that some experience in the general utility has been gained. Program implementation is restricted to Oregon State University (OSU) at present, FLEX1 being specific for the OS3 operating system on OSU's CDC 3300. If this approach proves sufficiently useful, translation to a more generally available and larger system is indicated.

An explicit paradigm (REFLEX) for hierarchical representation according to the U-C structure is currently under development, and a major part of the computer code has been written for its processor. The FLEX and REFLEX modes will be accomodated by a single processor FLEX2, which is scheduled for late 1973 (White and Overton, 1974).

Figure 2 illustrates the relationship between our explication of the two model definitions. Each proper subsystem in REFLEX is modeled either according to FLEX or according to REFLEX. The ghost system, S_0, is the integrator of the outputs and inputs of the proper subsystems. It is seen that S_0 contains all features of S, except the f functions; these are replaced by the subsystems.

In accordance with the concept that Fig. 2b is a finer resolution model than Fig. 2a, temporal resolution of the proper subsystem will be an integral fraction of the temporal resolution of S. S_0 will operate at both resolutions, being updated by the subsystems at their resolution and receiving outside inputs and sending outside outputs according to the resolution of S. Note,

* FLEX1 was programmed by J. A. Colby, C. White, and V. Hunt, with contributions by J. Gourley and E. Schroeder.

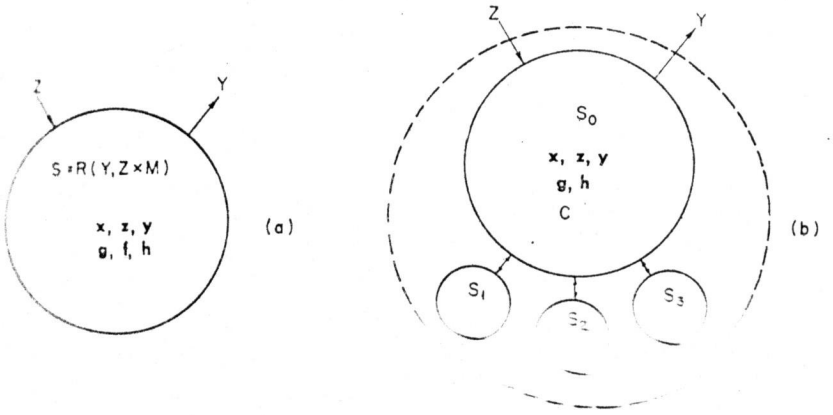

FIG. 2. Relationship between (a) FLEX and (b) REFLEX, $\mathscr{S} = \{\mathscr{S}_0, \mathscr{S}_1, \ldots, \mathscr{S}_n; C\}$.

also, that the model of a particular system, according to each of these forms, will involve *exactly* the same specification of system inputs and outputs and the same system resolution. Thus, one form may be substituted for the other without external change, this feature providing the modularity desired.

The management of all subsystem coupling through the ghost system serves two purposes. First, it eliminates the need for rigid sequential processing of subsystems. In the present form, order of subsystem processing is immaterial. Second, it provides for easy imposition of "regulation" of flow relations by both elements, donor *and* receiver. This point will be elaborated in the section on technical aspects.

In accordance with the *systems view* that a subsystem must be studied in the context of the system of which it is a part, it is anticipated that a specific question regarding ecosystem activities or behavior will be answered by simulation of a model structured something as illustrated in Fig. 3. The zero subscripts indicate ghost systems controlling the systems at the next lower echelon, and the *question* to be answered applies specifically to one of the lowest echelon subsystems. Note that each subsystem or coupled group of subsystems in the above structure can be studied individually (i.e., in isolation) with regard to its behavior, or tuned to yield the desired behavior. Then, after each is tuned to satisfaction, the entire system (or any part) can be coupled together to study behavior of any part in the context of the whole.

This, then, represents our current view of a working total system model, in variable resolution, and with the dimensionality of the coupling structure greatly reduced by the explicit specification of a hierarchy of subsystems.

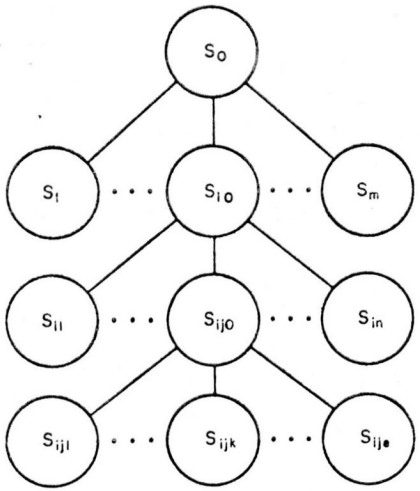

FIG. 3. Schematic representation of a working system in hierarchical structure and variable resolution by echelon. To add another finer level to any terminal system, append zero to the subscript of that system and couple in the next level of subsystems representing that system.

Hierarchical structure is provided by the REFLEX paradigm, this representing a special case of the U-C structure of Klir's general system theory. Terminal subsystems are defined by the FLEX paradigm, this representing a special case of Klir's definition according to *behavior*.

In anticipation of a later point of discussion, it is our current view that it will be necessary to develop a continuous (i.e., differential equation) version of FLEX, because some of the terminal subsystems studied will just not yield to the discrete formulation. However, the process of uncoupling is essentially one of discretizing at a specified resolution level, and continuous form need enter only at the terminal systems.

IV. Technical Aspects of Applying the Special Theory

A number of technical modeling problems are being examined within the Biome modeling program.

A. Spatial Heterogeneity

As in many other programs, we have attempted to reduce the effect of spatial heterogeneity by the device of stratification. Watershed 10 was stratified by vegetative and soil units into, first 13, then 15, then 17 strata such that at the resolution addressed, the system is relatively homogeneous within strata. It is our intent to construct models at the finer stratification, at intermediate stratification, and at the whole watershed level in order to

examine some of the aspects of changing resolution. The stratified forms will fit our REFLEX structure. Currently the stratification has been implemented only for the hydrologic model and only in a limited form. However, this is the part of the total system model which is most strongly coupled among strata, and it is anticipated that extension to the remaining structure will be straightforward.

B. The Estimation Problem

Generally, this problem can be expressed: Given a set of data and a model structure of a particular form, how does one "fit" the form to the data? Associated questions are: What model forms are compatible with particular data sets? What assumptions are implied by particular procedures? How does one generate a data set to conform to a particular model form?

The point is illustrated by a common example. Let F be an observed matrix of fluxes, $F=(F_{ij})$, where F_{ij} is the flux from compartment j to compartment i in a prescribed period of time, Δt. Let $\mathbf{x}_e$ be the estimated "average" state vector of the system over Δt, and let the proposed model be

$$\dot{\mathbf{x}} = \mathbf{A}\mathbf{x} + \mathbf{B}\mathbf{u}(t).$$

Then, if and only if $\mathbf{u}(t) = \mathbf{u}$, possibly $\mathbf{0}$, and $\mathbf{x}_e$ is a nonzero equilibrium value for the system, can one estimate the a_{ij}, $i \neq j$, by

$$\hat{a}_{ij} = F_{ij}/x_{ej},$$

where the unit of time for this representation is equal to the length of the interval over which F was observed, easily changed to any desired scale.

Now this is a common estimation procedure, but it is seldom pointed out, and seldom understood, in my experience, that $\mathbf{x}_e$ and $\mathbf{u}$ are greatly restricted—that the system must be in equilibrium while observing F and that the x_{ej} quantities used in calculating the $\hat{a}_{ij}$ quantities must be equilibrium values. An iterative procedure (determining $\mathbf{x}_e^{(1)}$ for a given $\hat{\mathbf{A}}^{(1)}$ and iterating) can correct for a poorly identified $\mathbf{x}_e$, but the assumption that F is observed in a state of equilibrium is critical and seldom, if ever, achieved in ecosystem study.

Of course, neither are the systems studied linear systems, so that the concern is really not with the particulars of this situation, but rather with its general aspects. Given either a nonstationary driving variable or a nonlinear system representation, an explicit identification of system parameters cannot be obtained from, say, an observed annual flux, F.

It *is* possible in such circumstances to estimate the parameters by some indirect method. However, one wonders if it might not have been better to observe some other quantity than F. Particularly in the light of the difficulties attendant to the measurement of total flux along each adjacency path over a meaningful finite interval, it is questionable if such a procedure is justifiable unless the system is truly stationary and in equilibrium.

Alternative measurements (e.g., time sequences of the output variables) are appropriate for some alternate circumstances, but the state of the art of parameter estimation in the general model circumstance is not very advanced, to understate the case greatly. It was a great disappointment to me that the Coniferous Biome would not support investigation of estimation problems in the 1973 and 1974 segments.

C. Modeling in Discrete vs Continuous Time

A linear system can be *exactly* transformed from continuous to discrete form,† with the inverse transformation usually defined. This follows the general expression of the two forms and the forms of the matrices of coefficients:

$$\dot{\mathbf{x}} = \mathbf{A}\mathbf{x} \Rightarrow \mathbf{x}_t = e^{\mathbf{A}t}\mathbf{x}_0 \Rightarrow \mathbf{x}_t{}^* = e^{\mathbf{\Lambda}_A t}\mathbf{x}_0{}^*,$$

$$\mathbf{x}(k+1) = (\mathbf{I}+\mathbf{B})\mathbf{x}(k) \Rightarrow \mathbf{x}(k) = (\mathbf{I}+\mathbf{B})^k\mathbf{x}_0 \Rightarrow \mathbf{x}^*(k) = (\mathbf{I}+\mathbf{\Lambda}_B)^k\mathbf{x}_0{}^*,$$

where

$$\mathbf{A} = \mathbf{Q}\mathbf{\Lambda}_A\mathbf{Q}^{-1}, \qquad \mathbf{B} = \mathbf{Q}\mathbf{\Lambda}_B\mathbf{Q}^{-1},$$

and where $\mathbf{\Lambda}_A$ and $\mathbf{\Lambda}_B$ are the canonical forms of $\mathbf{A}$ and $\mathbf{B}$, respectively; $\mathbf{Q}$ is a matrix whose columns are the eigenvectors of $\mathbf{A}$ and $\mathbf{B}$ (common to the two systems if the systems are identical at $t \in \{0, 1, 2, \ldots, k, \ldots\}$); and $\mathbf{x}^*$ is the modal variable.

It follows that for $t \in \{0, 1, 2, \ldots, k, \ldots\}$, one can write $\mathbf{x}_t{}^* = \mathbf{x}^*(k)$, $\mathbf{x}_t = \mathbf{x}(k)$, and

$$e^{\mathbf{\Lambda}_A} = \mathbf{I} + \mathbf{\Lambda}_B.$$

† This result does not seem to be generally known. It was discovered by the author and L. Hunt, and independently by Hal Caswell. A publication relating proofs is in preparation.

In this form it is a simple matter to translate $\mathbf{\Lambda}_A$ into $\mathbf{I} + \mathbf{\Lambda}_B$. For example, if $\mathbf{A}$ (and $\mathbf{B}$) are diagonalizable, then

$$e^{\mathbf{\Lambda}_A} = \begin{bmatrix} e^{\lambda_{1A}} & & & \\ & e^{\lambda_{2A}} & & \\ & & \ddots & \\ & & & e^{\lambda_{nA}} \end{bmatrix},$$

so that

$$e^{\lambda_{iA}} = 1 + \lambda_{iB}, \qquad \lambda_{iA} = \ln(1+\lambda_{iB}), \qquad \text{and} \qquad \lambda_{iB} = e^{\lambda_{iA}} - 1.$$

Note that λ_{iA} is undefined if $\lambda_{iB} \leq -1$, this constituting the major restriction on the inverse transformation. Special procedures are required for multiple or complex roots.

Several interesting properties of the continuous discrete transformation are easily observed. If $\mathbf{C}_A$ is the Boolean adjacency matrix of $\mathbf{A}$, having a 1 for every off-diagonal nonzero element of $\mathbf{A}$ and a zero for every zero and diagonal element, and $\mathbf{C}_B$ is the Boolean adjacency matrix of $\mathbf{B}$, then

$$\mathbf{C}_B = \mathbf{C}_A + \mathbf{C}_A{}^2 + \mathbf{C}_A{}^3 + \cdots + \mathbf{C}_A{}^k,$$

where k is the number of arms in the longest path of $\mathbf{A}$, and where the rules of Boolean algebra apply in evaluating the equation. It will be recognized that $\mathbf{C}_B$ is thus the reachability matrix of $\mathbf{A}$ (Rescigno and Segre, 1964). This result is of great value in modeling nonlinear discrete forms, as it calls attention to the fact that coupling must be provided for some elements that are not directly connected under a continuous conceptualization. Like many other such results, this is obvious when one's attention is called to it, but it was not obvious to me until we translated a continuous linear model into discrete form.

A general computer program (DISCON) has been written by L. Hunt for translation from discrete to continuous and continuous to discrete. In addition to its general translation value, it is useful in obtaining an exact solution to a linear continuous model and in changing the time increment of a linear discrete model. Modal model forms are also useful for study and characterization of behavior.

The modeling of nonlinear discrete and continuous forms, from the perspective of compartment systems, can be approached as the identification of nonlinear expressions to account for fluxes in the matrix F. Given that F was observed in equilibrium, and given a continuous nonlinear formulation for the flux, one can choose parameter values to yield the

observed flux. However, the choice among different forms and the estimation of multiple parameters require information or knowledge in addition to the flux. Further, a linear representation will fit the system just as well at equilibrium, so that a nonlinear representation should be formulated *only* in the attempt to achieve greater realism and only in the presence of additional knowledge.

Because of our orientation to discrete model forms for processing, we have also considered problems of translating continuous nonlinear representations into discrete form. Since the linear representation holds as well at the equilibrium point of observation, one obvious device is to translate the continuous linear interpretation of the flux F into the corresponding discrete form, and then model the elements of the discrete linear form nonlinearly in an attempt to achieve greater realism. As earlier indicated, a key feature of this approach is recognition that reachability of paths several arms in length must often be represented in the nonlinear discrete model, and that the importance of higher degree terms is lessened as step size is shortened.

We have expended considerable effort translating such a nonlinear representation into discrete form and then attempting to make modifications to yield the dynamics of the continuous version. This does not seem to be a fruitful activity, and our present position is that model components that are conceptualized as nonlinear continuous should be modeled in that form, and components conceptualized in nonlinear discrete form should be modeled in that manner. This position dictates the development of a differential analyzer form of FLEX to process terminal subsystems.

Our only current discretization of nonlinear continuous model forms is in cases in which it is reasonable to assume that the contribution of paths of length greater than one is negligible. Then, it is sometimes possible to "piecewise" discretize by substituting the appropriate integral of the respective terms. Note that this is effectively an uncoupling of the part from the whole, and understanding of this process is involved in identification of the U-C structure. Note also that REFLEX is by nature a discrete form, so that in our algorithm, continuous forms enter only at terminal points.

D. Achieving Desired Model Behavior

The technical problems of modeling specific relations among components illustrates one of the concerns regarding entire systems. The simple interactive representation of, say, predator and prey relations, is either unrealistic or unstable. For example, the linear "donor controlled" model calls for prey to force themselves on the predator, whether or not the predator

can handle the volume "donated."* The simple nonlinear version, in which predation is modeled in terms of expected contacts between predator and prey, say $\phi x_1 x_2$, behaves badly, particularly in the discrete form. In order to achieve realism in structure *and* behavior, one must explicitly recognize the two facets of predation, supply and demand, and construct some rule for resolving the equation if demand exceeds supply. Simple such forms are

$$\min\begin{cases} x_1(1 - e^{-\phi_1 x_2}) \\ \phi_2 x_2, \end{cases}$$

and

$$\min\begin{cases} \phi_2 x_2(1 - e^{-\phi_1 x_1}) \\ x_1 - \phi_2, \end{cases}$$

where x_1 is prey and x_2 predator.

But such forms imply that the system is well-behaved, that predation cannot decimate the prey. We should not be surprised if system models constructed from parts with this form are highly stable, or if we can find no perturbation which will upset them. There seems to be a dilemma here. We need mechanistic models in order to anticipate potential regions of instability. However, to achieve stability over the regions in which the system is thought to be well-behaved, we impose structures which are essentially stable, hence unperturbable elsewhere.

The solution to this problem now seems obvious. Stability questions should be asked only in the context of environmental variation and structural modification. Relationships must be parameterized in terms of the environment and so remain stable over some environments and become unstable in others.

This thought bears strongly on the concepts of holistic and mechanistic models. Holistic models should describe. They should faithfully reflect system behavior *in terms of what the system does*, in our experience.

Mechanistic models should explain and predict. They should also faithfully reflect system behavior over the region of our experience, but they should have the capacity of prediction beyond that experience *in terms of our understanding of how the system works.*

* The perspective that such behavior reflects adjustment of the system to capacity to support predation deserves some consideration, but this is a holistic behavior that can hold only in the neighborhood of an equilibrium, and so is dynamically uninteresting.

E. Study of Model Behavior

The characterization of ecosystem behavior, previously identified as a general research problem, has an exact counterpart in the study of models. Not only is it of interest to tune a model to yield desired behavior according to our understanding of how the system works, but it is also of interest to study model behavior such that it is difficult or impossible to study the real world counterpart, or perhaps to discover something that we just have not thought about yet.

The goal of development of system models is to contribute to understanding the system and how it works, where understanding is predicated as encountering no surprises. If the body of knowledge of a system would allow prediction of a particular event, or behavior, then the system is understood with regard to that event or behavior, whether or not the prediction is made.

However, it is also in the scientific and social interest to anticipate events and behavior of interest. The *capacity* to make accurate prediction must be accompanied by the *tendency* to make valuable predictions if the capacity is going to be of any social or scientific value. This tendency involves the tendency to build models incorporating essential knowledge and the tendency to discover valuable surprises about the model once it is constructed. The second is, in my opinion, potentially the most rewarding modeling activity of all.

Given the complex structures and the great dimensions of ecosystem models now being built, there seem to be, at this stage of development, many problems attendant to the study of model behavior. Given, say, a 50 variable model with 150 parameters and 20 driving variables, how can one possibly characterize in a succinct form the "behavior" of the model in terms of simultaneous variation of the 50 variables, in the 150 dimensions, and under the complexity of driving regimes which can be constructed from 20 driving variables? Clearly, something must be done to reduce the dimension of the task, and here the hierarchical model structure is seen to be extremely valuable.

We have just begun to address the problem of development of strategies for study of behavior, but several aspects are now apparent. Holon models should be tuned to yield desired behavior and then examined, in isolation, with regard to unanticipated properties. If surprising properties are discovered, i.e., properties and behavior which are inconsistent with current knowledge or opinion, then one should conduct sensitivity analyses to determine model features and parameters responsible for these properties. The next step is reexamination of these features and parameters with regard to ecological validity, which step may require specification of new field experiments.

This process can be repeated for each specified system and subsystem in its holistic *and* U-C forms, and the advantage of the hierarchical structure is that a U-C (or REFLEX) model form is an assemblage of subsystems, each of which can be examined in isolation, and such that the holistic (FLEX) representation of the system can be examined. The behavioral examination of the U-C structure need be oriented only to the nature of couplings among subsystems and the formulation of processes in ghost.

In this perspective, we can now concentrate on problems of describing behavior of a system with, say, five to eight output variables, ten to twenty parameters, and five to eight input variables, and have some reasonable faith that the strategies developed will be of value in the study of large ecosystem models.

An insight with regard to sensitivity is also provided by the preceding discussion. As sensitivity of a behavioral property to a parameter or structure is the clue to the importance of that parameter or structure to the property, and as we are interested in tuning models to achieve a desired behavior and in investigating the parameters and structures which cause surprising behavior, it is a good strategy to isolate sensitivity of a property onto as few parameters or structures as possible. In fact, it is a good strategy to build models in which the key behaviors are sensitive to identified parameters and structures and hence *controllable.*

V. Operational Aspects of Biome Modeling

The organizational structure of modeling efforts in the Coniferous Biome has changed during every year of the program. The general tendency has been toward fragmentation of the effort with little central integration. In 1972 an attempt was made to provide central focus through the Modeling Management Committee, but resistance was high. In 1973 (late 1972) this structure was abolished by the Biome administration and a formal split established between "Model Structure and Behavior" and "Model Assembly." I argued strongly against this split on the grounds that conceptualization and study of model behavior cannot be accomplished in isolation from the activities of assembly, and that integration of the two is essential. These arguments did not prevail.

Several particular operational activities interfacing the modeling effort to the rest of the Biome program are of interest. Perhaps the most important of these is the *translation of concepts and conceptual structures into field programs* oriented to provide needed data. Little progress has been

made in this direction. Modeling has not been close to the field activity and, with few exceptions, attempts to incorporate systems perspectives and model needs into field activities have been resisted. This situation is currently changing, and field investigators are becoming more involved in modeling. However, they are not inclined to follow the suggestions of "Central Modeling," and the current fragmentation in organization of the modeling effort does little to alleviate this situation.

Reduction of field data into a form useful to the model is in much the same state. Compilation and analyses are usually investigator specified, and follow much the same orientation as the data collection. Again, there are exceptions, but the data collected and the tabulation and analysis made have been primarily oriented toward traditional questions. At best, they are usually "process model" oriented.

The integration of diverse aspects of biome modeling through the structure of the ecosystem model was attempted by the Central Modeling group in 1971 in the form of a series of work sessions with subject and process groups. During this series, called "Round One," we identified the general subsystem structure, very similar to that presented in Fig. 4, and initiated the general approach we are now taking. Coupling variables between subsystems were identified, but internal structures were not specified for most of the systems. Plans for an immediate "Round Two" yielded to the press of other activities, and most of the results of this series of discussions appear in the proceedings of the symposium held at Bellingham, Washington in March 1972 (Franklin *et al.* 1972).

In the fall of 1972, subsystem modeling teams were established by the Biome administration for the purpose of developing working models of the study sites. Central Modeling then initiated an effort to integrate these efforts into an ecosystem model by specification of outputs of the various groups needed in development of the total system model:

(1) A narrative of the systems behavior, complete with data, graphs, and other supportive information, including details of couplings with other systems.
(2) A model, written in FLEXFORM, for the holistic behavior of the system.
(3) A mechanistic representation of the system in terms of its subsystems, with specification of couplings and a narrative of behavior of the subsystems.
(4) Later, models to be written in FLEXFORM of all subsystems defined in (3), each system model then to be modeled in REFLEX.

The modeling activities of the Central group, then, consists of integrating these inputs from the various groups to provide:

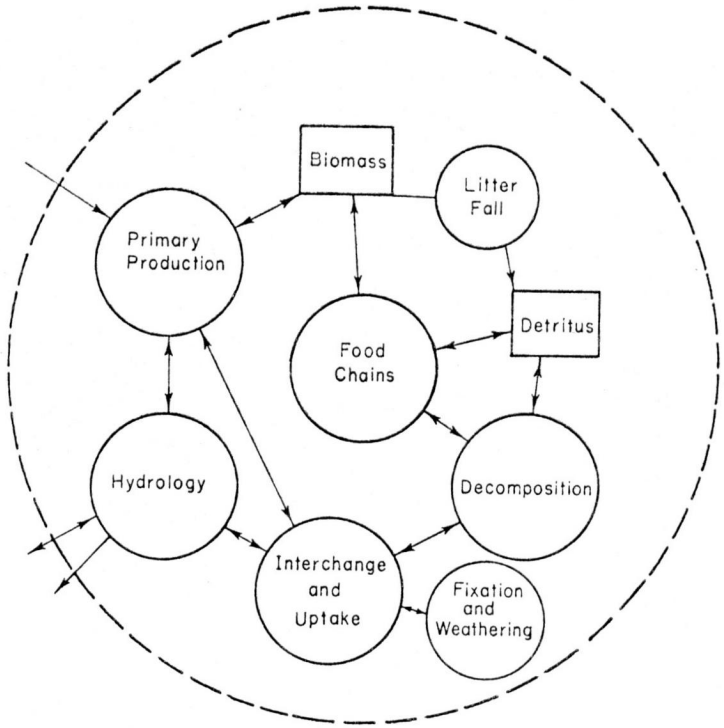

FIG. 4. Schematic representation of the mechanistic structure of the terrestrial subsystem.

(1) A holistic (FLEX) model for the entire system.
(2) A mechanistic (REFLEX) model consisting of the FLEX models provided by all the working groups, and integrated according to the behavior of the whole system.

Some progress has been made in this direction, but most of the needed inputs from working groups are not yet available. Meanwhile, Central Modeling has proceeded with development of the modeling capacity and elaboration of the total system structure in terms of the hydrologic model, which exhibits the same physical structure as does the entire watershed model. Stratified forms, quasistratified forms, and whole system forms have been developed. The complete stratification must wait until REFLEX is operative, but a system in two strata has been tested in FLEX.

The *critical review of submodels* is considered another important activity of Central Modeling. It is difficult, at best, to critique someone else's model, but the FLEX paradigm allows relatively quick translation into a simple convention, which is readily inspected for identification of specified

relations. I have proposed that all models developed in the Biome be translated into this form for review and subsequent examination of behavior.

To date, we have translated several models (four internal to the Coniferous Biome, and two external) in this fashion and have in each instance discovered mistakes of several forms. Most important are errors in executing the identified process in the program. However, errors in conceptualization and in documentation are also common. It is absolutely essential that such critical capacity be provided if we are not to generate model predictions based on erroneous or poorly understood models.

VI. Summary and Prospectus

The over-all strategy taken in development of an ecosystem modeling capacity in the Coniferous Forest Biome was (i) identification of properties which a general ecosystem model paradigm should have, by examination of current theory, (ii) identification of a general system theory which has the capacity to provide those properties, (iii) elaboration of a general paradigm for ecosystem models as a special case of the general system theory and in accordance with current ecosystem theory, and (iv) development of a general computer processor in the image of the proposed paradigm for ecosystem models.

The general system theory adopted is that of Klir (1969), and the general ecosystem model form is identified to have the following properties:

(1) The ecosystem model will be hierarchical and modular;
(2) Each system and subsystem will be conceptualized and modeled in two forms:
   (a) according to its holistic behavior,
   (b) according to its structure as a coupled collection of subsystems, each modeled according to its behavior;
(3) Modularity is to be achieved by explicit identification of the coupling variables between two subsystems. In principle, a model for a particular subsystem can be expanded or reduced in resolution without changing the resolution of the rest of the model. This is achieved by maintaining identical external variables, whatever the internal resolution;
(4) It will be possible, by the coupling feature, to model and study the behavior of any part (subsystem) either in isolation, or coupled with any other compatible part.

The developed paradigm, called FLEX (and REFLEX), is implemented in the computer programs FLEX1 and FLEX2, and accommodates the holistic (behavioral) and mechanistic (universe-coupling) components, respectively. FLEX is conceptualized as either a whole model processor or a module in REFLEX.

The current version of FLEX is a discrete form, and our view of discrete vs continuous model forms is essential to the paradigm. We do not view the *nature* of discrete models as approximation to continuous models, although they may be used in that capacity. Discrete models are legitimate forms in their own right. In some cases it is possible to determine the exact discrete counterpart of a continuous model. However, difficulty in adequately representing some continuous models in discrete form leads to the conclusion that both representations must be accommodated by a satisfactory modeling paradigm. A differential analyzer version of FLEX will be provided to fill this need.

At the time of this writing, some twenty models have been implemented on FLEX, six of which represent translations from another form. We have found the FLEX convention very useful in becoming familiar with a model built by someone else, whether constructed in FLEX or in another convention. We have also found that it is very convenient to examine the effect of structural change in the FLEX convention, as well as changes in parameters. REFLEX should be operative late in 1973, and we have already prepared test models in the appropriate modular form.

It is the intent of the Central Modeling group to concentrate in the last half of 1973 on development of the repetitive run capacity of FLEX and REFLEX, with the view of developing better fine tuning capacity and the capacity to examine the behavior of a working model quickly. The conceptual effort will be in development of strategies for study of model behavior and in the further development of general structural and relational forms.

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REFERENCES

Franklin, J. F., Dempster, L. J., and Waring, R. H. (1972). *Proc. Symp. Res. Coniferous Ecosystems.* Pac. N. W. Forest and Range Exp. Sta., Portland, Oregon.

Freeman, H. (1965). "Discrete-Time Systems: An Introduction to the Theory." Wiley, New York.

Klir, G. J. (1969). "An Approach to General Systems Theory." Van Nostrand-Reinhold, Princeton, New Jersey.
Klir, G. J. (1972). "Trends in General Systems Theory." Wiley, New York.
Koestler, A. (1967). "The Ghost in the Machine." Regnery, Chicago, Illinois.
Overton, W. S. (1972). Toward a General Model Structure for a Forest Ecosystem. *In Proc. Symp.-Res. Coniferous Forest Ecosyst.* (J. F. Franklin, L. J. Dempster, and R. H. Waring, eds.). Pac. N.W. Forest and Range Exp. Sta., Portland, Oregon.
Overton, W. S., Colby, J. A., Gourley, J., and White, C. (1973). FLEX1, Version 1.0. User's Manual Intern. Rep. Mimeo. IBP Coniferous Forest Biome.
Rescigno, A.., and Segre, G. (1964). *Bull. Math. Biophys.* **26**, 31.
Simon, H. A. (1962). *Proc. Amer. Phil. Soc.* **106**, 2.
Simon, H. A. (1973). The organization of complex system. *In* "Hierarchy Theory" (H. H. Pattee, ed.). Braziller, New York.
von Bertalanffy, L. (1968) "General Systems Theory." Brazillier, New York.
White, C., and Overton, W. S. (1974). Users Manual for the FLEX2 and FLEX3 Model Processors. Bull. 15, review draft. Forest Research Lab., Oregon State Univ., Corvallis, Oregon.