

SIMULATION MODELS OF ECOSYSTEMS

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*Come forth into the light of things,
Let Nature be your teacher.*

Wordsworth

MODELS AND NATURE

Simulations of the kind considered in this review are models of nature, living nature. As such, they are subject not only to the physical constraints on flow of matter-energy, but must conform to the multitudinous constraints required by the many species present in even the simplest of ecosystems. Indeed, it pays the ecological modeler to heed the words quoted above and to use the natural world, if not as teacher, as his guide when resolving questions of model form and function. The results of ignoring this advice are at best useless and at worst positively dangerous, for we live in a world where, more and more, decisions are shaped by the products of science and technology. One of those products that has heralded an exciting new area of ecology research is computer simulation modeling of ecosystems. I propose in this review to outline the origins, structure, and possible future of such models.

My dictionary defines simulation as "the act of feigning to be what one is not; the assumption of a deceitful appearance or character." Despite the somewhat pejorative character of this definition, it does describe well enough the modeler's intent, to simplify or substitute a model for the real thing, the ecosystem. But this "simulation model" should reflect the true nature of one or more aspects of reality and should not be a "dissimulation" model, one which, by definition, conceals the truth. In scope, simulation models vary from the detailed but small models of simple thermal communities (108) or microcosms (96) to simulation models of the world (52).

A word is needed about the scope of this review. I have deliberately avoided discussion of single population models or of two populations or competition models when these primarily concern predator-prey or competition theory. In the first place, the literature of predation and competition models is too vast an assemblage

even to attempt to summarize here. Second, such models are easily formulated without much attention to questions of matter-energy flows between compartments, the major concern both of simulation models of ecosystems and of this review. Some of the results of population modeling are discussed, however, in the context of equations describing the interactions between components.¹

Simulation modeling of a natural ecosystem is, to quote Steele (92),

... bound to involve extreme simplifications. It does not in any sense produce new facts, but merely permits the evaluation of laboratory experiments carried out on different components in isolation. By forcing one to produce formulas to define each process and put numbers to the coefficients, it reveals the lacunae in one's knowledge. Although the output of the model can be tested against existing field observations and experimental results, the main aim is to determine where the model breaks down and use it to suggest further field or experimental work.

It is my purpose in this review to essay a judgment about the success of simulation modeling in fulfilling and perhaps exceeding the functions outlined by Steele.

ORIGINS

Simulation modeling of ecosystems is a young subdiscipline even when compared to the relatively recent origins of ecology itself. Before the rapid development of analog and digital computers in the 1950s and early 1960s, the simulation modeling now taken for granted was impossible.

To my knowledge, the earliest actual applications of the idea of simulating the dynamics of ecosystems on computers were those of H. T. Odum (59) and J. S. Olson (124), on an analog device, and Garfinkel (30), using differential equations solved by numerical integration on a digital computer. By 1966, the field of systems ecology had been defined and incorporated in university level course work (72), and papers began to appear which discussed both the desirability and applicability of simulating ecosystems (24).

With the initiation of the International Biological Program (IBP) in 1966, simulation modeling received a great stimulus. The major theme of this worldwide cooperative program was the management of large biome-level ecological associations from the standpoint of long-term benefit to man. It was natural to approach most of these studies from a system-oriented standpoint, thus making simulation modeling and perturbation analysis a major and important part of each of the biome level studies. This emphasis has been particularly apparent in the US/IBP program (see for example, 10, 11, 35, 42, 69, 94).

Before leaving the topic of origins, it seems well to devote a few words to the distinction between simulation models, at least as they are defined and treated in

¹The literature search was aided greatly by the computer search profile service provided by the University of Georgia. All modeling and simulation titles were listed from four catalogues covering the years 1968–1969 through the first half of 1974. These were 1. Biological Abstracts, 2. Cataloguing and Indexing Bibliography of Agriculture, 3. Bioresearch Index, and 4. United States Government Research and Development Reports.

this review, and model or systems analysis. The pioneering series edited by Patten (74, 76, 78, 119) quite correctly made this distinction in its title, *Systems Analysis and Simulation in Ecology*. Constructing, validating, and running the model and assimilating the information derived—all these constitute the simulation process. Mathematical manipulations of the model designed to produce generalizations about such characteristics as stability, sensitivity, and frequency response are part of the analysis process. Patten (73) gave a comprehensive introduction to simulation, including some elementary programming for both the analog and digital computers. A different introductory approach has been outlined by Caswell et al (18). The analysis process is not considered in this review except insofar as it intrudes into simulation procedures, mainly concerning questions of the equations of interaction: how they should be written and methods of solution.

Taxonomy of Models and Their Uses

Simulation models of ecosystems may be separated according to a variety of criteria. As in any classification, much depends upon the viewpoint of the classifier. A basic distinction hinges on whether the model is theoretical or empirical. Theoretical simulation models attempt to provide some insight into the real world organization and operation of the modeling system. Perhaps these models can be said to be hypotheses as postulated by Reddingius (83). Or maybe Levins (46) was correct when he argued that a model cannot be a hypothesis because it cannot be directly verified by experiment. But one can at least, often rather easily, categorize models according to the above criteria. Empirical models make no pretense of explaining the real operation of the system. At best, they may faithfully reproduce the behavior of the system under a variety of conditions. Walsh & Dugdale (97) distinguished between these categories of model on the basis that a theoretical model uses causal relationships between variables and measured rate constants as opposed to the curve-fitting multiple regression techniques used to construct more empirical models. This is also similar to the distinction made by Caswell (17) whose ideas are considered in more detail when validation procedures are discussed later in this review.

Theoretical models, in common with all theory, cannot be proved correct; one can only attempt invalidation. Sufficient unsuccessful attempts to invalidate strengthen confidence in the model, but predictions are still justified only within the range of conditions spanned by the parameters of the model. Empirical models, known from the beginning to be developed directly from measured data representing known behavior of the system, are confined, in the sense of valid prediction, to that data set. Such models are of little value in those cases, probably a majority, where simulation is needed because experimentation is not possible (86), such as perturbations of large scale or dangerous proportions.

The semantic difficulties of trying to decide on a classificatory scheme for models have been explored thoroughly by Skellam (88). He pointed out the difficulty of deciding what is model and what is mimic by noting that DaVinci spoke of nature as his model! Biometricians interchangeably speak of fitting data to the model and of fitting the model to the data. Speaking on theoretical models, Skellam cautioned

that "... modelmakers dwell at rarefied conceptual levels and are prone to be carried away, particularly at their own constructions," or again, "Modelling is an area where that profound and disturbing remark of Lao Tse appears to hold: 'Those who know do not tell; those who tell do not know.'"—somewhat pessimistic perhaps, but nevertheless well to keep in mind when occupied in putting together a simulation model of a system as complex and obscure as an ecological community.

Models must have an explicit statement of purpose, else they lose their relevance (88). Besides as a statement of theory, models have been constructed for a variety of reasons. Some of these were alluded to in the earlier quote from Steele (92). A simple organization of thought and identification of gaps in the research plan may have great value. For this purpose, the actual simulation is secondary and it matters little whether the model is theoretical or empirical, correct or incorrect. To a great extent the world model put together by Forrester (27) like its sequel, *Limits to Growth* (53), was this kind of model; its purpose was to call attention to a little known problem and thus the numerous, often heated arguments about its validity are often superfluous (52).

Many present-day simulation models have been constructed for the express purpose of aiding in the management of a valuable resource. Through the use of such models the yield to man can be optimized (104) for a long-term stable system. Some currently popular areas of modeling emphasis range from vertebrate grazing systems (3, 56, 93), insect pest management (4), recreational game populations (99, 100), and fisheries management (86) to the control of oil refinery waste treatment facilities (48). A more detailed consideration is given some of these models in the latter half of this review. However, the management simulation models take us somewhat far afield of the central theme of ecosystems, for many of them consider only single populations or food chains. The principles needed in the development of such models are, however, identical with those of total ecosystem models.

Simulation models of ecosystems need not be all inclusive but they must be all encompassing, i.e. they must cover all the kinds of interactions present in the system without including all the interactions (42). This rather wide scope means that the modeling effort often requires a team approach; the team must be somewhat regimented yet simultaneously productive of theory. Regrettably, little information is available on how a good modeling team can be organized and maintained; for one short account of this type, see Innis (41).

MODEL STRUCTURE

Trophic Detail

Upon initiation of a simulation effort, an immediate decision must be made as to whether the model will reflect primarily a population or a trophic level organization. In other words, will the flow of matter-energy be directed through a set of variables of state representing the levels of a trophic flow diagram (113), or will the flow pass through a food web representing individual species? This decision is, for the most part, separate from the problem of model condensation (the lumping or combining of species into state variables) which is dealt with later. The decision at this stage is more one of emphasis. The primary interest may be in simulating the flows and

learning, for example, whether flow to the first order biophage consumer level is much less in a given system than is flow from the autotrophic level to the first order saprophage consumer level. In this case, the trophic level model is appropriate. If, however, the primary stress is on the dynamics and fate of individual species or species groups, one must model the species food web as a flow network. The trophic level approach offers (usually) the advantage of a much smaller number of state variables, but the construction of realistic interaction equations is made more difficult if not impossible. The species population food web modeling approach requires a sometimes bewildering array of state variables and parameters, but the chore of writing an equation for each interaction is lessened materially, since at most two species or species groups are involved with each equation. The latter approach has the additional advantage that the trophic model can be reconstructed from the simulation flow data of the population-oriented model, but the reverse is not true.

A variant of the population approach, which perhaps should be called a hybrid technique, and which melds both approaches, has been proposed by H. T. Odum (61). He has argued for simplicity in structure coupled with a total system overview, while maintaining the capability of a population orientation. Because this approach also employs a language variant, it is discussed later.

Model Construction—General

The steps necessary to construct a simulation model of an ecological system follow a fixed, generally agreed upon, logical sequence (4, 10, 34, 44, 104). The first stage begins with the initial ecological survey, which describes the list of biotic and abiotic variables. Generally, initial knowledge of the ecological relationships is slight, but all available information must be used to select a list of state variables. Naturally this initial list reflects not only the relative importance attached to the various species and/or trophic levels, but is also responsive to the objectives or purposes of the simulation model itself. For example, a model whose objective is to simulate and predict the effects of short-term (several years) management of quail populations in south Georgia stands of longleaf pine could ignore certain aspects of the population dynamics of the trees themselves, an oversight that would be ludicrous if the model also had the purpose of simulating a program of forestry management for timber production.

With the initial list of state variables selected, some indication of the interaction or degree of connectedness of the state variables must be drawn up. This often takes the form of a trophic model or a population food web. Some divergence at this point is expected depending on the type of model structure to be employed, i.e. on what "model" of modeling is chosen. For example, the kind of state space model proposed by Caswell et al (18) requires modeling the input and output relationships of each state variable by itself, i.e. free of constraints imposed by any other state variable. In general, however, a food web static model or diagram is sufficient.

Model Condensation

At this point, some latitude exists for different approaches to decreasing the complexity of the model organization. Broadly one may elect: 1. to set up smaller submodels, each having few state variables and interactions, 2. to make some gross

simplifications in the model, or 3. to utilize a two-stage modeling approach in which a first crude approximation is used to provide more refined parameter values for a second more detailed model (98).

The first approach is widely used when modeling large complex systems (e.g. see 75). With the gain in simplicity and the computer time economies gained by splitting the model into submodels come problems in properly interconnecting all the submodels. A major problem arises when the integration intervals needed for numerical solution of the differential equations differ between submodels. This is sometimes very difficult to implement in the program. Only if the submodels can be run or *exercised* alone is option 1 desirable.

The disadvantages of option 2, extreme condensation, are obvious. For a savings in computer time and programming difficulty, one sacrifices an (unfortunately unknown) amount of confidence in the predictions of the model. Although all simulation models, no matter how detailed they pretend to be, represent compromises with the complexity and diversity of the real world, the rule of thumb should be that only as much condensation is applied as is consistent with the needs and desires of the model objectives and the personnel involved. The degree of detail in simulation models is greatest when the time behavior of individuals must be simulated (38), and least when the trophic level approach is used or when complexity is deliberately suppressed to gain simplicity (61).

The third option for condensation, the two-stage approach, has the disadvantage of decreasing the objective a priori nature of the model by changing the parameter values in the second stage model on the basis of a previous simulation run. This first stage, a very much condensed version, may or may not be providing usable information. Thus the method seems to increase the chance of going wrong without materially helping with the problem at hand. Either methods 1 or 2, judiciously employed, should be better choices.

The majority of simulation models of ecosystems is of food webs, i.e. the dynamics of species populations are mimicked. Because of the vast assemblage of species in most communities, to say nothing of the large number of life history stages that should be accommodated as distinct state variables in the model, some condensation of almost all models is required at the outset.

When models are condensed there are certain obvious required constraints if the modeling of food web transfers is the objective. First, all species or life history stages that feed from the same resources must be lumped together in the same state variables or else considered as individual state variables. To be lumped together, these species should have similar life history characteristics; they may then be considered a single paraspecies (7). However, some caution must be exercised when combining species, and there exist few guidelines for this sort of procedure (36). A study having the specific objective of exploring the rules of model condensation is being conducted on the simple thermal algal-fly ecosystems of Yellowstone National Park (108, 112). To date, the best idea seems to be to lump together species that, as noted above, have similar food sources and life history characteristics, as long as they also possess similar intrinsic rates of increase. In cases where the different life history stages of a species are themselves ecologically distinct, but several species

are very similar with respect to each life history stage, it is best to lump the species within the life history stage, but to keep the stage itself as a separate state variable in the model (see 111). The next few years should witness a great improvement in our procedures for this phase of model construction.

Having decided on the objectives and structure of the model, with a food web diagrammed and questions of model condensation settled, the modeler can proceed to that phase of construction which is simultaneously the most ecologically demanding and scientifically controversial, the verbal and mathematical description of compartment interaction. The verbal description is essential to avoid nonsense biology creeping into the model. The mathematical description is necessary to implement the model. (Mathematical is used here in the sense of any set of formal symbols denoting relationships and implementable on analog or digital computers.)

Equations of Interaction

The central problem of this section is the translation of ecology into mathematical notation, a step with many logical and philosophical pitfalls (89). But before coming to grips with this central problem, a number of peripheral issues needs attention: stochastic vs deterministic models, the role of curve-fitting in modeling (realism), linear vs nonlinear equations, differential vs difference equations, the question of thresholds, spatial-temporal heterogeneity, and feeding preferences. All of these have been discussed at length in modeling literature.

Most ecologists and modelers have definite views on each of these topics, and I am no exception. I have reviewed the pertinent evidence in each case, but express some definite personal viewpoints in several instances.

STOCHASTIC VS DETERMINISTIC MODELS Because the individual organism is constantly faced with choices, and because the vagaries of the abiotic environment are largely unpredictable, particularly on a small scale, the argument for incorporating probabilistic elements into simulation models is a strong one. Garfinkel, MacArthur & Sack (31) described the circumstances under which either a Monte Carlo method or a Markov chain process could be used in place of a conventional set of equations to simulate the dynamics of simple ecosystems. To some extent, however, the need for stochastic elements in the model is tied to the level at which the modeling is to be done, i.e. upon which is to be simulated the behavior of an individual or the behavior of a large number of individuals (the population). If the latter, then many processes that are truly stochastic can be represented by a mean with very little effect on the resultant predictions. For example, birth and death must be regarded as probabilistic events at the individual level, but in a population of thousands a mean birth and death rate predicts quite well.

Some models dealing with the behavior of individual organisms have been presented in both deterministic (39) and stochastic forms (63). However, models as complex and detailed as those using the Holling approach have not yet been incorporated into simulations of ecosystems. In the early 1960s, the conclusion was that stochastic modeling would have only limited impact (103). Stochastic modeling is employed in ecosystem simulations but usually to model a specific process, for

example, the change in condition of algal mats (112). It usually adds only a small amount of realism; therefore at this time I see no need to revise Watt's opinion. An interesting sidelight, however, is the recent finding (50, 67) that even completely deterministic models may exhibit uncertain behavior because of mathematical properties of the feedback terms.

REALISM A vital question that must be decided before equations of interaction can be written concerns the degree of realism desired in the simulation model. Sufficient realism must be present to make the model suitable to achieve its stated objectives. Most disagreements originate over interpretation of the word *sufficient*. The issue is, to what extent should the model advance theory, i.e. how far should it be from a purely predictive model? This question is approached from a somewhat different viewpoint in the discussion of validation. Here I am concerned more with the degree to which system output should be used in the construction of the model.

Levins (46) suggested that a productive approach in model building is an emphasis on generality and realism, even if done at the expense of precision. A number of modelers have subsequently made a case for abandoning the idea that the model parameters should be arbitrarily adjusted or tuned until the model output resembles the time series behavior. Boling, Petersen & Cummins (7) emphasized the translation from the qualitative biological concepts to a mathematical model, i.e. from a verbal to a mathematical description. The older method of finding a mathematical function that can be fitted to a set of data is less useful. Ecologists regrettably have a common tendency to measure everything, to regard all patterns as meaningful, and to revere mathematics. Bunnell (11) found little use in accumulating elegant solutions of equations that make no sense biologically, and Lassiter & Hayne (45) argued that to admit mathematical functions to the model without a biological analog explains nothing. This kind of model would suffice only if the objective were to simulate a data set already at hand. Walsh & Dugdale (97) argued for a causal relationship to be established between variables and measured rate constants (parameter values). Goodall (34), in an excellent general article on construction and validation of ecosystem models, argued that only in the simplest of models can parameter values be estimated from observation of the whole system. Ad hoc studies of some kind are usually indicated. In many cases, data obtained separately from experiments or measurement of individual populations can be used to set the value of the model coefficients (57).

In general, a second prediction by Watt (103) is borne out, namely that the tendency is away from curve-fitting multiple regression techniques and toward models based on reasonably realistic equations.

The question now arises of the degree of nonlinearity required of the equation.

LINEAR VS NONLINEAR EQUATIONS Because this review specifically excludes the area of systems analysis and concentrates on simulation, it cannot cover the full scope of the controversy over the use of linear vs nonlinear equations in systems ecology. A good flavor of the arguments pro and con is obtained from three recent papers (5, 66, 77). Most of the justification for the use of totally (or at least piecewise)

linear models (79) is based on advantages gained in systems analysis, where a large body of theory is readily available to handle linear systems.

But I do want to consider the more limited question: Is there any advantage in restricting ecosystem simulation models to linear equations of interaction? In answering this question, one must keep in mind the purposes of simulation models are 1. to predict the effects of perturbations applied to the system, and 2. to explain some of the operation of the ecosystem itself, i.e. to contribute to theory.

Consider any two state variables x_i and x_j and F_{ij} a transfer of matter-energy from x_i to x_j , then if

$$F_{ij} = f(x_i, t), \quad 1.$$

F_{ij} may be described by a linear transfer equation, for example $\tau_{ij} x_i$. However, this is an uncontrolled relation, for x_j would grow without limit. Therefore, the more usual kind of linear transfer function encountered in ecosystem models is

$$F_{ij} = f(x_i, t). \quad 2.$$

An example might be $\tau_{ij} x_i$, where τ_{ij} is the specific rate of transfer with dimensions time⁻¹. This relationship is spoken of as a donor-controlled, or more properly as a donor-determined, donor-controlled, transfer because the state of the donor (resource) variable determines both the maximum rate and the realized rate of transfer. Common examples are respiratory energy loss and nonpredatory mortality. Indeed, any transfer of matter-energy to an abiotic compartment has a strong chance of fitting this model, assuming that the effects of other biotic and abiotic variables are negligible.

Transfers of matter energy to living or biotic components, however, often have the form

$$F_{ij} = f(x_i, x_j, t). \quad 3.$$

If an explicit form of this function involves (as it usually does) the product of the two variables, the function is nonlinear. A common form used in models of ecosystems is $\tau_{ij} x_i x_j$. In general, the linear formulations cannot represent some very common ecological phenomena. Specifically these are 1. the asymptotic approach of rates to a maximum or minimum value, 2. switching of behavior or rate of transfer when a threshold concentration is encountered, and 3. the multiplicative dependence exhibited by the example above, where a nonzero transfer rate depends upon a nonzero value of more than one state variable.

The consensus among ecological modelers is that many, if not most, processes operating to control the transfer of energy-matter between populations are nonlinear (5, 42-45, 47, 66). In contrast, a strong argument made for the consistent use of linear equations in simulation models (77) is that the nominal behavior of ecosystems, as their state variables fluctuate around some operating point, is linear, despite

the prevalence of nonlinear mechanisms in the interactions. This can easily be shown to be false for a number of ecosystems where a nonlinear response to a change in state variable or flux is observed. The nonlinear relationship between solar radiation intensity and photosynthesis exhibited by most C_3 plants is one case in point.

However, there are cases where linear models do predict changes reasonably well. If a system is in steady state and a radionuclide tracer is introduced, linear equations may describe adequately the movement through the system and the eventual establishment of an equilibrium (82). But the use of such linear equations, even where they may predict an adequate result, i.e. show how the system operates, cannot explain why it operates, because the interactions are not realistic (117).

Linear models have been justified on the grounds that they are well behaved and nonlinear models are not. Although nonlinear models employing simple, somewhat unrealistic, cross-product control functions are notoriously unstable, even they can be made to behave well (116). Realistic nonlinear models have been developed (108, 112, 115) that are well behaved (stable) with a single steady state or limit cycle trajectory. In fact none of the above criticisms applies to nonlinear models constructed in a manner reflecting the underlying ecological reality of the system (see also 42). On balance then, for simulation models at least, there seems no good reason for restricting the interaction equations to a linear model. Further arguments showing the positive advantages of nonlinear forms are reviewed in the following sections.

DIFFERENTIAL VS DIFFERENCE EQUATIONS The differential equation for exponential growth is

$$dx/dt = \rho \cdot x, \quad 4.$$

where ρ equals the specific rate of growth or decline. This equation postulates a continuous growth process. The alternative consideration of growth as a discrete process demands a difference form of this equation:

$$x_{t+1} = x_t \exp(\rho) \quad 5.$$

where t is the discrete interval of time.

At least one generalized ecosystem model relies on difference equations (45). There are some compelling arguments for the use of difference equations in such general models as well as in specific site models. Most ecological measurements are made during intervals that vary depending on the process studied (42). However, even though measurements are made over intervals, specific rates may still be calculated if the functional relationship is known. For example, in a population growing at an exponential rate, one may measure or count the population at two times t_0 and t_1 , find the ratio of x_{t_1}/x_{t_0} , and take the logarithm to base e of this value. This specific (often called instantaneous) rate is in units t^{-1} . In equation 5, the value of $\exp \rho \cdot t$ equals the ratio of population sizes over the intervals, thus the measured rate can be used directly in the calculated solution.

Difference equations also may conform more closely to the way ecologists think of the dynamic processes in their systems than do differential equations (40, 42). That observation, however, is a value judgment greatly dependent on individual circumstances. Certainly today the training of most ecologists includes considerable exposure to calculus.

The use of differential equations can be justified on the basis that the growth and decline of large populations of organisms approximate continuous processes very closely. Although rates cannot be measured instantaneously, the specific rates can be calculated, as above, from the discrete ratios of change. Unfortunately, few modeling studies employing specific rates and differential equations seem to recognize the problem involved in computing specific rates from measurements over discrete intervals. For example, assume one is measuring net photosynthesis of an aquatic community in a light bottle for one hour, and the populations fixed 100 mg of C, ending with 27,100 mg of C in the bottle. The specific rate of photosynthesis would usually be simply reported (incorrectly) as $100/27,000$ or $0.0037037 \text{ mg C} \times \text{mgC}^{-1} \times \text{hr}^{-1}$. In fact, the correct computation, assuming an underlying *exponential growth process*, is $\log_e(27,100/27,000)$ or 0.0036969. Not a large practical difference as long as the measured change is small compared to the standing stock, but, in any case, worth remembering.

Watt (106) also discussed the pros and cons of differential equations. Probabilistic alternatives to either equation, for example Monte Carlo models and Markov chain processes, were outlined by Garfinkel, MacArthur & Sack (31). Which form to use probably depends, in most cases, on personal preference as much as anything. In fact, when no analytical solutions are available, the solution of sets of differential equations involves approximating them with difference equations and solving the latter, choosing an appropriate step size (40). Major differences in overall system performance or prediction should seldom result with either.

THRESHOLDS At the outset of writing the equations of interaction, the modeler of ecosystems must decide whether to incorporate threshold responses. To do so means introducing discontinuities into the equations. This not only ensures non-linearity, but makes any single general analytical solution impossible. On the other hand, to rule out thresholds may render the equations so unrealistic or imprecise as to destroy their utility.

The thresholds considered here are not responses to such things as radiation and pollutants, which involve physiological responses, as some would argue thresholds do not exist in such instances, or at least can be ignored with little damage to the reality of the models (118). The thresholds of interest in ecosystem models involve the responses of consumers to: 1. changes in their own density, and 2. changes in the densities of their resources.

If, for example, a population shows distinct breaks in the relationship of ingestion to density, thresholds may be identified. Thus below a given threshold density one often observes a population growing, i.e. ingesting, at the maximum genetically determined rate, assuming food and other material resources are optimally abun-

dant. As the density increases, the mean interorganism distance decreases to the point at which perception of the neighbor occurs and a negative interaction is possible. At this point, density-dependent feedback has begun to decrease the growth rate. Similarly, at some upper density, negative interactions may become so severe that all feeding activity is interrupted and ingestion drops to zero. This must be represented as an upper threshold with respect to the relationship between density and ingestion.

Alternatively, one may examine the relationship of ingestion of a consumer population to the density of a resource. Again, if breaks in the curve are noted, threshold responses may be identified. A common threshold is a "refuge" level below which the resource is unavailable to the consumer. Such refuge densities may occur in the case of a bacterium unable to utilize dissolved organic compounds present in less than a threshold concentration. Or the threshold might be determined by the lower limit of prey density available to a predator because of physical structure in the environment suitable for a prey refuge.

Upper threshold concentrations of a material resource may induce saturation of the consumer. The population, if space is still optimum, may be growing, i.e. ingesting, at the maximum possible physiological rate. Thus further increases of that particular material resource would have no discernible effect, a useful test for a true threshold.

Some will argue that abrupt breaks or discontinuities do not occur in biological functions, that they are always smooth curves (85), but the weight of observational evidence is against this interpretation. Such threshold phenomena have been observed in ecosystems and have been incorporated into simulation models (1, 37, 45, 92). A simple method of incorporation is to use logical *IF* statements in the computer program [(37), see also the grassland model (42)]. This technique, however, is notationally clumsy. Abrosov, Kovrov & Rerberg (1) made use of the function *MIN* (a, b) i.e. the smaller value, a or b , to set threshold constraints in their model of an algal-bacterial community. The most generally useful technique is the use of the *DIM* function, where *DIM* (a, b) specifies that argument b is subtracted from argument a , returning the least positive difference, i.e. a positive value or zero (108). Thus whenever $b \geq a$, the value returned is zero. In mathematical notation, this function is closely related to a unit step function and is written $(a-b)_+$, where the subscript plus takes the place of the FORTRAN DIM. Examples of the use of this function in threshold equations are given in the section on equations of interaction.

HETEROGENEITY In addition to thresholds, the interactions between components of ecosystems operate within a mosaic of heterogeneity. Actions and reactions are delayed in time, and components are often clumped or otherwise nonrandomly arranged in space. In many cases, the importance of temporal and spatial heterogeneity is increased by greater diversity, and the relationship of these factors with stability (of various kinds) has been the subject of considerable discussion (49, 91). There is general agreement that this heterogeneity is vital to the validity or realism of an ecosystem simulation model (36, 47).

The incorporation of a time delay (temporal heterogeneity) in the interaction equations can be accomplished by making change a function of past states of the system (16), or by using vectors of population age (112). The use of difference equations (42, 45) automatically introduces the capability for time delays; instead of X_{t+1} being a function of X_t , it can be a function of X_{t-n} , where n is any chosen number of time intervals.

Handling spatial heterogeneity is a more difficult problem. The simplest solution is effectively to run as many concurrent models as there are spatially distinct areas. This is a solution if the areas themselves do not change in size, but the problem becomes more complicated when the spatial heterogeneity itself changes with time (112). At present this difficulty remains one of the major unsolved problems of ecological modeling.

FEEDING PREFERENCES Whenever any compartment in a model obtains resources from more than one source, some method of proportional allocation of these resources must be used to avoid biological unrealities in the equations when all resources are optimally abundant. Some simple and straightforward methods of accomplishing this have been discussed in the literature (62, 66, 108).

FUNCTIONAL FORMS The number of mathematical functions available with which to represent a verbal description of an ecological interaction is literally infinite. The modeler is faced initially with the choice of "tailor-made" versus "off-the-shelf," i.e. he may use standard mathematical notation to build an equation that faithfully represents the ecological situation, or he may opt for one of the standard mathematical representations used to describe material transfers in an ecological context. Unfortunately for the realism, accuracy, and generality of most models, the latter course is usually adopted. Of the many (2, 105) functions available "off-the-shelf," the logistic-based equations of Lotka and Volterra and adaptations of the Michaelis-Menten equations of enzyme kinetics are the most commonly used.

The Lotka-Volterra Equations

Two forms of the Lotka-Volterra equations of population growth may be identified. The first is a model of a population growing alone or, with the addition of a competition term, with another population (Equation 6a). It uses an asymptotic constant K to set a maximum density or carrying capacity. The second covers the case of a prey limited by being eaten by a predator (Equation 6b).

$$dx_j/dt = x_j(\rho_j - \rho_j x_j/K_j), \quad 6a.$$

$$dx_j/dt = x_j(\rho_j - \tau_i x_i). \quad 6b.$$

Perhaps the greatest single disadvantage of the first of these equations is that depletion of the environment is measured by the single value K . This means that the species utilizes the different resources of the environment (space, food of all kinds, etc) in ways that cannot be separately represented (87, 109). Another major

disadvantage is the linear relationship between the realized rate of increase and density. Often this is not observed. The second of the equations is notoriously unstable, for it permits growth at what may be biologically unreasonable rates. And finally, none of the Lotka-Volterra equations incorporates thresholds.

With these serious shortcomings, it is surprising that equations so devoid of biological reality (103) continue to be employed. Nevertheless, theoretical population biologists still make extensive use of the Lotka-Volterra equations, and they are found in simulation models as well, e.g. (48). Usually, however, some attention is paid to the shortcomings of these equations and variations are proposed. Thus O'Neill chose to represent the flux x_i to x_j as:

$$F_{ij} = kx_i x_j / (x_i + x_j).$$

Still, no thresholds are possible, and there is no incorporation of a density-dependent feedback from increases in x_j ; indeed, increasing x_j can only increase the ingestion of x_j , except insofar as very high values of F_{ij} may tend to reduce the resource x_i .

Lassiter & Hayne (45) discussed the pros and cons of the Lotka-Volterra equations at length, but ended up using similar equations, modified only insofar as separate feedback controls of birth and death rates were included.

Michaelis-Menten Equations

A second model utilizes the analogy between the feeding, assimilating living population and the equations describing the enzyme-catalyzed reactions taking place in the cell, the Michaelis-Menten formula. This is a two-step process involving the formation of an enzyme-substrate complex and the subsequent separation of the enzyme from the new product. Two rate constants are employed: one for the formation of the enzyme-substrate complex, one for the formation of product.



where F = food (substrate), x = population (enzyme), τ = rate of assimilation, and τ^1 = rate of production.

In enzyme chemistry these processes are reversible, but because reversibility is not a characteristic of biological growth, it is eliminated in ecological adaptations of this model. Smith (90) used this model to represent population growth, letting food and the feeding portion of the population combine at one rate to produce the biological equivalent of the enzyme-substrate complex. The latter is turned into new enzyme (population) at a second rate, then the total new production is computed. Because of the autocatalytic nature of growth, this new production is equivalent to new enzyme.

Where it applies, this formulation of the feeding equation is considerably more realistic than the Lotka-Volterra equations. Unfortunately, the ingestion of few populations can be considered even formally analogous to enzyme reactions in cells.

The assumptions of Michaelis-Menten-type models do not hold even for protozoa unless the cell size is constant (23). The Michaelis-Menten formula is best applied to the single-celled populations present in open water phytoplankton systems. Thus it is not surprising that this type of feeding interaction equation dominates the aquatic population model literature and is commonly used in simulation models of such ecosystems.

Choosing mathematical relationships that represent biological and ecological phenomena accurately is not simple. As Innis (40) noted in a refutation of the idea (20) that higher order derivatives are needed:

The established quantitative techniques were not developed for biological applications, but for physical applications. It results therefore, that these techniques may not be ideally suited to the biological and ecological realm and that, until some segment of the ecological community takes it upon itself to investigate these fundamentals more carefully, we may continue trying to fit square pegs into round holes.

A Generalized Realistic Model

Better interaction equations than the logistic Lotka-Volterra and Michaelis-Menten can be built if a suitable general, realistic foundation is used. One such model, with the capacity for incorporating techniques for building temporal and spatial heterogeneity, thresholds, and feeding preferences has been proposed (108–112, 115). An outline of the main arguments for this model follows.

For a model to be both realistic and general, the structure of the equations must: 1. reflect the important basic ecological parameters and 2. be flexible enough to accommodate additional special parameters whenever they are desired or deemed necessary.

Consider the transfer of matter-energy from a source (x_i) to a living component of the system (x_j). Without specifying the specific functional form of change in ingestion, five necessary parameters can be identified. The rate τ_{ij} is the maximum physiological rate of ingestion possible by x_j under a specified physical environment. If the latter does not vary, and if evolutionary change in physiological characteristics is negligible, then τ_{ij} is a constant. Otherwise it may be represented as a variable (28).

The flux of matter-energy into a population is represented by

$$F_{ij} = \tau_{ij} x_j \cdot f(x_i, x_j) \quad 0 \leq f(x_i, x_j) \leq 1. \quad 8.$$

When the feedback term $f(x_i, x_j)$ is unity, the population is ingesting at the maximum rate τ_{ij} ; when $f(x_i, x_j)$ is zero, ingestion is also zero. Between these two limits, x_j is ingesting at a rate between 0 and τ_{ij} .

If the limitation is imposed wholly by the condition of the food resource x_i , three basic pieces of information are needed in order to construct the proper feedback function $f(x_i)$. 1. The value of α_{ij} , the level of food density at which limitation first

begins (the saturation threshold) must be ascertained. 2. The value of γ_{ij} , the lower limit of food availability (the refuge threshold) must be measured, and 3. the relationship between the change in density of the food resource and the change in the function $f(x_i)$ must be chosen.

As an example, assume a linear relationship for 3, for which the feedback function is written

$$f(x_i) = [1 - \{(\gamma_{ij} - x_i) / (\gamma_{ij} - \alpha_{ij})\}_+]_+, \quad 9.$$

where the subscript + notation places the desired constraints through the convention that

$$(\bullet)_+ = \begin{cases} 0 & \text{if } (\bullet) \leq 0 \\ (\bullet) & \text{if } (\bullet) > 0 \end{cases}.$$

Note that $f(x_i)$ is zero whenever $x_i \leq \gamma_{ij}$ and unity whenever $x_i \geq \alpha_{ij}$, and that the change of $f(x_i)$ with change in x_i between α_{ij} and γ_{ij} is linear.

If the limitation on F_{ij} is wholly imposed by intrapopulation strife in x_j , that is, assume $x_i \geq \alpha_{ij}$, then evolution of the feedback function $f(x_j)$ depends upon knowing at least 1. the lower limit of density of x_j , where the effects of intrapopulation interaction first interfere with ingestion, i.e. α_{jj} or the threshold response density, 2. the upper asymptotic level of population density where interference has risen to the point at which ingestion is just equal to the maintenance costs of the population, i.e. the equilibrium threshold or carrying capacity, and 3. the relationship between the change in x_j and change in $f(x_j)$.

Again as an example, assume 3 to be linear, whence

$$f(x_j) = [1 - \{1 - \lambda_j / \tau_{ij}(1 - \epsilon_j)\} \{ (x_j - \alpha_{jj}) / (\gamma_{jj} - \alpha_{jj}) \}_+]_+. \quad 10.$$

The additional term involving λ_j (the specific maintenance losses) and ϵ_j (the proportion of ingestion that is egested) is necessary because the upper density level γ_{jj} is defined as the equilibrium point, not the point at which ingestion becomes zero. Thus when $x_j \leq \alpha_{jj}$, the flux F_{ij} is maximum, and when $x_j = \gamma_{jj}$, the flux F_{ij} equals $x_j [\lambda_j / (1 - \epsilon_j)]$, the amount of maintenance losses.

When both scarcity of resources (x_i) and intrapopulation (x_j) interaction are factors in limiting F_{ij} , equation 8 can be rewritten

$$F_{ij} = [1 - f(x_i) - \{1 - \lambda_j / \tau_{ij}(1 - \epsilon_j)\} f(x_j)]_+. \quad 11.$$

Equation 11 assumes that the repressive effects of each feedback term are additive. This is the simplest assumption, but in the face of experimental evidence to the contrary, other arrangements can be made.

The use of interaction equations constructed as outlined above produces models that combine aspects of generality, reality, and precision. Additional modifications in the mathematical functions can simulate the effects of time delays in development, spatial and temporal heterogeneity, variable parameters, and stochastic terms (111).

The equations are nonlinear and discontinuous, yet the models constructed from them are stable in the sense that no compartment can increase to infinity nor can a compartment go to extinction without a biological reason. There is only one positive steady state or limit cycle possible for a given set of parameter values. Models of this kind can be used to generate hypotheses concerning perturbations (109). Most important, every state variable and parameter in such models can be defined, and a procedure outlined for its observational or experimental measurement.

SIMULATION

Digital vs Analog

The mechanics of translating from a set of mathematical equations to a computer program are highly machine dependent. The initial choice facing many ecological modelers is whether to use an analog or a digital computer, assuming of course that both are available.

The analog computer is inherently less accurate than the large digital computers. But for solving simultaneous sets of differential equations, the analog machine has the advantage of not requiring a numerical approximation, i.e. its solutions are continuous and thus free of inherent error. In this application, the usual four-place accuracy of the analog machine may more than equal that of the high speed digital computer.

The analog computer also offers the advantages of low running cost and rapid operator-machine interaction. Once programmed, many simulations can be done rapidly. Because the output commonly shows up as a graph on an oscilloscope tube, or XY plotter, the modeler can quickly make decisions about the effects of parameter changes and perturbations.

Unfortunately, the process of programming and debugging the analog computer is relatively time consuming, and scaling restrictions reduce the dynamic range of model behavior. A shortcut method of programming the analog computer for models of ecosystems solves some of the worst of the scaling problems (61). The greatest single drawback of analog computers for ecological modeling is simply their unavailability, at least in the larger sizes, to most modelers. Models incorporating nonlinearities, spatial and temporal heterogeneities, and thresholds use components, particularly amplifiers, at a very great rate, and can be handled only by the largest analog machines, usually found only in schools of engineering. Digital computers capable of handling such models are commonly accessible, often via a terminal in the investigator's office.

Digital computers are ideal for handling spatial and temporal heterogeneities, threshold limits, and other nonlinearities (38). Their disadvantages are the cost of the simulations, a definite and sometimes great delay between making the parameter changes or perturbations and seeing the result, and the necessity of numerical methods for solving sets of differential equations.

The first two disadvantages are being eased by the rapid technological breakthroughs now being made in the computer industry. Unit costs are going down and speed is rising, causing a reduction in running expenses and making the computer

more accessible. Most ecological modelers can now arrange to spend time at an interactive terminal or console, where turnaround time is measured in seconds or, at most, minutes.

With regard to the third disadvantage, numerous numerical methods are available for the solution of simultaneous sets of differential equations with the digital computer (15). Probably because of the nature of ecological systems simulations (relatively imprecise parameters values and oscillating state variables) inaccuracies in the integration methods will remain relatively unimportant for some time. Distinct differences in results of simulations using four different integration techniques were noted in one unpublished study (R. V. O'Neill, An introduction to the numerical solution of differential equations in ecosystem models. ORNL-IBP-70-4. IBP UC-48-Biology and Medicine, 1970). Magnitude of the error with any of the techniques was relatively low. Usually, the simpler and more economical of time the method, the more inaccurate its results. However, it is sometimes possible to choose a shorter interval of integration and obtain equal results with a simpler technique at a much lower cost (114). Another way around the problem of numerical integration is simply to use difference equations in the model.

Simulation Language

Actually to simulate the dynamics of an ecosystem on a computer, the modeler is faced with the problem of translating a set of mathematical statements of the rules governing the operation of the system into something the computer can understand. For this purpose he has at his disposal a number of standard programming languages for the digital computer.

The most flexibility and often the most efficiency (from the standpoint of computer time) is frequently achieved by translating the mathematical model into a standard general purpose language such as FORTRAN. Many useful special on-line functions are available. Common examples are the logical *IF* statements and the replacement for the subscript plus notation [*DIM* (*a*, *b*)] discussed earlier. In addition, a number of other kinds of simulation languages have been developed to aid either in visualizing the system or in running it on the computer.

Both the system of diagrams developed by Forrester (26) and the energy circuit language developed by Odum (60, 61) are intermediary languages of the first type. As visual spans across the gap between a concept of the real ecosystem and its mathematical or computer language representation, both of these languages are extremely useful. The Odum circuit language, because of its greater numbers of symbols, is more explicit about relationships, but also more difficult to learn to use well. However, neither comes close to the richness of mathematical notation, and thus these languages are not suitable for direct implementation of the model from conception to simulation on the digital computer. The energy circuit diagram, with appropriate mathematical notation as addenda, can be implemented directly on the analog computer by someone experienced with both the analog and the energy circuit diagrams (61).

The second type of special category comprises those simulation languages developed to avoid the sometimes lengthy programs arising from a complete *FORTRAN*

translation of the mathematical model. In essence, these special languages act as partial translators and enable simulation modeling to be accomplished with a minimum of knowledge of and concentration on the programming itself.

Radford (81) presented an interesting and thorough discussion of the relative merits of three of these simulation languages. DYNAMO was discussed in the context of modeling the upstream migration of salmon. An application of the simulation language DSL 1130 to a lake ecosystem was illustrated, as was the use of the CSMP 360 language applied to management of a grassland cut for hay. Radford conceded somewhat more versatility to the CSMP language in terms of changing parameters between runs. The utility of CSMP 360 was also stressed by Brennan et al (9) who discussed its use in simulation models of four different kinds of system. However, Martin (48), comparing CSMP with the Dynamic Simulation Program (DYSIMP), was in favor of the latter on the basis of lower cost and the presence of optimization capabilities. SIMCOMP, a special simulation language, was developed specifically to ease the problems of communication of model changes between a large group of ecologists and modelers working on a common system, the short grass prairie (42).

The choice of programming approach and computer language depends on a combination of preference, availability, and training of the modeler, although some ecologists (97) see a trend from the special simulation languages and toward common use of FORTRAN by modelers of large biological systems.

Validation

The procedure necessary to validate a simulation model of an ecosystem depends on the type of model and the purpose for which it was designed. In an excellent general treatment of the difficult question of validation, Caswell (17) distinguished between predictive models, designed solely to provide information on the future behavior of the state variables, and theoretical models, those that purport to provide insight into how the real system operates internally. The validation of the latter must involve sufficient attempts at disproof so that confidence in the theory is established. Caswell noted the impossibility of proving the truth of a universal statement by inductive logic. Thus the validation (Caswell suggests the term *corroboration*) procedure for theoretical models must include hypothesis testing, the hypotheses being derived from the universal statements in the model plus certain initial conditions of the variables and parameters. A single instance of disagreement can be considered sufficient evidence for refutation of the model as a theoretical statement. This distinction between the two kinds of models was also implied by Morales (58) when exhorting modelers to criticize models not as true or false, but as useful/insightful vs ineffectual.

One point not made by Caswell concerns the role of measurement. The successful refutation of any scientific theory requires that the accuracy of measurement used to distinguish between alternative hypotheses be equal to the task. Thus the Newtonian view of the world could be refuted only when our standards of physical measurement became sufficiently precise to detect the minute discrepancies (under ordinary conditions and velocities) between theory and the real world. Relativity

now forms the theoretical model of our concept of the relation of mass and velocity, yet the predictive model used in everyday engineering retains the Newtonian ideas because they are simpler, and adequate under ordinary conditions.

In the ecological context, we are now at the stage where the refutation of theoretical models is possible only at the grossest level because of the relative crudity of our measurements. For example, Wiegert (108), in an ecosystem model simulating the growth of brine flies on thermal algal mats, employed a feedback control relationship in which the reduction of ingestion by flies upon an increase of the density was a nonlinear function. Further consideration of the biological factors involved prompted a revision of this theoretical model to incorporate a linear relationship into a feedback control of the flies (112) but to retain the experimentally corroborated inverse (nonlinear) feedback for the algae (28). Nevertheless, despite their different theoretical basis, the two models produced pictures of the successional dynamics of the thermal system that were virtually indistinguishable from each other, given the variance in the field data.

The opposite result was obtained in the case of a preliminary salt marsh model (115), where the initial linear feedback function used to represent the effects of resource scarcity on growth of anaerobic sediment bacteria produced such grossly aberrant estimates of the carbon dynamics of the salt marsh as to prompt re-evaluation and subsequent substitution of a new theoretical feedback relationship.

Predictive models, according to Caswell, are an entirely different matter. Because the reality or universal truth of the model is not an issue, the validation procedure is simply one of establishing the degree of accuracy with which the model predicts the system behavior, and the range of conditions and parameter values over which this degree of accuracy holds. In this sense, I suppose, one cannot really invalidate a predictive model, but only accept or reject its range of error in predictive ability. Thus, because Caswell argued for corroboration instead of validation for testing theoretical models, and because acceptance might be preferable to validation for predictive models, it may be wisest simply to drop the term *validation* from the simulation model literature. Perhaps the term can be used in the very general sense of suggesting the degree of confidence one has in models that combine both theoretical and predictive functions.

Simulated Ecosystems

At present, there are relatively few simulation models of ecosystems and fewer still attempt to include in detail more than a few of the component species or abiotic compartments. Nevertheless, in this review, space permits no more than a cursory description of several such models.

The simulations were divided into those whose object was to deal with the management of economically important systems and those primarily directed toward an understanding of a hypothetical or a natural system or process. In the former category are 1. terrestrial grazing systems, 2. marine fisheries, and 3. pest management. Although there is a vast literature on all three of these areas, relatively few ecosystem simulations model practical management problems.

In the latter category of simulation models are those dealing with 1. general (i.e. theoretical) ecosystems, 2. succession, 3. aquatic ecosystems, 4. forest, 5. grassland, 6. tundra, 7. desert, and 8. decomposers.

This is not an exhaustive list, yet it represents the total of relevant papers gleaned from a rather extensive search of the recent literature. Space does not permit more than a brief comment about each paper, but the following annotated list should serve to give the reader some appreciation for the kinds of model being developed and the future needs and possibilities of simulation modeling.

MANAGEMENT MODELS Five papers addressed the general topic of management of grazing systems. Goodall (32, 33) demonstrated the use of computers in the grazing management of semi-arid lands and simulated the grazing by a nonreproductive population of sheep in Australia with rainfall, the major abiotic variable, treated stochastically. Milner (56) also simulated the dynamics of vegetation and sheep on the St. Kilda Nature Reserve heath. The model defined harvest of vegetation by sheep and the resultant effects on sheep and vegetation, but lacked any feedback effect of vegetation changes in the present on vegetation and thus sheep in the future. Swartzman & Singh (93) discussed the value of the computer model in assessing the worth of alternative management schemes in a successional tropical grassland.

Many innovative ideas and techniques have been pioneered in the management of fisheries, an applied ecological area. Indeed, Volterra's original stimulus for his population work was an interest in an applied fisheries problem. Thus it is no surprise to find some early applications of simulation models in this field. Steele (92) provided a stimulating introduction to all phases of model building, with an example drawn from the phytoplankton-zooplankton food chain in the North Sea. An energy flow simulation model of a pelagic ecosystem in the tropical ocean (95) dealt with the problem of modeling vertical zones in an upwelling system. The state of the system was determined by intensity and nutrient dynamics. Models of both upwelling and marine outfalls (97) illustrate the use of submodels of nutrients. Saila (86), in a model of the Georges Bank haddock fishery, was concerned with economic factors as they interact with the biological model to influence catch. A model of a lobster fishery was also discussed briefly. Paulik (80) published a useful review of the economic simulation models used for biological management and for bioeconomic purposes relevant to fisheries. It contained a selected bibliography of references to computer modeling and simulation.

The third group of management models, those dealing with insect pests, was difficult to condense into a small list because of the vast literature on models of insect pest population (see 105). Berryman & Pienaar (4) developed an argument for simulation as a tool for investigating the dynamics and management of insects, and Walters & Peterman (101) provided an example applied to the spruce budworm in New Brunswick. A useful exposition of methods is found in Watt (106).

GENERAL MODELS Generalized models of ecosystem (no direct application to any existing community) were proposed for a resource population system (29), a

predator-prey food chain (45), and simple three-species predator-prey and competition ecosystems (109–111). Menshutkin (54) proposed a general algorithm for developing mathematical models of aquatic biological systems as did Walters, Park & Koonce (102). Park et al (122) proposed a generalized lake ecosystem model (CLEAN) for which some documentation and output were obtained for several lakes studied in IBP programs (123). But only Bledsoe & Van Dyne (6) developed a compartment model (linear) simulating successional changes on an old field.

AQUATIC MODELS A large number of simulation models describe aquatic ecosystems. Chen & Orlob (19) discussed a number of models ranging from the pollution-recovery system in Lake Washington to a hydrodynamic model, interfaced with an ecologic model of San Francisco Bay. Parker (70, 71) reviewed models of Kootenay Lake in British Columbia. He first concluded (70) that more knowledge of the nutrient cycling system was necessary, but later found (71) that phosphorus apparently did not limit the algae and that the length of the integration interval may have caused problems with the accuracy of the simulation predictions. Kremer & Nixon (121) developed a realistic model of the phytoplankton component of Narragansett Bay that employs the concept of maximum rates under optimum conditions. Because of stability problems, which necessitate a small integration interval, it is best used only for short-term simulations. Williams (116) based an aquatic model on the Cedar Bog Lake, Minnesota data as a class exercise to compare linear and nonlinear models, and Fagerstrom & Asell (25) used a model of methyl mercury movement to focus research effort on the ecology of aquatic food chains. This use was also one objective of the salt marsh model of Wiegert et al (115), which incidentally predicted that the *Spartina* marsh was a net producer, not importer, of organic carbon.

One of the most extensive aquatic models persuasively arguing the linear point of view was that of a cove in Lake Texoma (79). The opposite point of view, i.e. a philosophy of nonlinear, discontinuous yet realistic and stable models, was pursued in the detailed simulation model of a simple algal-fly-predator thermal spring community (108, 112).

FOREST MODELS Perhaps because of their complexity and the relative difficulties of sampling, ecosystem simulation models of forests are scarce. The IBP deciduous and coniferous biome modeling projects will help remedy this deficiency. O'Neill (65) provided a general discussion of the work on the eastern deciduous forest with a summary table showing type of model, statistics, and sites. A general description of the modeling process with specific reference to a tulip poplar forest was published (84), as well as a detailed nonlinear model of a forested ecosystem and its response to temperature and light (120).

Overton (68, 69) discussed the modeling problems encountered in the coniferous biome and presented a general model for forested ecosystems. Botkin has been very active in developing simulation models of forests that deal with the dynamics of individual trees (8).

GRASSLAND MODELS The grassland biome is another that has been the focus of much of the attention of IBP studies. Unfortunately, few of the models of this type

of ecosystem have been published. A general description of the grassland research program, with modeling as a major objective, was described by Van Dyne (94). Connor, Brown & Trlica (21) published a description of a photosynthesis submodel of the shortgrass prairie. The latest detailed nonlinear version of the grassland simulation model (ELM) was discussed. Also unpublished was the earlier nonlinear version (PWNEE), developed by Bledsoe. Both the ELM and PWNEE models are described in *US IBP Grassland Biome Technical Reports*, numbers 64 and 156. (United States International Biological Program, Ecosystem Analysis Studies, Grassland Biome, Natural Resource Ecology Lab., Colorado State University, Fort Collins, Colorado 80521.) A linearized version of the PWNEE model has been published (75).

TUNDRA, DESERTLAND, SOIL-LITTER MODELS Models of the tundra biomes are under development, but the only published works at the time of writing are those describing the effects of wind and radiation on primary production of the arctic tundra (55) and a 14-compartment carbon-flux simulation model (13). Unfortunately, the preprint copy of the latter, which I examined, did not contain the interaction equations, so I do not know what type of model was constructed. A history and description of the tundra modeling project can be obtained from the US IBP Tundra Biome Center *Tundra Biome Report No. 73-2*.

A general description of the simulation modeling efforts in the desert biome was given by Goodall (35, 37), but the extensive models themselves were unpublished. They are described in an extensive series of *US IBP Desert Biome Reports, Modelling Series 1-15*.

A number of specialized simulation models of the important soil-litter decomposition process have been constructed. Some of these are of course integral parts of larger overall ecosystem models. Others have been published by themselves. In the latter category are a generalized model of soil-litter decomposers (44), models of tundra (12, 14), a model of the soil-litter system in an eastern deciduous forest (120), a nitrogen flow model (96), and a bat guano ecosystem in a cave (51).

Cooper et al (22) presented a number of simulation models showing the effect of climatic change on a number of different biome models. Watt (107) has offered a critique of the entire biome modeling program and pointed out some of the major problems facing the reviewer when much of the material is in the "not for citation" literature.

CONCLUSIONS

One fact emerges clearly from the simulation models now in the literature. That is: the science (or art?) of simulation modeling, so concerned with the fluxes of matter-energy in ecosystems, is itself in a state of rapid flux. There seems to be a steady, if sometimes confused, search for new ways of approaching the modeling process and new sets of objectives for the models themselves. Simulation models could have advantages for prediction, for organizing research efforts, and as generators of new ecological hypotheses; all of these are being tried and discussed.

Modern high speed computers have made available to us a tool perhaps as important to ecology as the electron microscope was to cell biology. As with any new tool, much misuse and many distorted creations have followed in the wake of its first employment. The mistakes should wane and the important advances increase in number as our first clumsy efforts improve and as we employ ecological insights in the planning and construction of models, in other words, as we begin to let nature be our teacher. I believe that simulation models have great promise and that their use will advance ecology as a science. I hope this review will in some manner encourage this progress, thereby aiding the development of ecological theory and its application to pressing environmental problems.

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