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MODELLING REPORT SERIES NUMBER 12

AOE MODELLING MEETING
DISCUSSION PAPER

VERSION 1

DESERT BIOME
UTAH STATE UNIVERSITY
LOGAN, UTAH 84321
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INTRODUCTION

Reports in this series are intended for internal use by Desert Biome collaborators. They are not to be quoted or referred to in formal publications. These reports have been produced by the Desert Biome Modelling Group, with the assistance of participants in the Desert Biome and other researchers.

The main function of the models, at this stage of their development, is to provide guidance in the research efforts of the Biome. Therefore, it will be noted that most of the information which they contain is fragmentary evidence, best available estimates, arbitrary assumptions or non-Biome supported research. The collection and incorporation of more accurate data will come after these models have been prepared in this form. Validation of the models will also come later.

Any use of the models must recognize the limitations imposed by their development at this early stage of research.

(1) Biological interpretations must be performed with extreme caution. Output, for example, should be viewed in relation to system behavior (stability, general time relationships, relative magnitude of the variables, general responses to parameter modifications, etc.). These properties should be related to the processes incorporated in the model structure. No particular significance should be attached to the specific numbers given as output.

(2) Data included in these models must not be used without explicit approval of the investigators who have supplied them to us. Please contact the Desert Biome Central Office for details.

(3) The material contained in the models does not constitute publication. It is subject to revision. The modeling group requests that this material not be cited without their expressed permission.

As particular models are revised we will be re-issuing them in new versions. The versions will be numbered according to the general scheme:

Version 1. Models which have been developed by the modeling group in isolation from subject area specialists who have provided the question which has been modeled.

Version 2. Models revised to incorporate subject-areas specialist's criticisms.

Version 3. Models revised to incorporate finds of biome-sponsored research.

Discussion Paper for AOE Modelling Meeting

The modelling group of the Desert Biome has spent its first six months in building a variety of sub-models for generalized organisms. We tried to build each sub-model such that we could use it in simulating the major interactions in which the organisms were involved. For example, plant sub-models were developed with a view to herbivory. While the coding for these models can probably be written off, we feel that we have been able to assimilate the experience gained by these false starts, and organize it into a reasonably consistent philosophy for tackling the modelling of deserts. We believe this philosophy will help us to produce significant, useful results within the research framework which has been adopted for the biome. The remainder of this paper outlines the reasoning which has led us to adopt this approach, and describes the procedures we hope to use.

One of the strongest methods in science is that making and testing of hypotheses. The forcefulness of this method is discussed and illustrated by Platt (Science 146: 347-353, 1964). Ecology has suffered from an inability to use this approach effectively. The reason for this is that ecology deals with extremely complex systems. In order to make any single hypothesis about such a system it is necessary to simplify it conceptually to a point where it probably bears little relation to a natural ecological system.

The alternative to simplifying the system is to make the hypothesis more complex. This means making simultaneously a set of hypotheses about each of the components; that is, building a model. The problem with doing this is that it soon becomes difficult to work out the consequences of several simultaneous assumptions (hypotheses). Because the biologist does not know what he is trying to test when examining real ecological systems, he tends to relapse into a descriptive approach.

Digital computers and various programming techniques have made the handling of a large, interlocked set of hypotheses reasonably speedy. Even so, there are limits on the complexity of the sets of assumptions which can be handled. Apart from the physical limits of computers, an attempt to vary too many components makes interpretation of output difficult, and slows feedback from hypothesis to field test. In order to limit the number of hypotheses which are to be handled simultaneously, it is necessary to pose precise questions which the model should aim to answer.

A question is a statement of interest in a causal route, in the form "if A is varied, what happens to B?" Ideally, the form of variation in A is defined, or the question is given as "What type(s) of variation in A will give X variation in B?" In terms of a model, it defines important input and output. A hypothesis is a proposed mechanism or relationship on the path between the A and B defined by a question. The connection of a set of hypotheses into a model will give an answer to the question; the answer is a testable consequence of the set of hypotheses.

Some special skills, and probably a lot of experience, are needed to use computers fluently for model building. When the techniques of modelling become very specialized, as in large programs such as the AOE, there tends to be a division of labour between field-workers and modellers which raises problems.

The usual relationship between the researcher and his hypothesis is that of a molecular biologist. When he makes and tests a hypothesis, he has a close personal knowledge of the reasons why the hypothesis is crucial to a question, of the reasoning by which the testable consequences are deduced from it and of the methods by which the consequences can be tested. This kind of close acquaintance with all parts of the procedure is very important to interpreting the results and to generating further directions of work.

Ecological system studies, however, are of a different order of complexity from those of a molecular biologist. A group effort, with some division of labour, is unavoidable. As a consequence, the problems of interpreting results will be all the more severe, especially if the questions have not been carefully framed in the first instance, and if the interpreters as a group do not understand all the steps that have led to the results.

The question of communications between the modelling group of a Biome and its field workers is extremely important; in fact it is the key to making a modelling approach to ecological systems work. From the philosophy of modelling outlined, we believe that "communications", in the general sense of getting together from time to time, will not be enough. It is up to modellers to take the initiative in some quite specific processes:

(1) in acquiring and keeping up-to-date a set of questions about ecological systems which we would like to be able to answer, ranked in order of importance. The successive refinements of the answers we can give to these questions will constitute "advancing our understanding of ecosystems";

(2) in getting field biologists to put forward speculative statements about how the particular ecological systems and subsystems between the A and B of a question work, and helping them to formulate these in systems language;

(3) by explaining how an appropriately formulated hypothesis can be coded and simulated;

(4) and in taking model output (the consequences of hypotheses) back to the field workers for help in deciding what parts of the output are reasonable and what indicate faulty assumptions, and to generate improved hypotheses.

It should be noted that we are trying to achieve these aims in the context of maximizing the reinforcement to the investigators who are producing testable hypotheses. Consequently, we are concerned with such problems as the speed of the feedback (i.e., from hypothesis to testable consequence to new hypothesis).

It should not be thought that the approach we are proposing, answering a list of questions, will lead only to a set of fragmentary and specialized models. The causal routes which are simulated to give answers to particular questions will frequently intersect. Suppose, for example, two models are built, one dealing with the effect of chaining of vegetation on erosion, and another with the response of carrying capacity to changes in stocking density. The vegetation is common to both models; it is a node between them. The treatment of the vegetation will be different, however, in the two cases. For the grazing model, biochemical and other parameters affecting the palatability of the plants to stock must be included. The erosion model will require relatively more attention to the details of root distribution, and to spatial patterns on slopes.

Concentrating on answering the limited initial questions allows us to select parameters of the vegetation, simplifies the modelling, and gives faster feedback to field experimentation. Later, however, the models can be made compatible at the node by including both sets of vegetation parameters and we can answer questions such as "What is the effect of X change in stocking rate on erosion?" We feel that fitting our models together at the nodes in this way will enable us to build towards an integrative model for whole areas of desert.

At the present time we are asking the ecologists to put forward a number of questions about ecological systems they would like to be able to answer. This was put to the Desert Biome Policy and Management Committee, and a tentative set of relevant questions was selected. The top priority question to be tackled was "What would be the effect of a 100% change in the population density of a dominant herbivore on the dominant vegetation?"

Because the particular species hadn't been specified, we came up with the impact of *Dipodomys* on annual grasses. About five days later, after consultation with our investigators familiar with these species, it was suggested that normal population densities of *Dipodomys* could probably not be doubled, because of their rigorous territorial behaviour. This case did not, therefore, provide a good example of the question.

As an alternative, the combination of grasshoppers and perennial grasses was proposed for study. During the preliminary reading of the literature on this problem, we found that a doubling of any one grasshopper species would simply lead to the removal of twice the amount of the preferred grass species, since each grasshopper species has a relatively fixed preferred graze species and eats the remaining forage species with only slight discrimination. Again, this question gave no particularly informative results, and so a more interesting question was put forward; "What would happen if you doubled the population density of grasshoppers as a group, and what would be the long term effects of this manipulation on forage and grasshopper species diversity?"

The preliminary analysis of this work has led to two consequences. We are able to work toward a model which deals with grasshopper densities from year to year, and which also deals with an aspect of species diversity, the study of which is one of the AOE goals. In addition, we provided the field workers with a way of treating grasshopper diversity. Prior to this realization, they felt that they had to study the population dynamics of individual species, and had no sound criteria in deciding which species to study. We hope that they may now deal with quantities of grasshoppers as a group.

We feel that the posing of concrete questions has led to specific guidance of the research and helped us achieve progress toward an understanding of ecological systems. In particular, it has brought us up against a class of problems where our expression of the biology of a situation has been restricted by the mode of simulation.

If, for example, during a discrete-time-interval simulation, the supply of any one of the forage species is insufficient to foot the total demand, then in what order is one to distribute the food demands of the competing hopper species between the various grasses? Is the deficit to be shared amongst the hopper species equally, or does one species bear the brunt proportionately more heavily than another? On the same line, what happens to the preference array of a herbivore when one of its preferred forages is over-grazed? In this way, problems of the modelling process itself have highlighted aspects of biology which we might otherwise have assigned relatively low priority in the process studies.

There are several phases of the systems analysis procedure. These have been discussed recently by Dale (Ecology 51: 2-16, 1970), following the terminology of previous workers.

The procedure for systems analysis is divided into the following phases:

1. lexical--The elements of the system under study are identified;

2. parsing--The relationships between the elements are identified;

3. modelling--The mechanisms are established which will be used to change the state of the elements of the system;

4. analysis--The actual solution of the model is undertaken.

As Dale points out, the lexical phase is one of the most neglected areas of systems analysis. We are becoming convenced that the AOE has assumed that both this and the parsing phase have already been done. Modelling and analysis, on the other hand, upon which AOE has been placing considerable emphasis, already have a considerable number of techniques available (differential-equation-solving methodologies, for example).

Ecosystem modelling has yet to convince the majority of ecologists that it is anything but a drain on their financial resources. Unless we are careful to identify where the problems really exist in ecological-system modelling, we shall likely only confirm their worst expectations.