LARGE-SCALE SYSTEM PERSPECTIVES ON ECOLOGICAL MODELLING AND ANALYSIS

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ABSTRACT

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This paper suggests that it is time to shift emphasis from deterministic, numerical simulations of ecosystems, and consider more basic concerns about how to represent them. Approximating the entities of an ecological community is a problem of aggregation/decomposition. The most useful representations of ecosystems appear to be networks which are amenable to such techniques as input–output analysis, environ analysis, information theory and Markov chain calculations. There appears to be no formal way of adequately depicting ecosystems as thermodynamic systems, and there is a need to bridge the gap between micro and macro-perspectives in ecology. A-posteriori methods of identifying system interactions, such as group method of data handling (GMDH), compartmental diagnosis, reconstructability analysis and flow-based modelling, promise to be useful tools in ecological narration.

INTRODUCTION

As Jørgensen and Mejer (1983) pointed out in their introduction to a previous ISEM conference, this coming decade should see the development of a unified theory to describe ecosystems behavior. It should be a time of fervent theoretical discussion related to real ecosystems. This paper surveys some of the recent topics of interest in ecological modelling and analyses those which are relevant to large-scale systems.

In this discourse, computer-oriented models are not addressed. Although they are sometimes important, the era of computer-simulated, case-by-case discussions appears to be drawing to a close. The time is ripe to pause and think a little more theoretically before again resorting to computer numeri-

cal simulation. Of course, computers are very useful, if properly used, but blind faith and over-dependence on calculating machines can be dangerous and can also hinder the development of the unified, conceptual methods that lead one to true insights. Rather, one should strive to identify common properties of ecosystems and to develop more general methods of modelling and analysis. By so doing, one also saves resources (computer time and manpower) that would otherwise be spent on blind-search techniques.

The authors have found two excellent papers (Halfon 1983a,b) exemplifying the kind of theoretical discussion which should be done before resorting to computers: they outline a procedure to analyze several alternative model structures to identify the best one to subject to a more comprehensive simulation study. Although the method may not be complete, it is nonetheless a prime example of how theoretical discussion should precede practical computation. Such theoretical discussion should become increasingly more important in the future as a prelude to the modelling of ecosystems.

Aggregation is a subject of keen interest to ecological modellers, and one can expect a clearer picture of how best to aggregate systems to emerge over the next decade. This paper systematically discusses both the aggregation and decomposition problems as two aspects of the single issue of how to approximate ecosystems.

Because the ability to collect data is very limited in the ecological field, one of the most useful representations of ecosystems is their portrayal as a network. Input–output analysis, environ analysis, and the applications of information theory and Markov chain theory are surveyed, and the relationships among them are considered. It will be demonstrated that, as concerns flow partitions (propagation of cause), one can prove that the results obtained through input–output analysis are identical to those obtained by environ analysis.

The methods of thermodynamics and statistical mechanics are reviewed with an eye towards the construction of macroscopic models of ecosystems. Macroscopic models of closed ecosystems are also discussed as one aspect of macroecology. Discussion to bridge the gap between microscopic and macroscopic thinking in ecology should become more important during the next decade.

In general, there are two types of problems associated with model identification: black-box model identification and structure definition. In relation to black-box model identification, GMDH (the group method of data handling) is appraised; and with regard to structure identification, the methods of compartmental system analysis (tracer kinetics), reconstructability analysis and flow-based modelling are reviewed. Which method of identification an investigator should select will depend upon the nature of data available and upon the user's intentions.

Various other modelling methods, the modelling techniques of H.T. Odum, optimization based modelling, as well as econometric representations and an application of fuzzy set theory, are also briefly reviewed.

APPROXIMATION PROBLEM — AGGREGATION AND DECOMPOSITION

Because there are limitations on one's ability to observe and understand ecosystems, an approximation of the object ecosystem usually has to be made prior to the process of modelling. Even if the research budget were to permit huge amounts of measurement and simulation, one would probably not be able to digest the results obtained from such a complex model.

The approximation problem has two aspects: aggregation and decomposition. These problems have often been discussed during the past two decades in the fields of control and power systems (e.g. Aoki, 1968), and aggregation has been a frequent theme in economics (e.g. Simon and Ando, 1961; Theil, 1967; Fisher, 1969). As this review will show, research on the aggregation problem is in its early stages, and almost no consideration has been given to topological decomposition in ecology.

Explanation in simple mathematical terms should help one better to understand the meanings of both aggregation and decomposition. They are probably best discussed as dual aspects of the single problem of how to approximate ecosystems.

Systems consist of both elements and the relations among them, e.g., species and their ecological interactions. The task of approximating any systems consists of two processes: grouping the elements and deletion of relations among elements.

Define a grouping matrix, S, as:

$$S = [s_{ik}]_{i=1,\ldots,m,\,k=1,\ldots,n} \tag{1}$$

where

$$0 \leqslant s_{ik} \leqslant 1, \quad \sum_{i=1}^{m} s_{ik} = 1 \tag{2}$$

n is the number of elements, and m the number of groups. The nonzero positions of s_{ik} signify which elements should be gathered into the same group, i. If all s_{ik} are either 0 or 1, the grouping is referred to below as a 'discrete grouping'. Otherwise, it is called a 'weighted (or overlapping) grouping'. An example of discrete grouping represented by the matrix:

$$S = \begin{bmatrix} 1 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 \end{bmatrix} \tag{3}$$
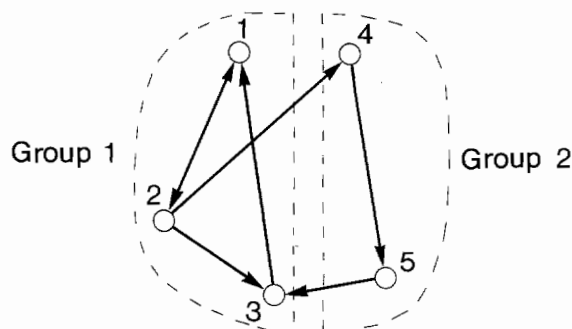
appears in Fig. 1.

Fig. 1. A discrete grouping of five elements into two modes. ○ shows an element; an arrow shows a relation between elements.

After gathering the elements, the deletion of relations between elements can occur in two ways: (a) aggregation, or the cancellation of relations between elements mapped into the same group, thereby condensing all the compartments of a given group into a single new element; and (b) decomposition, or the elimination of relations between elements in different groups, i.e., separating the original system into subsystems. Figure 2 schematically depicts the processes of discrete aggregation and discrete decomposition.

Two problems are apparent: (a) which elements should be gathered into the same group; and (b) how should the structure of the approximate model be determined? Because the method of aggregation is dictated by the purpose of the ensuing model (Cohen, 1985), the approximation criterion should be selected to serve the same purpose. Roughly speaking, there are two methods of approximation, one based on an examination of outputs and the other based on the internal structure of the system. The difference between the methods is portrayed in Fig. 3, and the following is a convenient, simplified explanation of aggregation using a state space (input–state–output) system representation as cast in the form of differential equations.

Vector x represents the state of the elements of an ecological system with inputs u and outputs y. Outputs are assumed to be based upon observation (or measurement). The pair of equations:

$$\frac{dx}{dt} = f(x, u)$$

$$y = g(x)$$

$$(4)$$

will represent the object (or real) ecological system, where:

$$x = \begin{bmatrix} x_1 \\ \vdots \\ x_n \end{bmatrix} \quad u = \begin{bmatrix} u_1 \\ \vdots \\ u_q \end{bmatrix} \quad y = \begin{bmatrix} y_1 \\ \vdots \\ y_r \end{bmatrix}$$
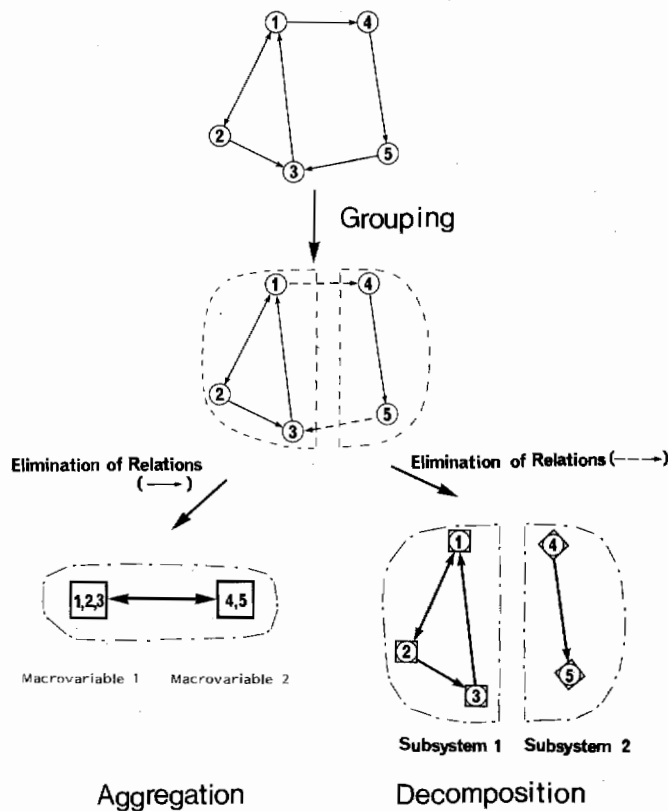
$$(5)$$

Fig. 2. Schematic diagram of aggregation and decomposition. An arrow is a relation between elements in the same group; a broken arrow is a relation between elements in different groups.

The equations:

$$\frac{d\bar{x}}{dt} = \bar{f}(\bar{x}, \bar{u})$$

and

$$\bar{y} = \bar{g}(\bar{x}) \tag{6}$$

depict the aggregated model for equation (4). Here $\dim(x) \geqslant \dim(\bar{x})$.

The criterion used to aggregate the system will be determined by the purpose of the modelling exercise and will fix the optimal forms of $\bar{x}$, $\bar{f}$, etc. One evaluates the difference between y and $\bar{y}$, i.e., the loss of output fidelity caused by the aggregation process. Then internal structure may be considered as a black box, because it does not directly affect the criterion, focused as it is on the outputs.
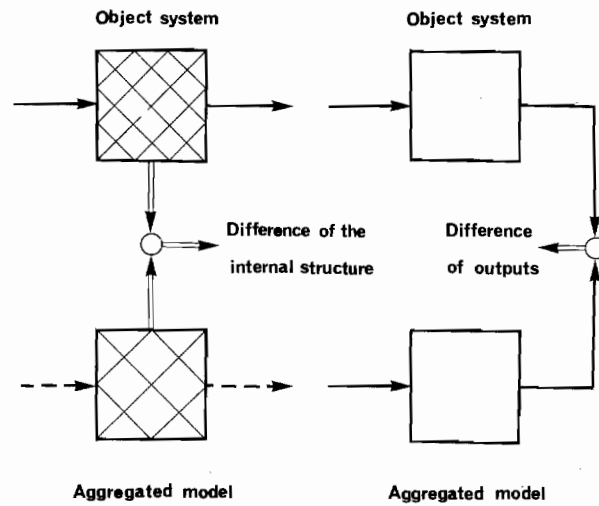
Fig. 3. Two ways of evaluating losses incurred by aggregation.

When one chooses not to fix the form of $g(x)$, the criterion is shifted to an appraisal of the structural difference between the objective system and the aggregated model. Although there were several ways to quantify the structure inherent in the original representation, the difference between original states and disaggregated states $\tilde{x}$ may be the most useful criterion to use for state space representation (e.g., Hirata, 1978). The disaggregated state vector $\tilde{x}$ has the same dimension as x and was created by subsequently decomposing the aggregated states, $\bar{x}$, according to one of several methods (e.g. Hirata, 1978; Roy et al., 1982).

Evaluating the changes in outputs or structures gives the criterion (cost) c as a function of either $y - \bar{y}$ or $x - \tilde{x}$. Generally, c may take the form of an integration or summation over time. Minimization of c then determines the optimal form of $\bar{x}$, $\bar{f}$, i.e.

$$c^* = \min_{\bar{x}, f} c \geqslant 0 \tag{7}$$

The aggregation problem is usually translated into an optimization problem. If $c^* = 0$, it is called a 'strict aggregation' (no introduced error), and if $c^* > 0$, it is an 'approximate aggregation'. No strict aggregation exists, except for a very special case.

When macro-variables are a composite form of micro-variables (x_i), the output functions must be defined by using the grouping matrix or identity matrix as:

$$\begin{aligned} y &= g(x) = Sx \\ \bar{y} &= \bar{g}(x) = I\bar{x} = \bar{x} \end{aligned} \tag{8}$$

Cost becomes:

$$c = c(y - \bar{y}) = c(Sx - \bar{x}) \tag{9}$$

The optimization problem (7) changes to:

$$\min_{S, f} c \tag{10}$$

i.e., the process of minimizing c determines the values of the elements in S. In the case of discrete aggregation the optimization identifies the positions of the 1's in S.

The decomposition problem can be analyzed in a manner similar to the above. Equations:

$$\frac{d\hat{x}_i}{dt} = \hat{f}_i(\hat{x}_i, \hat{u}_i)(i = 1, \ldots, p) \tag{11}$$
$$\hat{y} = \hat{g}(\hat{x}_1, \hat{x}_2, \ldots, \hat{x}_p)$$

depict the decomposed model for equation (4). Here:

$$\dim(x) \geqslant p, \dim(x) \geqslant \max_{1 \leqslant i \leqslant p} \{\dim(\hat{x}_i)\}$$

and p is the number of subsystems. The criterion is built upon either the function $y - \hat{y}$ or $x - \hat{x}$, where $\hat{x} = (\hat{x}_1 | \hat{x}_2 | \ldots | \hat{x}_p)'$. In the former case ($y - \hat{y}$), the decomposition is based on an examination of outputs, and in the latter instance ($x - \hat{x}$), upon the internal structure of the system. Minimization of c determines the optimal form of $\hat{x}_i$, $\hat{f}$, i.e.

$$c^* = \min_{\{\hat{x}_i, \hat{f}_i\}_{i=1,\ldots,p}} c \geqslant 0 \tag{12}$$

The decomposition problem is thereby also translated into an optimization problem. When x and $\hat{x}$ refer to the same basic elements, the optimization (12) changes to:

$$\min_{S, \{\hat{f}_i\}_{i=1,\ldots,p}} c \tag{13}$$

i.e., the process of minimizing c determines the value of the elements in S.

Modellers of ecosystems usually aggregate the object system into compartments according to experience and intuition. Halfon and Reggiani (1979) and Gardner et al. (1982) have highlighted the importance of aggregation in ecology. Hence, theoretical discussion about how best to aggregate an ecosystem is most desirable.

Zeigler (1976) was the first to introduce the aggregation problem into ecology in a mathematical framework. He has discussed the strict aggregation of linear dynamic systems, using the concept of a homomorphism which preserves either the transition structure or the input–output properties.

Under the special circumstances that one fixes a priori the function of one aggregation variable, $\bar{x}(t)$ — the structure of the aggregated model, $f(\bar{x})$ — and when the single macro-variable is the summation of all micro-variables — $S = (1, \ldots, 1) = 1$ (unit vector) — Cale and Odell (1979, 1980) and O'Neill and Rust (1979) studied the output aggregation error of several linear systems. They concluded that strict aggregation (no loss) is possible only when the elements all have identical turnover times. However, because systems are usually aggregated into several state variables, rather than into a single macro-variable, any results which are based on a single macro-variable can be of only limited applicability.

Cale et al. (1983) derived certain conditions under which strict aggregation based on observed outputs could be performed on nonlinear mass-balance-type ecological models. Their discussions, however, does not truly address nonlinear systems, because aggregating into a single state variable transforms the original nonlinear problem into a linear one. One can easily see that by grouping all the elements of a conservative system into one compartment, one neglects all the interactions between elements. The theoretical discussion of strict aggregation may be very useful in deriving some rules of thumb directly applicable to real situations, but it can also sometimes lead to trivial results.

In general, it is extremely difficult to aggregate nonlinear systems without introducing error. Luckyanov et al. (1983) gave some examples of nonlinear ecosystems which could be aggregated without loss of observed outputs. They used special types of macro-variables, which were not simply summations of micro-variables.

Gardner et al. (1982) wrote a most enlightening paper clarifying aggregation in ecology. They established the importance and meaning of aggregation in the field of ecology and proposed some rules of thumb directly applicable to local aggregation as practised in ecology. Although they constructed 40 different models to study four basic types of aggregation, some of their results can probably be derived from a theoretical treatment of aggregation based on system structure.

A particular instance of weighted aggregation based on the ecological exchange matrix has been utilized to transform an arbitrary network into a trophic chain (Ulanowicz and Kemp, 1979). There was no effort made to evaluate the consequent cost of such an aggregation.

As concerns aggregation based on structure, Hirata and Ulanowicz (1984) calculated the information contained in the structure of an ecological network and showed how the measure may be used to generate a hierarchical trophic structure (1985).

Although the meaning and purpose of decomposition as defined by M. Ikeda and Šiljak (e.g., 1980) differs somewhat from that described in this

paper, these investigators have used the concept of decomposition in their stability analysis of Lotka–Volterra equations.

Defining an acceptable amount of error due to aggregation (i.e., approximate aggregation) and how to aggregate when system parameters are uncertain (i.e., randomness of parameters), should be two topics generating keen interest in ecology during the next decade (e.g., Hirata, 1978; Gardner et al., 1982). Although almost no consideration has yet been given to topological decomposition in ecology, the subject is an important one, and deserves much attention in the near future.

ECOLOGICAL NETWORKS

One of the most useful representations of an ecosystem is its portrayal as a network.

Patten (e.g. Patten et al., 1976; Patten, 1982) has stressed the importance of addressing causality (indirect and direct effects, i.e., the propagation of conservative substances) in ecosystems. This is one of the most necessary and fundamental studies in ecology today. At present there are two methods to evaluate causality in ecological networks: input-output analysis and environ analysis.

The network representation is also useful for discussing other properties of ecosystems. There are two mutually related ways to analyze ecosystem networks quantitatively: the information theoretical treatment and the analysis based on Markov chains.

As concerns tracing causality in ecosystems, there are two directions in which one may proceed (shown in Fig. 4): (a) tracing the flows that contribute to a specific outflow (input approach, i.e., who receives what from whom?), and (b) tracing the flows that follow to a specific inflow
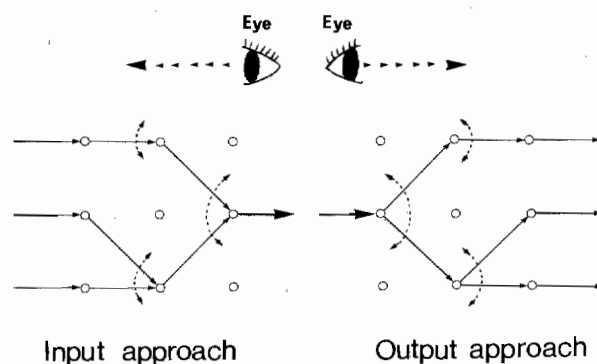

Input approach   Output approach

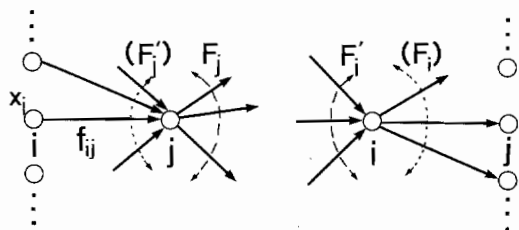Fig. 4. Schematic diagram of two ways of tracing influence in networks.

Fig. 5. Definitions of total flows used in flow analysis.

(output approach, i.e., who gives what to whom?). In a dynamic model, the input approach is backward in time and the output approach is forward in time.

Leontief (1966) first formulated input–output analysis (using the input approach) for the field of economics. Although several investigators had earlier developed the output approach, Augustinovics (1970) was the first clearly to formulate the output representation and to discuss the relation between the input and output approaches. Hannon (1973) introduced Leontief's input–output analysis to the field of ecology.

Environ analysis in ecology originated with Patten and Matis (e.g. Matis and Patten, 1981; Patten and Matis, 1982). The method has the potential to engender many extensions and applications in the future.

Let us first discuss the relationship between input–output analysis and environ analysis in an attempt better to understand those problems pertaining to causality. The fundamental difference between these two analyses is as follows: input–output analysis is based only on information (or data) about the flows, whereas environ analysis rests upon information about both flows and storages. As shown in Fig. 5, f_{ij} is the flow from the ith element to jth element, and x_i is the storage within the ith element. F_j is the total outflow from the jth element, i.e. $F_j = \sum_l f_{jl}$, and F_i' is the total inflow to the ith element, i.e., $F_i' = \sum_m f_{mi}$. At steady state the total inflow equals the total outflow at each element, i.e. $F_i' = F_i$. Input–output and environ methods define different coefficients for each flow and for each approach (input vs. output) as follows.

— Input–output analysis:

$$f_{ij} = a_{ij}F_j \quad \text{(for input approach)} \tag{14}$$

$$f_{ij} = b_{ij}F_i' \quad \text{(for output approach)} \tag{15}$$

— Environ analysis:

$$f_{ij} = a_{ij}'x_j \quad \text{(for input approach)} \tag{16}$$

$$f_{ij} = a_{ij}''x_i \quad \text{(for output approach)} \tag{17}$$

The difference between the definitions of the coefficients (a_{ij}, b_{ij}) of input–output analysis and (a'_{ij}, a''_{ij}) of environ analysis should be kept clearly in mind. Although their forms are similar, the degree of assumptions required for the two definitions differ. Equations (14) and (15), i.e. the a_{ij} and b_{ij} of input–output analysis, define the fractions of the compartmental flow that each individual flow comprises. In the static case this is a mathematical convenience requiring no assumption. On the other hand, equations (16) and (17), i.e., the a'_{ij} and a''_{ij} of environ analysis, postulate a relationship between two different kinds of variables, flows and storages. That is, equation (16) implies recipient-controlled compartmental dynamics and equation (17) assumes donor-controlled kinetics.

Because of these completely different kinds of relations, one has to exercise caution in applying these two methods to real ecosystems. As concerns input–output analysis, both input and output approaches can be applied to the same ecosystem so long as it is at stationary state, i.e., one can analyze the data on a static object ecosystem from two different directions: input and output approaches (e.g., Augustinovics, 1970). In the dynamic case, however, the mathematical manipulations (14 and 15) infer different assumptions about the dynamics of the system. Attempting to use both input and output approaches on a single object system at the same time would result in a physical contradiction.

As concerns environ analysis, because equations (16) and (17) imply different assumptions on the dynamics of the object system, one cannot simultaneously apply both input and output approaches to one object system even at steady-state. Of course this prohibition applies a fortiori in the dynamic case. Although both input and output environ indices can be calculated in dual fashion for a single object system at a given time, one is forced to choose between the input or the output sets. Two contradictory assumptions about the same system cannot be valid simultaneously. Because these implicit assumptions correspond to fixing the motive force of a system (i.e., in economics, assuming the input approach corresponds to controlling an economical system by the demand, while the assumption of the output perspective corresponds to control by supply), one has either to choose a perspective (input or output) for each object ecosystem suitable to its known properties, or else has to develop a new method which would make it possible to study both input and output approaches under a single assumption valid in ecology.

Although the purpose of environ analysis is to analyze not only flow partitions but also storage partitions, it was theoretically proved that the partitioning of flows by input–output analysis is the same as that obtained by environ analysis (Hirata, 1985). This means that when one wishes to know only about flow propagation, information on storages is superfluous.

Soon after Hannon (1973) first introduced the input perspective of input–output analysis into the ecological field and applied it to the Silver Springs ecosystem, Finn (1976) described the corresponding output approach and applied both approaches to three different ecosystems (Cone Spring ecosystem, etc.). He also derived several measures of ecosystem structure and function. In particular, he defined a cycling index, using the tools provided by input–output analysis.

Hannon used total system output and Finn employed total system through flow as indices of system size. Although Finn declared that both indices were identical, they are basically different. Finn defined the sum of the through flows of all elements as the index of system size, while Hannon used the sum of the through flows and the outputs from all elements as his total system output. (Because at steady-state total inputs equal total outputs, the total system output defined by Hannon becomes equal to Finn's index plus all inputs.) In open or non-stationary systems, Hannon's index may play an important role as a normalizing factor in information theoretic discussions of ecological networks (Hirata and Ulanowicz, 1984).

More recently, Hannon (1985) has proposed an accounting procedure which culminates in an index expressing the quality of energy flowing through each compartment.

Levine (1977) used input–output analysis to define an index of extended niche overlap.

There are several applications of input–output analysis to real ecosystems. Richey et al. (1978) compared direct and indirect carbon fluxes in four lake ecosystems, but were unable to discern any clear pattern. Patten and Finn (1979) applied flow analysis to the carbon cycling of the Ross Sea Pelagic ecosystem, Antarctica, and Finn (1980) analyzed several models of energy and nutrient flow on the Hubbard Brook ecosystem, New Hampshire, U.S.A. Dame and Patten (1981) discussed energy flows in an intertidal oyster reef.

Bosserman (1981) outlined the sensitivity analysis of parameters in an input–output analysis.

As mentioned earlier, Matis and Patten (1981) formulated environ analysis and Patten and Matis (1982) applied it to the Okefenokee swamp. Environ analysis may be applied to study: (a) flow partitions, (b) storage partitions, (c) intercompartmental transfers, and (d) residence time. The discussion of (c) and (d) relies on approximating linear differential equations in terms of a Markov chain (Walter, 1979). Although Walter's approximation form is valid when one wishes to formulate a difference equation as an approximation of a linear differential equation, when one starts with the dynamical system, it is uncertain how much relevance a dynamic property like the residence time calculated from a Markov chain model has to the

theoretical discussion of (c) and (d) as derived from static data. The question is how well dynamic information can be garnered from data on static systems.

Barber (e.g., 1978) proposed another type of Markovian model for ecosystem flow analysis which treated storage and flow in a single matrix form.

The ultimate goal of environ analysis is to describe the dynamics of systems. Hippe (1983) made some progress towards this end by studying the effects of time-varying inputs to linear, structurally invariant compartmental systems.

MacArthur (1955) and later Margalef (1968) introduced information theory into ecology by attempting to define macroscopic properties of ecosystems. Rutledge et al. (1976) refined these early attempts by introducing the conditional entropy as a model for choice which would also quantify ecological stability in closed systems. Ulanowicz (1980) later claimed that the emphasis in ecology should be shifted towards the mutal information, which could serve as an index of development for ecosystems. Hirata and Ulanowicz (1984) extended Rutledge et al.'s model for choice to include open ecosystems (ecological networks) and estimated the amount of information inherent in the network structure by using the concept of the mutual information of a channel. They also showed how the amount of information in a hierarchical structure could be assessed (1985). As mentioned in the previous section, this structural information is useful in discussing the aggregation (Hirata and Ulanowicz, 1985) and decomposition of ecological systems. Information theoretic treatments of ecological networks should be useful in clarifying the relations between the structure and the macro properties of ecosystems.

Another way to study ecological networks it to treat them as if they were Markov chains. Levine (1980) derived a measure of trophic position, i.e., the average trophic level at which a species feeds, by using a Markov chain analysis of energy flows. Walter (e.g., 1979, 1983a,b) discussed the relationship between the graphical structure of a network and its dynamical stability by using a Markov chain model to approximate the system's linear differential equations.

The four methods mentioned above should be the foci of further scrutiny and refinement during the coming decades. Most importantly, input–output and environ analysis have been developed to the point where investigators should begin to attempt to validate these techniques experimentally, for example, by using radioactive tracer techniques in ecological microcosms.

MACROSCOPIC DISCUSSION

Whether a system description is to be considered as macro or micro depends on the perspective of the observer. For example, when a population

is taken to exist at the macro level, then microscale phenomena become physicochemical processes such as energy transformation, respiration etc. When a population is said to be at the micro level, then the ecological community (or trophic grouping) become macro-level entities. Descriptions of macro properties of ecosystems and of the relations between micro and macro levels are important (e.g. Margalef, 1968). In a very general sense they are equivalent to problems of aggregation. It is, however, necessary to remember that the whole is not usually the simple sum of its parts.

In physics macroscopic discussion is most frequently encountered in thermodynamics, while statistical mechanics is a description of the relationship between molecular events and macroscopic thermodynamic properties. There are some applications of thermodynamics and statistical mechanics to ecosystems (e.g. Odum and Pinkerton, 1955; Kerner, 1957; Patten, 1959), as well as some new attempts based on accepted thermodynamic concepts (e.g., Jørgensen, 1982; Fukao, 1982). Bridging the gap between microscopic and macroscopic thinking in ecology will become more important in the next several years (e.g., Orians, 1980). As an important topic in macro-ecosystems, the discussion of closed ecosystems (energy flow and material — or nutrient — cycling) will be highlighted here as an aspect of macro-ecology.

Lindeman (1942) first studied the thermodynamic aspects of energy transfer in ecosystems. Odum and Pinkerton (1955) made use of irreversible thermodynamics to seek the optimal efficiency of biological systems. Patten (1959) discussed the energy transfer between trophic levels in both thermodynamic (especially entropy and information) and cybernetic terms. Jørgensen and Mejer have used exergy, which is defined as the maximum entropy-free energy that a system is able to transfer to the environment, to discuss ecological order (e.g., Jørgensen and Mejer, 1979; Jørgensen, 1982). When one considers ecosystems as open systems, the relation between energy flow and ecological structure becomes especially important (e.g., Morowitz, 1968) and should be discussed from a more theoretical viewpoint.

Smerage (1976) has used thermodynamic network analysis to discuss energy transformation processes like photosynthesis or respiration from a microscopic point of view. Meixner (1966) pioneered the development of thermodynamic network analysis, and Oster et al. (1973) and Schnakenberg (1977) extended the concepts and applied them to the dynamic modelling of biophysical systems. These methods are very useful and effective when it is possible to identify or assume the flows and forces in the object system. Such is usually the case when one is treating biophysical or physicochemical processes at the microscopic level of ecology. However, because wholes are not usually the simple sums of their parts, forces in physicochemical processes in micro-ecology cannot be simply aggregated to yield macroscopic forces at the population level of ecology. This is a very important

point. Therefore, the identification of the thermodynamic forces leading to the biological fluxes at the population or trophic level is a non-trivial and still unsolved problem.

Along the lines of thermodynamic network analysis, Fukao has constructed a macroscopic model of a decentralized, large-scale system to treat the system thermodynamics from the system-theoretic point of view. He applied the model to analyze the decentralization of resource competition as it occurs in ecology (Fukao, 1982; Fukao and Sugai, 1986).

Ulanowicz (1972) was among the first to discuss simultaneous energy flow and material cycling in closed ecosystems systematically. He, and later May (1973), suggested that a hierarchy in the specific energy content of the organisms should exist in simple food chains. Hirata and Fukao (1977) reformulated the model to correctly explain Ulanowicz and May's assertion, and obtained some additional results; for example, that a simple food chain possesses a hierarchy not only in the specific energy (energy amount per unit biomass) but also in the specific nutrient contents (the amount of fundamental nutrient elements like N, P, S, etc. per unit biomass). In complex foodwebs, inversions in the hierarchy of specific energy may happen in some parts of the foodweb, but they will disappear during subsequent succession (Hirata, 1984).

In discussing closed systems, it is essential to make the distinction between grazing flows and detrital returns, i.e., one should not neglect decomposers which change biological material to inorganic material (e.g., Nisbet and Gurney, 1976; Hirata and Fukao, 1977). Because nutrient cycling usually dominates ecosystem behavior, the study of closed ecosystems should lead to a better understanding of control processes at work in ecosystems in general (i.e., in both closed and open systems). Unfortunately, the literature about closed eco-community models is still rather sparse.

Nisbet and Gurney (1976) studied the local stability of any steady state in which all the standing crops are positive. Hirata (1980b) strengthened their results by proving that the model of nutrient–producer–consumer transfers was globally stable under certain conditions and that a similar model with an improved representation of the cycling process was always locally stable. Nisbet et al. (1983) discussed the role played by material cycling in stabilizing a closed system. To quantify the degree of trophic stability, they defined an index to measure the intensity of fluctuations of standing mass in a trophic level.

Hallam (1978) investigated the structural sensitivity of grazing formulations in a model of a closed community, and Antonios and Hallam (1984) pointed out that the persistence of the community is independent of the consumer density dependence in certain types of closed ecosystems.

Generally speaking, in ecology there is no single equation expressing the

total system energy and population dynamics analogous to Hamilton's equation in physical systems. Kerner (1957) originally derived a constant of motion for a community of populations governed by the Volterra predator–prey equations and discussed the statistical mechanics of such ecosystems. Kerner (1959) applied it to actual data on the catches of foxes in Labrador, Canada, from 1834 to 1925 and got good agreement between observation and theory after making the ergodic assumption. Some investigators question the relevance of Kerner's statistical mechanical treatment of the Volterra equations on the grounds that it is based on assuming both the antisymmetry of the interaction coefficients and ergodicity. As concerns the ergodic hypothesis, Goel et al. (1971) showed that it was a reasonable assumption so long as the numbers of species remained large. Several further developments have proceeded from Kerner's original work (e.g. Leigh, 1968; Goel et al., 1971; Kerner, 1978).

Demetrius (1977) defined some macroscopic parameters in ecosystems, using the statistical mechanical theory of lattice systems. Addressing the non-equilibrium dynamics of ecological succession, Allen (1975) used a Lotka–Volterra type model to show that the ratio of predator to prey populations should increase with time. Later, Hirata (1982a) was able to demonstrate that this ratio increased even when saturation effects are operating, and that under the same conditions the absolute value of the predator population should likewise increase. Even though ecological succession is clearly in the domain of non-equilibrium thermodynamics, there is still no consensus on a formal method for treating these phenomena.

As may readily be noticed, almost all of the tools used in the discussions of macroscopic properties and hierarchical relations have been borrowed from fields other than ecology. This only emphasizes the need to develop new methods originating from and pertinent to the field of ecology.

MODEL IDENTIFICATION

In general, there are two types of problems associated with model identification: black-box model identification and structure definition. The identification of black-box models is an effort to describe only input–output relationships while neglecting the internal dynamics or principles of system operation, whereas structure identification, as the name implies, is the attempt to identify the actual structure of systems. Usually internal descriptions of mass, momentum and energy conservation constitute the starting point for identification problems. Although there are several methods for approaching each type of problem (e.g., Beck, 1979), we concentrate here on those methods which have already been applied in ecology and are also of

some theoretical interest to ecologists. In relation to black-box model identification, the GMDH (the group method of data handling) is appraised; and with regard to structure identification, the methods of compartmental systems analysis (tracer kinetics), reconstructability analysis and flow-based modelling are reviewed. The method of identification selected will depend upon the nature of data available and upon the intentions of the investigator.

Ivakhnenko (1968) developed GMDH for the purpose of constructing an extremely high-order regression-type polynomial which relates multiple input variables to a single output variable. One wishes to establish this high-order, nonlinear input–output relationship with minimal a-priori information about the relationships between input–output variables. Although the GMDH algorithm faithfully reproduces the relationship between the input and output variables, it does not identify the actual internal structure of the system.

Many improved algorithms have succeeded the original one (e.g., Duffy and Franklin, 1975; Ivakhnenko et al., 1979; Tamura and Kondo, 1980, 1984; S. Ikeda, 1984).

Ivakhnenko and coworkers have also performed many applications of GMDH to the ecological field. For example, Ivakhnenko et al. (1971) used a GMDH algorithm to predict the quantity of bacteria in the Ryninsk reservoir. Ivakhnenko and Visotsky (1975) modeled a plankton ecosystem based on raw data. Duffy and Franklin (1975) used a modified GMDH algorithm to model a Corn Belt agricultural system producing high nitrate levels in the drain water.

Maciejowski (1979) made the observation that, in comparison with other types of models, GMDH is the best method for short-term prediction, but the worst for long-term forecasting. Tamura and Halfon (1980) confirmed this observation by comparing their model, created from a revised GMDH algorithm to identify water quality dynamics in Lake Ontario, with corresponding mechanistic water-quality models. It should be noted, however, that their results also have shown that GMDH can be usefully employed to develop models with a very low expenditure of manpower and computer time.

Farlow (1981) has written a very clear and comprehensive explanation of the GMDH method and has edited a book detailing applications of this algorithm to several different fields, including ecology (Farlow, 1984). He stressed the importance of incorporating more statistical methodology into GMDH, because it is not based on as solid a theoretical foundation as is, say, regression analysis, i.e., it is predominantly a heuristic procedure.

As mentioned above, GMDH not only has many merits, like certain computational advantages (e.g., Tamura and Halfon, 1980; Farlow, 1981),

but also has several defects. For example, it is not particularly good for long-term forecasting (e.g. Maciejowski, 1979; Tamura and Halfon, 1980). The model derived by GMDH is sometimes quite insensitive to inputs (Tamura and Halfon, 1980) and sometimes very sensitive (Ulanowicz and Caplins, 1983), i.e. the sensitivity depends upon the nature of data. It is, therefore, necessary to give consideration to which kinds of data and what particular classes of problems the GMDH algorithm can best be applied. Such a study should help this method become more useful and should engender numerous extensions of the GMDH algorithm.

Turning towards the problem of structure identification, Bellman and Åström (1970) first formalized the identifiability problem as it applies to compartmental systems, and many researchers have been following their lead, especially in creating applications for medical systems (e.g., Carson et al., 1983).

The goal of compartmental systems analysis (tracer kinetics) is the identification (estimation) of all unknown parameters of a model created in a-priori fashion from input–output experimental data. Tracer kinetics become appropriate under the following conditions: (a) linearity of structure, (b) arbitrary choice of the combinations of input–output positions (perturbation experiment), and (c) no restrictions on the number of times the experiment may be repeated.

Cobelli et al. (1979a,b) introduced compartmental analysis to the ecological literature and discussed its possible application to ecosystems (1979b). Beghelli et al. (1982) used the identification procedure of compartmental analysis along with data on phosphorus cycling in Kootenay Lake, Canada in order to determine the minimal number of compartments required to model the phosphorus dynamics.

Although there are many discussions centered on compartment models, no direct application of the original compartmental system analysis (tracer kinetics) exists outside of Beghelli et al. (1982). The reasons why this method has not found wider application in ecology are twofold: (a) the difficulty in repeating ecological experiments, (b) severe restrictions on the types of systems which may be treated by the method; i.e., compartmental system analysis can be applied only to small models (3–5 compartments) or to systems whose structure is very particular, e.g., those with catenary or mammillary topologies (e.g., Halfon, 1977). To make compartmental analysis more useful in ecology it must be extended to large-scale systems by employing the concepts of aggregation or decomposition (e.g., Brown and Norton, 1982).

Ashby recognized and clearly described the reconstructability problem (e.g., Ashby, 1964; Madden and Ashby, 1972). Many applications and elaborations followed, e.g., Klir (1979a) and Cavallo and Klir (1981). Klir

(1979b) was the first to introduce reconstructability analysis into ecology under the title of computer-aided systems modelling.

Generally speaking, reconstructability analysis may be divided into two problems: the decomposition into subsystems and the aggregation of the properties of subsystems into overall systems attributes, i.e. (a) the problem of determining which subsystems are adequate to reconstruct specific properties of the total system, and (b) the task of deriving specific properties of an unknown whole system from appropriate properties of given subsystems. Although ecologists may find reconstructability analysis a little hard to digest because of its complicated mathematical presentation, it may, nonetheless, have some application to real ecosystems.

The modelling of large-scale systems (like ecosystems) typically runs into the following difficulties: (a) very few quantitative observations of the systems are available; and (b) very little a-priori information about the true system structure is known (e.g. Maciejowski, 1979). In the light of these considerations, Hirata (1982b) proposed the method of flow-based modelling built around two points: (a) multi-aspects of large-scale systems, and (b) the relations inherent in the network of flows. Under the assumption that one knows the topology of the flows (information about the origins and terminal points of all flow streams), it becomes possible to compensate for the lack of data about one aspect of the ecosystem by the available information on another facet. For example, when there is insufficient data on the biomass of an ecosystem, one may use the data about energy to assist in estimating the biomass. This method was applied to simple ecosystems (Hirata and Fukao, 1977; Hirata, 1978, 1980a) and is in the process of being extended to complex ecosystems. The goal of this method is not only to approximate the equations of systems behavior, but also to make evident some properties and principles hidden in the system (e.g., Hirata, 1979).

VARIOUS OTHER MODELLING METHODS

Straškraba (1979) portrays the idea of hierarchical control in ecosystems from a cybernetic point of view and later (1983) gave it concrete expression in a simple predator-prey model. There exist four levels of control mechanisms in nature: feed-forward, feedback, self-adaptation and self-organization. Although Straškraba's thinking is incisive and his formulation of the optimization problem is straightforward, there nevertheless remain significant difficulties in actually solving the optimization problem for most object models.

H.T. Odum (e.g., Odum and Odum, 1976; Odum, 1983) has developed one of the most significant modelling methods based on energy flows. The approach has been applied not only to ecosystems but also to problems in

regional science (e.g. Boynton, 1977; Zucchetto, 1983). Although each particular model yields interesting insights, and his suggestions about the global properties of systems have broken new and fundamental ground; the paradigm should be subjected to further theoretical analysis (especially the work pertaining to total systems) before resorting to numerical or analog simulation on computers (e.g., Hirata, 1982c).

Zadeh (e.g., 1973) suggested that fuzzy set theory could address the uncertainty in complex systems and decision processes and Bosserman and Ragade (1982) were the first to apply this paradigm to ecosystems.

As mentioned in the section on ecological networks, input–output analysis stems from the field of economics. Hannon (1973) first introduced input–output analysis to the ecological field and later used it to define several concepts useful in discussing ecosystems evolution in terms of optimization (Hannon, 1976, 1979). Although ecosystems have many features in common with economic systems, some ecological researchers may feel that treating ecosystems in economic terms (input–output analysis excepted) is too tenuous an analogy.

CONCLUSIONS

The time for regarding ecosystems as collections of determinate processes (as has been the convention in most of simulation modelling) appears to be over. There is every reason to believe that individual processes actually change in nature as a result of their mutual interaction with other processes in the same community. Such circumstance would require that ecosystems be viewed as a unit with identifiable properties which exhibit some macroscopic regularities. (Dare we say laws?)

The tools necessary to describe ecosystems in this new perspective are evolving rapidly. It is altogether possible that this new direction will yield discoveries in 'macroscopic biology' which will rival the illustrious ones made in molecular biology during the past three decades.

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