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George M. Van Dyne

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HEALTH PHYSICS DIVISION

ECOSYSTEMS, SYSTEMS ECOLOGY, AND SYSTEMS ECOLOGISTS

George M. Van Dyne

Radiation Ecology Section, Health Physics Division
Oak Ridge National Laboratory, Oak Ridge, Tennessee
and
Associate Professor of Biology, University of Tennessee
Knoxville, Tennessee

JUNE 1966

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ECOSYSTEMS, SYSTEMS ECOLOGY, AND SYSTEMS ECOLOGISTS

George M. Van Dyne

ABSTRACT

This paper defines and discusses ecosystems, systems ecology, and systems ecologists, in that order. Some properties of ecosystems and the ecosystem concept are given as a basis for defining the area of study called systems ecology. Problems, methods, tools, and approaches of systems ecology are considered in defining tasks, problems, and training of systems ecologists. The interdisciplinary nature of systems ecology research and the importance of computers in this research are considered. Examples of methods, concepts, and applications are drawn from a diverse body of ecological, natural resource management, and mathematical literature, which further illustrate the interdisciplinary nature of systems ecology. Advantages and limitations, with respect to total-ecosystem problems, of research by ecologists in universities, in state and federal experiment stations, and in national laboratories are compared. An example is given wherein, possibly under International Biological Program support, the skills and resources of these three groups of ecologists might be combined for integrated attack on nationally important ecosystem problems.

ACKNOWLEDGMENTS

In any organization in which there is frequent and free interchange it is difficult to clearly identify the origin of concepts and ideas. Much of the material herein is a product of cross-fertilization of ideas with S. I. Auerbach, J. S. Olson, and B. C. Patten. Generally, we agree in principle, although our approaches differ in practice. Several other colleagues in the Radiation Ecology Section also have provided constructive criticisms of this paper. Acknowledgment also is extended to J. W. Barrett, J. E. Cantlon, F. B. Golley, A. M. Schultz, E. G. Struxness, and K. E. F. Watt, who have criticized the manuscript. G. C. Battle is thanked for his editorial assistance. The author assumes responsibility for any misconceptions or errors in this paper and would appreciate comments and criticisms. Part of this paper is based on a lecture given to the Radioecology Institute, Oak Ridge Institute of Nuclear Studies, June 1965.

INTRODUCTION

The Radiation Ecology Section of the ORNL Health Physics Division has initiated a new program of studies in "Systems Ecology." Neither is this area of work in ecology clearly defined nor do all ecologists view it equally. As with any new field, systems ecology is beset with vociferous skeptics (largely those who have done well under the old conditions) but supported primarily by lukewarm champions (largely those who may do well under the new conditions). It is desirable to examine the subject more closely as a further basis for clarification of objectives of work in this area.

Often we feel that our own work and interests are of extra importance, but I do not propose systems ecology to be a new panacea, nor that we neglect more conventional approaches in ecology. However, I feel that a systems approach has much to offer in various phases of ecology and especially in renewable resource management. This leads to a brief review of some ecological concepts and to suggestions about the tools, training, and work of systems ecologists. It is in this context that this essay is offered.

The purposes of this paper are twofold:

(1) To discuss important properties of ecosystems and to consider application of recent techniques from systems analysis and other fields. This is done not only to help define systems ecology and to help prevent semantic confusion, but also to help define some of the needs, training, and perspective of systems ecologists.

(2) To provide an introduction to a selected part of the large and diverse literature, through 1965, which encompasses the interdisciplinary area of systems ecology.

ECOSYSTEMS

Definitions

In 1935 Tansley (*106*) introduced the term ecosystem, which he defined as the system resulting from the integration of all the living and nonliving factors of the environment. Webster now defines the term as a complex of ecological community and environment forming a functioning whole in nature. An ecosystem is a functional unit consisting of organisms (including man) and environmental variables of a specific area (*3*). Macroclimate has an overriding impact on the other components, each of which is interrelated at least indirectly (Fig. 1). The term "eco" implies environment; the term "system" implies an interacting, interdependent complex.

Russian ecologists use the term ecosystem less frequently than the term biogeocoenosis, which Sukachev (*105*) defines as "any portion of the earth's surface containing a well-defined system of interacting living (vegetation, animals, microorganisms) and dead (lithosphere, atmosphere, hydrosphere) natural components. . . ." Biogeocoenosis is derived from the Greek "bio" or life, "geo" or earth, and "koinos" or common. Sukachev and others feel that biogeocoenosis is the more accurate and descriptive term from an etymological viewpoint, but Sukachev recognizes that ecosystem is the older term and that the two terms are widely used as synonyms.

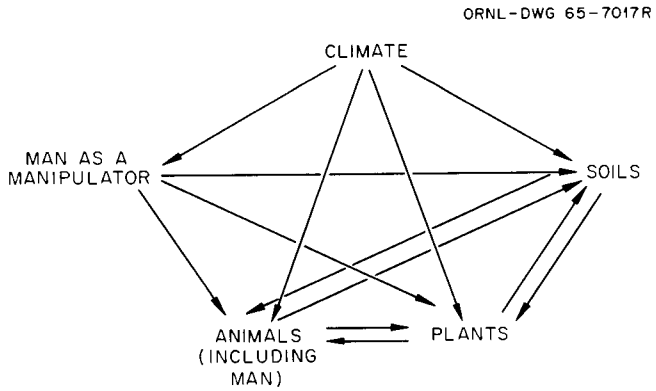

Fig. 1. An ecosystem is an integrated complex of living and nonliving components. Each component is influenced by the others, with the possible exception of macroclimate. And now man is on the verge of exerting meaningful influence over macroclimate.

For practical purposes and to avoid semantic argument, ecosystem and biogeocoenosis will be considered synonymous in this paper. Further discussion of ecosystem terminology is given by Schultz (*100*) and Maelzer (*73*).

The Ecosystem Concept: Unlimited Size and Complexity

A system is an organization that functions in a particular way. The functions of an ecosystem include transformation, circulation, and accumulation of matter and flow of energy through the medium of living organisms and their activities and through natural physical processes. Some specific functional processes include photosynthesis, decomposition, herbivory, carnivory, parasitism, and symbiosis (*31*). The ecosystem must be studied as a whole in order to understand energy transformations, the hydrologic cycle, or cycles of carbon, nitrogen, phosphorus, or other elements (*66, 68, 100*).

The ecosystem is the fundamental unit of study in "pure" and "applied" ecology (*31, 81, 106*). Directly or indirectly the ecosystem concept is useful in the management of renewable resources such as forests, ranges, watersheds, fisheries, wildlife, and agricultural crops and stock (*16, 26, 64, 72, 89, 91*). Understanding the ecosystem concept is required in the disposal of radioactive wastes and in analyses of environmental pollution (*108*). It has even found a place in medical studies of the digestive tract (*22*).

The ecosystem as a unit is a complex level of organization. It contains both abiotic and biotic components. The order of increasing complexity is: cell < tissue < organ < organism < population < community < ecosystem. Although the ecosystem is the most complex level, the study of a given ecosystem is less complex in many instances than the study of the lower levels (*33*).

We can consider steppe grasslands, deciduous forests, or oceans as examples of macroecosystems, as well as considering a given small plot or a spaceship and its contents as a microecosystem.

The term ecosystem is also used to describe a concept or approach of studying biotic-abiotic complexes. In applying the ecosystem concept there is no limit to size and complexity (*31, 34*). We delineate boundaries of ecosystems chiefly for convenience of study, although some natural boundaries may occur (e.g., shore lines and air-water or soil-water interfaces for aquatic systems), and man often introduces distinct boundaries, such as fences and field edges. Most ecosystems are bounded in nature by gradual and indistinct boundaries.

In the sense that the term ecosystem implies a concept and not a unit of landscape or seascape, the emphasis is that the biologist must look beyond his particular biological entity (e.g., cells, tissues, organs, etc.) and must consider the interrelationships between these components and their environment. For example, in applying the ecosystem concept to the tissue level of organization (Fig. 6) the environment of a specific tissue would include the fluids, such as blood and lymph, that may bathe or pass through the tissue as well as surrounding tissues. Part of the environment, therefore, consists of other parts of the same organism as well as external components. Generally, the ecosystem concept is used in situations where at least several organisms are being considered.

Trends in Ecological Research

Although the concept of the ecosystem and many methods for studying ecosystems have been available for some time, only recently have many ecologists given more than lip service to the idea. Recently it has been suggested that the ecosystem is the rallying point for ecologists. There has been a gradual but distinct shift in emphasis in ecological studies and training from the description or inventory of ecosystems, or parts thereof, to the study of energy flow, nutrient cycles, and productivity of ecosystems. More workers are extending knowledge from the "anatomy" to the "physiology" of the environment. This requires different concepts, tools, and methods. The gradual change in emphasis from inventory to experimentation also requires more use of scientific methodology; this will be discussed below in the section, "Systems Ecology."

Ecosystem Components

Jenny (*54–55*) discusses dependent and independent variables in ecosystems and shows their relationships by the following equations:

$$l,\ s,\ v,\ \text{or}\ a = f(L_0,\ P_x,\ t)\ ,$$

where the internal properties are l = ecosystem property, s = soil, v = vegetation, and a = animals. The external properties are L_0 = initial state of the system, P_x = external flux potentials, and t = the age of the system. External flux refers to the flux of nutrients, energy, etc. in from and out to adjoining systems and can be defined by

$$P_x = \left(\frac{P_{out} - P_{in}}{dX}\right) m ,$$

where P_{out} and P_{in} are the flux out and in over a boundary thickness dX which has a permeation parameter m.

The controlling factors of the ecosystem are macroclimate, available organisms, and geological materials, where the last term includes parent material, relief, and ground water. Time is considered as a dimension in which the controlling factors operate, rather than as an environmental factor. The controlling factors are partially or entirely independent of each other. Each of the controlling factors is a composite of many separate elements, and each element is variable in time or space. Operationally, we may consider each controlling factor as a multiple-dimensioned matrix. Each change in a controlling agent in the ecosystem produces in time a corresponding change in the dependent elements of the ecosystem. In space and time there is a continuum of ecosystems.

Internal properties of ecosystems, such as rate of energy flow, might be considered as dependent factors which vary through time under the influence of a series of independent controlling factors. The dependent factors of the ecosystem are soil, the primary producers (vegetation), consumer organisms (herbivores and carnivores), decomposer organisms (bacteria, fungi, etc.), and microclimate. Each of these factors is dynamically dependent on the others (Fig. 1), and each is a product of the controlling agents operating through time.

Producers, consumers, and decomposers are not distributed at random in the abiotic part of an ecosystem. To maintain either dynamic equilibrium or ordered change in an ecosystem requires that a tremendous number of ordered interrelations exist among its dependent elements (*82*). To function properly ecosystems must process and store large amounts of information concerning past events, and they must possess homeostatic controls which enable them to utilize the stored information. This information may be expressed in amino acid and nucleotide sequences in genetic codes which have developed over evolutionary time, or it may be expressed in spatial or temporal patterns (*20*). For example, the changing patterns of plant populations and communities in secondary succession can be considered as expressions of genetically coded information. One species, population, or community is replaced by another with greater genetic potential for utilizing the resources of the changing environment.

Dynamics

Ecosystem changes may be caused by fluctuations in internal population interactions or by fluctuations of the controlling factors. Such changes may be cyclical or directional (*14*). Directional change from less complex to more complex communities may be considered as progression or succession; directional change from more complex to less complex communities may be considered as regression or retrogression; both are shown in Fig. 2.

Autogenic succession occurs when the controlling factors are stable and change is due to the effect of the system or some part of it on the microhabitat. Clements (*15*) formalized this

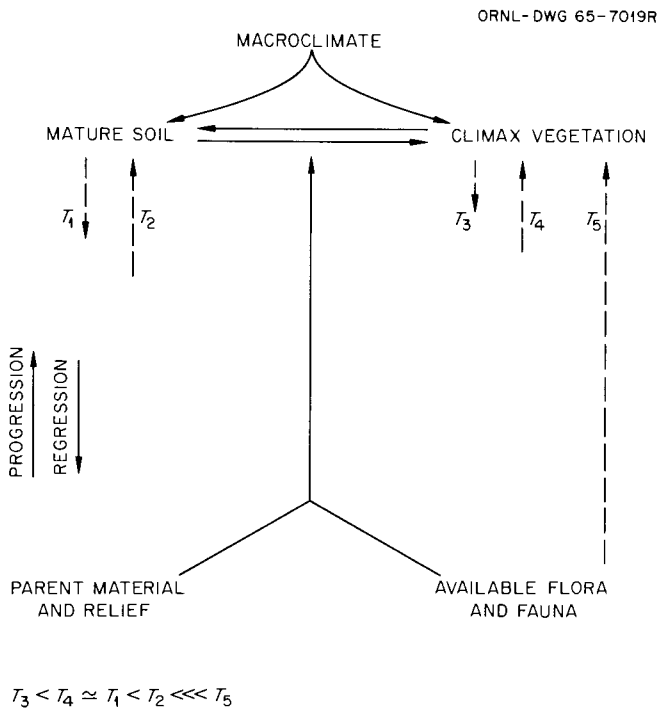

Fig. 2. Ecosystems develop through time, under climatic control, from the original flora and fauna under a given set of relief and parent material conditions. A final dynamic equilibrium is reached in which there exist a mature soil and climax plant and animal populations.

process as migration, ecesis, competition, reaction, and stabilization. This type of primary succession produces changes which are usually gradual and continuous. Allogenic succession occurs when there is a change in the controlling factors. Most changes in the ecosystem are products of both allogenic and autogenic successions. Most macroecosystems can be said to be polygeneic and are the result of several climatic changes and erosion cycles. Purposeful alterations, such as disruption by man, in the controlling and controlled factors of the ecosystem may induce relatively permanent changes in the ecosystem.

Because ecosystems vary both temporally and spatially, and to prevent ambiguity, it is important to specify at least semiquantitative time and space scales. The importance of specifying a time scale is illustrated in Fig. 2, where the time for primary succession (see T_5 for progression in Fig. 2) is shown as much greater than the time requirement for man to disrupt the system and alter soil or vegetation (T_1 and T_3 in Fig. 2). In the process of retrogression, changes take place in the vegetation more rapidly than they do in the soil. Generally, the ecosystem will recover towards the stable state through a progressive process called secondary succession (T_2 and T_4). Again, the rate of progressive changes of soil properties is usually lower than that for vegetation. Recovery of the vegetation to the climax state may take an amount of time similar to that required for deterioration of the soil. Change in a given ecosystem component or property may be negligible in T_3 but considerable in T_5.

During progressive succession there is usually an increase in productivity, biomass, relative stability and regularity of populations, and diversity of species and life forms within the ecosystem (*74*). Finally, the ecosystem reaches a steady state or equilibrium, which is characterized by dynamic fluctuation rather than by directional change. This steady state of the ecosystem is referred to as climax (*119*). At climax the dependent factors are in balance with the controlling factors; the climax is an open steady state (*101*). A diversity of species and life forms occupies every available ecological niche at climax and, because there is a maximum number of links in the food web, the stability of the system is maximized (*63*). A maximum amount of the entering energy is used in maintenance of life. Fosberg (*34*) considers "that climax communities [are those] in which there is the greatest range and degree of exploitation or utilization of the available resources in the environment." There is no net output from an ecosystem in the climax state (*86*). Three states of ecosystems exist with regard to energy or nutrient balance: steady state or climax, positive balance or succession occurring, and negative balance or decadence and senescence (*99*).

There is continual interchange of matter and energy among contiguous ecosystems. This interchange or flux is an essential property of ecosystems. The fluxes in and out of an ecosystem may be difficult to measure accurately, but there is relatively less error in measuring flux in a macroecosystem than in a microecosystem, because usually the error in measurements is inversely proportional to the magnitude of the object, rate, or processes being measured. Also, the relative amount of relevant surface or area around an ecosystem decreases as its size increases; many of the measurement errors or biases occur at such interfaces because of subjective decisions in defining boundaries. Still, we may find it convenient to study microecosystems such as a sealed bottle containing nutrients, gases, organisms, and water. Essentially, this is the type of system we need to study in preparing for interplanetary travel. But even such discrete microcosms are not adiabatic with their environment, and ultimately they are dependent upon their environment for a continuing energy input.

When flux of some element in and out of a given ecosystem is negligible for a defined period of time we consider that ecosystem to be stable with regard to that element. The equilibrium is referred to as climax only if it is reached naturally. Other equilibria, or disclimaxes, can be maintained by man's intervention. Here is the essence of renewable resource management: maintaining disclimaxes at equilibrium for the benefit of man.

Manipulation of Ecosystems

Man is a vital part of most major ecosystems, and there is an increasing human awareness of man's part in them and his influence on them (*108*) (Fig. 3). Traces of his pesticides probably can be found in living organisms throughout the world. Humans are both parts of and manipulators of ecosystems. Induced instability of ecosystems is an important cause of economic, political, and social disturbances throughout the world. In altering his environment in order to overcome its limitations to him, man learns that he often is faced with undesirable consequences

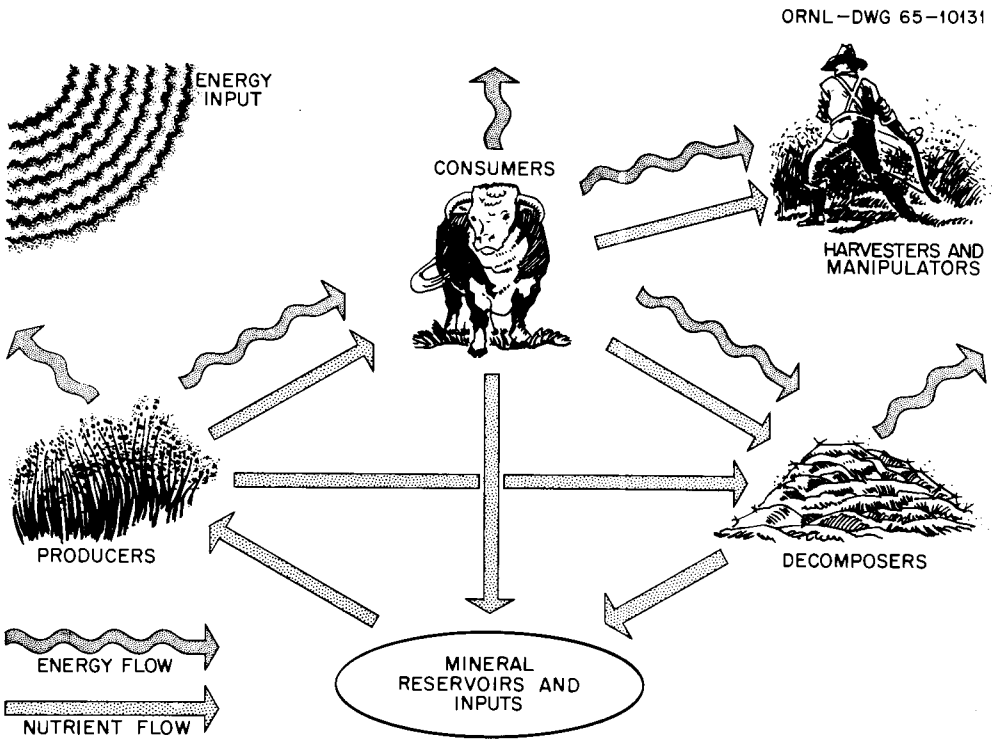

Fig. 3. Man is both a spectator of and a participant in the functioning of ecosystems. He has manipulated ecosystems to maximize the flow of nutrients and energy to him from the producers and primary consumers. He has attempted to minimize the respiratory losses of energy from producers, consumers, and decomposers.

of the environmental change (*13, 38, 39*). In manipulating his environment (e.g., felling forests, burning grasslands or protecting them from fire, and draining marshes), seldom has he foreseen the full consequences of his action (*104*).

Most ecosystems in our country were in climax states when civilized man began to affect them, but the economy of civilized man demanded that the ecosystems produce a removable product under his domination. In order to reach this goal he disrupted the climax ecosystems, perhaps by shortening food chains or by altering the diversity of life forms of primary producers. He has altered the rate of and amount of nutrients cycling through the system by such means as fertilization, both in aquatic and terrestrial systems (Fig. 3). In some instances the fertilization has been excessive and has led to undesirable side effects, such as algal blooms caused by excesses of organic wastes. In other instances man has altered the structure of ecosystems by simplifying them and diverting the flow of energy into his food products, such as in replacing a grassland and wild animals with a wheatfield. Eventually he has produced changes in some ecosystem properties, which in some instances has led to new quasi-stable levels. In other instances such changes have led to desertification, such as the result of centuries of overgrazing in the Middle East.

Man has also encountered difficulties when he attempts to return ecosystems to their native state or to preserve vegetation by the development of national parks or by control of predators (*104*). In several instances ungulate populations have multiplied rapidly, outstripped the natural control by predators, exceeded the carrying capacity of their ranges, and severely damaged their habitat. Examples include the classical Kaibab mule deer problem (*94*) and the elk problem in Yellowstone National Park (*64*). Man himself has had a direct and profound effect on some ecosystems he has attempted to maintain in a natural state, such as in Yosemite National Park (*39*).

Exploitation of ecosystems is still occurring throughout the world, although the consequences are yet unknown. Systems ecology may contribute to a better understanding of ecosystems and ecosystem processes, which will help civilized man produce new and useful quasi-stable equilibria. We still need to know the long-term effects and profits of ecosystem manipulation, such as even further shortening of food chains, as human populations continue to increase exponentially and impose greater stresses on our world ecosystem. Knowledge about the entire ecosystem has become so important that ecologists can no longer be satisfied to be concerned with specific individuals, species, or populations in the ecosystem. In addition to plant ecologists, animal ecologists, microbial ecologists, etc., we must now train more and more young ecologists to confront the entire complexity of the ecosystem.

We are still in the process of developing technology and scientific knowledge that will enable us to better perceive the influences of our manipulations of ecosystems. Intelligent manipulation of ecosystems is increasing, and there is increased interest in scientifically defining the carrying capacity of ecosystems, as in the proposed International Biological Program, for example. Scientific ecology has clarified many cause-and-effect relationships in environmental change. An example of the value of basic ecological knowledge may be found in studies relating community stability, diversity, and biological control practices (*116*).

SYSTEMS ECOLOGY

Definitions

The July 1964 issue of *Bioscience* contained perspective articles by several noted ecologists, and the term systems ecology was used. E. P. Odum (*83*), then president of the Ecological Society of America, used the term "systems ecology" as follows:

> "... the new ecology is thus a systems ecology – or to put it in other words, the new ecology deals with the structure and function of levels of organization beyond that of the individual and species."

We have been taught that ecology is the study of the relationships between organisms and their environment (*51*) and that ecology may be subdivided into autecology (of individuals or species), population ecology, and community ecology (*80*). Systems ecology in a sense approximates communities ecology. The terms system and ecology both imply a holistic viewpoint. Just as

ecology and ecosystems are considered by some people, systems ecology may be not so much an independent branch of study, but a point of view, a way of looking at things and explaining them, a concentration of pertinent concepts, facts, and data from various fields (*61*).

Some workers consider the realm of systems ecology to be that of using mathematics to study ecological systems. Although application of mathematical techniques to study ecosystems is an important part of systems ecology, it is far from being all of it. Systems ecology can be broadly defined as the study of the development, dynamics, and disruption of ecosystems. I consider systems ecology to have two main phases – a theoretical and analytical phase and an experimental phase.

Earlier I stated that for studying function in ecology we need methods and concepts which are different from those for studying structure. Essentially, study of problems in systems ecology requires three groups of tools and processes: conceptual, mechanical, and mathematical.

Study of Ecosystems

The tools and processes required for systems ecology are different from those for conventional phases of ecology because of the complexity of the total ecosystem as compared with a segment of it. When we consider the totality of interactions of populations with one another and with their physical environs – i.e., ecosystem ecology – we face a new degree of complexity (*10*). Other than some recent papers (e.g., ref. *41*) only a few reasonably adequate functional analyses of natural ecosystems exist (*80*).

One of the major problems in systems ecology is that of analyzing and understanding interactions. Events in nature are seldom, if ever, caused by a single factor. They are due to multiple factors which are integrated by the organism or the ecosystem to produce an effect which we observe (*45*). To further complicate the matter, various combinations of factors and their interactions may be interpreted and integrated by the ecosystem to produce the same end result.

Conceptual Requirements

A first conceptual requirement in systems ecology is clearer definition of problems. It is axiomatic that ambiguous use of terminology and an ambiguous statement of the problem lead to ambiguities of thought as well (*19*). These statements apply to many fields, but, particularly here, clear definitions are required because of the type of people systems ecologists will be and the types of people with whom they will work (discussed further below). Furthermore, in using computers, which are essential tools for systems ecologists, it is necessary to formulate the problems precisely and to clearly delineate the factors involved.

A second conceptual requirement in systems ecology is more and better use of logic and scientific and statistical methods. Essentially, we can define scientific method as the pursuit of truth as determined by logic and experimentation. In scientific method we use the approach

of systematic doubt to discover what the facts really are. Experimentation is one of several tools of scientific method used to eliminate untenable theories, that is, to test hypotheses (*32*). Other experiments may be conducted to determine existing conditions, or to suggest hypotheses, etc. The conclusions from experiments may be criticized because the interpretation was faulty, or the original assumptions were faulty, or the experiment was poorly designed or badly executed (*88*). Experimental design and statistical inference are aids in testing hypotheses.

Much past ecological research has not tested a hypothesis. There is a tendency for ecologists to pass over the primary phase of analysis. The lack of understanding of what is known already (inadequate knowledge of the literature, in part) is understandable because of the volume of material to be covered (*58*). Glass (*40*) has clearly stated this dilemma – "the vastness of the scientific literature makes the search for general comprehension and perception of new relationships and possibilities every day more arduous." But inadequate examination of facts and data and inadequate formulation of hypotheses lead to uncritical selection of experiments testing poorly formulated hypotheses, and ecologists are often at fault here (*51*). The experimental design is, essentially, the plan or strategy of the experiment to test clearly certain hypotheses (*32*). Statistical methods are especially important in experimentation with ecosystems, because not all factors influencing the system can be controlled in the experiment without altering the system (*29*). These uncontrollable factors lead to error or "noise" in our measurements, and inferences to be made from the results of experiments should be accompanied by probability statements (*32*).

Eberhardt (*27*) has discussed many of the problems ecologists encounter in sampling, and has stressed the importance of statistical techniques in analysis of such problems. Methods of statistical inference are also useful in suggesting improvements in our mathematical models and in suggesting alterations in the design of future experiments. Some of the work initiated and developed by the late R. A. Fisher on partial correlation and regression is invaluable to us in evaluating independent and interaction effects in complex ecosystems where experimental control is neither possible nor desirable (*45*).

The first two conceptual needs for systems ecology, mentioned above, lead naturally to the third, the approach of modeling (Fig. 4), with models which are mathematical abstractions of real world situations (*17, 107*). In this process some real world situation is abstracted into a mathematical model or a mathematical system. Next, we apply mathematical argument to reach mathematical conclusions. The mathematical conclusions are then interpreted into their physical counterparts. In some instances we are able to proceed from the real world situation via experimentation to reach physical conclusions. In other instances, however, we cannot experiment with a situation that does not exist but may become real; examples are such situations as thermonuclear war and wide-scale environmental pollution (*50*). In many cases we find it too costly to experiment; therefore mathematical modeling or mathematical experimentation may be especially useful.

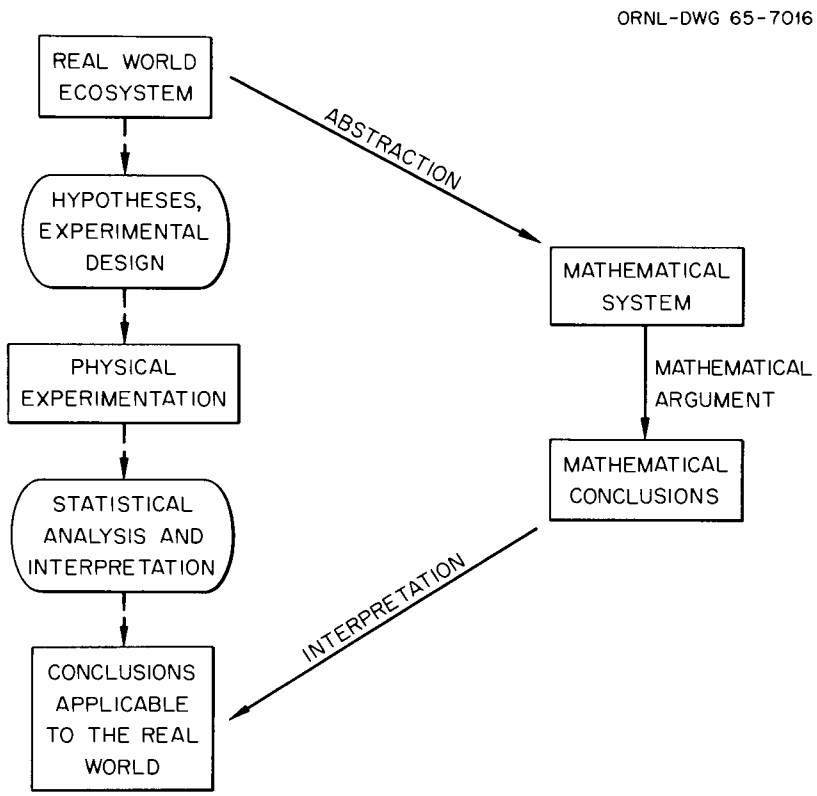

Fig. 4. Two ways of experimenting with ecosystems. One involves the conventional process of formulating hypotheses, designing and conducting experiments, and analysis and interpretation of results. The second involves the abstraction of the system into a model, application of mathematical argument, and interpretation of mathematical conclusions.

Mathematical modeling is somewhat new to many conventional ecologists and, in part, is just as much an art as a science. To ensure that the model will be valid, the mathematical axioms must be translations of valid properties of the real world system. The application of mathematical argument gives rise to theorems which we hope can be interpreted to give new insight into our real world system. However, the value of these conclusions should, where possible, be verified by experimentation. We must then accept the conclusions or reject them and start over again. This procedure of modeling, interpretation, and verification is used in many engineering and scientific disciplines. The success of the procedure, however, depends on the existence of an adequate fund of basic knowledge about the system. This knowledge permits predictive calculations. Hollister (*50*) outlines some of the problems to be encountered in modeling ecological phenomena.

Tools for Study of Ecosystems

The above conceptual tools should provide a framework in which to attack the complex problems of systems ecology. To implement these methods in studying ecosystems we will

need both physical and mathematical tools, including digital and analog computers and electrical, mechanical, and hydraulic simulation devices, and artificial populations (*44, 75, 85*). The act of expressing and testing biological problems with numerical, electrical, or hydraulic analogs often reveals some unsuspected relationships and leads to new approaches in investigation. In conducting experiments in systems ecology, more refined chemical analytical equipment will be needed, such as gas chromatographs, infrared gas analyzers, and recording spectrophotometers. Physical analytical equipment required includes micro-bomb calorimeters, biotelemetric equipment, and other electronic equipment useful for rapid, nondestructive sampling and measuring of plant and animal populations and parameters under field conditions.

The importance of these chemical and physical tools is apparent when one considers the amount and variety of apparatus required to construct and maintain even the simplest aquatic ecosystems or to transplant and manipulate naturally occurring ecosystems for detailed measurements (e.g., ref. *2*). A major reason for the scarcity of detailed studies of entire terrestrial ecosystems is that many ecologists are not trained to use many of the required, diversified tools. In other instances these tools may not be available to the ecologist. The systems ecologist cannot be an expert with each of these tools, but he must be aware of their applications and limitations in the study of components and processes in ecosystems. He will need to be conversant with the specialists in other disciplines who make increasing use of these modern and complex tools. For example, in the last 12 years there has been a sixfold increase in the use of large, expensive, and complex instruments in chemistry (*118*).

One of the important tools is tracing with radioisotopes. This is valuable for identifying food chains, for determining the mass of nutrients in various compartments of an ecosystem, and for determining the time and extent of transfer of matter and energy among compartments within the ecosystem. Possibly we can use two, three, or more tags simultaneously in many ecological experiments if we select tracers which have appropriate physiological properties and types of radiation. Ionizing irradiation and selective poisons are other tools or treatments that can enable us to learn more about the function of ecosystem components without physically dismantling the entire ecosystem.

One interesting feature is that many of the new methods and instruments are simpler to use, although more expensive, because much laboratory skill in manipulation has been eliminated by instrumentation (*40*). The systems ecologist will still require the tools of conventional ecology, but he cannot rely on them alone. An important caution for the systems ecologist is that the problem should dictate the tools to be used; the opportunity to use a complex tool should not dictate the problem to be studied.

Operations Research and Systems Analysis Applications

Mathematical analysis will become increasingly important in providing advances in systems ecology. Large, fast digital computers have become available in the last 15 years and have

allowed the development of special methods of analyzing and studying complex systems in industry and government. Most of these newer mathematical tools were developed in and are used primarily in two loosely defined and somewhat overlapping fields, operations research and systems analysis.

Operations research may be defined as the application of modern scientific techniques to problems involving the operation of a system looked upon as a whole (*77*). Included therein are any systematic, quantitative analyses aimed at improving efficiency in a situation where "efficient" is well understood (*103*).

Systems analysis is more difficult to define. Perhaps it can best be defined by opposites. The opposite of a systems approach is unsystematic or piecemeal consideration of problems; intuition may be taken as the opposite of analysis (*46*). Essentially systems analysis is any analysis to suggest a course of action arrived at by systematically examining the objectives, costs, effectiveness, and risks of alternative policies – and designing additional ones if those examined are found to be insufficient (*93*).

It is easily seen that operations research and systems analysis are both alike and different. They both contain elements from mathematical, statistical, and logical disciplines. In operations research, however, there usually is an unambiguous goal to be achieved, and the operations researcher is interested in optimization. The systems analyst faces a multiplicity of goals, a highly uncertain future, a frequent predominance of qualitative elements, and an exceedingly low probability of building an accurate and satisfactory model for his total problem (*103*). Because of the methods and techniques he can use effectively, the systems engineer has much to offer in study of ecosystems but he will need considerable guidance. In systems ecology he will be facing a collection and coupling of "green, pink, and brown" boxes (plants, animals, and physical environment) rather than the black boxes with which he is familiar (*56*). The interconnections between these boxes may be known only imperfectly, and the functional significance of the boxes will need to be established.

Some of the mathematical tools to be employed and examined in systems ecology include scientific decision-making procedures, theory of games, mathematical programming, theory of random processes, and methods of handling problems of inventory, allocation, and transportation (*77*).

Linear, nonlinear, and dynamic programming, which are especially important to the operations researcher, already show promise in ecology (*4, 112, 115*) and in management of renewable resources (*12, 60, 69*). Mathematical programming has already been used widely in agro-ecological problems, such as crop or yield prediction (*97*), in formulation of least-cost rations for livestock (*110*), and in farm management decisions (*5*). Game theory has been applied to decisions in cultivated-crop agriculture (*113*) and appears to have potential in dealing with wildland resources. Queuing theory and network flow appear to offer much in looking at problems of flow rates in ecosystems (*90*). Margalef (*74*) has discussed and indicated some important applications of information theory in ecology. Cybernetics principles and techniques are also useful

in studying biological systems (*37*). Simulation is another important tool in operations research, although not limited to it. Mathematical simulation models have been used to study important resource problems, such as salmon population biology (*59, 95*), and abstract systems (*36*).

Importance of Digital Computers

Probably most systems ecology problems will be attacked first with deterministic models as first approximations (*70, 71*). However, to increase their usefulness and their realism, stochastic elements will be involved in most models or an indeterministic point of view will be taken; for example, see Leslie (*65*), Neyman and Scott (*79*), and Jenkins and Halter (*53*). This will require extensive use of digital computers, not only in simulation but also in analysis. Most stochastic models in ecology to date have been concerned with only one or two species rather than populations or ecosystems (*6*). Stochastic simulation of biological models or processes has been a useful process in some problems (*109, 111*). Many problems of modeling and analysis will require study and examination of the underlying statistical distributions (*28*). In addition to the normal distribution, other distributions which will need examination and use in systems ecology problems include the Poisson, the exponential, and the log-normal. Monte Carlo methods will be especially valuable in developing, testing, and using stochastic or probabilistic models (*30, 67*). Computers are essential in studying and using these statistical techniques in systems ecology. Other statistical aspects are discussed by Eberhardt (*29*).

Compartment model methodology, implemented with both analog and digital computers, has proven its value in theoretical studies and is beginning to be put to use in analysis and extension of real data in medical (*9*) and ecological fields (*87, 90*). Thus far, however, compartmental simultation models have been restricted to relatively simple ecological and agricultural situations, because most investigators have worked with analog systems of limited capacity (*1, 35*), although simulation systems have been developed for and used with digital computers in the study of renewable resources (e.g., ref. *42*). Most systems ecologists will find it surprisingly easy to express many problems in the pseudoalgebraic languages, such as the many dialects of FORTRAN, used to communicate with digital computers.

An ecosystem might be depicted, as in Fig. 5, as composed of trophic levels represented as three-dimensional matrices. PRODUCER (I,J,K), CONSUMER (I,J,K), and DECOMPOSER (I,J,K) are matrices of species, individuals, and parts. The ranges of I, J, and K in each matrix are variable and depend upon the study. Matrices of transfer functions, depicted and simplified by the arrows in Fig. 5, are concerned with movement of matter or energy within individuals, between individuals, or between species. The latter two types of transfers may be between or within trophic levels. Also included in the figure is the fact that flux among contiguous ecosystems may be considered in matrix representation. Some of the transfer functions themselves may contain random noise and may be functions of a driving variable, such as macroclimate, acting on the system over time. Models or functions for macroclimatic influences may be constructed from actual data or may follow some prescribed hypothetical statistical distribution.

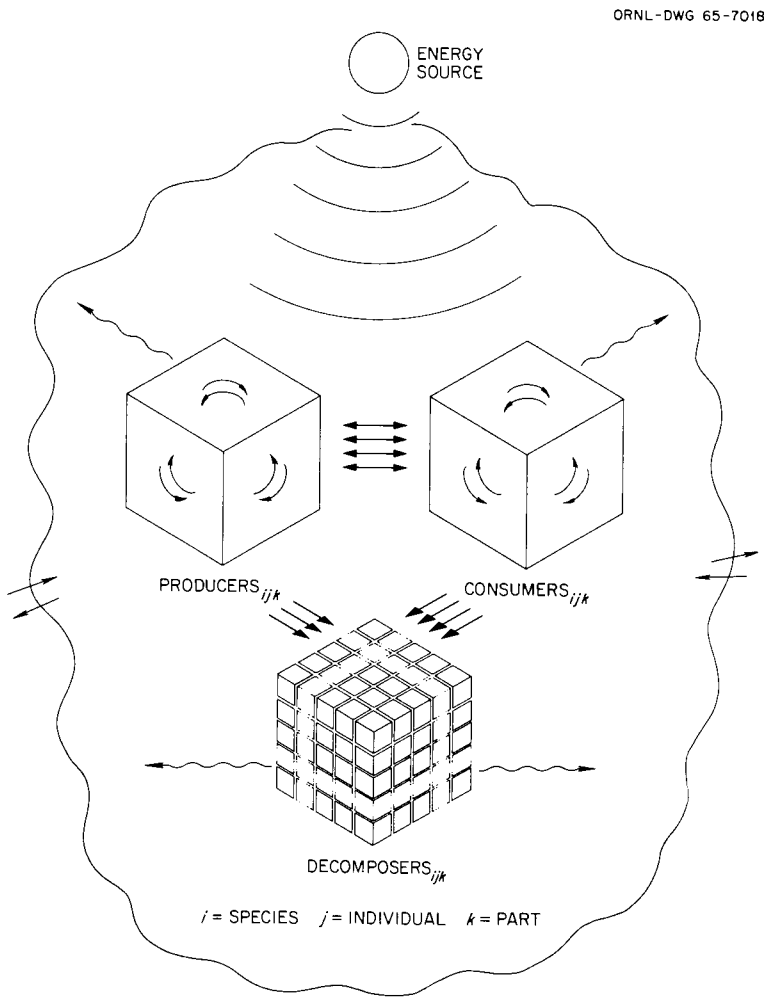

Fig. 5. A matrix representation of ecosystems adapted to pseudoalgebraic computer languages. Each trophic level is represented as a three-dimensional matrix. The arrows, wavy for energy and straight for matter, represent matrices of transfer functions interconnecting parts within individuals, individuals of a species to each other and to other species, etc., on up to connections between contiguous ecosystems. The transfer functions may contain probabilistic components and may be probabilistic functions of external variables such as macroclimate.

Consider the simplified case (Fig. 5) with only three parts per individual, three individuals per species, three species per trophic level, three trophic levels per ecosystem, and three ecosystems per problem. This leads to 3^5 microcompartments to be accounted for in addition to the many transfer functions interrelating the compartments. Many of the transfers will be zero, but this simplified model exceeds the capacity of most analog computers even if the problems of using various random function generators with an analog computer are bypassed. This example does not indicate that analog computers will not play an important role in systems ecology, but only that they may be of limited value in many realistically complex situations. Their major role may be as teaching (and learning) tools and as components of hybrid (digital-analog) sys-

tems. The capabilities and versatility of digital computers in general are far greater than those of analog computers (*62*).

Maximum use of most of the above mathematical tools and others by systems ecologists depends upon access to fast digital computers with large memory capacities (*115*). Such access will be especially important in working with large complicated models where remote-console access to large central computers will be essential for efficient and rapid progress. Computer technology is approaching the point where the rate of debugging of programs is the limiting factor.

The role of computers in the future of systems ecology is too readily underestimated. Computers in tomorrow's technology will have larger and faster memories, remote consoles, and time-sharing systems. Some may accept hand-written notes and drawings, respond to human voices, and translate written words from one language into spoken words in another (*96*). There will be vast networks of data stations and information banks, with information transmitted by laser channels over a global network. This network will be used not only by researchers but also by engineers, lawyers, medical men, and sociologists as well as government, industry, and the military. Computers could become tomorrow's reference library used by students in the university; they are already starting to revolutionize our present approaches to certain kinds of teaching. To utilize computers effectively in ecology we will have to state precisely what we know, what we do not know, and what we wish to know. Also, it will be necessary to assemble, analyze, identify, reduce, and store our ecological data and knowledge in a form retrievable by machine.

A Systems Approach

Systems ecology will call for an interdisciplinary team of systems ecologists, systems analysts and operations researchers (if they can be separated), conventional ecologists, mathematicians, computer technologists, and applied ecologists, including agriculturalists and natural resource managers of various disciplines. Systems ecologists studying ecosystems will devote at least as much time to delineating the problem as they will to solving it. This gives a hint as to the nature of the work of the systems ecologist.

The physical and mathematical tools to be used by this team are impressive, even though the list in the preceding sections is only partial. It serves to show that the systems ecologist will have to have more types of specialized training than did his predecessors. That different tools and methods may be needed to solve some of today's complex ecological problems is emphasized by the fact that many important contributors to advances in ecology in recent years may not be identified as ecologists (*92*). This will be especially true of systems ecology in the future, even though ecologists must be generalists and systems ecologists also will, in part, have to be generalists. Still, there are probably few if any authentic generalists or truly great minds who are not firmly grounded in a specialty (*18*). Most systems ecologists will serve their apprenticeship in basic fields. The conventional plant, animal, and aquatic ecologists will not be acceptable as systems ecologists, because they will lack the depth required in many specialties (*78*).

This raises the difficult question of how to train a man to be a specialist in at least one field, to be able to converse well with specialists in several fields, and yet to have a holistic or systems viewpoint.

SYSTEMS ECOLOGISTS

Definitions

The systems ecologist of tomorrow may be defined as one type of scientist who is a specialist in generalization (*100*). There are few if any systems ecologists today. Of today's biologists, perhaps some scientists in applied ecology can be considered systems ecologists (Fig. 6). In some applied ecology fields, such as forestry, it has been noted that the field is becoming so complex that more members of the profession will likely find it to their advantage to either specialize or become an exceptionally well-balanced generalist (*11*). This trend is well established in many professional fields. In addition to the growing need for specialists in resource management, there also is a niche for the generalist (*120*). Undergraduate programs have been developed to train such individuals.

The applied ecologists, shown as the second group of specialists in Fig. 6, to some degree have in their training many elements of the training of the four groups of specialists listed below them. The applied ecologists are closer akin to the systems ecologists than are the conventional ecologists, because in their training and in their work they usually are more cognizant of the total ecosystem and its interrelations than are many conventional ecologists.

Consider, for example, a scientist responsible for the trout population in a Rocky Mountain forest. He realizes that the trout's well-being is inextricably related to the total environment. He must consider the impact of grazing, lumbering, mining, and road-building upon the response of the watershed to uncontrolled and fluctuating precipitation. He must consider also the inherent fertility of the watershed and its impact on populations of fish and fish foods. Superimposed upon this are other factors, such as insect control by wide-scale pesticide spraying, the problems of optimum rates and places of artificial stocking of streams, of seasons and levels of bag limits, of public relations etc., ad infinitum. In contrast, for example, few plant ecologists thoroughly appreciate aquatic problems or communicate well with aquatic ecologists; few animal ecologists understand soil problems or communicate well with soil scientists.

The systems ecologist will require better mathematical, chemical, physical, and electronic training than either the applied or the conventional ecologist. Yet he must share their holistic way of thinking or approaching problems, and he must have a broad background in ecological subject matter. A lifetime may not be sufficient for any one person to prepare adequately to perform unassisted the synthesizing function, a major effort of the systems ecologist. This function requires the cooperation of specialists, and publication in each other's journals (*52*). No individual will be able to direct or conduct research without consulting others to obtain a complete understanding of the processes within even most fairly simple ecosystems (*80*). Future

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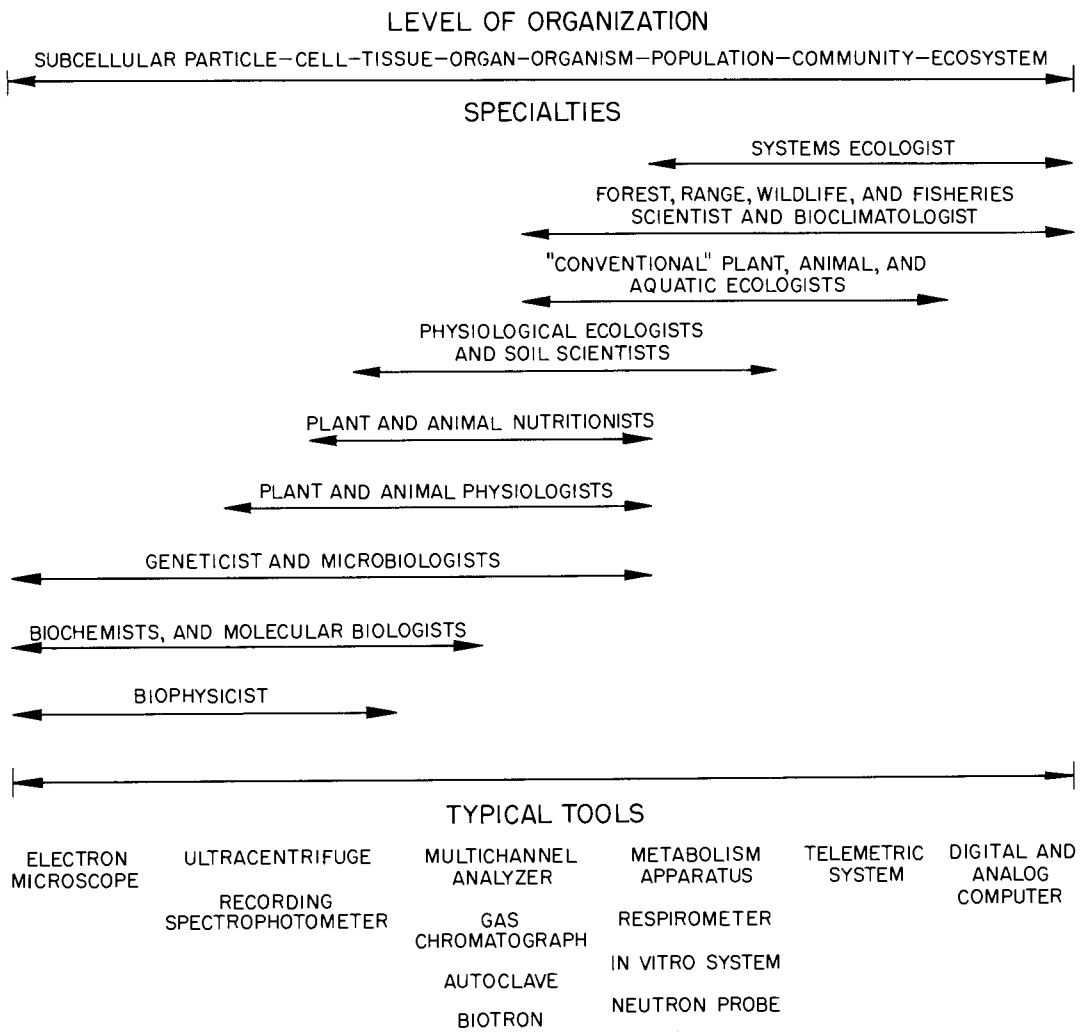

Fig. 6. A schematic comparison of biologists, the level of organization of the media with which they work, and the tools they use. The double-ended arrows indicate general positions of the specialties. Tools especially, and to some extent the media, overlap widely for different specialties.

leaders toward this goal must have the ability to organize concepts, things, and people.

It has long been apparent to those in physical sciences that the ecologist, in the broad sense, must be an environmental specialist. For example, Jehn (*52*) suggested that an ecologist must simultaneously be a meteorologist, a soils physicist, a geologist, and a geographer. But because no one man can encompass all the required specialties, he must ally himself with these specialists (*61*). Therefore, the greatest advances to be made in systems ecology will require the effort of an interdisciplinary team. How can this be done without losing the spontaneity and originality of the individual's personality?

Systems Ecologists: Interdisciplinarians and Multidisciplinarians

That interdisciplinary teams are required to solve many physicobiological problems of national importance is becoming more and more apparent (*43*). For example, the understanding of pollution processes requires the cooperation "of [systems] ecologists, physiologists, biomathematicians, microclimatologists, geneticists, microbiologists, biochemists, chemists, morphologists, and taxonomists..." (*108*). To work effectively as a member of an interdisciplinary team, the systems ecologist will need to establish a common vocabulary, an agreed-upon ideology, a set of reasonable goals, a common context for symbols, and ways for translating ideas into action (*57*).

The systems ecologist is one of the types of interdisciplinary scientists who should be in great demand in the near future. It has been estimated (*98*)

> "that about ten percent of our total national effort will be going into production, development, and research based on biophysics, biomedicine, bioengineering, and related computer projects by 1970. ...then we must hurriedly prepare to train several thousand additional students to the Master's or Ph.D. level per year in this difficult field and we must anticipate at least a doubling of our teaching and research facilities in this interdiscipline once in each three years during this decade."

Systems ecologists can and should contribute heavily to these efforts. But the increasing importance of group effort and interdisciplinary teams in the study of major, man-created environmental problems creates new paradoxes. Large-scale, expensive research activity may decrease the flexibility and freedom which are intrinsic to research. Operation of an interdisciplinary team requires unique coordination and appreciation of contributions by different skills at many levels (*23*). Interdisciplinary research must be reconciled with the continuing importance of distinctive contributions by highly talented and motivated individuals. Furthermore, it is historical fact that to date many major scientific achievements have been made by specialists – by scientists wearing blinders (*46*).

Imagination and inventiveness, like the ability to work in an interdisciplinary team, are difficult to develop by training (*47*). A successful systems ecologist will be one with the imagination to perceive an important problem before others do. He must have the inventiveness to devise and weigh alternatives for its solution. This emphasizes the multidisciplinary nature of systems ecologists. In order to contribute effectively in the interdisciplinary team they must have sufficient depth in more than one specialty in order to make significant contributions to the solution of the problem. Thus, systems ecologists will need both breadth and depth of interests.

The role of the systems ecologist is complex and not well defined, nor is it easy to analyze. He may be viewed by many specialists of the interdisciplinary team as an amateur, and he may be viewed by his fellow ecologists with suspicion. Both views are justified until he proves his worth to all concerned. A major problem of the systems ecologist will be to convince an ecologist that a mathematical attack is useful and to convince the mathematician that his time

and methods will be productive in ecology. Is there a natural course for this convincing to take? The interdisciplinary viewpoint does not rest solely on the biologist. A team composed of biologists with no mathematical and computer training and of engineers, mathematicians, and programmers with no biological training is doomed for failure (*62*).

Consider next the major activities of the systems ecologist in terms of combinations of old and new problems attacked with old and new methods [*sensu* Bellman (*7*)].

Old Problems – Old Techniques

In attacking old problems with old techniques, systems ecologists will be looked upon by their colleagues as useful intermediaries between themselves and biometricians. Therein, systems ecologists are used by their colleagues to provide guidance in the use of rather fundamental mathematical principles and methods. Soon, however, the average ecologist will be better trained mathematically and will not require as much of this service from the systems ecologist. How soon this will be is not certain. These activities may well be considered as one useful part of the training of the young systems ecologist, but should not be the major activity of the senior systems ecologist.

Old Problems – New Techniques

Old problems can also be attacked with some of the new and challenging techniques, such as those from operations research discussed above. These efforts should have considerable feedback influence on some fields of applied mathematics and may serve to initiate further developments of new methods. The attack on old problems by the systems ecologist armed with new methods should be rewarding and interesting and should produce further insight into ecological systems in a relatively short period of time. This is so because much time and effort has already been expended in the development and application of these techniques in fields with direct ecological analogies – examples are the conduct of war with species competition, the management of a firm with dynamics of ecosystems, the manufacture of a product with problems of nutrient cycling and energy flow, and the planning of an economy with optimization and adaptation in ecosystems. Today's systems ecologists (if they exist) probably will work primarily in this and in the next capacity.

New Problems – Old Techniques

The systems ecologists will still find uses for old techniques to attack new problems. Here he will serve an important consulting and interpreting service to other ecologists. He will be able to use his insight into the problem and its analysis by drawing upon his accumulated experience. This will be an effort of significant importance for the systems ecologist in the near future.

New Problems – New Techniques

New problems attacked with new techniques will be the most challenging, most demanding, most rewarding – and most discouraging – efforts of the systems ecologist of tomorrow. A hint of the challenge and importance of these efforts is seen if we attempt to foresee the consequences of being able to model accurately, to simulate, and to predict behavior of macroecosystems in various fields of renewable resource management. Another challenge for systems ecologists is to work effectively in interdisciplinary teams which are now required and which soon will start to study in detail the movement and degradation of pollutants through complexes of ecosystems. Of similar importance tomorrow is the application of knowledge of ecosystem behavior to the development of support systems for exploration of space (*84*). These efforts will be very demanding, because they will require the closest cooperation of competent and interested specialists.

Such efforts offer ecologists all the tangible and intangible rewards for being first to make major contributions to a new area of study. However, these efforts can be most discouraging because their impact may not be prompt and success is not certain. Furthermore, significant achievements by the systems ecologist in this area may not be recognized immediately for their worth by many conventional and applied ecologists. Most ecologists are not trained to evaluate the nature of this work. Slobodkin (*102*) states that "the number of good quantitative ecologists is in the thirties or forties for the entire world. . . ."

Some Pitfalls Facing Systems Ecologists

The availability of such powerful tools and equipment as gas chromatographs, telemetric devices, and computers will not make the solution of new problems trivial, nor will it make systems ecology research routine. Some of these powerful tools themselves are raising important problems.

A special problem exists with computers. In general, the larger and faster a computer is, the more economical it is, even for small problems, if there is sufficient work available. But, of necessity, operating procedures of large computer centers are rigid in order to maintain output. The "people problems" of getting small problems into large computers grow disproportionately with computer size (*98*), so remote access to and time sharing on these big computers will be essential. Without direct access to the computer, such as provided by remote consoles, many problems can be completed more rapidly with a hand calculator, although they may require several hours' work. Even though they could be run in a few seconds on a computer, the long delay or "turn-around" time in using a computer without direct access leads to inefficiency. Our research output is best and most efficient when we are able to progress at full speed, regardless of time of day or day of week, rather than to take days or weeks to complete a problem. Remote-console access to the large computers which will be required for many ecological problems will allow concentrated work and will in every sense give rapid results.

As compared with his predecessors, the systems ecologist will still have to acquire empirical data by means of experimental or literature research, but he will need a better grasp of the biological and physical interactions in the system he is studying, and he will have to apply more ingenuity and invention to formulating and analyzing his problems in order to make significant advances. The easy problems have been solved.

Another pitfall facing the systems ecologist of tomorrow, who may be an undergraduate today, is that often he has been given equations and their coefficients and has been asked to produce numerical or graphic solutions. The problem he faces when he leaves the "ivy-covered halls" is first to design experiments correctly and then to conduct them effectively before he even obtains experimental results. Then his problem will be to infer and derive the form of the equations and to determine analytically the magnitude of the coefficients. Needless to say, this will be a much different and more difficult task than that which he faces as a student. Perhaps it will be desirable to develop "co-op" training programs wherein the student may intersperse practical experience in his undergraduate program. Graduate students in systems ecology, of course, will have numerous opportunities to test the effectiveness of their training, especially in their research work.

Mathematical Training of Systems Ecologists

The training of systems ecologists in mathematics and computer sciences is an especially important part of their education. Watt's review (*114*) of the use of mathematics in population ecology gives numerous examples of mathematical methodologies and applications. Unfortunately, many ecologists receive little mathematical, statistical, or computer training, and this is only late in graduate school. An encouraging trend is the recent development of undergraduate biomathematical courses and curricula at several universities. For example, an undergraduate biologist at Colorado State University who has had college algebra can, in 12 quarter credits, complete courses in calculus and differential equations designed for biologists. Mathematical training for attacking four types of problems has been outlined for undergraduate students in biological, management, and social sciences (*24*).

Consider the four combinations generated by deterministic and stochastic phenomena, each with few or with many variables. Tools required in study of organized simplicity (i.e., deterministic × few variables) include the classical analytic geometry–calculus sequence, and difference and differential equations. Disorganized simplicity (i.e., stochastic × few variables) requires probability and statistics for analysis. Organized complexity requires linear algebra and many-variable advanced calculus. Study and use of complex stochastic models are needed for analysis of phenomena characterized as disorganized complexity. Computers are especially important in these last two areas, and computing practice in numerical analysis is equally important. For those systems ecologists who wish to specialize in computers in their undergraduate or graduate training, additional courses may be recommended (*25*).

Recently courses have been taught to ecologists which combine many systems-oriented mathematical approaches to ecological problems with practice in the use of digital computers (*117*) or use of both analog and digital computers (Systems Ecology, a yearlong graduate course at the University of Tennessee, which has been taught by B. C. Patten, J. S. Olson, and the author). Systems ecologists, however, should be trained in mathematics not so much for developing their skill in performing mass computations as for having the ingenuity of escaping them (*47*).

Systems Ecology Research

It is considered by some that existing ecological theory often has limitations in the rapid solution of many problems (*76*). Also, some consider that the reliance upon analogies from physics for the solution of ecological problems has distinct limitations (*102*). But the field essentially is a virgin area for tomorrow's better trained and better equipped systems ecologists. The dearth of quantitative ecologists has been mentioned above, and most ecologists have been isolated and not well supported. Hopefully, we will be able to develop centers wherein "critical masses" of systems ecologists will migrate and find suitable niches.

Perhaps a routine similar to the following will be of use to the systems ecologist (*7*). He will often have to guess at the fundamental cause-and-effect relationships in his system and may even have to guess about the basic variables. He will then test these hypotheses by comparing the quantitative and qualitative behavior of the real world with that predicted from his model. Fortunately, he will have varied and powerful tools available for the testing of complex (and realistic) as well as simple hypotheses. But there are an infinite number of hypotheses to test about any complex system, and most of these hypotheses will be wrong. Holling (*48–49*) shows by example how theory and experiment can be combined in a systems analysis of predation in a way to greatly reduce the number of hypotheses to be tested. The majority of the alternatives must be excluded by means which require, not computers, but only pencils, paper, and discriminating thought. The systems ecologist will have to develop the knack of feeding on negative information and use these negative hypotheses to guide his further experimentation and theory. In instances where experimentation or measurement of parameters is impossible without disruption of the system, perturbation of the system followed by measurements may still give new insight for the definition of a model (*8*).

A major hurdle to overcome in systems ecology research is lack of precedent in funding detailed and integrated research on complex ecological systems. This applies both to the theoretical and analytical phase and the experimental phase. In many respects no single organization has been working in depth on complex systems ecology problems, for such work may be beyond the role, objectives, or structure of existing organizations. Universities, national laboratories, and state and federal experiment stations each have some unique resources and capabilities for studying ecosystem problems. Some advantages and disadvantages of these three types of organizations with respect to "total systems" research, based on my experience in working in these organizations, are briefly outlined as follows.

In the past, ecological research conducted at universities generally has involved one investigator, or at most a few, on a part-time basis on problems of limited extent. Extensive and intensive interdepartmental cooperation in ecological research has been the exception rather than the rule. Many sources of funds are available to these researchers, but usually in amounts insufficient to attract permanent personnel and to support long-term ecosystem research. Although the economy of graduate student use has been exploited, often there is a lack of continuity in the conduct of long-term environmental researches. By the time the student gains competence and becomes capable of independent contributions to the project, he graduates and is lost to the project. Also, universities often lack controllable research areas or have conflicting needs for them.

Applied ecologists, in state fish and game departments or in state and federal agricultural experiment stations, for instance, often have controllable research areas on which to conduct long-term ecosystem research, but continuity again is impeded because of high turnover rate of personnel. Furthermore, their research funds often are restricted to only one or a few phases of the total ecosystem problem, and their funds have become more limited in recent years. Funds from many granting agencies may not be available to them for research, special training, or foreign study.

In the past ten years considerable ecological research has been conducted at several national laboratories. Ecologists in these laboratories have available many services, tools, and consultants which the university or experiment station scientists lack. Much of the ecological work in the national laboratories, however, has been concerned with specific needs of the funding agency. Most ecological researchers in these laboratories have come directly from liberal arts departments in universities, and these laboratory staffs are divided into subject matter groups for conduct of research. A total-system, interdisciplinary approach usually has not been implemented in their research. Although these ecologists are funded comparatively well, their costs are high due to the nature of their work. Although they may have long-term control over their research areas, the number of these laboratories is limited, and some important biomes, such as grasslands, are not within the boundaries of these laboratories.

I feel that perhaps research in systems ecology could encompass the advantages held by ecological researchers of the above three categories. This would require, however, some shifts concerning funding and conduct of research, and some shifts in administrative policy of the respective agencies or institutions. The exact nature and organization of such research is uncertain, although Dubos (*21*) has raised some interesting questions and has made some good suggestions about similar research in environmental biology.

The long-term impact on man of fundamental, total-ecosystem research should be recognized, and the framework should be developed for extensive and intensive intercooperation of these three groups of ecologists. Analytical and experimental research on total-ecosystem complexes should be initiated as soon as possible, if man is to benefit tomorrow, because most problems of environmental magnitude require many years of study before conclusions may be reached.

The proposed International Biological Program is, in several respects, a call for systems ecology research, both experimental and theoretical. This program could provide an incentive and a means for ecologists from universities, experiment stations, and national laboratories to work cooperatively and share funds, research areas, and talent. An example follows. Other such examples of needed research on total-system problems can be found in other parts of this continent and on other continents, in both terrestrial and aquatic ecosystems.

Consider the seminatural grassland ecosystems in the Great Plains. A more complete understanding of the structure and function of these ecosystems becomes increasingly essential as these lands are called upon to provide food, water, and recreation for tomorrow's growing populations. Several state and federal agricultural experiment stations hold sizable acreages of representative variations of grasslands, from the aspen parkland in Canada to the semidesert grasslands of Mexico. But at none of these stations is there a team equipped with suitable manpower or funds for intensive total-ecosystem research. Scientists at these experiment stations and nearby universities have accumulated considerable data and experience on and about these grassland ecosystems. There is no national laboratory in this vast area, and no university in the area can marshall many of the unique facilities, such as computing facilities and computer consultants, that are necessary for systems ecology research. Still, scientists at universities in the area can provide much necessary insight into these ecosystems and graduate students to help conduct ecosystem research in the area. With sufficient funds and planning it should be possible to combine the special skills and resources of all these groups and bring them to bear on problems of ultimate national importance at selected locations in the Great Plains.

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