MODELING ENVIRONMENTAL STRESS

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ABSTRACT

The word stress when applied to ecosystems is ambiguous. Stress may be
low-level, with accompanying near-linear strain, or it may be of finite magnitude,
with nonlinear response and possible disintegration of the system. Since there
are practically no widely accepted definitions of ecosystem strain, classification
of models of stressed systems is tenuous. Despite appearances, most ecosystem
models seem to fall into the low-level linear response category. Although they
sometimes simulate systems behavior well, they do not provide necessary and
sufficient information about sudden structural changes nor structure after
transition. Dynamic models of finite-amplitude response to stress are rare
because of analytical difficulties. Some idea as to future transition states can be
obtained by regarding the behavior of unperturbed functions under limiting
strain conditions. Preliminary work shows that, since community variables do
respond in a coherent manner to stress, macroscopic analyses of stressed
ecosystems offer possible alternatives to compartmental models.

Unfortunately, the term stress is not used uniformly in ecological
discussions. It comes to our discipline from mechanics, physiology,
and psychology and brings different shades of meaning from each
source. In clarifying what is meant by stress and its consequences, it
is useful to refer to the meaning given to the word by nineteenth
century engineers.

Stress represented "the forces or pressures exerted upon a
material" (Meier, 1972). In mechanics, stress had no utility without
its conjugate, strain, "a measure of the deformation brought about
by the action of the stresses." The relationship between applied
stress and observed strain (e.g., the elongation of a metal rod under

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tensile stress) was presumed linear. Twice the stress resulted in twice the strain.

The modulus of elasticity (the ratio of strain to stress) as a property of a solid is useful if we are designing a structure such as a bridge, but it is often necessary to know also the behavior of a solid system under extreme stresses. In fact, as the stress on a metal rod increases, a point is reached where the strain becomes disproportionately larger than the applied force. Not long thereafter the rod reaches the critical point; i.e., the strain is such that the rod will no longer return to its original state. Still further stress leads to increasingly disproportionate strain, culminating in a catastrophe when the rod loses its identity (yield point).

The behavior of a simple mechanical system under heavy stress differs markedly from its corresponding response to low stress. It is significantly nonlinear, and it culminates in loss of system structure. It is this response to heavy stress that is important to psychologists and physiologists, for whom stress has come to mean a "response to external or internal processes which reach those threshold levels that strain its physiological and psychological integrative capacities close to or beyond their limits" (Basowitz et al., 1955).

Stress, therefore, takes on different connotations for the engineer and the psychologist. Although it may not be obvious, this dual meaning of stress is found in ecological research. Ecologists have been slow to define and accept a useful measure of the response of the ecosystem to stress, i.e., ecological strain. Just as it is impossible to discuss mechanical stress without considering its conjugate, strain, the discussion of stress in ecological systems is fragmentary without some hypothetical measure of system strain. Before attempting a working definition of strain, however, we should consider how stress arises in ecosystem models.

Although ecosystem models may be stochastic, discrete, spatially heterogeneous, etc., much of systems analysis, following the lead of the early modelers, has concentrated on deterministic, first-order, ordinary differential equations, such as (see Lotka, 1957),

$$\dot{X} = f(X, P, t) \tag{1}$$

where X is a vector of state variables, t is time, and P is a vector of parameters. Parameters of a model include initial conditions, fluxes into and out of the system, and characteristics of the functional form of f (such as exponents or multiplicative constants).

The external world may impinge on the ecosystem (exogenous stress) through arbitrary variations in P and X; X may change

through cropping or mass infusion of a species; and P may change in
a number of ways. For example, the multipliers and exponents are
often strongly dependent on abiotic variables, such as temperature,
salinity, light, etc. These forcing functions, in turn, may possess both
regular and stochastic components. The input fluxes, necessary to
every living system, vary similarly.

Occasionally complex systems will exhibit the characteristics of
strain without any apparent imposed stress. The term endogenous
stress has been coined to describe such phenomena, but the previous
discussion reveals this to be a misnomer. Nonlinear systems some-
times produce an output without any corresponding input. "Endoge-
nous strain" would, therefore, be a more accurate descriptor for such
behavior.

Attempting to provide a workable definition for strain in an
ecosystem, Innis (1975) found it useful to invoke an arbitrary
function of the state of the system,

$$H = h(X, \dot{X}) \tag{2}$$

to measure the deviation from some prescribed state, H^*, character-
ized as unstressed. For example, H^* might be taken to be a
stationary state, i.e.,

$$H^* = h(X^*, 0) \tag{3}$$

where X^* is the solution of $f(X^*, P, t) = 0$. Any suitably defined
metric could be used to describe the distance between H and H^*, i.e.,
the ecological strain:

$$S = \|H - H^*\| \tag{4}$$

As Innis remarked, whether any particular deviation is indicative
of a stressed system is somewhat arbitrary and depends largely on the
context of the discussion. Woodwell (1975), for example, argued
against the threshold concept in ecology. In his view, any chronic
stress takes its toll on the ecosystem in the form of a chronic, albeit
sometimes small, deviation. The linear view of stress would be quite
useful for his purposes.

In contrast, Holling (1973) cited the possibility of multiple
stationary states for a given ecosystem——several H^*, each with its
own "domain of attraction" characterized by a finite deviation,
S_{crit}. Deviations in excess of the critical strain can lead to transition
into another domain. Furthermore, such transition may incur a

change in dimensionality of the problem and/or the necessity for a
new functional descriptor, $\hat{f}$, of the system dynamics. Deviations in
the neighborhood of S_{crit} are signs of a stressed ecosystem in the
physiological sense of the word.

Thus two classes of stress analyses are readily identifiable. In the
first, there is no explicit mention of a critical deviation, a change in
dimensionality, or a switch in function (topological form). The
second class is identified by the prominence of at least one of these
characteristics. The first class of models will be referred to as local
and the second as far-field.

Unfortunately, not all ecosystem stress analyses fall neatly into
these two classes. There are critics (e.g., Mann, 1975) who find
compartmental modeling reductionistic. They claim that time would
be better spent searching for emergent properties of the ecosystem as
a whole and that these properties would serve as more reliable
indicators of the response of the community to stress. To press the
earlier analogy (perhaps a little far!), this is akin to observing the
strain response of an assemblage of metal rods (such as a bridge truss)
to various imposed stresses without being concerned with the
properties of the individual members. Certainly there are character-
istic dimensions or dimensionless ratios of the total structure at
which strain responses are indicative of impending collapse. Such
approaches to ecosystem stress will be termed macroscopic in nature.

Finally, I indulge in speculation on a principle that I believe
would crystallize research on ecosystem response and, more impor-
tantly, might provide a theoretical basis to bridge the gap between
ecological systems research and evolutionary theory.

LOCAL ANALYSES OF STRESS

Most of the ecosystem models in existence today were con-
structed to elucidate the response of the community to a stress. As I
see it, most of these efforts have been local in nature. This is not to
imply that local analyses are necessarily uninteresting or uninforma-
tive. In fact, some appear to be nonlinear and have been quite
successful in portraying the response to exogenous stresses. For
example, the highly realistic aquatic ecosystems models of Nixon and
Kremer (1977), Di Toro et al. (1975), and Park, Scavia, and Clesceri
(1975) are capable of predicting significant changes in response to
exogenous stresses (e.g., temperature, nutrient input, and light
availability).

As an analysis of stress, however, these simulations are basically
local. To see this, we should appreciate that most of the exquisite

architecture of the models is in their parameter specifications. Thus, with changing driving forces, the "normal" state, H*, may vary considerably according to how the instantaneous stationary state,

$$f(X^*, P, t) = 0 \tag{5}$$

varies as P changes with exogenous stress. The behavior function, H, will tend to track H* closely. The hypothetical deviation may never be large, and the system is not stressed in the far-field sense of the word.

Nevertheless, the dramatic responses of some systems commonly referred to as stressed can be shown by a judicious choice of the functional dependence of the parameters on exogenous stress. Bierman et al. (1973), for example, chose *Chlorella* and *Microcystis* as two compartments of a nutrient-uptake model. Using separate laboratory information to describe the nutrient-uptake kinetics and the response to temperature, they investigated zones where one of the species dominated starkly. Lassiter and Kearns (1973) simulated an annual progression of six species as they dominated the phytoplankton of a hypothetical limnetic system. Falco and Mulkey (1976), using the law of mass action, anticipated the significant differential effect that pesticides can have on populations of bass and bluegills.

In these models all the information about the behavior of the system is contained in the functional form f and the parameter dependencies. Even when the population structure is predicted to be quite unbalanced (e.g., practically all blue-green algae), the system may be very near its stationary point, and, hence, by our definition it is only slightly stressed. Furthermore, the response is usually almost reversible (perhaps retrievable is a better word), meaning that, when the external influence is removed, the system returns to near its original condition.

The introductory examples of local low-stress models were purposely chosen for their nonlinear construction, but we more naturally associate low stress with linearity and, consequently, with linear models. Mathematically speaking, linear models have the form

$$\dot{X} = \underline{\underline{A}} \, X \tag{6}$$

where the matrix of coefficients is allowed to vary parametrically, i.e., $\underline{\underline{A}} = \underline{\underline{A}}(E, t)$. Any well-behaved nonlinear f can be approximated by a linear system in the neighborhood of a given point in phase space. The tremendous advantage of linear systems is the well-

developed mathematical tools that can be brought to bear on them—especially linear stability analysis.

In terms of the effects of low-level stress on a system, there is one key question, "Will the response to the stress remain small, or will it grow to the point of disrupting the integrity of the community?" For linearized systems the procedure for answering this question is well defined and has been reviewed by May (1971). All the eigenvalues of the matrix $\underline{\underline{A}}$ must have negative real parts. If the linear ecosystem model has constant coefficients, this test will show whether the model is properly behaved. More frequently, however, the coefficients of $\underline{\underline{A}}$ vary because of exogenous driving forces. In this case the eigenvalues vary also, and, under changing conditions, it is possible that some eigenvalue will acquire a positive real part (Halfon, 1976). Thus we can map out domains of driving forces for which the systems response is possibly unstable.

Much of the literature involving linear stability theory in ecosystems has been given over to debating the question of whether diversity will better enable an ecosystem to cope with an applied stress. MacArthur (1955) suggested such a causal link, and May (1973) reviewed the use of linear stability analysis to question this hypothesis. Central to the counter argument is the observation that increasing the dimensionality and connectivity of a randomly assembled system decreases the probability that all eigenvalues will be negative. Gardner and Ashby (1970) sampled randomly constructed matrixes to illustrate this point. Others have argued that ecosystems are not randomly constructed and that constraints on the form of $\underline{\underline{A}}$ can lead to different conclusions (Roberts, 1974; McMurtrie, 1975; Saunders and Bazin, 1975; Jeffries, 1974).

The diversity—stability controversy is actually a macroscopic issue, and further discussion is best deferred to that section of this paper. What is important here is that linear stability results are neither necessary nor sufficient to determine the persistence of an ecosystem under stress.

Despite their simplicity, linear models remain a popular medium for modeling total ecosystems (Patten, 1975). In fact, there are instances where linear models seem preferable for simulating total system behavior (Patten, 1976; Ulanowicz et al., 1978). Patten's success with linear descriptions led him to propose linearity as an evolutionary design criterion (Patten, 1975)—a much criticized stance (e.g., Wiegert, 1975). Leaving philosophical considerations aside, we see that the preceding discussion of local models of stress may help illuminate why linear models are such popular tools. As stated earlier, thus far most attempts to model ecosystem response to

stress have been local in nature; i.e., the system closely tracks the normal state, H*. Locally there is little difference between linear and nonlinear representations. Nonlinear representations tend to be more sensitive to parameter changes, however, and sensitivity and stability are closely related (Estberg and Patten, 1975). Thus a higher percentage of linear attempts at modeling are likely to survive into the final stages of an investigation.

Although they have served ecosystem science well, local models of stress response still leave much to be desired. The instability of a system to small stress serves as nothing more than a warning signal to the ecosystem manager. Local instability is neither necessary nor sufficient to cause a system to switch to a different configuration when subjected to a finite stress. Furthermore, the analysis reveals nothing about the future structure of the system if it should change character. Finally, in most local considerations little emphasis can be placed on endogenous strain, which may arise from finite excursions from the normal state.

FAR-FIELD STRESS ANALYSIS

The deficiencies of low-stress models are the cause of many ecological managers' suspicions of the modeling process. This point was underscored at a recent symposium on ecological modeling in a resource-management framework when three investigators—Schaaf (1975), O'Neill (1975), and Orlob (1975)—independently cited Holling's multiple steady-state hypothesis and the burning desire of ecologist and manager alike to understand more about the "collapsing" ecosystem syndrome. Managers are necessarily concerned with species changes within the systems in their charge. The conditions leading to structural changes in the system and the configuration of a collapsed or new ecosystem are matters of utmost importance in their eyes.

At the time of the symposium (1975), practically no research on the problem of switching between domains of attraction caused by finite amplitude stress was widely known. All investigators agreed on the need for theoretical research. In addition, Orlob called for controlled experimentation on collapsing ecosystems and systems subjected to low-level chronic stress.

The problem of mapping domains of attraction for an ecosystem is a formidable task. It is enough to cause a theoretical ecologist like May (1975) to remark: "I find it difficult to envision any simple number, or handful of numbers, which will quantify the resilience of a complicated natural ecosystem." There have been no major break-

throughs since May's comment to characterize the domain of attraction for a given stationary point. The task is as intriguing as it is important and formidable, however, and should continue to demand the attention of ecologists for several years to come. Nor will the problem remain of interest only to theoreticians. Lawton, Beddington, and Bower (1974) and Sutherland (1974), for example, have shown from empirical data that switching behavior occurs even among invertebrates.

Preliminary is perhaps the best word to describe the investigations on finite perturbations to date. An example of the nonreversibility of a nonlinear system is provided by McQueen (1975). His model for competition between two species of cellular slime mold exhibits two ranges of persistence in the sense of Holling. When he made the birthrate of one of the species highly dependent on climate and then shocked the model with a short burst of favorable climate, the model underwent transition from one domain to another where the favorably perturbed population was higher. Most interesting, however, was the model behavior that

> ... suggests that a population might fluctuate for long periods of time at a low level as it tracks the lower-stable [stationary] point, but given a short burst of favorable climatic conditions it could escape and rapidly grow to an upper-stable [stationary] level. From that point on, the population will remain at a high level tracking the high-stable [stationary point] as it moves in response to changing climate. Return to a low level is only possible when negative forces increase or when climate is very unfavorable to birthrate.

We can easily envision the reverse situation occurring in a collapsing ecosystem.

Although we cannot yet say with confidence how an ecosystem will be structured after it has undergone transition, there are two notable attempts to answer this question.

In the first, Smith (1975) occupied himself with species extinctions and the realm of possible stable subsystems that a known system may possess. He defined stability in a very fundamental way (see also Ulanowicz, 1972); a system is considered stable with regard to some defined stress if none of the component species become extinct as a result of that stress. In general, when one or more species of an ecosystem is removed, either a subsystem that is itself stable (in the sense just mentioned) results or one or more of the remaining species will drive the subsystem to collapse. Smith began by enumerating all possible subsystems by dropping various combinations of state variables in turn. To test whether any of these is a stable subsystem, we must view the behavior of the system when

stressed arbitrarily near the extinction of one or more species (stress in the second sense of the word). That is, if

$$\dot{X}i = fi(X_1, X_2, \ldots, X_m, X_{m+1}, \ldots, X_n) \quad i = 1, 2, \ldots, n \quad (7)$$

then we observe

$$\dot{X}i = fi(X_1, X_2, \ldots, X_m, 0, \ldots, 0) \quad i = 1, 2, \ldots, n \quad (8)$$

where variables X_{m+1} through X_n were chosen (without loss of generality) as those arbitrarily driven to near extinction. Smith then listed four criteria the reduced system must satisfy to be stable. For example, a stable subsystem cannot be obtained if any one of the fi describing an extinct species has become positive as a consequence of extinction, i.e., if any

$$\dot{X}i = fi(X_1, X_2, \ldots, X_m, 0, \ldots, 0) > 0 \quad i = m + 1, \ldots, n \quad (9)$$

He concluded his remarks by performing an analysis on a hypothetical four-species subsystem and identified three possible stable subsystems to which the original system might collapse.

Concern with environmental degradation in recent years has caused ecologists to become somewhat jaded and to focus on exogenous stress and its consequent simplification of the impacted ecosystem. In far-from-equilibrium nonlinear systems, however, endogenous strains occur which allow a chance perturbation (a mutant or migration) to flourish suddenly and to become an added dimension of the community. In the second example, Prigogine (1976) and Eigen (1971) examined this phenomenon as the crucial element in the prebiotic evolution of polymers, and Allen (1976) extended the analysis to the evolution of new populations in ecosystems. The methods used are similar to those used by Smith for collapsing systems.

Despite these interesting insights, the basic nature of structural transitions remains an enigma. This is caused in large measure by an inclination to think in terms of linear systems. It is not foreign to think of a system, an input (exogenous stress), and an output which results from that input (stability or instability), but it is discomfiting to be confronted with an output whose origin lies predominately within the system itself.

MACROSCOPIC TREATMENT OF ECOSYSTEM RESPONSE

In his presentation of evidence for multiple stable points and domains of attraction, Holling (1973) described the system from the

species or population level. The enormous analytical difficulties in properly describing most multistable systems, coupled with the high dimensionality of most real ecosystems, has led a number of investigators to explore the possibility that response to stress is best described in terms of macroscopic or emergent variables. Macroscopic variables are characteristic of the ecosystem as a whole and not just parts of it. They may and often do involve some combination of lesser order variables, however. There is still no consensus as to what consitutes a proper macroscopic variable.

Several investigators have suggested semiquantitative candidates for macroscopic variables as a consequence of their empirical studies. Kerr (1974) referred to structural transitions as "emergent surprises" and believed that they can be encompassed only by macroscopic theory. He cited the particle-size spectrum of an ecosystem as a convenient indicator of stress in a community. Exogenous stress seems to always affect the larger size organisms disproportionately. Jordan, Kline, and Sasscer (1972) emphasized the ratio of recycling to input as a system variable that characterizes the recovery time of an ecosystem from a temporary stress. Golley (1974) went further; he suggested a temporal hierarchy of three system properties to describe recovery from traumatic stress. First, the system responds to restore its extensive variables (mass); second, the functional options (topological diversity) increase; and, in the final stages of return to undisturbed climax, its response time to disturbance lengthens.

Presently the reconciliation of microscopic and macroscopic properties of an ecosystem is hampered by the inability of ecological theory to provide appropriate methods for observing community properties (Kerr, 1974). Actually this hierarchical problem has always been extremely important in ecological modeling. There are many opinions on how to aggregate organisms, species, etc., into trophic compartments or functional units (see Halfon, 1978), and it is especially difficult in highly connected or "webbed" ecosystems.

To address this problem, Kemp and Homer (1977) devised a method for assigning fractions of the energy storage in a given species compartment to various trophic levels. The key to their algorithm is the matrix of partial feeding coefficients, which describes the percentage of the total input to a given species, i, that flows from another species, j. To identify the contents of the fourth trophic level, for example, we identify all pathways three steps removed from a primary producer. The fraction of the end-point species to be assigned to the fourth trophic level is the product of the partial feeding coefficients of the three links along a pathway summed over all existing three-step pathways. Operationally the transformation is

calculated in a manner similar to Goh's (1975) vulnerability matrix (Ulanowicz and Kemp, 1978).

When Kemp and Homer's transformation is performed on energetics data from two comparable marsh ecosystems, one of which is impacted by thermal effluent, the results are striking. Energy flows through the lower trophic levels remain almost unchanged, but those through the higher levels fall off drastically under the thermal stress.

The observations of Kerr (1974), Golley (1974), and Kemp and Homer (1977) lead to the common conclusion that stress tends to result in more-simplified ecosystems. A great deal of debate has been devoted to the converse of this proposition, i.e., that more-diverse ecosystems are more resilient to stress. This proposition is properly macroscopic; i.e., diversity and stability are legitimate community properties. Few of the papers addressing this issue treat stability as a calculatable characteristic of the system, however. Two exceptions to this trend are Mulholland (1975) and Jorgensen and Mejer (1977).

Mulholland related the conditional entropy of an ecosystem to its buffering capacity. The conditional entropy, which comes from information theory, is the difference between the now-familiar Shannon—Wiener diversity index and the average mutual information, i.e., the amount of uncertainty about the distribution of energy from the various sources resolved by observing the behavior of the systems over a given time interval. Rutledge (1974) applied this measure to two short-grass prairie ecosystems, one under low-moisture stress. Surprisingly enough, the stressed system had higher conditional entropy (effective choice of pathways). Mulholland resolved this apparent contradiction by hypothesizing that the "ecological resilience of a system [which has not undergone transition] is maximum when conditions are harshest."

Jorgensen and Mejer defined the buffering capacity of a freshwater lake as the ratio of total phosphorous in the lake plus sediments to the steady-state value of soluble phosphorous in the lake. They found a tight correlation of this quantity with the exergy of the system (exergy is a measure of the mechanical energy equivalent of the distance from thermodynamic equilibrium).

In a third study of change in macroscopic variables in response to stress, Lane, Lauff, and Levins (1975) described the changes in several of Levins's (1968) community niche values in response to the eutrophication of a freshwater lake. Mean niche overlap, average competitive success, and mean number of organisms per unit of ecological space if no competitors were present, all increased significantly with increasing nutrient loading.

Finally, Harte and Levy (1975), borrowing from an analysis popular in physics around the turn of the century, constructed for three hypothetical ecosystems a community function whose existence ensured that the system would be stable to finite perturbations within a given domain. Briefly, if the differential equation

$$\dot{X} = f(X, P) \tag{10}$$

possesses a steady state or limit cycle, X_s, and is perturbed to $X_s + \Delta X$, it may or may not return to the neighborhood of X_s. If we can construct a function $L(\Delta X)$ (called a Liapunov function) which vanishes at the origin, is positive and monotonically increasing with ΔX in some domain about the origin, and has a negative time derivative, then the system is stable with respect to perturbations within that domain. The function L is not necessarily unique but is a conservative estimator of the stability properties of the system (and likewise a conservative estimator of the domain of stability). For certain classes of functions, f, there are standard methods for determining whether or not Liapunov functions exist. For these particular systems the question of stability is unequivocally resolved. In general, however, failure to find a Liapunov function does not imply instability of the system. The function may exist but may defy analytical description.

Despite these analytical difficulties, the Liapunov method has two things to recommend it. First, it bridges the gap between the microscopic (species level) and the macroscopic (L being a community function). Second, it offers the hope of ordinating the various domains of stability. Harte and Levy (1975) speculated that if succession is in the direction of ever more resiliency to stress, then

$$\Lambda = -\min\left(\frac{1}{2}\frac{d}{dt}\ln L\right)/\Delta X \tag{11}$$

provides a measure of the maturity of the system.

SUMMARY AND SPECULATIONS

There is a historical duality in the scientific meaning of the term stress, and this is reflected in the various models of ecosystem response to stress. Since strain, the conjugate to stress, is not well defined in ecology, discussion of the topic is difficult. If we assume a measure of system response to stress, two distinct groups of stress analysis arise, local and far-field.

I have classified most existing models of total ecosystems as local because either they are linear or they track the instantaneous

stationary state closely. Analysis of local systems is quite well developed, but application of the analytical results to real ecosystems is not free from ambiguities. Some of the models exhibit considerable realism and can be used as management tools to identify exogenous stresses that might jeopardize ecosystem integrity.

The observation that ecosystems undergo sudden, radical structural changes makes a nonlinear analysis of finite amplitude stress imperative. This endeavor is bound to be wrought with analytical difficulties. Even the simplest nonlinear model can exhibit bizzare behavior (May, 1974). To analyze finite amplitude stress, the mathematical ecologist may have to enlarge his skills to include such subjects as statistical mechanics, topology, nonlinear optimization theory, and variational calculus. The progress in this field treats the feasibility of alternate stable states.

The need for a holistic approach to ecosystem response has long been recognized (Odum, 1977), but the development of a macroscopic theory remains in its preliminary stages. Some correlation of total system variables to imposed stress has been noted, but much more empiricism seems necessary before the inductive leap to fundamental principles can be made.

Despite the remoteness of holistic principles, this review brings up several questions that may indicate a fruitful approach to macroscopic laws.

First, the language used in discussing nonlinear ecosystem response [e.g., "domain of attraction," "adsorbing set" (Botkin and Sobel, 1975), "strange attractor" (May and Oster, 1976)] is intriguing. If much of the experimentation with dynamic systems leads to the recognition of attractor surfaces, why not make an effort to describe the attractor surface, both mathematically and biologically?

Second, Kerr's (1974) emphasis on reconciling microscopic and macroscopic approaches to ecosystem research deserves consideration. Is it necessary to wait until theories at both levels are well developed before the two can be related, or can a single principle bridge the gap between them?

Third, Harte and Levy's (1975) speculation on the ordination of various stable states is appealing. What ecosystems manager would not rejoice at a quantitative comparison between two ecosystem states which distinguishes the more mature?

Fourth, and most relevant to this discussion, what is a definition of total system strain, H, which can be closely related to the dynamics of the system?

Finally, how might the gulf between the systems ecologists and the evolutionary biologists be bridged? Like the fluid dynamicist

who has the field representation of Newton's laws of motion from which to deduce the behavior of particular flows, most classically trained ecologists explain various species behavior in terms of Darwinian selection. Ecosystem models do not derive from any fundamental principle, however; they are a patchwork of empirical analogies and educated guesses.

No finished solutions are readily forthcoming, but I would like to speculate that all these questions can be addressed by a variational or optimizational statement. The clues that this might be so are found in the language of both the modeler and the evolutionist. Attractors can be described as points or surfaces of maximal properties. The evolutionist, in turn, is forever speaking in the superlative.

Others have hinted at an ecosystem variational principle (Glansdorf and Prigogine, 1971; Kerner, 1964; Ulanowicz, 1972). As early as 1925, Lotka suggested that living systems act to maximize the rate of energy capture. Odum and Pinkerton (1955) elaborated on this theme, and H. T. Odum treated the Lotka principle as axiomatic in many of his analyses. Energy is used in a very loose sense in these discussions. It is likely that one of the later definitions [e.g., exergy (Rant, 1956), the energetic measure of the departure of a system from the thermodynamic equilibrium state] is more suited to the descriptional task.

Thus we can envision a surface $H(X, \dot{X})$ in phase hyperspace such that any spontaneous movement along the surface maximizes the rate of energy storage (or some other suitable property). Domains of attraction are delimited by relative minimums. Attractors are points or surfaces of relative maximums. Strain in the ecosystem is defined as the distance between H and H^*. Presumably H would have its zero level at thermodynamic equilibrium so that the values of the relative maximums would indicate the maturity of each domain of attraction, allowing us to compare different ecosystem structures. Like Liapunov functions, H would be a system property defined from the components.

The requisite variational principle would be an extension of evolutionary theory. That is, current evolutionary dogma would be necessary but not sufficient to explain all the phenomena the new principle would presumably encompass. Surely such extension would be objected to by many as unnecessary. Some might even complain that an ecosystem variational principle smacks of teleology, but a glance at the application of variational principles in inanimate physics shows this fear to be groundless. Ultimately, however, the burden of proof is upon the proponents of the new principle to demonstrate the unifying powers alluded to.

Viewed in the context of such a unifying theory, labors with disturbed ecosystems take on an added importance. Beyond yielding answers to temporal questions of how best to manage impacted ecosystems, they provide pieces for the unending puzzle of where we come from and where we are headed.

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REFERENCES

Allen, P., 1976, Population Dynamics and Evolution, in *Evolution and Consciousness: Human Systems in Transition*, E. Jantsch and C. H. Waddington (Eds.), pp. 127-130, Addison—Wesley Publishing Co., Reading, Mass.

Basowitz, H., H. Persky, S. J. Korchin, and R. R. Grinker, 1955, *Anxiety and Stress*, McGraw-Hill Book Company, New York.

Bierman, V. J., F. H. Verhoff, T. L. Poulson, and M. W. Tenney, 1973, Multi-Nutrient Dynamic Models of Algal Growth and Species Competition in Eutrophic Lakes, in *Modeling the Eutrophication Process*, pp. 89-109, Utah Water Research Laboratory, Logan.

Botkin, D. B., and M. J. Sobel, 1975, The Complexity of Ecosystem Stability, in *Ecosystems: Analysis and Prediction*, SIAM—SIMS Research Application Conference on Ecosystems, Alta, Utah, S. A. Levin (Ed.), pp. 144-150, Society for Industrial and Applied Mathematics, Philadelphia.

Di Toro, D. M., D. J. O'Connor, R. V. Thomann, and J. L. Mancini, 1975, Phytoplankton—Zooplankton—Nutrient Interaction Model for Western Lake Erie, in *Systems Analysis and Simulation Ecology*, B. C. Patten (Ed.), Vol. 3, pp. 423-473, Academic Press, Inc., New York.

Eigen, M., 1971, Self-Organization of Matter and the Evolution of Biological Macromolecules, *Naturwissenschaften*, 58: 465-522.

Estberg, G. N., and B. C. Patten, 1975, The Relation Between Sensitivity and Persistence Under Small Perturbations, in *Ecosystems: Analysis and Prediction*, SIAM—SIMS Research Application Conference on Ecosystems, Alta, Utah, S. A. Levin (Ed.), pp. 151-154, Society for Industrial and Applied Mathematics, Philadelphia.

Falco, J. W., and L. A. Mulkey, 1976, Modeling the Effect of Pesticide Loading in Riverine Ecosystems, in *Environmental Modeling and Simulation*, Proceedings of a Conference, Apr. 19—22, 1976, Cincinnati, W. R. Ott (Ed.), EPA-600/9-76-016, Environmental Protection Agency, NTIS.

Gardner, M. R., and W. R. Ashby, 1970, Connectance of Large Dynamical (Cybernetic) Systems: Critical Values for Stability, *Nature*, 228: 784.

Glansdorf, P., and I. Prigogine, 1971, *Thermodynamic Theory of Structure, Stability and Fluctuations*, John Wiley & Sons, Inc., New York.

Goh, R. S., 1975, Stability, Vulnerability and Persistence of Complex Ecosystems, *Ecol. Model.*, 1: 105-116.

Golley, F. B., 1974, Structural and Functional Properties as They Influence Ecosystem Stability, in *Proceedings of the First International Congress of*

Ecology, The Hague, Netherlands, pp. 97-102, Centre for Agricultural Publishing and Documentation, Wageningen.

Halfon, E., 1976, Relative Stability of Ecosystem Linear Models, *Ecol. Model.,* 2: 279-286.

——, 1978, *Theoretical Systems Ecology,* Academic Press, Inc., New York, in press.

Harte, J., and D. Levy, 1975, On the Vulnerability of Ecosystems Disturbed by Man, in *Unifying Concepts in Ecology,* W. H. Van Dobben and R. H. Lowe-McConnel (Eds.), pp. 208-223, Dr. W. Junk Publishers, The Hague, The Netherlands.

Holling, C. S., 1973, Resilience and Stability of Ecological Systems, *Annu. Rev. Ecol. Systemat.,* 4: 1-23.

Innis, G., 1975, Stability, Sensitivity, Resilience, Persistence. What Is of Interest? in *Ecosystems: Analysis and Prediction,* SIAM—SIMS Research Application Conference on Ecosystems, Alta, Utah, S. A. Levin (Ed.), pp. 131-139, Society for Industrial and Applied Mathematics, Philadelphia.

Jeffries, C., 1974, Qualitative Stability and Digraphs in Model Ecosystems, *Ecology,* 55(6): 1415-1419.

Jordan, C. F., J. R. Kline, and D. S. Sasscer, 1972, Relative Stability of Mineral Cycles in Forest Ecosystems, *Am. Nat.,* 106: 237-253.

Jorgensen, S. E., and H. Mejer, 1977, Ecological Buffer Capacity, *Ecol. Model.,* 3: 39-61.

Kemp, W. M., and M. Homer, 1977, Functional Analysis of Complex Estuarine Food Webs, unpublished manuscript.

Kerner, E. H., 1964, Dynamical Aspects of Kinetics, *Bull. Math. Biophys.,* 26: 151-167.

Kerr, S. R., 1974, Structural Analysis of Aquatic Communities, in *Proceedings of the First International Congress of Ecology, The Hague, Netherlands,* pp. 69-74, Centre for Agricultural Publishing and Documentation, Wageningen.

Lane, P. A., G. H. Lauff, and R. Levins, 1975, The Feasibility of Using a Holistic Approach in Ecosystem Analysis, in *Ecosystems: Analysis and Prediction,* SIAM—SIMS Research Application Conference on Ecosystems, Alta, Utah, S. A. Levin (Ed.), pp. 111-128, Society for Industrial and Applied Mathematics, Philadelphia.

Lassiter, R. R., and D. K. Kearns, 1973, Phytoplankton Population Changes and Nutrient Fluctuations in a Simple Aquatic Ecosystem Model, in *Modeling the Eutrophication Process,* pp. 131-138, Utah Water Research Laboratory, Logan.

Lawton, J. H., J. R. Beddington, and R. Bower, 1974, Switching in Invertebrate Predators, in *Ecological Stability,* M. B. Usher and M. H. Williamson (Eds.), pp. 141-158, Halsted Press, New York.

Levins, R., 1968, *Evolution in Changing Environments: Some Theoretical Explorations,* Princeton University Press, Princeton, N.J.

Lotka, A. J., 1925, *Elements of Physical Biology,* The Williams & Wilkins Company, Baltimore.

——, 1957, *Elements of Mathematical Biology,* Dover Publications, Inc., New York.

MacArthur, R. H., 1955, Fluctuations of Animal Populations, and a Measure of Community Stability, *Ecology,* 36: 533-536.

McMurtrie, R. E., 1975, Determinants of Stability of Large Randomly Connected Systems, *J. Theor. Biol.,* 50: 1-11.

McQueen, D. J., 1975, Multiple Stability and Maximum Stability in a Model Population, *Can. J. Zool.*, 53: 1844-1854.

Mann, K. H., 1975, Relationship Between Morphometry and Biological Functioning in Three Coastal Inlets of Nova Scotia, in *Estuarine Research*, L. E. Cronin (Ed.), pp. 634-644, Academic Press, Inc., New York.

May, R. M., 1971, Stability in Multi-Species Community Models, *Math. Biosci.*, 12: 59-79.

———, 1973, *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, N.J.

———, 1974, Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos, *Science*, 186: 645-647.

———, 1975, Stability in Ecosystems: Some Comments, in *Unifying Concepts in Ecology*, W. H. Van Dobben and R. H. Lowe-McConnel (Eds.), pp. 161-168, Dr. W. Junk Publishers, The Hague, The Netherlands.

———, and G. F. Oster, 1976, Bifurcations and Dynamic Complexity of Simple Ecological Models, *Am. Nat.*, 110(974): 573-599.

Meier, R. L., 1972, Communications Stress, *Annu. Rev. Ecol. Systemat.*, 3: 289-314.

Mulholland, R. J., 1975, Stability Analysis of the Response of Ecosystems to Perturbations, in *Ecosystems: Analysis and Prediction*, SIAM–SIMS Research Application Conference on Ecosystems, Alta, Utah, S. A. Levin (Ed.), pp. 166-181, Society for Industrial and Applied Mathematics, Philadelphia.

Nixon, S. W., and J. N. Kremer, 1977, Narragansett Bay—The Development of a Composite Simulation Model for a New England Estuary, in *Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories*, C. A. S. Holland and J. W. Day, Jr. (Eds.), pp. 621-673, John Wiley & Sons, Inc., New York.

Odum, E. P., 1977, The Emergence of Ecology as a New Integrative Discipline, *Science*, 195(4284): 1289-1293.

Odum, H. T., and R. C. Pinkerton, 1955, Time's Speed Regulator, the Optimum Efficiency for Maximum Output in Physical and Biological Systems, *Am. Sci.*, 43: 331-343.

O'Neill, R. V., 1975, Management of Large-Scale Environmental Modeling Projects, in *Ecological Modeling in a Resource Management Framework*, C. S. Russell (Ed.), pp. 251-282, Resources for the Future, Inc., Johns Hopkins University Press, Baltimore.

Orlob, G. T., 1975, Present Problems and Future Prospects of Ecological Modeling, in *Ecological Modeling in a Resource Management Framework*, C. S. Russell (Ed.), pp. 283-312, Resources for the Future, Inc., Johns Hopkins University Press, Baltimore.

Park, R. A., D. Scavia, and N. L. Clesceri, 1975, CLEANER: The Lake George Model, in *Ecological Modeling in a Resource Management Framework*, C. S. Russell (Ed.), pp. 49-82, Resources for the Future, Inc., Johns Hopkins University Press, Baltimore.

Patten, B. C., 1975, Ecosystems Linearization: An Evolutionary Design Problem, *Am. Nat.*, 109(969): 529-539.

———, 1976, University of Georgia, personal communication.

———, D. A. Egloff, T. H. Richardson, 1975, Total Ecosystem Model for a Cove in Lake Texoma, in *Systems Analysis and Simulation Ecology*, B. C. Patten (Ed.), Vol. 3, pp. 206-243, Academic Press, Inc., New York.

Prigogine, I., 1976, Order Through Fluctuation: Self-Organization and Social System, in *Evolution and Consciousness: Human Systems in Transition*, E. Jantsch and C. H. Waddington (Eds.), pp. 93-126, Addison—Wesley Publishing Company, Reading, Mass.

Rant, Z., 1956, Exergie, ein neues Wort fuer technische Arbeitsfaehigkeit, *Forsch. Ingenieurwes.*, 22(1): 36-37.

Roberts, A., 1974, The Stability of a Feasible Random Ecosystem, *Nature*, 251(5476): 607-608.

Rutledge, R. W., 1974, *Ecological Stability: A Systems Theory Viewpoint*, Ph.D. Thesis, Oklahoma State University, Stillwater.

Saunders, P. T., and M. J. Bazin, 1975, Stability of Complex Ecosystems, *Nature*, 256(5513): 120-121.

Schaaf, W. E., 1975, Fish Population Models: Potential and Actual Links to Ecological Models, in *Ecological Modeling in a Resource Management Framework*, C. S. Russell (Ed.), pp. 211-239, Resources for the Future, Inc., Johns Hopkins University Press, Baltimore.

Smith, D. F., 1975, Quantitative Analysis of the Functional Relationships Existing Between Ecosystem Components, *Oecologia (Berlin)*, 21: 17-29.

Sutherland, J. P., 1974, Multiple Stable Points in Natural Communities, *Am. Nat.*, 108(964): 859-873.

Ulanowicz, R. E., 1972, Mass and Energy Flow in Closed Ecosystems, *J. Theor. Biol.*, 34: 239-253.

——, D. A. Flemer, D. R. Heinle, and R. T. Huff, 1978, The Empirical Modeling of an Ecosystem, *Ecol. Model.*, 4: 29-40.

——, and W. M. Kemp, 1978, Towards Canonical Trophic Aggregations, submitted to *Am. Nat.*

Wiegert, R. G., 1975, Simulation Models of Ecosystems, *Annu. Rev. Ecol. Systemat.*, 6: 311-338.

Woodwell, G. M., 1975, The Threshold Problem in Ecosystems, in *Ecosystems: Analysis and Prediction*, SIAM—SIMS Research Application Conference on Ecosystems, Alta, Utah, S. A. Levin (Ed.), pp. 9-23, Society for Industrial and Applied Mathematics, Philadelphia.