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ON THE VULNERABILITY OF ECOSYSTEMS

DISTURBED BY MAN**+**

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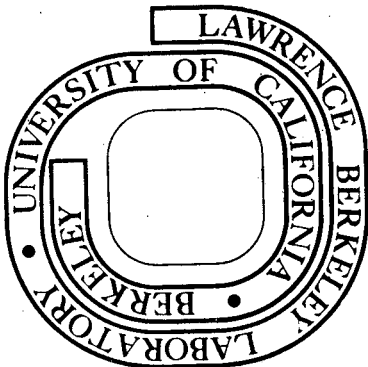
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ABSTRACT

The Liapunov stability theory is applied to models of
energy and nutrient flow in ecosystems. The domain of stability
under non-infinitesimal perturbations is discussed and signifi-
cant differences are pointed out between models with and with-
out detritus-decomposer feedback loops. Possible practical
implications are suggested. Speculations concerning the role
of fluctuations in ecosystems and the possibility of determining
successional trends from an optimization procedure are also
discussed.

I. INTRODUCTION

The ability to predict ecosystem instabilities is of great importance today because so many environmental conflicts are essentially disputes about stability--they boil down to a difference of opinion about whether a given man-induced distur- bance of a system is likely to result in a severe disruption or merely a gentle recoil. What intensifies the importance of this problem is the fact that our species is now capable of adding to or subtracting from our natural surroundings on a scale com- parable to the scale of natural processes. Thus, for example, the intensity at which waste heat is released by urban dwellers into their surroundings is in many cities 20% or more of the solar flux. Other disturbances such as the unsettling and dis- persal of heavy metals into marine food chains during dredging operations, the disruption of fresh water supplies and sub-sur- face organisms during and after strip mining operations, or the release of toxic substances in fuel combustion, are not merely perceptible, but gross alterations of our no-longer natural environment. Potential instabilities that may result from these and other perturbations range from the loss of certain species to the creation of local dustbowls to global climate modification.

Because the disturbances of our environment are not infinitesimal but finite, the traditional tools for studying the stability of complex systems are clearly inadequate. From a practical view, not only do we have to deal with finite perturba-

tions, but also with ecosystems which do not settle down to precisely their unperturbed states after we disturb them. Rather, what we can reasonably hope for is that the initial perturbation will not propagate in such a way that the system is pushed beyond tolerable limits.

Thus, we are led to the concept of practical stability.[1] This concept is intermediate between local and global stability. Local stability, utilizing the community matrix approach to a linearized system, is a mathematical nicety but, as we have mentioned, both too weak (as it is only reliable for infinitesimal perturbations) and too stringent (as it requires the system to return to its unperturbed state after the perturbation.) On the other hand, the requirement of global stability is too strong because we do not expect real systems to be stable under arbitrarily large perturbations.

A mathematical method exists for dealing with practical stability[1]-- a modification of the Liapunov Direct Method. The results of some ecosystem studies using this method will be described here. We have obtained some interesting results, especially pertaining to the role of decomposers and feedback loops in an ecosystem. Furthermore, our methods allow some new insight into the role of fluctuations in systems and a possible understanding of the direction of successional trends.

The goal of our studies is the elucidation of ecosystem parameters which correlate with stability. To be of practical

use, such quantities should depend upon general features of the
system such as the topology of the material and energy flow path-
ways and not upon detailed knowledge of all the system's components
and their dynamical interactions. Currently, much empirical acti-
vity in ecology is focused on measurements of quantities such as
the biomasses and productivities of the components of the system,
species diversity, and retention times of various nutrients. These
measurements, while important, do not reflect the organization
of an ecosystem and have not allowed ecologists to infer or under-
stand ecoystem stability properties. Rather, they are largely
indicators of the state of the components. If this work is to be
successful, that is verifiable and of practical use, then it must
ultimately point the way to measurable indicators of ecosystem
organization and stability. A lot of work lies ahead.

II. MATHEMATICAL PRELIMINARIES

Assume we are given a reasonable mathematical model
describing an ecosystem which can be written in the form of a
set of coupled, nonlinear, first order differential equations for
the time rate of change of the components of the system. By
'component' we refer, quite generally to the energy content, or
the carbon content, or any other convenient measure (e.g. DDT
content!) of individuals or species or conveniently chosen aggre-
gates of species or perhaps just physical sectors comprising the
ecosystem. These equations are assumed to have the form

$$\frac{dx_i}{dt} = X_i(x_1, \text{---},x_N;w_1, \text{---}\ w_m)$$

$$i = 1, \cdots,N \tag{1}$$

The x_i refer to the components of the system and the w_i are any

other parameters upon which the time derivatives may depend.

Phenomena such as time delays or stochasticity can be incorporated

within this general form.

Suppose we are given an initial, unperturbed state of

the system, $\bar{x}_i$, which may be time-independent (a steady state)

or time-dependent (e.g. a limit cycle.) In Fig. 1 we plot the

trajectory of such a state. If the state is perturbed at some

time to a new value $\bar{x}_i + \Delta x_i$ shown in the figure (Δx_i not necessarily

infinitesimal) then two options (see Fig. 1) are possible: i) the

perturbed state, x_i, may or may not return ultimately to the unper-

turbed state, $\bar{x}_i$, but it will never evolve further from the unper-

turbed state than some preassigned tolerance; ii) it will evolve in

time so as to exceed the preassigned tolerance. Our problem is to

determine which option occurs.

Fig. 2 summarizes the Liapunov direct method for stability

analysis. As shown, the crux of the method is to construct a

function, $L(\Delta x_1,\ldots,\Delta x_N)$, which vanishes at the origin, and within

some domain about the origin is positive and monotonically increasing

with Δx_i, and in addition has a negative time derivative. For ini-

tial perturbations confined to that domain, the existence of such a

function guarantees both the asymptotic stability of the system

(that is, the x_i will ultimately settle at $\bar{x}_i$) and a finite domain

of practical stability.[2] The size of this domain of practical

stability depends upon the preassigned tolerance. A slight modif-

cation[3] of the asymptotic stability criteria allows treatment of

the more realistic case in which it is not required that the system

return asymptotically to its unperturbed value. This, and other

subtleties of the method such as the extension to the case in which

the function L is explicitly time dependent or the case in which

the perturbation is made not only upon the $\bar{x}_i$ but also upon the

form of the equations of motion, are easily handled but will not be

delved into now as they would only obscure the underlying principles

which we wish to elucidate here.

For a wide class of ecological models[4], some of which are

described in the following section, a Liapunov function can be

constructed for any initial steady state or periodic[5] state, $\bar{x}_i$.

This function has the property that it vanishes at the origin, it

is monotonically increasing in the entire Δx_i plane, and

$$\frac{-dL}{dt} = \sum_i \sum_j B_{ij}(x,\bar{x},w)\ \Delta x_i \Delta x_j \tag{2}$$

where the B_{ii} are strictly positive for all values of the x_i.

Moreover, in realistic models, many of the B_{ij}, for $i \neq j$, are zero.

It is convenient to write the coefficients, B_{ij}, in the

form of a symmetric matrix, B, here after called the B-matrix. The

matrix elements are given by $[B]_{ij} = \frac{1}{2}(B_{ij} + B_{ji})$. Now, a theorem

on the positive definiteness of quadratic forms asserts that the

form

$$q = \sum_i \sum_j Q_{ij} Y_i Y_j \tag{3}$$

is positive for all values of the Y_i if and only if the determinants
of all the principal minors of the symmetric matrix of coefficients,
Q, are positive.[6] Therefore, the domain of asymptotic stability of
our system is at least as big[7] as the domain of the Δx_i for which
the determinants of the principal minors of the matrix $B(x, \bar{x}, w)$
are positive. We emphasize that the B-matrix is not the community
matrix. The latter describes infinitesimal stability of a linearized
system while the B-matrix encapsulates the finite stability proper-
ties of a nonlinear system.

Clearly, were it not for the presence of off-diagonal,
non-zero elements in the B-matrix, we would have global stability.
It is the organizational structure (patterns of pathways) of the
ecosystem which determines which of the off-diagonal elements
are non-zero, and therefore which places limits on the size of the
domain of stability. In the following section we explore the im-
plications of these ideas for various models of ecosystem.

III. MODELS AND APPLICATIONS

Let us consider three broad categories of ecological
organization:

i. Open flow without cycling. An example would be the flow
of energy through the pathways of the food web from photosynthesizers
on up to top carnivores. This is subsidized and therefore open flow,

the source of sustenance being the sun. Admittedly a certain frac-
tion of chemical energy is recoverable from detritus but it is
usually a good approximation to ignore this.

ii. Closed flow with cycling. An example would be any global
material cycle for which the number of molecules of the material is
conserved. A mathematical description of a closed cycle is, however,
likely to be elusive because of the difficulty in accounting for
all of the compartments in the cycle. Perhaps the global carbon
cycle is the most natural one to model, with the dominant compart-
ments being the atmosphere, plants, organic litter, decomposers, the
oceans, animals, fossil fuel, and the geosphere. In practice, most
models will be geographically non-global and will not incorporate
all compartments; thus one is led to:

iii. Open flow with cycling. The nitrogen flow in a field is
a fine example. Inputs and outputs such as the addition of fertilizer
or washout from erosion might be driving forces behind this open
flow, and yet the character and stability of the steady state or
limit cycle solutions will be strongly influenced by the cycling
capability of the system.

In Figs. 3, 4, 5 we illustrate examples of these three
types of organization. The pictures illustrate the pathway patterns.
In addition, model equations are present which correspond to the
flow diagrams. Other equations could be written-we have only shown
these in order to focus on specific examples. What can we learn
about the stability properties of these three systems from a Liapunov

analysis, and, in particular, what properties are reasonably inde-
pendent of the detailed mathematical model used to describe the
flow diagrams?

Type i Systems. The Liapunov method has been employed
by Huang and Morowitz[8] to analyze the stability properties of the
steady state solutions of the Lotka-Volterra equations for predator-
prey interactions. These authors show that if the $\bar{x}_i$ are constant,
then

$$L = \sum_i L_i = \sum_i \tau_i \, [x_i - \bar{x}_i - \bar{x}_i \, \ln(\frac{x_i}{\bar{x}_i})] \tag{4}$$

is a Liapunov function for the system. Moreover

$$B = - \begin{pmatrix} k_{11} & & \bigcirc \\ & k_{22} & \\ & & \ddots \\ \bigcirc & & k_{NN} \end{pmatrix} \tag{5}$$

for all x_i, indicating global stability if all $k_{ii} < 0$. Because the
steady state solutions are globally stable, the equations clearly
possess no limit cycle solutions. On the other hand, if we set the
$k_{ii} = 0$ then the equations do possess oscillatory solutions but
they are unfortunately not asymptotically stable nor are they
structurally stable against small changes in the form of the equations
of motion.

If a more general mathematical model describing the uni-
directional flow of energy through an ecosystem is employed, restricted
only by the constraints mentioned in footnote 4, then Eq. 4 is still
a Liapunov function but the structure of the B-matrix is more compli-
cated. In general, simply increasing the number of trophic levels

will not affect stability, but increasing the number of pathways in the food web by introducing, for example, more competitors at each trophic level will add off-diagonal elements to the B-matrix; this tends to diminish the size of the domain of stability.

Type ii Systems. Fig. 4 shows the pattern of pathways of a closed nutrient cycle. This cycle, and the model equations shown in the figure are a simple representation of carbon flow in a four level system consisting of photosynthesizers, the inorganic nutrient pool (which we take in this case to be the atmosphere), the decomposers, and organic Litter (fallen leaves, dead trees, etc.) We have assumed that negligible amounts of carbon are added to or lost from the system (for example, there is no exchange with the ocean.)

It is possible to construct a Liapunov function for this system and with it to establish the asymptotic stability of its steady state solutions under the class of finite perturbations which are constrained to conserve the total amount of carbon. The Liapunov function is

$$L = \sum_i c_i(\bar{x}_i, \alpha, \beta, \sigma)[x_i - \bar{x}_i - \bar{x}_i \ln(\frac{x_i}{\bar{x}_i})] \qquad (6)$$

where the c_i are moderately complicated functions of the $\bar{x}_i$.

Thus the closed system is asymptotically stable against the arbitrary sliding of carbon from one level to another. From this result, and the fact that a steady state solution exists for every value of the total quantity of carbon in the system, it follows that this closed system is not asymptotically stable against perturbations which do not conserve the total amount of carbon. If the perturbation

changes the total amount of carbon, then a new steady state will be approached asymptotically. An interesting question then arises: which steady state solutions are approached relatively rapidly when disturbed? This is amplified upon in Section 4 where we discuss successional trends.

It is straightforward but tedious to include more compartments such as the oceans into the model. We have not looked in detail at extremely complicated and inclusive models of the global carbon cycle, but from experience gained by working with relatively simple systems we suspect that the above results will remain valid for the quite general class of models characterized in footnote 4 provided the system is closed.

Type iii systems. If we open the system, that is allow for the incomplete cycling of the nutrient, then the situation changes. For example, consider the flow of a nutrient (such as nitrogen) in a six level system consisting of carnivores, herbivores, photosynthesizers, inorganic nutrient pool, decomposers, and organic litter (plant litter, excrement, and corpses)[9]. Referring to Fig. 5, we note that in our model equations we have adjoined a simple Lotka-Volterra-type predator-prey web upon the substratum of feedback dynamics describing the detritus - decomposer path ways.

A Liapunov function can be constructed, again of the general form of Eq. 6. Its properties are best encapsulated by the B-matrix, which for steady state solutions has the form:

$$
B = \begin{pmatrix}
a_{CC} & 0 & 0 & 0 & 0 & -b_{CL} \\
0 & a_{HH} & 0 & 0 & 0 & -b_{HL} \\
0 & 0 & a_{PP} & 0 & 0 & -b_{PL} \\
0 & 0 & 0 & a_{II} & -b_{ID} & -b_{IL} \\
0 & 0 & 0 & -b_{ID} & a_{DD} & -b_{DL} \\
-b_{CL} & -b_{HL} & -b_{PL} & -b_{IL} & -b_{DL} & a_{LL}
\end{pmatrix} \tag{7}
$$

where the a_{ii} and b_{ij} are always positive. The a's and b's are

simple functions of the $x_i, \bar{x}_i$ and the parameters c_i, α_i, Ω_i, γ_i,

β_{ij}, σ_{ij} (see Fig. 5 for an explanation of the symbols). By the

theorem on quadratic forms discussed above, our system is stable

for perturbations which are initially within a domain of the x_i

such that the determinant of the principal minors of B are positive.

Now the first four principal minors are diagonal and clearly posi-

tive. Adding more superstructure to the system (that is, more predator-

prey links in the Lotka-Volterra part of the system) would not affect

the positivity of the first N-2 determinants.[10] Constraints on the

domain of stability, if they exist, will show up in the evaluation of

the last two determinants. The fifth determinant is given by

$$
a_{CC}\, a_{HH}\, a_{PP}\, [a_{II}\, a_{DD} - b^2_{ID}]
$$

$$
= c_C \alpha_C c_H \alpha_H c_P \gamma_P \frac{[c_I c_D (\sigma x_D x_L + \Omega_I)\gamma_D}{x_I \bar{x}_I} \tag{8}
$$

$$
- \frac{c_I^2 \sigma^2 (x_L + \bar{x}_L)^2}{16\, \bar{x}_I^2}\,]
$$

We see that the domain of stability may now no longer be global; for

fixed $\bar{x}_i$ and for sufficiently small values of Ω_I and

x_D, or for sufficiently large values of x_I or x_L, the determinant

becomes negative. Thus type iii systems can be quite vulnerable to

perturbations in the litter, the inorganic nutrient pool or the

decomposers.

The sixth determinant is complicated and we have not yet

extracted all the information in it. For a range of cycling rate

parameters (Γ and σ) and external input and output parameters

(Ω_I, Ω_L, α_I, α_L) a finite domain of stability can be shown to exist.

It is possible to show that in type iii systems in which the exter-

nal input rate of litter is proportional to the amount of litter

present, that a certain critical minimum value of the cycling efficiency

parameter, Γ, is necessary in order to have a finite domain of asymptotic

stability. On the other hand, if the system is approximately closed,

i.e. external inputs and outputs relatively small, then the sixth

determinant can become negative. This is simply a reflection

of the fact discussed earlier that exactly closed systems are not

asymptotically stable against displacements which do not conserve

the total quantity of nutrient. This instability is a relatively

harmless one, however, as long as the perturbed system does not

evolve far away from where it is initially perturbed to. It remains

to be seen whether thresholds of dangerous instability are more likely

in high-Γ or low-Γ systems and in high-Ω_i or low-Ω_i systems. There

are many other unanswered questions which we hope to explore. For

example, do systems in which the inequality $\alpha_i \bar{x}_i \ll \gamma_i \bar{x}_i^2$ is satisfied

tend to have a greater stability domain than systems satisfying the opposite inequality? In other words, are resource-limited systems more stable than those existing well below a saturation level?

An amusing relation between diversity and stability also emerges from this analysis. Let us enlarge the Lotka-Volterra "superstructure" of the system by extending the matrix, Eq. 7, to the upper left so that we consider an N-component system. We denote by D_m^N the determinant of the mth principal minor of the N X N matrix and choose the values of x_D, x_L, and x_I so that D_{N-1}^N is positive. How does D_N^N then behave as $N \to \infty$? The answer depends upon two factors: the shape of the trophic structure of the system and the ratios β_{ij}/β_{ji}. In general, D_N^N will remain positive as N increases and thus systems with an ever-increasing number of inter-acting components, arranged vertically in trophic hierarchy, will remain stable.

In order to show this we number the rows and columns of the N X N matrix in an unorthodox manner, letting N denote the first row or column and 1 the last. Thus the matrix element a_{NN} is that appearing in the top left corner of the matrix and corresponds to the top carnivore. Then the following recursion relations are easily derived:

$$D_{N-1}^N = a_{NN} D_{N-2}^{N-1}$$

$$D_N^N = a_{NN} D_{N-1}^{N-1} - \frac{b_{1N}^2}{a_{NN}} D_{N-1}^N$$

(9)

These can be easily solved. Let $\phi = D_2^3$ and $\psi = D_3^3$ both of which

are assumed to be positive as is required for stability. Then

$$D_{N-1}^{N} = \phi \prod_{j=4}^{N} a_{jj}$$

$$D_{N}^{N} = \left(\psi - \phi \sum_{i=4}^{N} \frac{b_{1i}^2}{a_{ii}} \right) \prod_{j=4}^{N} a_{jj}$$

(10)

D_{N-1}^{N} clearly remains positive if the a_{ii}'s are positive (or γ_i positive in Fig. 5). The value of D_{N}^{N} will depend upon the b_{1i}'s and the a_{ii}'s. Now b_{1i} is proportional to the rate, per unit mass, at which x_i is cycled back to the organic litter level. We expect this quantity to be roughly independent of i and we henceforth take it to be a constant. Referring to Eq. 10 we note that if a_{ii} increases less rapidly than i, then the summation will diverge as $N \to \infty$ and D_{N}^{N} will become negative at some critical value of N. D_{N}^{N} can remain positive as $N \to \infty$ only if a_{ii} increases faster than i.

What does this imply? For $i > 3$, $a_{ii} = c_i \gamma_i$. The γ_i behave roughly proportional to x_i^{-1} and thus increase with i for ordinary trophic hierarchies. Moreover

$$\frac{c_i}{c_{i-1}} = \frac{\beta_{i-1,i}}{\beta_{i,i-1}} \gtrsim 1$$

(11)

since retention is $\lesssim 100\%$ and so the c_i's will not decrease with i. If $\beta_{i,i-1}$ is a constant multiple of $\beta_{i-1,i}$ then $c_i = c^i$ and the sum will not diverge. To create a divergence and thus drive the determinant negative, we would have to assume that both $\beta_{i,i-1} \to \beta_{i-1,i}$ and $x_i \to x_{i-1}$ as $i \to \infty$. Thus the trophic structure would not peak as rapidly as is usually observed in real systems. Such unpeaked systems

could exist but we have shown that they are likely to become unstable
rapidly, as N grows large. Moreover, systems with inverted struc-
ture in which the top levels are more "populated" than the lower
ones should be of very simple (small N) structure for stability.
For most systems, with peaked trophic structure and small retention
factors $(\beta_{i,i-1}/\beta_{i-1,i})$, increasing the value of N will not seriously
affect stability.

IV. SUMMARY AND SPECULATIONS

We have described here several results of an investigation
of the finite stability domain of ecosystem models including those
incorporating decomposer and detritus pathways. While only the
surface of this subject has been scratched by our work, several
pertinent results have emerged. Among these are two which may be
of practical interest:

i. Stability and diversity. We have distinguished several
kinds of diversity here. There is vertical diversity referring to
the number of levels in the trophic structure, and horizontal diver-
sity, referring to the variety of competitors at each level. And
then there is diversity of species and diversity of pathways. What
we have shown here is that increasing the number of trophic levels
generally has no effect on the size of the domain of asymptotic
stability. The exception to this occurs if the food web is not
pyramidal in shape but rectangular or inverted. Then the system
can rapidly destabilize as the number of levels grows. We have also

shown that increasing horizontal diversity generally leads to a decreasing domain of asymptotic stability, although if the ratio of the number of pathways to the number of species is kept sufficiently bounded, then both can increase without diminishing stability.

ii. Sensitivity of feedback systems. We have shown that damage to the decomposers or the organic or inorganic nutrient pools in an ecosystem is a potential source of instability - greater, perhaps, than that arising from tampering with the more visible predator-prey components of the system. Activities of man which diminish the cycling capability of an ecosystem should be viewed with caution if these results stand up under further analysis.

There are numerous practical problems to which stability analysis such as this might be applicable. Study of the global carbon cycle might reveal thresholds for climatic instability, or at least provide insight into the ultimate fate of the carbon dioxide released by fossil fuel consumption.

Our methods might also be useful for evaluating the potential for rehabilitating strip-mined lands which have had their detritus-decomposer pathways altered. Insight into the vulnerability of desert and tundra systems with low reserves of litter and slow cycling times might also be obtainable.

We close with several speculations. Let us recall the observation[11] that during the course of ecological succession, certain observables such as cycling rates, productivities, and biomass tend to show systematic time development. Is it possible

to view succession as the progression of the system into an ever
more resilient configuration? If so, then the evaluation of a suit-
able measure of resilience may provide a guide to the direction
of these successional trends.

As a suitable measure, we propose the use of either the
quantity

$$\Lambda = - \text{ minimum over } \Delta x_i \text{ of } (\frac{1d}{2dt} \ln L) \tag{12}$$

or, if one is only concerned with neighborhood stability,

$$\Lambda = - \text{ minimum over i of } (\lambda_i) \tag{13}$$

where the λ_i are the eigenvalues of the community matrix of the system.
For a stable system, either is roughly a measure of the lowest resilience
or recovery rate for a perturbed state to return to its unperturbed
value. In the limit of small Δx_i, the two definitions of Λ agree.
Λ is a quantity which should be of practical interest to those con-
cerned with environmental impacts. For even though mathematical
modeling may suggest that a system is asymptotically stable, a high
resilience is still desirable as it proves a safety factor against the
unexpected.

If we assume that Λ is maximized during succession, then
we may be able to understand the course of succession. Moreover,
if the equations of motion were sufficiently reliable, then if
Λ is evaluated for a time-dependent solution it may be possible to
use the dynamical equations to show that Λ _is_ increasing in time.

We have only been able to apply this idea so far to several
simple models. A number of simple two and three level systems

describing the flow of carbon have been analyzed and lead to the

result that Λ is maximized for a certain fixed ratio (which turns

out to be 4) of the equilibrum amount of carbon in plants to carbon

in the atmosphere. This result will be described in detail in a

forthcoming paper. It will be interesting to determine how Λ

depends upon such quantities as the total biomass, pathway diversity,

or productivity of model and laboratory systems.

We have also begun to assess the role of fluctuations or

noise in ecosystems. Several authors[12] have shown that fluctuations

in the k_{ii} terms in Fig. 3 are destabilizing. On the other hand we

have obtained some preliminary evidence from computer generated

solutions of our model equations that noise in the values of the

k_{ij}, for $i \neq j$, renders the system more resilient—more like a piece of

rubber than a crystal. To be more precise, consider the admittedly

over-simplified Lotka-Volterra equations as an example. If the

saturation effect is ignored ($k_{ii} = 0$) then the equations possess

solutions with interesting cyclic time dependence, but this system

is structurally unstable and the solutions possess no domain of

asymptotic stability; hence the model is unrealistic. On the other

hand, if the damping factors, k_{ii}, are negative definite, then the

system is structurally stable, but the solutions all approach

steady states. We hypothesize that in the latter case, with damping,

the presence of small fluctuations in the k_{ij} (for $i \neq j$) will not only

preserve the stability of the system but also excite the cyclic modes of the

undamped system. A linear system could not obey this hypothesis;
a more thorough study of nonlinear systems is needed before this and
other potential surprises are understood.

Much work remains in this exciting field. The search for
a deeper understanding of the workings of complex, non-linear, self-
organizing systems is a challenge in its own right; moreover, the
results may be of ultimate benefit to our species.

ACKNOWLEDGEMENTS

FOOTNOTES AND REFERENCES

1. J. Lasalle and S. Lefshetz, Stability by Liapunov's Direct Method, Academic Press, 1961.

2. For practical stability, we require that at finite times the pre-assigned tolerance is not exceeded. Thus the domain of asymptotic stability could be larger than the domain of practical stability.

3. See the discussion following P. 121 of Ref. 1.

4. This class of models includes those characterized as follows: Separate the net increasing and decreasing contributions to dx_i/dt by writing $\frac{dx_i}{dt} = f_i(x_1, \ldots, x_N) - g_i(x_1, \ldots, x_N)$ where f_i and g_i are positive and can be expanded in a sum of products of positive powers of the x_i. Further assume that $g_i(x_i = 0, x_{j \neq i}$ arbitrary$) = 0$, that f_i does not grow faster than linearly in x_i and that $f_i/g_i \underset{x_i \to \infty}{\longrightarrow} 0$

   Then such a B-matrix can be constructed. Of course, a wider class of models which are not expressible as sums of products of powers and which are quite difficult to characterize, will also lead to such a B-matrix.

5. The treatment of an unperturbed periodic or nearly periodic state involves an averaging procedure which will be discussed in a forthcoming paper. For the rest of this paper, attention will be limited to steady states.

6. See R. Fraser, W. Duncan, and A. Collar, Elementary Matrices, Cambridge University Press, 1957.

7. We say "at least as big" because the actual domain of stability can be larger than that calculated from the principal minors. This is true for two reasons. First, the condition on the determinants arose from the requirement that the quadratic form be positive for all values of the Δx_i's. Yet the condition restricts the Δx_i's and thus the requirement on the quadratic form was overly stringent. Secondly, even if some of the determinants are negative so that dL/dt is no longer negative definite, dL/dt is not necessarily positive definite and thus there may not necessarily be a true instability. A better Liapunov function might be needed to resolve this ambiguity. For both these reasons we have a built in "safety factor" in our analysis. We suspect that safety factors are desirable in practical ecosystem stability modeling if for no other reason than that model descriptions of ecosystems are inevitably only approximate. It remains to be seen whether this is the most appropriate way to build in the margin of safety.

8. H. Huang and H. Morowitz, Journal of Theoretical Biology, Vol. 35, p. 389, (1972).

9. A recent paper by M. Austin and B. Cook, Journal of Theoretical Biology, Vol. 45, p. 735, (1974) describes the results of some computer simulations of model systems with decomposers.

10. Provided, of course, that the horizontal structure of the web does not grow so complex that the Lotka-Volterra form of Eq. is impossible. The tendency will be for off-diagonal elements in the principal minors to diminish the domain of stability.

11. See, for example, E.P. Odum, Science, page 262, April 18, 1969.

12. See R. May, Stability and Complexity in Model Ecosystems, Princeton University Press, 1973 and references therein.

FIGURE CAPTIONS

FIGURE 1   Time evolution of unperturbed and perturbed states. The axes

label the component of the system. The solid line represents the

unperturbed system $(\bar{x}_i)$ and would be a single point for a

steady state $(\bar{x}_i = constant)$. The dashed line represents the

perturbed state and its subsequent time evolution. In the top

diagram the perturbed state remains near the unperturbed state,

while in the bottom diagram the perturbed state wanders into a

forbidden region (e.g. a region where algae concentration

accelerates dramatically).

FIGURE 2   An outline of the proceedure for using the Liapunov function

to determine stability properties of an ecosystem.

FIGURE 3   A schematic figure of a simple open system with no cycling of

energy flow. At each trophic level above the plants, energy

is lost. A typical set of equations describing such a system

is the Lotka-Volterra equations shown in the figure. In these

equations: The α_i are simple death rates, the k_{ii} are related

to carrying capacities, the k_{ij} are the interaction terms, and

the τ_i are retention factors. The simple form of the Lotka-

Volterra equations and the antisymmetry constraints limit their

usefulness.

FIGURE 4   A simple closed system with carbon cycling consisting of plants,

atmosphere (CO_2), decomposers, and organic litter. The x_i's

measure carbon content. The various numbered terms in the equations indicate:

1) plant death rate including resource saturation effect,

2) plant growth due to CO_2 absorption during photosynthesis,

3) decrease in CO_2 due to plant absorption,

4) production of CO_2 by decomposer action on litter,

5) decomposer death rate including resource saturation effect,

6) decomposers growth due to feeding on litter,

7) litter increase due to decomposer and plant death,

8) litter decrease by decomposer action.

(all constants are positive.)

FIGURE 5   A simple open system with nutrient cycling consisting of carnivores, herbivores, plants, inorganic nutrient pool, decomposers, and organic litter. The numbered terms indicate:

1) carnivore death rate including resource saturation effect,

2) carnivore growth due to eating herbivores,

3) herbivore death rate including resource saturation effect,

4) herbivore decrease due to carnivore grazing,

5) herbivore increase due to feeding on grass,

6) plant death rate including resource saturation effect,

7) plant decrease due to herbivore grazing,

8) plant growth due to absorbtion of inorganic nutrients,

9) addition of inorganic nutrient pool (e.g. fertilizer),

10) washout of inorganic nutrient,

11) nutrient decrease due to plant use,

12) nutrient increase due to decomposer action on litter,

13) decomposer death rate including resource saturation effect,

14) decomposer growth due to feeding on litter,

15) addition to litter (e.g. sewage dumping),

16) washout of litter,

17) litter increase from excrement (Γ is efficiency factor),

18) litter decrease due to decomposer action,

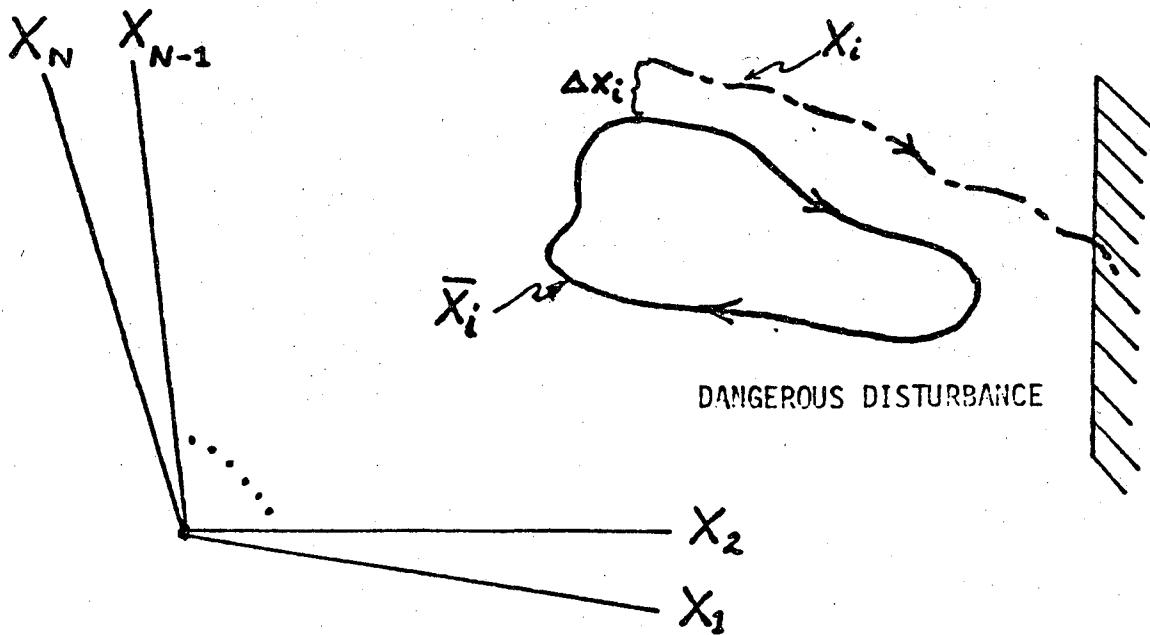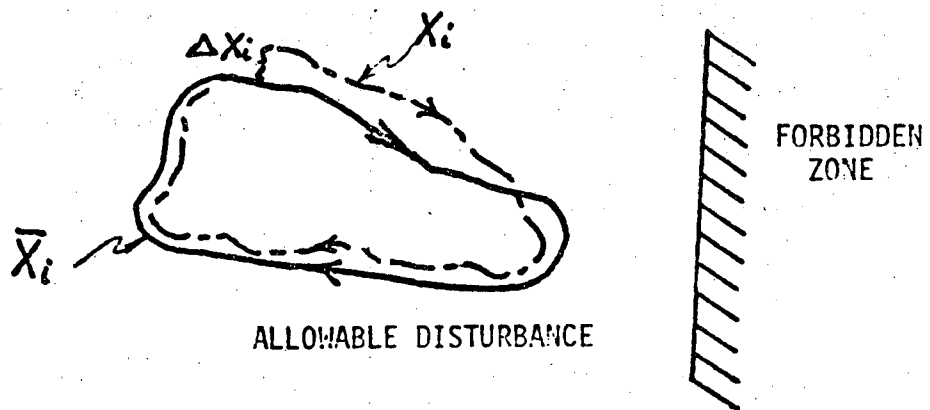19) litter increase due to death of organisms.

(all constants are positive.)

Fig. 1.

I) FIND A FUNCTION L ($\Delta X_1, \ldots \ldots, \Delta X_N$) WHICH SATISFIES

$$L = 0 \text{ IF ALL } \Delta X_i = 0$$

$$L > 0 \text{ IN SOME DOMAIN ABOUT } \Delta X_i = 0$$

II) EVALUATE $\dfrac{dL}{dt} = \sum_i \dfrac{\partial L}{\partial \Delta X_i} \dfrac{d \Delta X_i}{dt}$ USING THE EQUATIONS OF MOTION

III) IF $\dfrac{dL}{dt} < 0$, THE SYSTEM IS ASYMPTOTICALLY STABLE.

IF $'' '' = 0$, THE SYSTEM IS NEUTRALLY STABLE.

IF $'' '' > 0$, THE SYSTEM IS UNSTABLE.

THE DOMAIN OF PRACTICAL STABILITY DEPENDS UPON THE PREASSIGNED

TOLERANCE ON THE $\Delta X_i(t)$.   IT MAY BE LARGER THAN THE DOMAIN OF

ASYMPTOTIC STABILITY BECAUSE PRACTICAL STABILITY DOES NOT REQUIRE

$X_i(t) \to \bar{X}_i$ AS $t \to \infty$, OR IT MAY BE SMALLER BECAUSE THE $\Delta X_i(t)$,

FOR AN ASYMPTOTICALLY STABLE SYSTEM, MAY EXCEED THE TOLERANCE
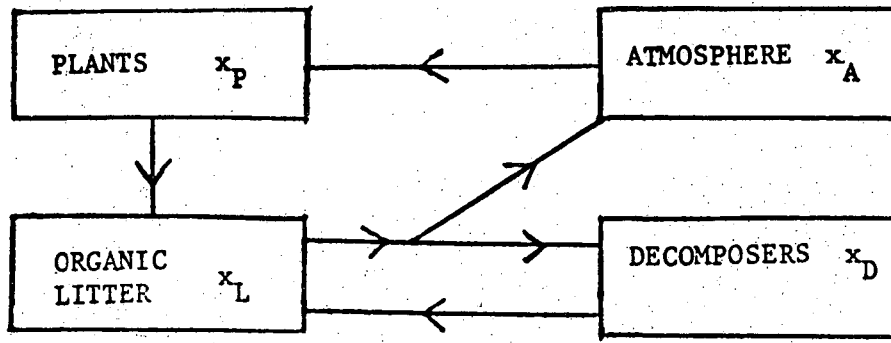
AT FINITE TIMES.

Fig. 2.

external input and/or output

TOP CARNIVORES

CARNIVORES

HERBIVORES

PLANTS
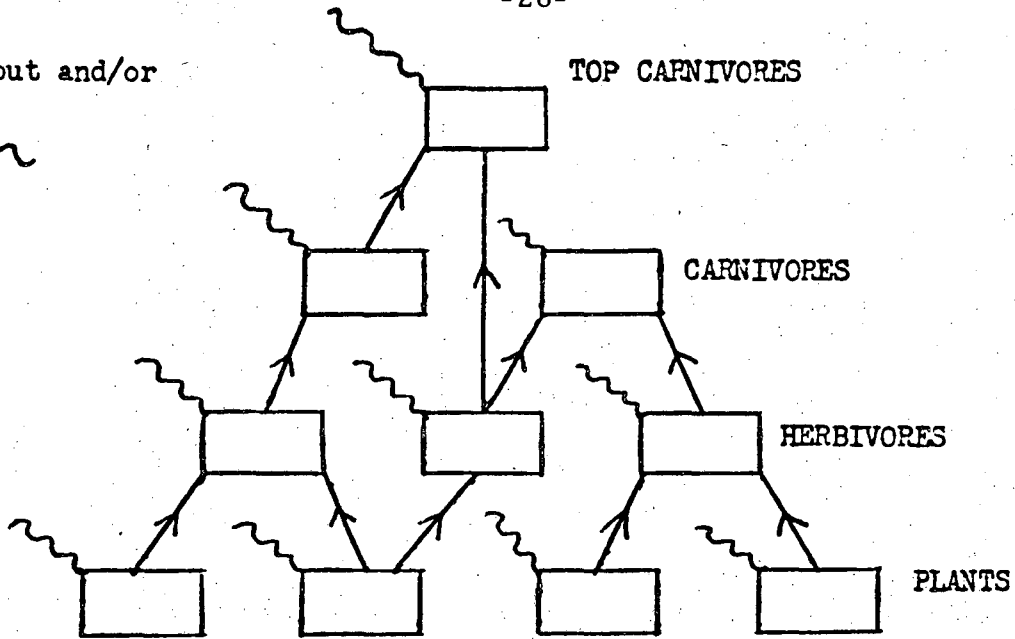
$$\frac{dX_i}{dt} = \alpha_i X_i + \sum_{j=1}^{N} \frac{k_{ij}}{\tau_i} X_i X_j$$

where $k_{ii} < 0$, $k_{ij} = -k_{ji}$ $(i \neq j)$

Fig. 3.

$$\frac{dX_P}{dt} = -\underbrace{\alpha_P X_P - \gamma_P X_P^2}_{1} + \underbrace{\beta_{PA} X_P X_A}_{2}$$

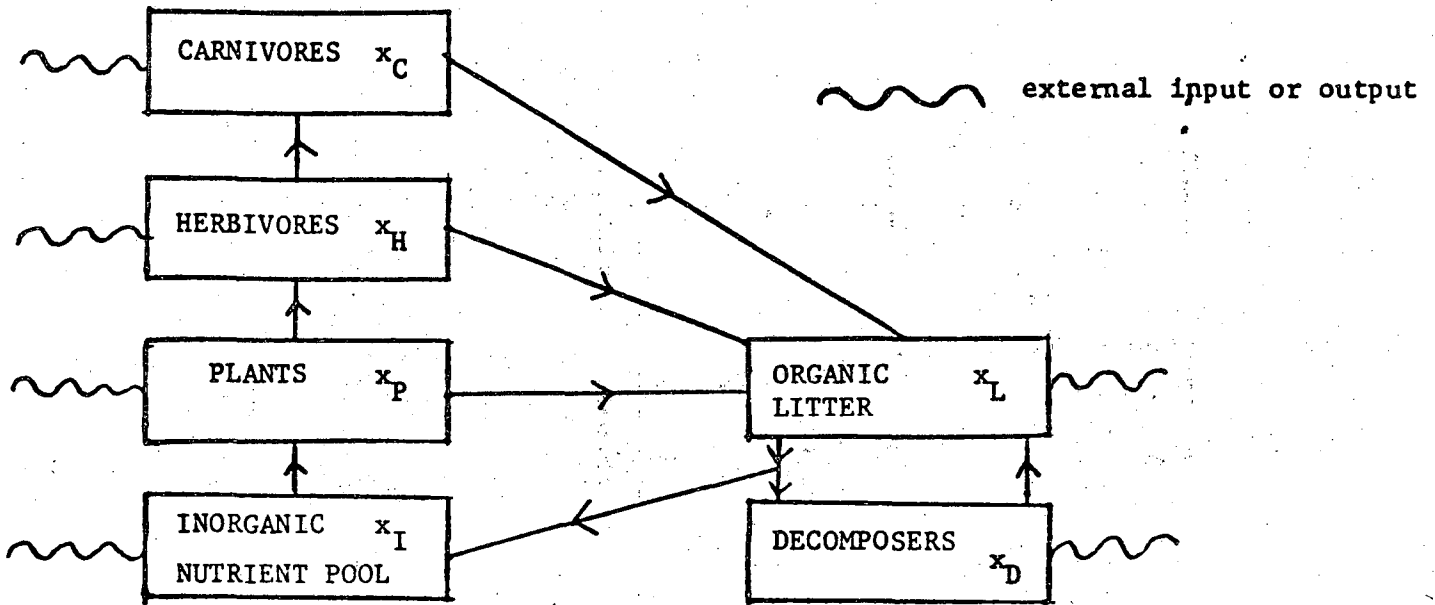$$\frac{dX_A}{dt} = -\underbrace{\beta_{PA} X_P X_A}_{3} + \underbrace{\sigma_{DL} X_D X_L}_{4}$$

$$\frac{dX_D}{dt} = -\underbrace{\alpha_D X_D - \gamma_D X_D^2}_{5} + \underbrace{\beta_{DL} X_D X_L}_{6}$$

$$\frac{dX_L}{dt} = \underbrace{\alpha_P X_P + \gamma_P X_P^2 + \alpha_D X_D + \gamma_D X_D^2}_{7}.$$

$$-\underbrace{(\beta_{DL} + \sigma_{DL}) X_D X_L}_{8}$$

note the system is closed, i.e.

$$\sum_i \frac{dX_i}{dt} \equiv 0 \quad \text{or} \quad \sum_i X_i = \text{constant}$$

Fig. 4.

external input or output

$$\frac{dX_C}{dt} = -\underbrace{\alpha_C X_C - \gamma_C X_C^2}_{1} + \underbrace{\beta_{CH} X_C X_H}_{2}$$

$$\frac{dX_H}{dt} = -\underbrace{\alpha_H X_H - \gamma_H X_H^2}_{3} - \underbrace{\beta_{HC} X_H X_C}_{4} + \underbrace{\beta_{HP} X_H X_P}_{5}$$

$$\frac{dX_P}{dt} = -\underbrace{\alpha_P X_P - \gamma_P X_P^2}_{6} - \underbrace{\beta_{PH} X_P X_H}_{7} + \underbrace{\beta_{PI} X_P X_I}_{8}$$

$$\frac{dX_I}{dt} = \underbrace{\Omega_I}_{9} - \underbrace{\alpha_I X_I}_{10} - \underbrace{\beta_{IP} X_I X_P}_{11} + \underbrace{\sigma_{DL} X_D X_L}_{12}$$

$$\frac{dX_D}{dt} = -\underbrace{\alpha_D X_D - \gamma_D X_D^2}_{13} + \underbrace{\beta_{DL} X_D X_L}_{14}$$

$$\frac{dX_L}{dt} = \underbrace{\Omega_L}_{15} - \underbrace{\alpha_L X_L}_{16} + \underbrace{\Gamma\{(\beta_{HC} - \beta_{CH})X_C X_H + (\beta_{PH} - \beta_{PH})X_P X_H\}}_{17}$$

$$-\underbrace{\beta_{LD} X_L X_D}_{18} + \underbrace{\Gamma\{\alpha_C X_C + \gamma_C X_C^2 + \alpha_H X_H + \gamma_H X_H^2 + \alpha_P X_P + \gamma_P X_P^2 + \alpha_D X_D + \gamma_D X_D^2\}}_{19}$$

Constraints are: $\beta_{HC} > \beta_{CH}$, $\beta_{PH} > \beta_{HP}$, $\beta_{LD} > \beta_{DL} + \sigma_{DL}$

Fig. 5.