

Lawrence Berkeley National Laboratory

Lawrence Berkeley National Laboratory

Title

ECOSYSTEM STABILITY AND THE DISTRIBUTION OF COMMUNITY MATRIX EIGENVALUES

Permalink

<https://escholarship.org/uc/item/9n15k5vq>

Author

Harte, J.

Publication Date

1977-07-01

0 03 03 48 70 00 09 09 01 1

LBL-6361 c./
UC-32
TID-4500-R65

For Reference
Not to be taken from this room

RECEIVED
LIBRARY
BERKELEY CALIFORNIA

JUL 13 1977

LIBRARY AND
DOCUMENTS SECTION

Energy and Environment Division



Ecosystem Stability And The
Distribution Of Community
Matrix Eigenvalues

John Harte

July 1977

Lawrence Berkeley Laboratory University of California/Berkeley
Prepared for the U.S. Energy Research and Development Administration under Contract No. W-7405-ENG-48

LBL-6361
c/

LEGAL NOTICE

This report was prepared as an account of work sponsored by the United States Government. Neither the United States nor the United States Energy Research and Development Administration, nor any of their employees, nor any of their contractors, subcontractors, or their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness or usefulness of any information, apparatus, product or process disclosed, or represents that its use would not infringe privately owned rights.

Printed in the United States of America
Available from
National Technical Information Service
U. S. Department of Commerce
5285 Port Royal Road
Springfield, VA 22161
Price: Printed Copy \$4.00 Microfiche \$3.00

0 9 9 8 4 8 7 9 9 9 2 2

LBL-6361

ECOSYSTEM STABILITY AND THE DISTRIBUTION
OF COMMUNITY MATRIX EIGENVALUES

by

John Harte

July 1977

Energy and Environment Division
Lawrence Berkeley Laboratory
Berkeley, California 94720

Work supported by the Energy Research and Development Administration

ABSTRACT

A definition or measure of ecological stability is introduced which is advantageous in that it may be empirically accessible and in that it relates to practical concerns in situations of environmental stress. It is shown how this measure can be analyzed, for an arbitrary system described by a community matrix, by model-independent mathematical methods. The relationship between the stability of any such system and both the distribution of community matrix eigenvalues and the pattern of pathway linkages is discussed.

I. Introduction

One of the central problems in ecology is to learn how to predict what will happen to a disturbed ecosystem. What one would like is to be able to measure certain properties (ideally, a few simple ones) of ecosystems before they are perturbed and then on the basis of the results of the measurements to be able to predict how gently or violently the system will respond to a disturbance. For this reason, much effort has been directed toward understanding what properties of ecosystems tend to enhance stability against external stresses. We call such properties stability indicators. A wide range of definitions of stability (May, 1973; Holling, 1973 ; Botkin and Sobel, 1974; Orians, 1974) and an even wider range of possible stability indicators for ecosystems have been considered by ecosystem theorists. Among the former are resistance, resilience, neighborhood asymptotic stability, global asymptotic stability, and structural stability, while the latter include species diversity, (Odum, 1969; May, 1973; Goodman, 1975), nutrient pathway diversity (MacArthur, 1955), nutrient transit-time diversity (Harte and Morowitz, 1975), time lags (May, 1973), spatial heterogeneity (Andrewartha and Birch, 1954; Horn and MacArthur, 1972), grazing strategies (Steele, 1974), density dependence (May, 1973), and stochasticity (May, 1973; Roughgarden, 1975).

A shortcoming of much theoretical work in ecology is that results often are not expressed or expressible as relations among readily measureable quantities. A familiar example is the oft-quoted result that a necessary and sufficient condition for asymptotic stability of a system described by a community matrix is the negativity of the real parts of all the eigenvalues of that matrix. While mathematically rigorous, this result unfortunately is not very useful for two reasons. First, measurement of all the community matrix eigenvalues for an actual ecosystem is nearly impossible. Secondly, the property of asymptotic stability, while mathematically precise, is unverifiable because it entails an infinite time of observation.

This work is motivated by our perceived need to bring theoretical stability analysis more in align with experimental constraints. Our objective is to introduce a relatively practical quantitative measure of stability and to explore how the value of this stability measure depends upon ecosystem parameters (such as averaged properties of the distribution of eigenvalues of the community matrix). In an earlier work, (Harte and Morowitz, 1975), summarized briefly below, we describe how a single function, characterizing in an approximate way the distribution of eigenvalues can be empirically

determined by an appropriate tracer experiment. Because measurement of this approximate distribution is far easier than measurement of all the community matrix eigenvalues (although still by no means easy!) analysis along these lines could enhance the empirical relevance of theoretical analysis.

II. A Practical Measure of Stability

All notions of stability in ecology pertain to the relation between a stressed state of a system and the state the system would have been in if there had been no stress. Where they differ is in the aspects of that relation which are selected as being especially important. No single measure of ecosystem stability can be suitable for all purposes and satisfy the interests of all ecologists. The notion of resistance to stress is very useful if one's interest is in the maximum extent of the deviation between the stressed and unstressed system. Resilience is of relevance to those concerned with the rate at which a system returns to pre-stress conditions. Asymptotic stability is a useful concept for those concerned with whether or not a system will eventually return to its pre-stressed state. Other concepts of stability likewise single out certain aspects of perturbed behavior for emphasis.

Asymptotic stability, together with the community matrix eigenvalue method of analysis, is perhaps the most widely applied of all. Yet it is not likely to be a practical concern in a situation in which, for example, effluent is dumped in a lake or a forest is clear-cut. First, it is too stringent a condition in the sense that return of a system to precisely its pre-stressed state is neither likely (especially if the stress is not removed!) nor essential to environmental acceptability. Secondly, the condition that a system ultimately returns to its predisturbed state may be too lenient if the system takes a very long time to do so and is displaced quite far from undisturbed conditions prior to its eventual return. In short, asymptotic stability, while mathematically convenient, is neither environmentally relevant nor, as mentioned in the introduction, empirically accessible.

The measure of stability analyzed here incorporates both resistance and resilience in a single integrated measure of the deviation between the stressed and unstressed states of the system. Suppose that in the absence of an external disturbance to an ecosystem, the state of the system is characterized by the functions of time, $\bar{x}_i(t)$, with $i = 1, 2, \dots, N$. The

\bar{x}_i describe the unperturbed components of the system; they are usually most conveniently taken to refer to the carbon contents of these compartments although that is not of importance to us here. Let the functions $\Delta x_i(t)$ be a measure of the magnitude of the effect on the i^{th} compartment resulting from some perturbation. The Δx_i 's are usually taken to describe the same property of the compartments that the \bar{x}_i 's describe although they could as well describe levels of a toxic substance or any other measure of system response. Assume that the perturbation begins at time $t=0$. Then we let

$$S^{-1} = \frac{1}{N} \sum_i \eta_i \int_0^{\infty} dt \rho(t) \left[\frac{\Delta x_i(t)}{\bar{x}_i(t)} \right]^2 \quad (1)$$

be our measure of stability. A large value of S corresponds to high stability. Note that this definition of stability incorporates a measure of both the magnitude of the deviation of the perturbed system from equilibrium and the rapidity with which it returns, if at all. The η_i may all be chosen to be equal to unity if each compartment is deemed to be of equal weight or importance, although a subjective judgment might favor choosing the η 's corresponding to some species to be larger than others. A time-weighting function, $\rho(t)$, under the

integral sign can be chosen to be different from a constant in order to reflect the observer's judgment about the relative importance of short-term or long-term effects. In order to compare the intrinsic stability of different systems, the integrals in Eq. 1 must be averaged over a set of initial perturbations of specified magnitude, as discussed further in the following section.

While Eq. 1 provides an index or measure of stability which is empirically convenient (or can be made so by appropriate choices of the η_i and $\rho(t)$) and appears to have the flexibility to reflect well many of the realities of environmental impact concerns, it does not connect in any transparent way with methods of mathematical analysis of theoretical models other than computer simulation. And yet if it is to provide more than just another empirical property of stressed ecosystems and is to be related in some way to properties of the pre-stressed system, such as diversity, then methods of theoretical analysis of this measure would be useful. By means of such methods, one could identify, for purposes of ultimate verification, interesting candidates for stabilizing or destabilizing properties of ecosystems. The rest of this article will develop an analytic

approach to the study of this stability index, and present some preliminary results about some possible candidates for stability indicators.

III. Analysis of S.

The value of S for a particular ecosystem subjected to a particular disturbance will depend upon how large the Δx_i grow and how rapidly, if at all, they damp out to zero. In order to see what generalities can be deduced, consider a quite general model description consisting of coupled, nonlinear, first order differential equations for the time dependence of the compartment variables. Assuming, now, that the ratios $\Delta x_i / \bar{x}_i$ are small, then a linearized matrix equation:

$$\frac{d}{dt} \Delta x_i(t) = \sum_j A_{ij} \Delta x_j(t) \quad (2)$$

is obtained. A is commonly referred to as the community matrix; its eigenvalues will be denoted by $-\lambda_\alpha$ (Note the minus sign in front of λ_α introduced for future convenience.) If, as we hereafter assume, the \bar{x}_i are time independent and the original non-linear equations have no explicit time dependence, and, in the absence of eigenvalue degeneracy, the time evolution of the Δx_i 's can be easily computed to be:

$$\Delta x_i(t) = \sum_{\alpha} a_{i\alpha} e^{-\lambda_{\alpha} t} \quad (3)$$

where the $a_{i\alpha}$ depend upon the matrix elements of A and the initial conditions, $\Delta x_i(0)$. If the eigenvalues of A all have negative real parts, as we hereafter assume, then the Δx_i 's are guaranteed to damp to zero as $t \rightarrow \infty$. The eigenvalues $-\lambda_{\alpha}$, which determine the damping times, are related in a moderately complicated way to the residence times of the compartments of the system; in general the damping time constants, or inverse negative real parts of the eigenvalues denoted by $\text{Re}^{-1}(\lambda_{\alpha})$, are large if the residence times are all long.

The qualitative dependence of integrals $\int dt (\Delta x_j(t))^2$ upon time constants, $\text{Re}^{-1}(\lambda_{\alpha})$, of the system can be conjectured. Dimension counting would suggest that when the time constants are small, the integrals are small. Therefore, small $\text{Re}^{-1}(\lambda_{\alpha})$ should be an indication of high stability. Moreover, equitability, or small dispersion, of the time constants tends to prevent a situation in which a subset of terms in Eq. 3 with, say, positive coefficients dominate the integrand at early times just subsequent to the perturbation, while the remaining terms with negative coefficients dominate at later times. Therefore, if the sum of the $\text{Re}^{-1}(\lambda_{\alpha})$ is fixed, the more equitably they are distributed,

the less the Δx_i should grow and the larger S should be. Below, we prove several theorems which establish rigorous connections between S and the distribution of eigenvalues.

Explicitly displaying the dependence of the $\Delta x_i(t)$ on the initial conditions, $\Delta x_i(0)$, we rewrite Eq. 3 as

$$\Delta x_i(t) = \sum_{j=1}^N \sum_{\alpha=1}^N \Delta x_j(0) C_{ji}^{\alpha} e^{-\lambda_{\alpha} t} \tag{4}$$

where C_{ji}^{α} is of the form:

$$C_{ji}^{\alpha} = D_{j\alpha}^{-1} D_{\alpha i} \tag{5}$$

and D is the matrix of eigenvectors of A . For future reference we note that the C_{ji}^{α} satisfy:

$$\sum_{\alpha} C_{ji}^{\alpha} = \delta_{ji} \tag{6}$$

and

$$\sum_i C_{ii}^{\alpha} = 1. \tag{7}$$

both of which constraints follow from Eq. 5. For the rest of this discussion we will assume that the η_i and $\rho(t)$ in Eq. 1 are equal to unity and that the eigenvalues are real and negative. This will simplify the algebra. It will also

influence our results; other cases can be treated, however, by the methods we develop here.

Substituting Eq. 4 into Eq. 1 and performing the integration, we obtain

$$S^{-1} = \frac{1}{N} \sum_{i=1}^N \sum_{j=1}^N \sum_{k=1}^N \sum_{\alpha=1}^N \sum_{\beta=1}^N \frac{\Delta x_j(0) \Delta x_k(0) C_{ji}^{\alpha} C_{ki}^{\beta}}{\bar{x}_i^{-2} (\lambda_{\alpha} + \lambda_{\beta})} \quad (8)$$

In order to proceed we must make an assumption about the $\Delta x_i(0)$. One possible initial condition would be to take a particular $\Delta x_i(0)$ different from zero and the others equal to zero. While in some situations this is a realistic initial condition and is, in fact, the most commonly considered one in theoretical studies, we choose instead to evaluate S by averaging over a set of many initial displacements. We adopt this procedure because we are interested in general, not specific, stability properties of ecosystems. That is, we do not want to know the value of S for a particular initial condition, but rather its value for a random average over a wide range of possible initial conditions. Our averaging procedure will be to take an average of S^{-1} , denoted $\langle S^{-1} \rangle$, over initial displacements which are randomly distributed subject to:

$$\langle \Delta x_i(0) \Delta x_j(0) \rangle = \delta_{ij} \bar{x}_i^{-2} \quad (9)$$

The "absence-of-correlation" assumption made here for the initial displacements is based simply on the absence of more detailed information. The methods we introduce here for analysing S could in principle be applied to other averaging procedures, with different results generally obtaining.

Using Eq. 9, to evaluate $\langle S^{-1} \rangle$, we obtain from

Eq. 8:

$$\langle S^{-1} \rangle = \frac{1}{N} \sum_{i=1}^N \sum_{j=1}^N \sum_{\alpha=1}^N \sum_{\beta=1}^N \frac{C_{ji}^{\alpha} C_{ji}^{\alpha} x_j^{-2}}{(\lambda_{\alpha} + \lambda_{\beta}) x_i^{-2}} \quad (10)$$

Consider, first, the case in which the community matrix is diagonal:

$$A = \begin{pmatrix} -\lambda_1 & & & \\ & -\lambda_2 & & \\ & & \circ & \\ & & \cdot & \\ \circ & & \cdot & \\ & & & -\lambda_n \end{pmatrix} \quad (11)$$

Letting

$$\lambda = \frac{1}{N} \sum_{\alpha} \lambda_{\alpha} \quad (12)$$

we write

$$\lambda_{\alpha} = \lambda + \epsilon_{\alpha} \quad (13)$$

where

$$\lambda > 0, \sum_{\alpha} \epsilon_{\alpha} = 0 \text{ and } \epsilon_{\alpha} > -\lambda. \quad (14)$$

It is then straightforward to show that

$$\langle S^{-1} \rangle = \frac{1}{2\lambda} - \frac{1}{N} \sum_{\alpha} \frac{\epsilon_{\alpha}}{2\lambda(\lambda + \epsilon_{\alpha})} \quad (15)$$

whether or not any degeneracies occur among the λ_{α} . This result follows from the fact that for this case,

$$C_{ji}^{\alpha} = \delta_{\alpha j} \delta_{\alpha i}.$$

Eqs. 14, 15 lead directly to the result that $\langle S^{-1} \rangle$ is minimum (corresponding to maximum stability) when all $\epsilon_{\alpha} = 0$. Moreover, for fixed values of the ϵ_{α} , $\langle S^{-1} \rangle$ decreases as the mean negative eigenvalue, λ , increases. Thus stability is enhanced when the mean eigenvalue is most negative and when the eigenvalues are most nearly equal in value, as suggested by the qualitative arguments given above. It is natural to inquire at this point as to what happens if the mean eigenvalue diminishes in absolute value and the dispersion, $\sum_{\alpha} \epsilon_{\alpha}^2 / N$, also decreases. It is easy to see from Eq. 15 that for small values of $\frac{\epsilon_{\alpha}}{\lambda}$, it is the ratio, $\sum_{\alpha} \epsilon_{\alpha}^2 / N\lambda^2$ which determines the index, S .

In order to analyze the case of an arbitrary (not necessarily diagonal) community matrix, we will need to use the relations given in Eqs. 6, 7 to simplify Eq. 10. A two component system will illustrate the techniques we use for non-diagonal A. We denote the two eigenvalues by $-\lambda_1$ and $-\lambda_2$, and set

$$\begin{aligned} \lambda_1 &= \lambda + \lambda' \\ \lambda_2 &= \lambda - \lambda' \end{aligned} \tag{16}$$

where

$$\lambda > 0, \quad |\lambda'| < \lambda \tag{17}$$

Substituting Eq. 16 into Eq. 10 we obtain

$$S^{-1} = \frac{1}{2} \sum_{i=1}^2 \sum_{j=1}^2 \frac{x_j^{-2}}{x_i^{-2}} \left(\frac{C_{ji}^1 C_{ji}^1}{2\lambda + 2\lambda'} + \frac{2C_{ji}^1 C_{ji}^2}{2\lambda} + \frac{C_{ji}^2 C_{ji}^2}{2\lambda - 2\lambda'} \right) \tag{18}$$

By adding and subtracting appropriate terms this becomes

$$\begin{aligned} S^{-1} &= \frac{1}{2} \sum_{i=1}^2 \sum_{j=1}^2 \frac{x_j^{-2}}{x_i^{-2}} \left[\sum_{\alpha=1}^2 \sum_{\beta=1}^2 \frac{C_{ji}^\alpha C_{ji}^\beta}{2\lambda} \right. \\ &+ C_{ji}^1 C_{ji}^1 \left(\frac{1}{2\lambda + 2\lambda'} - \frac{1}{2\lambda} \right) \\ &\left. + C_{ji}^2 C_{ji}^2 \left(\frac{1}{2\lambda - 2\lambda'} - \frac{1}{2\lambda} \right) \right] \end{aligned} \tag{19}$$

Using Eq. 6, we can simplify the first term on the right hand side of the above expression:

$$\frac{1}{2} \sum_{i=1}^2 \sum_{j=1}^2 \frac{\bar{x}_j^{-2}}{\bar{x}_i^{-2}} \sum_{\alpha=1}^2 \sum_{\beta=1}^2 \frac{C_{ji}^{\alpha} C_{ji}^{\beta}}{2\lambda} = \frac{1}{2} \sum_{i=1}^2 \sum_{j=1}^2 \frac{\bar{x}_j^{-2}}{\bar{x}_i^{-2}} \frac{\delta_{ji} \delta_{ji}}{2\lambda} = \frac{1}{2} \sum_i \frac{\delta_{ii}}{2\lambda} = \frac{1}{2\lambda} \quad (20)$$

Then, after a little algebraic rearrangement of the remaining terms, Eq. 19 becomes

$$\begin{aligned} S^{-1} &= \frac{1}{2\lambda} + \frac{1}{4\lambda^2} \sum_{i=1}^2 \sum_{j=1}^2 \frac{\bar{x}_j^{-2}}{\bar{x}_i^{-2}} \left(\left(C_{ji}^1 \right)^2 - \left(C_{ji}^2 \right)^2 \right) \\ &+ \frac{\lambda'^2}{4\lambda^2} \sum_{i=1}^2 \sum_{j=1}^2 \frac{\bar{x}_j^{-2}}{\bar{x}_i^{-2}} \left(\frac{\left(C_{ji}^1 \right)^2}{\lambda + \lambda'} + \frac{\left(C_{ji}^2 \right)^2}{\lambda - \lambda'} \right) \end{aligned} \quad (21)$$

The second term on the right hand side of Eq. 21 can be shown to vanish. This follows directly from Eqs. 6, 7:

$$\begin{aligned} &\sum_{i=1}^2 \sum_{j=1}^2 \frac{\bar{x}_j^{-2}}{\bar{x}_i^{-2}} \left[\left(C_{ji}^1 \right)^2 - \left(C_{ji}^2 \right)^2 \right] = \\ &\sum_{i=1}^2 \sum_{j=1}^2 \frac{\bar{x}_j^{-2}}{\bar{x}_i^{-2}} \left(C_{ji}^1 - C_{ji}^2 \right) \left(C_{ji}^1 + C_{ji}^2 \right) = \sum_{i=1}^2 \sum_{j=1}^2 \frac{\bar{x}_j^{-2}}{\bar{x}_i^{-2}} \left(C_{ji}^1 - C_{ji}^2 \right) \delta_{ij} \quad (22) \\ &= \sum_{i=1}^2 \left(C_{ii}^1 - C_{ii}^2 \right) = 1 - 1 = 0 \end{aligned}$$

Moreover, from Eq. 17, it follows that the last term in Eq. 21 is non-negative, and thus $\langle S^{-1} \rangle = 1/2\lambda +$ terms which are non-negative and do not vanish if $\lambda \neq 0$.

This result generalizes to an arbitrary community matrix. Let

$$\lambda_\alpha = \lambda + \epsilon_\alpha \quad (23)$$

where

$$\lambda > 0, \sum_\alpha \epsilon_\alpha = 0, \text{ and } \epsilon_\alpha > -\lambda \quad (24)$$

Then following the same procedures as in Eqs. 19, 20,

$$\langle S^{-1} \rangle = \frac{1}{2\lambda} - \frac{1}{2\lambda N} \sum_i \sum_j \frac{x_j^{-2}}{x_i^{-2}} \sum_\alpha \sum_\beta \frac{C_{ji}^\alpha C_{ji}^\beta (\epsilon_\alpha + \epsilon_\beta)}{2\lambda + \epsilon_\alpha + \epsilon_\beta} \quad (25)$$

In the appendix to this chapter it is shown that even in this general case, $\langle S^{-1} \rangle \geq 1/2\lambda$.

It should be pointed out that often in the limit of degenerate eigenvalues, Eq. 3 is no longer a correct form for ΔX_i and the C_{ji}^α develop singularities behaving like, for example, $1/\epsilon_\alpha$ as the ϵ_α approach zero. In such a degenerate limit, our proofs fail. By continuity, we still expect that $\langle S^{-1} \rangle \geq 1/2\lambda$ even in such a case. What we do not expect is that $\langle S^{-1} \rangle = 1/2\lambda$ in the

limit $\epsilon_\alpha \rightarrow 0$, should such singularities develop. If the community matrix has all zero matrix elements either above or below the diagonal, then such singularities do not arise, $C_{ji}^\alpha = \delta_{j\alpha} \delta_{\alpha i}$, Eq. 15 is exact, and $\langle S^{-1} \rangle \rightarrow 1/2\lambda$ as the $\epsilon_\alpha \rightarrow 0$. In general, the more sparse the off-diagonal terms of the community matrix the more likely that C_{ji}^α is non-singular in the degenerate limit and that Eq. 15 is exact.

From these results we draw the following conclusions:

- i. $\langle S^{-1} \rangle$ has a minimum value, $1/2\lambda$, where $-\lambda$ is the eigenvalue mean.
- ii. This minimum can only be reached if the dispersion, $(1/N)(\sum \epsilon_\alpha^2)$ of the eigenvalues vanishes (and thus each $\epsilon_\alpha = 0$).
- iii. This minimum is reached if the dispersion vanishes and the C_{ji}^α develop no singularities in that limit.

Additionally, the following qualitative results are suggested by the preceding arguments:

- i. For a fixed value of the eigenvalue mean and dispersion, stability is enhanced by community matrices which are either zero above or below the diagonal or are sparse with respect to off-diagonal elements. In an energy representation, the former is likely to be approximately valid because the

retention coefficients characterizing the ratio of the energy gained by a predator to the energy lost by a prey in a trophic interaction are typically very small. No matter what representation is used, our results suggest pathway simplicity (sparseness of off-diagonal community matrix) enhances stability, for a fixed value of the eigenvalue mean, and small eigenvalue dispersion. -

ii. The ratio of the eigenvalue dispersion to the square of the eigenvalue mean, $(1/N\lambda^2)(\sum \epsilon_\alpha^2)$ provides a parameter roughly characterizing the dependence of $\langle S^{-1} \rangle$ on the complete distribution of eigenvalues. Stability is enhanced as this parameter decreases.

IV. Discussion

Our results follow from relatively model-independent arguments. Nevertheless, it is useful to review the assumptions we have made in deriving Eq. 10 from Eq. 1. They are:

- i. The $\Delta x_i / \bar{x}_i$ are small so that a linear differential equation for Δx_i holds.
- ii. The \bar{x}_i are constants.

- iii. All the eigenvalues of A are negative and real.
- iv. The η_i and $\rho(t)$ in Eq. 1 are equal to unity.
- v. The initial conditions are as specified in Eq. 9.

If these assumptions are relaxed, methods may still exist for analyzing the implications of Eq. 1. For example, complex eigenvalues are easy to accommodate by our methods. If $\rho(t)$ is not constant, but some function of time weighing the future unevenly, then the λ -dependence of the time integrals in Eq. 1 will no longer look like $1/(\lambda_\alpha + \lambda_\beta)$. Whatever dependence on the λ 's emerges from the integrals, the constraints of Eqs. 6, 7 will still hold and our methods will give some result. Determination of the consequences of various forms for $\rho(t)$ and analysis of what happens when other assumptions in the above list are relaxed will be explored in future studies. It would also be of interest to determine how our results depend upon the specific functional dependence of the integrand in Eq. 1 upon the $|\Delta x_i|$. All our assumptions were chosen, in part, to simplify the mathematics, but only assumption i above appears impossible to relax, if analytical methods rather than numerical simulation are to be used to explore all these issues.

We conclude with a discussion of the question of measurement of an approximate eigenvalue distribution. Clearly, measurement of all the individual λ_{α} is impossible. In a previous report (Harte and Morowitz, 1975) we have described a tracer experiment which measures the transit-time distribution for a trace substance such as ^{14}C or ^{15}N to make a round trip through an ecosystem. This transit-time distribution provides a measure of the spread of the time constants characterizing the pathways for nutrient flow in the system. For a system in which there are only a small number of pathways with rapid flow rates, the distribution would be narrow and peaked at early times. For a system with many pathways, with greatly differing flow rates, the distribution would be spread out in time.

From a given distribution, we pointed out that a measure of pathway transit-time diversity can be constructed. This is obtained by forming the quantity $-\int g \ln(g/g_0) dt$ where g is the probability distribution for cyclic flow (i.e., $g(t)dt$ measures the probability that a signal which starts out at some point in the system at time $t=0$, will return to that point in the time interval $(t, t + dt)$. This diversity

measure has a dependence upon the mean and the dispersion of the transit-time distribution which is qualitatively the same as the dependence of $\langle S^{-1} \rangle$ upon the eigenvalue distribution. Increased transit-time diversity tends to increase $\langle S^{-1} \rangle$ or diminish stability. Development of tracer or other techniques for measurement of transit-time distributions for field systems (as distinct from the microcosm experiments proposed in our earlier report) would be of great value in verifying the ideas described here.

Appendix

In this appendix we prove that

$$J \equiv - \sum_i \sum_j \frac{x_j^{-2}}{x_i^{-2}} \sum_{\alpha} \sum_{\beta} \frac{C_{ji}^{\alpha} C_{ji}^{\beta} (\epsilon_{\alpha} + \epsilon_{\beta})}{2\lambda + \epsilon_{\alpha} + \epsilon_{\beta}} \geq 0 \quad \text{A-1}$$

subject to the constraints:

$$\begin{aligned} \sum_i C_{ij}^{\alpha} &= 1, \quad \sum_{\alpha} C_{ji}^{\alpha} = \delta_{ji}, \\ \sum_{\alpha} \epsilon_{\alpha} &= 0, \quad \epsilon_{\alpha} > -\lambda. \end{aligned} \quad \text{A-2}$$

Using Eq. 25, this will then establish that $\langle S^{-1} \rangle \geq 1/2\lambda$ in the most general case.

We first use the identity:

$$\frac{\epsilon_{\alpha} + \epsilon_{\beta}}{2\lambda + \epsilon_{\alpha} + \epsilon_{\beta}} \equiv \int_0^{\infty} d\sigma \left(-\frac{d}{d\sigma} - 2\lambda \right) e^{-\sigma(2\lambda + \epsilon_{\alpha} + \epsilon_{\beta})} \quad \text{A-3}$$

and the fact that:

$$\sum_{\alpha} \sum_{\beta} X_{\alpha} X_{\beta} \equiv \left(\sum_{\alpha} X_{\alpha} \right)^2, \quad \text{A-4}$$

for arbitrary X_{α} , to rewrite J in the form:

$$J = \int_0^{\infty} d\sigma \left(\frac{d}{d\sigma} + 2\lambda \right) \sum_i \sum_j \frac{x_j^{-2}}{x_i^{-2}} \left[\sum_{\alpha} C_{ji}^{\alpha} e^{-\sigma(\lambda + \epsilon_{\beta})} \right]^2 \quad \text{A-5}$$

The $d/d\sigma$ term easily simplifies, with the aid of Eq. A-2, as follows:

$$\int_0^{\infty} d\sigma \frac{d}{d\sigma} \sum_i \sum_j \frac{x_j^{-2}}{x_i^{-2}} \left[\sum_{\alpha} C_{ji}^{\alpha} e^{-\sigma(\lambda + \epsilon_{\alpha})} \right]^2 \quad \text{A-6}$$

$$= \sum_i \sum_j \frac{x_i^{-2}}{x_j^{-2}} \left[\sum_{\alpha} C_{ji}^{\alpha} \right]^2 = - \sum_i \sum_j \frac{x_j^{-2}}{x_i^{-2}} \delta_{ij}^2 = - \sum_i 1 = -N.$$

We now use the fact that the double sum over i and j is bounded below by the sum over $i = j$, and the general inequality

$$\sum_{i=1}^N x_i^2 \geq \frac{1}{N} \left(\sum_{i=1}^N x_i \right)^2, \quad \text{A-7}$$

to get

$$J \geq -N + 2\lambda \int_0^{\infty} d\sigma \frac{1}{N} \left[\sum_i \sum_{\alpha} C_{ii}^{\alpha} e^{-\sigma(\lambda + \epsilon_{\alpha})} \right]^2 \quad \text{A-8}$$

Using Eqs. A-2, A-4, this becomes

$$J \geq -N + \frac{2\lambda}{N} \sum_{\alpha} \sum_{\beta} \frac{1}{2\lambda + \epsilon_{\alpha} + \epsilon_{\beta}} \quad \text{A-9}$$

We next show that

$$K \equiv \sum_{\alpha} \sum_{\beta} \frac{1}{2\lambda + \epsilon_{\alpha} + \epsilon_{\beta}} \geq \frac{N^2}{2\lambda} \quad \text{A-10}$$

We begin by writing:

$$\begin{aligned}
 K &= \sum_{\alpha} \sum_{\beta} \int_0^{\infty} d\sigma e^{-\sigma(2\lambda + \epsilon_{\alpha} + \epsilon_{\beta})} \\
 &= \int_0^{\infty} d\sigma e^{-2\lambda\sigma} \sum_{\alpha} \sum_{\beta} e^{-\sigma(\epsilon_{\alpha} + \epsilon_{\beta})}
 \end{aligned}
 \tag{A-11}$$

But,

$$e^{-X} \geq 1 - X, \tag{A-12}$$

and so,

$$\begin{aligned}
 K &\geq \int_0^{\infty} d\sigma e^{-2\lambda\sigma} \sum_{\alpha} \sum_{\beta} (1 - \sigma\epsilon_{\alpha} - \sigma\epsilon_{\beta}) \\
 &= \frac{1}{2\lambda} \sum_{\alpha} \sum_{\beta} 1 \\
 &= \frac{N^2}{2\lambda}
 \end{aligned}
 \tag{A-13}$$

Thus, $J \geq 0$, and $\langle S^{-1} \rangle \geq 1/2\lambda$.

Acknowledgment

The proof in the appendix is due to Mark Davidson; we are extremely grateful to him.

References

- Andrewartha, H.G. and Birch, L.C., 1954 The Distribution and Abundance of Animals", Univ. Chicago Press, Chicago.
- Botkin, D. and Sobel, M., 1974. "Stability in Time-Varying Ecosystems", in Ecosystem Analysis and Prediction: Proceedings of a Conference on Ecosystems, Alta, Utah, July, 1974.
- Goodman, D. 1975, "The Theory of Diversity-Stability Relationships in Ecology", Quarterly Review of Biology 50:237-266.
- Harte, J., and Morowitz, H., 1975. "Nutrient Transit-Time Diversity: A measure of Ecological Organization and Stability", LBL-4441, Lawrence Berkeley Laboratory, Berkeley, California .
- Holling, C.S., 1973. "Resilience and Stability of Ecological Systems", in Annual Review of Ecology and Systematics Vol. 4, Annual Reviews Inc., Palo Alto, Calif.

- Horn, D. and MacArthur, R.H., 1972. "On Competition in A Diverse and Patchy Environment", Ecology, 53:749-752
- MacArthur, R.H., 1955. "Fluctuations of Animal Populations, and a Measure of Community Stability" Ecology, 36:533-536.
- Margalef, R., 1974, "Diversity, Stability, and Maturity in Natural Ecosystems", in Unifying Concepts in Ecology, Dr. W. Junk Publishers, The Hague.
- May, R., 1973, Stability and Complexity in Model Ecosystems, Princeton University Press, Princeton, N.J.
- Odum, E., 1969, "The Strategy of Ecosystem Development", Science 164:262-270.
- Orians, G., 1974, "Diversity, Stability and Maturity in Natural Ecosystems" in Unifying Concepts in Ecology, Dr. W. Junk Publishers, The Hague.
- Roughgarden, J., 1975 "A Simple Model for Population Dynamics in Stochastic Environments", The American Naturalist 109:713.
- Steele, J., 1974 The Structure of Marine Ecosystems, Harvard University Press, Cambridge, Mass.

This report was done with support from the United States Energy Research and Development Administration. Any conclusions or opinions expressed in this report represent solely those of the author(s) and not necessarily those of The Regents of the University of California, the Lawrence Berkeley Laboratory or the United States Energy Research and Development Administration.