

Lawrence Berkeley National Laboratory

Recent Work

Title

NUTRIENT TRANSIT TIME DIVERSITY: A NOVEL MEASURE OF ECOLOGICAL ORGANIZATION
and STABILITY

Permalink

<https://escholarship.org/uc/item/05q0z7g0>

Author

Harte, John

Publication Date

1975-12-01

Submitted for publication

LBL-4441
Preprint

NUTRIENT TRANSIT TIME DIVERSITY:
A NOVEL MEASURE OF ECOLOGICAL
ORGANIZATION AND STABILITY

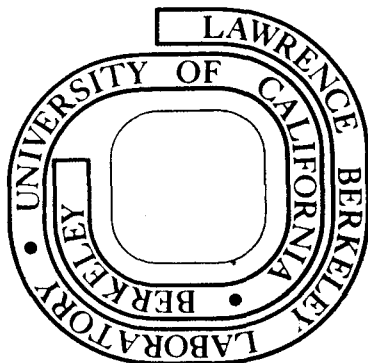
John Harte and Harold Morowitz

December 1975

Prepared for the U.S. Energy Research and
Development Administration under Contract W-7405-ENG-48

For Reference

Not to be taken from this room



LBL-4441
c.1

DISCLAIMER

This document was prepared as an account of work sponsored by the United States Government. While this document is believed to contain correct information, neither the United States Government nor any agency thereof, nor the Regents of the University of California, nor any of their employees, makes any warranty, express or implied, or assumes any legal 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. Reference herein to any specific commercial product, process, or service by its trade name, trademark, manufacturer, or otherwise, does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof, or the Regents of the University of California. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof or the Regents of the University of California.

NUTRIENT TRANSIT TIME DIVERSITY:
A NOVEL MEASURE OF ECOLOGICAL
ORGANIZATION AND STABILITY

John Harte*
Harold Morowitz**

December 1975

* Energy and Environment Division, Lawrence Berkeley Laboratory,
Berkeley, California, 94720

** Department of Molecular Biophysics and Biochemistry, Yale University
New Haven, Connecticut, 06520

ABSTRACT

A tracer experiment can be performed on ecosystems and shown to provide novel information about the distribution of transit times for a cycling nutrient in the system. A diversity index constructed from this distribution is mathematically associated with certain stability properties of ecosystems, and a natural ecological time-scale parameter is identified.

In this note, we point out the possibility of a tracer experiment which can be used to obtain a measure of the organization and structure of the pathways for nutrient flow in an ecosystem.¹ We will show that this measure is an index of the diversity of pathway transit times for a cycling nutrient and we will relate this index to certain stability properties of the ecosystem.

The cycling of a nutrient within an ecosystem can take place via a variety of alternate pathways. Cyclic flow patterns involving certain sequences of pathways are characterized by long transit times, while other cyclic flow patterns are characterized by short transit times. Moreover, some pathways produce a broad spread of transit times, while others are associated with a sharp, well-defined, transit time. We propose to measure the distribution of transit times for carbon (chosen because of the ubiquity of its pathways) to execute a cycle through the ecosystem. We will first describe briefly how such a measurement might be carried out and then explain how the result of this measurement can be interpreted as a stability indicator and how it provides a natural time scale for ecosystems.

As a concrete example of how such an experiment might be carried out in a laboratory microbiome, consider a closed terrarium under full illumination. A shot of $C^{14}O_2$ is introduced into the air in the terrarium and absorbed by plants in the system for a short time period. At the end of this period, the air in the tank is replaced by fresh air and the residual C^{14} in the removed air is measured. Call the time immediate subsequent to this initial replacement, $t=0$. The system at $t=0$ has a known amount of C^{14} , residing largely in the primary producers. This amount, X_0 , is equal to the quantity of C^{14} in the original shot minus the amount in the removed air. The soaking period should be taken to be as short as possible, but long enough to allow a useful amount of C^{14} to reach the primary producers.

Subsequent to time $t=0$, and at the end of regular time intervals, Δ , the air in the system is replaced by fresh air, and the residual C^{14} in the collected sample which accumulated during the previous interval is measured. The time period, Δ ,

should be chosen to be short enough to prevent significant re-uptake of gas phase C^{14} by primary producers,² yet not so short as to consistently yield undetectable amounts of C^{14} in the collected sample. Experience will be needed in order to determine a suitable time interval, Δ , and a suitable initial uptake period. Denoting by $f(n\Delta)$ the amount of C^{14} returned to the air in the time interval $(n\Delta, n\Delta + \Delta)$, and

$$\text{defining} \quad g(n\Delta) = f(n\Delta) / \sum_{m=0}^{\infty} f(m\Delta), \quad (1)$$

$$\text{we have} \quad \sum_{n=0}^{\infty} g(n\Delta) = 1. \quad (2)$$

Thus, g can be interpreted as a probability; viz, $g(n\Delta)$ is the probability of a C^{14} atom completing its cycle through the system in the time interval $(n\Delta, n\Delta + \Delta)$ if it is initially in the system at the time $t=0$ and ultimately completes a cycle. Note that the denominator on the right hand side of Eq. 1 need not equal X_0 if the cycling of carbon is incomplete due to sources and sinks.

The diversity index which we propose is motivated by the familiar information or diversity index, $-\sum_i p_i \ln p_i$, and is given by

$$I = - \sum_{n=0}^{\infty} g(n\Delta) \ln[g(n\Delta)]. \quad (3)$$

In the limit $\Delta \rightarrow 0$, and defining $h = g/\Delta$, it can easily be shown that

$$I \xrightarrow{\Delta \rightarrow 0} - \int_0^{\infty} dt h(t) \ln h(t) - \ln \Delta \quad (4)$$

where $h(t)$ is the fractional rate at which C^{14} completes its cycle

($\int_0^{\infty} h(t) dt = 1$). From Eq. 4 it follows that even if practical considerations

prevent the use of the same value of Δ for measuring the value of I of two ecosystems, $I_1 + \ln \Delta_1$, can still be compared directly with $I_2 + \ln \Delta_2$ when I_1 and I_2 are measured with Δ_1 and Δ_2 respectively.

It is straightforward to show that I is biggest if $g(n\Delta)$ is most uniformly distributed over the greatest number of intervals. In Fig. 1, two hypothetical, smoothed, distributions for g are shown. The solid line distribution corresponds to an I which is larger than the I corresponding to the dashed line distribution. This can be shown in the same way that one shows that having a large number of small

and equal probabilities maximizes $-\sum_i p_i \ln p_i$ in statistical physics.

Under what ecological circumstances would g resemble one or the other curve in Fig. 1? Intuitively, the dashed line distribution would be likely to be observed for an ecosystem in which an initial shot of carbon flows through the system rapidly and with little spread - i.e., the alternate pathways are characterized by roughly equal and short transit times. The solid line distribution, on the other hand, would be observed for an ecosystem in which a variety of pathway transit times generate a dispersal of the initial shot of carbon over a long time span. However, even if the system has only a single pathway for cyclic nutrient flow, the shape of g and hence the value of I would be expected to be dependent upon the magnitude and distribution of residence times characterizing the storage compartments (e.g., plants, bacteria, detritus) traversed by nutrients along their cyclic flow route.

This common sense picture is basically correct, although it can be refined with model calculations. The models we studied³ consisted of nonlinear differential equations for the flow of carbon through systems consisting of herbivores, primary producers, bacterial decomposers, organic detritus, and an inorganic nutrient. Under the assumption that the C^{14}/C^{12} ratio is small, the equations were linearized and the function $h(t)$ was explicitly calculated. The relevant time constants whose magnitude and equitability determine the shape of h or g are the inverse eigenvalues of a matrix whose elements are linear combinations of the individual inverse residence times in the various compartments of the system. The calculations show that if the sum of these time constants is small, and if, when their sum is fixed, they are equitably distributed (i.e., all close in value to each other), then g will resemble the dashed curve and I will be small. The solid line distribution for g , and hence a large value for I , will be observed if the time constants (inverse eigenvalues) are large in magnitude and if, for fixed sum, they are inequitably distributed (widely different from one another).

In order to relate our index, I , to stability properties of an ecosystem we must first specify a definition of stability. Suppose that in the absence of a

disturbance to an ecosystem, the state of the system is characterized by the functions $\bar{x}_i(t)$. The $\bar{x}_i(t)$ describe the unperturbed carbon contents of the important compartments of the system. Let the functions $\Delta x_i(t)$ be a measure of the time-dependent magnitude of the effect on the i^{th} compartment, resulting from the perturbation. The Δx_i 's might refer to changes in compartment carbon, or they might refer to the levels of a toxic substance in the compartments. Assume the perturbation begins at time t_0 . Then we let

$$S = \left(\sum_i c_i \int_{t_0}^{\infty} dt \left(\frac{\Delta x_i(t)}{\bar{x}_i(t)} \right)^2 \right)^{-1} \quad (5)$$

be our (unabashedly arbitrary) measure of stability⁴. A large value of S corresponds to high stability. The c_i may all be chosen to equal unity if each compartment is deemed to be of equal weight, although a subjective judgment might favor choosing the c 's corresponding to some species to be larger than others. In order to compare the intrinsic stability of different systems, the integrals in Eq. 5 must be averaged over a set of initial perturbations of specified magnitude.

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 carbon contents of the compartments. Assuming, now, that the ratios $\Delta x_i/\bar{x}_i$ are small, then a linearized matrix equation

$$\frac{d}{dt} \Delta x_i(t) = A_{ij} \Delta x_j(t) \quad (6)$$

is obtained. If the \bar{x}_i are time independent and the original non-linear equations have no explicit time dependence, then the time evolution of the Δx_i 's can be easily computed to be

$$\Delta x_i(t) = \sum_{\alpha} a_{i\alpha} e^{\lambda_{\alpha} t} \quad (7)$$

where the $a_{i\alpha}$ depend upon the matrix elements of A and the initial conditions, $\Delta x_i(t_0)$. 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, λ_α , 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, $Re^{-1}(-\lambda_\alpha)$ are large if the residence times are all long.

The qualitative dependence of the integrals $\int dt (\Delta x_j(t))^2$ upon the time constants, $Re^{-1}(-\lambda_\alpha)$ of the system can be readily deduced. Dimension counting would suggest that when the time constants are small, the integrals are small. Therefore, small $Re^{-1}(-\lambda_\alpha)$ should be an indication of high stability. Equitability of the time constants tends to prevent a situation in which a subset of terms in Eq. 7 with, say, positive coefficients dominate 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 $Re^{-1}(-\lambda_\alpha)$ is fixed, the more equitably they are distributed, the less the Δx_i should grow and the larger S should be.

We have evaluated S numerically for a variety of models³ and perturbations and have found such a systematic dependence of S upon the eigenvalues. In general, an integral $\int dt (\Delta x_j(t))^2$ will be smallest, and thus S largest, if the $Re^{-1}(-\lambda_\alpha)$ are small in magnitude and close in value to each other, provided the perturbation is not made directly on x_j , (i.e. provided $\Delta x_j(t_0)=0$). If the perturbation is made initially on x_j , then $\int dt (\Delta x_j(t))^2$ will be smallest in the limit in which all the $Re^{-1}(-\lambda_\alpha)$ are small, but in this case, the equitability condition is not obtained. In a multi-component ecosystem, only a small number of x_i are likely to be directly altered by a perturbation; most of the nonzero Δx_i 's will be generated indirectly as a result of the couplings within the system. Therefore, we expect the magnitude and equitability conditions⁵ to be important in estimating S.

Thus, if Eq. 6 is a good approximation, stability is enhanced if the time constants given by the $Re^{-1}(-\lambda_\alpha)$ are small and equitably distributed. But

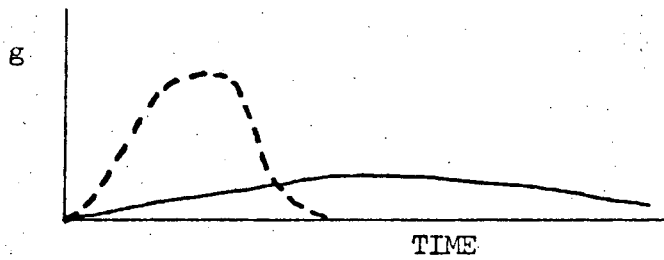
these time constants are related, and in some instances equal,⁶ to the time constants which determine the value of I. And the conditions that they be small and equitably distributed (resulting in large S) were precisely the conditions which we showed result in I being small. Our main result, then, is a qualitative one; namely: low pathway transit time diversity will tend to be associated with high stability.

For any ecosystem in which g is measured, a natural time constant, or mean transit time, $\tau = \sum_{n=0}^{\infty} g(n\Delta)(n+\frac{1}{2})\Delta$, can be constructed. It is then possible to define a new dimensionless stability index, $S' = \tau S$, scaled to the time constant, τ . An analogous scaled diversity index, $I' = I + \ln(\Delta/\tau)$, can also be defined. Consider, now, two ecosystems - one with rapid rate constants and the other with slow rate constants. Their respective values of I' and S' will still be correlated as above ; this correlation, however, now reflects differences between the distributions about the mean (i.e. equitabilities)⁷ of the two systems' rate constants, but does not reflect the difference between the natural overall time scales of the two systems. Use of these time-scaled indices may be more suitable for certain applications as they refer all ecosystems to the same time scale and thus reflect intrinsic structural differences.

We conclude that a measurement of g, and hence I (or I'), would provide interesting and useful ecological insight.⁸ Although I is only a single number for a given ecosystem at a given time period, and cannot describe all stability properties of an ecosystem, it does appear to encapsulate a great deal of information which could otherwise only be obtained, with far greater difficulty, from a very large number of measurements of individual pathways and population levels. Of course, it will not be an easy task to measure g. Measuring g in the field will be even more difficult than in the laboratory. We have begun to develop an aquatic microbiome facility at Lawrence Berkeley Laboratory in which measurements of g and an evaluation of the stability interpretation of I might be carried out.

Footnotes

1. A useful summary of applications of compartment theory and tracer methods to the study of pathway organization is: E. Eriksson, *Ann. Rev. Ecology and Systematics*, 2, 67(1971)
2. This condition can be stated: the ratio of Δ to the bio-uptake residence time of carbon dioxide in the system is small. A rough estimate is that for a typical terrarium or aquarium, Δ should be on the order of an hour to a day.
3. These models are described, and their stability properties computed, in Dudzik, M., J. Harte, D. Levy and J. Sandusky, "Stability Indicators for Nutrient Cycles in Ecosystems", LBL-3264, 1975.
4. A summary of a variety of other concepts of stability can be found in the paper by D. Botkin and M. Sobel, in "Ecosystem Analysis and Prediction: Proceedings of a Conference on Ecosystems", Alta, Utah, July, 1974.
5. The relative importance of these two conditions is difficult to generalize about. If the sum of the eigenvalues is decreased but their equitability is increased, the overall effect on S and I is model dependent. If some of the eigenvalues are very much larger than the others, then S and I become relatively insensitive to changes in the magnitude or equitability of the larger ones.
6. If the Δx_i refer to the levels of a trace substance whose flow rates among the compartments are proportional to those of the tracer used to evaluate g, then the time constants determining S and I will be identical. If the Δx_i refer to changes in biomass or total carbon contents of the compartments, then the matrix, A, in Eq.6 is the so-called community matrix of the system and the time constants determining S and I can differ. In particular, the eigenvalues of the community matrix reflect the existence of nonlinear damping effects such as Michaelis-Menten uptake kinetics or Verhulst crowding, whereas the eigenvalues determining the shape of h or g do not.
7. A sensible measure of the equitability of pathway transit times, which is invariant under time-scaling, is the ratio of the square of τ to the variance of the function h or g. Note that the mean and the variance of h or g are not necessarily identical to the mean and variance of the inverses of the eigenvalues which determine the shape of these functions.
8. A number of speculative questions arise: Does I (or I') systematically change when ecosystems are altered by succession or human intervention? Can a determination of I for the global carbon cycle be made by carrying out our proposed experiment using $C^{14}O_2$ from past nuclear weapons tests as the initial source? Is the notion of I of interest in the study of other complex systems such as economies?
9. One of us (J.H.) is grateful to Michael Dudzik, Alan Jassby, and Donald Levy for helpful comments and to the United States Energy Research and Development Administration for their support of this research.



Two hypothetical, smoothed, distributions for the probability function, g .

Fig. 1

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.

TECHNICAL INFORMATION DIVISION
LAWRENCE BERKELEY LABORATORY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720