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NUTRIENT RECYCLING AND THE STABILITY OF ECOSYSTEMS

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ABSTRACT

A theoretical perspective on ecosystems is elaborated which relates alternative strategies of stability to observable and measurable attributes of ecosystems. Arguments are presented for viewing nutrient cycling as positive feedback. Any resultant tendency for unlimited growth is resisted by (1) finiteness of resources, (2) kinetic limitations on resource mobilization, and (3) processes of nutrient regeneration. Ecosystem structure, a static inertia defined by the mass of biotic and abiotic components, is opposed by dynamic dissipative forces related to metabolism and erosion. Balance between these two factors (structural mass and dissipative force) guarantees the asymptotic stability of ecosystems. Attention is thus focused on two aspects of relative stability: resistance and resilience. Resistance, the ability of an ecosystem to resist displacement, results from the accumulated structure of the ecosystem. Resilience, the ability of an ecosystem to return to a reference state once displaced, reflects dissipative forces inherent in the ecosystem. A linear ecosystem model that embodies these concepts is discussed, and four relative stability indexes are derived. Random matrices, subject to mass-conservation limitations, and hypothetical ecosystem models, constructed according to a characterization of alternative properties of nutrient cycles, are analyzed to examine relationships between the relative stability indexes and specific properties of nutrient cycles.

Resistance is shown to be related to large storage, long turnover times, and large amounts of recycling. Resilience reflects rapid turnover and recycling rates. Thus resistance and resilience are inverse concepts. Factors that determine what balance between resistance and resilience an ecosystem exhibits are considered, including the degree and frequency of environmental fluctuation and the limitations placed on resource mobilization. The contribution of turnover rates of ecosystem components to the balance between resistance and resilience is also examined, involving consideration of (1) the population concepts of r and K selection, (2) the contribution of early successional species to ecosystem stability, and (3) the relation of herbivory to nutrient regeneration. The theory put forth in this paper is seen as a rigorous, operational approach to ecosystems which is testable by both observation and experimental analysis.

A dialectical point of departure for studying ecosystems is provided by the antithetical processes of biological growth and decay. At the cellular level, balance between the opposing forces of anabolism and catabolism determines both structure and reaction kinetics. Anabolic and catabolic phenomena similarly operate at the ecosystem level but are less well understood. On the one hand are the mobilization of energy and nutrient resources into organic configurations and the accretion of biomass; on the other are dissipative forces tending to erode whatever biotic structures have been realized, returning the system toward physicochemical equilibrium while regenerating assimilated nutrients.

Morowitz (1966) postulated that energy dissipation is sufficient to cause associated material cycles. Such a postulate is fundamental since in the materially closed biosphere, maintenance of life requires nutrient regeneration. For most natural ecosystems, recycling rates limit primary production and so regulate, at the source, biotic energy flows. A positive-feedback loop is thus inherent in the structure of every ecosystem: energy flow produces nutrient cycles, which lead to greater energy flow. Any tendency for unlimited growth is resisted by (1) finiteness of the resource base, (2) kinetic requirements of resource mobilization, and (3) restorative processes of nutrient regeneration.

Thus biotic growth tendencies are bounded by resource availability as well as by limitations on resource assimilation. The dialectical viewpoint outlined above must account for these facts. The biotic structure of ecosystems results from the tendency of living organisms to acquire resources, as limited by the requirements of resource mobilization. Acting to erode structure are dissipative forces that tend to degrade both organic and inorganic configurations. Degradation of biotic structure is related to metabolic processes of living organisms. Decay of abiotic structure relates both to the biotic decomposition of minerals and to the purely abiotic processes of weathering and erosion. Hence, on the one hand is the structure of the ecosystem, a static inertia defined by the mass of biotic and abiotic components. On the other hand is the dissipative force tending to erode this structure, a dynamic force defined by metabolism and erosion. At the ecosystem level these two factors (structural mass and dissipative force) are not necessarily antithetical. Both contribute, in different ways, to the stability of ecosystems.

A recurrent theme in ecological literature is that ecosystem stability is related to nutrient-cycling characteristics. E. P. Odum (1969) suggested that the closing of nutrient cycles through ecosystem development contributes to increased stability. Pomeroy (1970) related the stability of several ecosystem types to elemental standing crops and turnover times, biomass, and productivity. Jordan, Kline, and Sasscer (1972) examined ecosystem stability in relation to models of forest nutrient cycles. Hutchinson (1948a, 1948b), H. T. Odum (1971), Child and Shugart (1972), and Waide et al. (1974) also suggested causal links between nutrient cycling and ecosystem stability. These arguments were largely intuitive or heuristic, however, and did not seek the basis for causal relationships in specific properties of ecosystem nutrient cycles. In this paper we investigate relations between observable characteristics of nutrient cycles and system-level concepts of stability.

STABILITY CONCEPTS AND DEFINITIONS

Absolute Stability

Liapunov (1892) provided the basis of stability theory. Let $x(t)$ be a vector of n time-dependent state variables, with $\| x(t) \|$ a norm such as

$$\| x(t) \| = \sum_{i=1}^{n} |x_i(t)| \qquad (i = 1, 2, \ldots, n)$$

An equilibrium state $x^0(\dot{x} = 0$ when $x = x^0)$ is said to be stable in the sense of Liapunov if for every initial time t_0 and every $\epsilon > 0$ there exists $\delta > 0$ such that, if $\| x(t_0) - x^0 \| < \delta$, then $\| x(t) - x^0 \| < \epsilon$ for all $t > t_0$. In other words, a system is stable if, following displacement from equilibrium, its subsequent behavior is restricted to a bounded region of state space. A stronger stability concept involves return to equilibrium following initial displacement. An equilibrium state x^0 is said to be asymptotically stable (1) if it is stable in the sense of Liapunov and (2) if for any t_0 there exists $\alpha > 0$ such that, if $\| x(t_0) - x^0 \| < \alpha$, then $x(t) \rightarrow x^0$ as $t \rightarrow \infty$.

Holling (1973) suggested that such classical stability concepts are little more than theoretical curiosities in ecology. We suggest instead that natural ecosystems are asymptotically stable (Child and Shugart, 1972; Waide et al., 1974; Patten, 1974; Waide and Webster, 1975). A dynamic balance between the maintenance and dissipation of structure produces nonzero ecosystem states that are stable. Around this nominal (unperturbed, reference) trajectory exist basins or domains of attraction (Lewontin, 1970a; Holling, 1973) within which ecosystem displacements from nominal behavior are followed by return to the original condition. The relevant question for ecologists' attention is not "Are ecosystems stable?" but rather, "How stable?" Ecologists' concern should thus be focused on relative rather than absolute stability and on the mechanisms by which differing levels of relative stability are achieved.

Relative Stability

Attempts to measure the relative stability of ecosystems have met with limited success (e.g., MacArthur, 1955; Patten and Witkamp, 1967) because relative stability is not well defined mathematically or ecologically. Relative stability concerns the nature of an ecosystem's response to small displacement from a nominal trajectory. Two aspects of this response may be identified (Patten and Witkamp, 1967; Child and Shugart, 1972; Holling, 1973; Marks, 1974). The first aspect concerns the resistance of an ecosystem to displacement. An ecosystem that is easily displaced has low resistance, whereas one that is difficult to displace is highly resistant and is, in this sense, very stable. The second aspect of relative stability concerns return to the reference state, or resilience.* An ecosystem that returns to its original condition rapidly and directly following displacement is more resilient, more stable in this sense, than one that responds slowly or with oscillation.

Thus, given that an ecosystem is asymptotically stable, two aspects of its relative stability are (1) immovability, or resistance, which determines extent of displacement, and (2) recoverability, or resilience, which reflects rate of recovery to the original condition. This view of ecosystems identifies two alternatives for persistence. Resistance to displacement results from the formation and maintenance of large biotic and abiotic structures. Resilience following displacement reflects inherent tendencies for the dissipation of such structure, but, because it is related to ecosystem metabolism, it also reflects rates with which structure is reformed following its destruction. In the closed biogeochemical cycles of the biosphere, the observable structural and functional attributes of ecosystems are determined by the realized balance between factors favoring resistance and resilience. Nutrient cycling, a fundamental process inherent in ecosystems, thereby becomes a central issue in the consideration of mechanisms of macroscopic relative stability.

NUTRIENT CYCLING AND FEEDBACK

The use of flow diagrams to represent conservative energy and material flows in ecosystems has partly confused the concepts of input, output, and feedback. Input is any exogenous signal† that impinges on a system. Output is any endogenous attribute of a system transmitted as signal flow to an observer. Output generation is exclusively the province of the system, while output selection is the prerogative of the observer. Often output is equated with the state of the system, where state provides the necessary and sufficient information for a determinate mapping from input to output (Zadeh and Desoer, 1963).

Feedback exists in a system if any of its inputs are determined by its state. If the measure of state is directly related to such inputs, the feedback is positive; if the two are inversely related, the feedback is negative.

*Holling (1973) used *resilience* to denote what we term *resistance*, and *stability* for our *resilience*. Our use of resistance and resilience is consistent with common and accepted English usage (*Webster's New World Dictionary of the American Language*, Second College Edition, 1972, The World Publishing Company, New York).

†"Signal" denotes an observable and measurable flow of conserved (energy or matter) or unconserved (information) quantities.

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A flow diagram of an ecosystem or ecosystem component (Fig. 1) shows inflow of material or energy which is processed by the system, resulting in outflow. Inflows and outflows are conserved. In a control diagram of this system (Fig. 1), output has been equated to state. Inflow and outflow both constitute possible inputs to the system and may be subject to feedback control. Inflow and outflow are still conserved, but no such conservation restriction applies to input and output.

It can be argued that, if feedback control of outflow exists in ecosystems, it must be negative and therefore stabilizing. That is, ecosystem component losses are regulated by density-dependent mechanisms. These losses of conserved

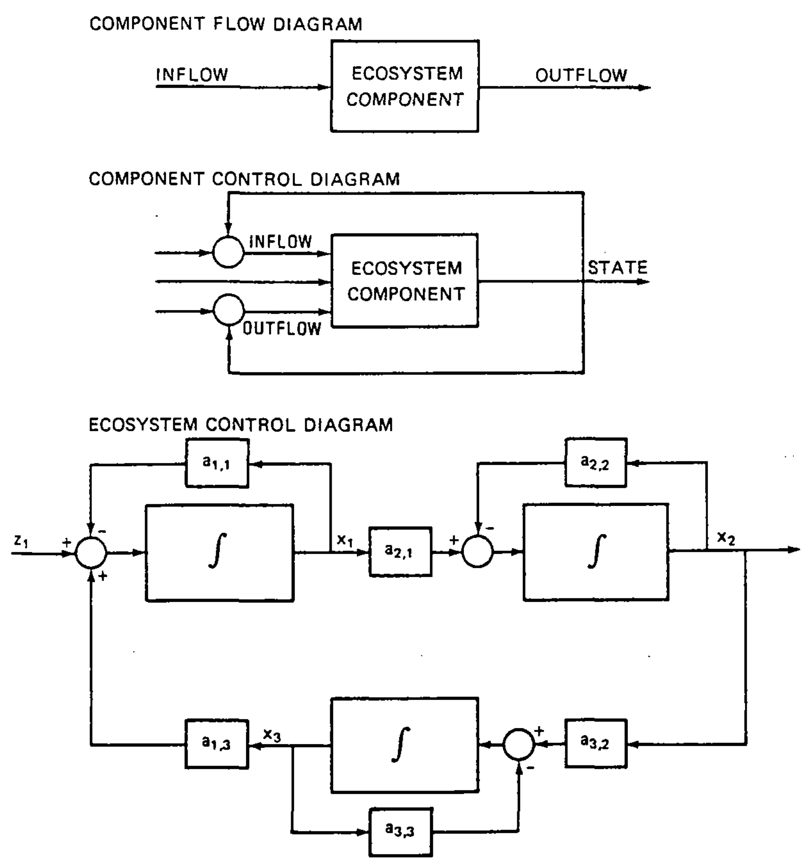

Fig. 1 Generalized flow diagram and control diagram of an ecosystem component and a control diagram of a three-component ecosystem model. Circles indicate summing junctions. Rectangles are storage (integrative) elements. z_i is an input; x_i is the state of the *ith* component; and $a_{i,j}$ is the rate coefficient for transfer from x_j to x_i.

quantities must be offset by inflows to maintain nonzero states. At the organism and population levels, positive-feedback mechanisms operate to promote inflow and are therefore potentially destabilizing (Milsum, 1968). Mobilization of resources is the essence of life processes (Smith, 1972); however, many density-dependent mechanisms exist which regulate inflow in a negative-feedback sense (Whittaker and Woodwell, 1972). Further, a macroscopic perspective leads to the conclusion that ecosystems and their components are ultimately resource limited (Hairston, Smith, and Slobodkin, 1960; Wiegert and Owen, 1971; Patten et al., 1974; Waide and Webster, 1975; Webster and Waide, 1975). Under unperturbed conditions ecosystems are maximally expanded within the resource hyperspace to the point of kinetic limitation of material transfers as set by the physicochemical environment (Blackburn, 1973). Thus inflow is limited by matter-recycling kinetics that ensure boundedness. Bounded inflow and negative-feedback control of outflow coupled with the first law of thermodynamics (mass conservation) form the basis of our argument for nonzero ecosystem states that are stable.

These ideas lead to a representation of ecosystems (Fig. 1) as sets of interacting components, each regulated by a negative-feedback loop related to its dissipative (i.e., turnover) character. Material recycling is displayed as feedback involving multiple system components. Because material flow is involved, recycling must be interpreted as positive feedback (H. T. Odum, 1971). This point emphasizes a fundamental difference between feedback in a control diagram and material recycling in a flow diagram. In the control diagram control is mediated by nonconservative information flows, whereas in the flow diagram control among components is exerted only through material or energy flows that must be conserved. Feedback mechanisms are not explicit in flow diagrams but must, nevertheless, be incorporated into any mathematical model of the system.

Thus a systems theoretic interpretation of nutrient cycling as feedback leads to the general conclusions already elaborated: (1) biotic tendency for unlimited growth is bounded by the first law of thermodynamics (mass conservation), as mediated through material-recycling kinetics and (2) negative-feedback decay to abiotic physicochemical equilibrium, if material and energy inflows are removed, is assured by the dissipative character of ecosystems and the second law of thermodynamics. The first conclusion guarantees Liapunov stability. The two conclusions together are sufficient to establish the stability of nonzero ecosystem trajectories (Patten, 1974).

MEASURES OF RELATIVE STABILITY

The General Linear Ecosystem Model

The dynamics of conserved quantities in an ecosystem with n components can be described mathematically as

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$$\dot{x}_i = \text{inflow} - \text{outflow} \qquad (i = 1, 2, \ldots, n) \tag{1}$$

Inflow can emanate from outside the ecosystem (z_i) or from other system components ($F_{i,j}$, $j = 1, 2, \ldots, n; j \neq i$). Outflow may pass to other components ($F_{j,i}$) or out of the system ($F_{0,i}$). Hence Eq. 1 may be reformulated in compartmental form as

$$\dot{x}_i = (z_i + \sum_{\substack{j=1 \\ j\neq i}}^{n} F_{i,j}) - (F_{0,i} + \sum_{\substack{j=1 \\ j\neq i}}^{n} F_{j,i}) \qquad (i = 1, 2, \ldots, n) \tag{2}$$

Material transfers within the ecosystem represent inflows to some components and outflows from others. On the basis of the arguments given above and elsewhere (Patten et al., 1974; Webster and Waide, 1975), these internal flows, as well as outflows from the system, can be modeled as donor-based according to the equation

$$F_{i,j} = a_{i,j} x_j \tag{3}$$

If we define component turnover rates as

$$a_{i,i} = - \sum_{\substack{j=1 \\ j\neq i}}^{n} a_{j,i} - a_{0,i} \qquad (i = 1, 2, \ldots, n) \tag{4}$$

Eq. 2 becomes

$$\dot{x}_i = z_i + \sum_{j=1}^{n} a_{i,j} x_j \qquad (i = 1, 2, \ldots, n) \tag{5}$$

Because all x_i and $F_{i,j}$ represent material or energy, they must be nonnegative, which ensures that

$$a_{i,j} \geqslant 0 \qquad (i \neq j) \tag{6}$$

Equation 5 can be expressed in matrix form as

$$\dot{x} = Ax + z \tag{7}$$

where x is the state vector, z is the input vector, and A is a matrix of (possibly time dependent) rate coefficients defined by Eq. 3. The mathematical constraints defined in Eqs. 4 to 6 are sufficient to guarantee the asymptotic stability of this model (Hearon, 1953, 1963). In addition, the model is sufficient for simulating nominal and small displacement dynamics of ecosystems (e.g., Olson, 1963; Patten, 1972; Patten et al., 1974). Implicit within the model structure defined by Eqs. 1 to 7 are both accumulative and dissipative tendencies; thus this model is useful for examining macroscopic questions of ecosystem relative stability.

nth-Order Measures

The system defined by Eq. 7 is an *nth*-order system, being composed of n first-order equations. Relative stability indexes can be derived for this system. Specifically, the characteristic roots or eigenvalues of the system defined by Eq. 7, denoted λ_k $(k = 1, 2, \ldots, n)$, can be found by solving the matrix equation

$$\det(\lambda I - A) = 0 \tag{8}$$

where det denotes the determinant of the indicated matrix, and I is the n X n identity matrix. The solution to Eq. 7 can be expressed in terms of these characteristic roots, where each eigenvalue defines a particular mode of system behavior, as

$$x = \sum_{k=1}^{n} c_k b_k e^{\lambda_k t} + p \tag{9}$$

where c_k is a constant, b_k is the eigenvector associated with the eigenvalue λ_k, and p is a particular solution to Eq. 7 determined by z.

Clearly, if any $\lambda_k > 0$, the system will grow exponentially. According to a theorem attributed to Liapunov and Poincaré (Bellman, 1968), a system is asymptotically stable if all the characteristic roots have negative real parts.

Two relative stability measures may be derived from these n eigenvalues. The first is the critical root, defined as the characteristic root with the smallest absolute value (Funderlic and Heath, 1971). Given that the system is asymptotically stable, the critical root is the one most likely to become positive. Hence this index indicates the system's margin of stability. This critical root is the smallest turnover rate (the longest time constant) in the system. Thus the system does not recover fully from displacement until this slowest component of the transient response decays away. Second, the trace of the matrix A (the sum of the diagonal elements) relates to the response time following perturbation (Makridakis and Weintraub, 1971b). Since the sum of the main diagonal elements of A equals the sum of the eigenvalues, we have used the mean root, defined as the mean value of the n eigenvalues, as an equivalent measure of response time. The mean root reflects the time required for most of the system, or for some hypothetical mean component of the system, to recover following displacement.

Second-Order Measures

Extensive experience in control-systems engineering has demonstrated the utility of approximating higher order linear systems as second order for analytical purposes (DiStefano, Stubberud, and Williams, 1967; Shinners, 1972). Child and Shugart (1972) provided a rationale for implementing such an approach in studying ecosystem behavior and applied it to an analysis of magnesium cycling in a tropical forest. Waide et al. (1974) used this approach in analyzing a model of calcium dynamics in a temperate forest. Hubbell (1973a, b) demonstrated the benefits of a frequency-domain analysis of second-order population models.

In this approach the behavior of an *nth*-order system of the form of Eq. 7 is approximated as second order with the equation

$$\ddot{y} + 2\zeta\omega_n\dot{y} + \omega_n^2 y = \omega_n^2 z \tag{10}$$

where ζ is the damping ratio and ω_n is the undamped natural frequency (DiStefano et al., 1967). The characteristic roots of this equation are given by

$$\lambda_1, \lambda_2 = -\zeta\omega_n \pm \omega_n (\zeta^2 - 1)^{1/2} \tag{11}$$

The roots of this second-order approximation represent the apparent roots of the original *nth*-order system. That is, these two eigenvalues, as well as the natural frequency, represent weighted mean roots of the higher order system. They capture most of the information contained in the *nth*-order trajectories. The weighting function that determines these second-order parameters from the n original eigenvalues is related to the magnitude of the eigenvector components of the *nth*-order system (Eq. 9).

From Eq. 11, if $\zeta = 1$, the system is said to be critically damped, the system responds rapidly and without oscillation following displacement, and $\lambda_1, \lambda_2 = -\omega_n$. If $\zeta > 1$, the system is overdamped, the response of the system is slower than that of a critically damped system, though still nonoscillatory, and the eigenvalues are real and unequal. If $\zeta < 1$, the system in underdamped, and the roots are complex and are given by

$$\lambda_1, \lambda_2 = -\zeta\omega_n \pm j\omega_n (1 - \zeta^2)^{1/2} \tag{12}$$

where $j = (-1)^{1/2}$. The response of such a system to displacement, though initially more rapid than a critically damped system, is oscillatory. If $\zeta = 0$, the roots are imaginary, and ω_n is the radian frequency of oscillation. If $\zeta < 0$, the eigenvalues have positive real parts, and the system is unstable.

Given that the system under study is asymptotically stable (i.e., $\zeta > 0$), the two parameters ω_n and ζ may be used as measures of relative stability. The natural frequency ω_n measures (inversely) the resistance of the system to displacement. A system with a large natural frequency is especially susceptible to disturbance, whereas a system with a small natural frequency strongly resists displacement. Similarly the magnitude of the damping ratio ζ indicates the rate of system response following displacement, the resilience of the system. If the system is overdamped, the return to steady state is monotonic but slow. If underdamped, the system responds in an oscillatory fashion. A critically damped system exhibits the most rapid response possible without oscillation and thus has maximum resilience.

In this paper we investigate relationships between specific properties of ecosystem nutrient cycles and discuss the four above-mentioned relative stability indexes: critical root, mean root, natural frequency, and damping ratio. We take two approaches. The first is a stochastic approach, using Monte Carlo techniques. In the second approach we construct hypothetical ecosystem models based on a characterization of alternative properties of nutrient cycles and investigate the relative stability of these models. We also provide further ecological understanding of the four relative stability indexes and extend the basis for their implementation. Attention is restricted to time-invariant systems for heuristic purposes.

STOCHASTIC APPROACH

Construction and analysis of random matrices was used successfully to further understanding of general system properties and to investigate effects of specific system characteristics (e.g., connectivity) on such system-level properties as stability (Ashby, 1952; Gardner and Ashby, 1970; Makridakis and Weintraub, 1971a, b; May, 1972, 1973; Makridakis and Faucheux, 1973; Waide and Webster, 1975; Webster and Waide, 1975). We initially followed such an approach to establish general relationships among relative stability indexes and system properties, focusing especially on the amount of recycling.

Methods

In constructing random matrices, off-diagonal elements $a_{i,j}$, $i \neq j$, of the A matrix (Eq. 7) were chosen from a specified statistical distribution (e.g., uniform on [0,1]). Rates of nutrient loss to the environment ($a_{0,i}$) were chosen from the same distribution and main diagonal elements calculated according to Eq. 4. For some analyses, off-diagonal elements were defined as nonzero according to a specified probability of connectivity. Only a single input z_1 was used for all analyses.

Following matrix construction, eigenvalues were calculated (Westley and Watts, 1970), and the critical root and mean root were determined. We also calculated an index of recycling (I) as the summed flows represented by the upper triangle divided by the input. That is, the ratio of nutrients recycled to nutrient input from the environment is

$$I = \frac{\left(\sum_{i=1}^{n-1} \sum_{j=i+1}^{n} F_{i,j} \right)}{z_1} \tag{13}$$

The synthetic division algorithm of Ba Hli (1971) was used to estimate the values of the natural frequency and damping ratio. A unit step input was applied se possible without oscillation and thus has

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$$\frac{\sum_{=1}^{i-1} \sum_{j=i+1}^{n} F_{i,j} \Big)}{z_1} \qquad (13)$$

n of Ba Hli (1971) was used to estimate the damping ratio. A unit step input was applied

to each randomly constructed matrix to generate the required discrete input–output time series. Synthetic division yielded the coefficients of a general second-order transfer function, which were equated with coefficients of the specific transfer function of Eq. 10, allowing estimation of the natural frequency and damping ratio (Hill, 1973).

The above process was repeated 50 or 100 times for each type of matrix constructed. The resulting sets of values were subjected to linear regression analysis to determine the presence of significant relationships among calculated variables. To ensure that results were not biased by methods of matrix construction, we analyzed a variety of matrices of three sizes ($n = 4, 6, 10$). In various experiments, matrix elements were sampled from uniform distributions of different ranges and from normal distributions with various means and variances. We tried a wide range of upper and lower triangle connectivity, and selected several different outputs for use in the synthetic division. In some cases modifications were made to obtain a pyramid-type structure of compartmental standing crops. We also examined results of increased input and recycling.

Results

The following trends were generally observed across the range of matrices analyzed. Increases in the amount of recycling relative to input led to increases in the critical root (moved closer to zero), decreases in the mean root (moved farther from zero), and decreases in the natural frequency. Also, larger critical and mean roots were both associated with smaller natural frequencies.

Trends in the damping ratio initially appeared to be variable. In some cases ζ tended to decrease with increasing recycling, critical root, and mean root. In other cases ζ showed the opposite behavior. Closer inspection revealed that, in the first case, all systems were underdamped, whereas in the second case they were overdamped. Thus, when the quantity $|1 - \zeta|$ was considered, the results were unambiguous: $|1 - \zeta|$ increased with increasing values of recycling, critical root, and mean root.

DETERMINISTIC APPROACH

Our second approach to investigating relationships between material recycling and ecosystem stability involved construction and analysis of hypothetical ecosystem models. Two basic assumptions are inherent in these analyses: (1) ecosystems are units of selection and evolve from systems of lower selective value to ones of higher selective value (we are not invoking any superorganism concept; this evolution is accomplished through species coevolution) (Slobodkin, 1964; Darnell, 1970; Lewontin, 1970; Dunbar, 1972; Whittaker and Woodwell, 1972; Blackburn, 1973); (2) those ecosystems with highest selective value are ones which optimize utilization of essential resources. Exceptions to the selection for ecosystems geared to efficient resource utilization would exist where resources were extremely abundant or where the system as a whole was operating under other environmental stress (Odum, 1967; Waide et al., 1974). An example might be a stream which receives large allochthonous inputs of detritus and which is strongly influenced by current action. In other ecosystems selective value involves efficient conservation and recycling of essential nutrients.

We suggest that three factors are involved in nutrient utilization in ecosystems: (1) the presence or absence of large abiotic nutrient reserves, (2) the degree of localization of nutrients within the biota, and (3) the turnover rate of the actively recycling pool of nutrients. Figure 2 schematically depicts these factors. In this figure a specific ecosystem type is associated with a given combination of factors. This conceptual scheme is clearly idealized since there exists a great range of each of these distinct types of ecosystems. However, this scheme is consistent with current ecological theory and represents a convenient method of examining relationships between nutrient cycling and stability.

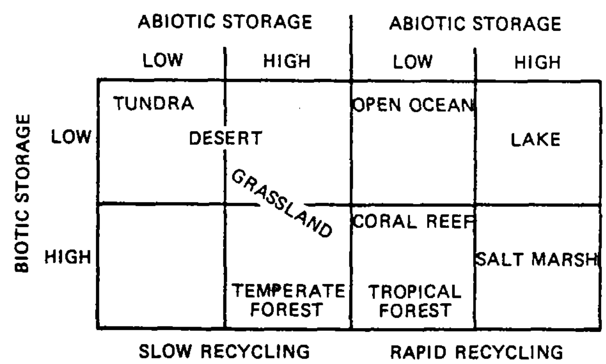
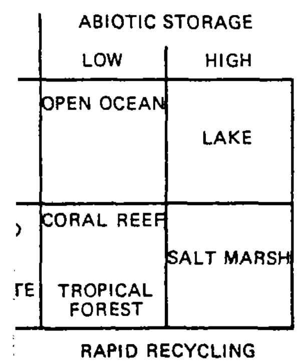


Fig. 2 Alternative properties of nutrient cycles. Shown in each box is an idealized ecosystem type that seems to exhibit the indicated combination of properties.

Methods

To facilitate quantitative comparisons among these various idealized ecosystems, we constructed a general model of nutrient cycling (Fig. 3). In this diagram the food base (x_1) may be either primary producers or detritus. Consumers (x_2) are organisms that feed directly on the food source. The $F_{3,1}$ is either death or mechanical breakdown of the food base to detritus (x_3). In an ecosystem with internal primary production, detritus is essentially dead primary producers (litter). In detritus-based systems this component is fine particulate ɜnt resource utilization would exist or where the system as a whole was ;s (Odum, 1967; Waide et al., 1974). :ceives large allochthonous inputs of ›y current action. In other ecosystems ›n and recycling of essential nutrients. involved in nutrient utilization in large abiotic nutrient reserves, (2) the the biota, and (3) the turnover rate of Figure 2 schematically depicts these tem type is associated with a given ;cheme is clearly idealized since there ıct types of ecosystems. However, this :al theory and represents a convenient n nutrient cycling and stability.



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organic matter. Decomposers (x_4) are those organisms which feed directly or indirectly on detritus. Available nutrients (x_5) are directly available for use in primary production. Nutrients in reserve (x_6) are not available but are tied up in sediments, primary minerals, clay complexes, or other refractory materials (e.g., humics). However, they may become available through transfer to x_5. Inflows and outflows occur primarily through the available nutrient pool.

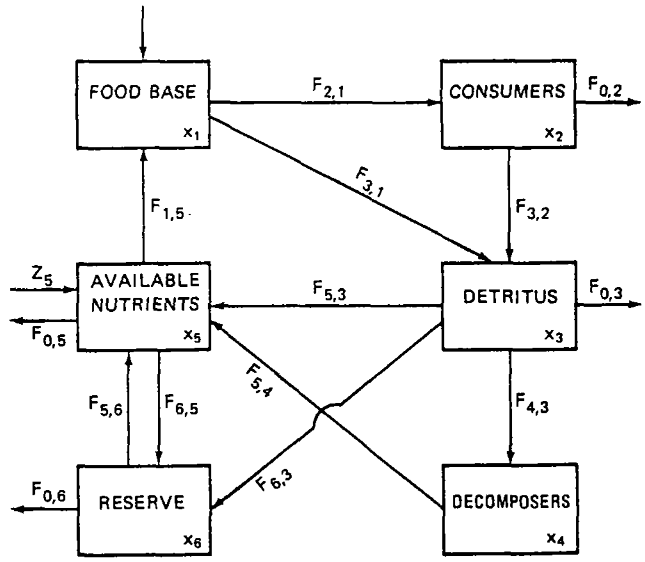

Fig. 3 **General nutrient-flow model of an ecosystem. x_i is the size of the *ith* compartment; z_i is inflow to compartment x_i; $F_{i,j}$ is the flow from x_j to x_i; and $F_{o,j}$ is the outflow to the environment from x_j.**

We have quantified this general model for seven of the ecosystem types shown in Fig. 2 (Table 1). We also applied this model to an idealized stream, which typifies an ecosystem without large abiotic reserves, with low biotic localization of nutrients, with little or no recycling, and with large nutrient throughflows. Standing-crop values were normalized to an available nutrient pool of 100 units. All transfers were per year. The values given in Table 1 are relative estimates that reflect differences among the idealized ecosystems, rather than exact, absolute estimates of nutrient transfers and standing crops. A variety of sources was consulted for each ecosystem type (Table 1). However, gaps and inconsistencies existed which were filled from general references or qualitative considerations. Each system was assumed to be at steady state.

From these numbers we derived several indexes which reflect structural characteristics of the eight ecosystems and which quantify the concepts of abiotic storage, biotic storage, and recycling (Table 2). Both the turnover time of the reserve ($T_6 = 1/|a_{6,6}|$) and the proportion of nutrients localized in the two abiotic pools $[(x_5 + x_6)/\Sigma x]$ are indexes of abiotic storage. Reserve turnover varies from slow in forests to fast in oceans and streams. The proportion of total nutrients in abiotic compartments is highest in temperate forests and lakes and lowest in tundra.

Biotic storage, given by the turnover time of biotic compartments $[(x_1 + x_2 + x_3 + x_4)/F_{1,5}]$, is higher in terrestrial ecosystems and lower in aquatic ecosystems.

We calculated two indexes of recycling. The turnover rate of the detritus pool ($F_{1,5}/x_3$) is higher in aquatic systems and generally lower in terrestrial ecosystems, except for tropical forests where there is a rapid turnover of detritus. The ratio of recycling to input ($F_{1,5}/\Sigma z$), as used in stochastic analyses, is approximately the inverse of the other recycling index. However, since systems with larger biotic pools typically recycle more nutrients than do systems with smaller biotic standing crops, this index partially confounds storage and recycling. This index ranges from 500 for grasslands to 0 for streams.

Two other useful indexes are the ratios of total standing crop to recycling material ($\Sigma x/F_{1,5}$) and total standing crop to total inflow ($\Sigma x/\Sigma z$). Both indexes estimate system turnover time. Longest turnover times occur in temperate forests and grasslands, whereas there is rapid turnover in stream and ocean ecosystems.

The specific values given in Table 1 have obvious deficiencies. Each idealized ecosystem represents a wide spectrum of actual ecosystems differing in many important characteristics. Similarly the kinetics of specific nutrients within a given ecosystem differ, quantitatively and qualitatively. In quantifying the general model shown in Fig. 3, we have attempted to suppress such specific details and to focus instead on the alternative properties of nutrient cycles depicted in Fig. 2. Our emphasis is thus on macroscopic properties of ecosystems rather than on specific differences between systems or nutrients. Comparison of the structural indexes (Table 2) with Fig. 2 reveals that the chosen values agree well with the idealized conceptualization.

Results

The eight models were analyzed in the same fashion as described previously, providing values for critical root, mean root, natural frequency, and damping ratio (Table 3). Both critical root and natural frequency were smallest (in absolute value) for the temperate forest and grassland models and largest for the stream model and tended to be smaller (in absolute value) for the four terrestrial ecosystem models. All values of damping were greater than 1, indicating all eight ecosystem models to be overdamped. The smallest value was obtained for the

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ocean, the largest for the stream. No clear separation between terrestrial and aquatic ecosystems was obvious.

The relative stability indexes were then compared with the structural indexes given in Table 2, using least-squares regression. Correlation coefficients are shown in Table 4. Both critical and mean roots were directly related to the turnover time of the reserve nutrient pool T_6, whereas the natural frequency exhibited an inverse relationship. For longer turnover times, critical and mean roots were nearer zero, and the natural frequency was smaller.

Regressions against the proportion of nutrients in the two abiotic pools were not significant. However, when terrestrial and aquatic ecosystems were considered separately, a trend was evident. Increased abiotic storage or slower abiotic turnover produced critical and mean roots nearer zero and smaller natural frequencies.

All four stability indexes were related to recycling. A greater recycling rate ($F_{1,5}/x_3$) or a smaller ratio of recycling to input ($F_{1,5}/\Sigma z$) resulted in roots farther from zero, a larger natural frequency, and greater damping.

Both critical and mean roots, as well as natural frequency, were significantly related to system turnover ($\Sigma x/F_{1,5}$). All four indexes were correlated with turnover as related to system input ($\Sigma x/\Sigma z$). In general, the slower the system turnover rate (the greater the turnover time), the nearer the critical and mean roots were to zero, the smaller the natural trequency, and the smaller the damping ratio.

The results clearly indicate that increased storage and turnover times (abiotic, biotic, or total), as well as increased amounts of recycling, lead to critical and mean roots nearer zero and to smaller natural frequencies. Increased recycling and turnover rates (of biotic or abiotic elements, or their sum), on the other hand, lead to critical and mean roots that are farther from zero and to larger natural frequencies. Relationships involving the damping ratio are less clear. However, if we ignore the stream, which has no recycling ($F_{1,5} = 0$) and for which the second-order approximation may not be accurate owing to dominance by the extremely large nutrient inflow, other trends become apparent (Table 4). Although correlations are not as large as for the other stability indexes, damping generally tended to be directly related to storage or turnover times but inversely related to recycling or turnover rates. Thus damping and natural frequency typically showed opposite behavior relative to the structural indexes considered.

DISCUSSION

The preceding arguments were presented for the asymptotic stability of ecosystems. This stability is guaranteed by limitations on resource mobilization and by the dissipative character of ecosystems. Resistance, the ability of an

TABLE 1

SUMMARY OF RELATIVE VALUES USED IN QUANTIFYING THE GENERAL NUTRIENT CYCLING MODEL (FIG. 3) IN THE EIGHT IDEALIZED ECOSYSTEMS INVESTIGATED (FIG. 2)

Parameter*	Tundra[a]	Grassland[b]	Temperate forest[c]	Tropical forest[d]	Ocean[e]	Lake[f]	Salt marsh[g]	Stream[h]
x_1	200	500	100	500	10	10	1,000	500
x_2	15	50	0.5	2.5	10	1	25	50
x_3	200	1,000	25	5	10	25	1,000	10
x_4	20	100	1	1	0.5	25	100	20
x_5	100	100	100	100	100	100	100	100
x_6	100	1,000	5,000	1,500	50	2,000	50,000	1,000
z_1	0	0	0	0	0	0	0	1,000
z_5	1	1	1	1	110	100	75	100,000
$F_{2,1}$	20	100	1	5	500	20	100	200
$F_{3,1}$	30	400	5	46	545	180	900	800
$F_{3,2}$	20	100	1	5	500	20	100	190
$F_{4,3}$	50	480	5.5	49.9	50	180	500	300
$F_{5,3}$	0	10	0.4	1	900	10	400	600
$F_{5,4}$	50	480	5.5	49.9	50	180	500	300
$F_{5,6}$	1	10	0.6	1.1	10	20	1,000	100
$F_{6,3}$	0	10	0.1	0.1	50	10	50	0
$F_{6,5}$	1	0	0.5	1	20	10	950	100
$F_{1,5}$	50	500	6	51	1,045	200	1,000	0
$F_{0,2}$	0	0	0	0	0	0	0	10
$F_{0,3}$	0	0	0	0	45	0	50	90
$F_{0,5}$	1	1	1	1	5	100	25	100,900
$F_{0,6}$	0	0	0	0	60	0	0	0

*x_i represents the size of the *ith* compartment; z_i is the input to x_i; $F_{i,j}$ is the flow of nutrients from x_j to x_i; and $F_{0,j}$ represents nutrient loss to the environment from x_j. All values are normalized against x_5, which was set to 100 units/unit area for each system. References consulted in deriving these values are listed below.

[a]Rodin and Bazilevich, 1967; Schultz, 1969.

[b]Reuss, 1971; Rodin and Bazilevich, 1967; Sims and Singh, 1971.

[c]Bormann and Likens, 1970; Likens and Bormann, 1972; Rodin and Bazilevich, 1967.

[d]Child and Shugart, 1972; McGinnis et al., 1969; Rodin and Bazilevich, 1967.

[e]Brylinsky, 1972; E. P. Odum, 1971; Riley, 1972.

[f]Juday, 1940; Likens and Bormann, 1972; Lindeman, 1941, 1942; Williams, 1971.

[g]E. P. Odum, 1971; Pomeroy et al., 1969; Teal, 1962; Wiegert et al., 1974.

[h]Boling et al., 1974; Cummins, 1971; Woodall, 1972.

Additional general references consulted include Collier et al., 1973; Golley, 1972; Pomeroy, 1970; Wiegert and Evans, 1964.

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'HE EIGHT IDEALIZED ECOSYSTEMS
D (FIG. 2)

ropical orest[d]	Ocean[e]	Lake[f]	Salt marsh[g]	Stream[h]
500	10	10	1,000	500
2.5	10	1	25	50
5	10	25	1,000	10
1	0.5	25	100	20
100	100	100	100	100
500	50	2,000	50,000	1,000
0	0	0	0	1,000
1	110	100	75	100,000
5	500	20	100	200
46	545	180	900	800
5	500	20	100	190
49.9	50	180	500	300
1	900	10	400	600
49.9	50	180	500	300
1.1	10	20	1,000	100
0.1	50	10	50	0
1	20	10	950	100
51	1,045	200	1,000	0
0	0	0	0	10
0	45	0	50	90
1	5	100	25	100,900
0	60	0	0	0

s the input to x_i; $F_{i,j}$ is the flow of nutrients
nvironment from x_j. All values are normalized
ach system. References consulted in deriving

Singh, 1971.
972; Rodin and Bazilevich, 1967.
din and Bazilevich, 1967.

, 1941, 1942; Williams, 1971.
; Wiegert et al., 1974.

ier et al., 1973; Golley, 1972; Pomeroy, 1970;

TABLE 2

INDEXES SUMMARIZING VARIOUS STRUCTURAL CHARACTERISTICS OF THE EIGHT HYPOTHETICAL ECOSYSTEMS AND DIFFERENTIATING AMONG THE PROPERTIES OF NUTRIENT CYCLES SHOWN IN FIG. 2*

System	Abiotic storage		Biotic storage	Recycling		System turnover	
	T_6	$\frac{x_5 + x_6}{\Sigma x}$	$\frac{x_1 + x_2 + x_3 + x_4}{F_{1,5}}$	$\frac{F_{1,5}}{x_3}$	$\frac{F_{1,5}}{\Sigma z}$	$\frac{\Sigma x}{F_{1,5}}$	$\frac{\Sigma x}{\Sigma z}$
Tundra	100	0.31	8.7	0.25	50	12.7	635
Grassland	1,000	0.86	3.3	0.5	500	23.5	11,750
Temperate forest	8,333	0.97	21.1	0.24	6	870.93	5,226
Tropical forest	1,364	0.76	9.97	10.2	51	41.34	2,108
Ocean	0.714	0.83	0.029	104.5	9.5	0.173	1.64
Lake	100	0.97	0.305	8	2	10.80	21.6
Salt marsh	50	0.96	2.12	1	13.3	52.22	696
Stream	10	0.65	∞	0	0	∞	0.017
			(0.58)†	(99)†	(0.0098)†	(1.70)†	

*x_i is the size of the *ith* compartment; z_i is the input to x_i; $F_{i,j}$ is the flow of nutrients from x_j to x_i; $F_{0,j}$ is the nutrient loss to the environment from x_j; and T_6 is the time constant of x_6.

†Since $F_{1,5} = 0$ for the stream, the indicated index was recalculated using the total loss from x_3 instead of $F_{1,5}$.

TABLE 3

RESULTS OF RELATIVE STABILITY ANALYSIS OF NUTRIENT-CYCLING MODELS FOR EIGHT HYPOTHETICAL ECOSYSTEMS

System	Critical root	Mean root	Natural frequency	Damping ratio
Temperate forest	−0.0001	−1.312	0.000227	1.2174
Grassland	−0.0001	−2.218	0.000228	1.1794
Tropical forest	−0.0003	−10.456	0.001039	1.2585
Salt marsh	−0.0013	−5.128	0.003898	1.1852
Tundra	−0.0015	−0.810	0.004413	1.1840
Lake	−0.0083	−9.718	0.02924	1.2954
Stream	−0.0999	−188.350	6.2947	1.4700
Ocean	−0.7678	−61.85	1.8478	1.1404

ecosystem to resist perturbation, results from the accumulated structure of the ecosystem. Resilience, the ability of an ecosystem to return to a nominal trajectory once displaced, reflects dissipative forces inherent in the ecosystem. These concepts were shown to be implicit within the linear donor-based model formulation of Eqs. 1 to 7, from which four relative stability indexes were derived: Critical root measures the system's margin of stability. Mean root is an index of system response time. Natural frequency measures resistance to displacement, and damping ratio measures resilience following displacement. Randomly constructed matrices (subject to the restriction of mass conservation; Eqs. 4 and 6) and hypothetical ecosystem models were analyzed to examine relationships between relative stability and specific properties of nutrient cycles.

Results of the stochastic analyses indicated that an increase in the amount of recycling relative to input resulted in a decreased margin of stability, faster mean response time, greater resistance, and less resilience. Analyses of the hypothetical ecosystem models revealed similar relationships among stability measures. Greater amounts of recycling were correlated with a smaller margin of stability, slower mean response time (not consistent with stochastic results), greater resistance, and less resilience (ignoring the stream value). Deterministic results also revealed that increased storage and turnover times resulted in exactly the same relationships as described for the amount of recycling. Increases in both recycling and turnover rates produced opposite results, however, leading to a larger stability margin, faster response time, smaller resistance, and greater resilience.

The inconsistent correlations between amount of recycling and mean response time can be explained. In the stochastic analyses, increases in recycling

TABLE 4

CORRELATION COEFFICIENTS FOR RELATIONSHIPS BETWEEN RELATIVE STABILITY MEASURES AND INDEXES OF STRUCTURAL PROPERTIES*

	Structural indexes						
	Abiotic storage		Biotic storage	Recycling		System turnover	
	T_6	$\frac{x_5 + x_6}{\Sigma x}$	$\frac{x_1 + x_2 + x_3 + x_4}{F_{1,5}}$	$\frac{F_{1,5}}{x_3}$	$\frac{F_{1,5}}{\Sigma z}$	$\frac{\Sigma x}{F_{1,5}}$	$\frac{\Sigma x}{\Sigma z}$
Critical root	1 0.99	1 0.10†	4 0.89	3 −0.89	4 0.59	4 0.90	4 0.90
Mean root	4 0.70	1 0.24	4 0.72	4 −0.97	2 0.85	4 0.72	2,4 0.88
Natural frequency	4 −0.89	1 0.22†	4 −0.81	3 0.91	2 −0.85	4 −0.85	4 −0.98
Damping ratio	3 0.36	1 0.14	1 0.20	2 0.49	2 −0.85	1 −0.10	2 −0.66
	(3 0.58)‡	(1 0.25)	(4 0.26)	(3 −0.50)	(2 −0.38)	(4 0.42)	(1 −0.16)

*Each indicated variable pair was tested for (1) linear; (2) semilog, log of structural index; (3) semilog, log of stability measure; and (4) log–log relationships. The model with the largest correlation is reported and indicated to the left of the correlation coefficient. Levels of significance are 0.666 (5%) and 0.798 (1%). x_i is the size of the *ith* compartment; z_i is the input to x_i; $F_{i,j}$ is the flow of the nutrients from x_j to x_i; $F_{0,j}$ represents the nutrient loss to the environment from x_j, and T_6 is the time constant of x_6.

†These relationships were greatly improved by considering terrestrial and aquatic ecosystems separately. In each case the correlation coefficient was 0.99 (model 4). The relationship was positive for critical root and negative for natural frequency damping factor.

‡Values in parentheses represent correlations and model numbers, if the stream system is not considered (ζ only).

coefficients forced increases in turnover rates of donor compartments ($|a_{i,i}|$, Eq. 4). Since randomly constructed matrices exhibited a narrow range of coefficient values, a change in any one turnover rate was reflected in the mean response time. The deterministic models exhibited a much wider range in values of transfer coefficients (several orders of magnitude), so that larger turnover rates of x_i did not correspond to longer mean response times. The opposite relationship, in fact, existed. Those systems with large amounts of recycling also had large storage and hence mean roots near zero. Indeed, the presence of rate coefficients that range over several orders of magnitude is one important characteristic of ecosystems that differentiates them from randomly organized systems.

Table 3 shows that the eight hypothetical ecosystems, ordered from least to most resistant (largest to smallest ω_n), were stream, ocean, lake, tundra, salt marsh, tropical forest, grassland, and temperate forest. The four terrestrial ecosystem models were, on the whole, much more resistant than the four aquatic models. Analyses did not reveal such a clear separation of ecosystems with high and low resilience, nor did the eight systems differ as much with respect to the resilience aspect of relative stability as they did in relation to resistance. From least to most resilient (largest to smallest ζ), the ecosystems were stream, lake, tropical forest, temperate forest, salt marsh, tundra, grassland, and ocean. This factor is tied to system characteristics (such as recycling) which do not differ strictly between aquatic and terrestrial ecosystems. Although several of the aquatic models were more resilient than most terrestrial ones, the lake model showed one of the smallest resilience values, probably related to slow turnover of the large abiotic storage pool. These results should be interpreted cautiously, in light of the data used in this analysis. Certainly the order-of-magnitude differences in the natural frequencies would seem to reflect real differences in the idealized ecosystems. The differences in damping ratios are apparently much smaller. However, these differences actually reflect large differences in the time dynamics of the ecosystem types because ζ appears as an exponent in the time-domain solutions (Eqs. 9 and 11).

These results agree well with previous analyses. Pomeroy (1970) related ecosystem stability to the presence or absence of abiotic reserves, system turnover rate, and predictability of the physical environment. Specifically, he noted that ecosystems with low abiotic storage and rapid recycling (tropical forests and coral reefs) are slow to recover following disturbance. Consistent with this observation, Table 3 shows the tropical forest to have one of the lowest resilience values. Also, the relative rankings of ecosystems in terms of stability given by Pomeroy correspond closely to rankings depicted in Table 4. Jordan et al. (1971) also showed an inverse relationship between recovery time following displacement and the amount of nutrient recycling relative to input. Comparisons between tropical and temperate forests in this study also agree with the analyses of Child and Shugart (1972) and Waide et al. (1974).

Inverse Relationships Between Resistance and Resilience

Taken together our results indicate an inverse relationship between resistance and resilience. Those factors which tend to increase resistance decrease resilience, and those factors which increase resilience decrease resistance. In addition, those systems which are highly resistant have low resilience, and vice versa. Thus ecosystem evolution would seem to involve a compromise or balance between resistance and resilience. In some situations, selection has favored ecosystems with large storage and a large amount of recycling, factors that contribute to ecosystem persistence by increasing resistance to displacement. Other ecosystems in other environments have low storage and rapid recycling and persist by responding rapidly following disturbance. The relationship is not an exact inverse, however. Results show, for example, the tropical forest to be both less resistant and less resilient than either the temperate forest or grassland. Also, the grassland model is next to the most stable in terms of both resistance and resilience, and the stream is least stable in both regards. Still, the notion of a functional balance between ecosystem properties favoring resistance or resilience is substantiated.

Environmental conditions that favor ecosystem resistance or resilience must be considered. In general, those environments in which resources are scarce or which place severe physicochemical limitations on resource mobilization will not favor the accumulation of large biotic stores of nutrients. Systems that recycle nutrients rapidly, and hence are highly resilient, should be favored in such environments. However, kinetic limitations on resource assimilation could be so severe as to produce systems that are neither resistant nor resilient, as streams seem to be. On the other hand, environments in which resources are available and which place less severe limitations on resource mobilization should favor the development of ecosystems that accumulate large nutrient reserves that turn over slowly and hence are relatively more resistant. Such considerations in part explain the separation between aquatic and terrestrial ecosystems in terms of resistance. With the exception of coral reefs, aquatic systems are generally limited in their ability to retain and recycle essential resources (Pomeroy, 1970; Riley, 1972). Such systems are typically more resilient, and less resistant, than terrestrial systems.

Also, as emphasized by Holling (1973), the balance between resistance and resilience is strongly influenced by the types of environmental fluctuations commonly encountered by an ecosystem. For example, results suggest that the hypothetical ocean is the least resistant ecosystem next to the stream. It is not reasonable to expect selection for maximum resistance of such an ecosystem since the environment typically encountered by oceanic ecosystems is buffered (by the surrounding water mass) compared to that impinging upon a temperate forest, the most resistant ecosystem considered. Similar buffering is attained in terrestrial ecosystems through large biotic storage.

As a corollary to these two last points, the kinds of environmental fluctuations an ecosystem "sees," and hence to which it responds, depend upon the degree of resistance or resilience it exhibits. A system will filter out or attenuate inputs with a frequency greater than its natural frequency but will pass and hence react to inputs with a lower frequency. Thus analyses indicate that terrestrial ecosystems are, on the average, currently responding to lower frequency environmental signals than are aquatic ecosystems. From the opposite perspective, we could perhaps argue that higher frequency inputs may be more damaging to terrestrial ecosystems and that selection has thus favored large, slowly recycling biotic structures that attenuate such persistent, potentially destabilizing inputs. Thus the degree of resistance or resilience a given ecosystem exhibits is determined by the types and frequencies of environmental fluctuations commonly encountered by the system, as well as by the environmental limitations on resource mobilization which the system experiences.

Contribution of Component Turnover Rates to Stability

It was suggested above that one of the factors which characterizes ecosystems is the presence of a large range in values of transfer rate coefficients and turnover rates, typically over several orders of magnitude. Each component turnover rate contributes to the resultant balance between resistance and resilience for a given ecosystem.

The concept of r and K selection define alternative evolutionary strategies at the population level (Pianka, 1970, 1972). These ideas may be reformulated in an ecosystem context by considering r selected species to be ones that have rapid turnover and low storage, thereby contributing to ecosystem resilience, whereas K specialists exhibit slow turnover and high storage, and thus contribute to resistance. Hence the degree of resistance or resilience observed in a given ecosystem results from the relative proportions of K and r selected components, respectively. This treatment does not seek to destroy the original meaning of these ideas but rather to suggest their implications for behavior at the ecosystem level.

During succession, ecosystems progress from stages that are relatively more resilient to ones that are relatively more resistant. Although differing degrees of environmental limitation and fluctuation will produce different balances between resilience and resistance, all developmental processes involve some amount of biomass accretion and nutrient storage. However, even at steady state a large variation in turnover rates of component populations is still present. It is the presence of such a variety of adaptations of component populations in steady-state ecosystems which ensures their ability to respond following disturbance and hence which confers the property of resilience on ecosystems. For example, pin cherry is an early successional woody plant common in

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northeastern deciduous forests, which ensures their rapid return to steady-state function following major perturbation (Marks and Bormann, 1972; Marks, 1974). Black locust seems to play a similar role in forest ecosystems in the southern Appalachians. Yet neither species is anything more than a minor component of steady-state ecosystems in either locality. Clearly, their persistence within these ecosystems represents a system-level adaptation for resilience which is not explained by considering dominant steady-state components alone. Similar examples could be cited for other ecosystem types.

The role of component turnover rates in regulating ecosystem stability is also emphasized by a consideration of the contribution of primary consumers to ecosystem stability. Primary biophages are generally viewed as being able to regulate their rate of resource supply and hence the ability of a specific ecosystem to accumulate biomass and store nutrients (Odum, 1962; Wiegert and Owen, 1971). Where environments favor ecosystem resistance, selection would thus seem to lead to mechanisms that suppress primary consumption, allelochemically, structurally, and via predators and parasites. However, in situations where ecosystem resilience is favored, mechanisms for reducing primary consumption would not necessarily be advantageous. Indeed, in such systems herbivory would seem to be a major mechanism of nutrient regeneration and recycling (Johannes, 1968; Pomeroy, 1970). Comparison of resilience values for the eight hypothetical ecosystems investigated with estimates of the amount of primary production passing through primary biophages (Wiegert and Evans, 1967; Wiegert and Owen, 1971; Golley, 1972) reveals a direct relationship between these two parameters, with those ecosystem types in which primary consumption is higher typically being more resilient. Such a relationship between herbivory and nutrient regeneration requires further experimental verification, especially in terrestrial ecosystems.

SUMMARY

The theoretical perspective embodied in this paper represents an attempt to account for alternatives for persistence at the ecosystem level and at the same time to relate ecosystem response to specific observable and measurable attributes of ecosystems. The argument that ecosystems are asymptotically stable focuses attention on the critical area of relative stability. It clearly identifies two aspects of ecosystem relative stability, resistance and resilience. Resistance is related to the formation and maintenance of persistent ecosystem structure. Resilience results from the tendencies inherent in ecosystems for the erosion of such structures. Thus this perspective offers to integrate various areas of ecological theory into a unified picture of ecosystem structure and function. Further research should help to establish the validity of these ideas. However, at present, they seem to represent a rigorous, operational approach to ecosystem theory which is testable by both observation and experimental analysis.

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