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## ENERGY FLOW, NUTRIENT CYCLING, AND ECOSYSTEM RESILIENCE<sup>1</sup>

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**Abstract.** The resilience, defined here as the speed with which a system returns to equilibrium state following a perturbation, is investigated for both food web energy models and nutrient cycling models. Previous simulation studies of food web energy models have shown that resilience increases as the flux of energy through the food web per unit amount of energy in the steady state web increases. Studies of nutrient cycling models have shown that resilience increases as the mean number of cycles that nutrient (or other mineral) atoms make before leaving the system decreases. In the present study these conclusions are verified analytically for general ecosystem models. The behavior of resilience in food web energy models and nutrient cycling models is a reflection of the time that a given unit, whether of energy or matter, spends in the steady state system. The shorter this residence time is, the more resilient the system is.

**Key words:** energy flow; food web model; mathematical model; nutrient cycling; resilience; stability.

### INTRODUCTION

A key aim of theoretical ecologists is the elucidation of relationships between the structure and stability of ecosystems. This is true both for ecologists concerned with food web or trophic level models involving population number, biomass, or energy (e.g., O'Neill 1976, Pimm and Lawton 1977) and for those primarily concerned with modeling of material cycles (e.g., Jordan et al. 1972, Webster et al. 1975).

A number of different meanings have been attached to the term, "stability." Probably the most common interpretation is that a system is stable when it tends to return to an equilibrium point from which it has been displaced. A related concept, relative stability, is a measure of both the resistance of the system to perturbations and the speed with which it returns to an equilibrium point following a perturbation. This latter property has been referred to as system "resilience" (e.g., Webster et al. 1975). The faster the perturbed system returns from its initial displacement back to the equilibrium point, the shorter its recovery time,  $T_R$ , and the greater its resilience is said to be. We shall, therefore, take  $1/T_R$  as a measure of system resilience.

This paper is concerned with the relationships between resilience and some basic aspects of model structure. A mathematical approach in this direction has been made for nutrient cycling (Child and Shugart 1972, Webster et al. 1975, Harwell et al. 1977), but these papers apply only to linear models that can be adequately condensed into two-compartment systems. In this paper, I attempt to deduce results applicable to general nonlinear models of both food webs and nutrient cycles. In particular, it will be shown that system resilience can be related to two fundamental

structural concepts: (1) the energy flux through the system per unit standing crop in the steady state, or its "power capacity" (Odum and Pinkerton 1955), and (2) the recycling index of the system or the mean number of cycles a unit of matter makes in the system before leaving it. A simple index that incorporates both concepts is proposed. The present work will not attempt to develop a rigorous, systematic mathematical theory, although the elements for such a theory exist (e.g., Ulanowicz 1972, Finn 1976, Patten et al. 1976, Barber 1978a, b).

Before examining the connections between resilience and model structure mathematically, let us consider some selected examples of food web and nutrient cycling models that serve as a reference for later theoretical work.

### EXAMPLES OF FOOD WEB AND TROPHIC MODELS

In an attempt to understand underlying similarities and differences among ecosystem types, O'Neill (1976) used data for six diverse ecosystems, representing tundra, tropical forest, deciduous forest, salt marsh, spring, and pond to parameterize a standard nonlinear energy flow model with compartments for active plant tissue, inactive plant tissue, and heterotrophs. The six models were each subjected to a standard perturbation, and their recovery towards equilibrium was followed through time. As a measure of recovery time, or return time to equilibrium,  $T_R$ , the sum of squares of deviations between the perturbed transient behavior and the steady state was integrated over time following a perturbation assumed to occur at time  $t = 0$ :

$$T_R = \int_0^{\infty} dt \frac{\sum_{i=1}^3 \{(X_i(t) - X_i^*)^2 / X_i^{*2}\}}{\sum_{i=1}^3 \{(X_{i,t} - X_i^*)^2 / X_i^{*2}\}}, \quad (1)$$

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where  $X_i^*$  is the equilibrium value of the  $i$ th component of the three-component model,  $X_{i,i}$  is the initial displacement of the  $i$ th component, and  $X_i(t)$  is the instantaneous value following the perturbation.

O'Neill (1976) found that  $T_R$  decreased as energy input (rate of flow of energy into the system via the autotroph compartment) per unit standing crop in the steady state increased. As might be expected, the tundra model had the longest recovery time, and hence the lowest resilience. The pond ecosystem, with a relatively low standing crop and a high rate of biomass turnover, had the shortest recovery time and hence the highest resilience. O'Neill related his results to an intuitive suggestion by Odum and Pinkerton (1955). These authors defined power capacity for ecological systems as the quantity of energy processed per unit living tissue, and hypothesized that greater power capacity would result in greater capability to counteract change, or greater resilience.

Pimm and Lawton (1977) examined the observation that food chains are seldom longer than four or five trophic levels. They employed a set of Lotka-Volterra equations,

$$\frac{dX_i}{dt} = \left( b_i + \sum_{j=1}^n a_{ij}X_j \right) X_i \quad (i = 1, 2, \dots, n), \quad (2)$$

to describe the flow of biomass through a variety of configurations of species, including straight chains of  $n$  species or trophic levels. Like O'Neill (1976), Pimm and Lawton assumed that the recovery time,  $T_R$ , would be an important characteristic of the system. They computed the equilibrium points,  $X_i^*$  ( $i = 1, 2, \dots, n$ ), and linearized the equations about this point to obtain the matrix equation,

$$\frac{dY}{dt} = \underline{A}Y, \quad (3)$$

where  $Y$  is the vector of perturbed biomasses,  $Y = (Y_1, Y_2, \dots, Y_n)$  and  $\underline{A}$  is the matrix

$$\underline{A} = \begin{pmatrix} a_{11}X_1^* & a_{12}X_1^* & \dots & a_{1n}X_1^* \\ a_{21}X_2^* & a_{22}X_2^* & \dots & a_{2n}X_2^* \\ \vdots & \vdots & & \vdots \\ a_{n1}X_n^* & a_{n2}X_n^* & \dots & a_{nn}X_n^* \end{pmatrix}. \quad (4)$$

Only stable systems were considered, i.e., systems for which all real parts of the eigenvalues of  $\underline{A}$  are negative. For such linear, stable systems, the return time,  $T_R$ , is usually defined as the inverse of the absolute value of the real part of the eigenvalues that has the least negative real part,  $\lambda_{\max}$ :

$$T_R = 1.0 / |\text{Real}(\lambda_{\max})|. \quad (5)$$

This expression is a measure generally similar to the expression for  $T_R$  defined by Eq. 1. To obtain results of a general nature, Pimm and Lawton (1977) used a

Monte Carlo technique, choosing values of  $a_{ij}X_i^*$  randomly within certain realistic limits and examining the resulting distribution of return times.

A significant finding of Pimm and Lawton's (1977) work is that, as the number of trophic levels in a chain of species increases, the average recovery time also increases. Hence, the resilience decreases, making the system remain away from equilibrium longer following perturbations. DeAngelis et al. (1978) confirmed these results, but also pointed out that decreases in recovery time can result when the energy flux through the system is increased. This result is similar to O'Neill's (1976) findings.

The two antecedent examples of nonlinear trophic and food web models demonstrate that the flux of energy or biomass through the system has an important influence on the resilience. The higher this flux, the more quickly the effects of the perturbation are swept from the system and the system approaches its equilibrium.

#### EXAMPLES OF NUTRIENT CYCLING MODELS

As chemical energy passes through successive trophic levels, it is degraded towards low-quality thermal energy, which is unable to perform useful work. For this reason, there is usually little recycling of energy (though the coprophagy model discussed by Finn [1976] is something of an exception). Atoms of a given material element, on the other hand, can be recycled indefinitely. Some nutrients may be held very tightly by the system and recycled many times before they are lost as "output" from the system.

The stability of material cycles has received attention in recent years. Jordan et al. (1972) considered the stability of mineral cycles in forest ecosystems and proposed a standard model consisting of compartments for minerals in soil, wood, canopy leaves, and litter. These compartments form a cycle, but the system is an open one since minerals enter the system from rainfall and from the weathering in the soil, and are lost via soil runoff and leaching. Data for various mineral cycles for three different forest types were used to parameterize the standard model, which was then run on the computer to obtain the recovery time,  $T_R$ , similar to that defined by O'Neill (1976).

An important conclusion reached by Jordan et al. (1972) was that models of nonessential elements tend to be more resilient than models of essential elements. They suggested, as a possible explanation for this peculiarity, that essential nutrients, such as calcium or phosphorus, tend to be tightly cycled. A perturbation to the system, therefore, damps away slowly. Minerals that are not essential, cesium for example, are lost at a high rate from the system, so the perturbation is quickly "washed out."

A similar observation was made by Pomeroy (1970), who pointed out that coral reefs and rain forests are examples of systems with tight nutrient cycles. When

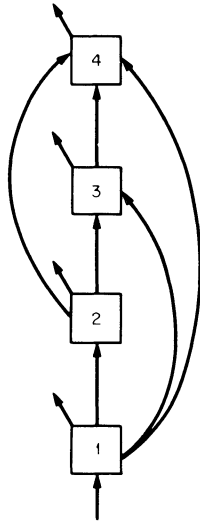


FIG. 1. A hypothetical four-species food chain, a special case of the system described by Eqs. (2). Energy enters the system through compartment 1, the autotroph level.

systems of this type are disturbed, recovery may be very slow because there is little throughflow of nutrients coming from outside the systems.

The basic factor determining the resilience of nutrient cycling models seems to be the degree of recycling, while the factor determining the resilience of food web or trophic models (with no feedback) is the energy or biomass flux per unit standing crop. Actually, these two factors are similar, as both relate to the rapidity with which a given unit of material or energy is carried through the system from the compartment where they enter (input compartment) to the compartment from which they exit the system (output compartment). In the next sections these intuitive ideas are formulated mathematically.

RESILIENCE AS A FUNCTION OF FLUX THROUGH THE SYSTEM

Since numerous food web models (e.g., Pimm and Lawton 1977) are based on the Lotka-Volterra system of equations (Eqs. 2), these form a useful starting point for the mathematical analysis. I shall consider an *n*-species model, a special case of which (*n* = 4) is shown in Fig. 1. In Eqs. 2, *b*<sub>1</sub> is allowed to be positive, while all the other *b*<sub>*i*</sub>'s (*i* = 2, 3, . . . , *n*) are negative, as might be the case if species 1 is an autotroph and the other species are heterotrophs.

One of the special features of Eqs. 2 is that the flux per unit standing crop through the system from input to output varies directly with the magnitude of the *b*<sub>*i*</sub>'s. By flux is meant the amount of matter (biomass or a particular nutrient) or energy flowing through a system or specified subsystem in a given amount of time. By standing crop is meant the total instantaneous amount of matter or energy in a system or specified subsystem.

Suppose each rate, *b*<sub>*i*</sub>, can be written as *b*<sub>*i*</sub> = *s**b*<sub>*i*</sub>' (*i* = 1, 2, . . . , *n*), where each *b*<sub>*i*</sub>' is a constant. The scaling parameter *s* is a measure of the magnitude of system throughput. As *s* increases, all *b*<sub>*i*</sub>'s increase proportionally, reflecting assumed simultaneous increases in primary production and the respirations. It is easy to show that the equilibrium values, *X*<sub>*i*</sub>\*, are all linear combinations of the parameters *b*<sub>*i*</sub> and, hence, are all proportional to the scaling parameter, *s*:

$$X_i^* = \sum_{k=1}^n C_{ik}b_k$$

$$= s \sum_{k=1}^n C_{ik}b_k' \quad (i = 1, 2, \dots, n), \quad (6)$$

where the *C*<sub>*ij*</sub>'s are constants.

Note from Eq. 4 that all elements in the matrix A contain factors of *X*<sub>*i*</sub>\*, and hence are proportional to *s*. The eigenvalue equation can now be written as

$$(s\underline{A}' - \lambda\underline{I})\underline{Y} = 0, \quad (7)$$

where the elements of A' have the form *a*<sub>*ij*</sub>  $\sum_{k=1}^n C_{ik}b_k'$ .

This implies that all eigenvalues, including  $\lambda_{max}$ , are proportional to *s*, and that *T<sub>R</sub>* = 1.0/Real( $\lambda_{max}$ ) is inversely related to *s*, or the magnitude of flux through the system.

The flux per unit standing crop through a specified subsystem, in this case a compartment of the system in steady state, is (for *i* > 1)

$$F_i = \sum_{j=1}^{i-1} a_{ij}X_j^* = \left| -\sum_{j=1}^n a_{ij}X_i^* - b_i \right|, \quad (8)$$

where || are absolute value signs. The flux *F*<sub>*i*</sub> is a linear function of *b*<sub>*i*</sub>' (*i* = 1, 2, . . . , *n*) and thus of *s*. The result is that the recovery time to equilibrium, *T<sub>R</sub>*, is inversely related to the flux per unit standing crop, or the power capacity. Therefore, resilience is directly related to this power capacity.

In general, the resilience of a model will not increase linearly with the rates of input to and output from the system, because increases in system input and output rates are not always linearly related to increases in the power capacity of the model. For example, in the simple linear model,

$$\frac{dX_1}{dt} = b_1 - a_{12}X_1 \quad (9a)$$

$$\frac{dX_2}{dt} = \gamma a_{12}X_1 - a_{22}X_2 \quad (\gamma < 1), \quad (9b)$$

increases in *b*<sub>1</sub> and *a*<sub>22</sub> would change the equilibrium values, *X*<sub>1</sub>\* and *X*<sub>2</sub>\*, but would not change the fluxes per unit standing crop, *a*<sub>12</sub> and  $\gamma a_{12}$ . Resilience of the system in this case can be shown to increase at a rate less than linear with respect to *a*<sub>22</sub>, while *b*<sub>1</sub> has no effect.

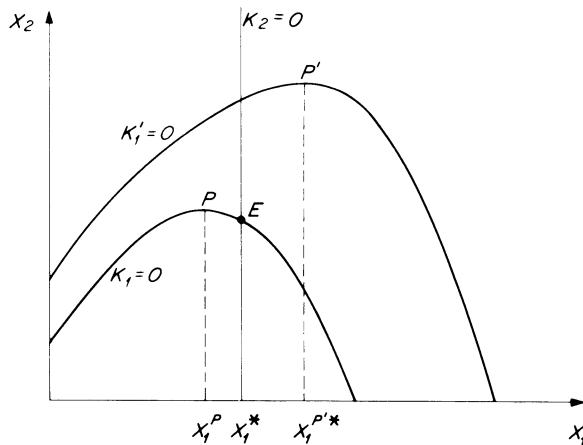


FIG. 2. The phase-plane plot of the zero isoclines associated with Eqs. (10a, b). The pair of isoclines ( $K_1 = 0, K_2 = 0$ ) represents a stable predator-prey system, while ( $K_1' = 0, K_2 = 0$ ) represents an unstable system. In the first case, the equilibrium point lies to the right of the peak, and in the second case this is reversed. Increasing the flux through the system by increasing  $b_1$  and  $b_2$  shifts both the peak and equilibrium point to the right.

Many food web models employ the Michaelis-Menten function to represent interactions. For example, consider the predator-prey model

$$\frac{dX_1}{dt} = \left( b_1 - \frac{fX_2}{C + X_1} - gX_1 \right) X_1 \equiv K_1(X_1, X_2)X_1 \quad (10a)$$

$$\frac{dX_2}{dt} = \left( \frac{fX_1}{C + X_1} - b_2 \right) X_2 \equiv K_2(X_1)X_2. \quad (10b)$$

For this type of model, the prey zero isocline forms a hump and the predator zero isocline is a vertical line (Fig. 2). This model is of special interest because Rosenzweig (1971) used it to demonstrate a "paradox of enrichment." As the input parameter,  $b_1$ , is increased, representing an enrichment of the prey's food or other resources necessary for growth, the prey isocline is heightened and shifted to the right ( $K_1' = 0$  curve in Fig. 2). If this shift is enough to move the new peak,  $P'$ , to the right of the equilibrium point,  $E$ , then the equilibrium point is unstable. Therefore, enrichment of the system can be deleterious. Even if the shift does not move the peak to the right of  $E$ , it can be shown that the resilience of the system is decreased.

As seen earlier for the Lotka-Volterra model, increases in the input flux tend to increase food chain resilience. An explanation of why an increase in input flux, or enrichment, destabilizes the system in the present case should be sought. One interpretation is that the steady-state flux of energy per unit standing crop of the predator population does not simultaneously increase, which would have represented increased predator turnover, but stays at the constant value,  $b_2$ . Hence, the predator population builds up and the prey become increasingly predator controlled.

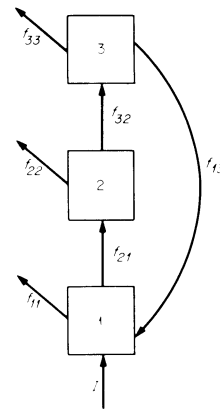


FIG. 3. An abstract model for material cycling in an ecosystem. There is an input  $I$  into compartment 1 and losses,  $f_{ii}$ , from each compartment. The  $f_{ij}$ 's are fluxes,  $f_{13}$  being a recycling flux.

If predator control of the prey population exceeds the self-regulation effects of the prey caused by the term  $gX_1$ , then a perturbation of  $X_1$  away from its equilibrium value will lead to deviation amplification, and a spiralling out to a limit cycle.

By allowing the flux through the predators to increase, either by increasing  $b_2$  as  $b_1$  is increased or by letting  $b_2$  be a function of  $X_2$  (e.g.,  $b_2 = b_2'X_2$ ), the paradox of enrichment can be avoided or at least delayed. Consider the former case, allowing both  $b_1$  and  $b_2$  to increase in proportion to a parameter  $s$ ;  $b_1 = b_1's$ ,  $b_2 = b_2's$ . The position of the peak,  $X_1^P$ , and of the equilibrium point,  $X_1^*$ , as functions of  $s$  are, respectively,

$$X_1^P = (sb_1' - gC)/2g, \quad \text{and} \quad (11a)$$

$$X_1^* = Cb_2's/(\gamma f + b_2's). \quad (11b)$$

Since the equilibrium point now shifts to the right, the tendency towards destabilization may not occur, or there may even be a tendency towards greater resilience as  $s$  is increased over certain ranges. Ultimately, if  $s$  is increased enough, the system must destabilize because there is a limit,  $f$ , on the flow of energy per unit standing crop of predators.

#### RESILIENCE AS A FUNCTION OF RECYCLING

Consider the abstract three-compartment model for a nutrient cycle shown in Fig. 3. An input of nutrient enters compartment 1, passes to compartments 2 and 3, and either leaves the system through any of these compartments or recycles to compartment 1. In the steady state, the magnitude of the input,  $I$ , is balanced by the total output from the three compartments. Before exiting from the system, individual atoms of nutrient may recycle a number of times through the system.



The model shown in Fig. 3 is not the most general that can be used to represent a nutrient cycle, but it is a fairly good analog of larger systems, and the results derived below should be broadly applicable. The general nonlinear equations for the system in Fig. 3 can be written

$$\frac{dX_1}{dt} = I + f_{13}(X_1, X_3) - f_{21}(X_1, X_2) - f_{11}(X_1) \quad (12a)$$

$$\frac{dX_2}{dt} = f_{21}(X_1, X_2) - f_{32}(X_2, X_3) - f_{22}(X_2) \quad (12b)$$

$$\frac{dX_3}{dt} = f_{32}(X_2, X_3) - f_{13}(X_1, X_3) - f_{33}(X_3). \quad (12c)$$

Let us consider the case in which recycling is strong, so that the steady-state flux out of the system from any given compartment is very small compared to other fluxes from the compartment; i.e.,

$$f_{ii}(X_i)/f_{ji}(X_i, X_j) \sim \epsilon \quad (\epsilon \ll 1) \quad (13)$$

Assume the system of equations (12a,b,c) has a stable equilibrium point  $X^* = (X_1^*, X_2^*, X_3^*)$ . The equations can be linearized about  $X^*$  by substituting  $X = X^* + y(t)$  and keeping only the terms linear in  $y(t)$ . The three eigenvalues of this nutrient cycling system can be determined from the equation

$$\lambda^3 + A_2\lambda^2 + A_1\lambda + A_0 = 0, \quad (14)$$

where  $A_0$ ,  $A_1$ , and  $A_2$  are constants. It is shown in the Appendix that the ratios  $A_0/A_1$  and  $A_0/A_2$  are very small ( $A_0/A_1 \sim \epsilon$ ,  $A_0/A_2 \sim \epsilon$ ).

If, as assumed,  $\epsilon \ll 1$ , it can be shown that one of the eigenvalues of this stable system is approximately equal to  $-A_0/A_1$  (see Appendix). This is a negative number because of the assumed stability, and is very small in magnitude, so it is likely that  $\lambda = -A_0/A_1$  is the eigenvalue whose real part is the largest of any of the system's eigenvalues. Even if this is not the largest real part, it is clear that the largest real part of an eigenvalue in the system must be at least as large as  $-A_0/A_1$ :

$$-A_0/A_1 \leq \text{Real}(\lambda_{\max}) < 0.0. \quad (15)$$

The return time,  $T_R$ , as defined by Eq. 5, then obeys the inequality  $1/T_R \leq A_0/A_1$ . Since  $A_0/A_1 \sim \epsilon$ , then

$$T_R \geq 1/\epsilon. \quad (16)$$

We can define an "index of recycling,"  $R$ , that measures the average number of times a unit of material is recycled before leaving the system. The probability that such a unit, upon leaving a particular compartment, will pass to another compartment in the system rather than leaving the system is  $1.0 - f_{ii}(X_i)/f_{ji}(X_i, X_j)$ , and the probability,  $P_c$ , of the unit making a complete circuit is, for the system in Fig. 3,

$$P_c = \prod_{i=1}^3 \{1.0 - f_{ii}(X_i)/f_{ji}(X_i, X_j)\}, \quad (17)$$

where  $j = i + 1$  except when  $i = 3$ , in which case  $j = 1$ . It follows that the mean number of cycles,  $R$ , a unit makes through the system before leaving it is

$$R \approx 1.0/(1.0 - P_c). \quad (18)$$

From (13) it can be seen that  $P_c \approx (1.0 - \epsilon)^3 \approx 1.0 - 3.0\epsilon$ , so that

$$R \sim 1.0/(3.0\epsilon). \quad (19)$$

By our definition, resilience is inversely related to  $T_R$ , so from (16) and (19), it follows that resilience varies inversely with the index of recycling,  $R$ .

#### AN INDEX OF RESILIENCE

Two factors that affect the resilience of a model have been determined: (1) the magnitude of flux (energy, biomass, or nutrient) per unit standing crop through the system, and (2) the index of recycling,  $R$ . Both factors will influence nutrient cycling models, but only the former is very significant for food web or trophic models because the magnitude of energy recycling is small. As mentioned earlier, both of these factors, though independent, relate to the rapidity with which a unit of energy or material is carried from the input to the output of the system. Because of this, it seems possible to define a single index that characterizes the resilience of the system.

Consider a general model, either a food web or a nutrient cycling model, consisting of  $n$  compartments. Assume that all of the input to the system passes through compartment 1 and all of the output passes through compartment  $n$ . It is always possible to define compartments (artificially, if necessary) to make this true. Let the equations governing the system have the general form

$$\frac{dX_1}{dt} = I + \sum_{j=2}^n f_{1j}(X_1, X_j) - \sum_{j=2}^n f_{j1}(X_1, X_j) \quad (20a)$$

$$\vdots$$

$$\frac{dX_i}{dt} = \sum_{j=1}^n f_{ij}(X_i, X_j) - \sum_{j=1}^n f_{ji}(X_i, X_j) \quad (20b)$$

$$\vdots$$

$$\frac{dX_n}{dt} = \sum_{j=1}^{n-1} f_{nj}(X_j, X_n) - \sum_{j=1}^n f_{jn}(X_j, X_n). \quad (20c)$$

The turnover time,  $\tau_i$ , for material or energy in compartment  $i$  in the steady state is defined here as the steady-state amount of material in the compartment divided by the total flux out of the compartment; i.e.,

$$\tau_i = X_i^*/F_i \quad (21)$$

where

$$F_i = \sum_{j=1}^n f_{ji}(X_i, X_j). \quad (22)$$

The probability that a unit of flux from compartment

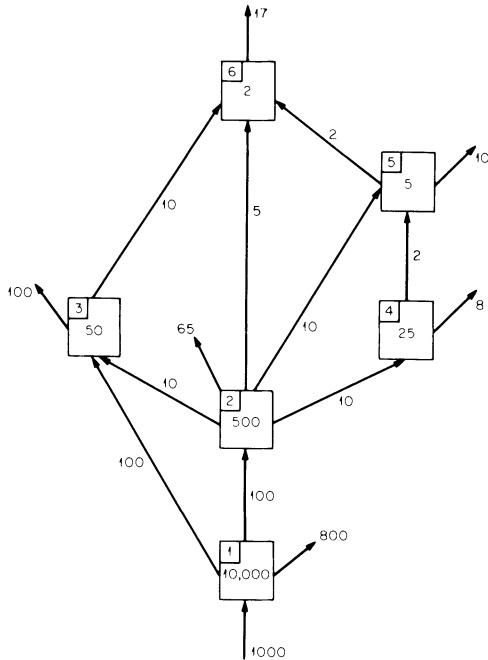


FIG. 4. An ecosystem model illustrating the concept of mean time of transfer,  $\overline{TT}$ . A unit of energy or matter enters compartment 1. The fluxes,  $f_{ij}$ , among the compartments are given in units of mass per unit time, say kilograms per day.

$i$  goes next to some particular compartment  $j$  is

$$P_{ji} = f_{ji}/F_i \tag{23}$$

Define the time it takes a unit of energy or material to pass from the input compartment to the output compartment (that is, from compartment 1 to compartment  $n$ ) as the transit time,  $TT$ . The transit time over a particular feasible path, say path  $k$ , is

$$TT_k = \left( \sum_i \tau_i \right)_k \tag{24}$$

where  $\sum_i$  represents the summation over all steps in pathway  $k$ . If there are  $M$  feasible paths, the mean transit time over all  $M$  feasible paths is

$$\overline{TT} = \sum_{k=1}^M p_{n1,k} \left( \sum_i \tau_i \right)_k \tag{25}$$

where  $p_{n1,k}$  is the probability of the unit of energy or matter taking the  $k^{\text{th}}$  path,

$$p_{n1,k} = P_{n1} P_{12} \dots P_{lm} P_{m1} \tag{26}$$

If there is recycling, then  $m$  will approach infinity.

As an example, consider Fig. 4, which represents energy flow through a hypothetical food web in steady state. The numbers in the compartments represent steady-state energy values in, say, kilojoules per hectare per year. Imagine a seventh compartment, an ar-

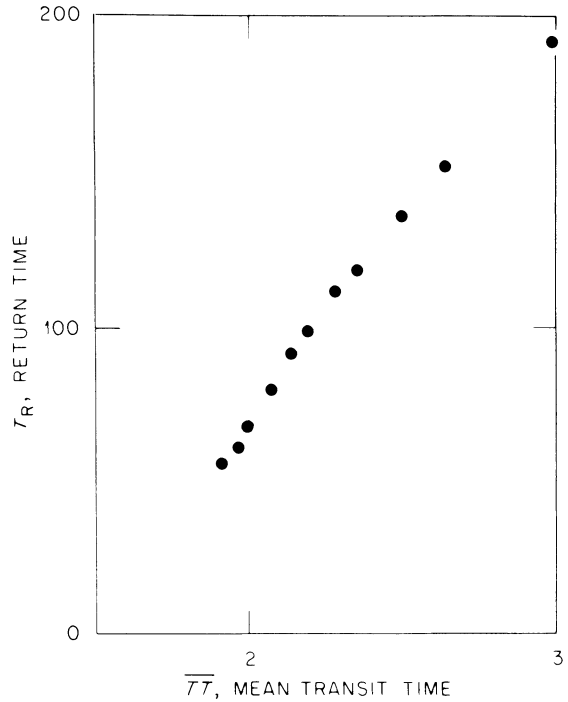


FIG. 5. The return time,  $T_R$ , plotted as a function of the mean time of transfer,  $\overline{TT}$ , for a Lotka-Volterra model of the form in Fig. 1. Each point in the plot represents the average of 1000 Monte Carlo samples for a different set of limits on the parameter values,  $a_{ij}$ .

tificial sink compartment into which the losses go from all six other compartments. Using the above procedure, the mean time it takes a unit of energy to pass from the input compartment 1 to the output compartment 7 can be computed to be  $\overline{TT} \approx 11.2$  yr.

There is no recycling in the above example, but the same procedure can be used in cases where recycling does occur. Barber (1978a, b) has recently presented a more general procedure for computing the transit time of a unit through a system.

Increases in the magnitude of fluxes,  $F_i$ , per unit standing crops in the compartments can be seen from the above analysis to decrease the mean transit time,  $\overline{TT}$ , by decreasing the  $\tau_i$ 's. Similarly, decreasing values of the recycling index,  $R$ , should obviously cause  $\overline{TT}$  to decrease. We showed earlier that increasing the flux through the system and decreasing  $R$  cause the return time to equilibrium,  $T_R$ , to decrease. Hence, there should be a positive correlation between  $T_R$  and  $\overline{TT}$  over a sampling of ecosystem models. This has been corroborated by numerous Monte Carlo simulations of Lotka-Volterra equations. For example, consider a four-compartment system similar to that shown in Fig. 1, but with feedback flows also included. Parameter values,  $a_{ij}$ , were chosen from uniform distributions between prescribed limits, the equilibrium points found, and  $T_R$  and  $\overline{TT}$  computed. In one such

case, I let  $a_{13} = a_{31} = a_{24} = a_{42} = 0$  and varied the limits on  $a_{41} = 0.1 a_{14}$ , taking 1000 Monte Carlo samples for each set of prescribed limits. The resultant averages of  $T_R$  and  $\overline{TT}$  were regressed as shown in Fig. 5, indicating a strong positive correlation.

CONCLUSIONS

Models of food web or trophic level energetics and models of nutrient cycles have been treated separately in the literature, and different conclusions have been drawn concerning the factors that affect the resilience of these models. The study of energetic models has led to the conclusion that the magnitude of flux, in this case energy or biomass, per unit standing crop through the system, or the power capacity, is positively correlated with the system's resilience (O'Neill 1976, DeAngelis et al. 1978). The analysis of nutrient cycles, on the other hand, indicates that the recycling index is a determinant of resilience, and that the resilience of a model decreases as the degree of recycling increases. These conclusions are not mutually exclusive, and both factors can operate in a given model. Both the power capacity and the recycling index are measures of how fast units of energy or matter are carried through the system from input to output. In fact, it is possible to define a single index, the mean transit time of a unit from input to output,  $\overline{TT}$ , that incorporates the two factors of power capacity and recycling. This mean transit time,  $\overline{TT}$ , should, in principle, be strongly positively correlated with the recovery time,  $T_R$ , of an ecosystem model from a perturbation, and therefore, inversely correlated with the resilience. Extensive Monte Carlo simulation appears to confirm this relationship. These results should bring us a little closer to understanding the influence of structure on stability in ecosystems, although this present work is only an outline of more thorough work that should be done.

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LITERATURE CITED

Barber, M. C. 1978a. A retrospective Markovian model for ecosystem resource flow. *Ecological Modelling* 5:125-135.  
 ———. 1978b. A Markovian model for ecosystem flow analysis. *Ecological Modelling* 5:193-206.  
 Child, G., and H. H. Shugart. 1972. Frequency response analysis of magnesium cycling in a tropical forest ecosystem. Pages 103-135 in B. C. Patten, editor. *Systems analysis and simulation in ecology*, Volume II. Academic Press, New York, New York, USA.  
 DeAngelis, D. L., R. H. Gardner, J. B. Mankin, W. M. Post, and J. H. Carney. 1978. Energy flow and the number of

trophic levels in ecological communities. *Nature* 273:406-407.  
 Finn, J. T. 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology* 56:363-380.  
 Harwell, M. A., W. P. Cropper, Jr., and H. L. Ragsdale. 1977. Nutrient recycling stability: a reevaluation. *Ecology* 58:660-666.  
 Jordan, C. F., J. R. Kline, and D. S. Sasser. 1972. Relative stability of mineral cycles in forest ecosystems. *American Naturalist* 106:237-253.  
 Lin, C. C., and L. A. Segel. 1974. *Mathematics applied to deterministic problems of the natural sciences*. Macmillan, New York, New York, USA.  
 Odum, H. T., and R. C. Pinkerton. 1955. Times speed regulator, the optimum efficiency for maximum output in physical and biological systems. *American Scientist* 43:331-343.  
 O'Neill, R. V. 1976. Ecosystem persistence and heterotrophic regulation. *Ecology* 57:1244-1253.  
 Patten, B. C., R. W. Bosserman, J. T. Finn, and W. G. Cale. 1976. Propagation of cause in ecosystems. Pages 457-579 in B. C. Patten, editor. *Systems analysis and simulation in ecology*. Volume IV. Academic Press, New York, New York, USA.  
 Pimm, S. L., and J. H. Lawton. 1977. Number of trophic levels in ecological communities. *Nature* 268:329-331.  
 Pomeroy, L. R. 1970. The strategy of mineral cycling. *Annual Review of Ecology and Systematics* 1:171-190.  
 Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385-387.  
 Ulanowicz, R. E. 1972. Mass and energy flow in closed ecosystems. *Journal of Theoretical Biology* 34:239-253.  
 Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. Pages 1-27 in F. G. Howell, J. B. Gentry, and M. H. Smith, editors. *Mineral cycling in southeastern ecosystems*. CONF-740513. National Technical Information Service, Springfield, Virginia, USA.

APPENDIX

Linearize Eqs. (12a,b,c) by letting  $X = X^* + y(t)$  and saving only terms linear in  $y(t)$ , to obtain

$$\frac{dy_1}{dt} = a_{11}y_1 - \frac{\partial f_{21}}{\partial X_2^*}y_2 + \frac{\partial f_{13}}{\partial X_3^*}y_3 \tag{A.1}$$

$$\frac{dy_2}{dt} = \frac{\partial f_{21}}{\partial X_1^*}y_1 + a_{22}y_2 - \frac{\partial f_{32}}{\partial X_3^*}y_3 \tag{A.2}$$

$$\frac{dy_3}{dt} = \frac{\partial f_{13}}{\partial X_1^*}y_1 + \frac{\partial f_{23}}{\partial X_2^*}y_2 + a_{33}y_3, \tag{A.3}$$

where

$$a_{ii} = \frac{\partial}{\partial X_i^*}(f_{ij} - f_{ki} - f_{ii}) \quad (i = 1, 2, 3), \tag{A.4}$$

and where  $j$  represents the compartment from which flux enters  $i$ , and  $k$  is the compartment to which flux goes from compartment  $i$ .

The eigenvalue equation for these equations is

$$\det \begin{vmatrix} a_{11} - \lambda & -\frac{\partial f_{21}}{\partial X_2^*} & \frac{\partial f_{13}}{\partial X_3^*} \\ \frac{\partial f_{21}}{\partial X_1^*} & a_{22} - \lambda & -\frac{\partial f_{32}}{\partial X_3^*} \\ -\frac{\partial f_{23}}{\partial X_1^*} & \frac{\partial f_{23}}{\partial X_2^*} & a_{33} - \lambda \end{vmatrix} = 0. \tag{A.5}$$



Expansion of this determinant leads to a third-order equation in  $\lambda$ , Eq. (14). A significant amount of cancellation occurs in the term  $A_0$  such that the surviving terms of  $A_0$  all contain at least one factor of the form  $\partial f_{ii}/\partial X_i$ . This is not generally true of the terms that constitute  $A_1$  and  $A_2$ , so from (13) these terms are much larger than  $A_0$ ;  $A_0/A_1 \sim \epsilon$  and  $A_0/A_2 \sim \epsilon$ .

Since, as deduced above,  $A_0/A_1 \ll 1.0$ , one eigenvalue of Eq. (14) is approximately  $\lambda_1 = -A_0/A_1$ , as can be shown by

techniques in any standard text covering asymptotic techniques (e.g., Lin and Segel 1974). This can be corroborated by substituting  $\lambda_1 = -A_0/A_1$  into Eq. (14). Since  $\lambda_1$  is very small, the first two terms of Eq. (14) are negligible, so the equation is approximately satisfied. The other eigenvalues are given approximately by solutions of the equation,

$$\lambda^2 + A_2\lambda + A_1 = 0. \quad (\text{A.6})$$