NOTES AND COMMENTS

MATERIAL CYCLING AND THE STABILITY OF ECOSYSTEMS

The cycling of matter in the form of nutrients, such as nitrogen or phosphorus, is an integral part of every ecosystem. As such, it is usually included in descriptive ecosystem models. Yet it has been ignored in most heuristic theoretical models, which have focused on communities rather than ecosystems (see, e.g., May 1974). A number of theoretical studies, however, have now been carried out on the effect of nutrient cycling on ecosystem stability (Jordan et al. 1972; Austin and Cook 1974; Webster et al. 1975; Nisbet and Gurney 1976; Harwell et al. 1977, 1981; Sjöberg 1977; Parker 1978; Harwell and Ragsdale 1979; DeAngelis 1980; Harrison and Fekete 1980; Nisbet et al. 1983; DeAngelis et al. 1989*a;* Nakajima and DeAngelis 1989). These studies, as well as many empirical investigations, have recently been reviewed extensively by DeAngelis and colleagues (DeAngelis et al. 1989*b;* DeAngelis 1992). They have led to the following conclusions: material cycling in model ecosystems that are closed with respect to matter increases the probability that these systems will be locally stable, but an increased degree of material cycling (i.e., an increased closure of the system) in open systems decreases their resilience, that is, the rate at which they return to their locally stable, steady state following a perturbation (DeAngelis et al. 1989*b*). An especially clear and general demonstration of this tendency toward decreased resilience with tighter recycling was provided by DeAngelis (1980).

The latter conclusion, however, seems to some extent to contradict the former: if resilience decreases with tighter recycling, how can closed systems be stable? It seems also to contradict the view of pioneer ecologists, who hypothesized that the tighter material cycling during the course of ecosystem succession might increase homeostasis (Odum 1969). A partial resolution of this paradox lies in the fact that a decrease in resilience may be accompanied by a concomitant increase in resistance (Webster et al. 1975; Harrison and Fekete 1980). Resistance to perturbations indeed approaches the concept of homeostasis much more than does resilience. My purpose here is to go further by laying a bridge between the conclusions from closed and open systems and clarifying the meaning of resilience as it has been investigated so far. I reexamine the general nonlinear model used by DeAngelis (1980) and show that resilience decreases with tighter material cycling only in a restricted sense; that is, what decreases is only the resilience of the total quantity of matter within the ecosystem, but not the resilience of its internal structure. I then discuss the implications of this fact.

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Resilience in stable model systems has usually been approximated by the absolute value of the real part of the critical eigenvalue of the system linearized about its steady state, because the critical eigenvalue ultimately governs the long-term rate of return of the system to its steady state after a small perturbation (see, e.g., Harwell and Ragsdale [1979]; Harwell et al. [1981]; DeAngelis [1980]; although some authors have also used the mean eigenvalue, e.g., Webster et al. [1975]; Halfon [1976]; Harwell et al. [1981]). The critical eigenvalue, λ_1, is the eigenvalue with the largest real part, $R(\lambda_1)$. To satisfy local (Lyapunov) stability, all eigenvalues of a linear model system must have negative real parts ($0 > R(\lambda_1) \geq R(\lambda_2) \geq R(\lambda_3) \geq \ldots$); thus, the critical eigenvalue is that which is nearest to zero. Harrison and Fekete (1980) proved that, in linear model ecosystems with strong nutrient recycling, λ_1 is approximately I/Q, where I is the total input of nutrient and Q is the total quantity of nutrient in the system at steady state. This has an important implication, the significance of which, to my knowledge, has not been fully appreciated; that is, the critical eigenvalue is associated only with the quantity of nutrient and is nearly independent of the structure of the system. Further, this property also holds for nonlinear model ecosystems.

To prove this, let us reexamine the general three-compartment nonlinear model used by DeAngelis (1980), which I rewrite as

$$dX_1/dt = \varepsilon I + f_{13}(X_1, X_3) - f_{21}(X_1, X_2) - \varepsilon f_{11}(X_1), \tag{1a}$$

$$dX_2/dt = f_{21}(X_1, X_2) - f_{32}(X_2, X_3) - \varepsilon f_{22}(X_2), \tag{1b}$$

and

$$dX_3/dt = f_{32}(X_2, X_3) - f_{13}(X_1, X_3) - \varepsilon f_{33}(X_3). \tag{1c}$$

An input of nutrient εI enters compartment 1 (nutrient pool), passes to compartments 2 and 3 (autotrophs and consumers) with fluxes f_{21} and f_{32}, and either leaves the system through any of these compartments (εf_{ii}) or recycles to compartment 1 (f_{11}) (fig. 1). The coefficient ε is chosen so that the functions f_{ii} and f_{ij} are of the same order of magnitude at steady state. In this way ε encapsulates the order of magnitude of the external fluxes relative to that of the fluxes internal to the system. A strong recycling is assumed; thus, $\varepsilon \ll 1$.

To illustrate our point, let us change variables and rewrite this system as a function of X_2, X_3, and the total quantity of nutrient, $Q = X_1 + X_2 + X_3$:

$$dQ/dt = \varepsilon[I - f_{11}(Q - X_2 - X_3) - f_{22}(X_2) - f_{33}(X_3)], \tag{2a}$$

$$dX_2/dt = f_{21}(Q - X_2 - X_3, X_2) - f_{32}(X_2, X_3) - \varepsilon f_{22}(X_2), \tag{2b}$$

and

$$dX_3/dt = f_{32}(X_2, X_3) - f_{13}(Q - X_2 - X_3, X_3) - \varepsilon f_{33}(X_3). \tag{2c}$$

In this form, it is apparent that the dynamics of the total quantity of nutrient is governed by slow processes of the order of ε, while that of the individual compartments occurs on a much shorter timescale. For $\varepsilon \to 0$, $dQ/dt \to 0$, and the system reduces approximately to the last two equations, with Q fixed at its initial value, Q_0. From this it is obvious that one eigenvalue of the full three-

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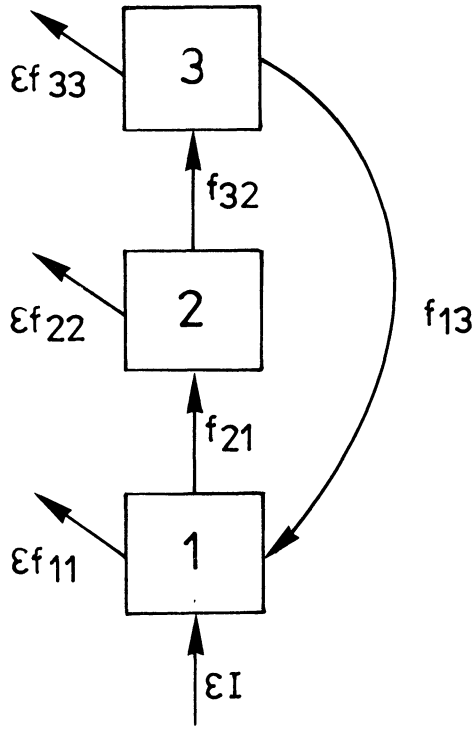

FIG. 1.—Flow diagram of the general three-compartment model (system [1]). Adapted from DeAngelis (1980).

variable system will be of the order of ε and determined by Q, whereas the other two eigenvalues will be of the order of the rates governing the dynamics of X_2 and X_3.

This can be proved formally by developing the characteristic equation of system (2) linearized near steady state, which can be written as

$$\lambda^3 + A_2\lambda^2 + A_1\lambda + A_0 = 0. \tag{3}$$

The coefficient A_0 in this equation is a sum of products of terms from the three linearized equations (eqq. [2a]–[2c]) and thus has the order of ε, whereas A_1 and A_2 are of the order of the rates governing equations (2b) and (2c). As shown by DeAngelis (1980), the critical eigenvalue is therefore approximately $\lambda_1 = -A_0/A_1$ and is of the order of ε, whereas the other two eigenvalues are given approximately by solutions of the equation

$$\lambda^2 + A_2\lambda + A_1 = 0. \tag{4}$$

Equation (4) is readily shown to approximate the characteristic equation of the reduced two-variable system (X_2, X_3) described by equations (2b) and (2c) without the loss terms in ε.

To summarize, systems (1) or (2) can be approximately decomposed into two

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disjunct sets of equations, with one equation governing the dynamics of the total quantity of matter and accounting for the critical eigenvalue and a set of two equations describing the internal dynamics of the system as if the latter were closed and accounting for the other eigenvalues. Note that this proof does not apply restrictively to a three-compartment system but can readily be extended to any system configuration. When recycling tends to be complete ($\varepsilon \rightarrow 0$), the critical eigenvalue tends toward zero and thus the system tends toward neutral stability, but this merely expresses the constraint of matter conservation or the closure of the system. Therefore, the resilience of the system's structure as expressed by the proportional importances of the compartments is determined by the other eigenvalues, in particular the subcritical eigenvalue λ_2 instead of λ_1.

Now, contrary to λ_1, there is no unequivocal relation between λ_2 or λ_3 and ε: λ_2 and λ_3 can either increase or decrease with decreasing ε, depending on the parameter values and the model structure, as can be shown through specific forms of model (system [1]). In any case, as a rule they are not of the order of ε since they are determined by an equation (eq. [4]), which is virtually independent of ε. Thus, a stronger recycling is accompanied by a decreased resilience to perturbations in the total quantity of matter but not necessarily by a decreased resilience to perturbations in the distribution of matter among the compartments.

But the more a system is closed, the smaller should be the perturbations in its quantity of matter, because these can only occur as perturbations in the input or output flows, which are of the order of ε (eq. [1] or [2]; see also Harrison and Fekete 1980). Thus, similar relative variations in nutrient input or output flows will translate into absolute perturbations of the order of ε. Therefore, the decrease in the resilience of the quantity of matter that accompanies a tighter recycling is normally offset by a parallel increase in resistance to perturbations, with the net result of there being no consistent effect on ecosystem stability. This conclusion holds only for "normal" perturbations, however—that is, for perturbations that preserve the relative closure of the ecosystem. When this closure is broken down by accidental or anthropogenic disturbances in the quantity of matter (e.g., by the introduction of pollutants), the return to the steady-state quantity of matter will indeed be governed by the critical eigenvalue and will be longer for ecosystems with stronger recycling; it will occur long after the internal distribution of matter, as governed by the subcritical eigenvalue, has stabilized.

The above theoretical conclusions regarding resilience and resistance should be amenable to experimental testing, but I do not know of any existing relevant data. Experiments that may provide information are being conducted by the stream nutrient cycling group at Oak Ridge National Laboratory (P. J. Mulholland, D. L. DeAngelis, A. D. Steinman, E. R. Marzolf, and M. Loreau, unpublished manuscript). In this experimental work, the nutrient and biomass dynamics of periphyton communities are being studied in laboratory artificial streams. In the streams, semi-isolated zones have been created with varying degrees of openness to the free-flowing water, some of which satisfy the condition $\varepsilon \ll 1$. Experiments are envisaged to test, among other things, the above theoretical results (*a*) that ecosystems respond differently to two types of perturbations, a perturbation

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in the input or output flows and a perturbation that redistributes matter within the system, and (*b*) that increased closure of the system is accompanied by decreased resilience but increased resistance of the quantity of matter. The first type of perturbation would be generated by increasing the nutrient concentration of the free-flowing water during a fixed time. The total quantity of matter within the semi-isolated zones is then expected to increase less during the perturbation and to decrease more slowly to its previous steady-state value after the perturbation, in the more closed zones than in the more open zones, because resistance of the quantity of matter is predicted to be higher, and resilience lower, in more closed systems. The second type of perturbation would be generated by killing part of the biomass in situ. In this case, no consistent relationship is expected between closure of a zone and the rate at which the various ecological compartments recover their previous steady-state values, because resilience of the internal structure of the ecosystem is predicted not to decrease in more closed systems. These experiments should help in the development and testing of a unified theory of resilience and resistance in nutrient-limited systems.

A few further remarks need to be made concerning the mathematical theory of such systems. It is important to realize that eigenvalue analysis does not allow proper consideration of the issue of ecosystem homeostasis. Eigenvalue analysis rests on the assumptions that a steady state does exist and that all parameter values are fixed. Not only do real perturbations usually involve perturbations in parameter values (Harrison and Fekete 1980), if not in the model's structure, but the external environment is also seldom constant. In particular, matter inputs can be highly variable. An open system subject to an intense flow of matter, like a fast-flowing stream, will appear highly resilient for fixed parameters (see, e.g., Webster et al. 1975; Harwell et al. 1977) but will follow external fluctuations in matter inflow in a more or less passive way. Unless the environment is constant enough, a certain degree of ecosystem homeostasis may be necessary before a meaningful steady state can exist at all. Material cycling does take part in ecosystem homeostasis because it buffers against external fluctuations in matter input.

DeAngelis (1980) attempted a synthesis of the relationship among energy flow, material cycling, and ecosystem resilience and proposed as a general law that resilience varies inversely as the mean transit time of a unit of either energy or matter within the system. On the basis of the above argument, I propose instead that the resilience of ecosystem structure varies directly with the energy flow through the system, or its power capacity (Odum and Pinkerton 1955; Odum 1983), independently of the degree of material cycling, whereas material cycling increases ecosystem homeostasis (Odum 1969). Recycling decreases the resilience of the quantity of matter within the ecosystem, but this effect is normally offset by a simultaneous increase in resistance.

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