

ALTERNATIVES TO RESILIENCE FOR MEASURING THE RESPONSES OF ECOLOGICAL SYSTEMS TO PERTURBATIONS

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Abstract. Resilience is a component of ecological stability; it is assessed as the rate at which perturbations to a stable ecological system decay. The most frequently used estimate of resilience is based on the eigenvalues of the system at its equilibrium. In most cases, this estimate describes the rate of recovery only asymptotically, as time goes to infinity. However, in the short term, perturbations can grow significantly before they decay, and eigenvalues provide no information about this transient behavior. We present several new measures of transient response that complement resilience as a description of the response to perturbation. These indices measure the extent and duration of transient growth in models with asymptotically stable equilibria. They are the reactivity (the maximum possible growth rate immediately following the perturbation), the maximum amplification (the largest proportional deviation that can be produced by any perturbation), and the time at which this amplification occurs. We demonstrate the calculation of these indices using previously published linear compartment models (two models for phosphorus cycling through a lake ecosystem and one for the flow of elements through a tropical rain forest) and a standard nonlinear predator–prey model. Each of these models exhibits transient growth of perturbations, despite asymptotic stability. Measures of relative stability that ignore transient growth will often give a misleading picture of the response to a perturbation.

Key words: compartment models; eigenvalues; pulse perturbations; reactivity; relative stability; resilience; return time; transient vs. asymptotic dynamics.

INTRODUCTION

Ecological systems are subject to continual perturbation. Their responses to perturbation are characterized qualitatively by *stability* (does the system return to its original state after perturbation, or does it not?), and quantitatively by *resilience*, or its reciprocal *return time*, which measure how rapidly a stable system returns to its original state after a perturbation (Holling 1973, Webster et al. 1975, Beddington et al. 1976, Harrison 1979, DeAngelis 1980, 1992, Pimm 1982, 1984, 1991). Theoretical and experimental ecologists have studied how resilience is affected by ecosystem characteristics including energy flow (O'Neill 1976, DeAngelis 1980), nutrient loads and nutrient cycling (Harwell et al. 1977, DeAngelis 1980, DeAngelis et al. 1989a, b, Steinman et al. 1991, Cottingham and Carpenter 1994, Loreau 1994), environmental stochasticity (Ives 1995), life history strategies (Lepš et al. 1982), food chain length (Pimm and Lawton 1977, Vincent and Anderson 1979, DeAngelis et al. 1989a, Steinman et al. 1991, Carpenter et al. 1992, Cottingham and Carpenter 1994), food web connectance (Pimm 1979, Lepš et al. 1982) and connectivity (Armstrong 1982), herbivory (Lee and Inman 1975), and omnivory (Pimm and Lawton 1978, Pimm 1979).

A number of indices have been suggested for mea-

suring resilience in model ecosystems (Patten and Witkamp 1967, Jordan et al. 1972, Pimm and Lawton 1977, Harte 1979, DeAngelis 1980). The most frequently used and easily calculated index is based on the eigenvalues of the system near its equilibrium. Consider a linear system

$$\frac{d\mathbf{x}}{dt} = \mathbf{Ax} \quad \mathbf{x}(0) = \mathbf{x}_0 \quad (1)$$

which may represent either an intrinsically linear system (such as certain compartment models) or the linearization of a nonlinear system near an equilibrium point. Eq. 1 has the unique solution

$$\mathbf{x}(t) = e^{\mathbf{At}} \mathbf{x}_0. \quad (2)$$

When the eigenvalues of \mathbf{A} are all negative, then $e^{\mathbf{At}} \rightarrow 0$ as $t \rightarrow \infty$, and the equilibrium solution $\mathbf{x}^* = 0$ is asymptotically stable. In fact, for almost all initial conditions,

$$\lim_{t \rightarrow \infty} e^{-\lambda_1(\mathbf{A})t} \mathbf{x}(t) \propto \mathbf{w}_1 \quad (3)$$

where $\lambda_1(\mathbf{A})$ is the eigenvalue of \mathbf{A} with largest real part and \mathbf{w}_1 is the corresponding eigenvector. Thus \mathbf{x} is approximately proportional to \mathbf{w}_1 and decays like $e^{\lambda_1(\mathbf{A})t}$ for t large.

Because, asymptotically, the magnitude of \mathbf{x} decreases by the factor $1/e$ in a time interval of length $-1/\text{Re}(\lambda_1(\mathbf{A}))$, Pimm and Lawton (1977) used

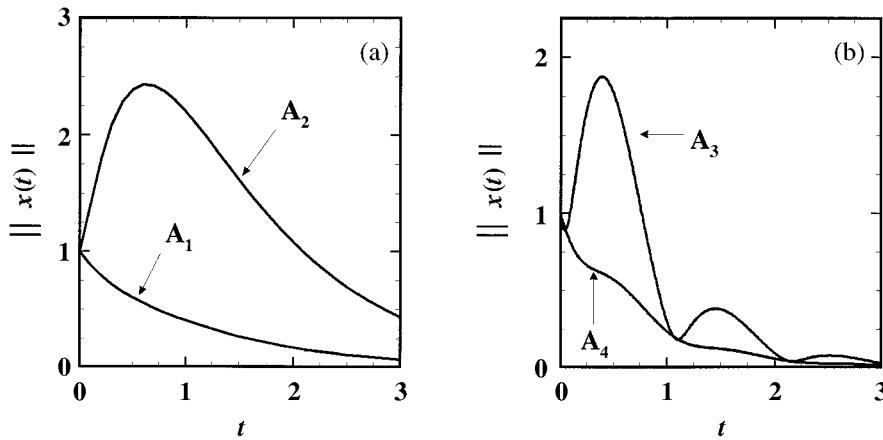


FIG. 1. The magnitude of four solutions of the linear system (Eq. 1). (a) The bottom curve represents the solution under \mathbf{A}_1 , the top under \mathbf{A}_2 (cf. Eq. 5). The initial conditions of both solutions are the same: $x_1(0) = 1/2$, $x_2(0) = \sqrt{3}/2$. (b) The top curve represents the solution under \mathbf{A}_3 , the bottom under \mathbf{A}_4 (cf. Eq. 7). The initial conditions of these two solutions are the same: $x_1(0) = \cos(2\pi/5)$, $x_2(0) = \sin(2\pi/5)$.

$-1/\text{Re}(\lambda_1(\mathbf{A}))$ as a measure of return time. Thus *resilience*, defined as

$$\text{resilience} = -\text{Re}(\lambda_1(\mathbf{A})) \quad (4)$$

is an asymptotic approximation of the decay rate of perturbations to the linear system (Eq. 1). The larger the resilience, the faster perturbations eventually decay. Expression 4, or the equivalent version for a discrete-time system, is widely used (e.g., Beddington et al. 1976, Pimm and Lawton 1977, 1978, Harwell and Ragsdale 1979, Pimm 1979, 1982, 1984, Vincent and Anderson 1979, DeAngelis 1980, Harwell et al. 1981, Armstrong 1982, DeAngelis et al. 1989a, b, Carpenter et al. 1992, Nakajima 1992, Cottingham and Carpenter 1994, Loreau 1994).

Resilience, measured in terms of the dominant eigenvalue of \mathbf{A} (Expression 4), is an asymptotic property, giving the rate of decay of perturbations as $t \rightarrow \infty$. Short-term transient behavior, immediately after the perturbation, is ignored. The question arises whether asymptotic behavior adequately characterizes the response to perturbations. Because of the short duration of many ecological experiments, transients may dominate the observed responses to perturbations. In addition, transient responses may be at least as important as asymptotic responses. Managers charged with ecosystem restoration, for example, are likely to be interested in both the short-term and long-term effects of their manipulations, particularly if the short-term effects can be large (National Research Council 1992). It is therefore the goal of this article to find mathematically simple measures of transient responses that complement resilience as a measure of the response to perturbation.

Our analysis shows that even in stable, resilient systems, transient behavior can be dramatic, long lasting, and counterintuitive. Although a perturbation eventually decays, its size can grow rapidly at first, and the

growth can continue for times on the order of the return time. This transient growth is not the result of nonlinearity, although nonlinearity can enhance the effect. It is a generic characteristic of linear or linearized equations with asymptotically stable equilibria and should therefore be common in ecosystem models.

Here is an example. Consider the solution to the system (Eq. 1) when \mathbf{A} is either

$$\mathbf{A}_1 = \begin{pmatrix} -1 & 1 \\ 0 & -2 \end{pmatrix} \quad \text{or} \quad \mathbf{A}_2 = \begin{pmatrix} -1 & 10 \\ 0 & -2 \end{pmatrix}. \quad (5)$$

Measuring the size of the solution by the Euclidean norm, i.e.,

$$\|\mathbf{x}(t)\| = \sqrt{x_1^2(t) + \dots + x_n^2(t)} \quad (6)$$

we can examine the dynamics under each matrix following a perturbation for which $\|\mathbf{x}_0\| = 1$. Since \mathbf{A}_1 and \mathbf{A}_2 have the same eigenvalues ($\lambda_1 = -1$, $\lambda_2 = -2$), they have the same resilience, and $\|\mathbf{x}(t)\|$ asymptotically approaches zero at the same rate for each. However, as shown in Fig. 1a, the solutions initially behave differently. One solution exhibits *transient growth*, temporarily moving farther away from the equilibrium, despite the negative eigenvalues. Fig. 1b shows that the same phenomenon can occur when the eigenvalues are complex by comparing

$$\mathbf{A}_3 = \begin{pmatrix} -1 & -12 \\ 0.75 & -2 \end{pmatrix} \quad \text{with} \quad \mathbf{A}_4 = \begin{pmatrix} -1 & -4 \\ 2.25 & -2 \end{pmatrix}. \quad (7)$$

Again the eigenvalues of \mathbf{A}_3 and \mathbf{A}_4 are identical ($\lambda_1 = (-3 + i\sqrt{35})/2$, $\lambda_2 = (-3 - i\sqrt{35})/2$), but the short-term behavior of the solutions they produce under system (Eq. 1) differs dramatically.

Fig. 1 highlights two key points: (1) perturbations to asymptotically stable equilibria of linear (or linearized) models may or may not exhibit significant transient growth, and (2) transient growth is not detectable

by eigenvalue analysis. These points have also been made in the contexts of numerical analysis (Trefethen 1992, Higham and Trefethen 1993), hydrodynamic stability and the transition to turbulence (Trefethen et al. 1993), and atmospheric dynamics (Farrell 1989).

Realizing that the approximation (Expression 4) may be good only a long time after the initial perturbation or for extremely small perturbations to nonlinear systems, O'Neill (1976), DeAngelis (1980, 1992), and Cottingham and Carpenter (1994) have used other measures of return time (T_R) that are similar to

$$T_R = \frac{1}{\|\mathbf{x}_0\|^2} \int_0^{\infty} \|\mathbf{x}(t)\|^2 dt. \quad (8)$$

That is, they integrate the magnitude of $\mathbf{x}(t)$ over the entire history of the system following the perturbation. The integral (Eq. 8) can be calculated analytically in the linear case (Eq. 1) (Harte 1979), or numerically when the equations are nonlinear. Note that Eq. 8 characterizes the return time for a particular perturbation and can vary widely for perturbations of the same size but in different directions. (For example, T_R varies between approximately 0.17 and 8.91 for Eq. 1 with matrix \mathbf{A}_2 and different perturbations with initial magnitude $\|\mathbf{x}_0\| = 1$.) In order to characterize return times of the system one must use some property of the distribution of the return times generated by a collection of different perturbations, such as the maximum or the mean. Indeed, if one is analyzing a nonlinear system, then the magnitude of the perturbation also matters and one must sample an n -dimensional ball in the state space. If the dimension of the system is large, these computations are time consuming, and the advantage of an easily calculated index, such as resilience as defined by Expression 4, becomes apparent.

In the next section, we introduce three measures that characterize the transient behavior of a system following a small perturbation. We call the first of these the *reactivity*; it is the maximal instantaneous rate at which perturbations can be amplified. The second, the *maximal amplification*, ρ_{\max} , is the factor by which the perturbation that grows the largest is amplified. Finally, we designate the time required to achieve this maximal amplification as t_{\max} . Each of these indices, in addition to resilience, can be derived from a curve we call the *amplification envelope*, which provides an upper bound on the possible responses to perturbations. Reactivity, ρ_{\max} , and t_{\max} are all measures of instability. As they increase, perturbations can grow faster, get bigger, and last longer. These measures of transient response give direct insight into short-term behavior and are easy to compute for linear or linearized systems. We give examples of transient growth in linear models of material cycling in ecosystems and in a nonlinear predator-prey model. We save our conclusions for a final discussion section.

CHARACTERIZING TRANSIENTS

Instantaneous behavior

We begin by considering a perturbation of magnitude $\|\mathbf{x}_0\|$ to an asymptotically stable equilibrium of a linear system. The perturbation will grow or shrink at a rate that depends on the initial condition. We define *reactivity* as the maximum amplification rate, over all initial perturbations, immediately following the perturbation:

$$\text{reactivity} \equiv \max_{\|\mathbf{x}_0\| \neq 0} \left[\left(\frac{1}{\|\mathbf{x}\|} \frac{d\|\mathbf{x}\|}{dt} \right) \right]_{t=0}. \quad (9)$$

The reactivity of a nonlinear system is computed from the linearization of the system near the equilibrium under consideration. Equilibria with positive reactivity we term *reactive*.

At first glance, the definition (Expression 9) seems to suggest that calculating reactivity requires evaluating the initial amplification of every possible perturbation. However, there is a formula that gives the reactivity without any sampling of initial conditions. First, the growth rate of perturbations governed by Eq. 1, at any time, is

$$\frac{d\|\mathbf{x}\|}{dt} = \frac{d\sqrt{\mathbf{x}^T \mathbf{x}}}{dt}, \quad (10a)$$

$$= \frac{\mathbf{x}^T (d\mathbf{x}/dt) + (d\mathbf{x}/dt)^T \mathbf{x}}{2\|\mathbf{x}\|}, \quad (10b)$$

$$= \frac{\mathbf{x}^T (\mathbf{A} + \mathbf{A}^T) \mathbf{x}}{2\|\mathbf{x}\|}. \quad (10c)$$

The matrix $(\mathbf{A} + \mathbf{A}^T)/2$ is called the *symmetric part* or *Hermitian part* of \mathbf{A} and is designated by the symbol $H(\mathbf{A})$. Thus

$$\frac{1}{\|\mathbf{x}\|} \frac{d\|\mathbf{x}\|}{dt} = \frac{\mathbf{x}^T H(\mathbf{A}) \mathbf{x}}{\|\mathbf{x}\|^2} = \frac{\mathbf{x}^T H(\mathbf{A}) \mathbf{x}}{\mathbf{x}^T \mathbf{x}}, \quad (11)$$

and

$$\left(\frac{1}{\|\mathbf{x}\|} \frac{d\|\mathbf{x}\|}{dt} \right) \Big|_{t=0} = \frac{\mathbf{x}_0^T H(\mathbf{A}) \mathbf{x}_0}{\mathbf{x}_0^T \mathbf{x}_0}. \quad (12)$$

The right-hand expression in Eq. 12 is known as the *Rayleigh quotient*. The maximum of this ratio over all \mathbf{x}_0 is the reactivity (cf. Expression 9). By Rayleigh's principle (e.g., Horn and Johnson 1985), the Rayleigh quotient is maximized by \mathbf{u}_1 , the eigenvector corresponding to the largest eigenvalue of $H(\mathbf{A})$. This eigenvalue, $\lambda_1(H(\mathbf{A}))$, is in turn the maximum value of the Rayleigh quotient. (As a real, symmetric matrix, $H(\mathbf{A})$ has real eigenvalues and orthogonal eigenvectors.) Hence

$$\text{reactivity} = \lambda_1(H(\mathbf{A})). \quad (13)$$

The eigenvalues of \mathbf{A} determine the asymptotic behavior of system (1); the eigenvalues of $H(\mathbf{A})$ —which do not necessarily have the same sign as the real parts of the eigenvalues of \mathbf{A} —determine its instantaneous be-

havior. If $\lambda_1(\mathbf{A}) < 0$ and $\lambda_1(H(\mathbf{A})) > 0$, the equilibrium will be stable but reactive, and some perturbations, no matter how small, will initially grow in magnitude. Returning to our example matrices (Eqs. 5 and 7), we compute that $\lambda_1(H(\mathbf{A}_1)) = -0.79$, $\lambda_1(H(\mathbf{A}_2)) = 3.52$, $\lambda_1(H(\mathbf{A}_3)) = 4.15$, and $\lambda_1(H(\mathbf{A}_4)) = -0.49$. \mathbf{A}_2 and \mathbf{A}_3 are reactive; \mathbf{A}_1 and \mathbf{A}_4 are not.

The amplification envelope

Reactivity is a measure of solution behavior as $t \rightarrow 0$, and thus complements resilience, which describes solution behavior as $t \rightarrow \infty$. In most cases, neither describes all the transient behavior between zero and infinity. (There are rare instances, however, such as when \mathbf{A} has orthogonal eigenvectors, when reactivity is impossible and the eigenvalues of \mathbf{A} capture both transient and asymptotic behavior.) If \mathbf{A} is reactive and solutions can grow in magnitude, we can ask how large a perturbation can possibly get, and how long growth can continue. If perturbations are amplified in the short term but decay in the long term, there must be a largest possible amplification of a perturbation, ρ_{\max} , and a time, t_{\max} , when it is achieved. These two quantities, along with reactivity, are characteristics of a curve we call the *amplification envelope*.

We define the amplification envelope, $\rho(t)$, as the maximum possible amplification that any perturbation could achieve at a given time $t \geq 0$:

$$\rho(t) \equiv \max_{\mathbf{x}_0 \neq 0} \frac{\|\mathbf{x}(t)\|}{\|\mathbf{x}_0\|}. \quad (14)$$

Using the solution (Eq. 2) to write $\mathbf{x}(t)$ in terms of the matrix $e^{\mathbf{A}t}$, we have

$$\rho(t) \equiv \max_{\mathbf{x}_0 \neq 0} \frac{\|e^{\mathbf{A}t}\mathbf{x}_0\|}{\|\mathbf{x}_0\|}. \quad (15)$$

The right-hand side of Eq. 15 is the definition of the matrix norm of $e^{\mathbf{A}t}$, $\|e^{\mathbf{A}t}\|$, induced by the Euclidean norm (Expression 6) that we use to measure the length of vectors (see, for example, Horn and Johnson 1985). ρ_{\max} is simply the maximum value of $\rho(t)$,

$$\rho_{\max} = \max_{t \geq 0} \rho(t) \quad (16)$$

and t_{\max} is the value of t at which the maximum of $\rho(t)$ occurs,

$$\rho(t_{\max}) = \rho_{\max}. \quad (17)$$

Fig. 2 illustrates that, along with ρ_{\max} and t_{\max} , resilience and reactivity are also characteristics of the amplification envelope. Resilience, $\lambda_1(\mathbf{A})$, is the slope of $\ln[\rho(t)]$ as t goes to infinity. Reactivity, $\lambda_1(H(\mathbf{A}))$, is the slope of $\ln[\rho(t)]$ as t goes to 0. In the following section we use these four quantities (summarized in Table 1) to demonstrate that transient growth is predicted by compartment models from the ecological literature. We also examine the transient behavior of a

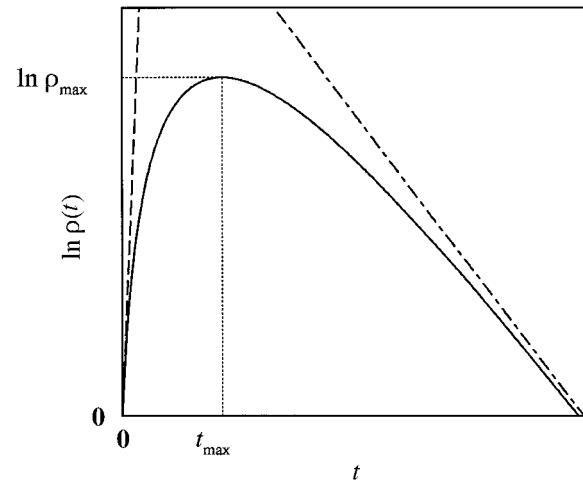


FIG. 2. The natural logarithm of the amplification envelope, $\rho(t)$, of a typical stable node (—, cf. Eq. 15). The slope of $\ln(\rho(t))$ as $t \rightarrow 0$ is the reactivity (left, ---); the slope as $t \rightarrow \infty$ is the resilience (right, ----). t_{\max} and ρ_{\max} locate the maximum of the amplification envelope.

nonlinear predator-prey model to demonstrate that the relationship between these quantities can be complex.

The amplification envelopes for our example matrices are shown in Fig. 3. Calculation of the amplification envelope has been of some interest in the field of numerical analysis (Van Loan 1977, Moler and Van Loan 1978). To calculate the matrix exponential we used the MATLAB function “`expm()`” which is based upon the Padé approximation (cf. method 3 of Moler and Van Loan 1978). The matrix norm in Eq. 15 is quickly calculated as the largest singular value of $e^{\mathbf{A}t}$ (Strang 1988), as in the MATLAB function “`norm()`.”

EXAMPLES

A tropical rain forest compartment model

Compartment models describe the flow of some quantity (nutrients, energy, etc.) from one compartment to the next. For example, McGinnis et al. (1969), characterized the flow of elements through a tropical rain forest as in Fig. 4. Matter is input to the system through the leaves and litter and flows through plants, herbivores, carnivores, and detritivores before leaving the system through the soil.

A linear compartment model assumes that the flow rate between compartments is proportional to the amount of material in the donor compartment, and that inputs to a compartment from outside of the system are independent of the amount of material in that compartment. Thus, using $y_i(t)$ for the amount of material in the i^{th} of n compartments at time t , a_{ij} for the proportionality constants, and b_i for the external inputs, we have the linear, donor-controlled model

$$\frac{dy_i}{dt} = \sum_{j=1}^n a_{ij}y_j + b_i \quad i = 1, 2, \dots, n, \quad (18)$$

along with prescribed initial conditions

TABLE 1. Measures of the response of a linear or linearized system ($\dot{\mathbf{x}} = \mathbf{A}\mathbf{x}$), to perturbations ($\mathbf{x}(0) = \mathbf{x}_0$) of the asymptotically stable equilibrium $\mathbf{x} = 0$, and how to calculate them.

Quantity	Definition	Calculation method
Resilience [†]	asymptotic proportional decay rate of perturbations:	$-\text{Re}(\lambda_1(\mathbf{A}))$
	$\lim_{t \rightarrow \infty} \left(\frac{1}{\ \mathbf{x}(t)\ } \frac{d\ \mathbf{x}\ }{dt} \right) \quad \mathbf{x}_0 \neq \mathbf{w}_i$	
Reactivity [‡]	maximum possible instantaneous proportional amplification rate of perturbations:	$\lambda_1(H(\mathbf{A}))$
	$\max_{\ \mathbf{w}_0\ \neq 0} \left[\left(\frac{1}{\ \mathbf{x}(t)\ } \frac{d\ \mathbf{x}(t)\ }{dt} \right) \Big _{t=0} \right]$	
Amplification envelope [§] , $\rho(t)$	maximum possible amplification at time t :	$\ e^{\mathbf{A}t}\ $
	$\max_{\ \mathbf{x}_0\ \neq 0} \frac{\ \mathbf{x}(t)\ }{\ \mathbf{x}_0\ }$	
ρ_{\max}	maximum possible amplification:	$\max_{t=0} \rho(t)$
	$\max_{\substack{t=0 \\ \ \mathbf{x}_0\ \neq 0}} \frac{\ \mathbf{x}(t)\ }{\ \mathbf{x}_0\ }$	
t_{\max}	time at which maximum amplification occurs:	$\rho(t_{\max}) = \rho_{\max}$
	$\left\{ t : \max_{\ \mathbf{x}_0\ \neq 0} \frac{\ \mathbf{x}(t)\ }{\ \mathbf{x}_0\ } = \rho_{\max} \right\}$	
Sensitivity of resilience [†]	matrix whose ij^{th} entry gives the change in resilience due to an infinitesimal change in the ij^{th} element of \mathbf{A} :	$-\text{Re}\left(\frac{\mathbf{v}_i \mathbf{w}_i^T}{\mathbf{v}_i^T \mathbf{w}_i}\right)$
	$\left(\frac{\partial}{\partial a_{ij}} (\text{resilience}) \right)$	
Sensitivity of reactivity [‡]	matrix whose ij^{th} entry gives the change in reactivity due to an infinitesimal change in the ij^{th} element of \mathbf{A} :	$\frac{\mathbf{u}_i \mathbf{u}_i^T}{\mathbf{u}_i^T \mathbf{u}_i}$
	$\left(\frac{\partial}{\partial a_{ij}} (\text{reactivity}) \right)$	

[†] The dominant eigenvalue of \mathbf{A} is $\lambda_1(\mathbf{A})$; the associated right and left eigenvectors are \mathbf{w}_i and \mathbf{v}_i .

[‡] $H(\mathbf{A}) = (\mathbf{A} + \mathbf{A}^T)/2$. The dominant eigenvalue and eigenvector of $H(\mathbf{A})$ are $\lambda_1(H(\mathbf{A}))$ and \mathbf{u}_1 .

[§] The matrix norm $\|e^{\mathbf{A}t}\|$ can be calculated in MATLAB via ‘‘norm(expm(A*t))’’.

$$y_i(0) = y_{0,i}, \quad i = 1, 2, \dots, n. \quad (19)$$

Each of the a_{ij} , for $i \neq j$, gives the fraction of the material in compartment j that flows into compartment i per unit time. $a_{ij} \geq 0$ when $i \neq j$, but the a_{jj} are negative, as they represent total fractional losses from compartment j per unit time. In fact,

$$a_{jj} \leq -\sum_{i \neq j} a_{ij} \quad j = 1, \dots, n, \quad (20)$$

since fractional losses from compartment j are exactly the fractional contributions from j to other compartments plus any losses from the system from compartment j .

Eqs. 18 and 19 can be rewritten as

$$dy/dt = \mathbf{A}\mathbf{y} + \mathbf{b} \quad \mathbf{y}(0) = \mathbf{y}_0, \quad (21)$$

where \mathbf{y} is the vector of compartment contents, \mathbf{A} is the matrix of transfer coefficients a_{ij} , \mathbf{b} is the vector of inputs, and \mathbf{y}_0 is the vector of initial conditions. The system has a stable equilibrium at $\hat{\mathbf{y}} = -\mathbf{A}^{-1}\mathbf{b}$. (We assume that \mathbf{A} is invertible.) In terms of the deviation from the equilibrium, $\mathbf{x}(t) = \mathbf{y}(t) - \hat{\mathbf{y}}$, we have from Eq. 21:

$$d\mathbf{x}/dt = \mathbf{A}\mathbf{x}, \quad \mathbf{x}(0) = \mathbf{x}_0. \quad (22)$$

Table 2 exhibits the matrix of transfer coefficients (\mathbf{A}) for the tropical rain forest compartment model of Fig. 4, as reported by McGinnis et al. (1969). For this matrix $\lambda_1(\mathbf{A}) = -0.002 \text{ yr}^{-1}$ and $\lambda_1(H(\mathbf{A})) = 65.4 \text{ yr}^{-1}$.

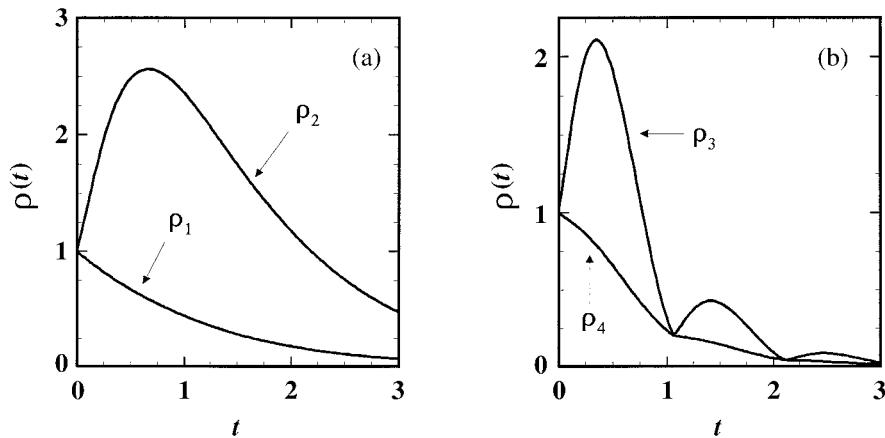


FIG. 3. The amplification envelopes of example matrices \mathbf{A}_1 through \mathbf{A}_4 (cf. Eqs. 5 and 7, Fig. 1). Note that ρ_2 and ρ_3 initially grow, indicating that \mathbf{A}_2 and \mathbf{A}_3 are reactive. In contrast, ρ_1 and ρ_4 decay, indicating that \mathbf{A}_1 and \mathbf{A}_4 are not reactive.

This system is clearly reactive. Fig. 5 shows the logarithm of the amplification envelope for this matrix at two different time scales, $t \in (0, 100 \text{ yr})$ and $t \in (0, 0.1 \text{ yr})$ (inset). From this graph we can read off $t_{\max} \approx 7 \text{ yr}$ and $\rho_{\max} \approx 280\%$. Because equilibria of this model are reactive, and $\lambda_1(\mathbf{A})$ is so small, it is possible to perturb this system so that even after a century, perturbations remain $>200\%$ of their original size.

The inset of Fig. 5 highlights an interesting phenom-

enon: transient growth actually occurs on two different time scales in the rain forest compartment model. The first corresponds to $\lambda_1(H(\mathbf{A}))$ and is extremely short. The second corresponds to $\lambda_2(H(\mathbf{A}))$, which also happens to be positive (8.5 yr^{-1}). The rest of the eigenvalues of $H(\mathbf{A})$ are negative. It appears that the competition between transient growth on the time scale $1/\lambda_2(H(\mathbf{A}))$ and asymptotic decay on the time scale $-1/\lambda_1(\mathbf{A})$ sets the value of t_{\max} . Thus we may not be able to find a generally applicable relationship between reactivity and the time to maximum amplification.

The tropical rain forest matrix is not a special case; reactive equilibria appear in parameterized models of real systems. O'Neill (1971) compiled 66 examples of estimated transfer matrices like Table 2, extracted from 23 papers in the ecological literature. Of these, 18 are matrices for closed systems and therefore had $\lambda_1(\mathbf{A}) = 0$; one matrix is unstable and another matrix is derived from this unstable one. Of the remaining 46 matrices, 31 are reactive. These 46 matrices are not independent, however, as 22 represent either aggregated versions of other matrices, or the flow of different elements through the same ecosystem, or slightly different experimental treatments of the same system.

An aquatic food chain manipulation

Pimm and Lawton (1977) predicted that resilience should decrease as food chains get longer. DeAngelis et al. (1989a, b) predicted that resilience should increase as the turnover rate of a limiting nutrient increases. These hypotheses were recently tested by Carpenter et al. (1992), who measured the flow of phosphorus through a lake ecosystem before and after a food web manipulation.

In 1984, Tuesday Lake in Wisconsin was dominated by planktivorous minnows. In 1985, Carpenter et al. added another trophic level to Tuesday Lake by introducing piscivorous largemouth bass, while removing enough minnows to maintain total fish biomass (Car-

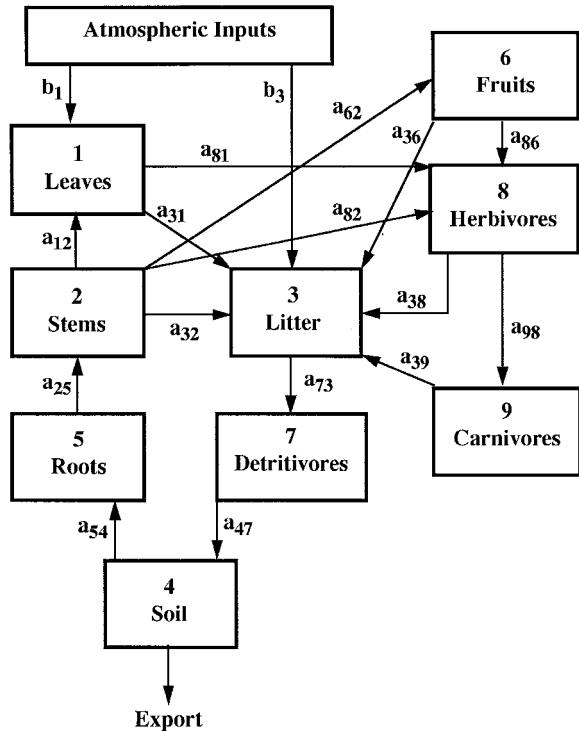


FIG. 4. A compartment model for the flow of elements through tropical rain forests. Matter flows in the direction of the arrows, from compartment j to compartment i at the fractional rate a_{ij} (modified after McGinnis et al. 1969).

TABLE 2. Transfer matrix for elemental dynamics in a Panamanian tropical forest (cf. McGinnis et al. 1969).

Compartment and number	1	2	3	4	5	6	7	8	9
Leaves	1	-1.5622 [†]	0.6685						
Stems	2		-0.7119						
Litter	3	1.4627	0.0364	-6.4091					
Soil	4				-0.0222				
Roots	5				0.0201	-2.5632			
Fruits and flowers	6		0.0070				-2.0348		
Detrivores	7			6.4091			-315.9443		
Herbivores	8	0.0995				0.8902		-62.6458	
Carnivores	9						6.8257	-17.2972	

[†] All entries are in units of yr⁻¹.

penter et al. 1987). Transfer matrices were estimated for both the 1984 planktivore-dominated system and for the piscivore-dominated system of 1986. These matrices (and their resiliences) were originally reported in Carpenter et al. (1992); we have reproduced them in Table 3. Using these matrices, the authors showed that the food web manipulation decreased phosphorus turnover rate by approximately 75%.

The resilience of the 1984 matrix (0.035) is approximately seven times larger than the resilience of the 1986 matrix (0.005), supporting the food chain length and nutrient turnover rate hypotheses. The piscivore-dominated lake is less stable in the long run.

In the short run, however, the food web manipulation had the opposite effect (Table 4). Reactivity, maximum amplification (ρ_{\max}), and the time to maximum amplification (t_{\max}) all decreased between 1984 and 1986. Fig. 6 shows how the manipulation changed the shape of the amplification envelope.

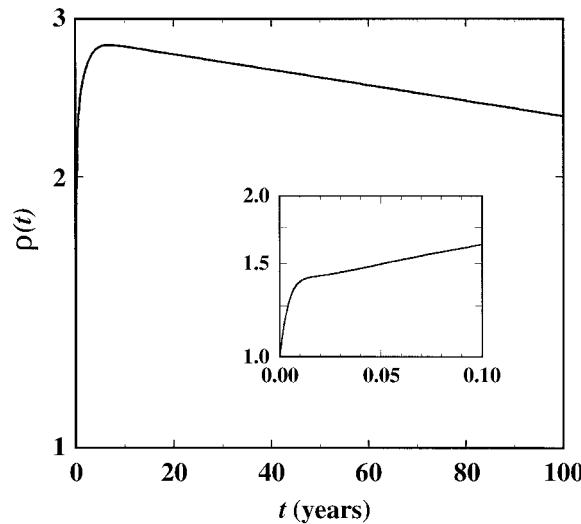


FIG. 5. The amplification envelope of the tropical rain forest matrix (cf. Table 2). The inset, an expanded view of the interval $0 < t < 0.1$, exhibits the two phases of transient growth that occur because both $\lambda_1(H(\mathbf{A}))$ and $\lambda_2(H(\mathbf{A}))$ are positive. (Note that P is plotted on a logarithmic scale.)

Carpenter et al. also calculated the sensitivity of the resilience to changes in the elements of \mathbf{A} . If the dominant right and left eigenvectors of \mathbf{A} are \mathbf{w}_1 and \mathbf{v}_1 , the matrix of sensitivities of $\lambda_1(\mathbf{A})$ is

$$\left(\frac{\partial \lambda_1(\mathbf{A})}{\partial a_{ij}} \right) = \frac{\mathbf{v}_1 \mathbf{w}_1^T}{\mathbf{v}_1^T \mathbf{w}_1} \quad (23)$$

(Jacobi 1846, Caswell 1978). The matrix of resilience sensitivities is then

$$\frac{\partial \text{resilience}}{\partial a_{ij}} = -\text{Re} \left(\frac{\mathbf{v}_1 \mathbf{w}_1^T}{\mathbf{v}_1^T \mathbf{w}_1} \right). \quad (24)$$

We have recalculated the sensitivities for the matrices in Table 3 and present them in Table 5. (The sensitivities in Table 5 differ from those reported by Carpenter et al. [1992] because we used a more accurate method for calculating eigenvectors [S. R. Carpenter, *personal communication*.]) Two facts emerge on examination of Table 5. First, in both the 1984 and 1986 matrices, resilience is most sensitive to changes in flow rates to and from the top trophic level (planktivores and piscivores, respectively). These were the lowest flow rates in the system (Table 3). Second, sensitivities to changes in each of the flow rates that existed in 1984 decreased by at least one order of magnitude after the addition of piscivores.

It is also possible to calculate the sensitivity of reactivity to changes in the elements of \mathbf{A} . Let h_{ij} denote the (i, j) element of $H(\mathbf{A})$, then

$$\frac{\partial \lambda_1(H(\mathbf{A}))}{\partial a_{ij}} = \frac{\partial \lambda_1(H(\mathbf{A}))}{\partial h_{ij}} \frac{\partial h_{ij}}{\partial a_{ij}} + \frac{\partial \lambda_1(H(\mathbf{A}))}{\partial h_{ji}} \frac{\partial h_{ji}}{\partial a_{ij}}, \quad (25a)$$

$$= \frac{1}{2} \frac{\partial \lambda_1(H(\mathbf{A}))}{\partial h_{ij}} + \frac{1}{2} \frac{\partial \lambda_1(H(\mathbf{A}))}{\partial h_{ji}}. \quad (25b)$$

Eq. 23 can be used to calculate the partial derivatives in Eq. 25b. Because the left and right eigenvectors of $H(\mathbf{A})$ are the same (call them \mathbf{u}_1) the resulting matrix of sensitivities is given by

$$\left(\frac{\partial \lambda_1(H(\mathbf{A}))}{\partial a_{ij}} \right) = \frac{\mathbf{u}_1 \mathbf{u}_1^T}{\mathbf{u}_1^T \mathbf{u}_1}. \quad (26)$$

The reactivity sensitivities for the 1984 and 1986

TABLE 3. Phosphorus transfer matrices for Tuesday Lake before and after the addition of piscivorous fish (cf. Carpenter et al. 1992).

Variable and number	1	2	3	4	5	6
1984						
Soluble phosphorus	1	-0.9503 [†]		0.0130	0.0056	0.0257
Seston	2	0.9500	-0.5900			
Zooplankton	3		0.0290	-0.2622		
<i>Chaoborus</i>	4			0.2000	-0.1752	
Planktivore	5			0.0192	0.0026	-0.0389
1986						
Soluble phosphorus	1	-0.9503		0.0690	0.0002	0.0027
Seston	2	0.9500	-0.1800			0.0034
Zooplankton	3		0.1500	-0.2569		
<i>Chaoborus</i>	4			0.1000	-0.0138	
Planktivore	5			0.0019	0.0002	-0.0124
Piscivore	6				0.0001	0.0028

[†] All entries are in units of d^{-1} .

matrices (Eq. 26, Table 6) contrast with the resilience sensitivities (Eq. 24, Table 5). In both years, resilience is more sensitive to changes in the flow rates near the top of the food chain (fishes), while reactivity is more sensitive to changes near the bottom of the food chain (plankton). The Tuesday Lake phosphorus cycle is regulated by plankton in the short term and by fishes in the long term. As a result, adding a new top predator (piscivores) did not change reactivity as dramatically as it changed resilience (Table 4). These results fit nicely with the conventional wisdom on nutrient dynamics (DeAngelis 1992; S. R. Carpenter, *personal communication*): lower trophic levels, with faster turnover rates, control short-term responses to perturbation, while higher trophic levels, with slower turnover rates, control long-term responses. Reactivity and resilience analyses quantify these relationships and combine to give a more complete understanding of the time scales of nutrient cycling.

A nonlinear predator-prey model

The compartment models we have examined so far are unusual among ecological models in that they are linear. In this section, we compare resilience and reactivity in a simple nonlinear predator-prey model, the stability of which can be adjusted by varying parameters. The model incorporates logistic growth of the prey population in the absence of its predator and saturating (Holling Type II) functional and numerical responses. If N and P , respectively, represent the densities of the prey and predator populations, we can write this model as

TABLE 4. Relative stability measures derived from the 1984 and 1986 phosphorus transfer matrices.

Measure	1984	1986
Resilience (d^{-1})	0.035	0.005
Reactivity (d^{-1})	0.148	0.069
Maximum amplification, ρ_{\max}	1.198	1.059
Time to maximum amplification, t_{\max} (d)	2.340	1.420

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{aNP}{N + b} \quad (27a)$$

$$\frac{dP}{dt} = \frac{caNP}{N + b} - dP. \quad (27b)$$

The model is parameterized by the prey's intrinsic growth rate (r) and carrying capacity (K), the saturation level (a) and half-saturation constant (b) of the predator's functional response, and the predator's yield coefficient (c) and mortality rate (d). The change of variables

$$y_1 = N/b \quad y_2 = aP/(rb) \quad \tau = rt \quad (28a)$$

$$\kappa = K/b \quad \alpha = (ac)/r \quad \beta = d/(ac) \quad (28b)$$

has the advantage of casting Eq. 27 into the dimensionless form

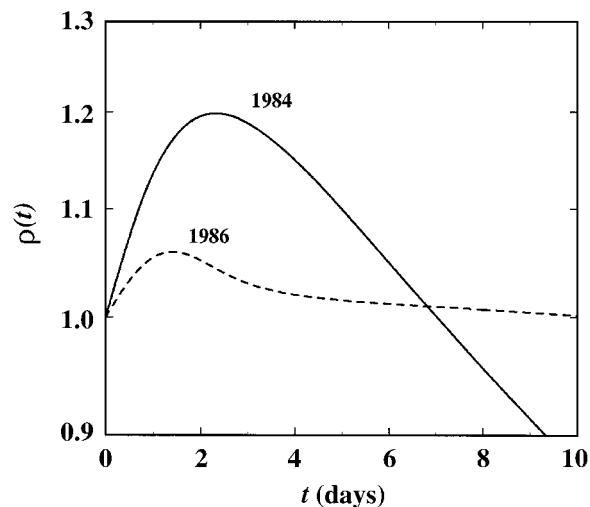


FIG. 6. Amplification envelopes of the 1984 and 1986 Tuesday Lake phosphorus flow matrices (cf. Table 3). After adding piscivorous fish in 1985, resilience (a measure of long-term stability), reactivity, t_{\max} , and ρ_{\max} (measures of short-term instability) all decreased.

TABLE 5. Sensitivities of resilience to changes in the elements of the Tuesday Lake phosphorus transfer matrices.

Variable and number	1	2	3	4	5	6
1984						
Soluble phosphorus	1	-0.0038		-0.0194	-0.0278	-0.1199
Seston	2	-0.0037	-0.1465			
Zooplankton	3		-0.1203	-0.0154		
<i>Chaoborus</i>	4			-0.0033	-0.0047	
Planktivore	5			-0.1345	-0.1921	-0.8296
1986						
Soluble phosphorus	1	-0.0001		-0.0002	-0.0021	-0.0001
Seston	2	-0.0001	-0.0003			-0.0120
Zooplankton	3		-0.0004	-0.0002		
<i>Chaoborus</i>	4			-0.0003	-0.0034	
Planktivore	5			-0.0058	-0.0644	-0.0032
Piscivore	6				-0.1715	-0.0084
						-0.9929

$$\frac{dy_1}{d\tau} = y_1 \left(1 - \frac{y_1}{\kappa} \right) - \frac{y_1 y_2}{y_1 + 1} \quad (29a)$$

$$\frac{dy_2}{d\tau} = \alpha \left(\frac{y_1 y_2}{y_1 + 1} - \beta y_2 \right) \quad (29b)$$

which has only three parameters.

The model (Eq. 29) has three equilibria. We will consider only the equilibrium (y_1^*, y_2^*) , at which the predator and prey coexist:

$$y_1^* = \frac{\beta}{1 - \beta} \quad y_2^* = (1 + y_1^*) \left(1 - \frac{y_1^*}{\kappa} \right). \quad (30)$$

In a small enough neighborhood of this equilibrium, the linear approximation (Eq. 1) holds, with a community matrix \mathbf{A} given by

$$\mathbf{A} = \begin{pmatrix} \left(1 - \frac{2y_1^*}{\kappa} - \frac{y_2^*}{(1 + y_1^*)^2} \right) & -\beta \\ \frac{\alpha y_2^*}{(1 + y_1^*)^2} & 0 \end{pmatrix}. \quad (31)$$

When β and κ satisfy the inequalities

$$\frac{\kappa - 1}{\kappa} < \frac{\beta}{1 - \beta} < \kappa, \quad (32)$$

the eigenvalues of \mathbf{A} have negative real parts, and thus

the equilibrium is stable. If the left-hand inequality is violated, the eigenvalues cross the imaginary axis as a complex conjugate pair, and the equilibrium gives way to a stable predator-prey cycle. Violation of the right-hand inequality produces real eigenvalues, one of which is positive, and results in extinction of the predator.

Fig. 7 (a, c, and e) displays resilience, reactivity, ρ_{\max} , and t_{\max} , as functions of β , for fixed α and κ , over the range of predator mortality rates (β) where Eq. 32 is satisfied. Resilience peaks at intermediate values of β , whereas reactivity tends to increase with increasing β , eventually levelling off and even declining slightly at the highest values. Thus, increasing predator mortality over the range (0.05, 0.25) increases long-term stability (resilience goes up), but reduces short-term stability (reactivity also goes up). But, over the interval (0.25, 0.5) long-term stability declines sharply whereas reactivity changes very little. Clearly, there is no simple relationship between these four relative stability measures. Parameter changes that produce increased asymptotic stability (by increasing resilience) can simultaneously produce increased transient instability (by increasing reactivity, ρ_{\max} , or t_{\max}).

Note that in the limit as β goes to zero, $\lambda_1(\mathbf{A})$ goes to zero and the linearization (Eq. 31) incorrectly pre-

TABLE 6. Sensitivities of reactivity to changes in the elements of the Tuesday Lake phosphorus transfer matrices.

Variable and number	1	2	3	4	5	6
1984						
Soluble phosphorus	1	0.1576		0.0173	0.0068	0.0118
Seston	2	0.3637	0.8393			
Zooplankton	3		0.0399	0.0019		
<i>Chaoborus</i>	4			0.0007	0.0003	
Planktivore	5			0.0013	0.0005	0.0009
1986						
Soluble phosphorus	1	0.1672		0.1084	0.0653	0.0042
Seston	2	0.3510	0.7369			0.0039
Zooplankton	3		0.2275	0.0702		
<i>Chaoborus</i>	4			0.0423	0.0255	
Planktivore	5			0.0027	0.0016	0.0001
Piscivore	6				0.0015	0.0001

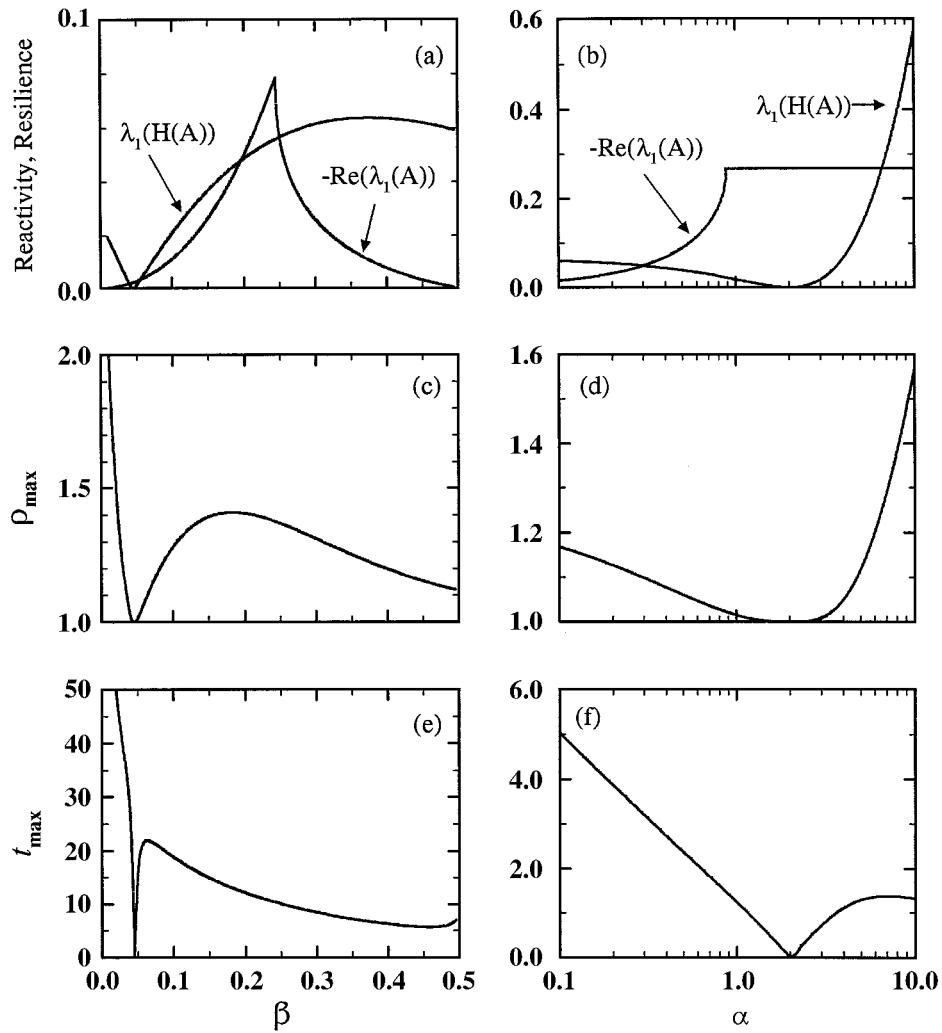


FIG. 7. Resilience (a, b), reactivity (a, b), ρ_{\max} (c, d), and t_{\max} (e, f), of model (29) as functions of the predator mortality rate β and the maximum predator growth rate α (cf. 28b). In panels (a), (c), and (e), $\alpha = 0.05$; in panels (b), (d), and (f), $\beta = 0.4$. The carrying capacity was held constant at $\kappa = 1$.

dicts that the magnitude of almost all perturbations will grow without bound. (In fact the nonlinearities in Eq. 29 prevent this from happening.) Thus ρ_{\max} and t_{\max} diverge in the limit $\beta \rightarrow 0$, where they become undefined.

Fig. 7 (b, d, and f) also shows the effects of changes in the maximum predator growth rate α on our relative stability measures. For $\alpha > 1$, the equilibrium is a focus, and the real parts of its eigenvalues are independent of α . But the eigenvalues of $H(A)$ do depend upon α , producing changes in the measures of short-term instability ($\lambda_1(H(A))$, ρ_{\max} , and t_{\max}) without affecting asymptotic stability.

DISCUSSION

Most ecological theory, even that theory dealing with the wildest of nonequilibrium dynamics, chaos, focuses on asymptotic behavior (Hastings et al. 1993).

The theory of the resilience of ecosystems, communities, and populations is one example. This emphasis on asymptotic behavior partly reflects a belief that dynamics are more important than history, but it is also partly due to the usefulness of linearization in studying nonlinear systems near asymptotically stable attractors. The asymptotic behavior of solutions of the linearized system is easily described by the dominant eigenvalue—hence ecological theory's obsession with eigenvalues. The purpose of this paper has been to point out one of the pitfalls of eigenvalue analysis in the context of ecological models, and to provide some simple alternatives for characterizing transient behavior.

As is true for almost all ecological stability theory, we have focused on linear dynamics near an equilibrium. Nonlinearity, in contrast, is notorious for producing longer and/or larger transients. It can produce long, apparently chaotic transients in simple discrete-

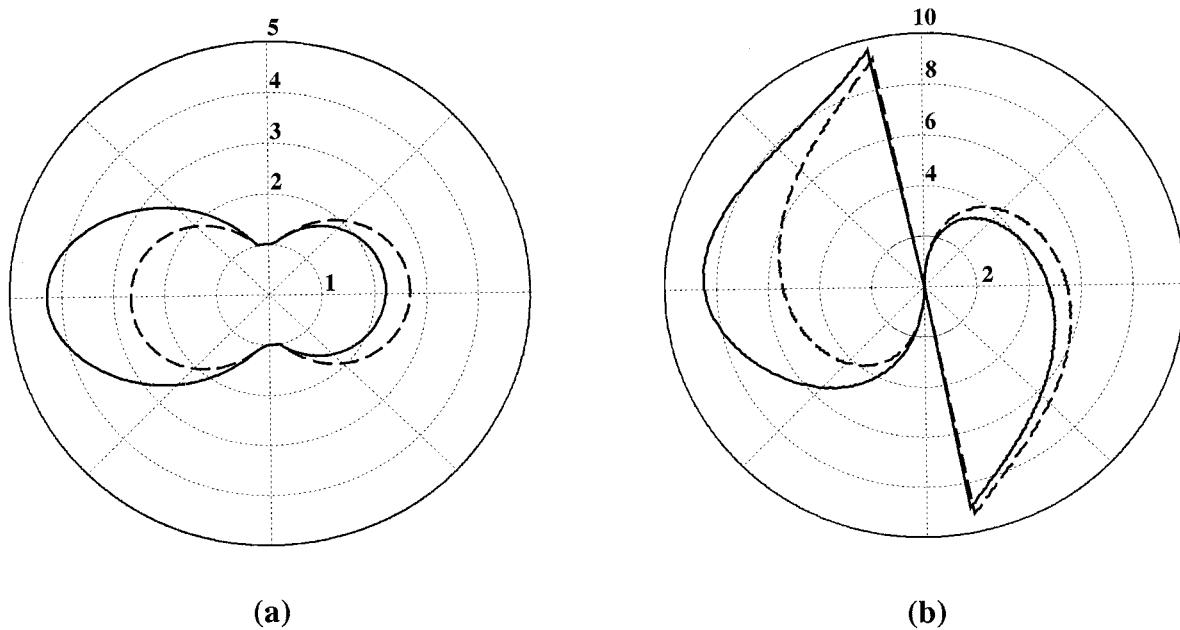


FIG. 8. The effect of nonlinearity and initial conditions on maximum amplification and time to maximum amplification. For each angle θ , the equilibrium (30) of the nonlinear model (29) was perturbed 0.1 units in the direction θ . The model and its linearization were then integrated (with parameter values $\alpha = 1$, $\beta = 0.1$, $\kappa = 1$). The maximum amplification of each perturbation (a) and the time to maximum amplification of each perturbation (b) are plotted (in polar coordinates) as the distance from the origin for each θ . Solid curves correspond to the nonlinear model; dashed curves correspond to its linearization.

time predator-prey models (Hadeler and Gerstmann 1990, Neubert and Kot 1992) and in spatial models of single populations (Hastings and Higgins 1994). A nonlinear model of nontransitive competition (May and Leonard 1975) produces solutions that are essentially entirely transient, asymptotically approaching cycle-graphs.

Nonlinearity can also enhance the amplification of perturbations predicted by the analysis of a linearized system. As an example, Fig. 8 compares the results of integrating the predator-prey model (Eq. 29) and its linearization from initial conditions representing small perturbations to the stable equilibrium. Each perturbation had the same magnitude (0.1) but was in a different direction. In Fig. 8a, the maximum amplification of the perturbation is plotted (in polar coordinates) as the distance from the origin (r) as a function of its direction (θ , the angle between the perturbation and the positive x axis). The time needed for a perturbation to achieve its maximal amplification is plotted as a function of its direction in Fig. 8b. Of the perturbations that grew at all, and that initially decreased the prey population, all grew larger than predicted by the linearization, and most grew larger than predicted by ρ_{\max} . They also took longer to do so than predicted by the linearization. The opposite is true for perturbations that initially increased the prey population.

In addition to displaying the way nonlinearity can modify the predictions of the linear theory, Fig. 8 highlights another limitation of that theory. The reactivity

of a system is the growth rate of a *particular* perturbation. There is also a *particular* perturbation that achieves the amplification ρ_{\max} at time t_{\max} —usually not the perturbation corresponding to the reactivity. In some reactive systems, the majority of perturbations may decay monotonically! The amplification envelope, and its characteristics, including resilience, are “worst case” measurements. This leads us to suggest the integral

$$T_R = \int_0^\infty \rho(t) dt \quad (33)$$

as an alternative to Eq. 8, and as a worst case measure of return time.

Throughout this paper we have measured the magnitude of a vector \mathbf{x} by its Euclidean norm (Expression 6). The results we derived are specific to this norm, and will be different in other norms. In particular, for a given linear system with an asymptotically stable equilibrium and distinct eigenvalues, one can always find a norm in which the size of perturbations is bounded above by a monotonically decaying exponential (Lozinskij 1958, Dahlquist 1959, Coppel 1965). Using this norm is equivalent to changing the coordinates so that the eigenvectors of \mathbf{A} become perpendicular. Such a change of coordinates obscures the biological meaning of the variables, and in effect hides the existence of transient growth in the original variables. In addition, this norm will be different for different systems,

making comparisons between systems difficult. We have used the Euclidean norm because it corresponds to the physical notion of length and because it has been used almost universally by other authors studying the subject of stability in ecological models.

Our results suggest a number of interesting open questions. For example, in the Introduction, we mentioned a number of ecosystem properties that have been studied with respect to their effects on resilience. It would be interesting to see how these properties affect the reactivity and the amplification envelope of simple models. Although our main results here are in terms of calculation from mathematical models, they have implications for empirical studies. If a system is stable but reactive, a perturbation experiment may produce a trajectory that moves farther away from the initial state, rather than returning to it. If the transient growth lasts long enough (say, longer than the median duration of NSF grants), conclusions about stability and resilience based on the response to the perturbation may be erroneous.

Finally, we note that real ecosystems are seldom if ever subject to single, temporally isolated perturbations. Nevertheless, our analyses, together with most theoretical and experimental studies of resilience, ignore the effects of continual stochastic disturbances in the hope that the deterministic results will shed light on the stochastic case. Developing a theory of reactivity for stochastic systems is a significant problem in its own right, but our preliminary results suggest that reactive systems are more variable than nonreactive systems subject to the same stochastic forcing.

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