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MEASURING RESILIENCE IN STOCHASTIC SYSTEMS

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Abstract. This paper develops mathematical and statistical techniques for measuring the resilience of inherently stochastic ecological systems. To correspond to the deterministic idea of resilience measured by the return time to equilibrium following perturbation, resilience in stochastic systems is defined as the variability in population densities relative to environmentally driven variability in population growth rates. Stochastic resilience defined in this way is calculated from a community matrix describing the average interaction strengths within and among species. The procedure to calculate stochastic resilience is demonstrated on simulated data sets consisting of time series of population densities. The simplicity of the procedure makes it a potential tool for application to a wide range of ecological communities.

Key words: community ecology; population dynamics; resilience; stability; stochastic models.

INTRODUCTION

The concept of stability is one of the most challenging in ecology. Although the term “stability” can take a variety of meanings (Leigh 1965, 1975, May 1974, Bender et al. 1984, Pimm 1984a, DeAngelis and Waterhouse 1987), many definitions involve the time required for populations to return to equilibrium following external perturbations; the more stable the population, the more rapidly it returns to equilibrium, while unstable populations never return. A conceptual difficulty with this definition is that it requires population densities to remain relatively constant (in the absence of a disturbance), allowing the identification of both equilibrium densities and environmental perturbations. Although there are communities in which population densities are sufficiently constant, and perturbations sufficiently large and infrequent to estimate return times to equilibrium (e.g., Steinman et al. 1991, Carpenter and Kitchell 1993, Cottingham and Carpenter, 1994), these communities are probably exceptions to the general rule of highly variable population densities in nature (e.g., Bigger 1976, Wolda 1978, Weins 1984, Strong 1986a, b). To apply generally to ecological communities, stability needs to be defined for stochastic systems in which environmental perturbations are continuous and equilibrium densities are never achieved.

For stochastic systems, two factors determine the degree of variability in population densities. First, variability in population densities depends on the sensitivity of population growth rates to environmental fluctuations; populations with birth or death rates that respond strongly to environmental changes will consequently have greater fluctuations in density. For example, mosquitoes are more sensitive to daily temperature fluctuations than are moose and therefore show greater population fluctuations from one day to the next. The deterministic counterpart of this sensitivity of population growth rates to environmental fluctuations is resistance, defined as the magnitude of change in population density brought about by an instantaneous environmental perturbation (Pimm 1984a). Second, population variability depends on the degree to which fluctuations in population growth rates are buffered by density-dependent feedbacks operating through interactions within and among species. For example, if high population densities lead to intense intraspecific competition while low population densities produce large population growth rates, competition will act to buffer populations against environmental variability. The deterministic counterpart to this second component of population variability in stochastic systems is the characteristic return time to equilibrium following perturbations, or the resilience of the system (Pimm 1984a). Just as the characteristic return time measures the rate of return to equilibrium independently of the size of the perturbation, the variability in population densities relative to the variability in population growth rates is independent of the sensitivity of population growth rates to environmental fluctuations. Therefore, to give a definition of stochastic resilience that is comparable to characteristic return times in deterministic systems, this paper develops the idea of stochastic resilience as the ratio of variability in population densities to variability in population growth rates. The more variable the population densities relative to population growth rates, the less resilient is the system.

For this definition of stochastic resilience, the same mechanisms that increase resilience in deterministic systems increase resilience in stochastic systems. In deterministic systems, if populations perturbed far from equilibrium return rapidly to equilibrium, then the system will have greater deterministic resilience
(May 1974). In stochastic systems, perturbations are continuous, so a deterministic equilibrium is never reached. However, if populations perturbed far from mean densities tend to move rapidly back towards mean densities, then the system will have greater stochastic resilience, since this will reduce the variability in population density. The similarity between deterministic and stochastic resilience is more than heuristic. As shown below, the procedure for calculating characteristic return times in deterministic systems is similar to the procedure for calculating the variance in population densities in stochastic systems. For deterministic systems, the procedure involves constructing a community matrix that gives the strength of interactions among all species at their equilibrium densities. The maximum eigenvalue of the community matrix then gives the characteristic return time of the system to equilibrium. For stochastic systems, the procedure to measure variances in population densities involves constructing a stochastic community matrix composed of the average interaction strengths among species. The eigenvalues of this stochastic community matrix give the variances in population densities relative to the environmentally driven variances in population growth rates. This relationship between stochastic and deterministic resilience allows the transfer of much of our understanding of deterministic stability directly to stochastic systems.

In experimental studies, researchers have measured resilience in two ways. First, resilience can be measured after a perturbation as the time it takes for populations to return to some pre-disturbance condition. Resilience measured in terms of recovery time has been used in both laboratory (e.g., Steinman et al. 1991) and field (e.g., Grimm and Fisher 1989) studies in which either manipulated or natural perturbations are large. The difficulty with this procedure is determining when a population has recovered (DeAngelis et al. 1989). Second, resilience has been measured in terms of variability in population densities in both the laboratory (e.g., Luckinbill and Fenton 1978, Lawler and Morin 1993) and the field (e.g., Pimm 1984b). A potential problem with this approach is confounding resilience with resistance. Low observed variability in population densities could result either from high resilience or from high resistance. An additional problem with measuring resilience from population variability is deriving a community-level measure of resilience—how should population variability of different species be combined to give a single measure to characterize resilience? Since resilience is determined by the interactions among species, it is a property of the entire system rather than of separate species.

The purpose of this paper was to develop techniques to measure stochastic resilience that can be applied directly to time series data of population densities. The techniques are based on characterizing the variability in population densities relative to the environmental variability driving population fluctuations. The paper is divided into three sections. First, a numerical example is given to illustrate the problem of determining the source of population variability in stochastic systems. Second, a general procedure is developed to calculate the stochastic resilience of a system from time series data. Finally, the ability of this procedure to capture the sources of variability in population dynamics is tested using the numerical example.

A Stochastic Predator–Prey Model

In this section, I develop a stochastic model for predator–prey interactions to illustrate how environmental variability and population interactions combine to drive variability in population densities. The model is given by the equations:

\[ x_1(t + 1) = \text{Exp}[\mu_1(t)][rx_1(t)(1 - x_1(t)/K) - ax_1(t)x_2(t)/(1 + ux_1(t))] \]

\[ x_2(t + 1) = \text{Exp}[\mu_2(t)][vax_1(t)x_2(t)/(1 + ux_1(t)) - dx_2(t)]. \]

Here, \( x_1(t) \) and \( x_2(t) \) are the densities of prey and predator, respectively, at time \( t \). The dynamics of the prey are governed by logistic growth with intrinsic rate of increase \( r \) and carrying capacity \( K \). Predation follows a Type II functional response in which \( u \) determines how rapidly the predation rate saturates at high prey density (Holling 1959); large values of \( u \) imply that per capita predation rates decrease rapidly at high prey density. The predator attack rate at low prey density is given by the parameter \( a \). The parameter \( v \) scales the assimilation of depredated prey into the predator population growth rate, and \( d \) is the density-independent death rate of the predator. Both prey and predator suffer environmental fluctuations in population growth rates incorporated into the random variables \( \mu_1(t) \) and \( \mu_2(t) \), which are assumed to follow independent normal distributions with means of 0. This general form of equations describing predator–prey interactions has been used in a variety of contexts (May 1981) and has been found to approximate reasonably some natural systems (Carpenter et al. 1994).

Four trajectories generated from Eq. 1 are shown in Fig. 1. In all four, parameters are chosen to give mean prey and predator densities of 10 and 1, respectively. The difference between Fig. 1a and b is caused by differences in the environmentally driven variability in population growth rates: in Fig. 1b the variances of \( \mu_1(t) \) and \( \mu_2(t) \) are four times those in Fig. 1a, resulting in greater population variability. In contrast, the difference between Fig. 1a and c is caused by an increase in the intrinsic rate of increase of the prey, \( r \); the variances of \( \mu_1(t) \) and \( \mu_2(t) \) are the same in both graphs. Fig. 1d differs from Fig. 1a in that the variance in \( \mu_1(t) \) is increased by a factor of four, while the variance in \( \mu_2(t) \) is decreased to 0.

This example illustrates the problem of resilience in
stochastic systems. Comparing Fig. 1a and c, increasing \( r \) decreases the resilience in the system, in the sense that it increases the variance in population densities under the same environmental regime. Comparing Fig. 1b and c, variability in population densities depends on both the degree of environmental variability and interaction among species; although in both graphs the variances in densities are similar, in Fig. 1b the variances are driven more by environmental variability and in Fig. 1c they are driven more by interactions among species. Fig. 1d illustrates the confounding effect of species interactions in determining the source of variability in population densities of individual species. Even though there is no direct effect of environmental fluctuations on the predator population growth rate, variation in prey density drives variation in predator density. The objective in defining stochastic resilience is to disentangle the sources of population variability into those driven by environmental variability and those driven by interactions among species. If the component driven by interactions among species is relatively small, then the system is relatively resilient.

**Stochastic Resilience**

The goal of this section is to develop tools to look generally at the sources of population variability in stochastic systems. The procedure outlined below partitions population variability into that driven by external, environmental influences and that driven by the interactions among organisms in the community. By partitioning the sources of population variability, this procedure makes it possible to measure stochastic resilience as the degree of population variability relative to environmentally driven variability in population growth rates.

The basic procedure for measuring stochastic resilience begins by applying linear regression to the data to extract the linear component of the interactions among species. This produces a matrix of interaction terms comparable to the community matrix used in calculating characteristic return times in deterministic models. It is then possible to calculate the variance in population densities along the eigenvectors corresponding to the eigenvalues of the matrix of interaction terms. Calculating variances along the eigenvectors has the pragmatic advantage of greatly simplifying the covariance structure of the population densities in a community; the covariances between population densities along different eigenvectors are 0. Comparing the variance in population densities to the environmental variance along the same eigenvectors gives the desired measure of stochastic resilience. This analysis is presented in the first subsection below.

The basic analysis uses linear regression, and because interactions among species will most likely not be linear, the second subsection addresses the problem of non-linear interactions among species. The third subsection analyzes the case in which data on the pop-
ulation dynamics of only a single species are available, even though the pattern of dynamics in the single-species data suggest interactions with other species (Royama 1981, Turchin and Taylor 1992). Since good data sets on the population dynamics of all species in a community are rare, this subsection attempts to broaden the applicability of the analysis. Finally, the fourth subsection addresses temporal autocorrelation in the environmental variability that drives fluctuations in population densities. Environmental autocorrelation may increase the observed variance in population densities and therefore presents a potential problem in characterizing the stochastic resilience of a system.

**Linear analysis**

The initial step is to formulate the equations governing population dynamics in terms of the linear components of interactions within and among species. For a community with $S$ species, the population dynamics of each species can be described by equations of the form:

$$x_i(t + 1) = b_{i,0} + b_{i,1}x_i(t) + b_{i,2}x_j(t) + \ldots + b_{i,S}x_S(t) + \epsilon_i(t, x_1(t), \ldots, x_S(t)). \quad (2)$$

Eq. 2 has the form of multiple linear regression of $x_i(t + 1)$ against population densities in the preceding generation, with regression coefficients $b_{ij}$ and error term $\epsilon_i(t, x_1(t), \ldots, x_S(t))$. Environmental variability affecting the system occurs in the variance of the error term. As an important departure from standard regression models, the error term $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ may depend on the independent variables $x_j(t)$. Therefore, Eq. 2 is not an approximation of a more general non-linear model, but is instead a formulation of a non-linear model that extracts out the linear dependence of population dynamics on densities. Even though Eq. 2 represents a non-linear model, the coefficients $b_{ij}$ are calculated using least squares regression in the standard fashion.

In Eq. 2, $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ represents the residuals of linear regression with population densities as independent variables. Therefore, $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ includes not only variability in population growth rates driven by environmental variability, but also variability in population growth rates that is not explained by the linear interactions among species. For example, if Eq. 2 is non-linear, even in the absence of environmental variability there will be variance in $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ whenever the populations show non-stationary dynamics, such as stable limit cycles. The inclusion of the effects of non-linearities means that $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ does not measure only environmental variability. However, this being acknowledged, the analysis can proceed and the issue of separating the true environmental component of $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ left to the next subsection.

Several additional comments are necessary about Eq. 2. First, all stochastic variability in the model occurs in the error term $\epsilon_i(t, x_1(t), \ldots, x_S(t))$. Therefore, the cause of environmental variability is not explicitly included in the model, and $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ may represent a combination of many environmental events. Also, environmental variability is assumed to affect population growth rates directly, rather than some other property of population dynamics, such as the carrying capacity of the species (May 1973, 1974, Feldman and Roughgarden 1975, Turelli 1977, Pimm 1984). Second, in Eq. 2 environmental variability is calculated from the observed variance in population growth rates rather than from measurements of known environmental factors influencing populations. This distinction has important consequences for the case when environmental factors influencing population growth rates are positively autocorrelated, producing a greater chance of successively “good” or successively “bad” environmental conditions. Eq. 2 assumes there is no autocorrelation in the error terms, so $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ is independent of $\epsilon_i(t - 1, x_1(t - 1), \ldots, x_S(t - 1))$. The problem of environmental autocorrelation is treated separately in the subsection entitled Delayed density dependence, below. Third, the estimation of parameter values depends on the range of population densities in the data set. Therefore, the estimated parameters only represent the observed data, and if the data set is short relative to the naturally occurring variation in population densities and environmental variability, then the estimated parameters may not represent the long-term dynamics of the community. This limits the technique to being primarily an interpretive tool for the population dynamics observed in a particular data set rather than a predictive tool for population dynamics beyond the range of observed population densities. Fourth, Eq. 2 does not include error associated with the measurement of population densities; exact population densities are assumed to be known (Walters and Ludwig 1981). Measurement error can be introduced into the analysis, although at this stage it is excluded for simplicity. Fifth, just as in standard linear regression, independent variables $x_i(t)$ may be transformed to increase the linearity of the data and improve the fit of the model. This will increase the precision of estimates of the parameters $b_{ij}$ and will decrease the variance in $\epsilon_i(t, x_1(t), \ldots, x_S(t))$ resulting from non-linear interactions among species. Finally, the regression parameters $b_{ij}$ are phenomenological descriptors of interactions among species that are not intended to recover the underlying mechanisms governing these interactions. Precise characterization of interactions among species will necessarily require more detailed non-linear analyses. Rather than investigate the details of interactions among populations, the focus here is identifying community scale patterns of population variability.

Calculating the regression coefficients $b_{ij}$ using least squares produces a critical property for the analysis. Even though Eq. 2 represents a non-linear model, both
the mean of the error term, \( M[\varepsilon_t, x_1(t), \ldots, x_n(t)] \), and the mean of the product of error term and densities, \( M[x_1(t) \varepsilon_t, x_2(t), \ldots, x_n(t)] \), equal 0; this result follows from the derivation of least squares linear regression (Appendix 1). From this, the variance in the sum of the random variables \( x(t) + \varepsilon(t, x_1(t), \ldots, x_n(t)) \), denoted \( V[x(t) + \varepsilon(t)] \), equals the sum of the variances, since:

\[
V[x(t) + \varepsilon(t)] = M[(x(t) + \varepsilon(t))^2] - (M[x(t)] + M[\varepsilon(t)])^2
\]

\[
= M[x(t)^2] + 2M[x(t)\varepsilon(t)] + M[\varepsilon(t)]^2 - (M[x(t)] + M[\varepsilon(t)])^2
\]

\[
= V[x(t)] + V[\varepsilon(t)]. \tag{3}
\]

Thus, even though \( x(t) \) and \( e(t, x_1(t), \ldots, x_n(t)) \) are not independent, the covariance between them is 0. The significance of this result is shown later.

The equations governing the population dynamics of the \( S \) species in a community can be written in matrix form as:

\[
X(t + 1) = bX(t) + U(t), \tag{4}
\]

where

\[
X(t) = [x_1(t), x_2(t), \ldots, x_n(t)],
\]

\[
U(t) = [\varepsilon_1(t) + b_{13}, \varepsilon_2(t) + b_{23}, \ldots, \varepsilon_n(t) + b_{n3}],
\]

and \( b \) is the \( S \times S \) matrix with elements \( b_{ij} \) (\( i, j = 1, \ldots, S \)). Matrix \( b \), in all but the rarest cases, will have \( S \) distinct eigenvalues (May 1974). Let \( n \) be the number of real eigenvalues, \( \lambda_i \), and \( 2m \) be the number of complex eigenvalues occurring as \( 2m \) conjugate pairs of the form \( \alpha_i \pm \beta_i I \) (\( n + 2m = S \)). Matrix \( b \) can be written in terms of its eigenvalues and corresponding eigenvectors as \( b = \sum I \) (Cronin 1980), where \( I \) is an \( S \times S \) diagonal matrix with diagonal elements \( J_i \) of the form:

\[
J_i = \lambda_i \quad \text{for } 1 \leq i \leq n
\]

\[
J_j = [\alpha_j, \beta_j, -\beta_j, \alpha_j] \quad \text{for } n < j \leq n + m. \tag{5}
\]

For \( 1 \leq i \leq n \), column \( i \) of \( \tau \) consists of the eigenvector corresponding to the real eigenvalue \( \alpha_i \), while for \( n < j \leq n + m \), consecutive columns consist of the real and complex parts of the eigenvector corresponding to the eigenvalue \( \alpha_i \pm \beta_i I \). The magnitude of eigenvectors, defined as the square root of the sum of squared terms, is arbitrary. Therefore, the magnitude of the columns of \( \tau \) may be set to 1 in the case of real eigenvalues, and for complex eigenvalues the average magnitude of consecutive columns may be set to 1.

If new variables \( Y(t) \) and \( W(t) \) are defined by the equations \( \tau Y(t) = X(t) \) and \( \tau W(t) = U(t) \), Eq. 4 can be written as

\[
Y(t + 1) = jY(t) + W(t). \tag{6}
\]

Eq. 6 describes the same dynamical system as Eq. 4, but in terms of axes given by the eigenvectors of \( b \) rather than axes given by the density of each species. Since each element of \( Y(t) \), \( y_i(t) \), is a linear combination of values of \( x(t) \), \( y_i(t) \) represents a composite measure of population densities within the community along the axes defined by the eigenvector of the \( i \)th eigenvalue. Similarly, \( W(t) \) represents the residuals from linear regression along the axes given by the eigenvectors of \( b \).

The objective of this approach is to identify how much of the variance in population densities is driven by environmental variability. This problem is complicated if the distribution of environmental variability changes over the course of the data set. For example, if the variance in environmental factors influencing population growth rates increased through time, the variance in population densities will also increase.

There would then be no time-independent variance in population densities, and the problem of identifying the component of population variability attributable to environmental variability becomes more difficult. Identifying and removing environmental trends is a common problem in analyzing time series that extends beyond the scope of this paper (Wei 1990, Turchin and Taylor 1992). Therefore, I assume that the environmental distribution is stationary, implying that the distribution of population densities is also stationary.

The variance in population densities at the stationary distribution can be calculated from Eq. 6 in terms of the composite density variables \( y_i(t) \). When the eigenvalue is real, \( y_i(t + 1) = \lambda_i y_i(t) + w_i(t) \), and taking variances on both sides of the equality gives:

\[
V[y_i(t + 1)] = V[\lambda_i y_i(t) + w_i(t)]
\]

\[
= \lambda_i^2 V[y_i(t)] + V[w_i(t)]. \tag{7}
\]

Separating the variances of \( y_i(t) \) and \( w_i(t) \) in this equation is possible because \( y_i(t) \) and \( w_i(t) \) are linear combinations of \( x(t) \) and \( \varepsilon_i(t, x_1(t), \ldots, x_n(t)) \), respectively, and Eq. 3 demonstrates that the covariance between \( x(t) \) and \( \varepsilon_i(t, x_1(t), \ldots, x_n(t)) \) is 0. At the stationary distribution, the variances in \( y_i(t) \) and \( y_i(t + 1) \) must be equal. Therefore, letting \( V[y_i] \) denote the variance in \( y_i(t) \) at the stationary distribution,

\[
V[y_i] = V[w_i]/(1 - \lambda_i^2). \tag{8}
\]

As shown in Appendix 2, the eigenvalue \( \lambda_i \) must be between \(-1\) and \( 1 \). Thus, for a given value of \( V[w_i] \), the variance in \( y_i \) decreases as \( \lambda_i \) approaches 0.

When the eigenvalues are complex, equations governing the variances of consecutive values of \( y_{2j}(t) \) and \( y_{2j+1}(t) \) corresponding to eigenvalues \( \alpha_j \pm \beta_j I \) are
This set of equations can be solved to give the sum of variances of \( y_{2,1}(t) \) and \( y_{2,1}(t) \) at the stationary distribution of population densities:

\[
V[y_{2,1}(t + 1)] = \alpha_i^2 V[y_{2,1}(t)] + \beta_i^2 V[y_{2,1}(t)] + 2\alpha_i \beta_i \text{COV}[y_{2,1}(t), y_{2,1}(t)] + V[w_{2,1}(t)]
\]

This equation is similar to Eq. 10.

The strategy of this analysis is to recast the equations governing population dynamics in terms of composite measures of population densities along axes determined from the eigenvectors of the community matrix \( B \). The easiest way to visualize the results is with a phase portrait that gives the combinations of population densities \( [x_1(t), x_2(t), \ldots, x_n(t)] \) at each point in time; this is illustrated for a hypothetical community of two species in Fig. 2. In the example, both eigenvalues \( \lambda_1 \) and \( \lambda_2 \) are real, and the corresponding axes given by the eigenvectors are labeled \( A_1 \) and \( A_2 \). From Eq. 8, the amount of observed variability in population densities along \( A_1 \) equals the composite variance of \( \epsilon_i(t), x_i(t), x_j(t) \) and \( \epsilon_j(t), x_i(t), x_j(t) \) along \( A_1 \) divided by \( (1 - \lambda_i^2) \). The variance in population densities along \( A_2 \) is calculated analogously. The lower the values of \( \lambda_1 \) and \( \lambda_2 \), the lower the variances in population densities along \( A_1 \) and \( A_2 \), implying greater stochastic resilience. The case for complex eigenvalues \( \alpha_i \pm \beta_i \) given by Eq. 10 is similar, although rather than defining a single direction, the eigenvectors of \( \alpha_i \pm \beta_i \) define a plane. Lower values of \( \lambda_i \) imply lower population variance in this plane, and hence greater resilience.

Conceptually, this stochastic analysis is similar to principal components analysis. Given a multivariate data set, principal components analysis calculates variances along principal and minor axes. These axes correspond to eigenvectors and the variances correspond to eigenvalues of the variance–covariance matrix for the data set (Sokal and Rohlf 1981). The variance–covariance matrix contains the variances of each of the variables along the diagonal, and the covariances in the off-diagonal elements. In the analysis here, the matrix \( B \) contains regression coefficients rather than variance–covariance terms. This difference is due to the fact that stochastic resilience is measured from time series data, while there is no temporal structure to the data used in principal components analysis. As a result, eigenvalues calculated from \( B \) may be complex, while eigenvalues in principal components analysis are always real.

This stochastic analysis has close parallels to standard eigenvalue analysis of deterministic systems. The eigenvalues for deterministic systems are calculated from a linear approximation of the equations at equilibrium. Each eigenvalue gives the population dynamics in the direction of its corresponding eigenvector. Thus, for a real eigenvalue \( \lambda_i \) (where the squiggle bar denotes the deterministic case), the dynamics along \( A_i \) are governed by \( \Delta y_i(t + 1) = \lambda_i \Delta y_i(t) \), where \( \Delta y_i(t) \) denotes the deviation of population densities from equilibrium along \( A_i \). Here, \( \Delta y_i(t) \) serves the same role as \( y_i(t) \) in the stochastic model. The smaller the magnitude of \( \lambda_i \), the more rapid the return to equilibrium, while values of \( \lambda_i > 1 \) produce instability. In the stochastic case, smaller magnitudes of \( \lambda_i \) produce lower variances in population densities in the direction of \( y_i(t) \). The comparison between deterministic and stochastic analyses is similar for complex eigenvalues; in the deterministic case small values of \( |\lambda_i| \) produce rapid return to equilibrium in a spiral fashion in the plane given by \( A_j \) and \( A_{j+1} \), and in the stochastic case small values of

![Fig. 2. Hypothetical phase portrait showing axes A1 and A2 calculated from the eigenvectors of the community matrix B (Eq. 4). Both eigenvalues are real, so the lengths of A1 and A2 equal 1.](image)
$\|A\|$ decrease the variance in population densities in the same plane.

Similar results to Eqs. 8 and 10 can be derived for models based on stochastic differential equations in which stochasticity is added to population growth rates (May 1973, Bulmer 1976, Turelli 1977). In this previous work, the variance in population densities depends both on the environmental variance and the deterministic stability of the model. Despite the similarity between previous results from stochastic differential equations and those presented here, they differ both technically and philosophically. Methods based on stochastic differential equations are designed to analyze models of population dynamics rather than real data. To apply them to data, it is first necessary to specify a particular model for a given ecological system and estimate its parameters. Given a parameterized model, the model can be analyzed using stochastic calculus and transfer functions (for a general overview, see Nisbet and Gurney 1982). Applying analytical techniques to stochastic models has been particularly useful in exploring how variability in different model parameters affects population dynamics (e.g., Feldman and Roughgarden 1975, Beddington and May 1977, Turelli 1978, Horwood and Sheppard 1981). Constructing a specific model for the ecological system makes it possible to examine sources of population variability in a mechanistic fashion.

The approach presented here differs from previous approaches because it bypasses the construction of a particular model for a system. Parameters pulled from the data (the regression coefficients) are used directly to assess resilience. The philosophy is to describe the population dynamics observed in a data set in an ecologically meaningful way. The advantage of the approach is that it gives a valid measure of resilience without extracting a defensible mechanistic model for the system. The disadvantage is that it does not give information about the mechanistic role of environmental stochasticity in the system. This means that the approach is most useful to compare the dynamics in different data sets; for example, do lakes with different trophic structures differ in resilience? (Pimm and Lawton 1977, Carpenter and Kitchell 1993).

The results given by Eqs. 8 and 10 are cast in terms of variances in population densities along axes given by the eigenvectors of $A$. How do the results translate into variances in the population densities of individual species? The sum of variances in population densities is:

$$\sum_{i=1}^{S} V[x_i] = \sum_{i=1}^{S} \|A\|^2 V[y_i] + 2 \sum_{i=1}^{S}$$

where $\|A\|$ is the magnitude of the axis corresponding to eigenvalue $i$, $\theta_{ij}$ is the angle between $A_i$ and $A_j$, and $\text{COV}[y_i, y_j]$ is the covariance between $y_i$ and $y_j$. This expression can be simplified by noting that for real eigenvalues, eigenvectors can be scaled so $\|A\| = 1$, and for complex eigenvalues, eigenvectors can be scaled so $(\|A_{1i}\| + \|A_{2i}\|)/2 = 1$. However, unless axes $A_i$ are orthogonal so $\cos \theta_{ij} = 0$, the sum of variances in population densities depends on values of $\text{COV}[y_i, y_j]$. The complication of covariance terms also arises in transferring from variances in $\epsilon(t)$ to variances in $w(t)$. Therefore, the precise role of eigenvalues in determining the stochastic resilience of a system is lost when transferring from variances along the axes $A_i$ to variances in individual species densities.

Despite the difficulty of translating stochastic resilience into variances in individual species densities, focusing on variances along the axes $A_i$ has an important advantage over variances in the densities of individual species. The variance in density of a species depends not only on the environmental fluctuations that affect its population growth rate, but also on the variability in population densities of other species in the community; this is illustrated in Fig. 1d in which all of the stochastic variation in predator density is driven by stochastic variation in prey density. Due to the confounding effects of variation in the density of interacting species, the ratio $V[y_i]/V[\epsilon_i]$ gives a poor measure of stochastic resilience for species $i$. To give an extreme example of this, if interactions among species were linear, and species $i$ experienced no environmental variability, $V[\epsilon_i]$ would be 0. However, $V[x_i]$ need not be 0, since variance in the population density of species $i$ could be caused by variance in the population densities of interacting species. In this case, $V[x_i]/V[\epsilon_i]$ would approach infinity and give a nonsensical measure of resilience. In contrast, along the axes $A_i$, the variance in population densities, $V[y_i]$, depends only on the variance in population growth rates along the same axis, $V[w_i]$ (Eqs. 8 and 10); variability in population densities along the axes other than $A_i$ do not affect the variance in population densities along $A_i$. Therefore, the ratio $V[y_i]/V[w_i]$ incorporates completely the sources of variance in population growth rates and gives a more complete measure of resilience. The important point here is that resilience is a property of the entire community as opposed to its constituent species. Resilience depends on the interactions among species, and therefore it cannot be measured for single species separately.

**Separating true environmental variability from non-linear population dynamics**

In the analysis in the previous subsection, variability in population growth rates driven by both environmental variability and non-linear population dynamics were lumped into the term $\epsilon(t)$, and hence also $w(t)$. Therefore, $w(t)$ represents a maximum estimate of the environmental variance along its corresponding eigen-}

\|$\|A\|\|$ decrease the variance in population densities in the same plane.

Similar results to Eqs. 8 and 10 can be derived for models based on stochastic differential equations in which stochasticity is added to population growth rates (May 1973, Bulmer 1976, Turelli 1977). In this previous work, the variance in population densities depends both on the environmental variance and the deterministic stability of the model. Despite the similarity between previous results from stochastic differential equations and those presented here, they differ both technically and philosophically. Methods based on stochastic differential equations are designed to analyze models of population dynamics rather than real data. To apply them to data, it is first necessary to specify a particular model for a given ecological system and estimate its parameters. Given a parameterized model, the model can be analyzed using stochastic calculus and transfer functions (for a general overview, see Nisbet and Gurney 1982). Applying analytical techniques to stochastic models has been particularly useful in exploring how variability in different model parameters affects population dynamics (e.g., Feldman and Roughgarden 1975, Beddington and May 1977, Turelli 1978, Horwood and Sheppard 1981). Constructing a specific model for the ecological system makes it possible to examine sources of population variability in a mechanistic fashion.

The approach presented here differs from previous approaches because it bypasses the construction of a particular model for a system. Parameters pulled from the data (the regression coefficients) are used directly to assess resilience. The philosophy is to describe the population dynamics observed in a data set in an ecologically meaningful way. The advantage of the approach is that it gives a valid measure of resilience without extracting a defensible mechanistic model for the system. The disadvantage is that it does not give information about the mechanistic role of environmental stochasticity in the system. This means that the approach is most useful to compare the dynamics in different data sets; for example, do lakes with different trophic structures differ in resilience? (Pimm and Lawton 1977, Carpenter and Kitchell 1993).

The results given by Eqs. 8 and 10 are cast in terms of variances in population densities along axes given by the eigenvectors of $A$. How do the results translate into variances in the population densities of individual species? The sum of variances in population densities is:

$$\sum_{i=1}^{S} V[x_i] = \sum_{i=1}^{S} \|A\|^2 V[y_i]$$

where $\|A\|$ is the magnitude of the axis corresponding to eigenvalue $i$, $\theta_{ij}$ is the angle between $A_i$ and $A_j$, and $\text{COV}[y_i, y_j]$ is the covariance between $y_i$ and $y_j$. This expression can be simplified by noting that for real eigenvalues, eigenvectors can be scaled so $\|A\| = 1$, and for complex eigenvalues, eigenvectors can be scaled so $(\|A_{1i}\| + \|A_{2i}\|)/2 = 1$. However, unless axes $A_i$ are orthogonal so $\cos \theta_{ij} = 0$, the sum of variances in population densities depends on values of $\text{COV}[y_i, y_j]$. The complication of covariance terms also arises in transferring from variances in $\epsilon(t)$ to variances in $w(t)$. Therefore, the precise role of eigenvalues in determining the stochastic resilience of a system is lost when transferring from variances along the axes $A_i$ to variances in individual species densities.

Despite the difficulty of translating stochastic resilience into variances in individual species densities, focusing on variances along the axes $A_i$ has an important advantage over variances in the densities of individual species. The variance in density of a species depends not only on the environmental fluctuations that affect its population growth rate, but also on the variability in population densities of other species in the community; this is illustrated in Fig. 1d in which all of the stochastic variation in predator density is driven by stochastic variation in prey density. Due to the confounding effects of variation in the density of interacting species, the ratio $V[y_i]/V[\epsilon_i]$ gives a poor measure of stochastic resilience for species $i$. To give an extreme example of this, if interactions among species were linear, and species $i$ experienced no environmental variability, $V[\epsilon_i]$ would be 0. However, $V[x_i]$ need not be 0, since variance in the population density of species $i$ could be caused by variance in the population densities of interacting species. In this case, $V[x_i]/V[\epsilon_i]$ would approach infinity and give a nonsensical measure of resilience. In contrast, along the axes $A_i$, the variance in population densities, $V[y_i]$, depends only on the variance in population growth rates along the same axis, $V[w_i]$ (Eqs. 8 and 10); variability in population densities along the axes other than $A_i$ do not affect the variance in population densities along $A_i$. Therefore, the ratio $V[y_i]/V[w_i]$ incorporates completely the sources of variance in population growth rates and gives a more complete measure of resilience. The important point here is that resilience is a property of the entire community as opposed to its constituent species. Resilience depends on the interactions among species, and therefore it cannot be measured for single species separately.

**Separating true environmental variability from non-linear population dynamics**

In the analysis in the previous subsection, variability in population growth rates driven by both environmental variability and non-linear population dynamics were lumped into the term $\epsilon(t)$, and hence also $w(t)$. Therefore, $w(t)$ represents a maximum estimate of the environmental variance along its corresponding eigen-
vector, and consequently \( V_\cdot \sqrt{V_\cdot} \) is a minimum estimate of the variance in population densities relative to environmental variance. To estimate the environmental variance more accurately, the variance in \( w(t) \) due to non-linear interactions among species can be removed using non-linear regression.

Following the analysis in the last subsection, non-linear regression may be applied to the changes in population densities along the eigenvectors using the general form:

\[
y(t + 1) = f(y(t)) + z(t)
\]

for population densities along eigenvectors corresponding to real eigenvalues, and

\[
y_2(t + 1) = f_2(y_2(t), y_2(t) + z_2(t))
\]

\[
y_{2j+1}(t + 1) = f_{2j+1}(y_2(t), y_{2j+1}(t)) + z_{2j+1}(t)
\]

for population densities along eigenvectors corresponding to complex eigenvalues. Here, \( f() \), \( f_2() \), and \( f_{2j+1}() \) represent non-linear functions, and \( z(t), z_2(t), \) and \( z_{2j+1}(t) \) give the residual variability in population growth rates not explained by non-linear regression. If \( f() \) is a simple linear equation, \( V[z] \) will equal \( V[w] \). If the relationship between \( y(t + 1) \) and \( y(t) \) is non-linear, \( V[z] \) will be less than \( V[w] \). In applying non-linear regression, some judgment should be given to the choice of the functions \( f() \), although simple plots of Eqs. 12 and 13 should reveal appropriate functions.

This application of non-linear regression follows the same spirit as the linear analysis. Environmental variability is measured by the residual variance in population growth rates following regression of population densities at time \( t + 1 \) against population densities at time \( t \). Following the correction for non-linear population interactions, the measures of stochastic resilience are \( V[y]/V[w] \) and \( (V[y] + V[y_2])/(V[z] + V[z_{2j+1}]) \) for eigenvectors corresponding to real and complex eigenvalues, respectively.

**Delayed density dependence**

The analysis so far has assumed that population densities at time \( t + 1 \) can be predicted from densities at time \( t \). There is no effect of densities before time \( t \); i.e., there is no delayed density dependence. Delayed density dependence may arise if populations are age-structured, since population densities at some time \( t + 1 \) may depend on the number of individuals born more than one time interval before. Alternatively, delayed density dependence may indicate density-dependent interactions with other species that have not been recorded in the data set (Royama 1981, Turchin and Taylor 1992). Turchin (1990) found evidence for delayed density dependence in 8 of 14 data sets for single species of forest insects; the delayed density dependence is most likely caused by interactions with other species the densities of which were not recorded. Delayed density dependence can be incorporated into the analysis of stochastic resilience in a straightforward manner, as follows.

For delayed density dependence where the delay is one time unit, the linear regression equation for the population density of species \( i \) at time \( t + 1 \) has the form:

\[
x(t + 1) = b_i + \sum_{j=1}^{S} b_{ij} x(t) + \sum_{j=1}^{S} c_{ij} x(t-1) + \epsilon_i(t).
\]

This can be rewritten as two equations to remove the time delay by letting \( \xi(t) = x(t-1) \):

\[
x(t + 1) = b_i + \sum_{j=1}^{S} b_{ij} x(t) + \sum_{j=1}^{S} c_{ij} \xi(t) + \epsilon_i(t).
\]

If all species in the community have delayed density dependence of lag 1, this process will lead to 2 \( S \) equations for the system. Greater lags can be handled in an analogous fashion. The analysis of the entire system of equations can then proceed in exactly the same way as before.

When delayed density dependence is produced by interactions with unidentified species in the community, this method of handling delayed density dependence may give different estimates of stochastic resilience than would be obtained given data for the population densities of the additional species. There are two reasons for this. First, consider the hypothetical case of a predator–prey pair (as in the simulation example given in the last section) for which data are only available for the prey. Calculating the stochastic resilience for the single-species data set will estimate the variance in (transformed) prey density relative to the (transformed) environmental variance. The variance in the unobserved predator density may be greater than that observed in the prey density, since strong intra-specific density dependence in the prey population could buffer prey density against large fluctuations in predator density. If this were the case, the estimated resilience from the prey data alone would be greater than that estimated for the combined predator–prey data, simply because the more variable predator is not included. Second, in the same predator–prey example, the effect of the predator on the prey dynamics is observed through the delayed term \( x(t-1) \). The delayed term, however, might be a poor predictor of the predator density in time \( t \), since increased time delays will accumulate environmental variability. This will lead to an underestimate of the true effect of population densities (including the predator) at time \( t \) on the population density of the prey at time \( t + 1 \). With under-estimates of the true impact of density dependence, the estimate of the environmental variability will be exaggerated, increasing the estimated resilience of the
system. Despite the possible lack of correspondence between resilience measured for the prey data alone and that measured for the combined predator–prey data, this does not in itself diminish the usefulness of the technique. It is still useful in comparing among single-species data sets which are analyzed in the same manner.

This procedure is related to that used by Turchin (1990) and Turchin and Taylor (1992) to detect delayed density dependence in single-species data sets. These authors apply a response surface method to detect density dependence in a fashion that flexibly describes a wide range of non-linear patterns. Since Turchin and Taylor's method identifies density dependence, stochastic resilience could be calculated as the variance in population density divided by the variance that is not explained by the variance around the response surface. This has the advantage of not transforming data along eigenvectors, so the population variance is measured for untransformed density. For single-species data sets, this approach makes good sense. The advantage of my method is that it can be used when there are data for many but not all species in a community. When there are many species, some or all with delayed density dependence, interspecific density-dependent interactions may produce very complicated patterns of covariances between densities of different species. Transforming densities along eigenvectors removes the complicating effect of these covariances. Furthermore, my method makes it possible to account for temporal autocorrelation in the environmental factors driving population fluctuations. This is explained in the next subsection.

**Environmental autocorrelation**

Thus far, the analysis has assumed that there is no temporal autocorrelation in the environmental variance driving population fluctuations. Existence of environmental autocorrelation depends strongly on the time scale of population sampling relative to the time scale of environmental variability; the slower the environmental fluctuations, the greater the chance of observing autocorrelation in the population dynamics. Environmental autocorrelation can increase the variance in population densities, because consecutively "good" or "bad" environments may push population densities farther from the mean. This subsection shows how to analyze data when population dynamics are affected by a known temporally autocorrelated environmental factor.

The analysis assumes that data are available for the autocorrelated environmental factor or some surrogate measure. If there is no independent measure of the autocorrelated environmental factor, then statistically distinguishing environmental autocorrelation from delayed density dependence is difficult at best. To illustrate this problem with a simple example, suppose a data set has the following statistical structure:

\[ x(t + 1) = b_0 + b_1 x(t) + \hat{\epsilon}_1(t) \]

\[ \hat{\epsilon}_1(t + 1) = c \hat{\epsilon}_1(t) + \hat{\epsilon}_2(t). \]

Here, the environmental factor affecting the population growth rate, \( \hat{\epsilon}_1 \), is temporally autocorrelated, since \( \hat{\epsilon}_1(t + 1) \) depends on its value at time \( t \), discounted by the parameter \( c \). \( \hat{\epsilon}_2(t) \) represents the uncorrelated component environmental variability. This pair of equations can be rearranged into a single equation of the form:

\[ x(t + 1) = (1 - c) b_0 + (b_1 + c) x(t) - c b_1 x(t - 1) + \hat{\epsilon}_2(t - 1). \]

This has the same structure as a statistical model for delayed density dependence (Eq. 14), demonstrating the impossibility of distinguishing environmental autocorrelation from delayed density dependence in this data set without additional information. Of course, real data sets may not have the simple structure of this example, but, in general, distinguishing autocorrelated environmental variability from delayed density dependence will be difficult. Therefore, the focus of this subsection is to analyze the case when a potentially autocorrelated environmental factor has been measured.

The analysis including environmental autocorrelation proceeds in a similar fashion as before. First, linear regression is applied to the changes in population densities of species \( i \) using the equation:

\[ x_i(t + 1) = g_1 y(t) + b_{i0} + b_{i1} x_1(t) + b_{i2} x_2(t) + \ldots + b_{i,j} x_j(t) + \epsilon_i(t). \]

This differs from Eq. 2 by the addition of the term \( g_1 y(t) \) for the environmental factor. The regression coefficient \( g_1 \) gives the effect of \( y(t) \) on the population growth rate of species \( i \). The variable \( y(t) \) may represent any kind of environmental factor that has been transformed to produce linearity in the regression. If environmental measurements have not been taken simultaneously with estimates of population densities, \( y(t) \) can be a surrogate measure of an environmental factor that is potentially autocorrelated. For example, if seasonal changes in the environment potentially affect population dynamics, \( y(t) \) could represent the day of the year. The effect of \( y(t) \) on all species in the system is given by the vector \( G = [g_1, \ldots, g_3] \).

As before, population densities can be projected onto the eigenvectors of the matrix \( B \) to give the matrix equation:

\[ Y(t + 1) = H y(t) + J Y(t) + W(t), \]

where \( H = T G \) (see Eq. 6). Consider first the case for real eigenvalue \( \lambda \). The densities along the corresponding eigenvector satisfy \( y_i(t + 1) = h_1 y_i(t) + \lambda y_i(t) + w_i(t) \). Assuming stationarity and taking variances of both sides,
Note that there is potentially covariance between \( y(t) \) and \( y(t) \). This will occur if \( y(t) \) is temporally autocorrelated. For example, if \( y(t) \) is positively autocorrelated, an environmentally "good" year that leads to relatively higher population densities will likely be followed by yet another "good" year, thereby producing a positive covariance between \( y(t) \) and \( y(t) \). There is no covariance between \( y(t) \) and \( w(t) \), since as before linear regression guarantees that \( \text{M}[y(t)w(t)] = 0 \).

Using the identity \( y(t) = h_1y(t - 1) + h_\gamma y(t - 1) + w(t - 1) \), \( \text{COV}[y(t), y(t)] \) can be expressed as:

\[
\text{COV}[y(t), y(t)] = h_1\text{COV}[y(t - 1), y(t)] + \lambda_1\text{COV}[y(t - 1), y(t)] + \text{COV}[w(t - 1), y(t)].
\]

Since \( y(t) \) is transformed to linearize its relationship to the population growth rate, \( \text{COV}[w(t - 1), y(t)] = 0 \). In a similar fashion, \( \text{COV}[y(t - 2), y(t)] \) can be expanded and the process continued for \( \text{COV}[y(t - 3), y(t)] \), etc. Letting \( p[y(t - k), y(t)] \) denote the correlation coefficient between \( y(t - k) \) and \( y(t) \),

\[
2h_1\lambda_1\text{COV}[y(t), y(t)] = 2h_1^2\text{V}[\gamma(t)]\lim_{t \to \infty} \sum_{k=1}^{T} \lambda_1^k p[y(t - k), y(t)] = 2h_1^2\text{V}[\gamma(t)]R[p],
\]

where \( R[p] \) summarizes the effect of autocorrelation in the environmental factor \( y(t) \). Thus, from Eq. 20,

\[
V[y] = h_1^2\text{V}[\gamma(1 + 2R[p]) + V[w]] / (1 - \lambda_1^2).
\]

This result is very similar to its counterpart when there is no environmental autocorrelation (Eq. 8). The variance in population densities along the eigenvector equals the environmental variance divided by \( 1 - \lambda_1^2 \). The variance of the autocorrelated environmental factor \( y(t) \) is multiplied by the square of the regression coefficient for the effect of \( y(t) \) on population growth rates, \( h_\gamma \), and by a term for the pattern of autocorrelation of \( y(t) \). The term \( R[p] \) describes the manner in which the environmental autocorrelation is perpetuated in the population dynamics. The closer \( \lambda_1 \) to 0, the more rapidly the effects of environmental autocorrelation dissipate. This makes sense, since values of \( \lambda_1 \) close to 0 imply a strong tendency for population densities to return to equilibrium, which effectively reduces the "memory" of past environmental conditions. If both \( \lambda_1 \) and \( p[y(t - k), y(t)] \) are positive, environmental autocorrelation will lead to relatively greater population variance. This corresponds to the case in which "good" or "bad" years occur in succession, driving populations successively further from mean densities. If \( \lambda_1 \) is positive and \( p[y(t - k), y(t)] \) is negative, "good" and "bad" years alternate, thereby leading to negative values of \( R[p] \) and reductions in the population variance. The situation becomes somewhat more complicated when density dependence is overcompensating, giving \( \lambda_1 \), a negative value. In this case, positive environmental autocorrelation may lead to decreases in the population variance, although the overall result depends on the structure of environmental autocorrelation.

The analysis for the complex eigenvalue \( \alpha_j + \beta J \) is more complicated, but leads to essentially the same result:

\[
V[y_2] + V[y_{2+t}] = (h_1^2 + h_\gamma^2)\text{V}[\gamma(1 + 2R[p]) + V[w_2] + V[w_{2+t}]] / (1 - R_\gamma^2)^2,
\]

where

\[
J_j = \begin{bmatrix} \alpha_j & \beta_j \\ -\beta_j & \alpha_j \end{bmatrix},
\]

\[
R[p] = \frac{\lim_{t \to \infty} \text{tr}(J_j^t)p[y(t - k), y(t)]}{2^t}\]

and \( \|\lambda\| \) denotes the magnitude of the eigenvalues \( \alpha_j \pm \beta J \). This equation is similar to that for the case of real eigenvalues (Eq. 23), and \( R[p] \) plays exactly the same role as \( R[p] \) in summarizing the effect of environmental autocorrelation on the population variance.

Eqs. 23 and 24 solve an important problem that arises in the study of temporal variability in stochastic models. As Turelli (1977) strongly points out, there is not always a correspondence between characteristic return times in deterministic models (the measure of deterministic resilience) and population variability in stochastic models (see Pimm 1984b, Taylor 1992, 1993, Horwood 1993 for further discussion). The best example of the lack of correspondence between characteristic return times and population variability comes from analyzing the continuous-time logistic equation for a single species:

\[
\frac{dx}{dt} = rx(1 - x/K)
\]

where \( x \) is the density of the species, \( r \) is its intrinsic rate of increase, and \( K \) is its carrying capacity. When environmental variability is added to \( r \), rapid return times in the deterministic system correspond to small population variances in the stochastic system. However, the reverse is true when variability is added to \( K \); rapid return times in the deterministic model lead to large variances in population densities in the stochastic model (Turelli 1977, Nisbet and Gurney 1982, Horwood 1993). This seemingly counterintuitive effect of adding stochasticity to \( K \) can be explained in terms of the ability of the species to track environmental fluc-
tations. Rapid return rates in the deterministic model will increase the ability of populations to track environmental fluctuations in the corresponding stochastic model. If populations track the environment well, then population densities will exhibit high variances over long periods of time when there are large fluctuations in the carrying capacity. On the other hand, if return to carrying capacity in the deterministic system is slow, the population will not track the carrying capacity well, and environmental fluctuations will be averaged out before population densities show a strong response (Turelli 1977, Pimm 1984b). Therefore, dynamic characteristics producing rapid return rates to a fluctuating (Turelli 1977, Pimni 1984). If populations track the environment well, then environmental fluctuations will be averaged out before population densities show a strong response.

This problem of adding stochasticity to different parameters in a particular model leads to parallel problems when analyzing data. For example, using 75 data sets for farmland and woodland birds, Pimm (1984b) attempted to distinguish population variability driven by environmental variability in either $r$ or $K$. By fitting a discrete logistic equation to the data and comparing the estimates of $r$ and $K$ to the coefficient of variation in population densities, he concluded that variability in $r$ is the better explanation of population variances. Eqs. 23 and 24 give a more direct way to identify how environmental variability affects population variability. The difference between variability in $K$ versus $r$ is whether there is environmental autocorrelation or not. In real data, this strict dichotomy is unlikely, since some sources of environmental variability are likely autocorrelated while others are not. By analyzing data for environmental autocorrelation rather than fitting particular models, Eqs. 23 and 24 give a more direct method for estimating the resilience of stochastic systems. Rather than fit particular parameters that have particular effects in a model of the data, the methods developed hee search for the effects directly in the data. Since the methods for analyzing models with stochastically varying parameters become mathematically difficult as the number of species in a community increases, the method proposed here provides a much simpler solution.

A limitation of Eqs. 23 and 24 is the need for independent measurements of environmental factors that might be autocorrelated. In fact, this is not a strict mathematical requirement, but due to the difficulty of differentiating environmental autocorrelation from delayed density dependence, it is the safest approach. If one is willing to assume a particular structure for delayed density dependence, specifying which species experience what length of delays, it is possible to construct an artificial variable for autocorrelated environmental variance. This requires examining the pattern of residuals following regression to identify autocorrelations and then placing the autocorrelated component of environmental variance in the parameter $\gamma(t)$. Because I think this technique would be suspect on a variety of grounds, I will not pursue the mathematical derivation for this analysis in detail.

**APPLICATION OF THE STOCHASTIC ANALYSIS**

To illustrate the procedure developed above, here it is applied to the data in Fig. 1 for a hypothetical predator–prey system (Eq. 1). Relative to Fig. 1a, the greater variability in population densities in Fig. 1b is produced by an increase in environmental variability; in Fig. 1c, greater variability is caused by an increase in the prey intrinsic rate of increase ($r$ in Eq. 1). In Fig. 1d, all of the environmental variability occurs in the prey population growth rate, and variation in predator density is driven by variation in prey density. The specific challenge for the procedure developed in the last section is whether it can distinguish the relative contribution of species interactions and environmental variability to the variance in population densities directly from the data in Fig. 1. To perform the analysis, I used Systat (Wilkinson 1988) to calculate regression coefficients and Mathematica (Wolfram 1991) to find eigenvalues, although a wide range of other programs is available for the analysis. I will provide programs for the analysis on request.

**Linear analysis**

For the data in Fig. 1a, the first step is to use Eq. 2 to regress population densities of predator and prey at time $t + 1$ against densities at time $t$ (Eq. 2). The resulting regression coefficients $b_{ij}$ are given in Table 1. Fig. 3 shows the regression of prey density at time $t + 1$ against prey (Fig. 3a) and predator (Fig. 3b) densities at time $t$. The scatter around the regression lines is driven by variance in the prey population growth rate that is incorporated into the environmental “error” term $\varepsilon_i$. The eigenvalues of the system are complex conjugates, $\lambda_z = 0.527 \pm 0.313 I$, and the eigenvectors are $0.39 - 0.57 I$ and $1.30 I$ (Table 1). Fig. 4 shows a phase portrait in which predator density is graphed against prey density. The gray lines depict

**Table 1.** Parameter estimates for stochastic analysis of the data in Fig. 1a.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$b_{1,0}$</td>
<td>1.23</td>
</tr>
<tr>
<td>$b_{1,1}$</td>
<td>0.069</td>
</tr>
<tr>
<td>$b_{2,0}$</td>
<td>-1.03</td>
</tr>
<tr>
<td>$b_{2,1}$</td>
<td>1.04</td>
</tr>
</tbody>
</table>

**Eigenvalues and eigenvectors**

$\lambda_z = 0.527 \pm 0.313 I$  
$t = \begin{bmatrix} 0.39 & -0.57 \\ 0 & 1.30 \end{bmatrix}$

**Variances in population densities**

$V[x_1] = 0.0045$  
$V[y_1] = 0.0031$

**Variances of transformed variables**

$V[y_2] = 0.0094$  
$V(x_1, x_2) = -0.0032$

**Resilience**

$1/(1 - \|\lambda_z\|^2) = 1.60$
FIG. 3. The prey density at time \( t + 1 \) as a function of (a) prey and (b) predator densities at time \( t \) for the data in Fig. 1a. Regression lines were calculated using multiple linear regression (Eq. 2; Table 1). To portray variability around the regression lines, the residuals from the multiple regression were added to the regression lines produced by setting predator density to 0 in (a) and prey density to 0 in (b). Thus, the points around the regression lines represent the projections of residuals onto the plane of \( x_i(t + 1) \) vs. \( x_i(t) \) and \( x_i(t + 1) \) vs. \( x_j(t) \) in (a) and (b), respectively.

The axes \( A_1 \) and \( A_2 \) given by the columns of \( T \) (Table 1). If the eigenvalues were real, these axes would have a length of 1. However, since the eigenvalues are complex, the axes are of unequal length, although their average length is 1. The variances in population densities along \( A_1 \) and \( A_2 \) are \( V[y_1] = 0.031 \) and \( V[y_2] = 0.0094 \), respectively. From Eq. 10, the ratio of population variance to environmental variance, \( 1/(1 - ||A_2||^2) \), equals 1.60.

To compare different systems, the analysis can be applied to the data in Fig. 1b–d. In Fig. 1b, the environmental variance is greater than in Fig. 1a by a factor of 4, resulting in a roughly four-fold increase in the variance in population densities (Table 2). The resilience of the system, measured by \( 1/(1 - ||A_2||^2) \), is 1.62, very close to the value 1.60 for Fig. 1a. This is expected, since the strengths of interactions between predator and prey are the same in both cases. Consequently, the resilience of both systems should be the same. In Fig. 1c, the roughly four-fold increase in population variances relative to Fig. 1a is caused by increasing the prey intrinsic rate of increase; the environmental variance in each of the figures is the same. The resilience calculated from the data in Fig. 1c is \( 1/(1 - ||A_2||^2) = 4.93 \) (Table 2). This is less than what might be expected. Since the environmental variances in Fig. 1a and c are the same, while the population variances are four times greater in Fig. 1c, one would expect a larger increase in the value of \( 1/(1 - ||A_2||^2) \). The explanation is that the variance in \( \epsilon_2 \) calculated from Fig. 1c is greater than that calculated in Fig. 1a (Table 2). This is because the regression for the predator density at time \( t + 1 \) (Eq. 2) is more nonlinear in Fig. 1c than in a; application of stepwise multiple regression including quadratic terms to the data in Fig. 1c produced a significant interaction term for \( x_i(t) \times x_j(t) \) (\( P < 0.01 \)), while the interaction term was not significant for Fig. 1a. Because the non-linearity increases the estimated environmental variability, the estimated resilience of the system is exaggerated. This results in a lower value of \( 1/(1 - ||A_2||^2) \). Correcting for this effect of non-linearities is done in the next subsection.

For Fig. 1d, interactions among species are the same.
as in Fig. 1a and b, although all variability occurs through the prey population growth rate. The calculated value of $1/(1 - ||\lambda_1||^2)$ is 1.94 (Table 2), 1.60 and 1.62, the values calculated for Fig. 1a and b, respectively. This discrepancy is due to different estimates of the regression coefficients $b_{ij}$ in Eq. 2 caused by differences in sources of variability in population growth rates. The effect of non-linearities in Eq. 1 is seen in the non-zero estimate for $V[\varepsilon_1]$, even though there is no environmentally driven variance in predator population growth rate. Although the value of $1/(1 - ||\lambda_1||^2)$ for this data set is different from those calculated for Fig. 1a and b, the value is still much lower than that for Fig. 1c, in which interactions among species give much lower resilience.

Rather than calculate eigenvalues, an alternative approach is to measure resilience in terms of variances in population densities of individual species. Two possible measures of resilience are the sum of the ratios of variance in density to variance in $\varepsilon$, $V[x]/V[\varepsilon]$, and the ratio of the sum of variances in population densities to the sum of variances in $\varepsilon$, $(V[x_1] + V[x_2])/V[\varepsilon_1] + V[\varepsilon_2]$; values of these ratios are given in Table 2 for each of the four data sets in Fig. 1. Neither of these measures captures the underlying sources of variability as well as $1/(1 - ||\lambda_1||^2)$. The value of $V[x_1]/V[\varepsilon_1] + V[x_2]/V[\varepsilon_2]$ fails particularly obviously in the case of Fig. 1d, since $V[\varepsilon_2]$ is very small and the variance in predator density $V[x_2]$ is large due to variation in the prey density. The value of $(V[x_1] + V[x_2])/V[\varepsilon_1] + V[\varepsilon_2]$ is less consistent than $1/(1 - ||\lambda_1||^2)$, giving relatively more variable values for Fig. 1a, b, and d, despite the same interactions among species, and distinguishing the instability of Fig. 1c relatively less clearly than $1/(1 - ||\lambda_1||^2)$.

Separating true environmental variability from non-linear population dynamics

The linear analysis does not account for variance in population densities driven by non-linear species interactions. Since $\varepsilon(t)$ includes variability due to both environmental fluctuations and non-linear species interactions, the linear analysis overestimates stochastic resilience, leading to minimum values of $1/(1 - ||\lambda_1||^2)$. To account for non-linear population dynamics, first $x(t)$ and $\varepsilon(t)$ are transformed to produce variables $y_1(t)$ and $w(t)$ as in the linear analysis Eq. 6). Then non-linear regression is applied using Eq. 13 to extract the component of the variance in $y_1(t)$ due to non-linear species interactions. The choice of regression model [functions $f_1$ and $f_{2,2}$ in Eq. 13] depends on the structure of the data. The better the fit of the regression model, the greater the separation of environmental variability from non-linear species interactions. For the data in Fig. 1, I used quadratic regression including the terms $y_1(t)^2$, $y_2(t)^2$, and $y_1(t)y_2(t)$; other regression models did not improve the fit. The variances of the error terms from non-linear regression are $V[z_1]$ and $V[z_2]$ that give the environmental variances.

The final column in Table 2 gives values of $(V[y_1] + V[y_2])/V[z_1] + V[z_2]$ calculated for the data in Fig. 1a–d. All estimates of $(V[y_1] + V[y_2])/V[z_1] + V[z_2]$ are necessarily higher than values of $1/(1 - ||\lambda_1||^2)$. There is a particularly large difference between $(V[y_1] + V[y_2])/V[z_1] + V[z_2]$ and $1/(1 - ||\lambda_1||^2)$ for the data in Fig. 1c, reflecting the increased non-linearities introduced into the interactions among species by increasing the intrinsic rate of increase of the host. This correction gives an even clearer pattern of resilience in the four different data sets.

**Delayed density dependence**

In the analyses above, data were provided for both prey and predator densities. What could be said about the resilience in each data set if only data were available for the prey species? Since the interaction with the predator produces delayed density dependence in the prey population dynamics, resilience in the prey data set can be estimated using the techniques for delayed density dependence in the last section.

Transforming the data for the prey alone as in Eq. 15, the analysis of delayed density dependence proceeds in the same fashion as that used in the preceding

---

**Table 2.** Population variances, error terms, and resilience calculated for data in Fig. 1.

<table>
<thead>
<tr>
<th>Data source</th>
<th>Prey density</th>
<th>Predator density</th>
<th>$\varepsilon_1$</th>
<th>$\varepsilon_2$</th>
<th>$V[x_1]/V[\varepsilon_1]$</th>
<th>$V[x_2]/V[\varepsilon_2]$</th>
<th>$V[z_1]$</th>
<th>$V[z_2]$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fig. 1a</td>
<td>0.0045</td>
<td>0.016</td>
<td>0.0023</td>
<td>0.0023</td>
<td>1.60</td>
<td>8.91</td>
<td>4.46</td>
<td>1.84</td>
</tr>
<tr>
<td>Fig. 1b</td>
<td>0.016</td>
<td>0.059</td>
<td>0.010</td>
<td>0.0095</td>
<td>1.62</td>
<td>7.81</td>
<td>3.85</td>
<td>1.81</td>
</tr>
<tr>
<td>Fig. 1c</td>
<td>0.017</td>
<td>0.062</td>
<td>0.0029</td>
<td>0.0068</td>
<td>4.93</td>
<td>15.0</td>
<td>8.14</td>
<td>9.39</td>
</tr>
<tr>
<td>Fig. 1d</td>
<td>0.015</td>
<td>0.045</td>
<td>0.0098</td>
<td>0.00081</td>
<td>1.94</td>
<td>55.0</td>
<td>5.61</td>
<td>2.16</td>
</tr>
</tbody>
</table>

**Table 3.** Resilience measured from predator–prey data versus that measured from prey data alone.

<table>
<thead>
<tr>
<th>Date source</th>
<th>Predator–prey data</th>
<th>Prey data alone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$(V[y_1] + V[y_2])/V[z_1] + V[z_2]$</td>
<td>$(V[y_1] + V[y_2])/V[z_1]$</td>
</tr>
<tr>
<td></td>
<td>$1/(1 -</td>
<td></td>
</tr>
<tr>
<td>Fig. 1a</td>
<td>1.60</td>
<td>1.15</td>
</tr>
<tr>
<td>Fig. 1b</td>
<td>1.62</td>
<td>1.06</td>
</tr>
<tr>
<td>Fig. 1c</td>
<td>4.93</td>
<td>2.97</td>
</tr>
<tr>
<td>Fig. 1d</td>
<td>1.94</td>
<td>1.15</td>
</tr>
</tbody>
</table>
two subsections. In Table 3, the first two columns give the results from Table 2 for the predator–prey data, and the final two columns give the corresponding results for the prey data alone. Values of both $1/(1 - \|\lambda_i\|^p)$ and $(V[y_1] + V[y_2])/(V[z_1] + V[z_2])$ are lower for the prey data alone. This reflects the fact that the predator density showed greater variance than the prey density (Table 2), so excluding the predator density will necessarily give lower estimates of $1/(1 - \|\lambda_i\|^p)$. Nonetheless, comparing the results for the four data sets shows that the analysis accurately identifies Fig. 1c as having the lowest resilience, and the other data sets have similar resilience despite very different levels of variance in population densities. Therefore, although resilience measured for the prey data alone cannot be directly compared to resilience measured for the predator–prey data, $1/(1 - \|\lambda_i\|^p)$ and $(V[y_1] + V[y_2])/(V[z_1] + V[z_2])$ can be used to compare data sets analyzed in the same manner.

**DISCUSSION**

This paper has developed conceptual and mathematical tools for analyzing resilience in stochastic systems. Resilience in stochastic systems is defined in terms of the variability in population densities resulting from interactions among species; given the same environmentally driven variability in population growth rates, the more resilient system has the lower variability in population densities. Resilience is measured by calculating the eigenvalues of the matrix whose elements consist of linear regression terms for the effect of each species’ density on the population growth rates of the other species in the community. As in the deterministic case, small magnitudes of the eigenvalues imply greater resilience.

The greatest value of deterministic stability analysis is that resilience can be calculated directly from equations governing population dynamics (May 1974). The ease with which deterministic stability analysis can be applied and the usefulness of the information it provides has made deterministic stability analysis a cornerstone in the study of the dynamics of deterministic systems. However, deterministic stability analysis is difficult to apply to data (DeAngelis and Waterhouse 1987, Grimm et al. 1992, Cottingham and Carpenter 1994). The strengths and weaknesses of stochastic stability analysis are the reverse. Application to data is easy, since it involves standard linear regression. Application to stochastic models of population dynamics is more difficult, since it requires calculating the average interaction strengths among species, $b_{ij}$, at the stationary population distribution. In general, there is no simple way to derive stationary population distributions for non-linear population dynamic models when the number of species in the system is greater than two (Turelli 1978, Turelli and Gillespie 1980, Nisbet and Gurney 1982). Therefore, the stochastic stability analysis derived here does not lend itself to analytical examination of the mechanisms producing resilience.

The strengths of deterministic resilience in analyzing models and stochastic resilience in analyzing data complement each other, since the types of interactions among species that lead to greater resilience are similar. In both, greater resilience implies a greater tendency of populations to move towards mean densities. The conceptual similarity between the two analyses makes it possible to extend our understanding of deterministic models to real data in a formal manner. The relationship between resilience in deterministic and stochastic models has been argued on several occasions (May 1973, Turelli 1977, Taylor 1992, 1993, Horwood 1993). The problem when comparing resilience in deterministic and stochastic models is that stochasticity added to different parameters in a deterministic model will produce different conclusions; if adding stochasticity to a parameter produces autocorrelated environmental fluctuations, the variance in population densities may be greater than in the absence of environmental autocorrelation (see Section entitled Stochastic resilience, subsection environmental autocorrelation). This problem can be overcome when analyzing data by accounting directly for autocorrelation in the environment. This greatly reduces previous ambiguities in the relationship between deterministic and stochastic concepts of resilience.

The definition of stochastic resilience used here was chosen to be the analog of characteristic return times in deterministic systems, but other definitions are possible (May 1973, Turelli 1978, Chezzon and Case 1986). A particularly useful alternative is the expected time to extinction, or expected time to reach a low, critical boundary. This definition is analogous to global stability or persistence in deterministic systems, and has been applied both to stochastic models (Ludwig 1975, Turelli 1978, Chezzon 1982) and to data (Soule 1987 and references therein, Mangel and Tier 1993). The issue of persistence is important for conservation biologists predicting the viability of small populations that are currently decreasing in density. In contrast, the definition of stochastic resilience used here is appropriate for large, persistent populations.

Despite the importance of stability in ecological systems, there have been relatively few empirical tests of the different facets of stability (Pimm 1984a, DeAngelis et al. 1989, Carpenter et al. 1992, but see Luckinbill and Fenton 1978, Pimm 1984b, Steinman et al. 1991, Lawler and Morin 1993). Difficulties in measuring resilience in natural systems include estimating return times in inherently stochastic systems and deriving a common currency for return times when comparing different ecological systems. In the method developed here, calculating return times is replaced by estimating variances in population densities and population growth rates, which can be done in a relatively straightforward fashion. The method also provides a
natural common currency for comparative studies. For example, two communities may contain species with very different generation times and therefore operate on very different time scales; long-lived organisms may be less affected by short-term (e.g., daily) environmental changes, and long generation times will produce slow responses to longer term environmental changes. However, since stochastic resilience is defined in terms of the relative degree of variance in population density to environmentally driven variability in population growth rates, it is possible to compare systems that operate on different time scales. For example, it should be possible to compare the effect of trophic structure on resilience for such diverse communities as laboratory populations of protozoans (Lawler and Morin 1993) and freshwater lake communities (Carpenter and Kitchell 1993). Furthermore, although the analysis has been discussed in terms of population densities, the analysis could equally be framed in terms of other ecological measures, such as densities of aggregated species groups, population biomasses, or energy and nutrient flow through different functional groups in the community. Thus, the techniques developed here are a major step towards developing an operational concept of resilience that can be applied to a wide variety of ecological systems.

ACKNOWLEDGMENTS

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LITERATURE CITED


APPENDIX 1

When applying linear least squares regression, the mean value of the error terms, $M[\epsilon(t)$, $x_1(t)$, . . . , $x_n(t)]$, and the mean value of the product of error term and any population density, $M[\epsilon(t)x_1(t)$, $x_1(t)$, . . . , $x_n(t)]$, equal zero. Here, $M[ ]$ is used to denote the mean taken across all sample times $t$ excluding the last sample. These results can be demonstrated following the derivation of least squared estimates of the regression parameters $b_i$ in Eq. 2 (Neter et al. 1989). To keep the presentation simple, let there be only two species in the system; the case for more species follows in an obvious fashion.

For the model $x_1(t + 1) = b_0 + b_1x_1(t) + b_2x_2(t) + \epsilon_1(t)$, the least square estimates of $b_0$, $b_1$, and $b_2$ are obtained by minimizing

$$Q(b_0, b_1, b_2) = \sum_{t=1}^{N} [x_1(t + 1) - (b_0 + b_1x_1(t) + b_2x_2(t))]^2,$$

where $N$ is the number of sample periods minus 1. $Q$ reaches a minimum when its derivatives with respect to $b_0$, $b_1$, and $b_2$ are 0:

$$0 = \delta Q/\delta b_0 = -2 \sum_{t=1}^{N} [x_1(t + 1) - (b_0 + b_1x_1(t) + b_2x_2(t))]$$

$$= -2 \sum_{t=1}^{N} \epsilon_1(t)$$

$$0 = \delta Q/\delta b_1 = -2 \sum_{t=1}^{N} [x_1(t + 1) - (b_0 + b_1x_1(t) + b_2x_2(t))]x_1(t)$$

$$= -2 \sum_{t=1}^{N} \epsilon_1(t)x_1(t)$$

$$0 = \delta Q/\delta b_2 = -2 \sum_{t=1}^{N} [x_1(t + 1) - (b_0 + b_1x_1(t) + b_2x_2(t))]x_2(t)$$

$$= -2 \sum_{t=1}^{N} \epsilon_1(t)x_2(t).$$

Thus,

$$M[\epsilon_1] = M[\epsilon_1x_1] = M[\epsilon_1x_2] = 0.$$
This appendix demonstrates that the magnitudes of the eigenvalues calculated from the matrix \( B \) are \( \leq 1 \). To simplify the presentation, only the case when \( B \) is a \( 2 \times 2 \) matrix is derived in detail, although the analysis for more species follows directly from the two-species case.

From Eq. 2, the regression coefficients calculated by least squares satisfy the matrix equation:

\[
\begin{bmatrix}
  b_{11} & b_{12} \\
  b_{21} & b_{22}
\end{bmatrix}
\begin{bmatrix}
  \text{SS}[x_i(t), x_j(t)] \\
  \text{SS}[x_i(t), x_j(t)]
\end{bmatrix} =
\begin{bmatrix}
  \text{SS}[x_i(t + 1), x_j(t)] \\
  \text{SS}[x_i(t + 1), x_j(t)]
\end{bmatrix}
\]

(A3)

where

\[
\text{SS}[x_i(t), x_j(t)] = \sum_{i=1}^{N} (x_i(t) - \bar{x}_i)(x_j(t) - \bar{x}_j).
\]

Thus, \( \text{SS}[x_i(t), x_j(t)] \) is the sample covariance between \( x_i(t) \) and \( x_j(t) \), and \( \text{SS}[x_i(t + 1), x_j(t)] \) is the sample covariance between \( x_i \) and values of \( x_j \) at the next time period. The value of the eigenvalue of \( B \) can be real or complex. Assuming first it is real, \( B \) can be written as \( B = T \Gamma T^{-1} \) (Eqs. 4 and 5) where \( \Gamma = \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix} \). Applying this to Eq. A3 results in two equations in \( \lambda_i \):  

\[
\begin{align*}
\lambda_1(s_{11} \text{SS}[x_i(t), x_j(t)] + s_{12} \text{SS}[x_i(t), x_j(t)]) &= s_{11} \text{SS}[x_i(t + 1), x_j(t)] + s_{12} \text{SS}[x_i(t + 1), x_j(t)] \\
\lambda_2(s_{21} \text{SS}[x_i(t), x_j(t)] + s_{22} \text{SS}[x_i(t), x_j(t)]) &= s_{21} \text{SS}[x_i(t + 1), x_j(t)] + s_{22} \text{SS}[x_i(t + 1), x_j(t)],
\end{align*}
\]

(A4)

where \( s_{ij} \) is the \( ij \)th element of \( T^{-1} \). Multiplying the top equation by \( s_{11} \) and the bottom by \( s_{22} \), adding both equations, and noting that the population densities along the eigenvector of \( \lambda_i \), \( y_i(t) \), equal \( s_{11} x_i(t) + s_{12} x_j(t) \) (Eq. 6),

\[
\lambda_i = \frac{\text{SS}[y_i(t + 1), y_j(t)]/\text{SS}[y_i(t), y_j(t)]}{\text{SS}[x_i(t + 1), x_j(t)] - \text{SS}[x_i(t), x_j(t)]}
\]

(A5)

The terms \( y_i(t) \) and \( y_i(t + 1) \) represent the same sequence of numbers, except \( y_i(t) \) excludes the last number of \( y_i(t + 1) \), and \( y_i(t + 1) \) excludes the first number of \( y_i(t) \). Therefore, the sample variance of \( y_i(t + 1) \) is approximately equal to the sample variance of \( y_i(t) \), and \( \lambda_i \) approximately equals the correlation coefficient between \( y_i(t + 1) \) and \( y_j(t) \). Whenever the sample size is large enough that the sample variance of \( y_i(t + 1) \) is close to the sample variance of \( y_i(t) \), \( \lambda_i \) is constrained to have magnitude \( \leq 1 \).

If the eigenvalues are complex, taking the determinant of both sides of Eq. A3 and noting that \( \det(B) = \alpha^2 + \beta^2 \),

\[
(\alpha^2 + \beta^2)(\text{SS}[x_i(t), x_j(t)] \text{SS}[x_i(t), x_j(t)] - \text{SS}[x_i(t), x_j(t)]^2) = \text{SS}[x_i(t + 1), x_j(t)] - \text{SS}[x_i(t + 1), x_j(t)]\text{SS}[x_i(t + 1), x_j(t)].
\]

(A6)

Since \( \text{SS}[x_i(t), x_j(t)] = \text{SS}[x_i(t + 1), x_j(t + 1)] \), dividing by \( \text{SS}[x_i(t), x_j(t)] \text{SS}[x_i(t), x_j(t)] \) and solving for \( \alpha^2 + \beta^2 \) gives

\[
(\alpha^2 + \beta^2) = (r(x_i(t + 1), x_j(t))r(x_i(t + 1), x_j(t)) - r(x_i(t + 1), x_j(t))r(x_i(t + 1), x_j(t))(1 - r(x_i(t), x_j(t))^2),
\]

(A7)

where \( r(x_i(t), x_j(t)) = \text{SS}[x_i(t), x_j(t)]/\text{SS}[x_i(t), x_j(t)] \) is the correlation coefficient between \( x_i(t) \) and \( x_j(t) \), and \( r(x_i(t + 1), x_j(t)) = \text{SS}[x_i(t + 1), x_j(t)]/\text{SS}[x_i(t + 1), x_j(t)] \). The approximate correlation coefficient between \( x_i(t + 1) \) and \( x_j(t) \). From Eq. A7, \( \alpha^2 + \beta^2 \) must be \( \leq 1 \) for sufficiently large sample sizes, since for correlation coefficients for any four variables, \( 1 - r_{12}^2 - r_{13}r_{24} + r_{12}r_{24} \approx 0 \).

These results can be extended to more than two species by first applying the transform \( B = T \Gamma T^{-1} \). This separates sets of equations corresponding to each of the eigenvalues in the system, reducing the problem to a single equation for real eigenvalues (Eq. A5) and to a \( 2 \times 2 \) matrix for complex eigenvalues (Eq. A7).