

The Many Growth Rates and Elasticities of Populations in Random Environments

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ABSTRACT: Despite considerable interest in the dynamics of populations subject to temporally varying environments, alternate population growth rates and their sensitivities remain incompletely understood. For a Markovian environment, we compare and contrast the meanings of the stochastic growth rate (λ_s), the growth rate of average population (λ_M), the growth rate for average transition rates (λ_A), and the growth rate of an aggregate represented by a megamatrix (shown here to equal λ_M). We distinguish these growth rates by the averages that define them. We illustrate our results using data on an understory shrub in a hurricane-disturbed landscape, employing a range of hurricane frequencies. We demonstrate important differences among growth rates: $\lambda_s < \lambda_M$, but λ_A can be $<$ or $>$ λ_M . We show that stochastic elasticity, E_{ij}^s , and megamatrix elasticity, E_{ij}^M , describe a complex perturbation of both means and variances of rates by the same proportion. Megamatrix elasticities respond slightly and stochastic elasticities respond strongly to changing the frequency of disturbance in the habitat (in our example, the frequency of hurricanes). The elasticity E_{ij}^A of λ_A does not predict changes in the other elasticities. Because E^s , although commonly utilized, is difficult to interpret, we introduce elasticities with a more direct interpretation: E^{sm} for perturbations of means and E^{sv} for variances. We argue that a fundamental tool for studying selection pressures in varying environments is the response of growth rate to vital rates in all habitat states.

Keywords: temporal variation in demography, plant population biology, *Ardisia escallonioides*, hurricanes, canopy-gap forest dynamics, sensitivity, elasticity, stochastic demography, norm of response.

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Many populations experience random temporal variation in demography. There is considerable interest in analysis of population dynamics in temporally varying environments not only for life-history theory and ecology but also for conservation and management (Lande and Orzack 1988; Nations and Boyce 1997; Beissinger and Westphal 1998; Fieberg and Ellner 2000; Menges 2000). The theory of structured populations subject to random temporal variation (Cohen 1977a, 1977b, 1979; Tuljapurkar 1990) has been applied to field data (reviews by Nakaoka 1996; Engen and Saether 1998; examples include Bierzychudek 1982; Cohen et al. 1983; Benton et al. 1995; Dixon et al. 1997). Recently, sensitivity analysis in the context of temporally variable environments has received much attention (Benton and Grant 1999; de Kroon et al. 2000).

However, two main areas remain incompletely developed both in concept and in application to data. The first concerns comparisons of several growth rates that can be calculated for a given set of habitat and population dynamics, and the second concerns sensitivity of one of them, the stochastic growth rate, to changes in life-history transitions. We elucidate the relationships among four different concepts for a population living in a range of habitats or successional states: the stochastic growth rate of a single population, the growth rate of an average population, a growth rate calculated from a matrix of average transition rates, and the growth rate of an aggregate population as described by Horvitz and Schemske (1986) and Pascarella and Horvitz (1998). We examine these concepts for populations in a Markovian environment and describe how they measure (or do not measure) distinct aspects of population dynamics.

Part of the comparison among growth rates concerns how sensitive they are to vital rates or habitat dynamics. In a varying environment, a life-history trait is described by a function—a norm of response—that shows how trait value changes with temporal changes in habitat state. By habitat we mean a particular variant of the environment that is associated with particular values of the vital rates,

for example, the amount of light in the understory of a patch of forest. Our second main issue emerges in this context: stochastic growth rate will respond to changes in the habitat-specific values of a life-history trait. Thus, in a varying environment, a derivative of growth rate with respect to a life-history component must be recognized as being habitat specific (technically, as a functional derivative rather than as an ordinary derivative). This seemingly complex view actually makes it possible to compute and interpret elasticities in variable environments. We first show how to use an exact formula (Tuljapurkar 1990) to compute numerical values of such derivatives. Next we obtain the properties of and differences between three different summary measures of elasticity and sensitivity. It is common to think about sensitivity of growth rate to perturbations of such characteristics as the mean and variance of vital rates. We show how to compute exactly the elasticity to perturbation of the mean by itself corresponding to directional selection in all habitats and the elasticity to a perturbation of the variance by itself corresponding to selection on plasticity of vital rates. A simultaneous perturbation of means and variances is not easily interpretable as a selective force since the entire pattern of variation, that is, the life history in all habitats, is being perturbed. However, we show that one commonly employed elasticity (Tuljapurkar 1990; Benton and Grant 1996; Caswell 2001) measures the effect of perturbing both means and variances in such a way that the coefficient of variation is held fixed. We show that these elasticities are different in properties and interpretation. Our results on elasticity apply for any stochastically varying environments; we do not assume that variability is small or otherwise restricted. In particular, we do not use Tuljapurkar's (1982) small-noise expansions (see Caswell 2001 for their use in studying sensitivity).

Several previous studies (Benton and Grant 1996, 1999; Caswell 2001) have suggested that sensitivity analysis of a growth rate given by the average demographic rates sometimes yields results similar to those from sensitivity analysis of the stochastic growth rate. We provide a striking illustration that this conclusion is not true in general. Analysis of a matrix of average demographic rates misses the importance of habitat sequencing and variance in life-history rates in a temporally stochastic environment.

We consider the dynamics of structured populations modeled by population projection matrices. Temporal variation is described by associating a distinct projection matrix with each of several distinct environments, such as those arising over time following a disturbance. The (random) sequence of environments is generated by a Markov chain (Cohen 1977*b*; Tuljapurkar 1982; Horvitz and Schemske 1986). This setup can be used to describe a wide variety of cases of temporally varying demography (Tul-

japurkar 1997; Caswell 2001). Throughout, we illustrate our arguments with an example of a plant population living in an environment characterized by recurrent, patchy disturbance. The species is an understory shrub (*Ardisia escallonioides* Schlecht. & Cham. [Myrsinaceae]) in a forest landscape where canopy-gap dynamics are driven by hurricanes. The demography is estimated from empirical data and exhibits a complex pattern of temporal variation with accompanying variation in vital rates. This example provides a contrast to more stylized models that impose relatively simple temporal variation around an average demography (as do some of the examples in Tuljapurkar and Caswell 1997 and Caswell 2001).

The next section of the article presents our model of population dynamics and the background on the species used for our example. The following sections present the results for growth rates and then for sensitivities. We end with a summary and discussion of the conclusions and implications.

Model and Study Species

Structure and Assumptions of the Model

We consider a stage-structured population that has S distinct life-history stages, occupying a fixed spatial location, a patch. The population is censused at discrete times $t, t + 1$, and so on. In every time period, the patch is in one of K possible habitat states. Each habitat state, α , determines a particular matrix, \mathbf{A}_α , of life-history transition rates. The matrix element $A_{\alpha ij}$ is the rate at which individuals in stage j produce individuals in stage i over one time step. Each \mathbf{A}_α is irreducible and primitive, and the matrices constitute an ergodic set (Hajnal 1976).

The probability that the habitat state changes from state β to state α over one time step is written $c_{\alpha\beta}$. These probabilities make up a $K \times K$ Markov transition matrix \mathbf{c} . We are mainly concerned with situations in which this transition matrix is irreducible and primitive. The relative frequency of habitat states over time for a single patch (or equivalently, at one time for a large set of independently varying patches that change according to the same Markov process) converges to the components of the right eigenvector \mathbf{f} of \mathbf{c} corresponding to the eigenvalue of largest magnitude (equal to 1). In the interval $t - 1$ to t , the patch's environmental state is written as $E(t)$, a random variable that takes one of the values $1, 2, \dots, K$. In the next time interval, t to $t + 1$, the habitat state $E(t + 1)$ is chosen in accordance with the transition probabilities \mathbf{c} . A sequence of habitat states $E(1), E(2), \dots, E(t), E(t + 1), \dots$ is not predictable from the stable distribution \mathbf{f} but depends on habitat transition probabilities.

The eigenvalue of \mathbf{c} of second-largest magnitude, a mag-

nitude we call ρ , usually summarizes serial correlation between habitat states: a value of ρ near 1 means serial correlation is strong. The population numbers by stage at time t are enumerated in vector $N(t)$; there is a known population vector $N(0)$ at time $t = 0$. The population is governed between $(t - 1)$ and t by a random vital rate matrix $X(t)$ that takes on values determined by the habitat state at time t . The population changes through time according to

$$N(t) = X(t)N(t - 1). \quad (1)$$

Study Species and Habitats

We employ an example based on empirical work on the population and habitat dynamics (Pascarella 1995, 1998a, 1998b; Pascarella and Horvitz 1998) of *Ardisia escallonioides* Schlecht. & Cham. (Myrsinaceae) (fig. 1), a tropical understory shrub living in a hurricane-prone tropical hardwood forest on a limestone rock substrate. The habitat state is measured by openness of the forest canopy. In the absence of hurricanes, forest canopies tend to close gradually and the forest understory becomes darker; hurricanes open the forest canopy, creating a large light gap. The system is described by eight life-history stages ($S = 8$) and seven habitat states ($K = 7$), that is, the percent of canopy openness. The eight life-history stages are seeds, seedling-sized plants, juveniles, prereproductives, and four size classes of reproductives (small, medium, large, and very large). Single habitat vital rates are contained in matrices A_1, A_2, \dots, A_7 (see app. A in the online edition of the *American Naturalist*). For this understory species, hurricanes have positive effects because they open the canopy and kill the major seed predator. State 1 of the habitat (the most open canopy and the lightest habitat) has the highest asymptotic single-habitat population growth rate and state 7 (the closed canopy and the darkest habitat) has the lowest (fig. 1A).

The effect of a hurricane on a patch of plants depends on its intensity and on the location of the patch relative to the hurricane's path. From the historical record, Pascarella and Horvitz (1998) calculated the probability of a hurricane at the study site in any given year as $P(\text{hur}) = 0.081$ and from this, combined with other data, estimated the habitat transition probabilities c (see app. B in the online edition of the *American Naturalist*). The steady state distribution of habitats at the historical hurricane frequency is shown in figure 1B; corresponding values of the average vital rates and their coefficients of variation are in figure 1C, 1D. Our numerical illustrations follow Pascarella (1995) in using a range of hurricane frequencies higher or lower than historical for several reasons.

Higher hurricane frequency will be expected in our study region as the global climate warms. Hurricane frequency currently varies across the geographic range of our study species; in particular, the noncoastal Central American populations are affected by hurricanes less often than the populations in our study region. Also, consideration of how disturbance frequency affects population dynamics increases the general applicability of our model to other similar environments (i.e., typhoon-disturbed environments).

For our system, we find that both historical and low hurricane frequencies yield environments in which the most frequently occurring habitat state is the closed canopy (state 7), whereas high hurricane frequency results in a habitat dominated by state 1 (the most open canopy; fig. 2). The serial correlation of the habitat (ρ) ranges from a high of 0.9 at the historical hurricane frequency to a low near 0.4 at high hurricane frequency (fig. 2).

Growth Rates as Averages

Stochastic Growth Rate

The total population $P(t)$ in the patch at time t is the sum of the elements of $N(t)$ and depends on the history of habitat states that the patch has experienced and is therefore a random variable. The long-run growth rate

$$\log \lambda_s = \lim_{t \rightarrow \infty} (1/t) \log [P(t)/P(0)] \quad (2)$$

is also denoted $a = \log \lambda_s$ by Tuljapurkar (1990, 1997). This stochastic growth rate can be obtained from numerical simulations of many time steps of a population in a single patch or of many independent patches (table 1; Caswell 2001).

Average or Megamatrix Growth Rate

A temporally random environment is observed as a sample path, a sequence of habitats. Over t time steps, an average of population at time t over many independent simulations is an estimate of the expected population (table 1). From a starting population $P(0)$, suppose that n independent simulations, each over t time steps, yields population numbers $P(j, t)$ for $j = 1, \dots, n$. Then we estimate the growth rate of average population using large n to get the average population and then large t to get

$$\log \lambda_M = \lim_{t \rightarrow \infty} (1/t) \log \left\{ \lim_{n \rightarrow \infty} (1/n) \sum_{j=1}^n [P(j, t)/P(0)] \right\}. \quad (3)$$

However, we may find λ_M by a different conceptual and

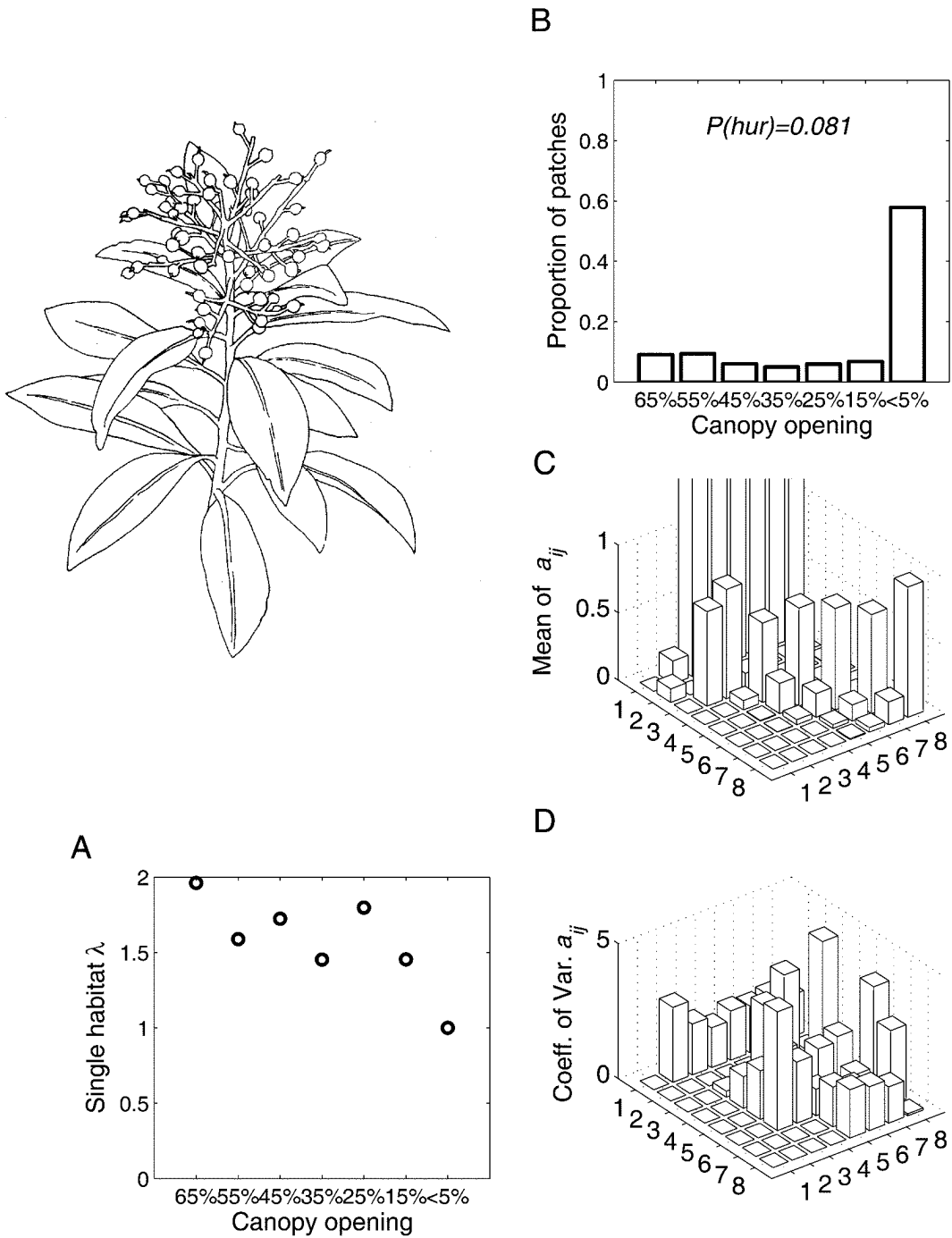


Figure 1: The example species, *Ardisia escallonioides*. **A**, Single-habitat population growth rates, dominant eigenvalues of A_1, A_2, \dots, A_7 . At historical hurricane frequency $P(\text{hur}) = 0.081$, the following are illustrated: **B**, the equilibrium proportion (f) of habitat states; **C**, the mean vital rates (except reproduction, which is clearly on a different scale); and **D**, the coefficient of variation of vital rates in matrix form. In **C** and **D**, stages are numbered 1–4 for seeds, seedlings, juveniles, and prereproductive, and 5–8 for small, medium, large, and very large reproductives (stage at time t as columns are depicted left to right and stage at time $t + 1$ as rows are depicted back to front).

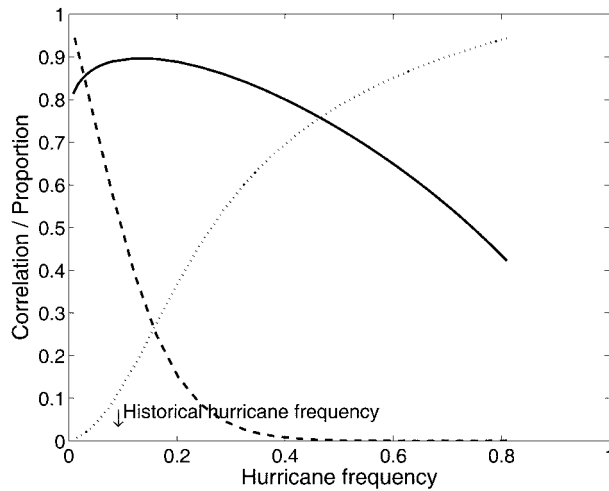


Figure 2: Effects of hurricane frequency on serial correlation ρ (solid line) of the habitats and on the equilibrium frequency of open-canopy (dotted line) and closed-canopy (dashed line) patches. The arrow indicates historical hurricane frequency.

computational route. Consider an ensemble of many independent patches, in each of which a population follows the dynamics of our single-patch model. Individuals do not move between patches, and there is no correlation in the transitions of different patches (i.e., the scale of the patches is such that they are independent in their responses to the overall expected regime of hurricanes in the region [Pascarella and Horvitz 1998]). Each patch undergoes changes in its habitat state according to the same Markov transition matrix \mathbf{c} . At time t , let us enumerate habitat states and populations in the individual patches to obtain a joint distribution of population by life-history stage and habitat state. Now find all patches that have a given habitat state and add the population vectors across all the patches of that state. The aggregated population in habitat state β will be subject to the population vital rate matrix \mathbf{A}_β , and then on average, a fraction $c_{\alpha\beta}$ of this aggregate will make a transition to habitat state α . So the average rate at which the aggregate in habitat state β at time t will contribute to the aggregate in state α at time $(t + 1)$ is given by the product $c_{\alpha\beta}\mathbf{A}_\beta$. Clearly the dynamics of this aggregation (table 1) are described by powers of the megamatrix

$$\mathbf{M} = \begin{pmatrix} c_{11}\mathbf{A}_1 & c_{12}\mathbf{A}_2 & \cdots & c_{1K}\mathbf{A}_K \\ \vdots & \vdots & \vdots & \vdots \\ c_{K1}\mathbf{A}_1 & c_{K2}\mathbf{A}_2 & \cdots & c_{KK}\mathbf{A}_K \end{pmatrix} \quad (4)$$

that was described by Horvitz and Schemske (1986) and Pascarella and Horvitz (1998). Write λ_M for the dominant eigenvalue of \mathbf{M} . When there is a large number of patches,

this habitat-by-stage aggregation keeps track of the average population at each time step, and the annual growth rate of average population must converge to λ_M . This connection between the megamatrix method (as an aggregate habitat-by-stage time average) and the stochastic dynamics is presented here for the first time. The megamatrix was derived in a different way by Cohen (1977b) to compute growth rate of average population in Markovian models.

The Mean Matrix: Whose Dynamics?

The dominant eigenvalue λ_A of the mean (weighted arithmetic average) matrix of vital rates, $\mathbf{A} = \sum_\alpha f_\alpha \mathbf{A}_\alpha$, does not describe the dynamics of the average population or the time-averaged dynamics in a single path (table 1), unless there is no serial correlation of habitat states (app. C). In any case, \mathbf{A} and λ_A contain no information about sequences of habitat states that are key to dynamics in temporally varying environments. Still, λ_A is equivalent to the growth rate estimated in many past demographic studies, and so we consider how it relates to λ_S and λ_M .

Growth Rate Comparisons

We illustrate the differences between these growth rates using our example. For any given hurricane frequency, the megamatrix yields the growth rate λ_M of average population; the average matrix likewise yields λ_A . For the stochastic growth rate λ_S , we used a 100,000-long simulation sequence, and we present a numerical estimate λ_S^* as well as approximate 90% confidence intervals computed as in Caswell (2001, p. 396).

Note that the three growth rates respond differently to hurricane frequency (fig. 3). We cannot predict change in one by the change in one or both of the others: λ_S is most sensitive to hurricane frequency; λ_M is the least; $\lambda_S < \lambda_M$ throughout. In contrast, $\lambda_A > \lambda_M$ only for hurricane frequency below about 0.4, but at higher frequencies, the relationship is reversed. As hurricane frequency rises above 0.4, the frequency f_1 of the most open habitat state exceeds 0.8 (fig. 2), so most habitat sequences contain a high proportion of open habitat states that have high vital rates. The three λ 's converge at high hurricane frequency for two reasons. One is that the serial correlation of habitat states is much smaller than at low hurricane frequencies (which reduces the difference between λ_A and λ_M), and the other is that as transitions to the darker habitat states become uncommon, the variability experienced by a population (or ensemble of independent populations) over time becomes increasingly small (which reduces the difference between λ_M and λ_S).

As hurricane frequencies drop below 0.4, darker habitat states become more common. Therefore, at low hurricane

Table 1: Growth rates

Name	Symbol	Meanings and methods
Cumulative growth	$P(t)/P(0)$	Population growth after t time steps (which depends upon the sequence of habitat states).
Stochastic growth rate	$\lambda_s = \exp(a)$	(1) Time-averaged cumulative growth in a patch over many time steps in one sample path; (2) average over many sample paths of each sample path's time-averaged cumulative growth.
Megamatrix growth rate	λ_M	(1) For many sample paths (or many patches), perform the following steps to obtain the time-averaged mean cumulative growth: First, take the cumulative growth of each path (or patch), $P(t)/P(0)$; second, take the mean cumulative population growth over many sample paths (or patches); third, take the time average of this mean cumulative growth rate. (2) The growth rate of the average population. (3) The dominant eigenvalue of the megamatrix constructed for an aggregation of patches.
Growth rate of the matrix of average transition rates	λ_A	The dominant eigenvalue of the matrix of average transition rates

frequencies, we expect and observe (fig. 3) a large difference between λ_M and λ_s . The distinction between the most favorable sequences and the most probable sequences is sharpest when the best habitat is the rarest. In our example, this occurs at the lowest hurricane frequency.

The megamatrix growth rate λ_M is best understood as the aggregate growth rate of an ensemble of a large number of independent patches. It is improved by rare but favorable habitats because, at each time step, the “wealth” of the high growth makes a large contribution to the ensemble average. In a large number of patches, some few will have a persistently favorable sequence of habitats over

many time steps. In contrast, λ_s is the exponential growth rate of a single patch or a set of patches that experience the same habitat sequences; here, rare favorable habitats have less effect because the “wealth” passes from one time step to the next only within a patch, and a patch is likely to transition to poorer environments before experiencing another rare favorable one. The growth rate λ_A cannot in general predict the other growth rates.

Sensitivity and Elasticity

Sensitivity to What?

In a fixed habitat, sensitivity is unambiguously defined by the (partial) derivatives of the growth rate with respect to the vital rates. In a varying environment, a vital rate for transition (i, j) may have different values in each habitat state. Each of the population growth rates we have discussed is a function of each of these values, that is, a function of the phenotypic norm of response of the trait over environments. Therefore, the “derivative” of a growth rate with respect to the (i, j) trait is not a single number but a set of numbers (one for each habitat state) that make up a functional derivative. When we consider how a growth rate changes in response to a perturbation of a mean, variance, or any other statistic, we are summarizing these derivatives in special ways (table 2).

Computing Derivatives of λ_s

Recall that Caswell (1978) showed how to compute deterministic elasticities by using eigenvectors of a fixed projection matrix to compute an exact derivative of the growth rate. We can do a similarly exact calculation for a stochastic

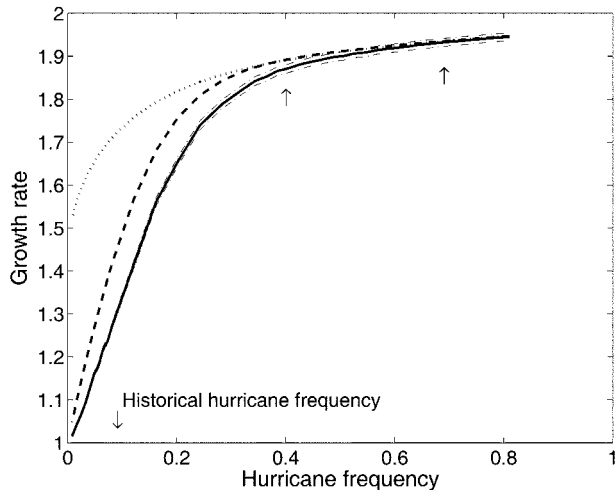


Figure 3: Effects of hurricane frequency on three growth rates: λ_M (dotted line), λ_A (dashed line), and λ_s (solid line). The downward arrow indicates historical hurricane frequency. The upward arrows indicate the range of hurricane frequencies in which λ_A exceeds λ_M .

Table 2: Elasticities of λ_s to perturbations of the mean and the variance of matrix entries X_{ij} , where random matrix \mathbf{X} takes values \mathbf{A}_α , which are determined by habitats α in a Markovian environment

Elasticity	Symbol	Mean	Variance	CV	ΣE_{ij}
Stochastic	E^S	+	+	No	= 1
Average	$E^{S\mu}$	+	No	-	>0, $\neq 1$
Variance	$E^{S\sigma}$	No	+	+	<0, >0, $\neq 1$

Note: Plus sign indicates what is changed. CV = coefficient of variation.

growth rate, using Tuljapurkar's (1990, ch. 11) exact formula for the derivatives.

We first use equation (1) to obtain statistically stationary sequences of population structures $\mathbf{u}(t)$ and reproductive value vectors $\mathbf{v}(t)$ (Tuljapurkar 1990, 1997). The population growth rate between $t - 1$ and t from equation (1) is

$$\lambda(t) = |\mathbf{X}(t)\mathbf{u}(t - 1)|.$$

We record a numerical set of the $\mathbf{X}(t)$, $\mathbf{u}(t)$, and $\mathbf{v}(t)$ by doing a long numerical simulation (we used 100,000 iterations and discarded the first 500) and storing the matrices and vectors. These vectors and matrices describe the statistical dynamics of the model. Note that there is no restriction here on the size of the random variation in vital rates (we are not using Tuljapurkar's [1990] small-noise approximation techniques).

We now examine the elasticity of the stochastic growth rate $a = \log \lambda_s$. The growth rate $a = a(\mathbf{X})$ is a function of the sequence of random projection matrices $\mathbf{X}(t)$. To examine elasticity is to examine the effect of a small change in the vital rates, which amounts to a change in $\mathbf{X}(t)$ for each t . Suppose that for the (i, j) life-history transition, we change the vital rate from $X_{ij}(t)$ to $X_{ij}(t) + \delta C_{ij}(t)$, where $\delta > 0$. Then the stochastic growth rate must change from $a(\mathbf{X})$ to $a(\mathbf{X} + \delta\mathbf{C})$. A proportional derivative of a corresponding to the perturbations \mathbf{C} can now be defined as the limit

$$D_{ij} = \lim_{\delta \rightarrow 0} \left(\frac{1}{\delta} \right) [a(\mathbf{X} + \delta\mathbf{C}) - a(\mathbf{X})]. \quad (5)$$

Tuljapurkar (1990) showed that this derivative can be computed in terms of the stationary sequences $\mathbf{X}(t)$, $\mathbf{u}(t)$, $\mathbf{v}(t)$ by

$$D_{ij} = \lim_{T \rightarrow \infty} \left(\frac{1}{T} \right) \sum_{t=1}^T \frac{v_i(t)C_{ij}(t)u_j(t-1)}{\lambda(t)[\mathbf{v}(t), \mathbf{u}(t)]}. \quad (6)$$

In our initial simulation, we stored the long sequences of

the vectors, so for any perturbation we compute the entire matrix \mathbf{D} in one pass through the summation. We can adjust T to reduce the estimated sampling error to any desired accuracy. Our computations use MATLAB (2001) code that we will provide upon request.

The computation in equation (6) is a direct estimate of the exact derivative and can be used to examine habitat-specific perturbations in rates or perturbation of correlations or serial correlations between rates. The definitions and computation of elasticity used here also apply when the rates have continuous distributions. In this article, we will focus on only three of the many kinds of elasticity that could be investigated for the stochastic growth rate.

Three Kinds of Elasticity of λ_s

Consider first the effect of perturbing the mean μ_{ij} of vital rate $X_{ij}(t)$, with no change in variance. To achieve this we must perturb the vital rate in every habitat state by an equal amount, so in equation (5) and equation (6), set

$$\mathbf{C}_{ij}(t) = \mu_{ij}. \quad (7)$$

The derivative in equation (6) now becomes precisely an elasticity with respect to the mean rate, which we write as

$$E^{S\mu} = \frac{\partial \log \lambda_s}{\partial \log \mu_{ij}}. \quad (8)$$

Here the variance of the rate stays fixed, but its coefficient of variation decreases (table 2). Dixon et al. (1997) were the first to compute this particular elasticity using this method, although they do not interpret it as we do. These $E_{ij}^{S\mu}$ are always positive or 0, but their sum over vital rates does not equal 1.

Our second case is elasticity with respect to standard deviation (variance), with no change in means. In equation (5) and equation (6), set

$$\mathbf{C}_{ij}(t) = \mathbf{X}_{ij}(t) - \mu_{ij}. \quad (9)$$

Such a perturbation increases the variance (plasticity) of the (i, j) rate by a factor of $(1 + \delta)^2$ but does not change the mean. The number δ is the proportional increase in the standard deviation σ_{ij} of the rate, and it is also the proportional increase in the coefficient of variation of the rate. The derivative in equation (6) obtained when using equation (9) is precisely the elasticity with respect to the standard deviation, which we write as

$$E_{ij}^{S\sigma} = \frac{\partial \log \lambda_s}{\partial \log \sigma_{ij}} = \frac{\sigma_{ij} \partial \lambda_s}{\lambda_s \partial \sigma_{ij}}. \quad (10)$$

Here the mean of the rate stays fixed, but its coefficient of variation increases (table 2). Caswell (2001) has defined this elasticity but does not show how to compute it exactly (he uses Tuljapurkar’s small-noise approximation; we do not) and does not provide the interpretation we give here. These elasticities need not be positive, and they will not add to 1, either.

Our third and final example is a perturbation of both mean and standard deviation by equal proportions, and we write the elasticity with respect to such perturbation by E^S . In equation (5) and equation (6), set

$$C_{ij}(t) = X_{ij}(t). \tag{11}$$

Here, and only here, do we get the same proportional change in every i, j element of each matrix in the sequence, which means that averages and standard deviations change by the same proportional factor. Denote the elasticity of λ_s to this change by

$$E_{ij}^S = \frac{\partial \log \lambda_s}{\partial \log X_{ij}}. \tag{12}$$

We are the first to point out that this elasticity describes only changes in which the coefficient of variation stays fixed (table 2). We follow Caswell (2001) in referring to E_{ij}^S as “the” stochastic elasticity. These elasticities are non-negative, and as Caswell shows, always sum to 1 over all elements for any stochastic model (this sum provides a convenient check on the computation; see table 2). In this regard, these elasticities are analogous to deterministic elasticities. Benton and Grant (1999) were the first to use E_{ij}^S , although they used numerical differences to estimate the necessary derivative of λ_s .

Computing Elasticities of λ_M and λ_A

The elasticity of λ_M with respect to changes in habitat-stage transitions, $E_{ij\alpha\beta}^M$, is obtained by standard analytical methods from the eigenvectors of the megamatrix. These

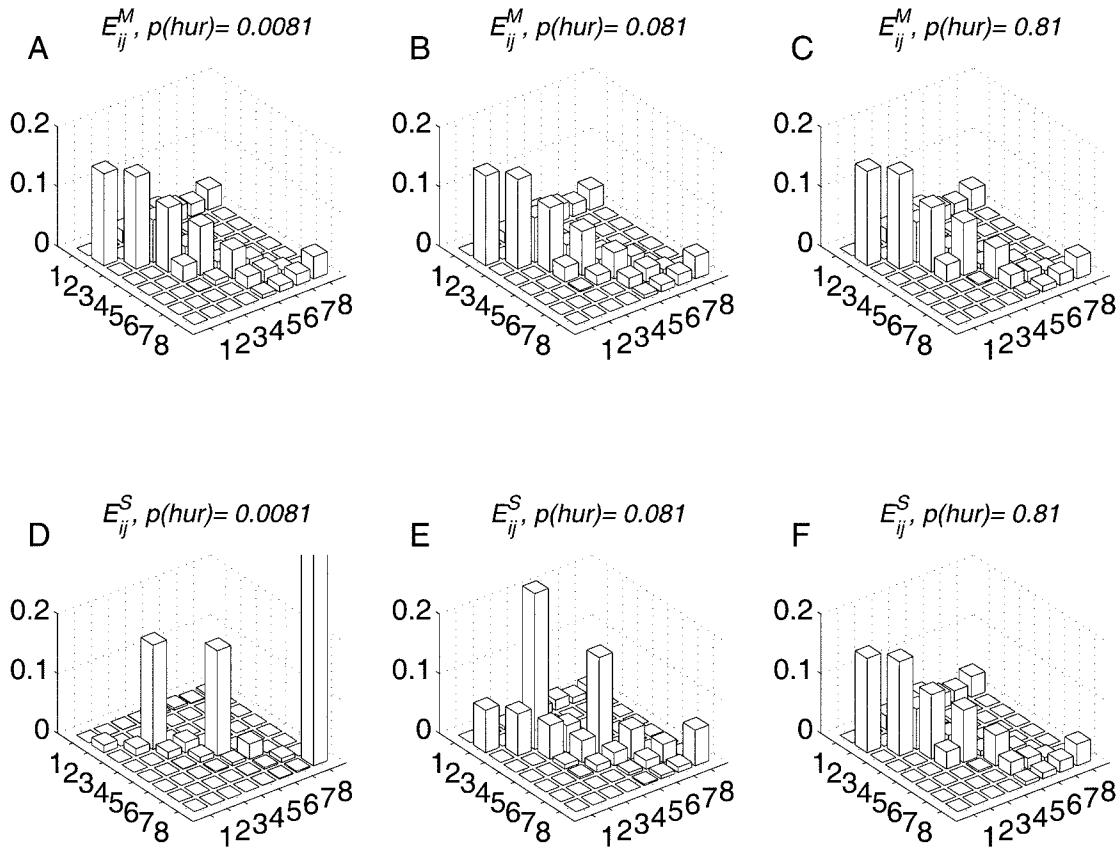


Figure 4: Effects of hurricane frequency on elasticity of the megamatrix growth rate E_{ij}^M and of the stochastic growth rate E_{ij}^S . The entire elasticity matrix is illustrated for (A, D), 0.1 ×; (B, E), 1 ×; and (C, F), 10 × the historical hurricane frequency. Stages are numbered as in figure 1C, 1D.

elasticities sum to 1 across the entire megamatrix; they can be summed in subsets with respect to habitats, stages, habitat transitions, or stage transitions (Pascarella and Horvitz 1998). Summing with respect to stage transitions yields elasticities E_{ij}^M that are analogous to E_{ij}^S . The elasticity of λ_A is obtained by standard analytical methods from the matrix \mathbf{A} .

Elasticity Comparisons

We now compare the stochastic elasticity E^S with the megamatrix elasticity E^M and the elasticity of the matrix of average vital rates E^A . We also examine the elasticities $E^{S\mu}$ and $E^{S\sigma}$ and compare them with E^S , computed for our example at the historical hurricane frequency.

Comparing E^M , E^S , and E^A . The elasticities E_{ij}^S and E_{ij}^M for all vital rates are shown for low, historical, and high hurricane frequencies in figure 4. The megamatrix elasticities appear similar across hurricane frequencies, but there are large changes in the stochastic elasticities of elements representing stasis of juveniles and adults (e.g., E_{33}^S , E_{55}^S , and E_{88}^S), seed germination (E_{21}), and seedling growth (E_{32}).

At low and historical frequencies, there is very low correlation among the elasticities of the three growth rates (fig. 5). We emphasize that elasticities of λ_A do not accurately predict E_{ij}^M or E_{ij}^S , although at high hurricane frequency the correlation between E_{ij}^A and E_{ij}^S increases. As hurricane frequency changes, the relative importance of some vital rates to λ_s changes dramatically. The effects of early life-cycle growth transitions on λ_s increase with hurricane frequency; for example, there is an eightfold increase in the elasticity of seed germination (element 2,1; fig. 6A) and a similar change in the elasticity of seedling growth (not pictured). In contrast, the elasticity of stasis of later stages, for example, juveniles (element 3,3; fig. 6B) and small reproductives (element 5,5; not pictured), first increase and then decrease. In general, changes in stochastic elasticity E_{ij}^S with hurricane frequency are not predicted by changes in E_{ij}^M or E_{ij}^A (illustrated in fig. 6).

E^S , $E^{S\mu}$, and $E^{S\sigma}$. The elasticities $E^{S\mu}$ and $E^{S\sigma}$ can be readily translated into sensitivities. For the (ij) rate, the absolute change in $a = \log \lambda_s$ produced by a change of $(\Delta)(\mu_{ij})$ in the average μ_{ij} is $(\Delta)E_{ij}^{S\mu}$. Note that here we keep the variance fixed so the vital rate increases by the same amount in every habitat state. In our example, λ_s responds strongly to a proportional change in the average value of seed production by small reproductives (element 1,5) and of growth of juveniles (element 4,3; fig. 7A). If we keep the mean value of the (ij) rate fixed and change only σ_{ij} by $(\Delta)(\sigma_{ij})$, the resulting change in $\log \lambda_s$ will be $(\Delta)E_{ij}^{S\sigma}$. Tran-

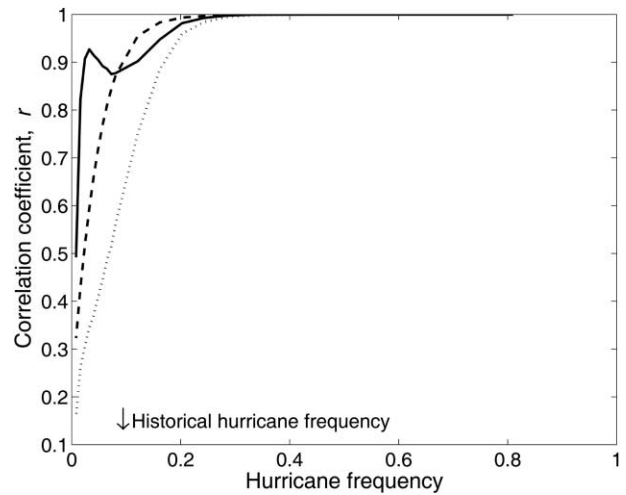


Figure 5: Effects of hurricane frequency on correlations of E_{ij}^M (solid line), E_{ij}^S (dotted line), and E_{ij}^A (dashed line). The arrow indicates historical hurricane frequency.

sitions with a relatively high positive value of $E^{S\sigma}$, such as stasis of juveniles (element 3,3) in our example (fig. 7B), identify transitions in which increasing plasticity will increase stochastic growth rate. Increasing plasticity for transitions with negative $E_{ij}^{S\sigma}$, such as the growth of juveniles (element 4,3), will decrease λ_s .

The pattern of stochastic elasticity E^S (fig. 4E) does not describe the pattern of $E_{ij}^{S\mu}$ or the sign structure of $E_{ij}^{S\sigma}$. The evolutionary implication is that for many vital rates, the strength of directional selection on the mean value (measured by $E_{ij}^{S\mu}$) can be quite different from the strength of selection for a proportional change in all habitats (measured by E_{ij}^S). There is a correlation of 0.63 between E^S and $E^{S\mu}$ (fig. 8A) and very little correlation (0.19) between E^S and $E^{S\sigma}$ (fig. 8B). One can directly interpret the $E^{S\mu}$ in terms of changes that act in a similar direction and magnitude in all habitats. The $E^{S\sigma}$ describe changes in the variability of rates around their mean values. However, the E^S reflect changes in the same direction but with different magnitudes proportional to the habitat-specific rates, making them harder to interpret in terms of a force of selection.

Reinterpretation of the Dynamics of Ardisia escallonioides. Previous megamatrix analyses of this (Pascarella and Horvitz 1998) and similar systems (Horvitz and Schemske 1986; Alvarez-Buylla 1994; Cipollini et al. 1994) pointed out the need to examine habitat as well as stage dynamics but were missing a perspective on population dynamics within a patch. Our results enable us to supplement Pascarella and Horvitz's (1998) results about population dynamics of the study species at the historical hurricane

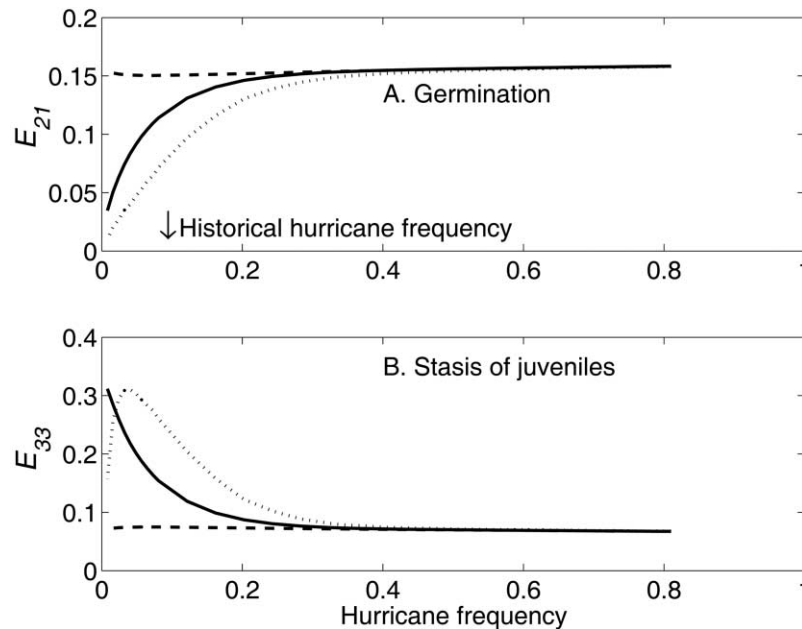


Figure 6: Differences in the effects of hurricane frequency on E_{ij}^M (dashed line), E_{ij}^S (dotted line), and E_{ij}^{λ} (solid line), illustrated for (A) germination and (B) stasis of juveniles. The arrow indicates historical hurricane frequency.

frequency. First, the stochastic growth rate $\lambda_s = 1.27$ is much lower than the aggregate growth rate $\lambda_M = 1.71$. This difference means that in an ensemble of many independent patches, only a small fraction of patches experiences favorable habitat sequences and achieves a very high growth rate. Second, the principal influences on λ_M are through seed germination, seedling growth, and juvenile growth, whereas λ_s is influenced most by stasis of juveniles and small reproductives. Pascarella and Horvitz (1998) pointed out that elasticities of the life-history matrix in the most frequent habitat (state 7) do not predict E_{ij}^M . Our results here show that they also do not predict E_{ij}^S . Specifically, juveniles have higher E_{ij}^M and E_{ij}^S than do very large reproductives; the opposite is true for the single-habitat elasticity analysis of the dynamics in the most frequent habitat (state 7; see Pascarella and Horvitz 1998).

Conclusions

We have analyzed growth rates and their elasticities for populations in which the environmental state affects the life-history rates of the organism and in which the sequencing of environments is determined by natural forces. The sequence of environments matters: There is a probability distribution of sequences encapsulated in the dynamics that cannot be seen simplistically. We illustrated our analysis with an empirically based example, an un-

derstory plant in a hurricane-disturbed forest. Our theory and illustration should be especially relevant in studying patchy, recurrent disturbances such as may be experienced by a broad range of organisms. The stochastic growth rate is best understood as a geometric mean growth rate for a particular patch, where the realized cumulative growth of the patch is the result of a long temporal sequence of habitats. The stochastic growth rate is also the geometric mean growth rate for a collection of patches if there is high spatial correlation between the patches in the habitat sequences they experience. The megamatrix growth rate is best understood as an aggregate growth rate of an ensemble of a large number of independent patches and thus as a spatial average over many patches experiencing uncorrelated temporal sequences of the same length.

We compared three types of elasticity: the proportional sensitivities of stochastic growth rate to proportional perturbations of the mean, or of the variance, or of all the habitat-specific values of each vital rate. These elasticities are called $E^{S\mu}$, $E^{S\sigma}$, and E^S , respectively. They may appear complex, but they only describe the effect of changes in the norm of response of phenotypes to environment. In particular, the $E^{S\mu}$ describe change in growth rate when a vital rate changes by the same magnitude in every habitat, whereas the E^S describe the effect of changing a vital rate by the same proportion in every habitat. In life-history theory, elasticities are used to explore potential selection gradients, and our approach provides a tool for studying

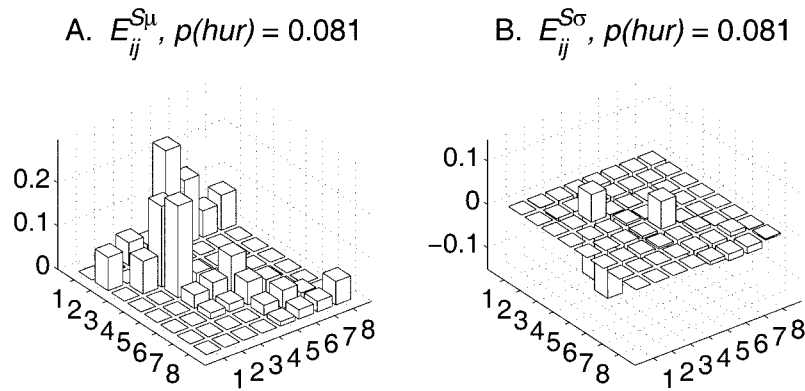


Figure 7: Elasticity of λ_s to perturbations at the historical hurricane frequency. A, Perturbations of the mean only, $E^{S\mu}$. B, Perturbations of the variance only, $E^{S\sigma}$. Stages are numbered as in figure 1C, 1D.

not just average phenotypes but the entire structure of phenotypes as they depend on the environment. We have shown that elasticity is shaped by the response of the organism not just to environments but also to the patterning of environments through time. These results extend previous work on life-history evolution in correlated environments (Orzack 1985). More generally, our results show that a fundamental concept in varying environments is the elasticity of growth rate to the value of each vital rate in each possible habitat state.

In our example species, as in many understory plants, the population is not limited by its own density but rather by reduced light created by canopy closure of the overstory trees. The principal positive effect of hurricanes for such species comes not from reducing density but rather from an increase in light, which stimulates flowering. In addition, particular to our study species, hurricanes extirpate

the major predispersal seed predator, a small specialist moth (*Periploca*). This combination of increased flowering and freedom from predation is what makes posthurricane conditions so favorable. It is not a density effect. In more general ecological settings we may expect density-dependent dynamics (Benton and Grant 1999), and our methods can and should be adapted to such cases.

Our example illustrates that analysis of a matrix constructed from the arithmetic mean of vital rates does not predict the value or the elasticity of either type of average growth rate, except in special conditions. An important question was raised by Benton and Grant (1996, 1999) and Caswell (2001): When is it not safe to use the elasticities of the average matrix? Our analysis and previous examples identify two situations in which a full stochastic analysis is likely to be essential: when there are many habitat states with correlated transitions over time or when

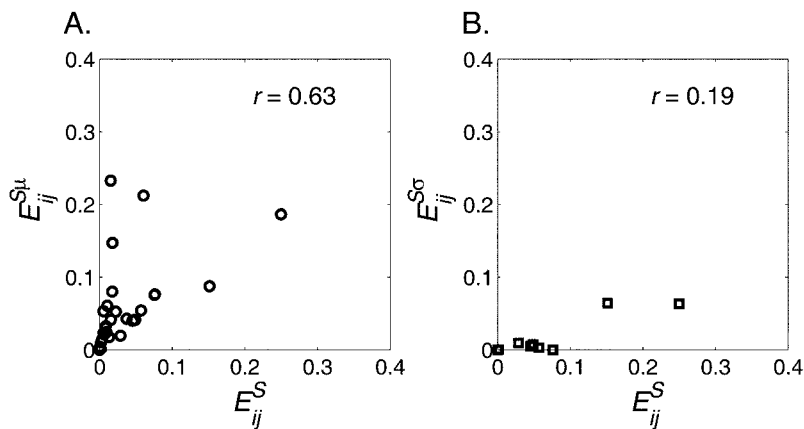


Figure 8: Correlation of E^S with (A) $E^{S\mu}$ and (B) $E^{S\sigma}$

the demography of the average matrix displays slow and cyclical convergence to a stable population structure.

Stochastic elasticities can be used to compute stochastic versions of what van Tienderen (1995, 2000) calls “integrated elasticity” by incorporating the biological (not environmental) covariation between life-cycle transitions. We have assumed that we know accurately the parameters that determine the population dynamics. In fact (Wisdom et al. 2000), the model parameters will be known only to within some error. We could use the method of Wisdom et al. to examine the relative impact of uncertainty about parameters and the actual dynamic uncertainty of environments over time.

What are the management implications of these analyses? Management, whether to conserve, control, or exploit species, is an activity framed by a particular time period, particular landscape constraints, and particular goals. Our analyses show that to manage for an increase in the population growth of an aggregate (an ensemble of a large number of patches) can be different than managing for the long-term population growth rate in a particular patch.

Our elasticity analysis makes it possible to focus on both stage transitions and habitat states. Managers may wish to manipulate the habitat dynamics, if possible (e.g., controlled burns, logging practices that simulate tree-fall dynamics, etc.), to increase the probability of favorable sequences of habitat states, not merely the frequency of a favorable habitat. Finally, our results concerning population variability are relevant to management that aim to control population variance over space or time. For example, harvesting that is directed at particular life stages can alter the overall variability in habitat-by-stage population structure.

Acknowledgments

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APPENDIX C

Megamatrix with No Serial Correlation

First we show that when there is no serial autocorrelation, $\lambda_M = \lambda_A$. From equation (4), the eigenvector \mathbf{u}_M of the megamatrix \mathbf{M} corresponding to eigenvalue λ_M is a stack of $S \times 1$ vectors:

$$\begin{pmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \vdots \end{pmatrix}. \quad (\text{C1})$$

Multiply this by the megamatrix to get

$$\sum_{\beta} c_{\alpha,\beta} \mathbf{A}_{\beta} \mathbf{u}_{\beta} = \lambda_M \mathbf{u}_{\alpha} \quad (\text{C2})$$

for every α . Zero serial correlation means that $c_{\alpha,\beta} = c_{\alpha}$ for all β , and the stationary habitat frequencies are $f_{\alpha} = c_{\alpha}$. Equation (C2) now becomes

$$c_{\alpha} \sum_{\beta} \mathbf{A}_{\beta} \mathbf{u}_{\beta} = \lambda_M \mathbf{u}_{\alpha},$$

which implies that the \mathbf{u}_{α} are proportional to each other. If we could find a vector \mathbf{w} such that $\mathbf{u}_{\alpha} = c_{\alpha} \mathbf{w}$, the preceding equation would become

$$\left(\sum_{\beta} c_{\beta} \mathbf{A}_{\beta} \right) \mathbf{w} = \lambda_M \mathbf{w}. \quad (\text{C3})$$

The average vital rates are $\mathbf{A} = \sum_{\beta} f_{\beta} \mathbf{A}_{\beta} = \sum_{\beta} c_{\beta} \mathbf{A}_{\beta}$. Therefore, equation (C3) is just the eigenvalue equation for the average matrix \mathbf{A} , which means that $\lambda_M = \lambda_A$ and \mathbf{w} is the corresponding eigenvector of \mathbf{A} .

Earlier analysis of λ_M (Tuljapurkar 1982) shows further that when there is serial autocorrelation we have $\lambda_M \neq \lambda_A$, except perhaps for very special constraints on the vital rates.

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Correction

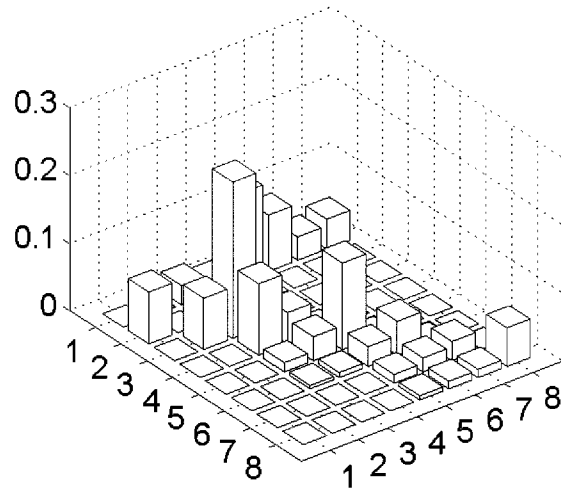
In “The many growth rates and elasticities of populations in random environments” by Shripad Tuljapurkar, Carol C. Horvitz, and John B. Pascarella (*American Naturalist* 162:489–502), two of the graphs were incorrect and certain numerical assertions in the text need to be corrected. On page 497, column 1, last paragraph, lines 7–9, replace “seed ... fig. 7A)” with “stasis of juveniles (element 3,3) and seed production by small reproductives (element 1,5; fig. 7A).” On page 497, in the legend to figure 5, replace “correlations ... (*dashed line*)” with “correlations of E^S with E^A (*solid line*), E^A with E^M (*dashed line*), and E^S with E^M (*dotted line*, lowest curve).” On page 497, column 2, replace line 2, “stasis of juveniles (element 3,3)” with “stasis of small reproductives (element 5,5)”; lines 5–6, “growth of juveniles (element 4,3)” with “seed production by small reproductives (element 1,5)”; line 13, “0.63” with “0.90”; line 14, “0.19” with “0.14.” On page 499, replace figures 7 and 8 with the figures that appear on the following pages.

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A. $E_{ij}^{S\mu}, p(hur) = 0.081$



B. $E_{ij}^{S\sigma}, p(hur) = 0.081$

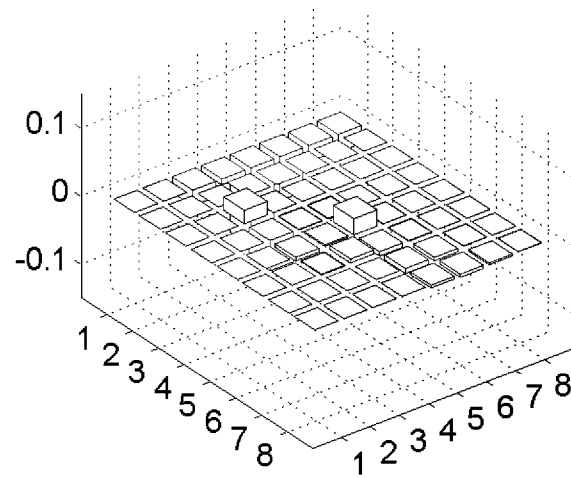


Figure 7: Elasticity of λ_s to perturbations at the historical hurricane frequency. *A*, Perturbations of the mean only, $E^{S\mu}$. *B*, Perturbations of the variance only, $E^{S\sigma}$. Stages are numbered as in figure 1C, 1D.

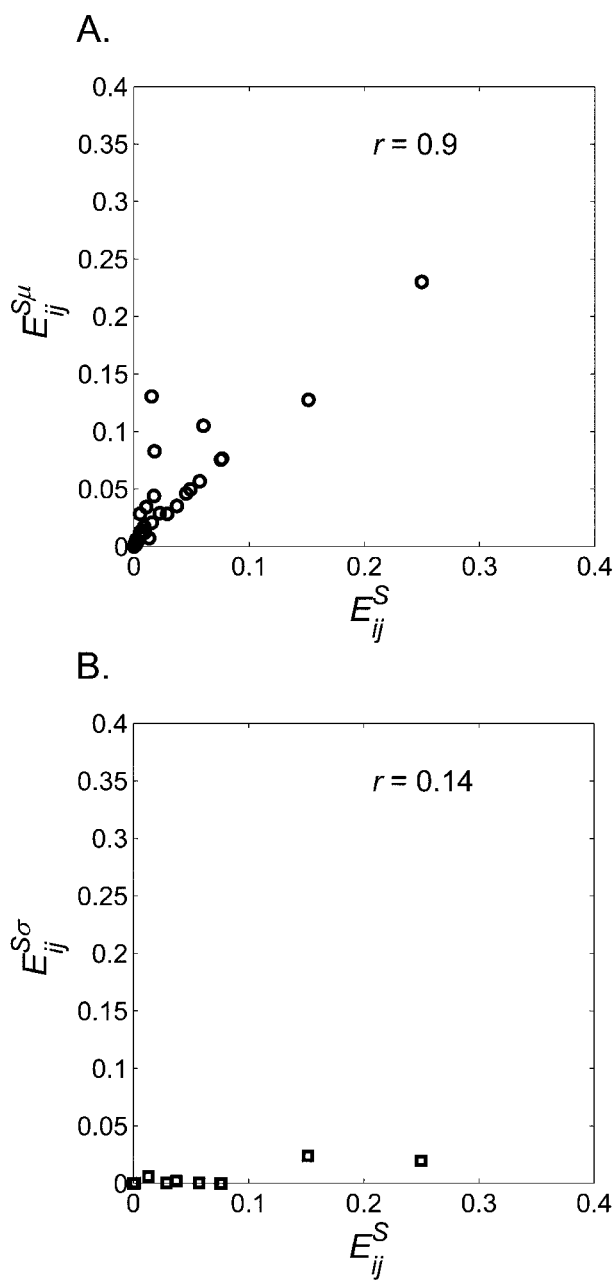


Figure 8: Correlation of E^S with (A) $E^{S\mu}$ and (B) $E^{S\sigma}$