

FROM STAGE TO AGE IN VARIABLE ENVIRONMENTS: LIFE EXPECTANCY AND SURVIVORSHIP

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Abstract. Stage-based demographic data are now available on many species of plants and some animals, and they often display temporal and spatial variability. We provide exact formulas to compute age-specific life expectancy and survivorship from stage-based data for three models of temporal variability: cycles, serially independent random variation, and a Markov chain. These models provide a comprehensive description of patterns of temporal variation. Our formulas describe the effects of cohort (birth) environmental condition on mortality at all ages, and of the effects on survivorship of environmental variability experienced over the course of life. This paper complements existing methods for time-invariant stage-based data, and adds to the information on population growth and dynamics available from stochastic demography.

Key words: *age structure; Calathea; demography; life expectancy; Markov chains; stage structure; survivorship.*

INTRODUCTION

Structured populations are studied and modeled in terms of stages when stage is better than age at predicting survival, growth, and reproduction, or when stage is more readily determined in the field than age. Stage-based demographic data are now available for many populations. Analyses of population dynamics using stage data recognize that time-invariant models do not capture the effects of temporal variability in vital rates. Temporal variability can be due to disturbances such as fire or hurricanes (Pascarella and Horvitz 1998, Kaye et al. 2001, Pico et al. 2003), land-use patterns (Donahue et al. 2000), disease (Davelos and Jarroz 2000), and climate (Aberg 1992). Methods of stochastic demography (Tuljapurkar 1990, Caswell 2001, Tuljapurkar et al. 2003) describe the effects of temporal variability on dynamics and have been widely used (Orzack 1985, Aberg 1992, Morris and Doak 1998, 2002, Gaillard et al. 2000, Caswell and Kaye 2001). But stage-based data also contain age-specific demographic information, such as life expectancy or age-specific schedules of survivorship and fertility. For time-invariant stage-structured models, there is a theory to extract age-based demographic information (Cochran and Ellner 1992, Caswell 2001), which has recently been applied to many plant species (Silvertown et al. 2001, Ehrlén and Lehtilä 2002) to address questions about the evolution of senescence. However, the consequences of

environmental variability for life span and other age-related demographic rates have not been explored.

This paper presents theory to extract age-specific mortality, survivorship, and life expectancy from stage-based models for populations in temporally varying environments. Here, the environment changes through a sequence of states determined by climate, disturbance, or other factors. Correspondingly, individuals move through a sequence (an event history) of life history stages, with transition rates between stages that depend on the individual's current stage, the current environment, and the pattern of environmental change. Age-specific information is obtained by tracking individuals through stages and states before they (eventually) die. Our results, which to our knowledge are new not only to ecology but to mathematics, are closed form, analytical expressions for the expectations and variances of demographic functions in periodic, random identically and independently distributed (i.i.d.), and random (finite state) Markovian environments.

Temporal variability in stage transition rates has two kinds of effect. A cohort effect results from the environmental conditions affecting individuals at the time and stage where they are first observed. A period effect results from environmental variability that is revealed through the course of life. Our results quantify the biological consequences for survival and senescence of cohort and period effects. We illustrate cohort effects on the average life expectancy of newborns, remaining life expectancy (future life expectancy after reaching a particular stage), and survivorship. For all models of environmental variability, the average survivorship changes exponentially at old ages at an asymptotic rate independent of cohort birth conditions. But the initial state of the environment influences the level of the

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asymptote, the speed at which it is reached, and the early age pattern of survivorship and mortality. The formulas also describe variance in age-specific survivorship resulting from differences in environments after birth (e.g., for cohorts born in different years or different locations subject to the same environmental probabilities), and show in general that the coefficient of variation of survivorship increases with age. We illustrate the analytical results with an example and results from numerical simulations.

FROM STAGE TO AGE: THEORY

We consider a stage-structured population with S distinct life history stages censused at discrete times $n, n + 1$, and so on. In every time period, the population's environment is in one of K possible habitat states. Each habitat state, b , determines a particular population projection matrix, \mathbf{A}_b , that contains all life-history transition rates including reproduction, fission, and cloning. Cochran and Ellner (1992:347) distinguish fission, in which individuals split to form two or more individuals, and cloning, which results in two or more individuals including parent and offspring. Following Cochran and Ellner (1992) and Caswell (2001), we focus on life history transitions other than reproduction, fission, or cloning, and split the population projection matrix into two parts:

$$\mathbf{A}_b = \mathbf{F}_b + \mathbf{q}_b \tag{1}$$

so that the matrix \mathbf{F}_b contains rates for all reproductive events, and the matrix \mathbf{q}_b contains only probabilities for transitions other than reproduction, such as growth, stasis or shrinkage. Henceforth the term "life history transition matrix" refers only to the matrices \mathbf{q}_b . At time n , call the life history transition matrix $\mathbf{T}(n)$; if the environment at time n is in state b , then $\mathbf{T}(n) = \mathbf{q}_b$. An individual in life history stage j at time n makes a transition to stage i with probability $T_{ij}(n)$. Changing environments produce changing transition probabilities $\mathbf{T}(1), \mathbf{T}(2), \dots$. We assume that eventual death is certain, i.e., the probability of death is >0 for every starting stage j .

An individual starting in stage j at time $n = 1$ will spend Y_{1j} time intervals in stage 1, Y_{2j} time intervals in stage 2, and so on until death. These stage durations Y_{ij} are random because some individuals may make only a few transitions and die whereas others may make many transitions before death. What matters are the averages and variances of the stage durations Y_{ij} . We first show how to compute these quantities for arbitrary temporal variation in the $\mathbf{T}(n)$, and then provide exact analytical expressions in three useful cases: periodic (cyclic) environments, independent random variation, and environments that follow a Markov chain and display serial autocorrelation.

Notation is summarized in Table 1, to which we refer throughout, and derivations are in the Appendix.

General temporal variability

Temporal variability means that individuals experience a particular sequence of environmental states over time. Consider an individual who is in stage j at time $n = 1$. At time $n = 2$, the individual will be in some state i after making a stage transition according to the probabilities $\mathbf{T}(1)$, and so on over successive intervals. At each time n , the matrix $\mathbf{T}(n)$ is determined by the environmental state at that time. Conditional on a particular environmental sequence, define the fundamental matrix as follows:

$$\mathbf{N} = \mathbf{I} + \mathbf{T}(1) + \mathbf{T}(2)\mathbf{T}(1) + \mathbf{T}(3)\mathbf{T}(2)\mathbf{T}(1) + \dots \tag{2}$$

where \mathbf{I} is the identity matrix, and the series runs over all integers $n \geq 1$. Our assumption of certain death guarantees that the series will converge (see Appendix). The n th term in Eq. 2, written as $\hat{\mathbf{T}}(n)$, is a product of matrices that contains the probabilities of life history transitions between times 1 and n . Conditional on the environmental sequence, the average stage durations are

$$[E(Y_{ij} | \text{environments})] = \mathbf{N} \tag{3}$$

where the expectation is taken with respect to the transition probabilities $\mathbf{T}(n)$. Here and below we omit the outermost parentheses in Eq. 3 and use the shorthand that the quantity on the left is the (i, j) element of the matrix on the right.

The total remaining life time of an individual who starts in stage j at time $n = 1$ is

$$\eta_j = \sum_{i=1}^{i=S} Y_{ij} \tag{4}$$

so the sum of the first column of \mathbf{N} is expected lifetime for an individual starting in state 1 at time 1, and the sum of any other column j is the expected remaining lifetime for an individual who starts in state j at time 1. In this general case, there is no closed-form analytical expression for the variances of the above quantities, but variances can be computed for any given environmental sequence by numerical simulation.

The conventional survivorship to age x of any individual is written $l(x)$. In our setting, a newborn individual of age $x = 0$ is censused as being in some stage j at time $n = 1$. If the individual survives it will attain age $x = 1$ at time $n = 2$ and so on to attain age x at time $n = (x + 1)$. Therefore, survivorship to age x is computed from the $\hat{\mathbf{T}}(x + 1)$, conditional on the environmental sequence. In what follows, we also compute averages and variances of these quantities with respect to environmental variability, by averaging over environmental sequences.

Cyclical environments

Cyclical changes in environments are driven by, for example, seasonal changes or long-period oscillations in weather. Environments are not random but may differ in the phase of the cycle. In a cycle of period P there is a

TABLE 1. Notation.

Variable	Definition
S	number of life history stages
K	number of environmental states
n	time (discrete units)
x	age (discrete units)
a, b	indices for environmental states, values from 1 to K
i, j	indices for life history stages, values from 1 to S
\mathbf{Z}'	transpose of a vector or matrix \mathbf{Z}
$\text{dg}(\mathbf{L})$	diagonal matrix whose entries are the diagonal elements of matrix \mathbf{L}
$\mathbf{L} \otimes \mathbf{M}$	Kronecker product of \mathbf{L} and \mathbf{M}
$\mathbf{L} \circ \mathbf{M}$	Hadamard product whose i, j element is the product of the i, j elements of \mathbf{L} and \mathbf{M}
$\mathbf{0}$	a square matrix of zeros
\mathbf{I}	$S \times S$ Identity matrix
$\bar{\mathbf{I}}$	$SK \times SK$ Identity matrix
\mathbf{e}	a vector with every element equal to 1
$\tilde{\mathbf{e}}_a$	$SK \times S$ matrix = $(\mathbf{0} \cdots \mathbf{0} \mathbf{I} \mathbf{0} \cdots)'$
$\tilde{\mathbf{e}}$	$SK \times S$ matrix = $(\mathbf{I} \mathbf{I} \cdots \mathbf{I})'$
E	expectation of the random variable that follows
Var	variance of the random variable that follows
$\mathbf{T}(n)$	matrix of transition probabilities of life history transitions determined by environmental state at time n
$\hat{\mathbf{T}}(n)$	n th term in series in Eq. 2; equal to \mathbf{I} for $n = 1$; for $n > 1$, equals product of matrices $\mathbf{T}(n) \cdots \mathbf{T}(1)$.
\mathbf{N}	fundamental matrix, sum of series whose n th term is $\hat{\mathbf{T}}(n)$; a subscript a indicates starting state is a
Y_{ij}	stage duration: time spent in stage i by an individual starting in stage j at time $n = 1$
η_j	total remaining lifetime of an individual who starts in stage j at time $n = 1$
$l(x);$ $l(x w, a)$	age-specific survivorship (probability of surviving from birth to age x); survivorship conditional on starting stage a and environments w
\mathbf{q}_a	matrix of probabilities of life history $>$ transitions when environment is in state a
w	random environmental sequence
P	period of an environmental cycle
$(K(a, 1), \dots,$ $K(a, P))$	sequence of states in P -period cycle starting at state a
\mathbf{Q}_a	$K \times K$ cycle matrix = $\mathbf{q}_{K(a,P)} \mathbf{q}_{K(a,P-1)} \cdots \mathbf{q}_{K(a,1)}$
λ	dominant eigenvalue of cycle matrix \mathbf{Q}_a
π_a	stationary probability of observing environmental state a
$\bar{\mathbf{q}}$	average life history transition matrix = $\sum_{a=1}^K \pi_a \mathbf{q}_a$
λ_1	dominant eigenvalue of $\bar{\mathbf{q}}$
$\bar{\mathbf{R}}$	$\sum_{a=1}^K \pi_a (\mathbf{q}_a \otimes \mathbf{q}_a)$
β_1	dominant eigenvalue of $\bar{\mathbf{R}}$
$\mathbf{c} = (c_{ab})$	Markov matrix of transition probabilities between environmental states
$\tilde{\mathbf{q}}_a$	$SK \times S$ matrix = $(\mathbf{0} \cdots \mathbf{0}(\mathbf{q}_a)'\mathbf{0} \cdots \mathbf{0})'$
\mathbf{m}	$SK \times SK$ matrix whose a, b block is $\mathbf{m}_{ab} = \mathbf{q}_a c_{ab}$
λ_2	dominant eigenvalue of \mathbf{m}
$\bar{\mathbf{R}}_2$	$KS^2 \times KS^2$ matrix whose a, b block is $(\mathbf{q}_a \otimes \mathbf{q}_a)c_{ab}$
β_2	dominant eigenvalue of $\bar{\mathbf{R}}_2$

sequence of transition matrices $\mathbf{q}_1, \mathbf{q}_2, \dots, \mathbf{q}_P$. Suppose that the environment is in state 1 at time $n = 1$, so that $\mathbf{T}(1) = \mathbf{q}_1, \mathbf{T}(2) = \mathbf{q}_2$, and so on. Defining the cycle matrix starting in state 1 as

$$\mathbf{Q}_1 = \mathbf{q}_P \mathbf{q}_{P-1} \cdots \mathbf{q}_2 \mathbf{q}_1 \tag{5}$$

the fundamental matrix for life cycles that begin in state 1 at time $n = 1$ is

$$\mathbf{N}_1 = (\mathbf{I} + \mathbf{q}_1 + \mathbf{q}_2 \mathbf{q}_1 + \cdots + \mathbf{q}_{P-1} \cdots \mathbf{q}_2 \mathbf{q}_1)(\mathbf{I} - \mathbf{Q}_1)^{-1}. \tag{6}$$

For individuals who are in state j at time $n = 1$ with the cycle in state 1, the expected stage durations are

$$E(Y_{ij} | \text{start in state 1}) = \mathbf{N}_1. \tag{7}$$

Expected total lifetimes by initial stage are

$$E(\eta_j | \text{start in state 1}) = \mathbf{e}' \mathbf{N}_1. \tag{8}$$

Here \mathbf{e} is a $S \times 1$ vector whose elements all equal 1.

The cycles here can, of course, begin at time $n = 1$ in state $a \neq 1$. But in that case the sequence of environments follows a new “cycle” starting with state a . We can use our results for cycles starting in state 1 simply by relabeling

TABLE 2. Cycles.

Variable	Value
\mathbf{N}_a	$(\mathbf{I} + \mathbf{q}_{K(a,1)} + \mathbf{q}_{K(a,2)}\mathbf{q}_{K(a,1)} + \dots + \mathbf{q}_{K(a,P-1)} \dots \mathbf{q}_{K(a,1)})(\mathbf{I} - \mathbf{Q}_a)^{-1}$
$E(Y_{ij} \text{start in state } a)$	\mathbf{N}_a
$E(\eta_j \text{start in state } a)$	$\mathbf{e}'\mathbf{N}_a$
$\hat{\mathbf{N}}_a[1]$	$(\mathbf{I} - \mathbf{Q}_a)^{-1}$
$\hat{\mathbf{N}}_a[b]$	$\mathbf{q}_{K(a,b-1)} \dots \mathbf{q}_{K(a,b-2)}\mathbf{q}_{K(a,1)} (\mathbf{I} - \mathbf{Q}_a)^{-1}$ for $2 \leq b \leq P$
$E(Y_{ij}^2 \text{start in state } a)$	$2 \sum_{b=1}^{b=P} \text{dg}(\mathbf{N}_{K(a,b)})\hat{\mathbf{N}}_a[K(a, b)] - \mathbf{N}_a$
$E(\eta_j^2 \text{start in state } a)$	$2\mathbf{e}' \sum_{b=1}^{b=P} \mathbf{N}_{K(a,b)} \hat{\mathbf{N}}_a[K(a, b)] - \mathbf{e}'\mathbf{N}_a$
$l_a(x)$	sum of first column of $\mathbf{q}_{K(a,m)} \dots \mathbf{q}_{K(a,m-1)}\mathbf{q}_{K(a,1)} \mathbf{Q}_a^x$ with $x = JP + m$
$\mathbf{v}_a, \mathbf{u}_a$	left, right eigenvectors for dominant eigenvalue λ of \mathbf{Q}_a
$\log l_a(x)$	$\sim -[(\log(\lambda))/P]x + \log z_a(m)$ for high ages x
$z_a(0)$	$\log(v_{a,1}) - \log(\mathbf{v}'_a\mathbf{u}_a)$; $v_{a,1}$ is first element of \mathbf{v}_a
$z_a(m)$	$\log(\mathbf{e}'\mathbf{q}_{K(a,m)}\mathbf{q}_{K(a,m-1)} \dots \mathbf{q}_{K(a,1)}\mathbf{u}_a) + z_a(0)$ for $1 \leq m \leq P - 1$

states in the new cycle, as follows. For any a from 1 to P , define $(K(a, 1), K(a, 2), \dots, K(a, P))$ to be the cycle of states starting at state a . E.g., if $a=3, P=4$, then $(K(3, 1), K(3, 2), K(3, 3), K(3, 4))=(3, 4, 1, 2)$. Table 2 lists the cycle matrix \mathbf{Q}_a and fundamental matrix \mathbf{N}_a as well as other results for cohorts that start with the cycle in state a .

To obtain variances, first define $\hat{\mathbf{N}}_1[1] = (\mathbf{I} - \mathbf{Q}_1)^{-1}$, and for integers b with $2 \leq b \leq P$ define

$$\hat{\mathbf{N}}_1[b] = \mathbf{q}_{b-1}\mathbf{q}_{b-2} \dots \mathbf{q}_1(\mathbf{I} - \mathbf{Q}_1)^{-1}. \tag{9}$$

Then for cycles starting in state 1 (see Table 1 for notation, also see Table 2) we have

$$E(Y_{ij}^2 | \text{start in state 1}) = 2 \sum_{b=1}^{b=P} \text{dg}(\mathbf{N}_b)\hat{\mathbf{N}}_1[b] - \mathbf{N}_1. \tag{10}$$

Variances follow by using the means in Eq. 7 to get

$$\text{Var}(Y_{ij} | \text{start in state 1}) = E(Y_{ij}^2 | \text{start in state 1}) - \mathbf{N}_1 \circ \mathbf{N}_1.$$

For total lifetimes, variances follow from

$$E(\eta_j^2 | \text{start in state 1}) = 2\mathbf{e}' \sum_{b=1}^{b=P} \mathbf{N}_b\hat{\mathbf{N}}_1[b] - \mathbf{e}'\mathbf{N}_1. \tag{11}$$

Table 2 lists the corresponding results for life cycles that start when the environment is any state a .

Survivorship to age x is the probability of living past that age, which is the probability that total lifetime (=age at death) η_j exceeds x :

$$\Pr\{\eta_1 > x, \eta_2 > x, \dots, \eta_S > x\} = \mathbf{e}'\hat{\mathbf{T}}_{x+1}. \tag{12}$$

The conventional survivorship of individuals born in life history stage 1 with the environment in state a is thus

$$l_a(x) = \text{sum (first column of } \hat{\mathbf{T}}_{x+1}) = (\mathbf{e}'\hat{\mathbf{T}}_{x+1})_1. \tag{13}$$

The age pattern of survivorship at high ages n has a characteristic exponential shape (see Appendix for derivation). The nonnegative cycle matrix \mathbf{Q}_a has a dominant eigenvalue $\lambda < 1$, the same for all a , and for high ages as $x \rightarrow \infty$:

$$\left(\frac{1}{x}\right)\log l_a(x) \rightarrow \left[\frac{\log(\lambda)}{P}\right] < 0. \tag{14}$$

Thus age-specific mortality rate at high ages is constant and equal to $-\log(\lambda)/P$. The eigenvalues of the different cycle matrices are identical so this plateau in mortality is independent of the initial state of the environment. If matrix \mathbf{Q}_a is irreducible and primitive, it also has left, right eigenvectors $\mathbf{v}_a, \mathbf{u}_a$ corresponding to eigenvalue λ ; we normalize \mathbf{u}_a to sum to 1. Then, at high ages,

$$\log l_a(x) \sim \left[\frac{\log(\lambda)}{P}\right]x + \log z_a(m) \tag{15}$$

where $z_a(m)$ changes only over each cycle $m=0, 1, \dots, P - 1$ (see Table 2 and Appendix). Thus the level of the survivorship curve at old ages does depend on the initial environment at the time of birth. The stage structure of a surviving cohort at high ages will be proportional to the vector \mathbf{u}_a ; this is the quasi-stationary stage distribution for the cohort. In some cases, \mathbf{Q}_a may not be primitive, but we can apply the above arguments to a suitable primitive submatrix using the classification described in Seneta (1981, Chapter 1). Biologically, the effect of an imprimitive matrix is to force the quasi-stationary distribution to concentrate on a few stages.

Random i.i.d. environments, no serial correlation

Here the transition probability matrix $\mathbf{T}(n)$ at time n is chosen with

$$\text{Probability}\{\mathbf{T}(n) = \mathbf{q}_a\} = \pi_a, \quad \text{for } a = 1, \dots, K. \tag{16}$$

The average transition matrix is

$$E_w[\mathbf{T}(n)] = \bar{\mathbf{q}} = \sum_{a=1}^{a=K} \pi_a \mathbf{q}_a \tag{17}$$

where E_w is an average over environments.

Suppose that, at time $n=1$, the environment is in state a , so that $\mathbf{T}(1)=\mathbf{q}_a$. Conditional on the starting state, the expected stage durations (averaged over environments for $n > 1$ and over transition probabilities) are:

TABLE 3. Independent identically distributed random environments.

Variable	Value
$E(Y_{ij} \text{start in state } a)$	$\mathbf{N}_a = \mathbf{I} + (\mathbf{I} - \bar{\mathbf{q}})^{-1} \mathbf{q}_a$
$E(Y_{ij})$	$\bar{\mathbf{N}} = (\mathbf{I} - \bar{\mathbf{q}})^{-1}$
$E(\eta_j \text{start in state } a)$	$\mathbf{e}' \mathbf{N}_a$
$E(\eta_j)$	$\mathbf{e}' \bar{\mathbf{N}}$
$E(Y_{ij}^2 \text{start in state } a)$	$2\text{dg}(\mathbf{N}_a) + 2\text{dg}(\bar{\mathbf{N}})(\mathbf{N}_a - \mathbf{I}) - \mathbf{N}_a$
$E(\eta_j^2 \text{start in state } a)$	$\mathbf{e}'[\mathbf{N}_a + 2\bar{\mathbf{N}}(\mathbf{N}_a - \mathbf{I})]$
$l_a(x)$	sum of first column of $\bar{\mathbf{q}}^{x-1} \mathbf{q}_a$
\mathbf{v}, \mathbf{u}	left, right eigenvectors for dominant eigenvalue λ_1 of $\bar{\mathbf{q}}$
$\log l_a(x)$	$\sim x \log(\lambda_1) + z_a$ for high ages x
z_a	$\log((\mathbf{v}' \mathbf{q}_a)_1) - \log(\mathbf{v}' \mathbf{u})$
$(1/x) \log(\text{Var } l_a(x))$	$\rightarrow \log \beta_1$ for high ages x
cv of $l(x w, a)$	grows at rate $((1/2) \log \beta_1 - \log \lambda_1)$ at high ages

$$E(Y_{ij} | \text{start in state } a) = \mathbf{N}_a = \mathbf{I} + (\mathbf{I} - \bar{\mathbf{q}})^{-1} \mathbf{q}_a. \tag{18}$$

Averaging over the initial environment as well yields

$$E(Y_{ij}) = \bar{\mathbf{N}} = (\mathbf{I} - \bar{\mathbf{q}})^{-1}. \tag{19}$$

Expected total lifetimes by stage are

$$E(\eta_j | \text{start in state } a) = \mathbf{e}' \mathbf{N}_a \tag{20}$$

and the average over the initial state is $E(\eta_j) = \mathbf{e}' \bar{\mathbf{N}}$.

The variances of stage durations follow from

$$E(Y_{ij}^2 | \text{start in state } a) = 2\text{dg}(\mathbf{N}_a) + 2\text{dg}(\bar{\mathbf{N}})(\mathbf{N}_a - \mathbf{I}) - \mathbf{N}_a. \tag{21}$$

The variances of total lifetimes by stage follow from

$$E(\eta_j^2 | \text{start in state } a) = \mathbf{e}'[\mathbf{N}_a + 2\bar{\mathbf{N}}(\mathbf{N}_a - \mathbf{I})]. \tag{22}$$

Indicating the environmental sequence by w, a where a is the environment at birth and w is the sequence of environments between birth and age x , write survivorship to age x as $l(x | w, a)$. The average survivorship over all environments w except the initial one is $l_a(x) = E_w l(x | w, a)$. For $x \geq 1$

$$E_w(\hat{\mathbf{T}}_{x+1} | \text{start in state } a) = \bar{\mathbf{q}}^{x-1} \mathbf{q}_a. \tag{23}$$

Exact average survivorship $l_a(x)$ at age x is given by the first column sum of the above matrix.

Survivorship at high ages depends on high powers of $\bar{\mathbf{q}}$ which has a dominant eigenvalue $\lambda_1 < 1$. Hence at old ages as $x \rightarrow \infty$

$$\left(\frac{1}{x}\right) \log l_a(x) \rightarrow \log(\lambda_1) < 0 \tag{24}$$

an asymptotic slope independent of the starting environmental state a . If in addition matrix $\bar{\mathbf{q}}$ is irreducible and primitive, to the eigenvalue λ_1 there will correspond a left eigenvector \mathbf{v} , and right eigenvector \mathbf{u} (we normalize the latter to sum to 1). Then,

$$\log l_a(x) \sim x \log(\lambda_1) + z_a \tag{25}$$

where z_a is given in Table 3. The asymptotic slope of \log survivorship is independent of initial state but the level z_a is not. The stage structure of a surviving cohort (the quasi-stationary distribution) at high ages will be proportional to the vector \mathbf{u} . If $\bar{\mathbf{q}}$ is not primitive we must proceed as discussed above for cyclical environments.

Because survivorship $l(x | w, a)$ depends on the environments w experienced after birth, we expect differences in survival between cohorts born in different years (or in different locations subject to the same environmental probabilities). Environmentally driven variability in survivorship is measured by the variance in $l(x | w, a)$ with respect to environments w . Using the environmental probabilities π_a in Eq. 16, compute the following $S^2 \times S^2$ matrix:

$$\bar{\mathbf{R}} = E_w[\mathbf{T}(n) \otimes \mathbf{T}(n)] = \sum_{a=1}^{a=K} \pi_a (\mathbf{q}_a \otimes \mathbf{q}_a). \tag{26}$$

This will not equal $\bar{\mathbf{q}} \otimes \bar{\mathbf{q}}$ because environmental variation results in within-period covariances between elements of the transition matrix. Letting the dominant eigenvalue of $\bar{\mathbf{R}}$ be $\beta_1 < 1$, at high ages $x \rightarrow \infty$,

$$\left(\frac{1}{x}\right) \log[\text{Var } l_a(x)] \rightarrow \log \beta_1. \tag{27}$$

The asymptotic rate of growth β_1 of the variance is independent of the initial environmental state a (see Appendix for derivation). The dispersion of survivorship $l(x | w, a)$ around the average survivorship $l_a(x)$ can be measured by the coefficient of variation. From Eqs. 24 and 27, observe that at old ages the variance of $l(x | w, a)$ changes roughly as $e^{x \log(\beta)}$ whereas the mean $l_a(x)$ changes roughly as $e^{x \log(\lambda)}$. In general, it is known that $\beta_1 > \lambda_1^2$ (Tuljapurkar 1982) and therefore the coefficient of variation of $l(a | w, x)$ will grow roughly exponentially with age at a positive rate of $(1/2) \log(\beta_1) - \log(\lambda_1)$. In words, there are environmental sequences that can produce extremely high survivorship at old ages.

Markovian environments

At time n , the life history transition matrix $\mathbf{T}(n)$ is chosen according to

$$\text{Probability}\{\mathbf{T}(n) = \mathbf{q}_a | \mathbf{T}(n-1) = \mathbf{q}_b\} = c_{ab}. \tag{28}$$

The $K \times K$ Markov matrix $\mathbf{c} = (c_{ab})$ describes environmental transitions. The stationary probability of observing environment a is π_a with $\sum_b c_{ab} \pi_b = \pi_a$, for $a, b = 1, \dots, K$.

Define an $SK \times SK$ matrix as follows:

$$\mathbf{m} = \begin{pmatrix} \mathbf{q}_1 c_{11} & \mathbf{q}_1 c_{12} & \cdots \\ \mathbf{q}_2 c_{21} & \mathbf{q}_2 c_{21} & \cdots \\ \vdots & \vdots & \vdots \end{pmatrix}. \tag{29}$$

Similar block matrices (megamatrices) have been used to describe population growth (but not life span distribu-

TABLE 4. Markovian environments.

Variable	Value
$E(Y_{ij} \text{start in state } a)$	$\mathbf{N}_a = \mathbf{I} + \tilde{\mathbf{e}}'(\tilde{\mathbf{I}} - \mathbf{m})^{-1}\tilde{\mathbf{q}}_a$
$E(\eta_j \text{start in state } a)$	$\mathbf{e}'\mathbf{N}_a$
$\tilde{\mathbf{N}}_a$	$\tilde{\mathbf{e}}'\mathbf{m}(\tilde{\mathbf{I}} - \mathbf{m})^{-1}\tilde{\mathbf{e}}_a$
$\tilde{\mathbf{N}}_{ba}$	$\tilde{\mathbf{e}}_b\mathbf{m}(\tilde{\mathbf{I}} - \mathbf{m})^{-1}\tilde{\mathbf{e}}_a$ for $a, b = 1, \dots, K$
$E(Y_{ij}^2 \text{initial start in state } a)$	$\mathbf{N}_a + 2 \sum_{b=1}^{b=S} \text{dg}(\tilde{\mathbf{N}}_b) \tilde{\mathbf{N}}_{ba} + 2\text{dg}(\tilde{\mathbf{N}}_a)\mathbf{q}_a + 2\text{dg}(\mathbf{N}_a - \mathbf{I})$
$E(\eta_j^2 \text{start in state } a)$	$\mathbf{e}'[\mathbf{N}_a + 2 \sum_{b=1}^{b=S} \tilde{\mathbf{N}}_b \tilde{\mathbf{N}}_{ba} + 2\tilde{\mathbf{N}}_a\mathbf{q}_a + 2(\mathbf{N}_a - \mathbf{I})]$
$l_a(x)$	sum of first column of $\tilde{\mathbf{e}}'\mathbf{m}^{x-1}\tilde{\mathbf{q}}_a$
\mathbf{v}	left eigenvector for dominant eigenvalue λ_2 of \mathbf{m} ; written as $S \times 1$ blocks \mathbf{v}^i for $i = 1, \dots, K$
\mathbf{u}	right eigenvector for dominant eigenvalue λ_2 of \mathbf{m} ; written as $S \times 1$ blocks \mathbf{u}^i for $i = 1, \dots, K$
$\log l_a(x)$	$\sim x \log(\lambda_2) + z_a$ for high ages x at high ages x
z_a	$\log((\mathbf{v}^a)'\mathbf{q}_a)_1 - \log(\mathbf{v}'\mathbf{u})$
$(1/x) \log(\text{Var } l_a(x))$	$\rightarrow \log \beta_2$ at high ages x
cv of $l(x w, a)$	grows at rate $((1/2)\log \beta_2 - \log \lambda_2)$ at high ages

tions) in Markovian environments (Cohen 1977, Tuljapurkar 1982, Horvitz and Schemske 1986).

Conditional on the initial environment a at time 1, the average stage durations (averaged over environments for $n > 1$ and over transition probabilities) are as follows:

$$E(Y_{ij} | \text{start in state } a) = \mathbf{N}_a = \mathbf{I} + \tilde{\mathbf{e}}'(\tilde{\mathbf{I}} - \mathbf{m})^{-1}\tilde{\mathbf{q}}_a \quad (30)$$

using the matrices $\tilde{\mathbf{e}}, \tilde{\mathbf{q}}_a$ and $\tilde{\mathbf{I}}$ defined in Table 1. Note that \mathbf{N}_a is an $S \times S$ matrix. To average over initial states weight these values by the stationary probabilities π_a . Average total lifetimes are given by the following:

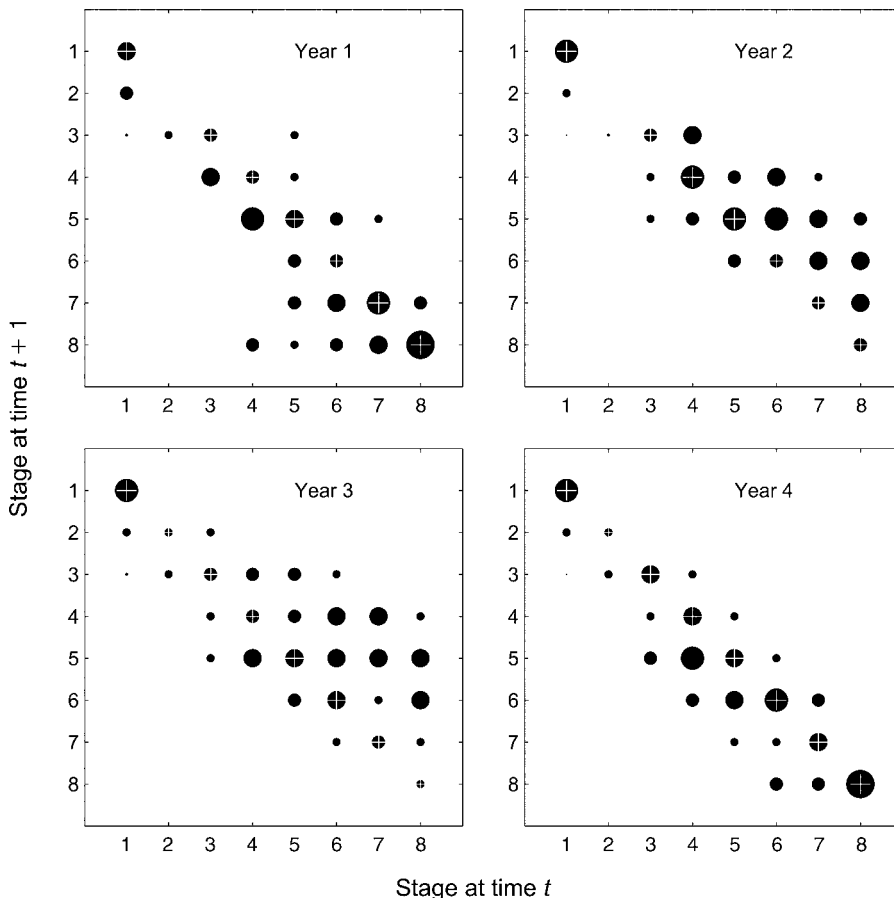


FIG. 1. Dot pattern diagram for life history transition matrices (\mathbf{q}_b) for each of the four years. Distinct dot sizes, from small to large, are used for values of transitions > 0 that fall within intervals defined by the following points (0, 0.0001, 0.001, 0.01, 0.1, 0.25, 0.5, 0.75, 1), where each interval (except for the first) includes its lower bound.

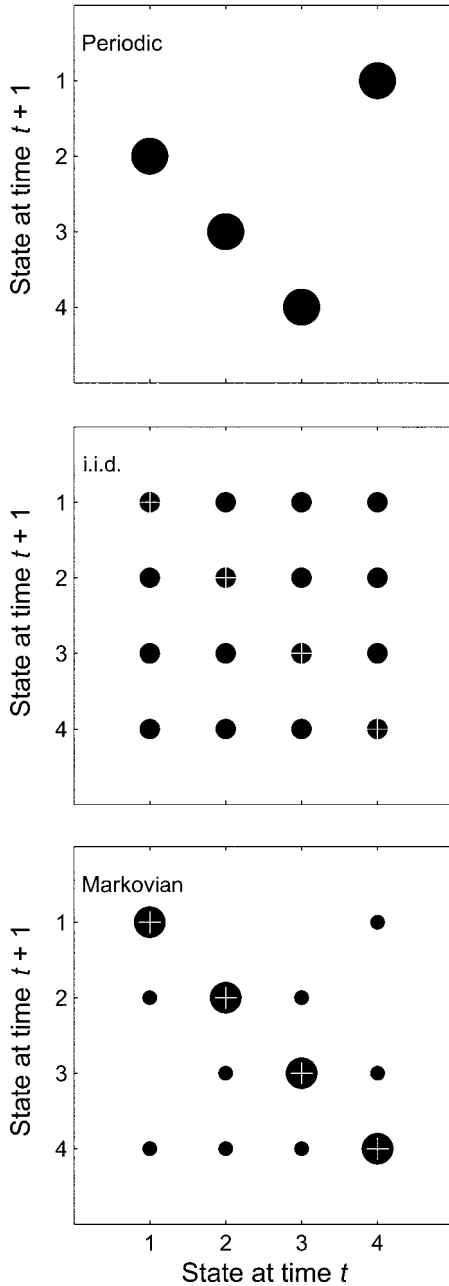


FIG. 2. Dot pattern diagram for habitat transitions ($c = c_{ab}$) exemplifying different types of variable environments: periodic, i.i.d. (random identically and independently distributed), and Markovian. Distinct dot sizes were used for values of transitions, as in Fig. 1.

$$E(\eta_j | \text{start in state } a) = \mathbf{e}' \mathbf{N}_a. \quad (31)$$

Using matrices $\tilde{\mathbf{N}}_a$ and $\tilde{\mathbf{N}}_{ba}$ as defined in Table 4, we find

$$E(Y_{ij}^2 | \text{initial start in state } a) = \mathbf{N}_a + 2 \sum_{b=1}^{b=K} \text{dg}(\tilde{\mathbf{N}}_b) \hat{\mathbf{N}}_{ba} + 2 \text{dg}(\tilde{\mathbf{N}}_a) \mathbf{q}_a + 2 \text{dg}(\mathbf{N}_a - \mathbf{I}) \quad (32)$$

which, together with the mean values above, yields variances. Variances of total lifetimes follow from

$$E(\eta_j^2 | \text{start in state } a) = \mathbf{e}' \left[\mathbf{N}_a + 2 \sum_{b=1}^{b=K} \tilde{\mathbf{N}}_b \hat{\mathbf{N}}_{ba} + 2 \tilde{\mathbf{N}}_a \mathbf{q}_a + 2(\mathbf{N}_a - \mathbf{I}) \right]. \quad (33)$$

To compute average survivorship $l_a(x) = E_w l(x | w, a)$ we average the product of transition matrices over all environments except the initial one. For ages $x \geq 1$,

$$E_w(\hat{\mathbf{T}}_{x+1} | \text{start in state } a) = \tilde{\mathbf{e}}' \mathbf{m}^{x-1} \tilde{\mathbf{q}}_a \quad (34)$$

The exact value of $l_a(x)$ is the sum of the first column of the matrix in (34).

At old ages x the average survivorship depends on high powers of the matrix \mathbf{m} which has a dominant eigenvalue $\lambda_2 < 1$, so again old age survivorship changes exponentially as $x \rightarrow \infty$:

$$\left(\frac{1}{x}\right) \log l_a(x) \sim \log(\lambda_2). \quad (35)$$

The asymptotic slope of \log survivorship, $\log(\lambda_2)$, is independent of the initial environmental state. If in addition matrix \mathbf{m} is irreducible and primitive, to the eigenvalue λ_2 there will correspond left, right eigenvectors \mathbf{v} , \mathbf{u} . Note that because \mathbf{m} is a matrix of $K \times K$ blocks of $S \times S$ matrices, we have a block structure for the eigenvector so that $\mathbf{v} = (\mathbf{v}^1, \mathbf{v}^2, \dots, \mathbf{v}^K)$ where each \mathbf{v}^i is an $S \times 1$ vector. We can decompose \mathbf{u} in the same way: we normalize this right eigenvector so that its components add to 1. Using these, as age x increases we have

$$\log l_a(x) \sim x \log(\lambda_2) + z_a \quad (36)$$

where the level z_a is written out in Table 4. The stage structure of a surviving cohort (the quasi-stationary distribution) at high ages will be proportional to the $K \times 1$ vector $\tilde{\mathbf{e}}' \mathbf{u}$. For cases of imprimitive \mathbf{m} we must proceed as discussed above for cyclical environments.

To compute environmentally driven variance in survivorship, define a new $KS^2 \times KS^2$ block matrix,

$$\bar{\mathbf{R}}_2 = [(\mathbf{q}_a \otimes \mathbf{q}_a) c_{ab}] \quad (37)$$

where the block indices a, b take values from 1 to K . The structure of $\bar{\mathbf{R}}_2$ is similar to that of \mathbf{m} in Eq. 29. Let the dominant eigenvalue of $\bar{\mathbf{R}}_2$ be $\beta_2 < 1$. At high ages, the variance of survivorship changes when $x \rightarrow \infty$ as

$$\left(\frac{1}{x}\right) \log[\text{var } l_a(x)] \rightarrow \log \beta_2. \quad (38)$$

The asymptotic rate of growth β of the variance is independent of the initial environmental state a . As with purely random environments, here the coefficient of variation of $l(a | w, x)$ will grow roughly exponentially with age at a positive rate of $(1/2)\log(\beta_2) - \log(\lambda_2)$. In words, there are environmental sequences that can produce extremely high survivorship at old ages.

TABLE 5. Remaining life expectancy (in units of years) of reproductives ($\bar{X} = E[\eta_j]$, the mean; and $cv = (\text{Var}[\eta_j])^{1/2}/E[\eta_j]$, the standard deviation/mean) according to a time-invariant model.

Environment	Size class of reproductives							
	Small		Medium		Large		Very large	
	Mean	cv	Mean	cv	Mean	cv	Mean	cv
1	47.45	1.29	54.44	1.16	61.52	1.04	66.73	0.96
2	10.49	0.80	10.27	0.79	10.56	0.80	11.08	0.76
3	4.18	0.72	4.70	0.65	4.85	0.62	5.37	0.57
4	490.89	1.02	497.23	1.00	498.62	1.00	500.00	1.00

Note: Each environment is described by a single population projection matrix.

EXAMPLE

The study system

We employ an example based on empirical work on population dynamics and habitat states of *Calathea ovandensis* (Marantaceae), a tropical understory herb living in a moist tropical forest on volcanic substrate. Temporal variability in the state of the habitat was measured by evaluating demographic rates across four different year-to-year time steps at the same site. The most distinct of these was an El Niño year (Horvitz and Schemske 1995). We describe the system by eight life history stages ($S=8$) and four environmental states ($K=4$). The eight life history stages are seeds, seedling-sized plants, juveniles, pre-reproductives, and four size classes of reproductives (small, medium, large, and very large). Vital rates for the four environmental states are

contained in matrices A_b , $b = 1, \dots, 4$ which were parameterized directly from field data (Horvitz and Schemske 1995). Here we use the matrices from one of four study sites (site 3 in Horvitz and Schemske 1995). Differences in habitat quality are summarized by the asymptotic growth rates λ_b of the four matrices, which varied from $\lambda_3 = 0.736$ to $\lambda_1 = 1.156$.

We used the protocols in Caswell (2001) to partition the A_b and find the life history transition matrices q_b as in Eq. 1 (for stages estimated as having perfect survival in the original matrix, we converted to a survival probability of 0.998). Fig. 1 displays the stage pattern of life history transitions in the q_b . The long term pattern of change among environmental states at this site is unknown. For illustration, we use (1) a four-period cycle (top panel of Fig. 2), (2) an i.i.d. environment with all states equally probable (middle panel of Fig. 2), and (3)

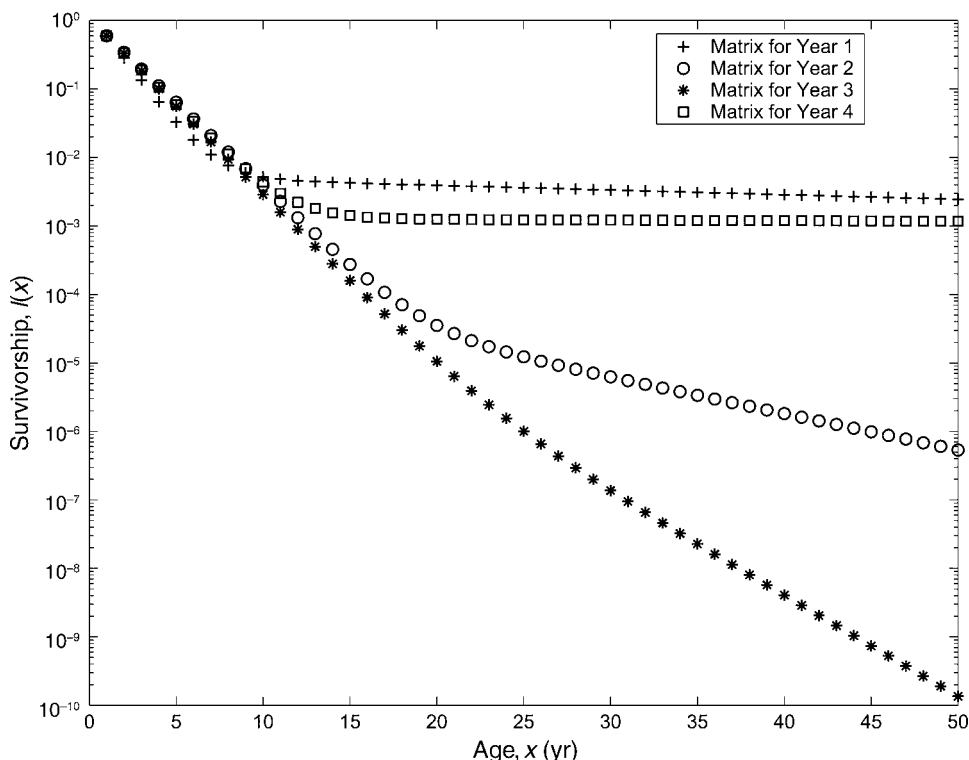


FIG. 3. Age-specific survivorship ($l(x)$) parameterized from single states of the environment shown for each of four years.

TABLE 6. Remaining life expectancy (in units of years) of reproductives ($\bar{X} = E[\eta_j | \text{start in state } a]$, the mean; and $cv = (\text{Var}[\eta_j | \text{start in state } a])^{1/2} / E[\eta_j | \text{start in state } a]$, the standard deviation/mean) in variable environments.

Environment and initial state	Size class of reproductives							
	Small		Medium		Large		Very large	
	Mean	cv	Mean	cv	Mean	cv	Mean	cv
Periodic								
1	10.16	0.99	11.30	0.91	12.50	0.83	13.47	0.77
2	10.60	0.95	10.29	0.97	11.48	0.90	12.69	0.82
3	10.46	0.97	11.96	0.86	12.69	0.81	13.28	0.78
4	11.77	0.87	12.62	0.82	13.42	0.78	14.44	0.72
Average	10.75		11.54		12.52		13.47	
Random (i.i.d.)								
1	11.55	0.97	12.80	0.89	14.01	0.81	14.94	0.76
2	11.87	0.93	12.07	0.91	12.33	0.91	13.36	0.85
3	10.10	1.06	11.62	0.95	12.31	0.90	13.08	0.85
4	12.97	0.86	13.75	0.82	14.26	0.79	15.09	0.75
Average	11.62		12.56		13.23		14.12	
Markovian								
1	15.94	1.05	17.78	0.94	19.72	0.84	21.11	0.77
2	12.83	1.16	12.66	1.19	13.02	1.17	13.79	1.13
3	8.34	1.70	9.60	1.53	10.02	1.48	11.20	1.37
4	18.79	0.83	19.59	0.81	20.08	0.80	20.96	0.77
Average	14.09		14.97		15.66		16.68	

Notes: Average refers to the expectation when the process is averaged over initial states; i.i.d. indicates random identically and independently distributed.

Markovian transitions with relatively high environmental stasis (bottom panel of Fig. 2).

We verified our theoretical results using numerical simulations (1000 sample paths, each 200 time steps long). For i.i.d. and Markovian environments, we estimate the fundamental matrix from a cumulative sum, noting that there is rapid convergence along each sample path although none among paths. For the periodic environment, we calculated the fundamental matrix for each initial state directly. Here we present simulation results only to illustrate the environmentally driven dispersion of survival curves.

All of our computations were performed using MATLAB.

Age-specific demography from single habitat states

Vastly different conclusions may result from using one state of the habitat vs. another as if it were the environment for all time. For example, using the matrix from year 4 of the study, reproductive plants would be expected to remain alive for nearly 500 years while using the matrix from year 3 of the study, they would be expected to remain alive for only about five years, a difference of two orders of magnitude (Table 5). An interesting pattern common to all four matrices is that remaining life expectancy, $E(\eta_j)$, of reproductives, stages 5–8, increases with increasing stage. Since stage mostly reflects size, this means larger reproductives are likely to live longer. Similarly, survivorship (l_x) and mortality estimated from these matrices differ markedly (Fig. 3). For example, the survivorship curve constructed from the matrix for year 1 of the study has a unique combination of high early mortality and low late

mortality in contrast to the other years. Thus in this example, no single year’s matrix can correctly describe age-specific survival in temporally changing conditions.

Our example does not, of course, imply that the equivalent time-invariant methods are not valuable in the proper context. Those methods will likely provide a useful picture of demography when temporal variability is weak. The present methods are likely to be important when environmental variability is strong, as with disturbances such as treefalls, fires, or hurricanes (as in the examples chosen here).

Age-specific parameters in the variable environment

Remaining life-expectancy, $E(\eta_j)$, of reproductives.—The remaining life expectancy of reproductives answers the question, given that an organism has reached a particular reproductive stage, how many years of life are expected to remain? Table 6 displays the mean and cv for life expectancy $E(\eta_j | \text{start in state } a)$ of four reproductive stages, stages 5 through 8. First, note that conditional life expectancies of reproductives increase with plant size, as in the time-invariant case. Second, in the variable environment, life expectancies are affected by the initial state of the environment as well as the pattern of environmental variability. Life expectancies in variable environments range from about 8 to 21 yr, in contrast with the two-orders-of-magnitude range among the matrices for the time-invariant case. In our example, initial state 4 is associated with the longest life expectancies in all three environments, implying that environmental sequences beginning with state 4 are better for long term survival of reproductives. In contrast, the relative ranking of life expectancies among initial states

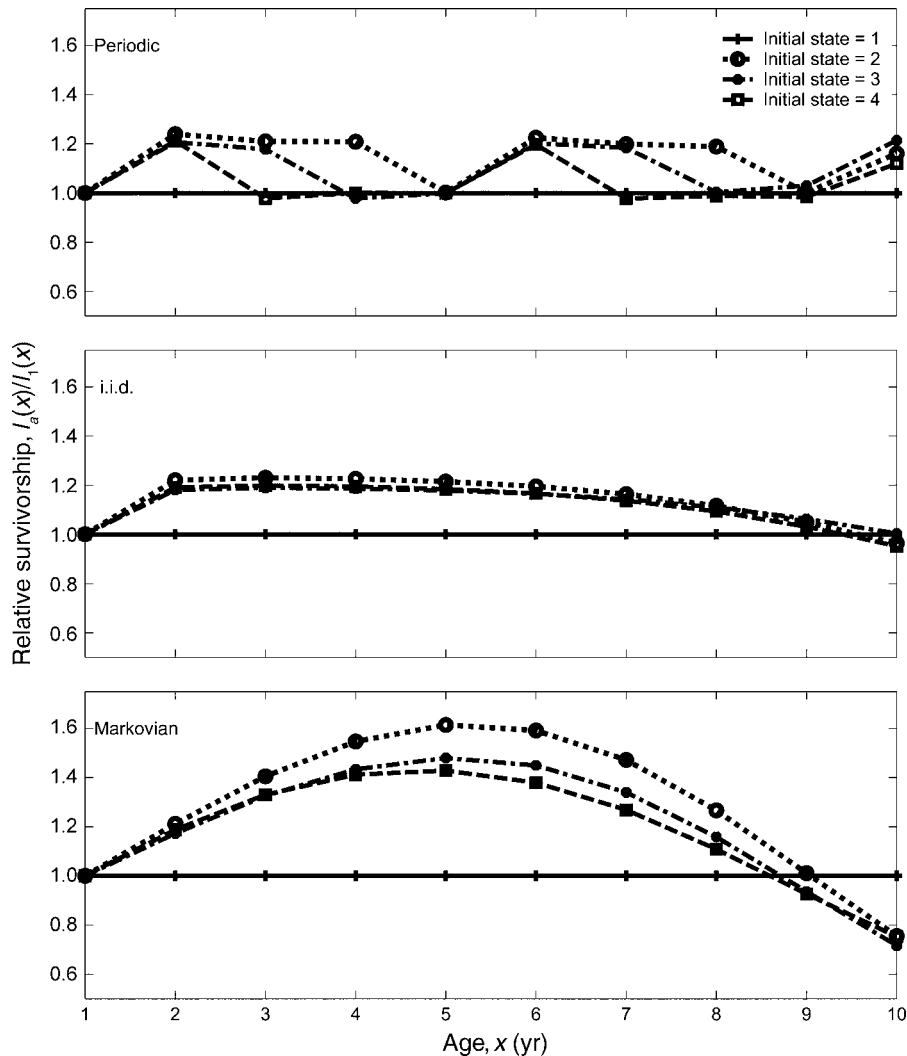


FIG. 4. Relative early survivorship conditional on initial state, $l_a(x)/l_1(x)$, for periodic, i.i.d., and Markovian environments.

1, 2, and 3 is not consistent across stages or environments. When considering remaining life span the “initial state” is not the birth year, but is the state of the environment in the year that the individual is observed in a given stage, counting from that point in time onward. The age of an individual first observed in a given stage is not known, and for large plants in advanced stages, the age distribution is likely to be quite wide (Caswell 2001, Boucher 1997). We find that the Markovian environment predicts longer life spans for reproductives than the periodic or the i.i.d. environment.

The coefficients of variation (cvs) in Table 6 reflect variability due both to environments and to the intrinsic randomness of individual transitions. Interestingly, environmental variability does not always increase the cv of remaining life span as compared with the cv obtained with fixed matrices alone. The Markovian environment, which has positive serial autocorrelation,

results in significantly larger cvs than the i.i.d. or cyclical environments.

Survivorship to age x conditional on birth state a , $l_a(x)$.—Environmental state at birth affects age-specific survivorship differently under different patterns of environmental change. In our example, seed survival is quite similar among all states of the environment and first year survival is thus quite similar for all three patterns of environmental change (i.i.d., periodic, and Markovian). In all three of these cases, survivorship over the next few years (ages 2–8) is frequently lowest for individuals born in state 1 and highest for individuals born in state 2, although the relative advantages of the states show oscillations in the periodic environment (Fig. 4). Between ages 8 and 10, shifts occur in the relative advantages of being born in one state or another, and one birth state or another gradually begins to show a consistent survival advantage at all later ages.

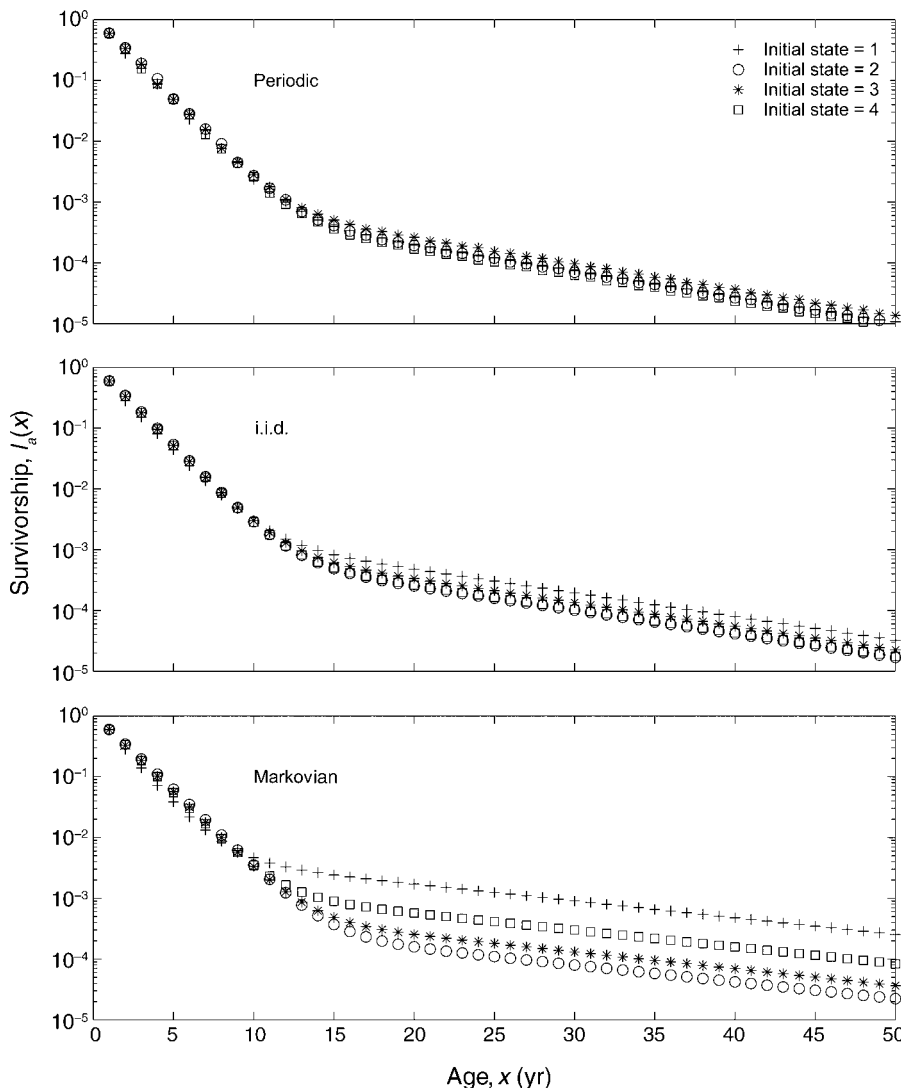


FIG. 5. Survivorship curves conditional on initial state, $l_a(x)$, for periodic, i.i.d., and Markovian environments.

Mid to late survivorship (ages 11 yr and up), shows marked effects of environmental pattern. In the periodic environment, individuals born in state 3 have a higher mid to late life survivorship than those born in other states, but the effect is small (top panel of Fig. 5). In the i.i.d. and Markov environments, individuals born in state 1 have higher mid to late life survivorship (lower two panels of Fig. 5), respectively. The largest impact of initial state on mid to late life survivorship is in the Markov environment, which also has the highest level of late age survivorship overall (Fig. 5). The same patterns are reflected in mortality curves (not pictured).

The survivorship curves drawn on a log scale all exhibit long-term convergence to a particular slope at late ages that is independent of initial state (Fig. 5). The state of the environment in the birth year affects the height of the curve. In practice, it is not clear that a

given cohort lives long enough or is numerous enough to have living survivors at the age when the asymptotic survivorship begins to dominate the picture. It is possible that for many populations, the ages lived are all within the zone of the transient dynamics.

Variability in age-specific survivorship.—Our theoretical results for i.i.d. and Markov environments show generally that cohorts experiencing different environmental sequences (even when the sequences are generated by the same probability rules) will have different survivorships. Thus we expect differences in survivorship for cohorts established at different times in one spatial location, or living in different locations whose environments are not correlated. One measure of this variability is given by the rate of growth of the coefficient of variation of survivorship at old ages (top panel of Fig. 6). A more dramatic picture of this

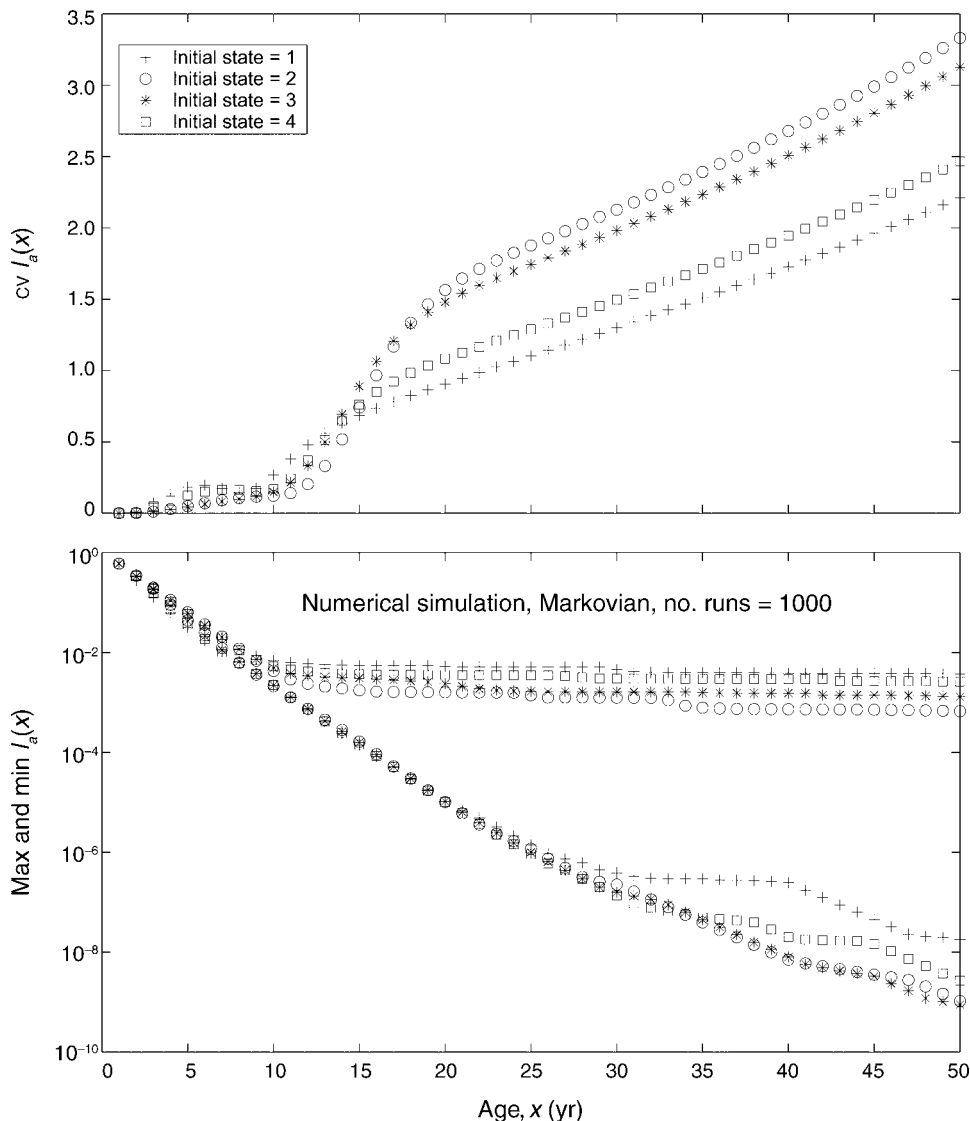


FIG. 6. Variability of survivorship curves in the Markovian environment: coefficient of variation, $\sqrt{\text{Var}_w l(x|w, a)} / [E_w l(x|w, a)]$, (standard deviation/mean), of $l_a(x)$ from analytical results, and minimum and maximum of $l_a(x)$ from numerical simulations of 1000 sample paths.

variation is given by numerical simulations of different environmental sequences (lower panel of Fig. 6) which show how rapidly survivorship curves diverge with age.

CONCLUSIONS

We provide exact computable formulas for life expectancy and age-specific survivorship and mortality when stage transition rates follow one of three general patterns over time, cycles, independent random variation, or a Markov chain. Application of these formulas shows that temporal variability has significant effects on age-specific mortality and survival rates. The use of a fixed transition matrix can predict quite inaccurate age-based survival when transition rates actually vary significantly over time. The environment at birth,

affecting the first transitions made by new recruits into a population, has effects on age-specific survivorship at all ages, including very high ages. Current environmental conditions also have lasting effects on the remaining life expectancy of an individual who is first observed at some later stage of the life cycle.

Over the course of an individual's life, environmental changes accumulate to determine both the average and variance of life expectancy and survivorship. The pattern of survivorship at old ages always converges to an exponential decrease with age. Initial environments have a small effect on average survivorship at old ages, but a large effect on the variance of old-age survivorship.

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LITERATURE CITED

- Aberg, P. 1992. Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology* **73**:1488–1501.
- Boucher, D. H. 1977. General patterns of age by stage distributions. *Journal of Ecology* **85**:235–240.
- Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Second Edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Caswell, H., and T. Kaye. 2001. Stochastic demography and conservation of an endangered perennial plant (*Lomatium bradshawii*) in a dynamic fire regime. *Advances in Ecological Research* **32**:1–51.
- Cochran, M. E., and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs* **62**:345–364.
- Cohen, J. E. 1977. Ergodicity of age-structure in populations with Markovian vital rates III. Finite-state moments and growth rates: an illustration. *Advances in Applied Probability* **9**:462–475.
- Davelos, A. L., and A. M. Jarosz. 2004. Demography of American chestnut populations: effects of a pathogen and a hyperparasite. *Journal of Ecology* **92**:675–685.
- Donohue, K., D. R. Foster, and G. Motzkin. 2000. Effects of the past and present on species distribution: land-use history and demography of wintergreen. *Journal of Ecology* **88**:303–316.
- Ehrlén, J., and K. Lehtilä. 2002. How perennial are perennial plants? *Oikos* **98**:308–322.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Togo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**:367–393.
- Horvitz, C. C., and D. W. Schemske. 1986. Seed dispersal and environmental heterogeneity in a neotropical herb: a model of population and patch dynamics. Pages 169–186 in A. Estrada and T. F. Fleming, editors. Symposium on frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht, The Netherlands.
- Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: Projection matrix analysis. *Ecological Monographs* **65**:155–192.
- Kaye, T. N., K. L. Pendergrass, K. Finley, and J. B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. *Ecological Applications* **11**:1366–1380.
- Morris, W. F., and D. F. Doak. 1998. Life history of the long-lived gynodioecious cushion plant, *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. *American Journal of Botany* **85**:784–793.
- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.
- Orzack, S. H. 1985. Population dynamics in variable environments. V. The genetics of homeostasis revisited. *American Naturalist* **133**:901–923.
- Pascarella, J. B., and C. C. Horvitz. 1998. Hurricane disturbance and the population dynamics of a tropical understory shrub: megamatrix elasticity analysis. *Ecology* **79**:547–563.
- Pico, F. X., P. F. Quintana-Ascencio, E. S. Menges, and F. Lopez-Barrera. 2003. Recruitment rates exhibit high elasticity and high temporal variation in populations of a short-lived perennial herb. *Oikos* **103**:69–74.
- Seneta, E. 1981. Non-negative matrices and Markov chains. Second edition. Springer-Verlag, New York, New York, USA.
- Silvertown, J., M. Franco, and R. Perez-Ishiwara. 2001. Evolution of senescence in iteroparous perennial plants. *Evolutionary Ecology Research* **3**:393–412.
- Tuljapurkar, S. 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theoretical Population Biology* **21**:114–140.
- Tuljapurkar, S. 1990. Population dynamics in variable environments. Springer-Verlag, New York, New York, USA.
- Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. *American Naturalist* **162**:489–502.

APPENDIX

Mathematical derivations (*Ecological Archives* E087-089-A1).