Leslie Matrix II

Formal Demography
Stanford Summer Short Course 2006
James Holland Jones

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Outline

1. Spectral Decomposition
2. Keyfitz Momentum
3. Transient Dynamics in terms of Eigenvectors
4. Matrix Perturbations
   (a) Sensitivity
   (b) Elasticity
   (c) Second Derivatives

Spectral Decomposition of the Projection Matrix

Suppose we are given an initial population vector, $\mathbf{n}(0)$

We can write $\mathbf{n}(0)$ as a linear combination of of the right eigenvectors, $\mathbf{w}_i$ of the projection matrix $\mathbf{A}$

$$\mathbf{n}(0) = c_1\mathbf{w}_1 + c_2\mathbf{w}_2 + \cdots + c_k\mathbf{w}_k$$

where the c_i are a set of coefficients

We can collect the eigenvectors into a matrix and the coefficients into a vector and re-write this equation as:

$$\mathbf{n}(0) = \mathbf{W}\mathbf{c}$$

From this it is clear that

$$\mathbf{c} = \mathbf{W}^{-1}\mathbf{n}(0)$$

Now, $\mathbf{W}^{-1}$ is just the matrix of left eigenvectors (or their complex conjugate transpose), so:

$$c_i = \mathbf{v}_i^*\mathbf{n}(0)$$

Spectral Decomposition II

Project the initial population vector $\mathbf{n}(0)$ forward by multiplying it by the projection matrix $\mathbf{A}$

$$
\begin{aligned}
\mathbf{n}(1) &= \mathbf{A}\mathbf{n}(0) \\
&= \sum_i c_i \mathbf{A}\mathbf{w}_i \\
&= \sum_i c_i \lambda_i \mathbf{w}_i
\end{aligned}
$$

Multiply again!

$$
\mathbf{n}(2) = \mathbf{A}\mathbf{n}(1)
$$

$$
\begin{aligned}
&= \sum_i c_i \lambda_i \mathbf{A} \mathbf{w}_i \\
&= \sum_i c_i \lambda_i^2 \mathbf{w}_i
\end{aligned}
$$

We could keep going, but at this point it isn't hard to believe that the following holds:

$$
\mathbf{n}(t) = \sum_i c_i \lambda_i^t \mathbf{w}_i \tag{1}
$$

Equivalently:

$$
\mathbf{n}(t) = \sum_i \lambda_i^t \mathbf{w}_i \mathbf{v}_i^* \mathbf{n}(0) \tag{2}
$$

This is known as the **Spectral Decomposition** of the projection matrix $\mathbf{A}$

It is instructive to compare this to the solution for population growth in an unstructured (i.e., scalar) population, characterized by a geometric rate of increase a:

$$N(t+1) = aN(t)$$

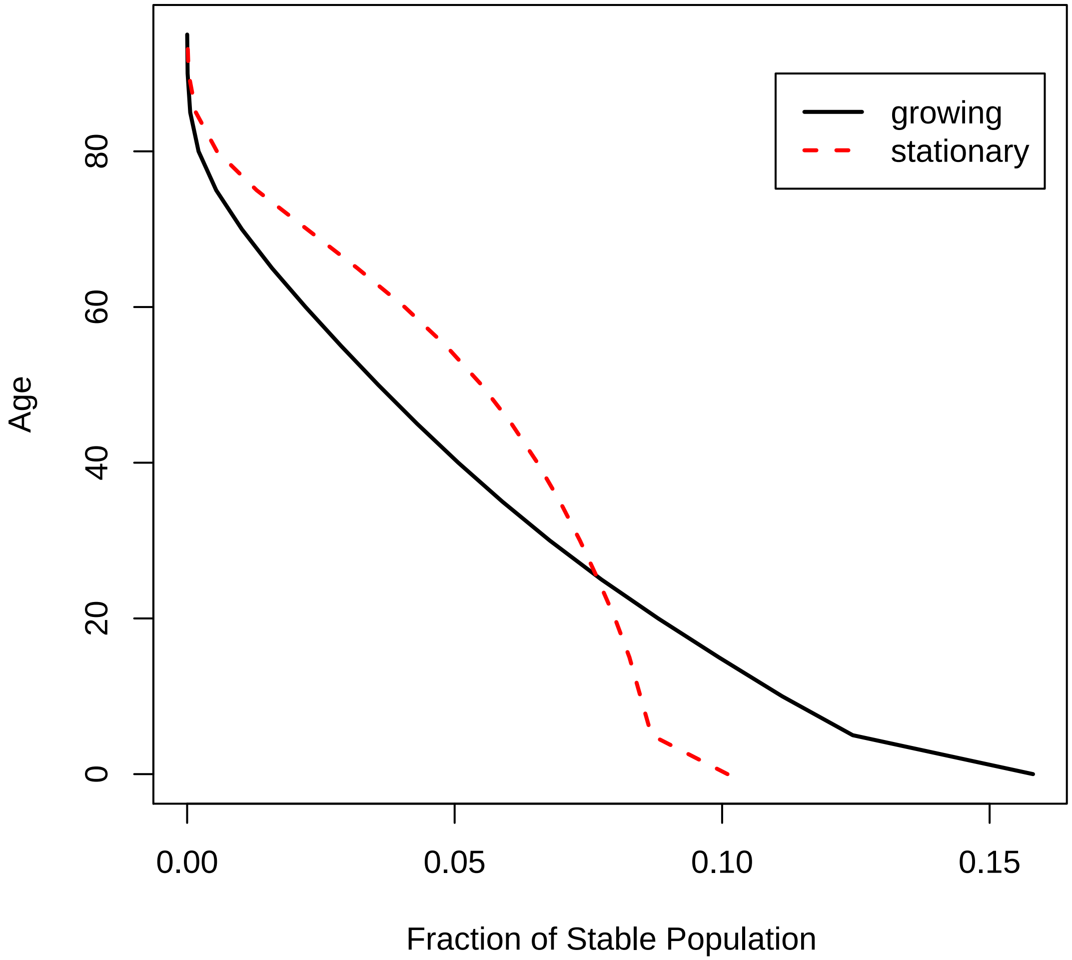
$$N(t) = N(0)a^t$$

For the scalar case, the solution is exponential

For a k-dimensional matrix, this solution means that the population size at time t is a weighted sum of k exponentials

While both depend on the initial conditions, the k-dimensional case weights the initial population vector by the reproductive values of the k classes

Population Momentum



Keyfitz (1971) Formulation for Population Momentum

The ratio of population size at the ultimate equilibrium and just before the fertility transition

$$M = \frac{b \, \mathring{e}_0}{r\mu} \left(\frac{R_0 - 1}{R_0} \right) \tag{3}$$

where b is the gross birth rate:

$$b = \frac{1}{\int_\alpha^\beta e^{-rx} l(x) dx}$$

$\mathring{e}_0$ is the life expectancy at birth

μ is the mean age of childbearing in the stationary population:

$$\mu = \frac{\int_\alpha^\beta x l(x) m(x) dx}{\int_\alpha^\beta l(x) m(x) dx}$$

R_0 is the net reproduction ratio:

$$R_0 = \int_\alpha^\beta l(x) m(x) dx$$

Momentum in Terms of Matrix Formalism

First recall the spectral decomposition of the projection matrix $\mathbf{A}$:

$$\mathbf{n}(t) = \sum_i c_i \lambda_i^t \mathbf{w}_i$$

where the coefficients of the sum c_i are

$$c_i = \mathbf{v}_i^* \mathbf{n}(0)$$

The (scalar) product of the initial population size and the reproductive value vector corresponding to the ith eigenvalue

Momentum is the Ratio of Eventual Size to the Size at Fertility Drop

$$M = \lim_{t \to \infty} \frac{\|\mathbf{n}(t)\|}{\|\mathbf{n}(0)\|} \tag{4}$$

where $\|\mathbf{n}\| = \sum_i n_i$ is the total population size

The population under the old and new rates will be characterized by eigenvalues, $\lambda_i^{(\mathrm{old})}$ and $\lambda_i^{(\mathrm{new})}$

$$\lim_{t \to \infty} \frac{\mathbf{n}(t)}{\lambda_1^{(\mathrm{new})}} = \lim_{t \to \infty} \mathbf{n}(t) \tag{5}$$

$$= \left(\mathbf{v}_1^{(\mathrm{new})*}\mathbf{n}(0)\right) \mathbf{w}_1^{(\mathrm{new})} \tag{6}$$

This follows directly from the spectral decomposition of the projection matrix

Substitute this into equation 4

$$M = \frac{\mathbf{e}^\mathsf{T} \left(\mathbf{v}_1^{(\mathrm{new})*} \mathbf{n}(0) \right) \mathbf{w}^{(\mathrm{new})*}}{\mathbf{e}^\mathsf{T} \mathbf{n}(0)} \tag{7}$$

where $\mathbf{e}$ is a vector of ones.

This much simpler computationally than the original Keyfitz (1971) formulation

Transient Dynamics and Convergence

Re-write the spectral decomposition for the projection matrix $\mathbf{A}$, expanding the sum for expository purposes

$$\mathbf{n}(t) = c_1 \lambda_1^t \mathbf{w}_+ c_2 \lambda_2^t \mathbf{w}_2 + \cdots + c_k \lambda_k^t \mathbf{w}_k$$

If $\mathbf{A}$ is irreducible and primitive, then the Perron-Frobenius theorem insures that one of the eigenvalues, λ_1, of $\mathbf{A}$ will be:

- Strictly positive
- Real
- Greater than or equal to all other eigenvalues

Because of this, all the exponential terms in the spectral decomposition of $\mathbf{A}$ become negligible compared to the one associated with λ_1 when t gets large

To see this divide both sides of the spectral decomposition of $\mathbf{A}$ by the dominant eigenvalue raised to the t power λ_1^t:

$$\frac{\mathbf{n}(t)}{\lambda_1^t} = c_1\mathbf{w}_1 + c_2\left(\frac{\lambda_2}{\lambda_1}\right)^t \mathbf{w}_2 + \cdots + c_k\left(\frac{\lambda_k}{\lambda_1}\right)^t \mathbf{w}_k \tag{8}$$

Since $\lambda_1 > \lambda_i$ for $i \geq 2$, each of the fractions involving the eigenvalues will approach zero as $t \to \infty$

Taking this limit, we see that:

$$\lim_{n\to\infty} \frac{\mathbf{n}(t)}{\lambda_1^t} = c_1\mathbf{w}_1 \tag{9}$$

This is the **Strong Ergodic Theorem**

The long term dynamics of a population governed by primitive matrix $\mathbf{A}$ are described by growth rate λ_1 and population structure $\mathbf{w}_1$

Yes, But How Soon to Convergence?

Clearly, a population will converge to its asymptotic behavior faster is λ_1 is large relative to the other eigenvalues

That's because λ_i/λ_1 $(i > 1)$ will be smaller and approach zero more rapidly as it is powered up

The classic measure of convergence is the ratio of the dominant to the absolute value of the subdominant eigenvalue

$$\rho = \lambda_1/|\lambda_2|$$

The quantity ρ is known as the damping ratio

From equation 8, we can write

$$\lim_{t \to \infty} \left(\frac{\mathbf{n}(t)}{\lambda_1} - c_1 \mathbf{w}_1 + c_2 \rho^{-t} \mathbf{w}_2 \right) = 0$$

For large t and some constant k

$$\begin{aligned} \left\| \frac{\mathbf{n}(t)}{\lambda_1} - c_1 \mathbf{w}_1 \right\| &\leq k\rho^t \\ &= ke^{-\log \rho} \end{aligned}$$

Convergence to stable structure (and therefore growth at rate λ_1) is asymptotically exponential at a rate at least as fast as $\log \rho$

Note that convergence *could* be faster (e.g., if $\mathbf{n}(0) = \mathbf{w}_1$)

The time t_x it takes for the influence of λ_1 to be x times larger than λ_2 is

$$\left(\frac{\lambda_1}{|\lambda_2|} \right)^{t_x} = x$$

or

$$t_x = \log(x)/\log(\rho)$$

How Far is a Population from the Stable Age Distribution?

The classic measure of distance is attributable to Keyfitz (1968) and is a standard measure of the distance between two probability vectors

$$\Delta(\mathbf{x}, \mathbf{w}) = \frac{1}{2} \sum_i |x_i - w_i|$$

Keyfitz's Δ takes a maximum value of $\Delta = 1$, clearly, $\Delta = 0$ when two vectors are identical

Cohen developed two metrics that account not just for the population vector but for the possible route through which a population structure can converge to stability

$$\mathbf{s}(\mathbf{A}, \mathbf{n}(0), t) = \sum_{u=0}^{t} \left(\frac{\mathbf{n}(u)}{\lambda_1^u} - c_1 \mathbf{w}_1 \right)$$

$$\mathbf{r}(\mathbf{A}, \mathbf{n}(0), t) = \sum_{u=0}^{t} \left| \frac{\mathbf{n}(u)}{\lambda_1^u} - c_1 \mathbf{w}_1 \right|$$

Cohen's measures of distance between the observed population vector and the stable vector is simply the sum of the absolute values of these vectors as $t \to \infty$

$$D_1 = \sum_i \lim_{t \to \infty} |s_i(\mathbf{A}, \mathbf{n}(0), t)|$$

$$D_1 = \sum_i \lim_{t \to \infty} |r_i(\mathbf{A}, \mathbf{n}(0), t)|$$

Matrix Perturbations

This derivation follows Caswell (2001)

We start from the general matrix population model:

$$\mathbf{A}\mathbf{w} = \lambda\mathbf{w} \tag{10}$$

Now we perturb the system

$$(\mathbf{A} + d\mathbf{A})(\mathbf{w} + d\mathbf{w}) = (\lambda + d\lambda)(\mathbf{w} + d\mathbf{w}) \tag{11}$$

Multiply all the products and discard the second-order terms such as $(d\mathbf{A})(d\mathbf{w})$

$$\mathbf{A}\mathbf{w} + \mathbf{A}(d\mathbf{w}) + (d\mathbf{A})\mathbf{w} = \lambda\mathbf{w} + \lambda(d\mathbf{w}) + (d\lambda)\mathbf{w} \tag{12}$$

Simplify this to yield

$$\mathbf{A}(d\mathbf{w}) + (d\mathbf{A})\mathbf{w} = \lambda(d\mathbf{w}) + (d\lambda)\mathbf{w} \tag{13}$$

Multiply both sides by $\mathbf{v}^*$ to get

$$\mathbf{v}^*\mathbf{A}(d\mathbf{w}) + \mathbf{v}^*(d\mathbf{A})\mathbf{w} = \lambda\mathbf{v}^*(d\mathbf{w}) + \mathbf{v}^*(d\lambda)\mathbf{w} \tag{14}$$

From the definition of a left eigenvector, we know that the first term on the left-hand side is the same as the first term on the right-hand side. Similarly, because the right and left eigenvectors are scaled so that $\langle \mathbf{w}, \mathbf{v} \rangle = 1$, the last term simplifies to $d\lambda$. We are left with

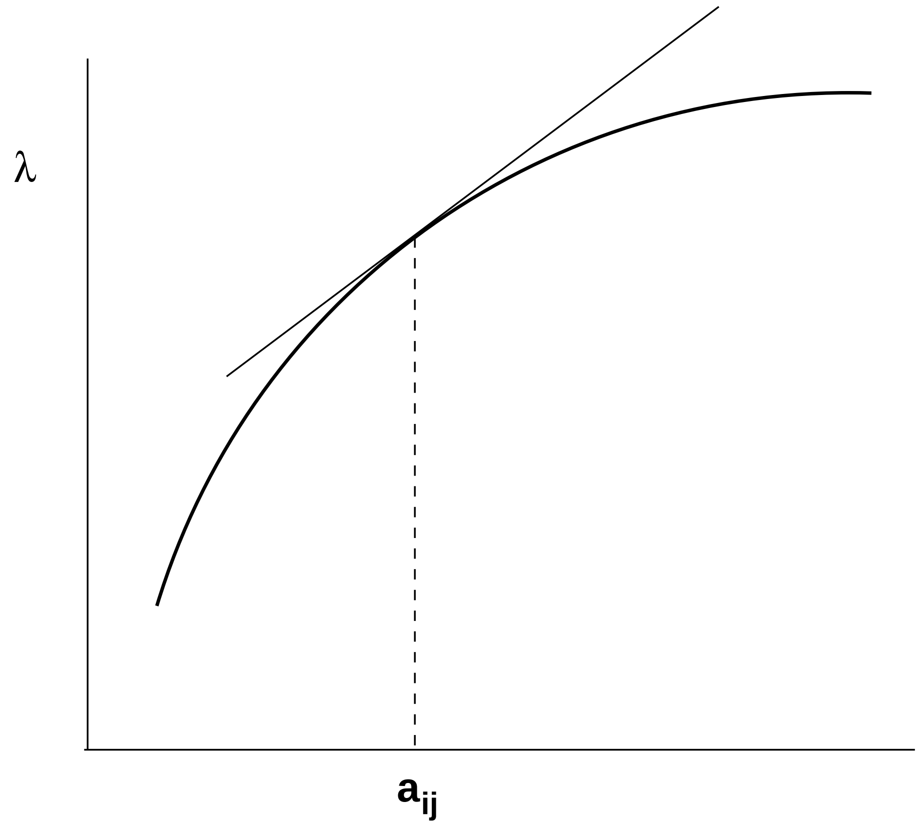
$$\mathbf{v}^* d\mathbf{A}\mathbf{w} = d\lambda \tag{15}$$

When we do a perturbation analysis, we typically only change a single element of $\mathbf{A}$. Thus the basic formula for the sensitivity of the dominant eigenvalue to a small change in element a_{ij} is

$$\frac{\partial \lambda}{\partial a_{ij}} = v_i w_j \tag{16}$$

In other words, the sensitivity of fitness to a small change in projection matrix element a_{ij} is simply the ith element of the left eigenvector weighted by the proportion of the stable population in the jth class (assuming vectors have been normed such that $\langle \mathbf{v}\mathbf{w} \rangle = 1$)

Eigenvalue Sensitivities are Linear Estimates of the Change in λ_1, Given a Perturbation



Lande's Theorem

Imagine a multivariate phenotype (e.g., a life history) $\mathbf{z}$

Lande (1982) shows that when selection is weak, the change in the phenotype $\Delta\mathbf{z}$ is given by

$$\Delta\mathbf{z} = \lambda^{-1}\,\mathbf{G}\,\mathbf{s}$$

wher $\mathbf{G}$ is the additive genetic covariance matrix for the transitions in the life-cycle and $\mathbf{s}$ is a column vector of all the life-cycle transition sensitivities

The sensitivities therefore represent the *force of selection* on the phenotype

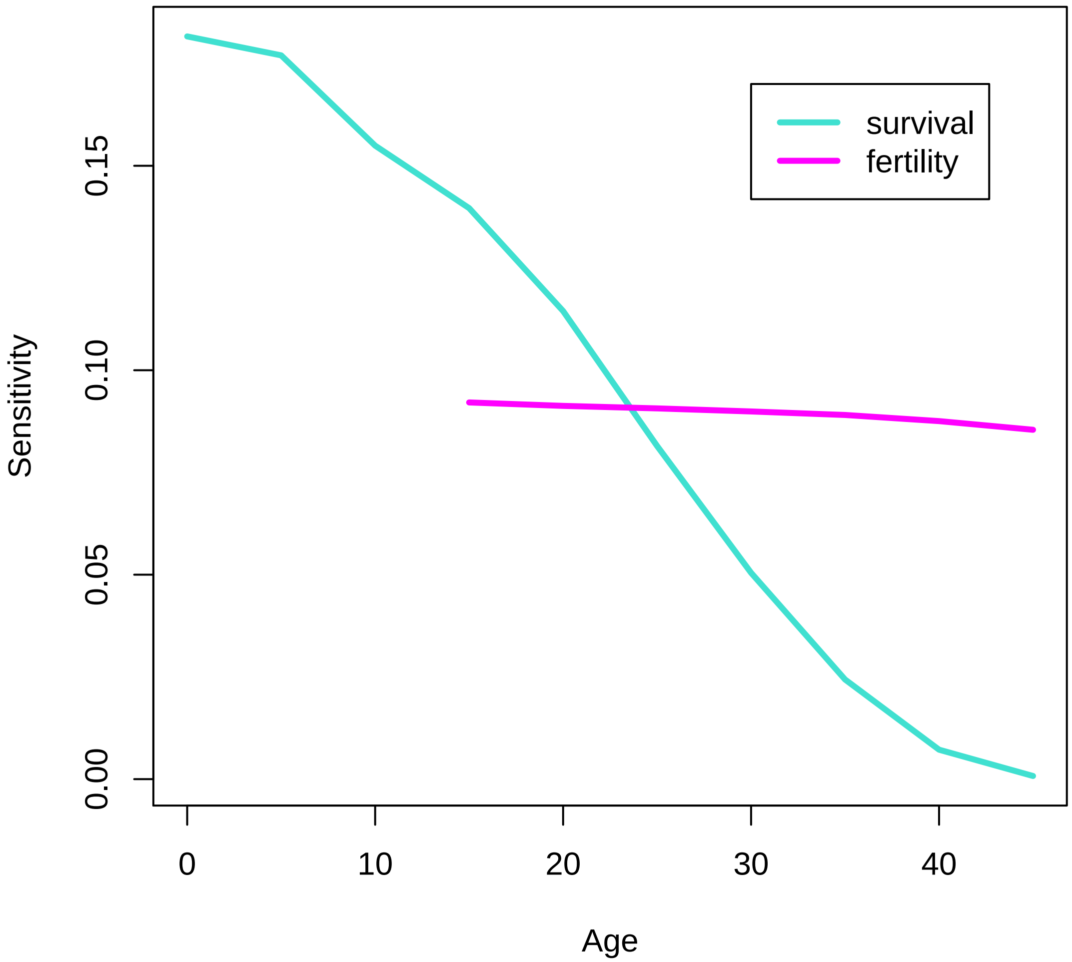
Some R Code for Calculating Sensitivities

A recipe!

```
> lambda <- eigen(A)
> W <- lambda$vectors
> w <- abs(Re(W[,1]))
> V <- solve(Conj(W))
> v <- abs(Re(V[1,]))
> s <- v%o%w
> s[A == 0] <- 0
```

Extract and plot them

```
> surv.sens <-  s[row(s) == col(s)+1]
> fert.sens <- s[1,]
> age <- seq(0,45,by=5)
> plot(age,surv.sens,type="l",lwd=3,col="turquoise")
> lines(age[4:10], fs[4:10], lwd=3, col="magenta")
> legend(30,.17,c("survival","fertility"), lwd=3, col=c("turquoise","magenta"))
```



survival
fertility
Sensitivity
0.00
0.05
0.10
0.15
0
10
20
30
40
Age

Elasticities

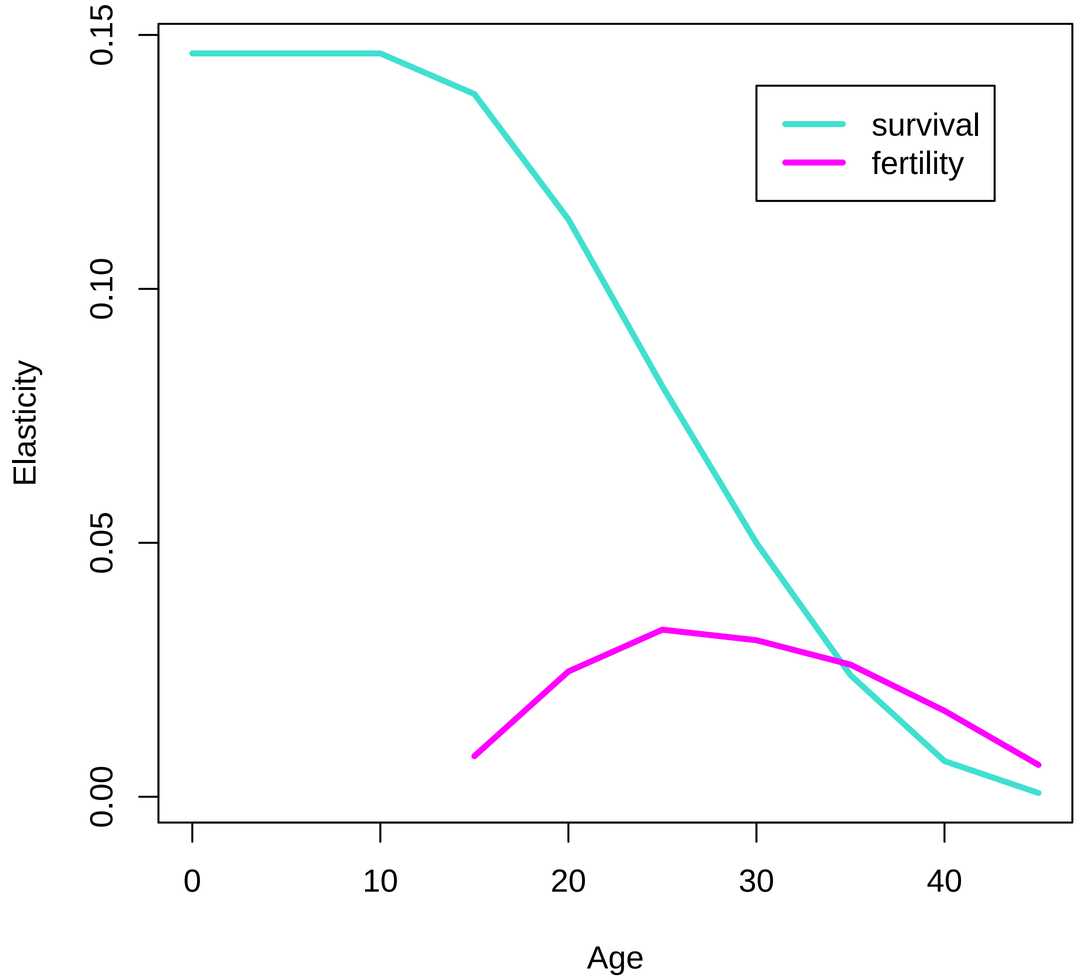
Another measure of the change in a matrix given a small change in an underlying element is the eigenvalue elasticity:

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}}$$

Elasticities are proportional sensitivities: they measure the linear change on a log scale

An important property of elasticities is that they sum to one

$$\sum_{i,j} e_{ij} = 1$$



survival
fertility
Elasticity
0.00
0.05
0.10
0.15
0
10
20
30
40
Age

The Universality of the Human Life Cycle

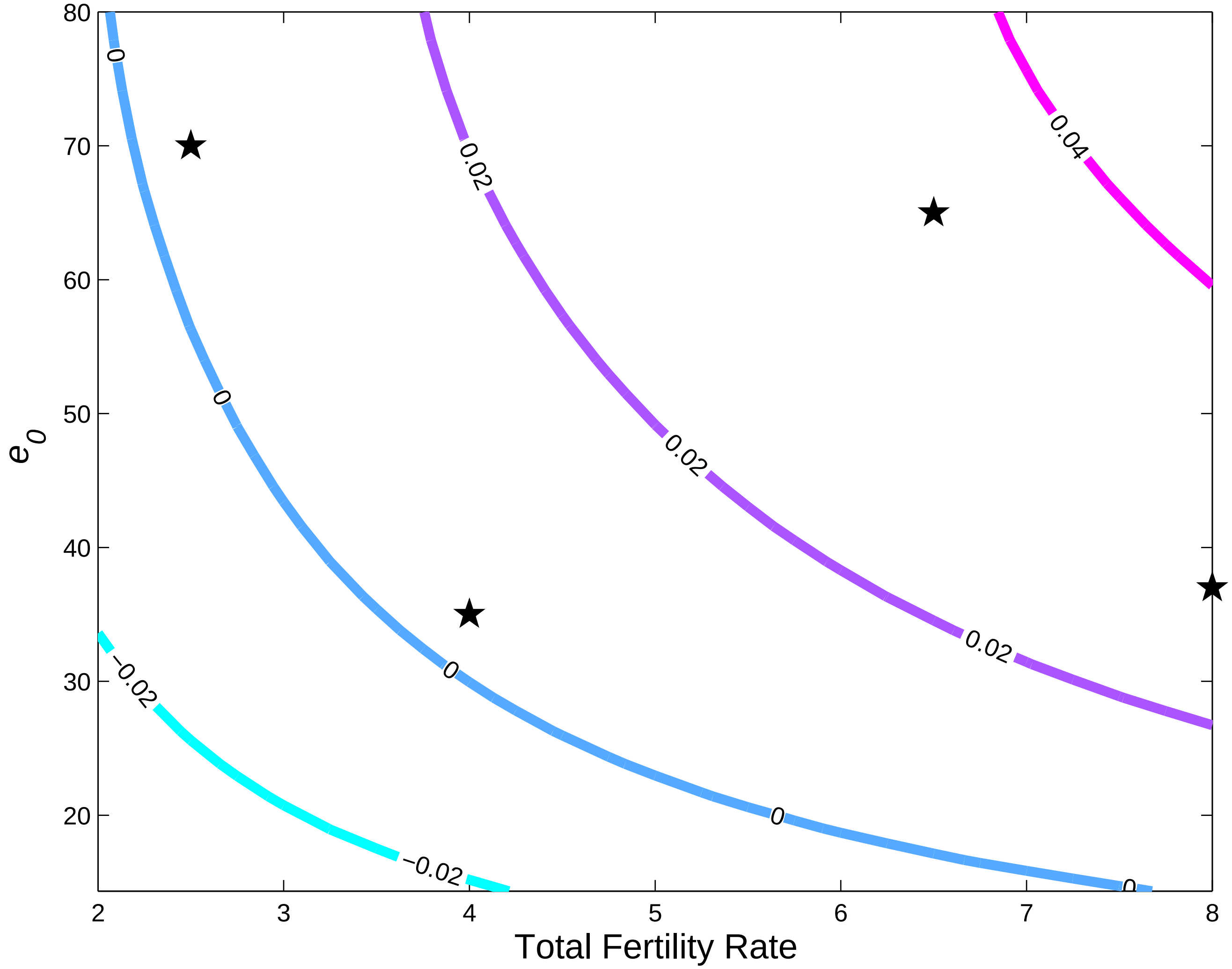
There is a great variety of human demographic experience

How does this variation translate into the force of selection on the human life cycle?

Sampling the full variety of human demographic variation is hopeless

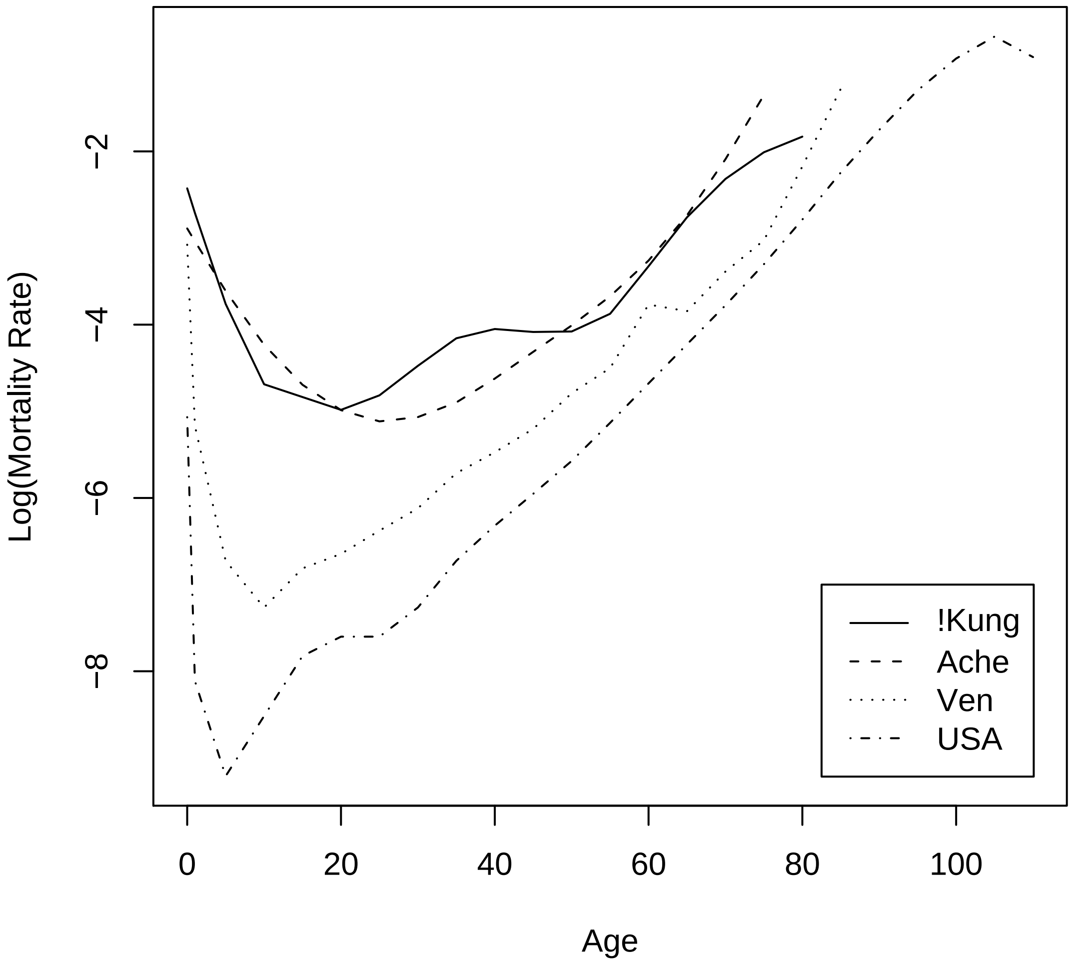
Adopt a strategy (following Livi-Bacci) of filling out a demographic space and exploring the boundaries of the region

The Human Demographic Space

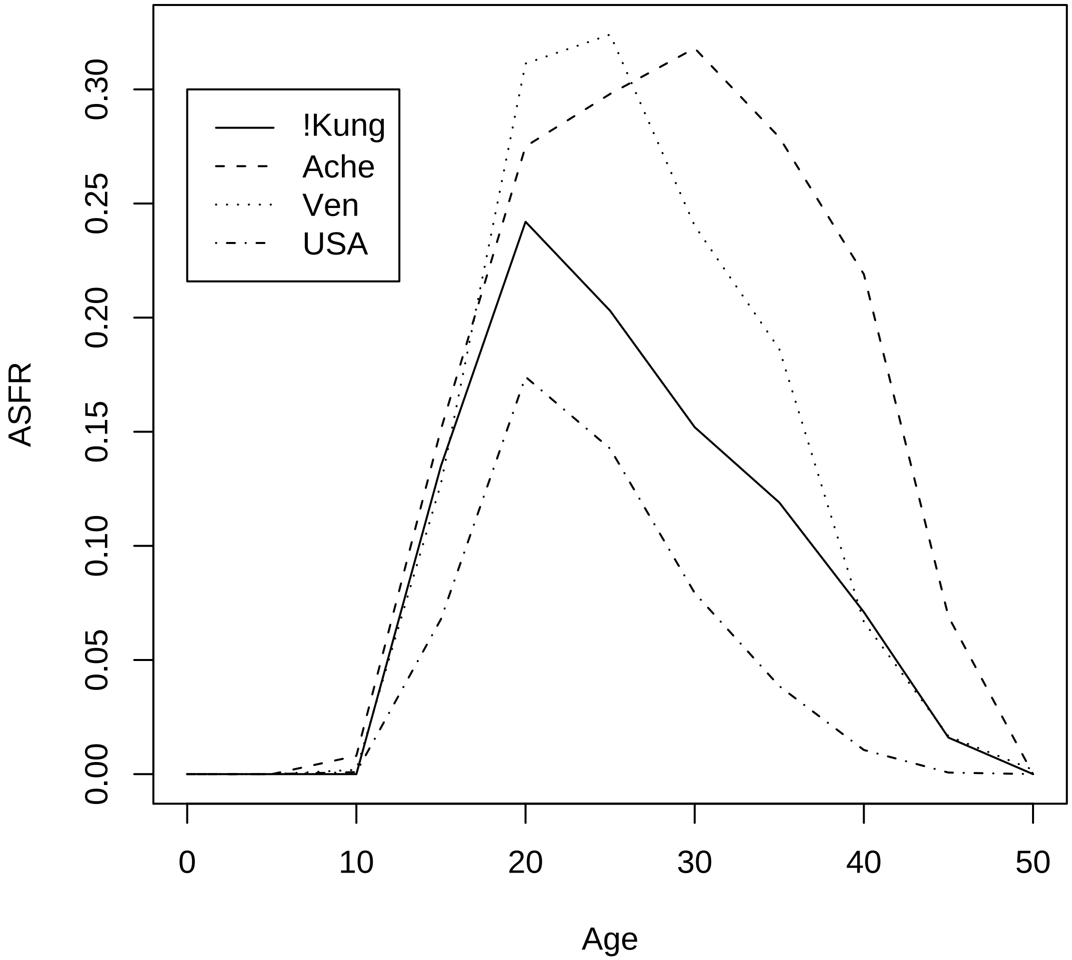


80
70
60
50
40
30
20
e_0
2
3
4
5
6
7
8
Total Fertility Rate
0
0.02
0.04
−0.02

Mortality

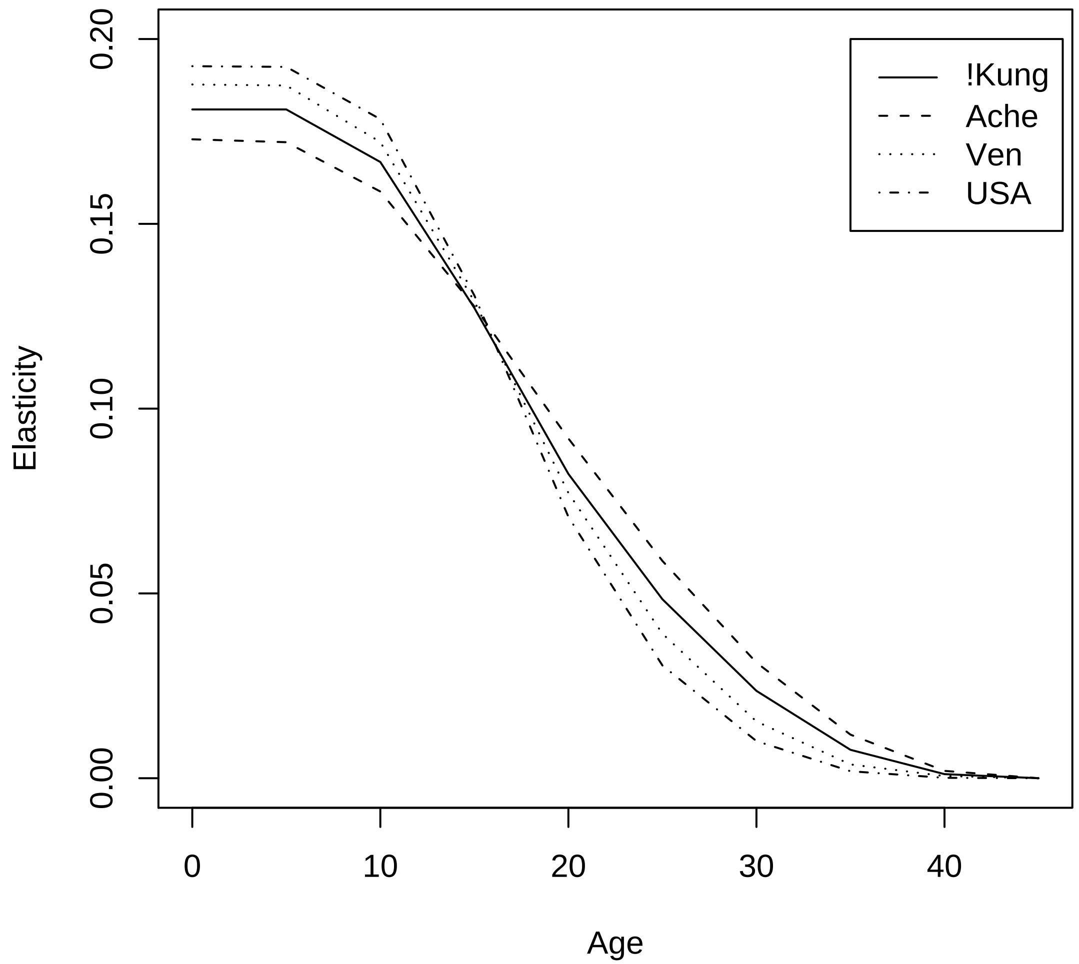


Fertility

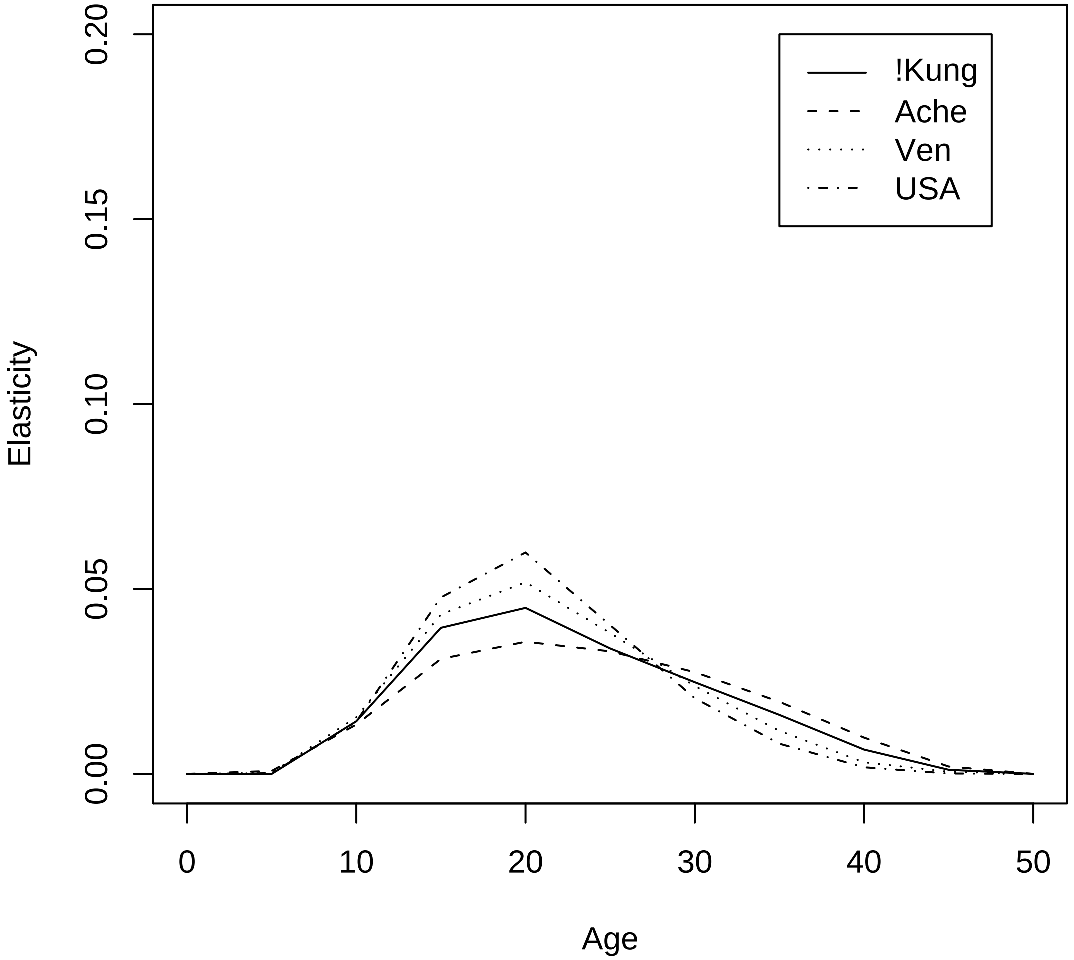


!Kung
Ache
Ven
USA
ASFR
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0
10
20
30
40
50
Age

Survival Elasticities



Fertility Elasticities



Eigenvalue Second Derivatives

We can measure the curvature of the fitness surface

$$\frac{\partial^2 \lambda^{(1)}}{\partial a_{ij} \partial a_{kl}} = s_{il}^{(1)} \sum_{m \neq 1} \frac{s_{kj}^{(m)}}{\lambda^{(1)} - \lambda^{(m)}} + s_{kj}^{(1)} \sum_{m \neq 1} \frac{s_{il}^{(m)}}{\lambda^{(1)} - \lambda^{(m)}}, \qquad (17)$$

where m is the rank of the projection matrix,

$$s_{ij}^{(m)} = \partial \lambda^{(m)} / \partial a_{ij},$$

and $\lambda^{(m)}$ is the mth eigenvalue of the projection matrix

Sensitivity of Elasticities

One application of the eigenvalue second derivatives is calculating how elasticities will change when vital rates are perturbed

i.e.., the sensitivities of the elasticities:

$$\frac{\partial e_{ij}}{\partial a_{kl}} = \frac{a_{ij}}{\lambda} \frac{\partial^2 \lambda}{\partial a_{ij} \partial a_{kl}} - \frac{a_{ij}}{\lambda^2} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}} + \frac{\delta_{ik} \delta_{jl}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \tag{18}$$

where δ_{ik} and δ_{jl} indicate the Kronecker delta function where $\delta_{ik} = 1$ if $i = k$, otherwise $\delta_{ik} = 0$

More Uses for Sensitivities: Stochastic Population Growth

Assume a population living in an i.i.d. random environment

The population is characterized by a mean projection matrix $\bar{\mathbf{A}}$, with its associated eigenvalue $\bar{\lambda}$

Tuljapurkar's small noise approximation for the stochastic growth rate is:

$$\log \lambda_s = \log \bar{\lambda} - \frac{\sigma^2}{2}$$

where

$$\sigma^2 = \mathbf{s}^T \, \mathbf{C} \, \mathbf{s}$$

where $\mathbf{C}$ is the covariance matrix for life-cycle transitions across time