#### Leslie Matrix II

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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 the right eigenvectors,  $\mathbf{w}_i$  of the projection matrix  $\mathbf{A}$ 

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

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  $\mathbf{A}$ 

$$\mathbf{n}(1) = \mathbf{A}\mathbf{n}(0)$$

$$= \sum_{i} c_{i} \mathbf{A}\mathbf{w}_{i}$$

$$= \sum_{i} c_{i} \lambda_{i} \mathbf{w}_{i}$$

Multiply again!

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

$$= \sum_{i} c_{i} \lambda_{i} \mathbf{A} \mathbf{w}_{i}$$

$$= \sum_{i} c_{i} \lambda_{i}^{2} \mathbf{w}_{i}$$

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:

$$\mathbf{n}(t) = \sum_{i} \lambda_{i}^{t} \mathbf{w}_{i} \mathbf{v}_{i}^{*} \mathbf{n}(0)$$
 (2)

This is known as the **Spectral Decomposition** of the projection matrix **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:

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

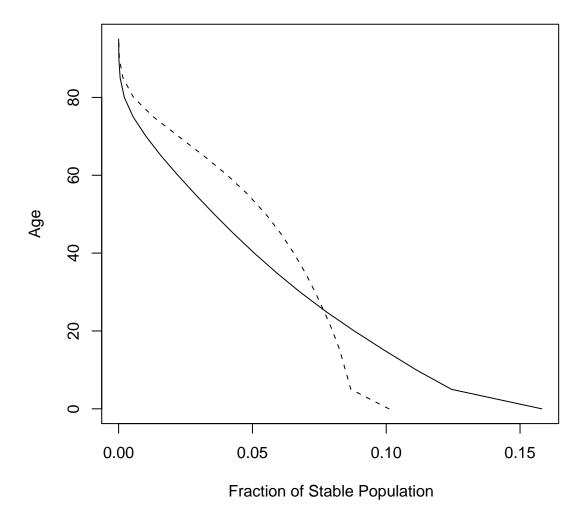
$$N(t) = N(0)a^t$$

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**



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# Keyfitz (1971) Formulation for Population Momentum

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

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

where b is the gross birth rate:

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

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

 $\mu$  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 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,  $\lambda_i^{({\rm old})}$  and  $\lambda_i^{({\rm new})}$ 

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

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

This follows directly from the spectral decomposition of the projection matrix

Substitute this into equation 4

$$M = \frac{\mathbf{e}^{\mathsf{T}} \left( \mathbf{v}_{1}^{(\text{new})*} \mathbf{n}(0) \right) \mathbf{w}_{i}^{(\text{new})*}}{\mathbf{e}^{\mathsf{T}} \mathbf{n}(0)}$$
(7)

where 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 A, expanding the sum for expository purposes

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

If **A** is irreducible and primitive, then the Perron-Frobenius theorem insures that one of the eigenvalues,  $\lambda_1$ , of **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  $\bf A$  become negligible compared to the one associated with  $\lambda_1$  when t gets large

To see this divide both sides of the spectral decomposition of A by the dominant eigenvalue  $\lambda_1$ :

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

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  ${\bf A}$  are described by growth rate  $\lambda_1$  and population structure  ${\bf w}_1$ 

# Yes, But How Soon to Convergence?

Clearly, a population will converge to its asymptotic behavior faster is  $\lambda_1$  is large relative to the other eigenvalues

That's because  $\lambda_i/\lambda_1$  (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  $\rho$  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

$$\left\| \frac{\mathbf{n}(t)}{\lambda_1} - c_1 \mathbf{w}_1 \right\| \leq k \rho^t$$

$$= k e^{-\log \rho}$$

Convergence to stable structure (and therefore growth at rate  $\lambda_1$ ) 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  $\lambda_1$  to be x times larger than  $\lambda_2$  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  $\Delta$  takes a maximum value of  $\Delta=1$ , clearly, is  $\Delta=0$  when two vectors are identical

Cohen developed two metrics that account not just for the population

vector byt 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  $(d\mathbf{A})(d\mathbf{w})$ 

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

Simplify this to yield

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

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

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

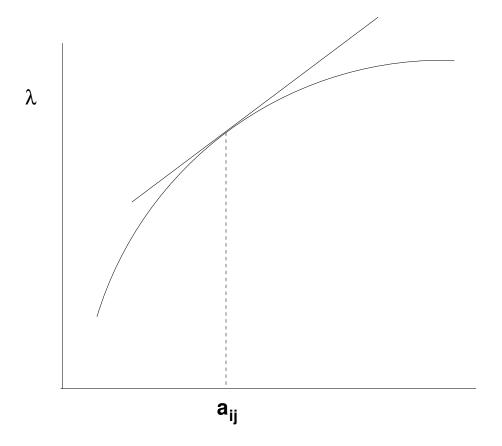
$$\mathbf{v}^* d\mathbf{A} \mathbf{w} = d\lambda \tag{15}$$

When we do a perturbation analysis, we typically only change a single element of 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 $\lambda_1$ , Given a Perturbation



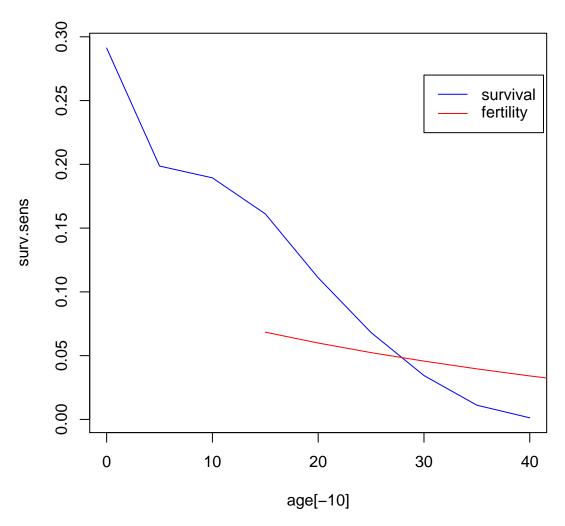
# Some R Code for Calculating Sensitivities

#### 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</pre>
```

#### Extract and plot them

```
> surv.sens <- s[row(s) == col(s)+1]
> fert.sens <- s[1,]
> age <- seq(0,45,by=5)
> plot(age[-10],surv.sens,type="l",col="blue")
> lines(age[4:10],fert.sens[4:10],col="red")
> legend(30,.27,c("survival","fertility"),col=c("blue","red"),lty=c(1,1))
```



#### **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

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

# **Eigenvalue Second Derivatives**

We can measure the curvature of the fitness surface

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

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:

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

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