Matrix Population Models: deterministic and stochastic dynamics

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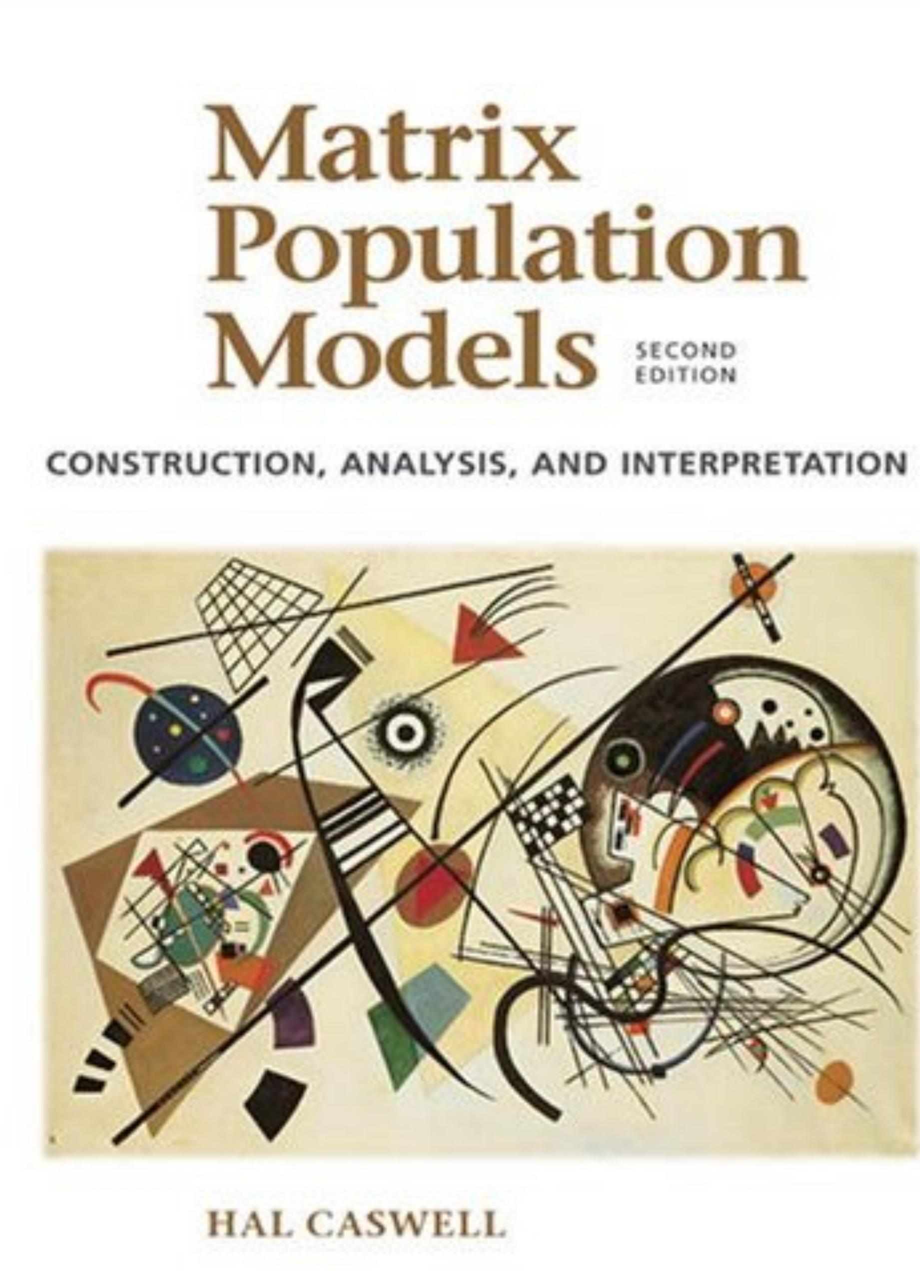
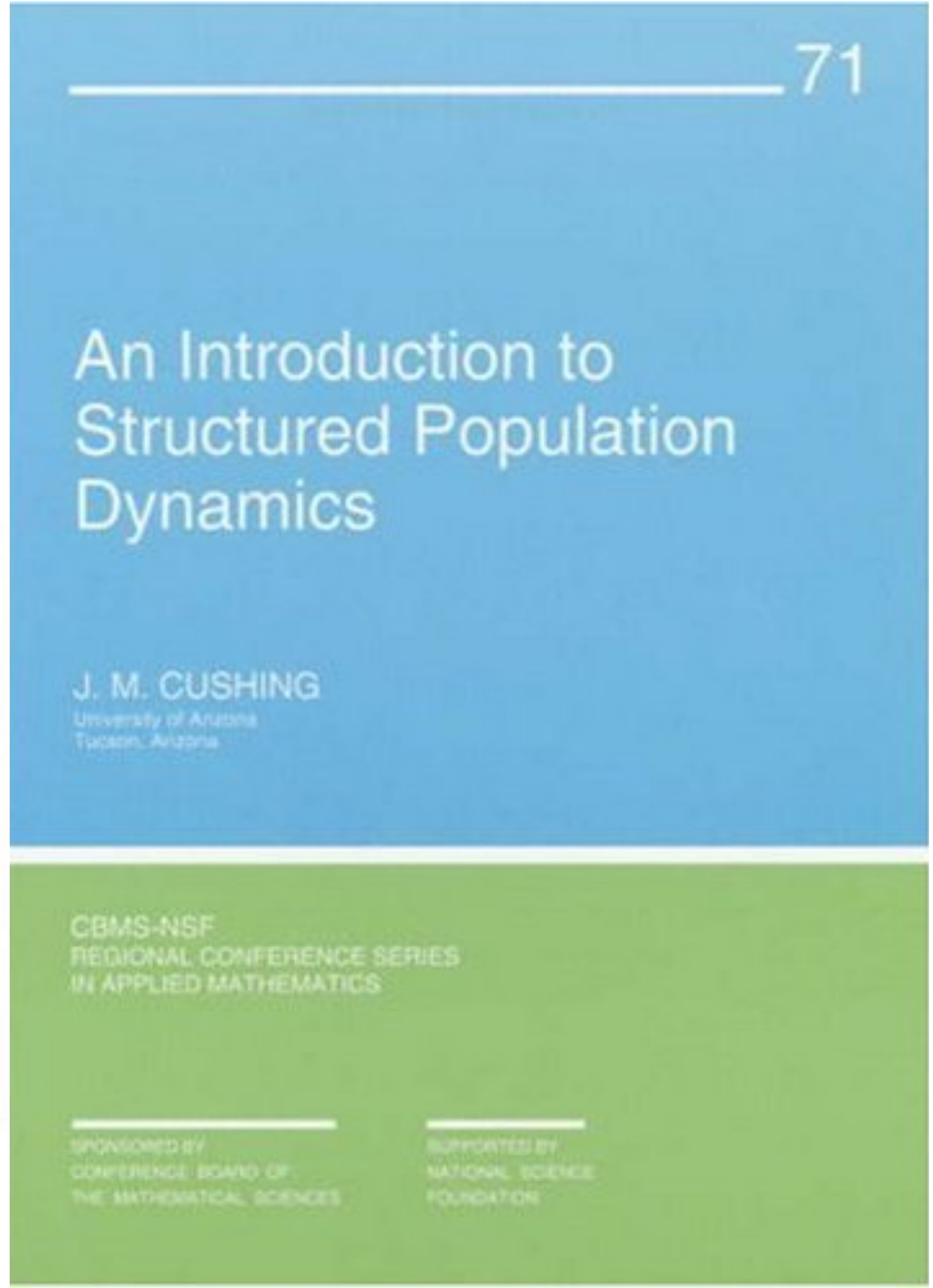

Matrix
Population
Models
SECOND EDITION
CONSTRUCTION, ANALYSIS, AND INTERPRETATION
HAL CASWELL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An Introduction to
Structured Population
Dynamics
J. M. CUSHING
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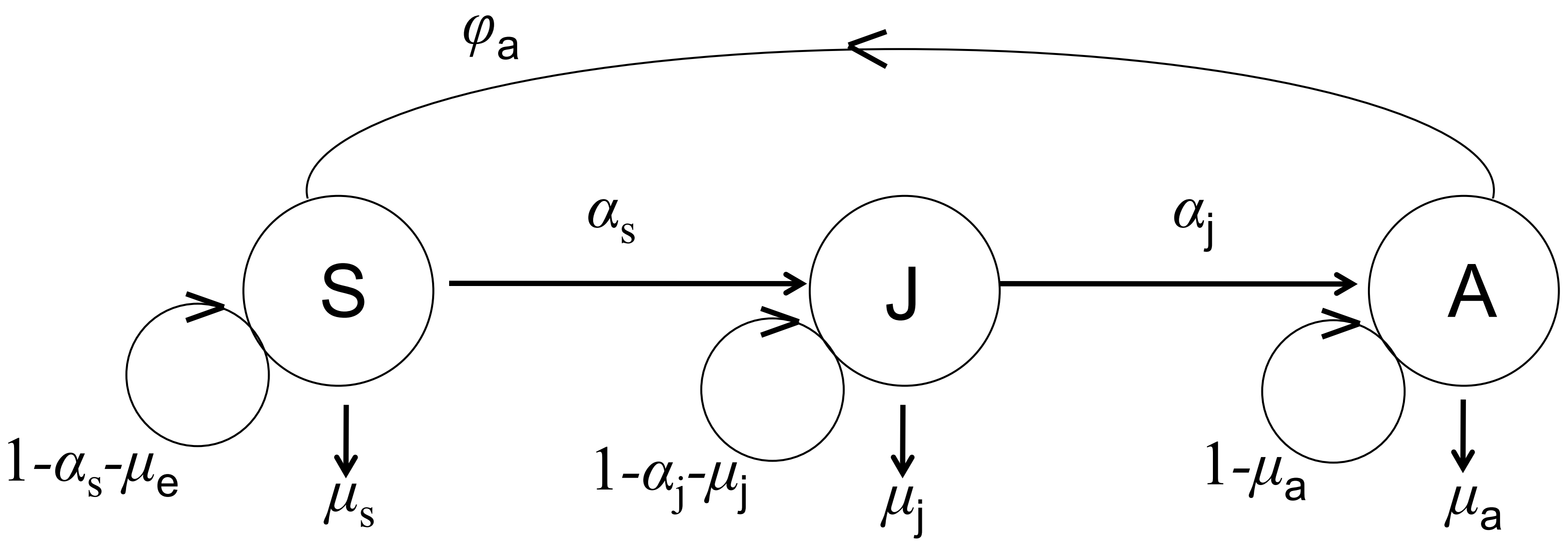
System of difference equations



$$S(t+1) = (1-\boldsymbol{\alpha}_s-\boldsymbol{\mu}_s)S(t)+0J(t)+\boldsymbol{\varphi}_a A(t)$$

$$J(t+1) = \boldsymbol{\alpha}_s S(t)+(1-\boldsymbol{\alpha}_j-\boldsymbol{\mu}_j)J(t)+0A(t)$$

$$A(t+1) = 0S(t)+\boldsymbol{\alpha}_j J(t)+(1-\boldsymbol{\mu}_a)A(t)$$

Matrix population model

$$S(t+1) = (1 - \boldsymbol{\alpha}_s - \boldsymbol{\mu}_s)S(t) + 0J(t) + \boldsymbol{\varphi}_a A(t)$$
$$J(t+1) = \boldsymbol{\alpha}_s S(t) + (1 - \boldsymbol{\alpha}_j - \boldsymbol{\mu}_j)J(t) + 0A(t)$$
$$A(t+1) = 0S(t) + \boldsymbol{\alpha}_j J(t) + (1 - \boldsymbol{\mu}_a)A(t)$$

$$\begin{pmatrix} S(t+1) \\ J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 1 - \boldsymbol{\alpha}_s - \boldsymbol{\mu}_s & 0 & \boldsymbol{\varphi}_a \\ \boldsymbol{\alpha}_s & 1 - \boldsymbol{\alpha}_j - \boldsymbol{\mu}_j & 0 \\ 0 & \boldsymbol{\alpha}_j & 1 - \boldsymbol{\mu}_a \end{pmatrix} \begin{pmatrix} S(t) \\ J(t) \\ A(t) \end{pmatrix}$$

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

A is nonnegative.

(St)Age-Structured matrix model

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \qquad (1)$$

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

$$\mathbf{n}(2) = \mathbf{A}\mathbf{n}(1) = \mathbf{A}(\mathbf{A}\mathbf{n}(0)) = \mathbf{A}^2\mathbf{n}(0)$$

$$\mathbf{n}(3) = \mathbf{A}\mathbf{n}(2) = \mathbf{A}(\mathbf{A}^2\mathbf{n}(0)) = \mathbf{A}^3\mathbf{n}(0)$$

$$\vdots$$

$$\mathbf{n}(t) = \mathbf{A}^t\mathbf{n}(0) \qquad (2)$$

For a *p* x *p* matrix A, there are *p* eigenvalues; some of them are complex. The *dominant eigenvalue* λ of A is **the long-term population growth rate.**

<u>λ>1: growing population; λ<1: declining population; λ=1: constant population.</u>

Long term growth rate: eigenvalues

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

At equilibrium,

$$\mathbf{n}(t+1) = \boldsymbol{\lambda}\mathbf{n}(t)$$

Then,

$$\mathbf{A}\hat{\mathbf{n}} = \boldsymbol{\lambda}\hat{\mathbf{n}}$$

$$(\mathbf{A} - \boldsymbol{\lambda}\mathbf{I})\hat{\mathbf{n}} = 0$$

we can solve this equation for λ using the determinant

$$\det(\mathbf{A} - \boldsymbol{\lambda}\mathbf{I}) = 0$$

Right and left eigenvectors of **A**

From the matrix model we can find the right (**w**) and left (**v**) eigenvectors of **A** associated with the *dominant eigenvalue* λ. These eigenvectors satisfy

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

$$\mathbf{v}^T \mathbf{A} = \lambda \mathbf{v}^T$$

The right eigenvector **w** of A is the **stable (st)age distribution** or the long-term equilibrium states. The left eigeinvector **v** is **the reproductive value**.

Reproductive values

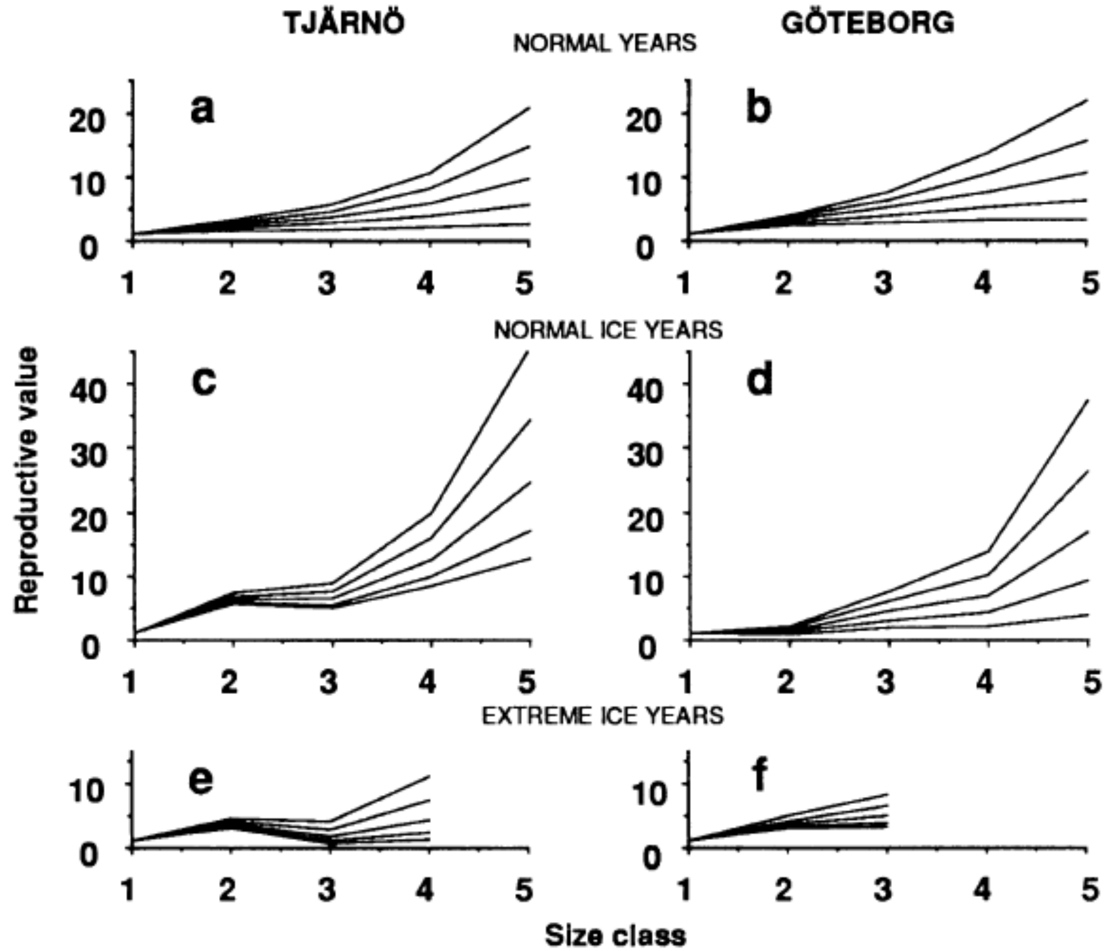


FIG. 7. Reproductive values for each year and population. Each line in subfigure (a)–(f) represents the reproductive values for a survival matrix scaled to a specific value of λ_1. For (a) and (b) lines are drawn for $\lambda_1 = 1.00$ to $\lambda_1 = 1.40$ in steps of 0.10. For the specific values of λ_1 for (c)–(f) see Table 4. The lines with highest reproductive values are those with the highest λ_1.

Brown alga (*Ascophyllum nodosum*)

Stable stage distribution

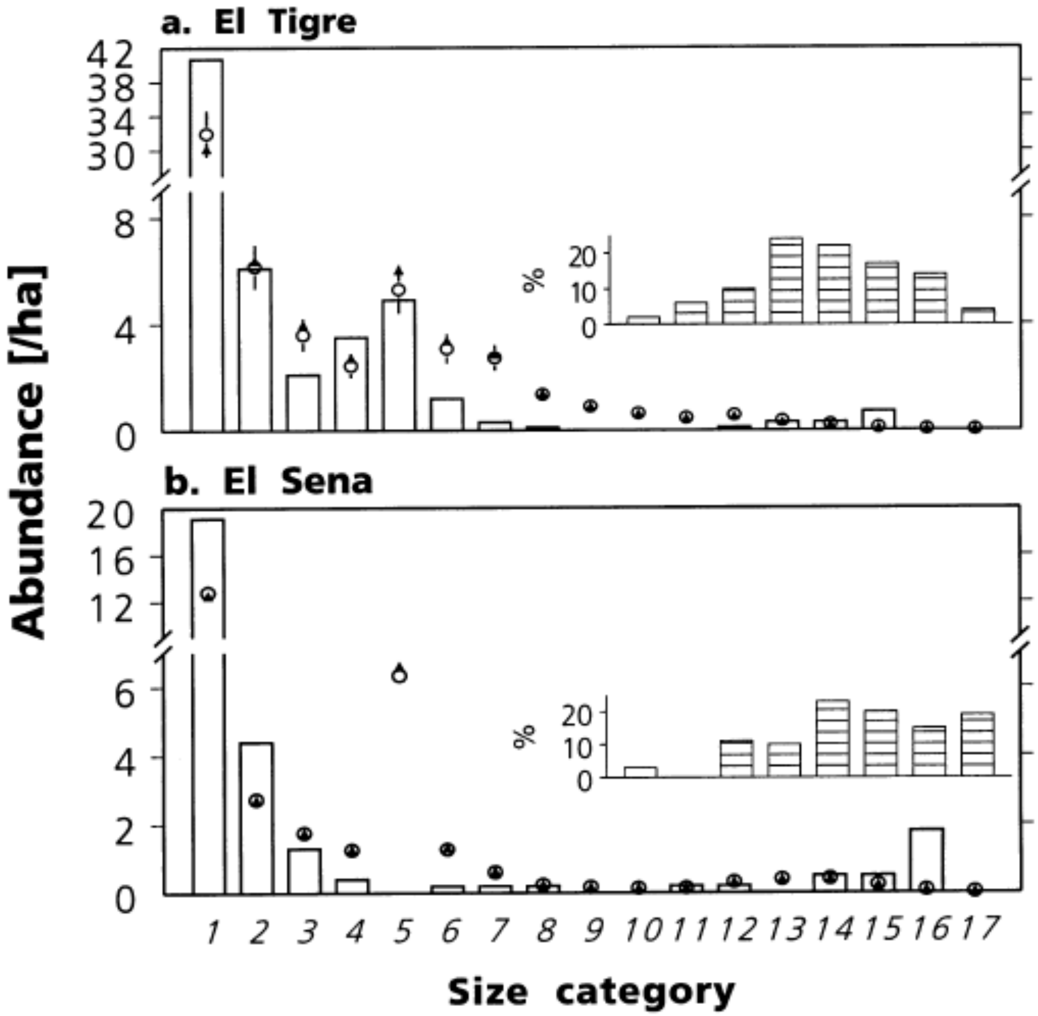


Figure 1

Population structures of *Bertholletia excelsa* in two sites in the Bolivian Amazon where Brazil nuts are extracted: El Tigre (a) and El Sena (b). Shown are observed population structure from study plot data (bars) and stable stage structures resulting from a time-invariant matrix model for a normal year (triangles) and a stochastic time-varying model for normal and dry years (dots; error is 1 SD of 3000 structures). The hatched bars in the inset denote the proportion of individuals measured outside the study plots in categories *10-17* (*n*=127 for El Tigre and 120 for El Sena).

Zuidema 2000

Distance to stable (st)age distribution

Keyfitz's Δ

Let **x**(t) be the observed stage distribution with element x_i; **w** the stable stage distribution with component w_i. The distance between the two vectors of probabilities is measured by

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

$$0 \leq \Delta(\mathbf{x},\mathbf{w}) \leq 1$$

Findings eigenvalues and eigenvectors in R

r-project.org

```
e<-eigen(A)                    # eigenanalysis
lambda<-Re(e$values[1])        # dominant eigenvalue

## right eigenvector
w<-Re(e$vectors[,1])           # stable (st)age distribution
w<-v/sum(v)                    # standardize to total density

## left eigenvector
et<- eigen(t(A))
v<- Re(et$vectors[,1])
v<-w/w[1]                      # reproductive value
```

```
## Keyfitz function
keyfitz<-function(x,y){        # you provide the observed x
    sum(abs(x-y))/2            # and stable stage dist vectors
    }
```

Sensitivity and Elasticity of λ

Given a Leslie matrix **A** with transition elements a_{ij},

Sensitivity of λ to changes of transition elements

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{v^T w}$$

Elasticity of λ to changes of transition elements

$$e_{ij} = \frac{\partial (\log \lambda)}{\partial (\log a_{ij})} = \left(\frac{a_{ij}}{\lambda} \right) \left(\frac{\partial \lambda}{\partial a_{ij}} \right) = \left(\frac{a_{ij}}{\lambda} \right) s_{ij}$$

Sensitivities and Elasticities in R

```
e<-eigen(A)                    # eigenanalysis
lambda<-Re(e$values[1])        # dominant eigenvalue
w<-Re(e$vectors[,1])           # stable (st)age distribution
w<-v/sum(v)                    # standardize to total density
et<- eigen(t(A)
v<- Re(et$vectors[,1])
v<-w/w[1]                      # reproductive value
```

```
tp <- as.vector(v%*%w)
tw <- t(w)
mat <- v %*%tw

## Sensitivities of lambda to matrix elements
sens <- mat/tp

## Elasticities of lambda to matrix elements
elas <- A/lambda*sens
```

Elasticity patterns

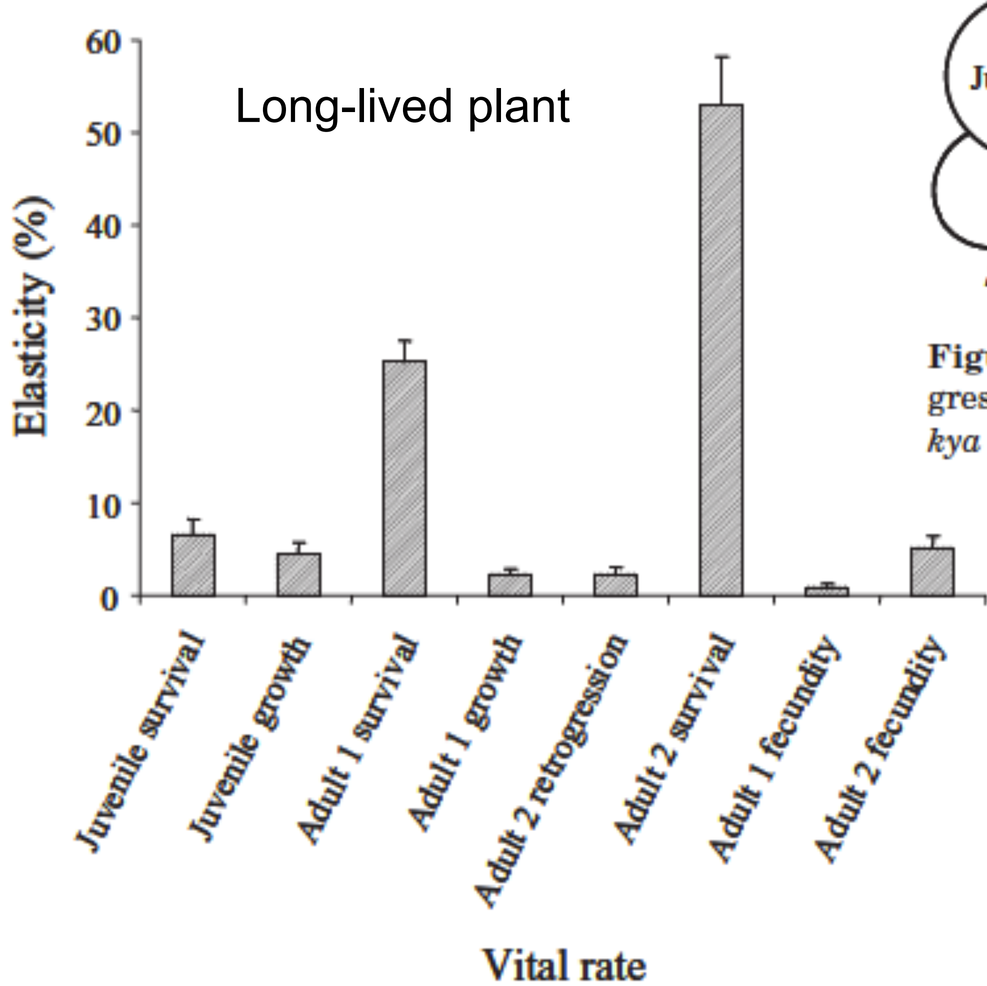


Figure 3. Average (± SE) elasticity values of vital rates for the *Kosteletzkya pentacarpos* study population.

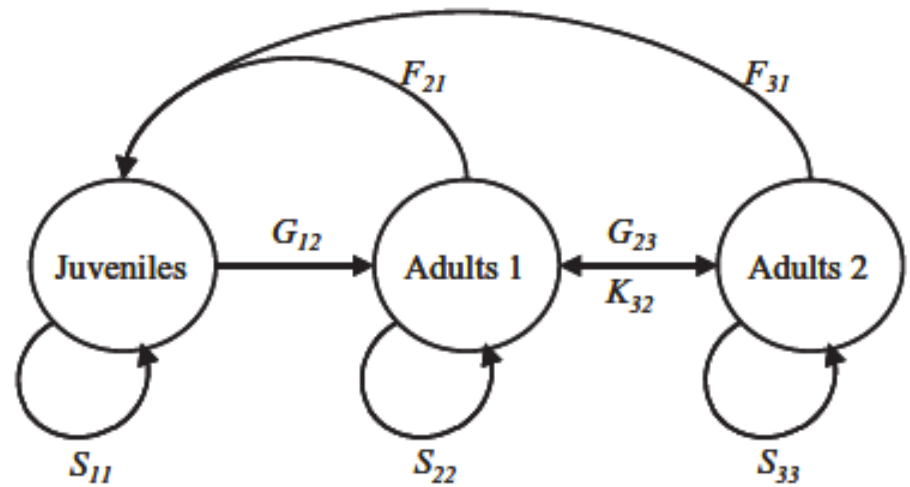
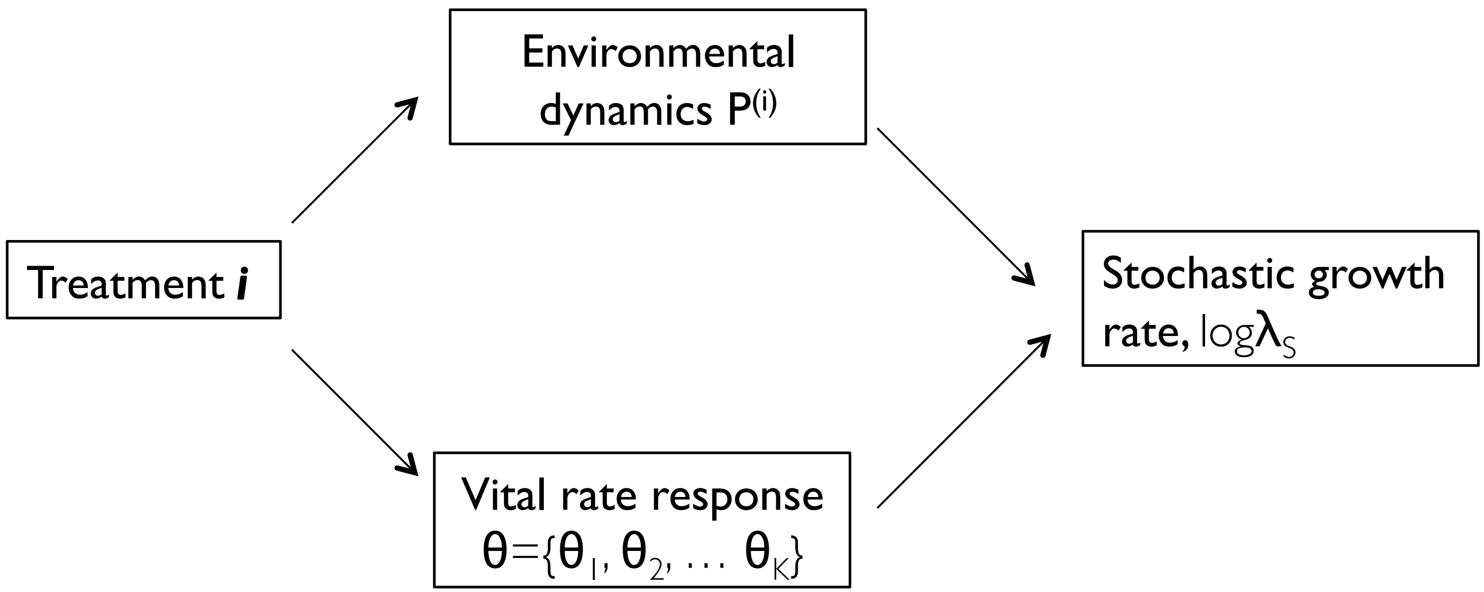


Figure 1. Life-cycle graph indicating growth (G_{ij}), retrogression (K_{ij}), survival (S_{ij}) and fecundity (F_{ij}) of *Kosteletzkya pentacarpos* plants.

Pino et al. 2007. *Botanical Journal of the Linnean Society* 153, 455–462

Stochastic population dynamics, log λ_s



Caswell, 2010. *Journal of Ecology* 98: 324 - 333

Stochastic matrix population models

$$\mathbf{n}(t) = \mathbf{A}(t)\mathbf{n}(t-1)$$

$$\mathbf{n}(t) = \mathbf{A}_{t-1}\mathbf{A}_{t-2}\ldots\mathbf{A}_0\mathbf{n}_0$$

$$\begin{pmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \end{pmatrix} = \begin{pmatrix} P_1(t) & 0 & F_3(t) & F_4(t) \\ G_1(t) & P_2(t) & 0 & 0 \\ 0 & G_2(t) & P_3(t) & 0 \\ 0 & 0 & G_3(t) & P_4(t) \end{pmatrix} \begin{pmatrix} n_1(t-1) \\ n_2(t-1) \\ n_3(t-1) \\ n_4(t-1) \end{pmatrix}$$

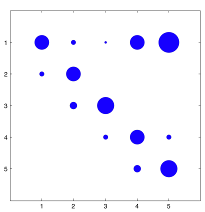
$$\log \boldsymbol{\lambda}_S = \lim_{t\to\infty} \frac{1}{t} \log \left\| \mathbf{A}_{t-1}\mathbf{A}_{t-2}\ldots\mathbf{A}_0\mathbf{n}_0 \right\|$$

Log λ_s is the stochastic population growth rate.

Case study: Harvesting as Markov Process

Harvest states

L



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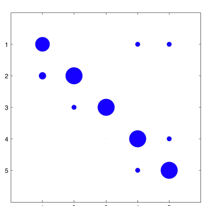

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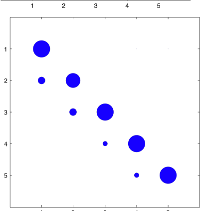

$$\mathbf{n}(t) = \underline{\mathbf{A}(t)}\,\mathbf{n}(t-1)$$

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