An Introduction to Discrete-time Structured Population Models

Mark Lewis

University of Alberta

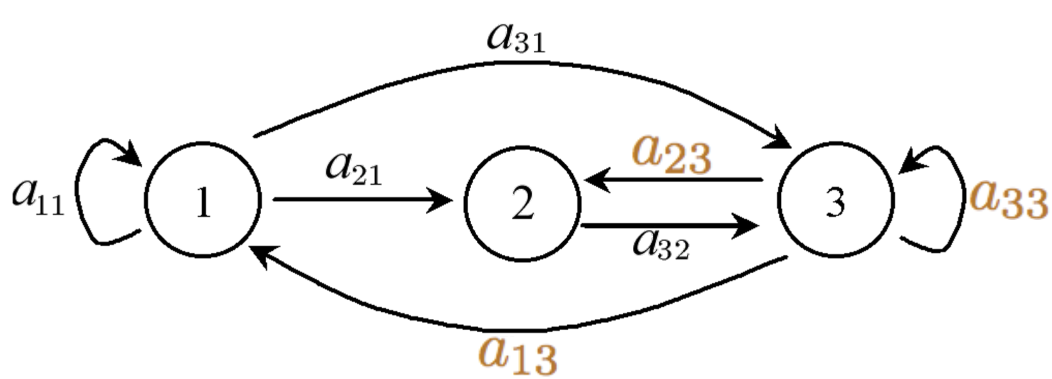
Outline

- The problem of invasive weed control.
- Classical methods for evaluating discrete-time structured population growth, including eigenvalue and elasticity analysis
- Calculation and analysis of basic reproduction number/net reproductive rate (R_0).
- Insight regarding control of scentless chamomile.
- A graphical method for calculating R_0.
- Generation time and fecundity profile

The problem of invasive weed control

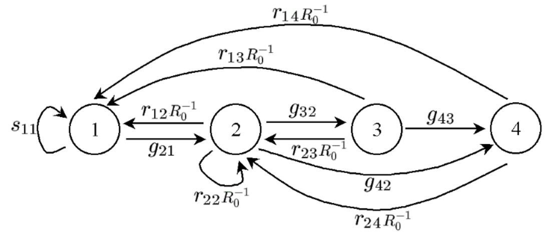
Case Study:
Scentless chamomile (*Matricaria perforata*)

- Annual, biennial or short-lived perennial
- Prefers disturbed habitats (poor competitor)
- Invades agricultural ecosystems
- Three distinctive life cycle stages: (1) seeds (2) rosettes, and (3) flowering plants
- Stage-structured life cycle:

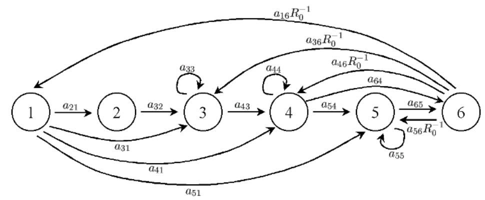


Complex Stage-Structures of Some Invaders

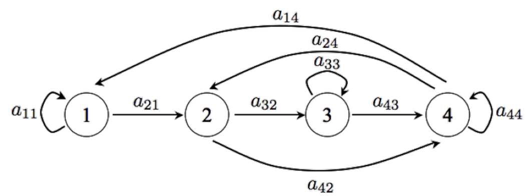
Nodding thistle
(*Carduus nutans*)



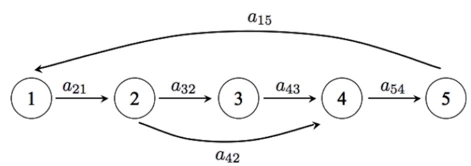
Common teasel
(*Dypsacus sylvestris*)



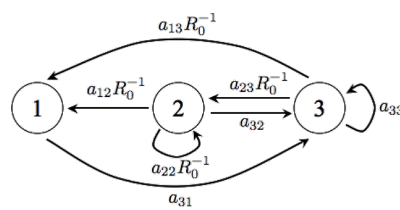
Tansy ragwort
(*Senecio jacobaea*)



Bullfrog
(*Rana catesbeiana*)



Common cat's ear
(*Hypochaeris radicata*)



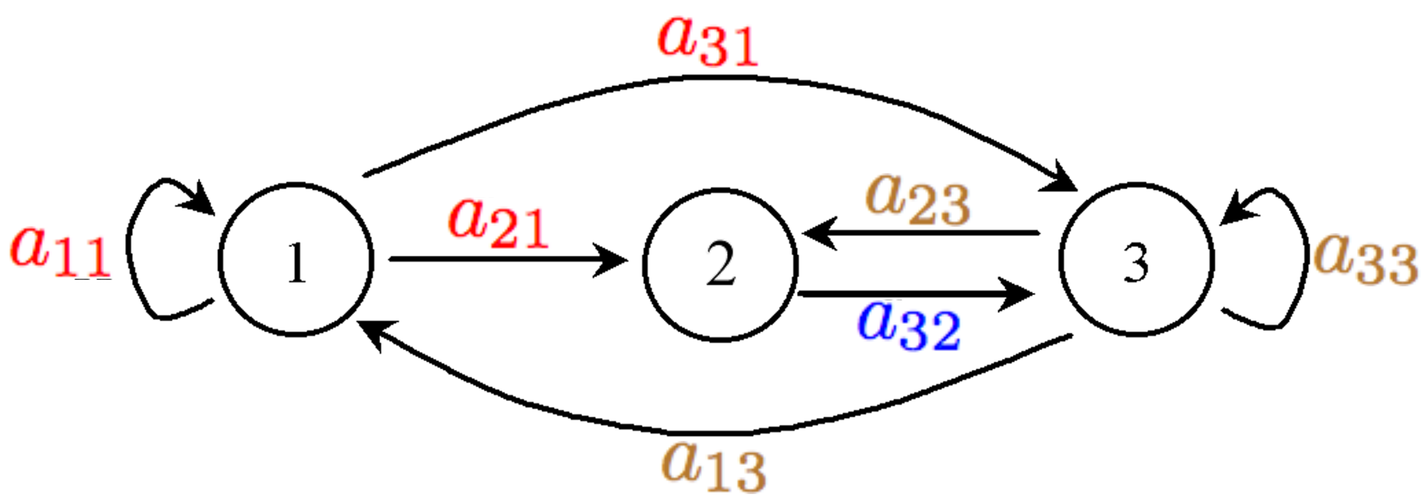
Matrix Population Models

Matrix model:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t}$$

Life cycle graph:



Asymptotic Growth Rate

- If **A** is primitive (**A**$^k > 0$ for some k) the *Perron-Frobenius* theorem ensures there is a positive and simple dominant eigenvalue with a corresponding positive eigenvector.
- This eigenvalue yields the *asymptotic growth rate* of the population and the corresponding eigenvector yields the *stable age distribution,* which the population asymptotically achieves.
- This dominant eigenvalue λ must be determined from the characteristic polynomial.

Dominant Eigenvalue

Population growth rate (λ):

Dominant eigenvalue of **A**

$$\begin{cases} \lambda < 1 & \text{decrease} \\ \lambda = 1 & \text{constant} \\ \lambda > 1 & \text{increase} \end{cases}$$

(λ_i, n_i) eigenvector-eigenvalue pair satisfy

$$An_i = \lambda_i n_i$$

There will be k such pairs for a k x k matrix. λ is the largest of these λ_i and denotes the long term geometric growth rate of the population

Caswell (2001)

Elasticity Analysis

Population growth rate (λ):

Dominant eigenvalue of **A**
$$\begin{cases} \lambda < 1 & \text{decrease} \\ \lambda = 1 & \text{constant} \\ \lambda > 1 & \text{increase} \end{cases}$$

Elasticity analysis:

Measures the relative contributions of transitions to population growth

$$\mathbf{E} = \left[\frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \right]$$

E_{ij} denotes the proportionate change in λ with respect to a proportionate change in a_{ij}.

Caswell (2001)

Demographic Analysis

Matrix models for control:

1. Determine life cycle and estimate parameters
2. Calculate population growth rate λ
3. Calculate **E** and target transitions with higher elasticities
4. Verify is control agents affect transitions with high elasticities

Scentless Chamomile

Case Study:
Scentless chamomile (*Matricaria perforata*)

- Annual, biennial or short-lived perennial
- Seed production of up to 256,000 seeds/plant
- Three distinctive life cycle stages: seeds (n_1), rosettes (n_2), and flowering plants (n_3):

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_t$$

Data collection

Case Study: Scentless chamomile (*Matricaria perforata*)

Data collected in Vegreville, AB, 2003-2005




Demographic Analysis

Case Study: Scentless chamomile (*Matricaria perforata*)

2004

$$\mathbf{A} = \begin{bmatrix} 0.08 & 0 & 36376.45 \\ 0.27 & 0 & 517 \\ 0.04 & 0.45 & 297.85 \end{bmatrix}$$

$$\lambda = 303.46$$

$$\mathbf{E} = \begin{bmatrix} 0.00041 & 0 & \mathbf{1.57} \\ 0.016 & 0 & 0.25 \\ \mathbf{1.55} & 0.26 & \mathbf{96.35} \end{bmatrix}$$

2005

$$\mathbf{A} = \begin{bmatrix} 0.08 & 0 & 1775.22 \\ 0.27 & 0 & 25.24 \\ 0.04 & 0.45 & 14.53 \end{bmatrix}$$

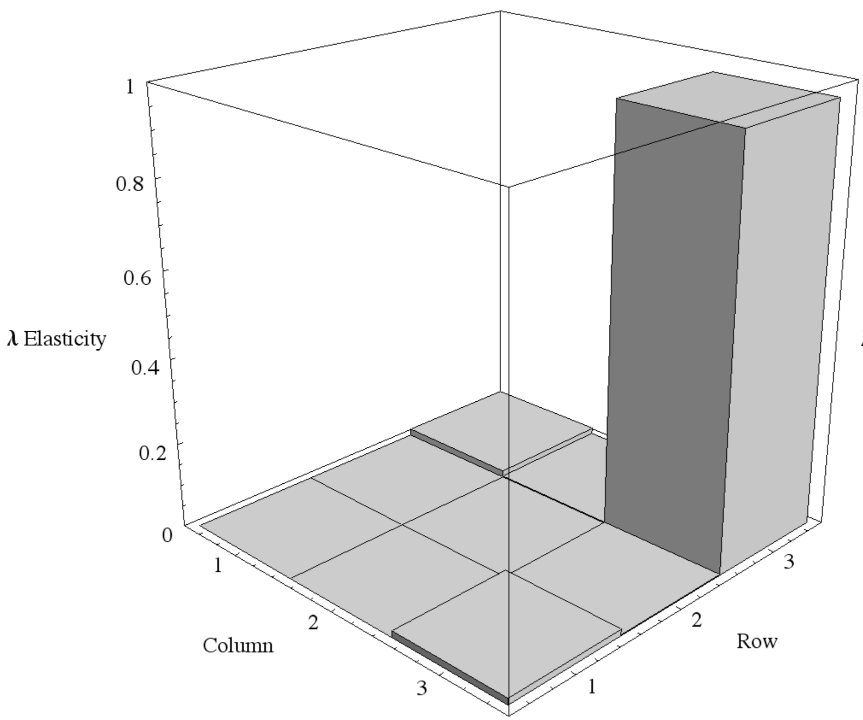
$$\lambda = 19.37$$

$$\mathbf{E} = \begin{bmatrix} 0.071 & 0 & \mathbf{17.16} \\ 2.32 & 0 & 2.36 \\ \mathbf{14.83} & 4.69 & \mathbf{58.56} \end{bmatrix}$$

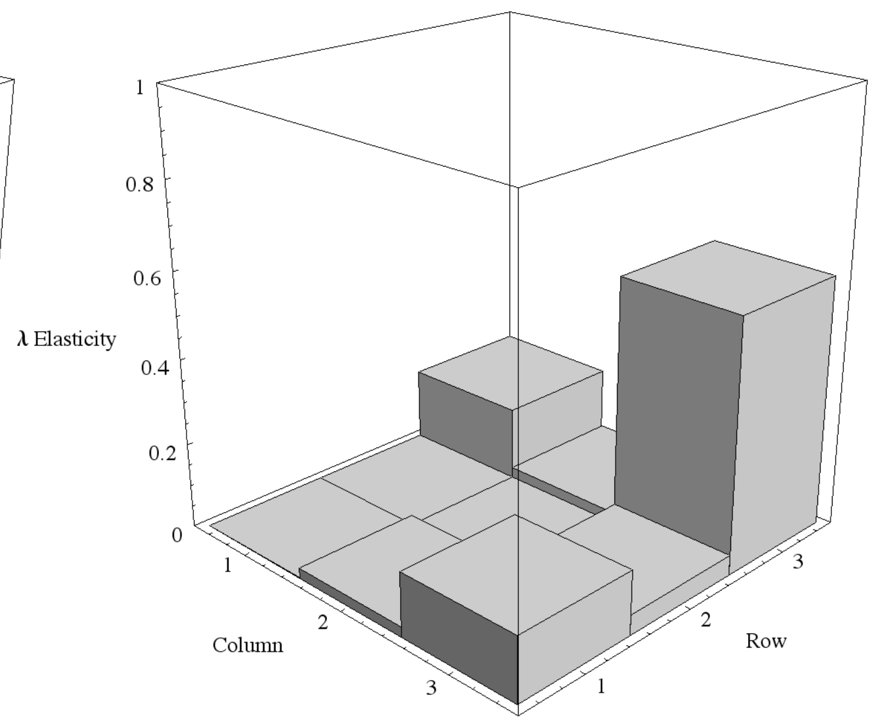
(Here the elasticities have been rescaled to add to 100.)

Control Target: flower to flower transition

Demographic Analysis—Elasticity



2004



2005

Demographic Analysis

Matrix models for control:

1. Determine life cycle and estimate parameters.
2. Calculate population growth rate λ.
3. Calculate **E** and target transitions with higher elasticities
4. Verify if control agents affect transitions with high elasticities.

Is this the best method for assessing control?

Demographic Analysis

Matrix models for control:

1. Determine life cycle and estimate parameters.
2. Calculate population growth rate λ .
3. Calculate **E** and target transitions with higher elasticities.
4. Choose control agents that affect transitions with high elasticities.

Is this the best method for assessing control?

1. There is no simple formulae for the eigenvalue λ for high order polynomials.
2. Both **E** and λ have to be calculated numerically for a particular dataset.
3. Assessment of the impacts of control is indirect.

Net Reproductive Rate

Transition and fecundity matrix:

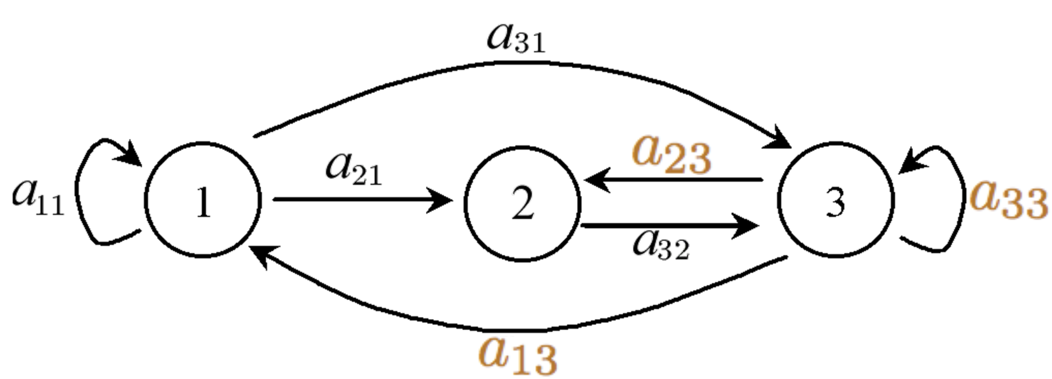
$$\mathbf{A} = \mathbf{T} + \mathbf{F} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$

$$\mathbf{T} = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}$$

Transition matrix
(Survival)

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

Fecundity matrix
(Fecundity)



Net Reproductive Rate

Next generation operator (**Q**):

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t = (\mathbf{T} + \mathbf{F})\mathbf{n}_t \qquad \rho(\mathbf{T}) < 1$$

$$\mathbf{n}_{t+gen} = \mathbf{Q}\mathbf{n}_t = (\underbrace{\mathbf{F}}_{\text{Year 1}} + \underbrace{\mathbf{F}\mathbf{T}}_{\text{Year 2}} + \underbrace{\mathbf{F}\mathbf{T}^2}_{\text{Year 3}} + \ldots)\mathbf{n}_t = \mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}\mathbf{n}_t$$

Net Reproductive rate (R_0):

This is the number of individuals that one individual produces over its lifetime. It is the largest eigenvalue of the next generation operator **Q**. The population asymptotically grows if $R_0 > 1$ and dies out if $R_0 < 1$.

$$R_0 > 1 \quad \text{if and only if} \quad \lambda > 1$$

Cushing and Yicang (1994)

Net Reproductive Rate

Transition and fecundity matrix:

$$\mathbf{T} = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}$$

Transition matrix
(Survival)

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

Fecundity matrix
(Fecundity)

$$[I-T]^{-1} = \begin{bmatrix} \dfrac{1}{1-a_{11}} & 0 & 0 \\ \dfrac{a_{21}}{1-a_{11}} & 1 & 0 \\ \dfrac{a_{32}a_{21}+a_{31}}{1-a_{11}} & a_{32} & 1 \end{bmatrix}$$

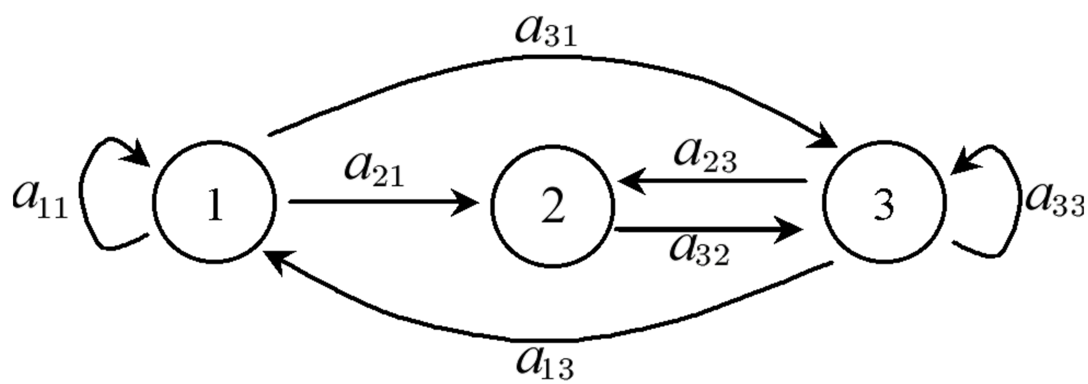
$$F[I-T]^{-1} = \begin{bmatrix} \dfrac{a_{13}(a_{32}a_{21}+a_{31})}{1-a_{11}} & a_{13}a_{32} & a_{13} \\ \dfrac{a_{23}(a_{32}a_{21}+a_{31})}{1-a_{11}} & a_{23}a_{32} & a_{23} \\ \dfrac{a_{33}(a_{32}a_{21}+a_{31})}{1-a_{11}} & a_{33}a_{32} & a_{33} \end{bmatrix}$$

$$R_0 = \frac{(a_{31}+a_{21}a_{32})a_{13}}{1-a_{11}} + a_{32}a_{23} + a_{33}$$

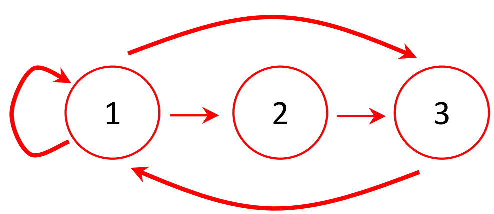
Net Reproductive Rate

Scentless chamomile:

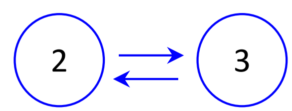
1. Seeds
2. Rosettes
3. Flowering plants



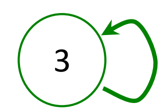
$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$



Seed
bank pathway



Rosette
pathway



Flowering plant
pathway

Calculating the Net Reproductive Rate

- Analytical formula for R_0 yields insight regarding effective control
- Is there a simple way to calculate R_0 ?
- It turns out that R_0 can be calculated directly from a graph related to the fecundity and transition matricies **F** and **T**.
- Method is based on the fact that R_0 can be defined implicitly as

$$R_0 = \rho(R_0\mathbf{T} + \mathbf{F})$$

- Then graph reduction rules are used to solve this equation.

de Camino Beck and Lewis (2006)

Characteristic Polynomial from the Graph of A

- The z-transformed graph of $\mathbf{A}$, $G_{\mathbf{A}}(\lambda)$ is defined as the graph obtained by replacing each entry by $a_{ij}\,\lambda^{-1}$
- The characteristic polynomial can be defined terms of the graph $P(G_{\mathbf{A}}(\lambda)) = \det(\mathbf{A}\,\lambda^{-1}\text{-}\mathbf{I})$

$$P(G_{\mathbf{A}}(\lambda)) = 1 - \sum_i L^{(i)} + \sum_i^{*} L^{(i)} L^{(j)} - \sum_i^{*} L^{(i)} L^{(j)} L^{(k)} + \ldots$$

  - $L^{(i)}$ is the product of arc coefficients in the i^{th} loop of $G_{\mathbf{A}}(\lambda)$
  - * indicates the sum is taken over pairs, triplets,..., n−tuples of disjoint loops

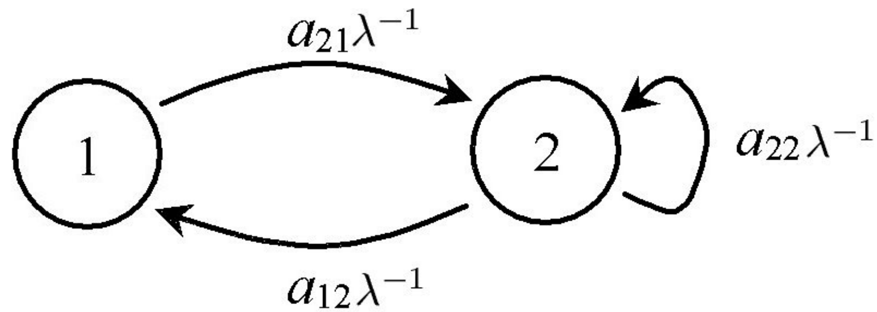
- Eigenvalues are found by solving $P(G_{\mathbf{A}}(\lambda)) = 0$ and the largest of these is $\lambda = \rho(\mathbf{A})$.

Hubbell and Werner (1979)

Mason and Zimmerman (1960)

A Simple Example

$$\mathbf{A} = \begin{bmatrix} 0 & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$



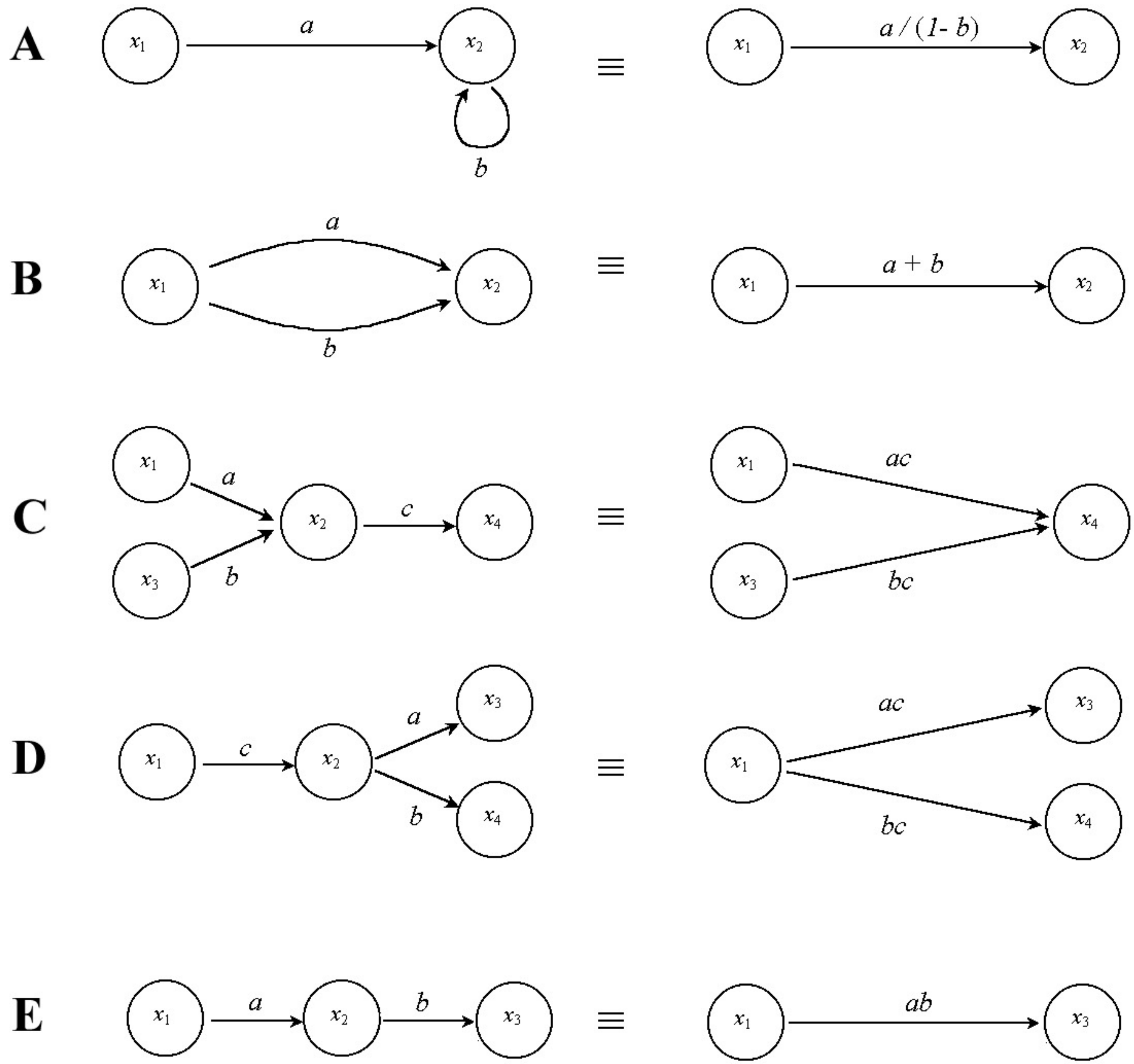
$$P(G_{\mathbf{A}}(\lambda)) = 1 - \sum_i L^{(i)} + \sum_{i,j}^{*} L^{(i)} L^{(j)} - \sum_{i,j,k}^{*} L^{(i)} L^{(j)} L^{(k)} + \ldots$$

- $L^{(i)}$ is the product of arc coefficients in the i^{th} loop of $G_{\mathbf{A}}(\lambda)$
- * indicates the sum is taken over pairs, triplets,..., n−tuples of disjoint loops

$$P(G_{\mathbf{A}}(\lambda)) = 1 - a_{22}\,\lambda^{-1} - a_{12}\,a_{21}\,\lambda^{-2}$$

Mason and Zimmerman (1960)

Graph reduction leaves polynomial unchanged



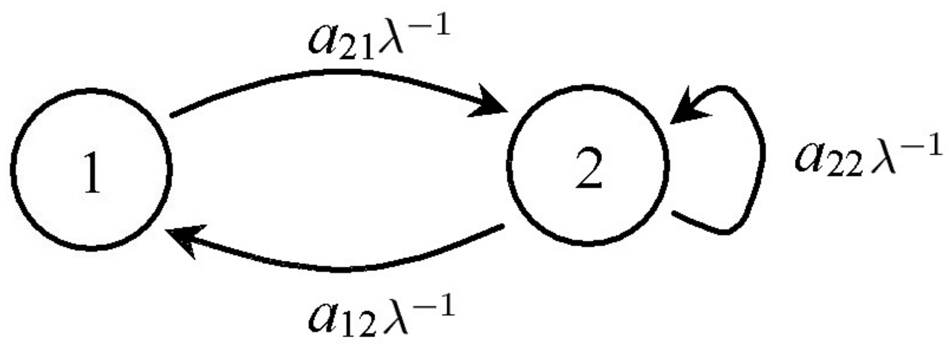
Chen (1976)

Caswell (2001)

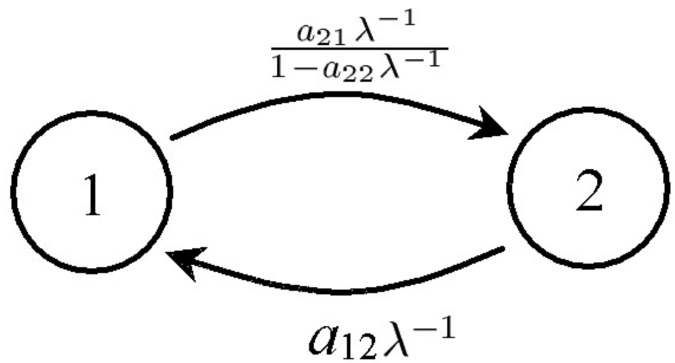
The Simple Example using Graph Reduction

$$\mathbf{A} = \begin{bmatrix} 0 & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

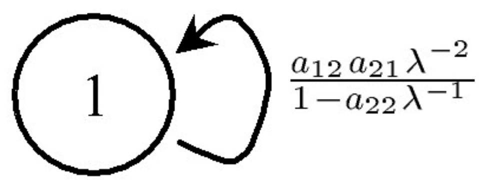
A



B



C

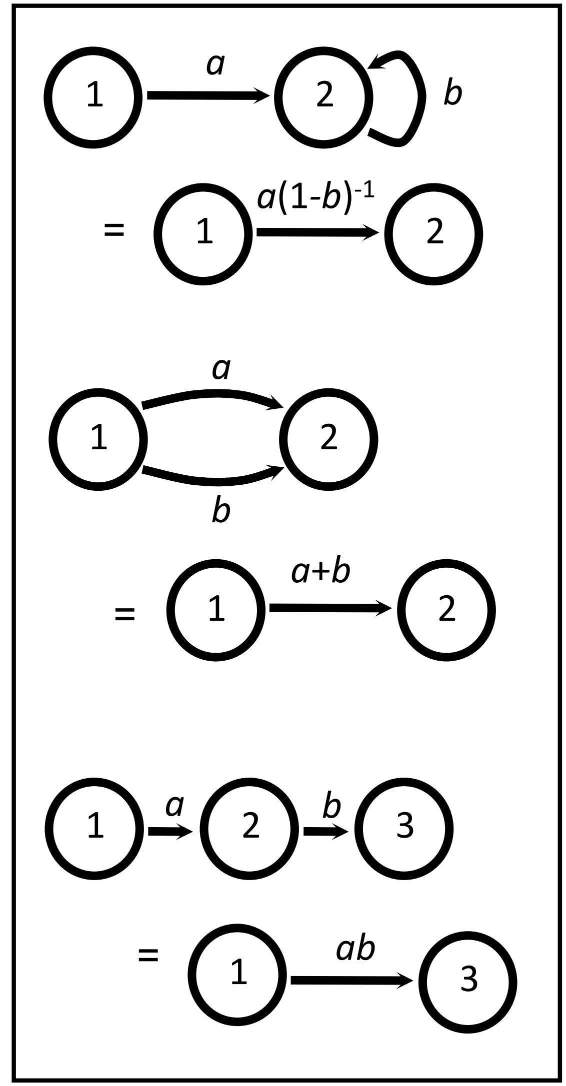


D

$$a_{21}a_{12}\lambda^{-2} + a_{22}\lambda^{-1} - 1 = 0$$

Graphical method for calculating $R_0 = \rho(R_0\mathbf{T} + \mathbf{F})$

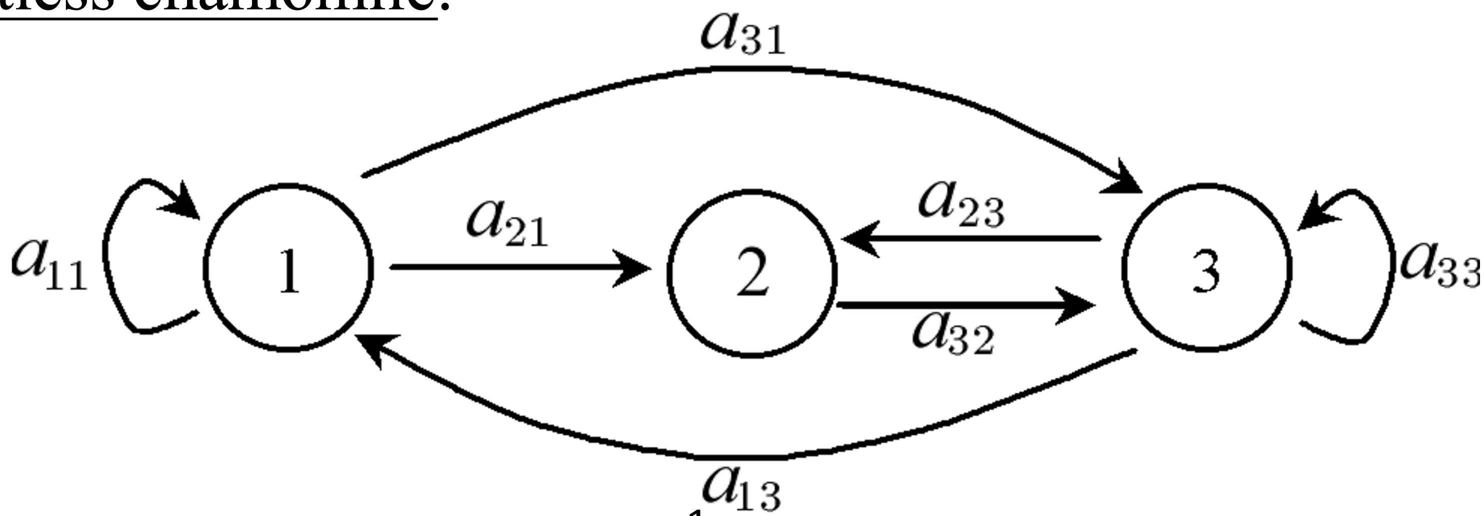
1. Create a graph of the *controlled matrix*, where the fecundities (entries of **F**) are multiplied by R_0^{-1}
2. Reduce graph to a single node, using Mason's graph reduction rules.
3. Set the weight for the final node equal to 1 and solve for R_0



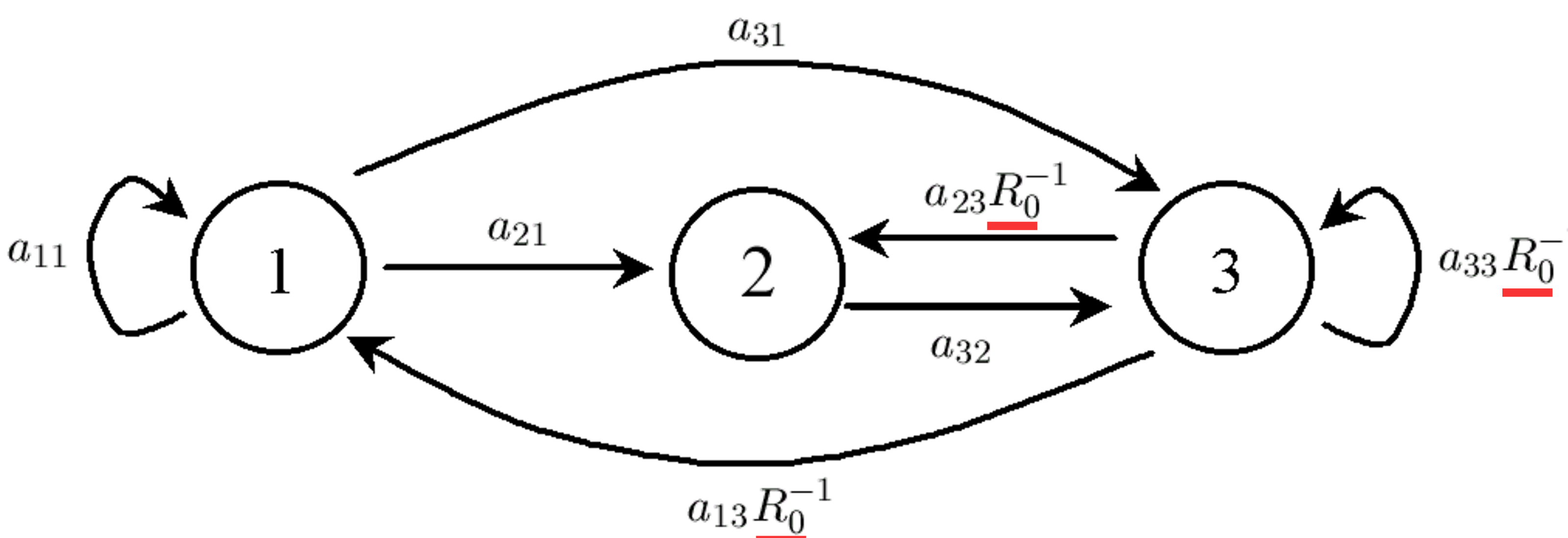
De Camino Beck and Lewis (2006)

$$\mathbf{T} = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}, \text{ and } \mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

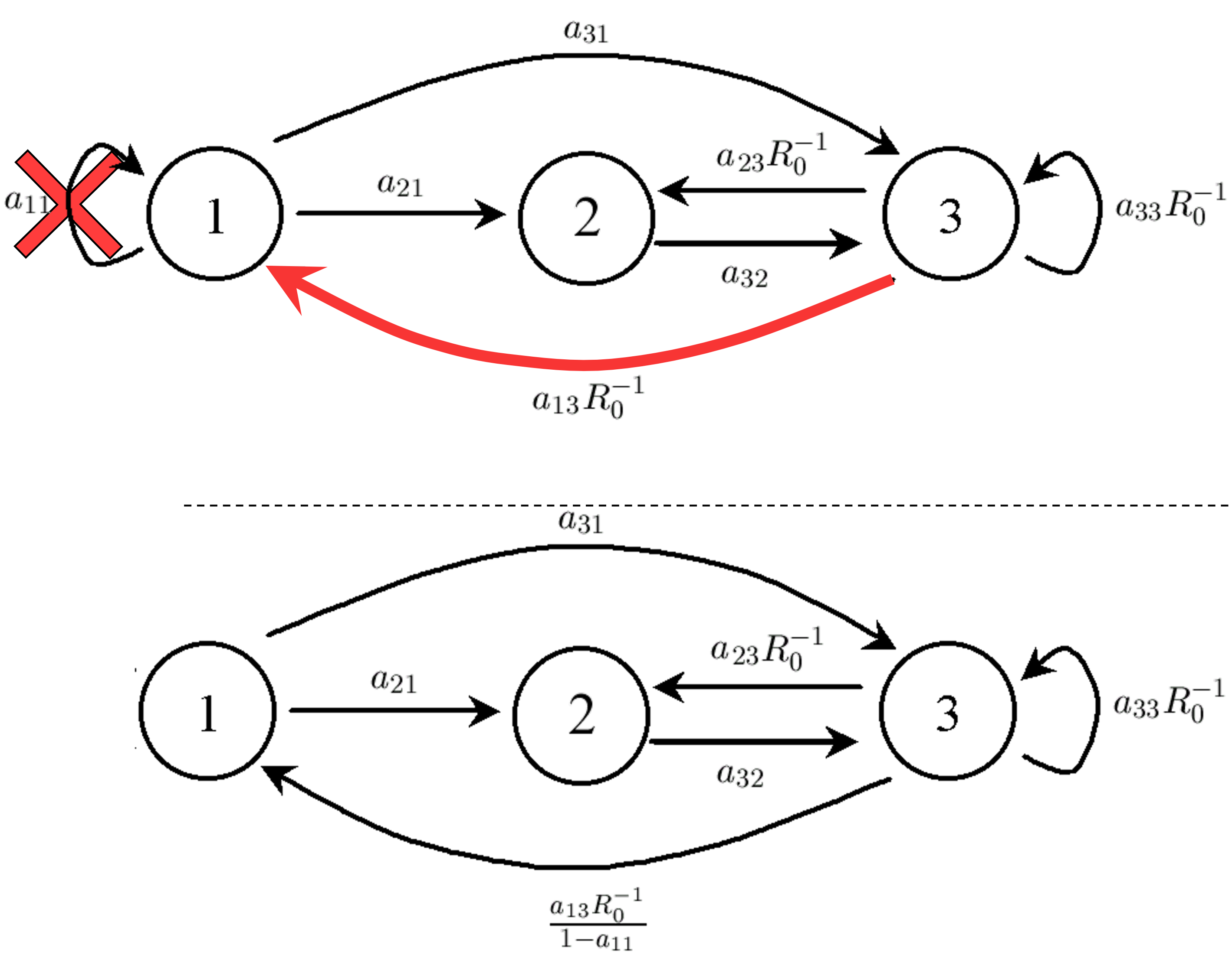
Scentless chamomile:

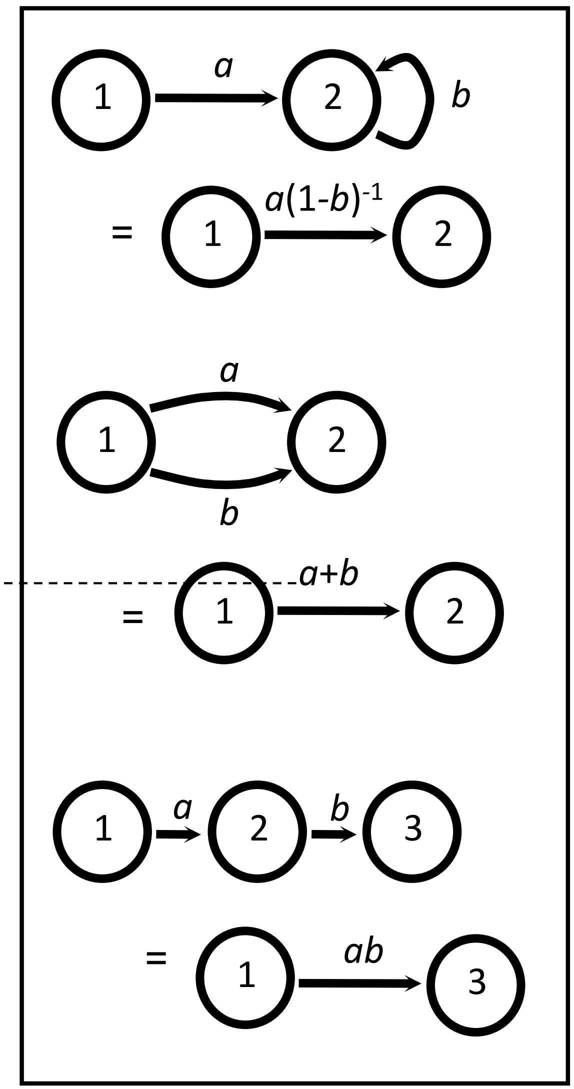


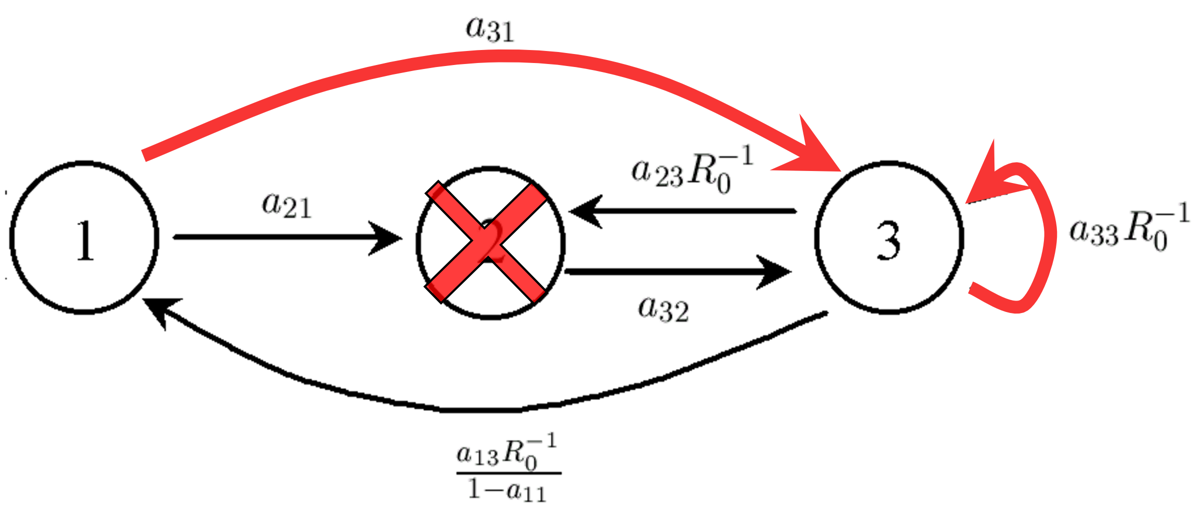
1. Multiply fecundities by R_0^{-1}



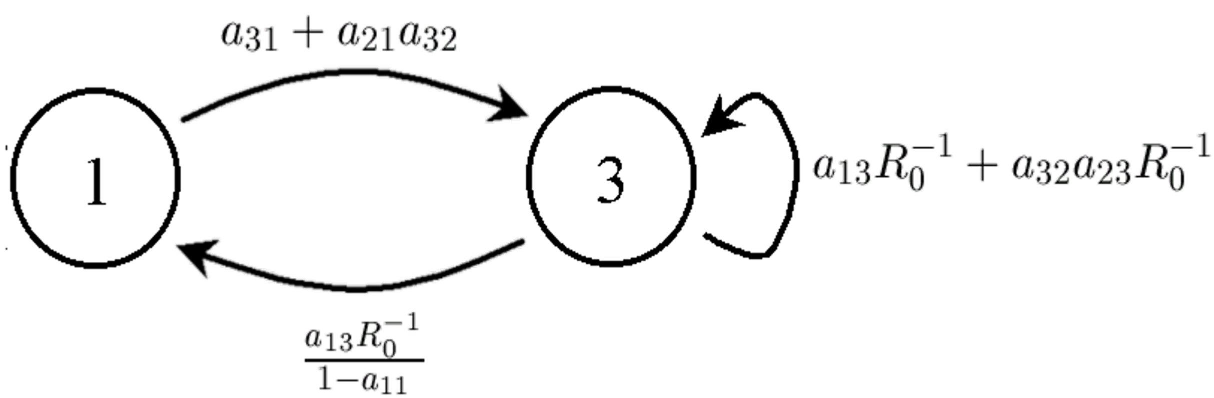
2. Reduce graph

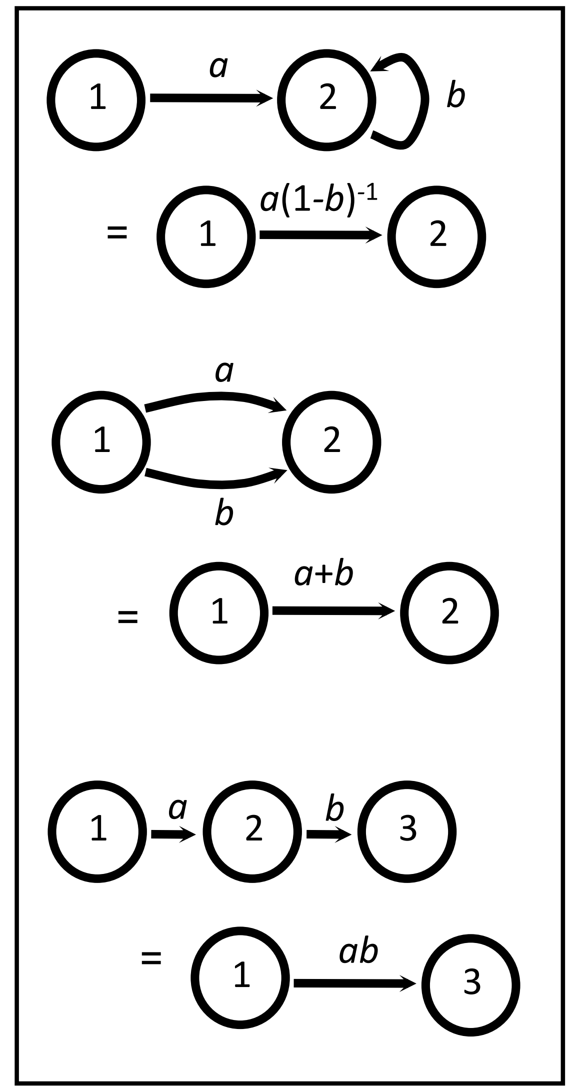




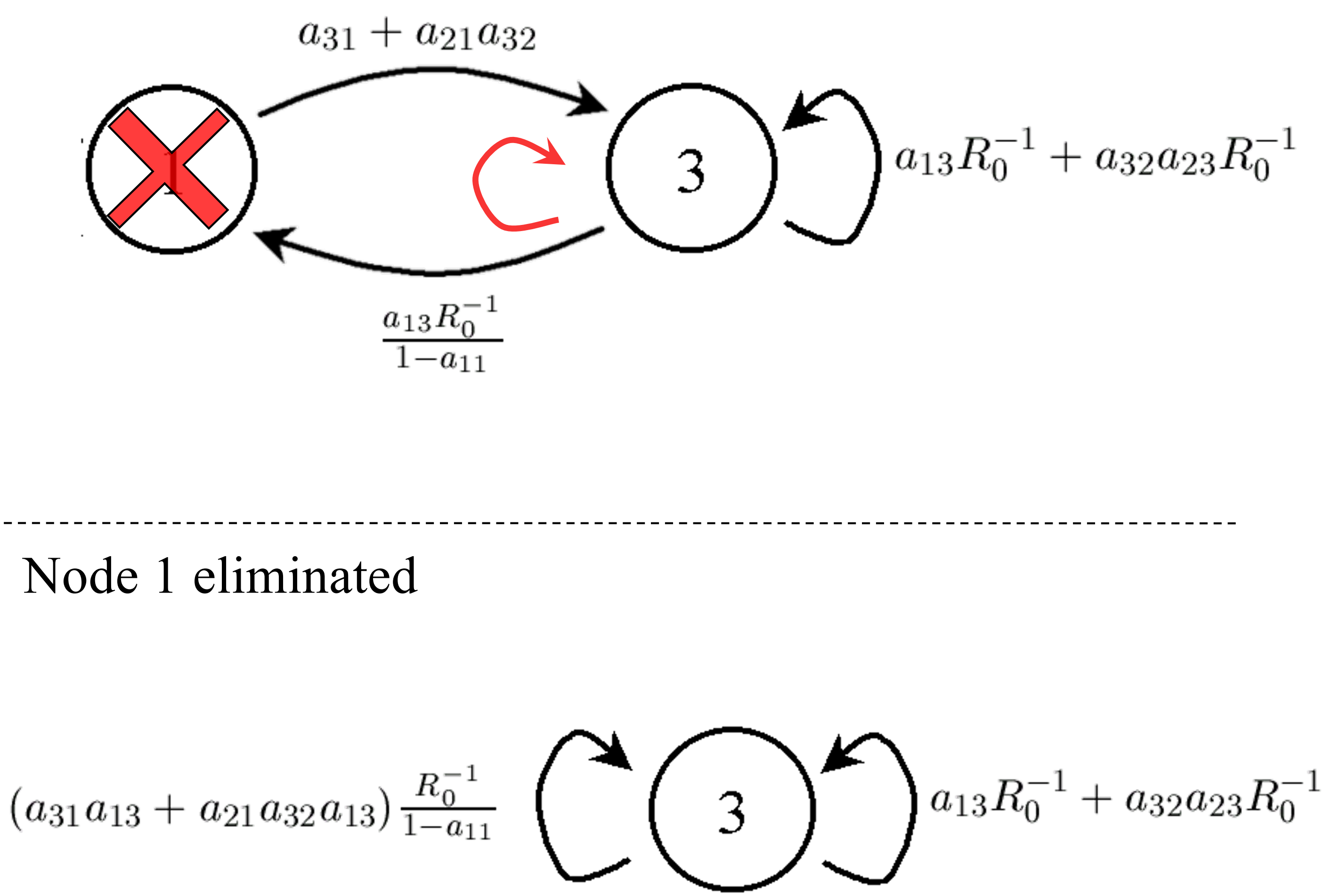


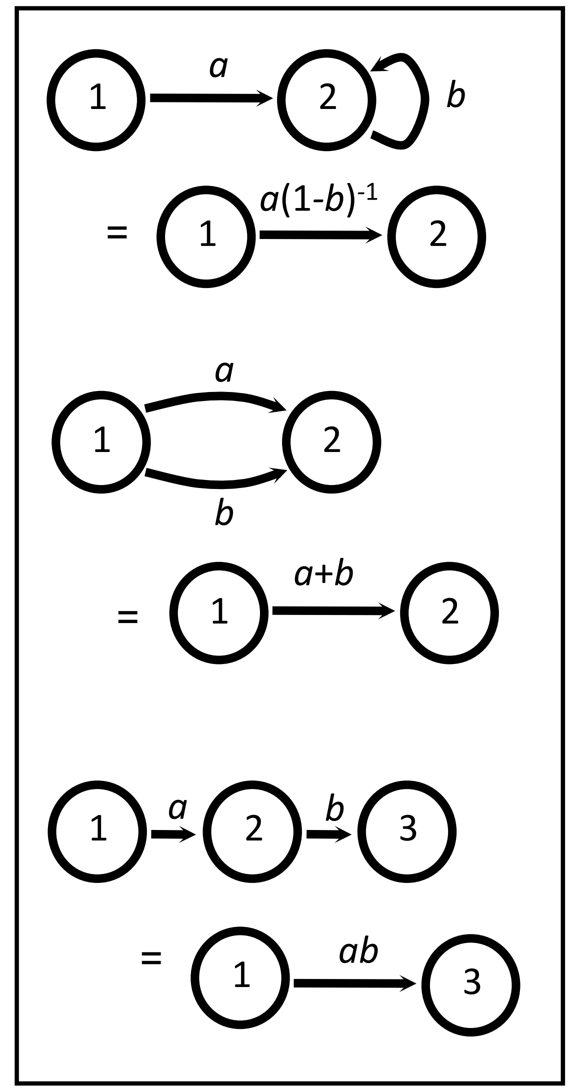
Node 2 eliminated





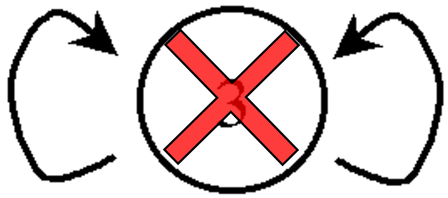
Mason's rules





Mason's rules

Set the final node equal to 1 and solve for R_0



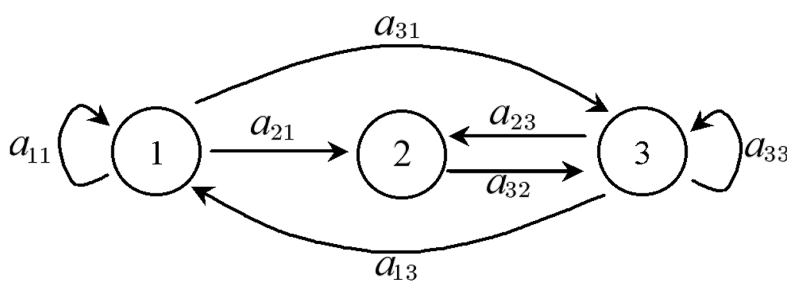
$$R_0 = \frac{(a_{31} + a_{21}a_{32})a_{13}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

Back to the control of scentless chamomile

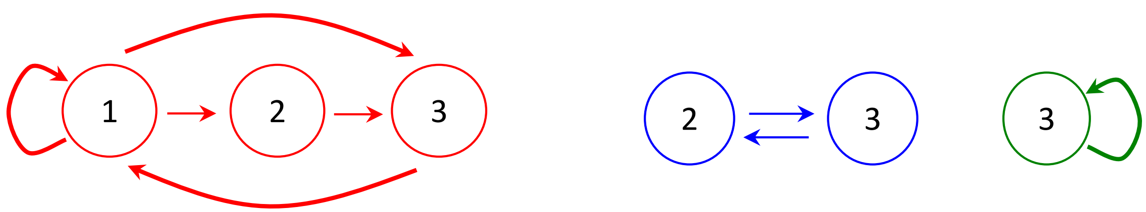
Scentless chamomile:

2004	2005
$R_0 = 6385.65 + 232.74 + 297.85$	$R_0 = 311.63 + 11.36 + 14.53$

1. Seeds
2. Rosettes
3. Flowering plants



$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$



Seed bank pathway

Rosette pathway

Flowering plant pathway

Back to the control of scentless chamomile

Scentless chamomile:

2004

$$R_0 = 6385.65 + 232.74 + 297.85$$

2005

$$R_0 = 311.63 + 11.36 + 14.53$$

$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

Seed bank pathway

Rosette pathway

Flowering plant pathway

Control Agents:

□ Seed Weevil (*Omphalapion* (Apion) *hookeri*)

□ Gall midge (*Rhopalomyia sp.*)

Tomas de Camino Beck (*Grad* (Mathbio) *studenticus*)

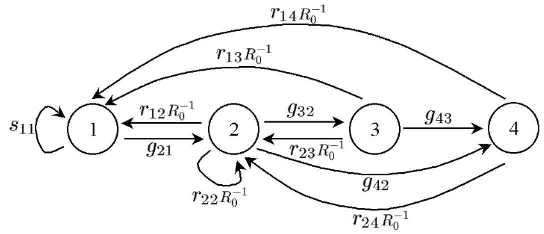
Mechanical control (removal of seed head and destruction of stems) used to simulate control agents and validate model

Back to the control of scentless chamomile

1. It is not possible to control scentless chamomile by reducing growth alone.
2. It is possible to control via reduced fecundity or a mixed strategy
3. However, the biocontrol agents are not sufficiently effective to completely control because of very high fecundity.
4. Both of these biocontrol agents (seed weevil and gall midge) have now been released in Alberta.

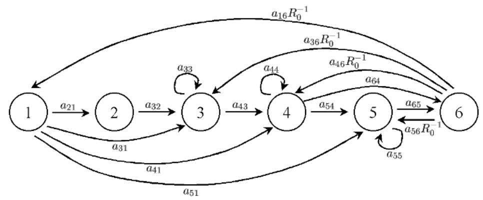
Net Reproductive Rate

Nodding thistle
(*Carduus nutans*)



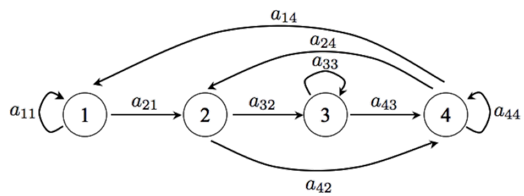
$$R_0 = r_{22} + g_{42}r_{24} + g_{32}r_{23} + g_{32}g_{43}r_{24} + \frac{g_{21}r_{12} + g_{21}g_{32}r_{13} + g_{21}g_{42}r_{14} + g_{32}g_{43}g_{21}r_{14}}{1 - s_{11}}$$

Common teasel
(*Dypsacus sylvestris*)



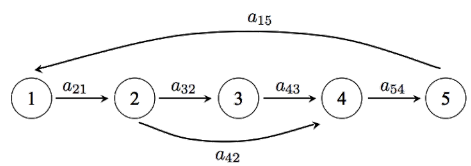
$$R_0 = a_{16}\alpha_1 + \alpha_2$$

Tansy ragwort
(*Senecio jacobaea*)



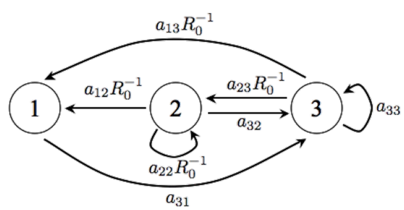
$$R_0 = \left[\frac{a_{21}a_{14}}{1 - a_{11}} + a_{24}\right]\left[\frac{a_{32}a_{43}}{(1 - a_{33})(1 - a_{44})} + \frac{a_{42}}{(1 - a_{44})}\right].$$

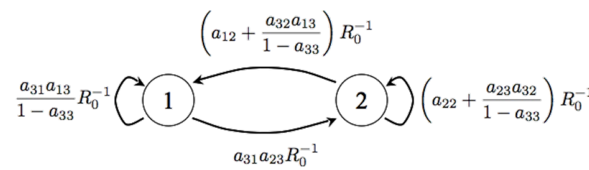
Bullfrog
(*Rana catesbeiana*)



$$R_0 = a_{12}a_{42}a_{54}a_{15} + a_{21}a_{32}a_{43}a_{54}$$

Common cat's ear
(*Hypochaeris radicata*)



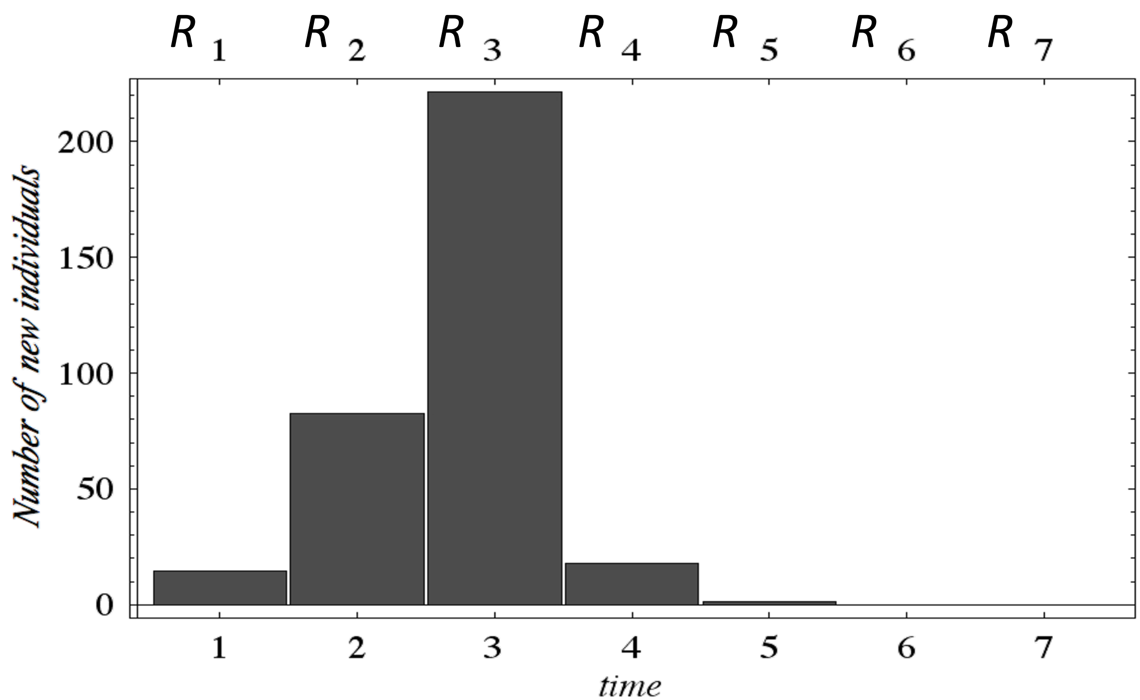


Generation Time

Explicit R_0 formulae can be used to determine when the new offspring are produced (fecundity profile)

Relates to Cole (1954):

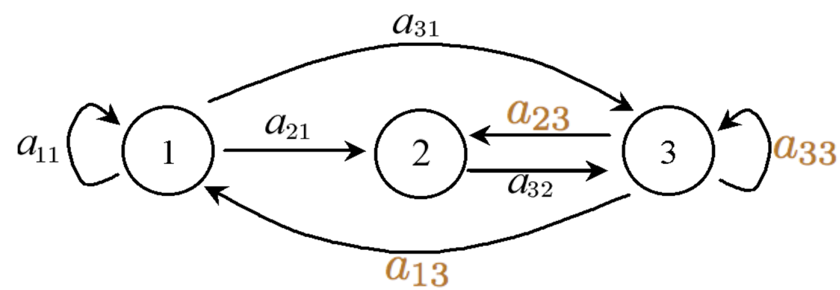
Effect of life history traits on population growth and Generation-Law method



De Camino Beck and Lewis (2007)

Generation Time

Number of new individuals:



$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

R_0 generating function

$$R(T) = \frac{a_{31}a_{13}T^2 + a_{13}a_{21}a_{32}T^3}{1 - a_{11}T} + a_{32}a_{23}T^2 + a_{33}T$$

$$= R_1 T + R_2 T^2 + \ldots$$

$$R_0 = R(1) = R_1 + R_2 + \ldots$$

$$R_1 = R'(0)$$

$$R_2 = R''(0)/2$$

$$\vdots$$

From this it is possible to calculate mean generation time $\bar{T}$ and generation time variance $\mathrm{Var}[T]$

Conclusions

- Our focus is on structured population models which can be described by a model with a nonnegative matrix which is a primitive.
- We have only considered linear models, although it is reasonable to make this assumption when population levels are low (relevant to endangered species or initial stages of an invasion).
- Eigenvalue analysis and sensitivity analysis are the classical approaches for modelling asymptotic population growth.
- R_0 provides a convenient and transparent formula describing life-time contribution of offspring by a single individual, particularly when life-cycle details are complex.
- A straightforward graph reduction method can be used to calculate R_0.
- The methods can be applied to give insight about the generation time and fecundity profile.

R_0 versus a target reproduction number

R_0 provides an easier method for assessing whether growth occurs

As with λ we still need to calculate an eigenvalue, now of the next generation operator $\mathbf{Q}$

However, this eigenvalue R_0 typically be written down easily and explicitly and yields insight into factors driving growth

How do we address the problem of targeted control agents?

It turns out that the idea of R_0 can be generalized to deal specifically with targeted control to give a *target reproduction number*.

Biocontrol agents

Scentless chamomile:

$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

Seed bank pathway | Rosette pathway | Flowering plant pathway

Control Agents:

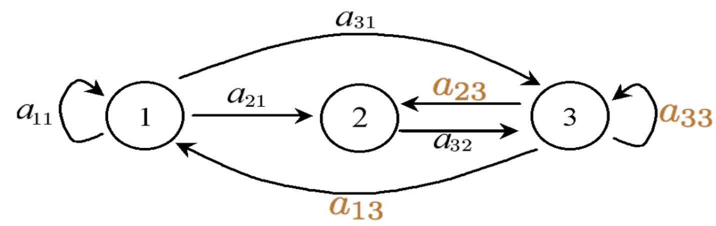
- Seed Weevil (*Omphalapion* (Apion) *hookeri*)

- Gall midge (*Rhopalomyia sp.*)

How much does the seed weevil need to reduce seed production in order to control the weed?

Target reproduction number for fecundity

Effect of seed weevil:



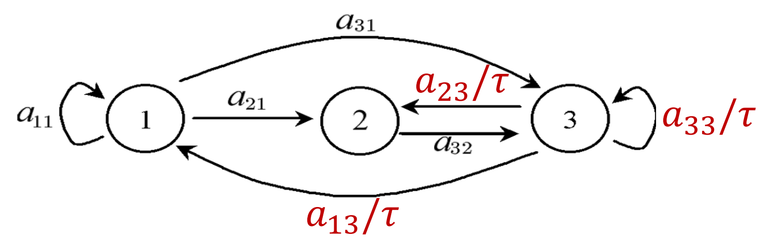
$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}\, a_{23} + a_{33}$$

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

- The seed weevil would control the population by reducing fecundity **F**.
- Suppose we want to target fecundity by rescaling it by factor $1/\tau$ so as to control population growth. What value should τ at least be?

$$1 = \frac{a_{31}a_{13}/\tau + a_{13}/\tau\, a_{21}a_{32}}{1 - a_{11}} + a_{32}\, a_{23}/\tau + a_{33}/\tau$$

$$\Longrightarrow \tau = R_0$$



- To control the population, we need $\tau \geq \tau_F = R_0$.
- $\tau_F = R_0$ can be thought of as the *target reproduction number* that is needed to rescale fecundity sufficiently to control the population.

Target reproduction number for growth

Scentless chamomile:

$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

Seed bank pathway | Rosette pathway | Flowering plant pathway

Control Agents:

- ☐ Seed Weevil (*Omphalapion* (Apion) *hookeri*)
- ☐ Gall midge (*Rhopalomyia sp.*)

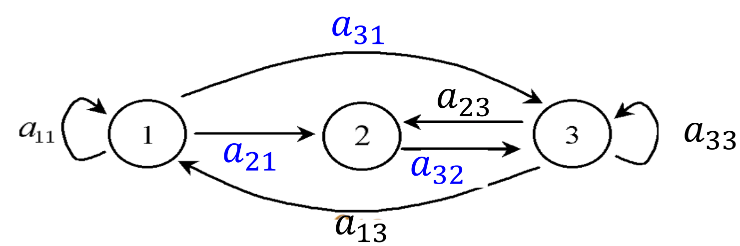
What if we were to try to control the population by rescaling growth (via the gall midge)?

Can we come up with a *target reproduction number* for growth?

Target reproduction number for growth

Transition and fecundity matrix:

$$\mathbf{A} = \mathbf{B} + \mathbf{C} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$



$$\mathbf{B} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

Residual matrix

$$\mathbf{C} = \begin{bmatrix} 0 & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}$$

Target matrix

require $\rho(\mathbf{B}) < 1$ for controllability

Target reproduction number theory

Definition: For $\mathbf{A}$, $\mathbf{B}$, $\mathbf{C}$, nonnegative matricies such that $\mathbf{A} = \mathbf{B} + \mathbf{C}$ is irreducible, $\mathbf{C} \neq \mathbf{0}$ and $\rho(\mathbf{B}) < 1$, τ_{C} is defined as

$$\tau_{\mathrm{C}} = \rho\left(\mathbf{C}(\mathbf{I} - \mathbf{B})^{-1}\right).$$

(Note: if $\mathbf{C} = \mathbf{A}$ then $\tau_{\mathrm{C}} = \lambda$. If $\mathbf{B} = \mathbf{T}$ (transition) and $\mathbf{C} = \mathbf{F}$ (fecundity) then $\tau_{\mathrm{C}} = R_0$.)

Theorem 1: Let $\mathbf{A}_C(\tau) = \mathbf{B} + \frac{1}{\tau}\mathbf{C}$ be the *controlled matrix*. Then $\rho\left(\mathbf{A}_C(\tau)\right) = 1$ if and only if $\tau = \tau_{\mathrm{C}}$. (This yields the practical method for calculating τ_{C}.)

Theorem 2:

(1) $\rho(\mathbf{A}) > 1$ iff $\tau_{\mathrm{C}} > 1$;
(2) $\rho(\mathbf{A}) = 1$ iff $\tau_{\mathrm{C}} = 1$;
(3) $\rho(\mathbf{A}) < 1$ iff $\tau_{\mathrm{C}} < 1$.

Interpretation:

(1) a growing population has a target reproduction number greater than 1
 (entries of C must be shrunk if the population is to be controlled, e.g. weed);
(2) a stationary population has a target reproduction number equal to 1;
(3) a shrinking population has a target reproduction number less than 1
 (entries of C must be made larger if the population is to grow, e.g. at risk pop'n).

Target reproduction number for growth

Transition and fecundity matrix:

$$\mathbf{A} = \mathbf{B} + \mathbf{C} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$

$$\mathbf{B} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

Residual matrix

$$\mathbf{C} = \begin{bmatrix} 0 & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}$$

Target matrix

Let $\mathbf{A}_C(\sigma) = \mathbf{B} + \frac{1}{\sigma}\mathbf{C}$ be the controlled matrix. Then

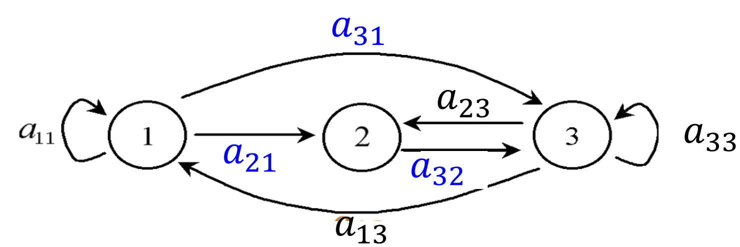
$$\mathbf{A}_C(\sigma) = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21}/\sigma & 0 & a_{23} \\ a_{31}/\sigma & a_{32}/\sigma & a_{33} \end{bmatrix},$$

and σ_C is found by (1) solving $\rho\big(\mathbf{A}_C(\sigma)\big) = 1$ (by Theorem 1) or, (2)alternatively,

$$\sigma_C = \rho\big(\mathbf{C}(\mathbf{I} - \mathbf{B})^{-1}\big).$$

Target reproduction number for growth

$$\mathbf{A}_C(\sigma) = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21}/\sigma & 0 & a_{23} \\ a_{31}/\sigma & a_{32}/\sigma & a_{33} \end{bmatrix},$$



(1) Solving $\rho\big(\mathbf{A}_C(\sigma)\big)=1$ for σ_C yields

$$1 = \frac{\boxed{a_{31}/\sigma}\, a_{13} + a_{13}\boxed{a_{21}/\sigma}\,\boxed{a_{32}/\sigma}}{1-a_{11}} + \boxed{a_{32}/\sigma}\, a_{23} + a_{33},$$

or equivalently

$$1 = \frac{a_{13}a_{21}\,a_{32}}{1-a_{11}}\,\sigma^{-2} + \left(\frac{a_{31}\,a_{13}}{1-a_{11}} + a_{32}\,a_{23}\right)\sigma^{-1} + a_{33}.$$

σ_C is the real root to this polynomial equation. (We know there is only one by Theorem 1.)

We know that $\sigma_C > 1$ providing $\rho(\mathbf{A}) > 1$ by Theorem 2.

(2) Alternatively, we calculate $\mathbf{C}(\mathbf{I}-\mathbf{B})^{-1} = \begin{bmatrix} 0 & \dfrac{a_{13}\,a_{21}}{(1-a_{11})(1-a_{33})} \\ a_{32} & \dfrac{a_{13}\,a_{31}}{(1-a_{11})(1-a_{33})} + \dfrac{a_{23}\,a_{32}}{(1-a_{33})} \end{bmatrix}$

Which gives the same characteristic polynomial for σ_C.

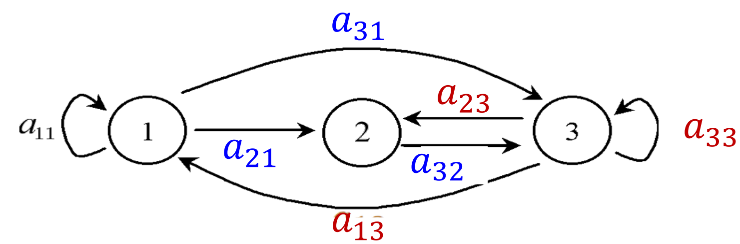
Steps to determine a target reproduction number

1. Break down the population projection matrix $\mathbf{A}$ into a nonnegative target matrix $\mathbf{C}$ and a nonnegative residual matrix $\mathbf{B}$ such that $\mathbf{C} \neq \mathbf{0}$. Ensure that $\rho(\mathbf{B}) < 1$ so as to be able to control the system.
2. Let $\mathbf{A}_C(\tau) = \mathbf{B} + \frac{1}{\tau}\mathbf{C}$ be the *controlled matrix*. This system can be controlled (τ can be found such that $\rho\big(\mathbf{A}_C(\tau)\big) = 1$) so long as $\rho(\mathbf{B}) < 1$.
3. Set $\rho\big(\mathbf{A}_C(\tau)\big) = 1$ to get a polynomial in τ.
4. Solve for τ_C over the real numbers to get the target reproduction number.
5. This determines the level of control τ needed to stabilize the population (so that $\rho\big(\mathbf{A}_C(\tau_C)\big) = 1$).

<u>Note 1</u>: If the original population was growing, then $\tau_C > 1$ and, if the original population was shrinking, then $\tau_C < 1$.
<u>Note 2</u>: If $\mathbf{B}$ is the transition matrix and $\mathbf{C}$ is the fecundity matrix then the above method determines the net reproductive rate R_0. (This is also referred to as the basic reproduction number.)
<u>Note 3</u>: If you have an expression for R_0 then steps 2 and 3 can be replaced by setting R_0 =1 in that expression and then rescaling elements of $\mathbf{C}$ by τ.

Target reproduction with two controls

$$\mathbf{A}_C(\sigma) = \begin{bmatrix} a_{11} & 0 & a_{13}/\tau \\ a_{21}/\sigma & 0 & a_{23}/\tau \\ a_{31}/\sigma & a_{32}/\sigma & a_{33}/\tau \end{bmatrix},$$



We assume that the cost of control is $\mathrm{D}(\tau,\sigma) = d_1(\tau - 1) + d_2\,(\sigma - 1)$ and look for the least cost solution

Solving $\rho\big(\mathbf{A}_C(\sigma,\tau)\big)$=1 for σ_C yields

$$1 = \frac{a_{31}/\sigma\; a_{13}/\tau + a_{13}/\tau\; a_{21}/\sigma\; a_{32}/\sigma}{1-a_{11}} + a_{32}/\sigma\; a_{23}/\tau + a_{33}/\tau,$$

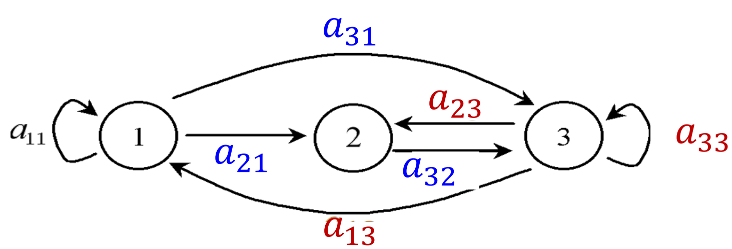
or equivalently

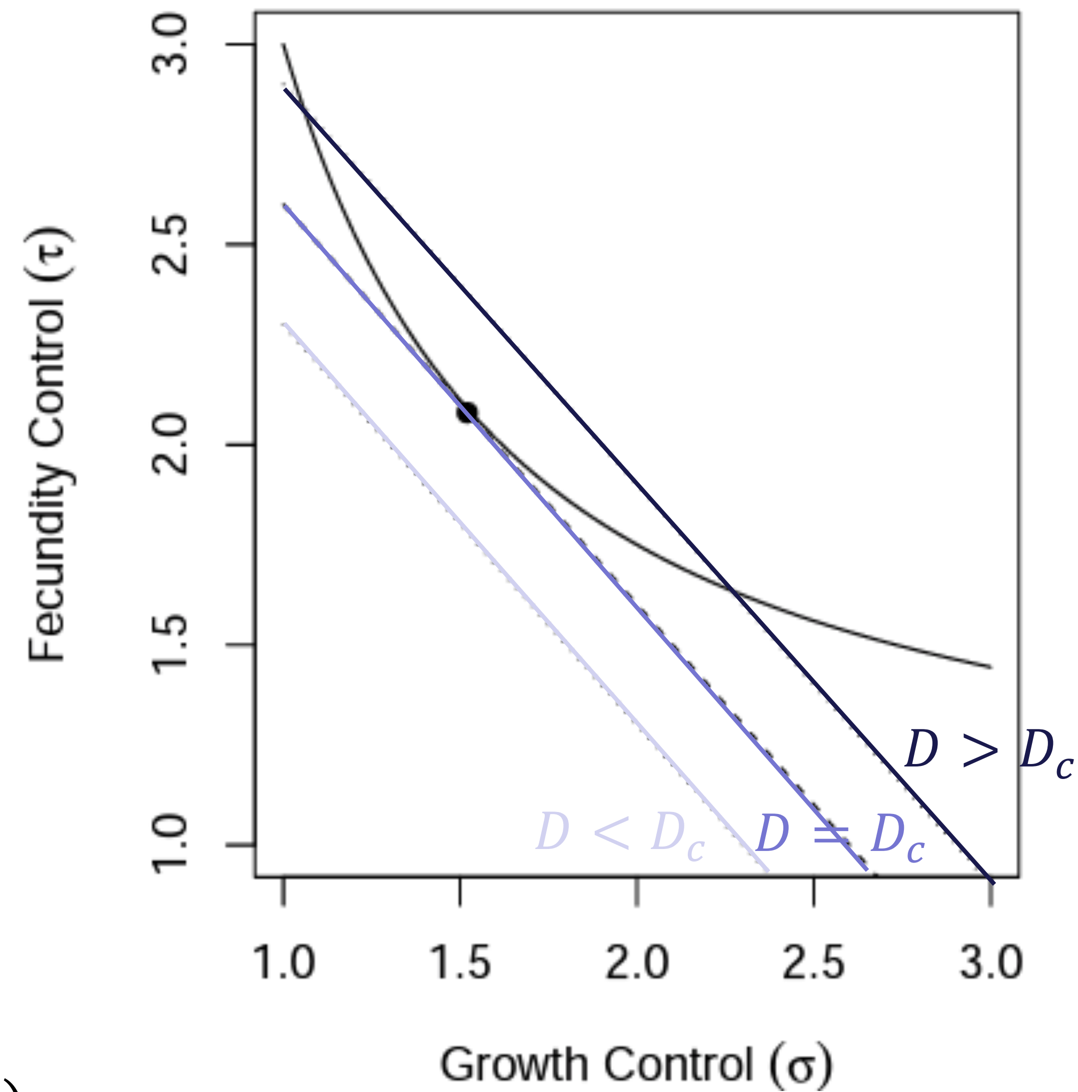
$$\tau = \frac{a_{13}a_{21}\,a_{32}}{1-a_{11}}\,\sigma^{-2} + \left(\frac{a_{31}\,a_{13}}{1-a_{11}} + a_{32}\,a_{23}\right)\sigma^{-1} + a_{33}.$$

Parameters for control of fecundity (τ) and growth (σ)are given by a curve in $\tau - \sigma$ space.

Target reproduction with two controls

$$\mathbf{A}_C(\sigma) = \begin{bmatrix} a_{11} & 0 & a_{13}/\tau \\ a_{21}/\sigma & 0 & a_{23}/\tau \\ a_{31}/\sigma & a_{32}/\sigma & a_{33}/\tau \end{bmatrix}$$





$$\mathrm{D}(\tau, \sigma) = d_1(\tau - 1) + d_2\,(\sigma - 1)$$

$$\tau = \frac{a_{13}a_{21}\,a_{32}}{1-a_{11}}\,\sigma^{-2} + \left(\frac{a_{31}\,a_{13}}{1-a_{11}} + a_{32}\,a_{23}\right)\sigma^{-1} + a_{33}.$$