

Matrix Models

EFB 370: Population Ecology

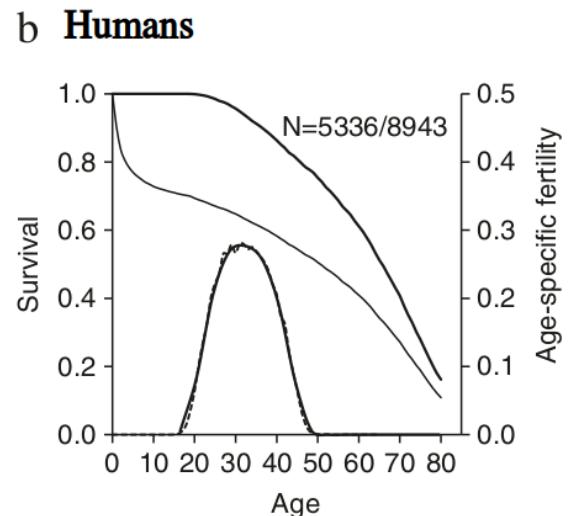
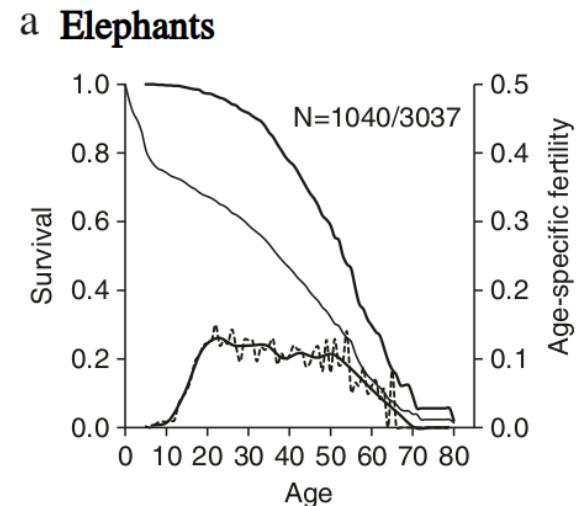
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Quick recap of last lecture

1. Survival and Fecundity vary with age / class / stage
2. Life history tables organize that variability:
 - age distribution $S(x)$
 - survival schedule $l(x)$
 - birth schedule $b(x)$
3. With those schedules we can compute:
 - Growth rate r
 - Generation time G
 - Stable age distribution N^*
 - Reproductive value v_x (*But the calculations are fussy!*)
4. Different schedules point to different life history strategies



Estimating Life Histories: Cohort Life Table

Follow a cohort (or cohorts) through time.

Track survival. Track age at birth.

Minus:

- Can take a really long time!

Plus:

- Population always decreasing!

Age	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr 7
0	<u>1000</u>	1005	1010	995	1007	990	1002
1	800	<u>801</u>	799	789	810	805	802
2	600	598	<u>601</u>	609	601	595	603
3	400	406	403	<u>401</u>	390	399	400
4	200	202	202	196	<u>205</u>	198	199
5	100	105	101	103	99	<u>96</u>	97

Estimating Life Histories: Vertical Life Table

Take a snapshot of the age distribution and build survival schedule

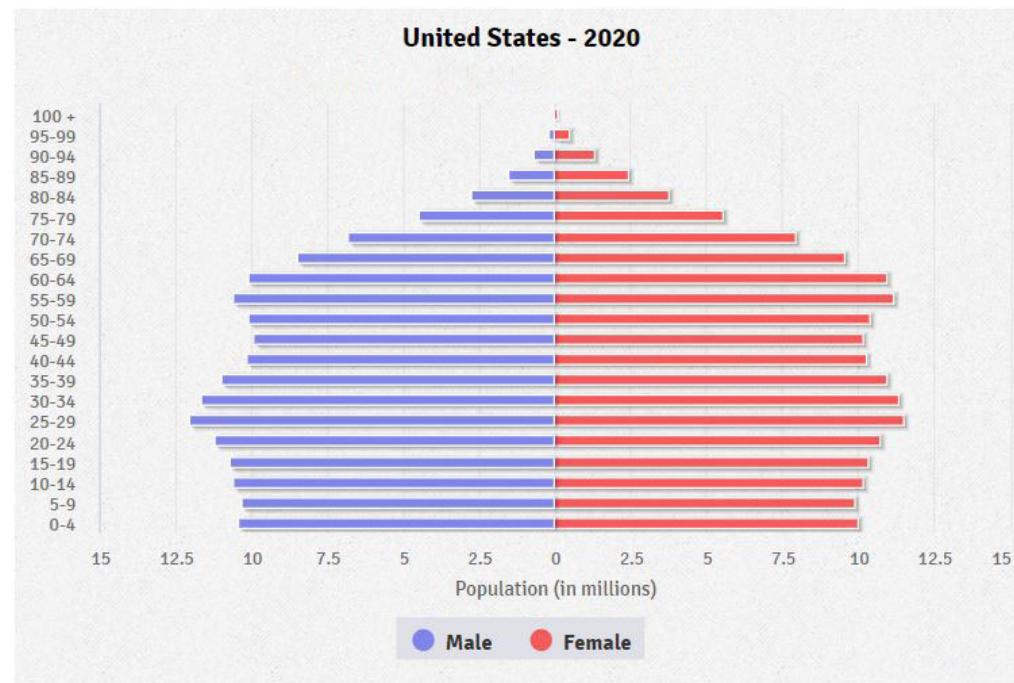
Strong assumptions:

- $r = 0$ or $\lambda = 1$
- processes (birth and survival schedules) are **stationary**, meaning *parameters* don't change over time.
- Of course - you also need to know **birth schedule**.

Age	Yr 1	Yr 2	Yr 3	Yr 4	Yr 5	Yr 6	Yr 7
0	1000	1005	<u>1010</u>	995	1007	990	1002
1	800	801	<u>799</u>	789	810	805	802
2	600	598	<u>601</u>	609	601	595	603
3	400	406	<u>403</u>	401	390	399	400
4	200	202	<u>202</u>	196	205	198	199
5	100	105	<u>101</u>	103	99	96	97

Do these assumptions hold?

US population pyramid - 2020



Life history strategies: *r*-selected, vs. *K*-selected species

For a long time a popular **paradigm** (conceptual model purporting to explain a wide range of phenomenon) for understanding evolutionary drivers of life-history variation. Still popularly taught:



r-selected species

strategy:

- lots of offspring
- little or no parental investment
- semelparous
- early maturity
- Type III survivorship
- low survivorship
- short life-expectancy

drivers:

- small size
- unstable / unpredictable environments

consequence

- highly fluctuating populations



K-selected species

strategy:

- few offspring
- lots of parental investment
- high survivorship
- late maturity
- iteroparous
- long life-expectancy
- Type I survivorship schedule

drivers:

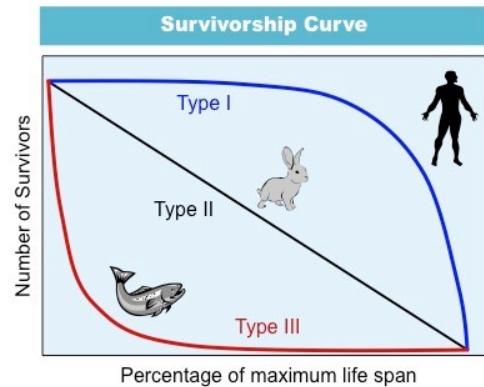
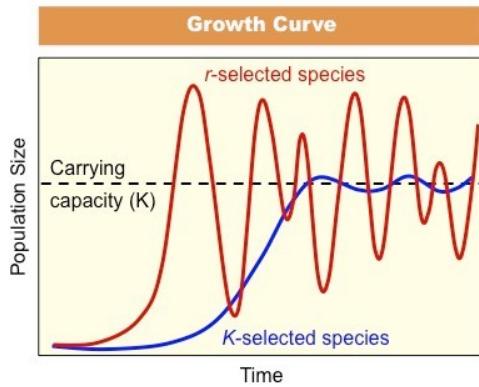
- stable environments
- large

consequence

- more stable / slowly-fluctuating populations

Nice theory you've got there, but lots of counter-examples

- What about **trees**? They're big, they're long-lived (very **K**), but they produce and disperse a **heckload** of seeds (very, very **r**).



- What about **iteroparous** species (**K**) that are hedging their bets against high inter-annual variation in environmental conditions (very **r**)?

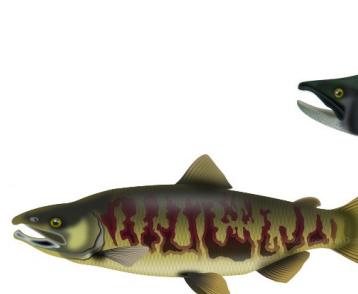
The r- and K-selection paradigm was focussed on **density-dependent selection**. This paradigm was challenged as it became clear that ... **age-specific mortality** provide[s] a more mechanistic link between an environment and an **optimal life history** ...

(Reznick et al. (2002) Ecology)

Salmonid (counter)-example



Sockeye salmon
Oncorhynchus nerka



Chum salmon
Oncorhynchus keta



Pink salmon
Oncorhynchus gorbuscha

Semelparous species

Much bigger eggs ($189 > 86$ mg).

Also nest building and guarding behavior, before dying,

i.e. greater investment in **Juvenile Survival over Adult Survival.**

The iteros just keep staying alive and trying to
breed again and again.

Inconsistent with r-K paradigm!



Arctic char
Salvelinus alpinus



Rainbow trout
Oncorhynchus mykiss



Brown trout
Salvelinus trutta

Tasmanian devil (*Sarcophilus harrisii*)



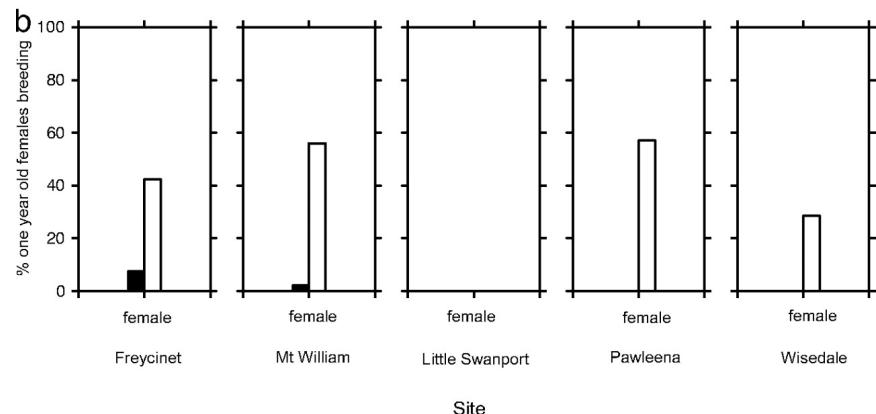
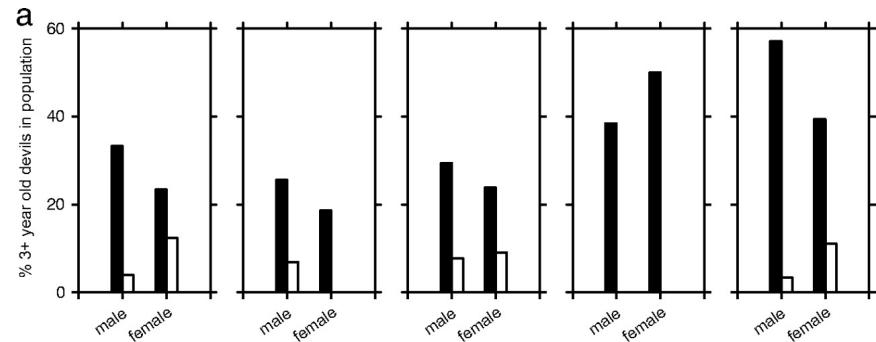
Only marsupial carnivore | range restricted to Tasmania

Dying of *facial tumor disease*; an infectious cancer (!) which kills nearly all adults > 3 years



Switch to Semelparity

Previously: Longer-lived, and iteroparous, with later birth (over 1 year old)



Now: Semelparous, one-shot, younger mothers (almost NO 2-3 year old animals!) (Jones et al. (2013))

Matrix population modelling

Total populations vs. structured populations

Scalar:

$$N_t$$

Vector:

$$\vec{N}_t = \begin{pmatrix} n_{1,t} \\ n_{2,t} \\ n_{3,t} \\ \vdots \\ n_{k,t} \end{pmatrix}$$

Exponential Growth - Structured Population Growth

Exponential Growth

$$N_{t+1} = \lambda N_t$$

λ is a scalar population growth multiplier

Structured Population Growth

$$\vec{N}_{t+1} = \mathbf{M} \vec{N}_t$$

M is a **Matrix** population **structure** growth multiplier

Population transition (aka **Leslie**) matrix

A **matrix** is a tool for **transforming vectors**.

A **population matrix** transforms a structured population **vector** by

1. adding newborns, [fecundity: f_i]
2. killing off older classes, [survival: s_i]
3. scootching everyone up the stage ladder [aging]

$$\begin{bmatrix} n_0 \\ n_1 \\ \vdots \\ n_{\omega-1} \end{bmatrix}_{t+1} = \begin{bmatrix} f_0 & f_1 & f_2 & \dots & f_{\omega-2} & f_{\omega-1} \\ s_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & s_{\omega-2} & 0 \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ \vdots \\ n_{\omega-1} \end{bmatrix}_t$$

The Leslie matrix

- is square
- the rows and columns represent age classes
- the top row is the number of **births** coming in from older age classes
- the lower rows are the number of **survivors** into the next age class

Remember *Monocerus academicus* ...

.	Larva	Sophomore	Emeritus
Monoceros academicus			
Survival	0.5	1	0
Fecundity	0	1.5	0.5

Here's the matrix:

$$M = \begin{bmatrix} 0 & 1.5 & 0.5 \\ 0.5 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}$$

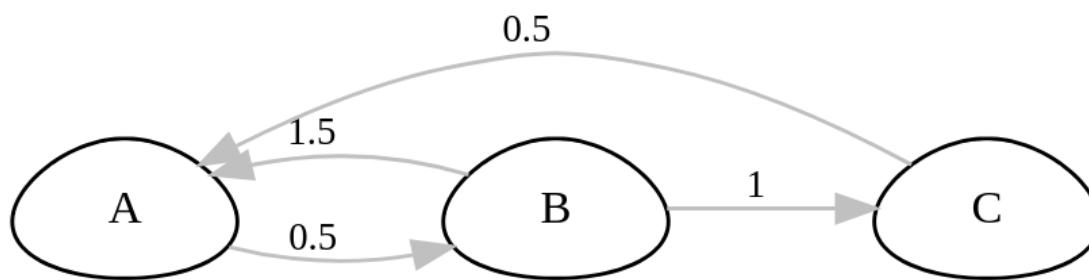
Leslie matrix as diagram

The population matrix maps to a diagram! These are very useful:

Matrix

$$M = \begin{bmatrix} 0 & 1.5 & 0.5 \\ 0.5 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}$$

Diagram



- Arrow **A** to **B** (0.5) is represented by matrix entry **column 1 to row 2** - survival to second stage.
- Arrow **B** to **C** (1) is matrix entry **column 2 to row 3** - survival to last stage.

Ok, but how does it work?

Matrix Multiplication looks scary!

$$MV^T = \begin{bmatrix} a_{11} & a_{12} & \dots & a_{1n} \\ a_{21} & a_{22} & \dots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nn} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{bmatrix} = \begin{bmatrix} a_{11}x_1 + a_{12}x_2 + \dots + a_{1n}x_n \\ a_{21}x_1 + a_{22}x_2 + \dots + a_{2n}x_n \\ \vdots \\ a_{n1}x_1 + a_{n2}x_2 + \dots + a_{nn}x_n \end{bmatrix}.$$

But it basically just takes each element of your vector (e.g. population at a stage) and tracks how it is affected by all the other stages.

Start with our experiment: 8 larvae

$$N_0 = \begin{bmatrix} 8 \\ 0 \\ 0 \end{bmatrix}$$

$$N_1 = MN_0^T = \begin{bmatrix} 0 & 1.5 & 0.5 \\ 0.5 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix} \times \begin{bmatrix} 8 \\ 0 \\ 0 \end{bmatrix} = \begin{bmatrix} 0+0+0 \\ 4+0+0 \\ 0+0+0 \end{bmatrix} = \begin{bmatrix} 0 \\ 4 \\ 0 \end{bmatrix}$$

$$N_2 = MN_1^T = \begin{bmatrix} 0 & 1.5 & 0.5 \\ 0.5 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix} \times \begin{bmatrix} 0 \\ 4 \\ 0 \end{bmatrix} = \begin{bmatrix} 6 \\ 0 \\ 4 \end{bmatrix}$$

$$N_3 = MN_2^T = M \times \begin{bmatrix} 6 \\ 0 \\ 4 \end{bmatrix} = \begin{bmatrix} 2 \\ 3 \\ 0 \end{bmatrix}$$

etc.

Super simple in R!

```
M <- rbind(c(0,1.5,.5), c(.5,0,0), c(0,1,0))
row.names(M) <- c("larvae", "sophs", "emeriti")
```

One step:

```
M %*% N0
```

```
##          [,1]
## larvae      0
## sophs       9
## emeriti     0
```

Two steps:

```
M %*% M %*% N0
```

```
##          [,1]
## larvae   13.5
## sophs    0.0
## emeriti  9.0
```

Three steps:

```
M %^% 3 %*% N0
```

```
##          [,1]
## larvae   4.50
## sophs    6.75
## emeriti  0.00
```

20 steps:

```
M %^% 20 %*% N0
```

```
##          [,1]
## larvae   8.000124
## sophs    3.999882
## emeriti  4.000225
```

Plotting the results

$$N_t = M^t \times N_0$$

(if no animation shows up, click [here](#))

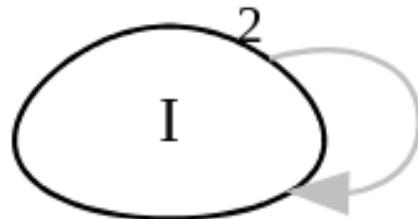
Amazing property of (many) matrices ...

$$M \times N^* = \lambda N^*$$

For every **(population) matrix** there is a **vector (age distribution)** for which the matrix transformation **(population growth process)** increases the vector by a fixed proportion λ (**population growth rate**).

- N^* - is the **eigenvector** = **stable population distribution**
- λ - is the **eigenvalue** = **population growth factor**

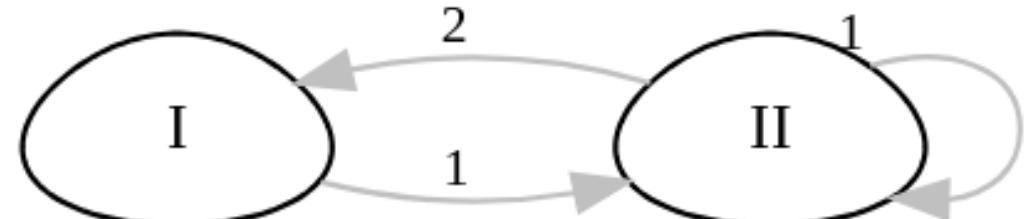
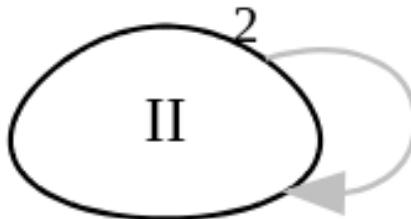
Some simple examples (to work out by hand)



$$M = \begin{bmatrix} 2 & 0 \\ 0 & 2 \end{bmatrix}$$

Everything doubles!

- $\lambda = 2$
- no unique distribution.

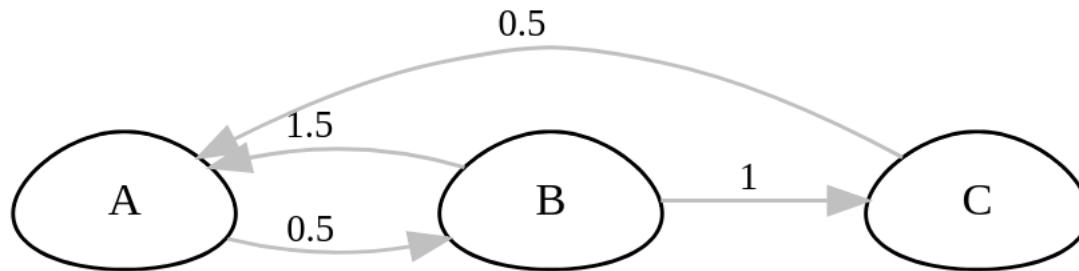


$$M = \begin{bmatrix} 0 & 2 \\ 1 & 1 \end{bmatrix}$$

Eventually everything doubles!

- $\lambda = 2$.
- stable distribution = $N^* = \{1, 1\}$

Monocerus academicus



```
matA <- rbind(c(0, 1.5, .5),
               c(.5, 0, 0),
               c(0, 1, 0))
```

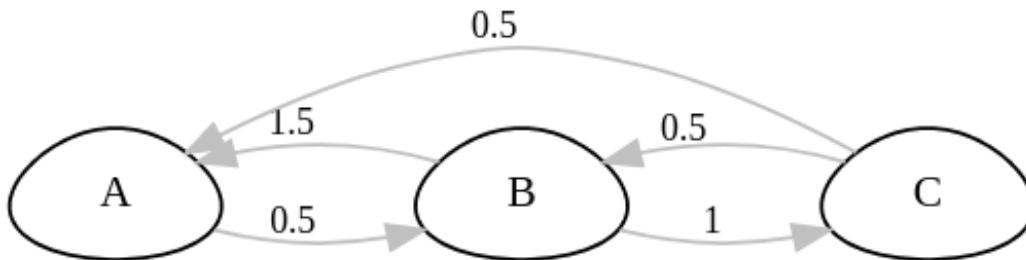
$$M = \begin{bmatrix} 0 & 1.5 & 0.5 \\ 0.5 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix}$$

```
eigen(matA)

## eigen() decomposition
## $values
## [1] 1.0 -0.5 -0.5
##
## $vectors
## [,1]      [,2]      [,3]
## [1,] -0.8164966 -0.4082483  0.4082483
## [2,] -0.4082483  0.4082483 -0.4082483
## [3,] -0.4082483 -0.8164966  0.8164966
```

- First eigenvalue: $\lambda = 1$
- Ratio of first eigenvector: 50% : 25% : 25%

What if some emeriti decide to go back to school?



$$M = \begin{bmatrix} 0 & 1.5 & 0.5 \\ 0.5 & 0 & \textcolor{red}{0.5} \\ 0 & 1 & 0 \end{bmatrix}$$

```
eigen(matB)

## eigen() decomposition
## $values
## [1] 1.2071068 -1.0000000 -0.2071068
##
## $vectors
## [,1]      [,2]      [,3]
## [1,] 0.7736915 0.5773503 0.6669930
## [2,] 0.4878914 -0.5773503 0.1511012
## [3,] 0.4041824  0.5773503 -0.7295812
```

- First eigenvalue: $\lambda = 1.21$
- Ratio of first eigenvector: 46% : 29% : 24%

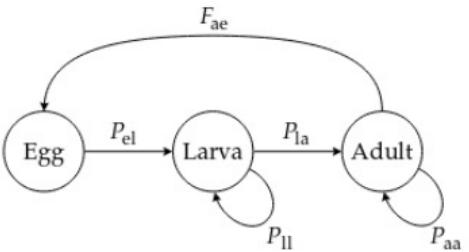
How does this look?

(If animation does not work, click [here](#))

Complex life histories

(a) Insect

$$\begin{matrix} 0 & 0 & F_{ae} \\ P_{el} & P_{ll} & 0 \\ 0 & P_{la} & P_{aa} \end{matrix}$$

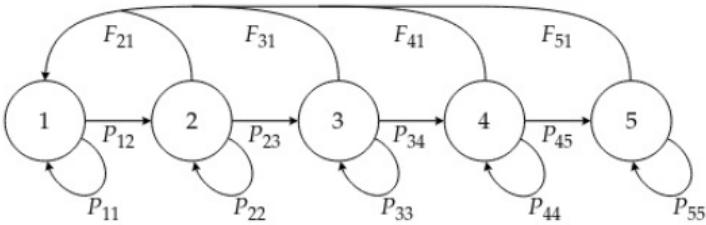


In short ...

... matrix models do it all!
And do it fast, and intuitively.

(b) Forest tree

$$\begin{matrix} P_{11} & F_{21} & F_{31} & F_{41} & F_{51} \\ P_{12} & P_{22} & 0 & 0 & 0 \\ 0 & P_{23} & P_{33} & 0 & 0 \\ 0 & 0 & P_{34} & P_{44} & 0 \\ 0 & 0 & 0 & P_{45} & P_{55} \end{matrix}$$



(c) Coral

$$\begin{matrix} P_{ss} + F_{ss} & P_{ms} + F_{ms} & P_{ls} + F_{ls} \\ P_{sm} & P_{mm} & P_{lm} \\ P_{sl} & P_{ml} & P_{ll} \end{matrix}$$

