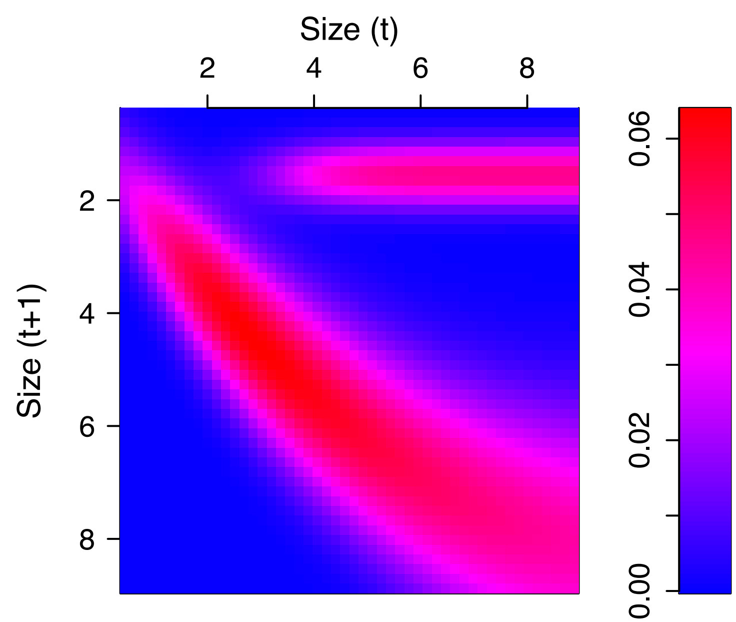
AN INTRODUCTION TO INTEGRAL PROJECTION MODELS (IPMS)

Cory Merow



Methods in Ecology and Evolution

Methods in Ecology and Evolution 2013 doi: 10.1111/2041-210X.12146

REVIEW

Advancing population ecology with integral projection models: a practical guide

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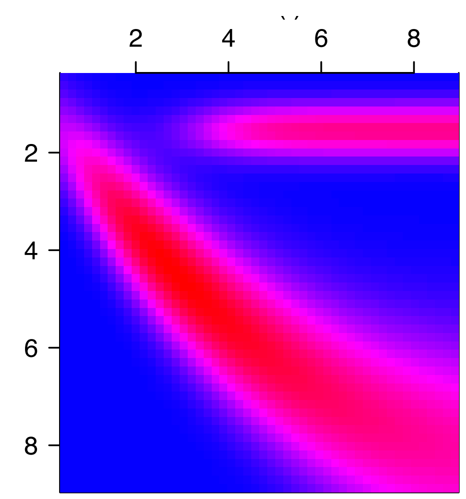
IPMs

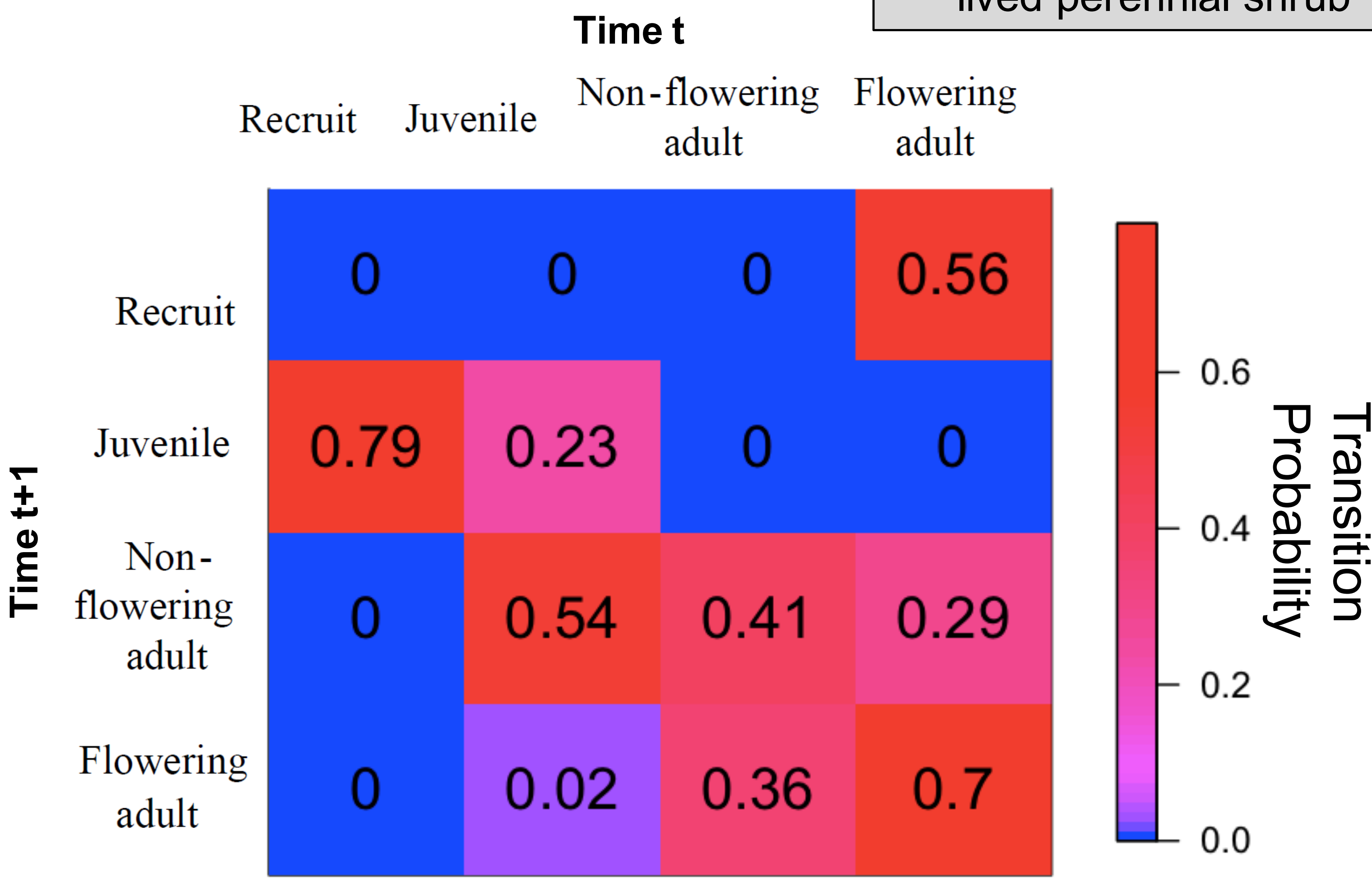
Process-based demography:

- Accurate stage structure
- Decompose life history to desired level of detail
- Link vital rates to covariates
- Heterogeneity among individuals

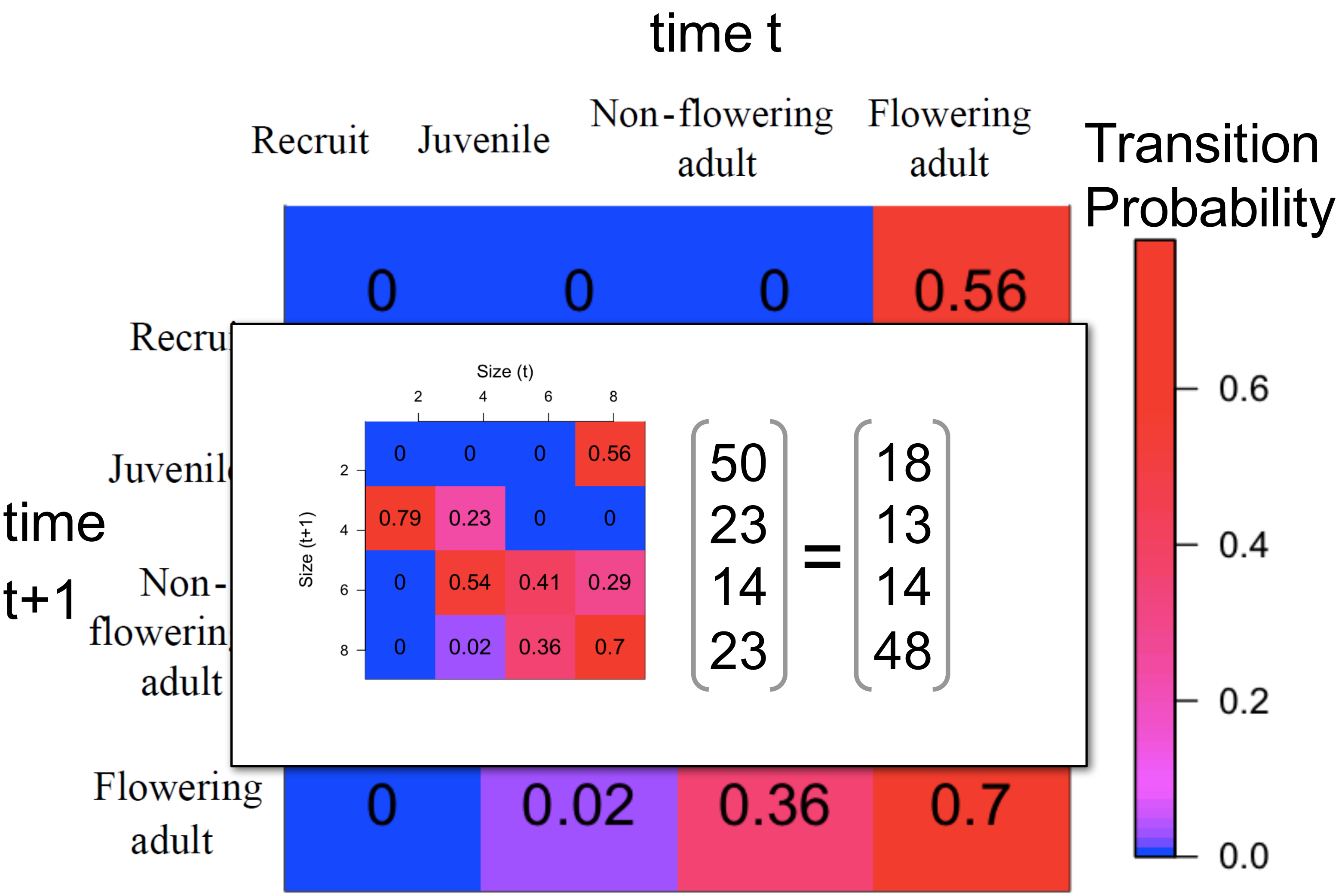


What is an IPM?

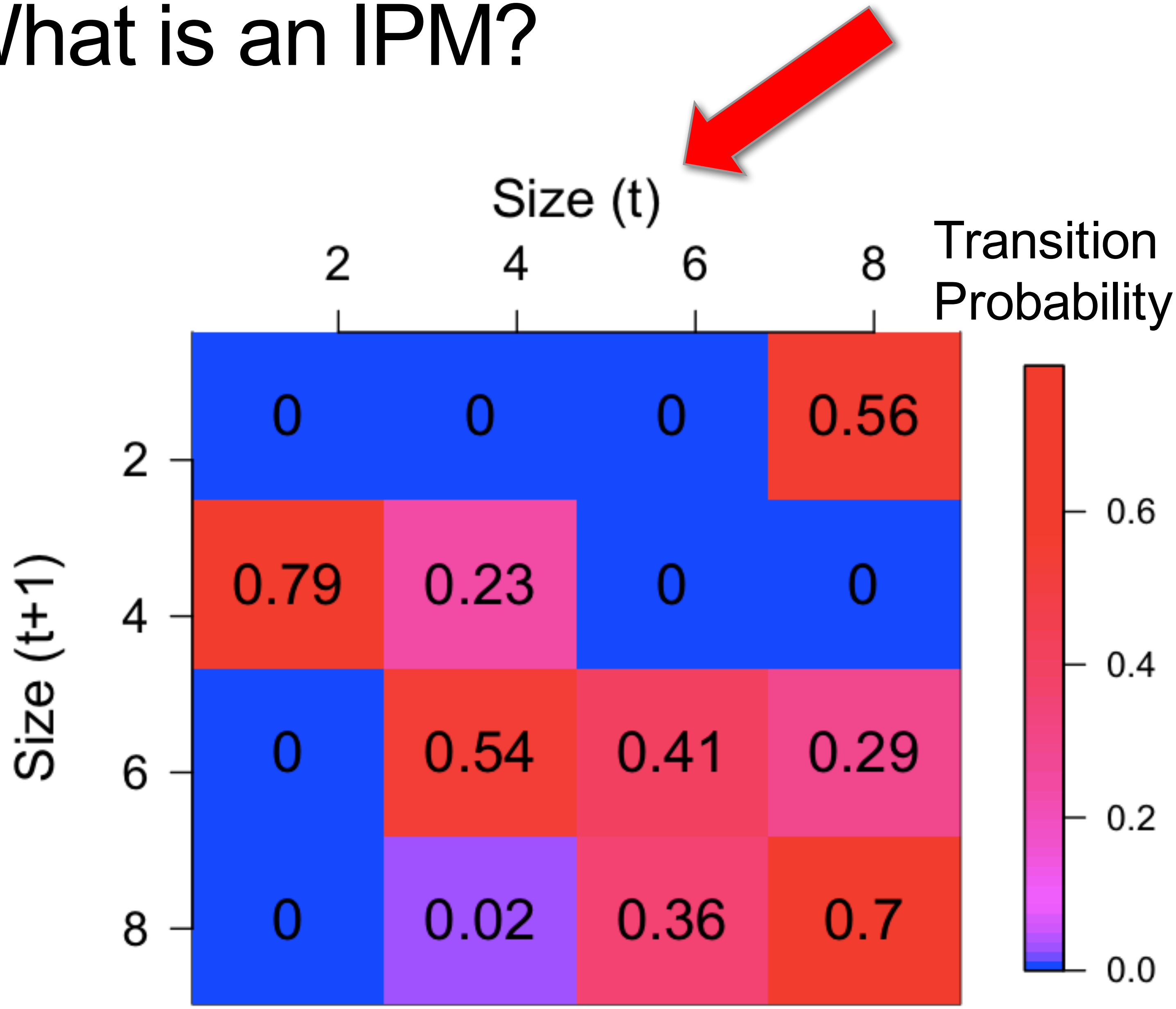
Lefkovich matrix for a long-lived perennial shrub



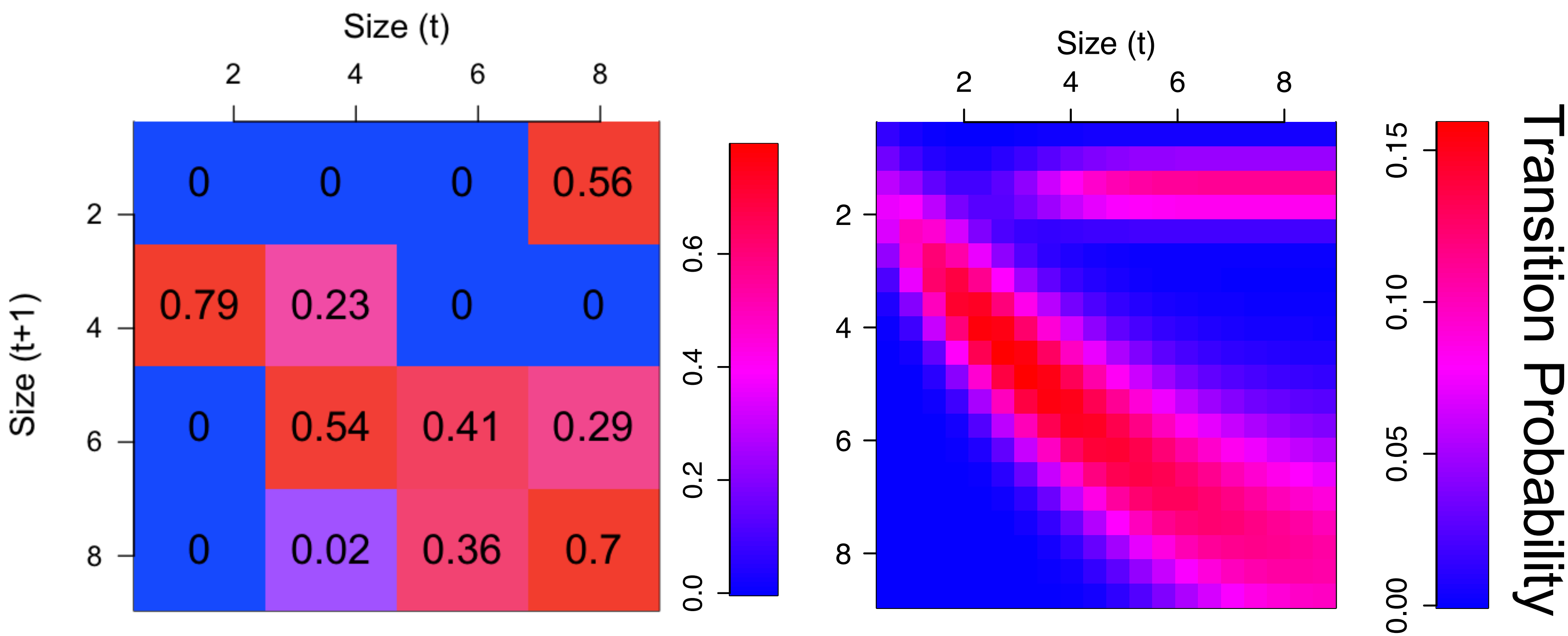
What is an IPM?



What is an IPM?

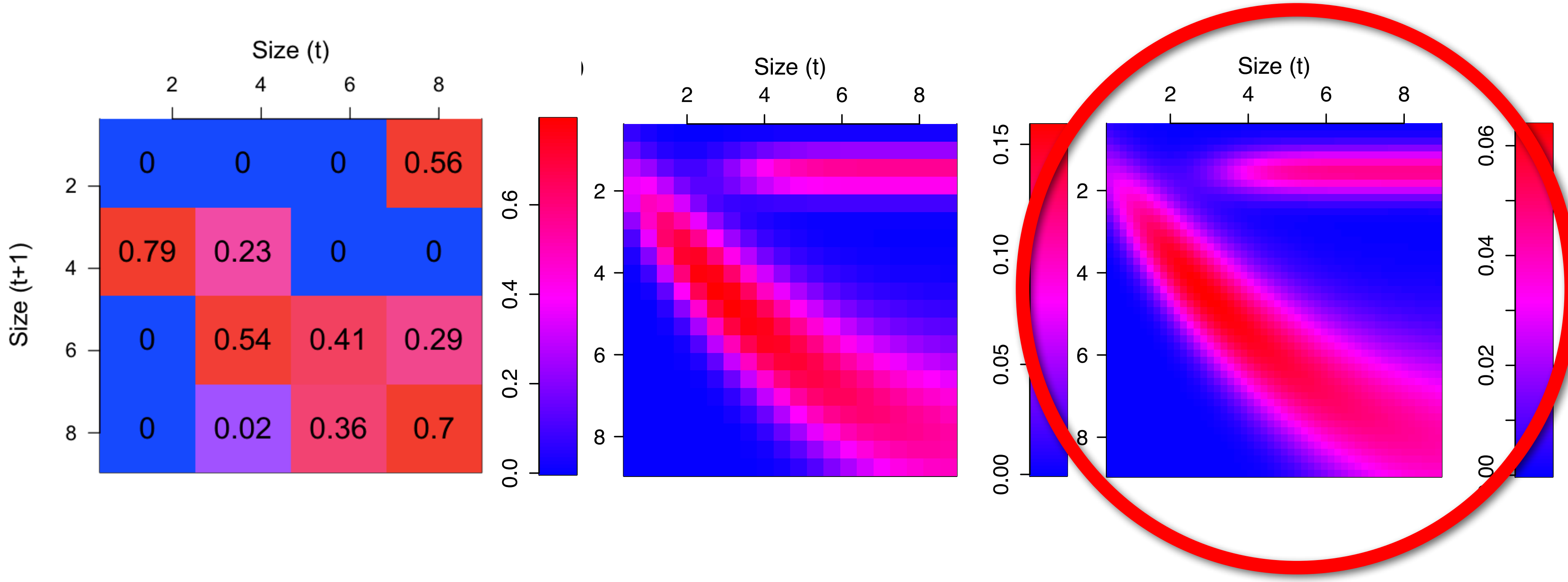


What is an IPM?



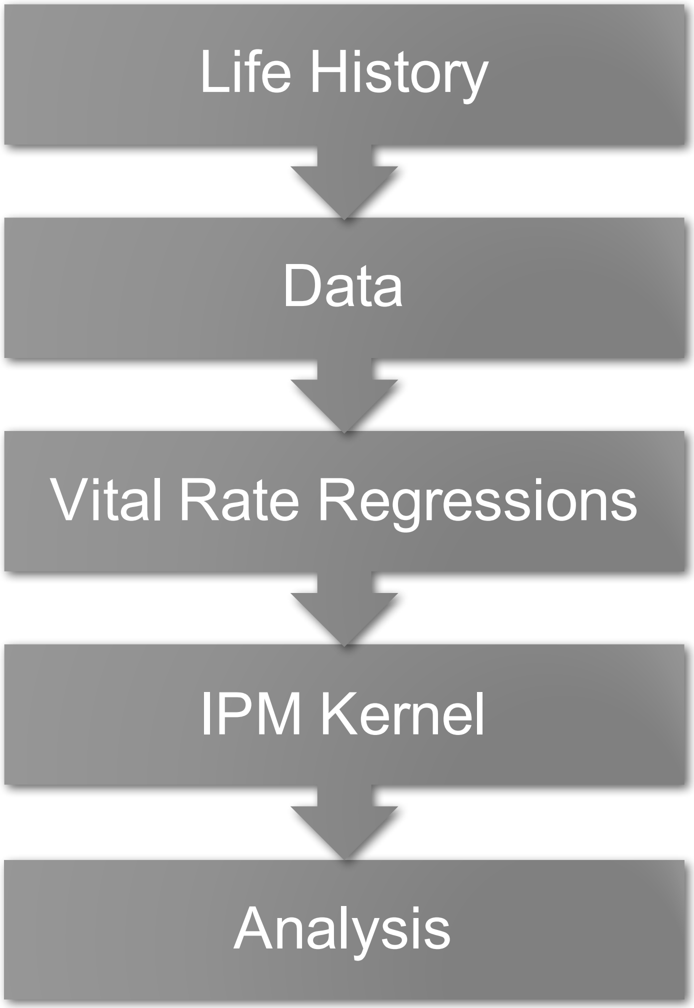
More stages = more heterogeneity among individuals

What is an IPM?

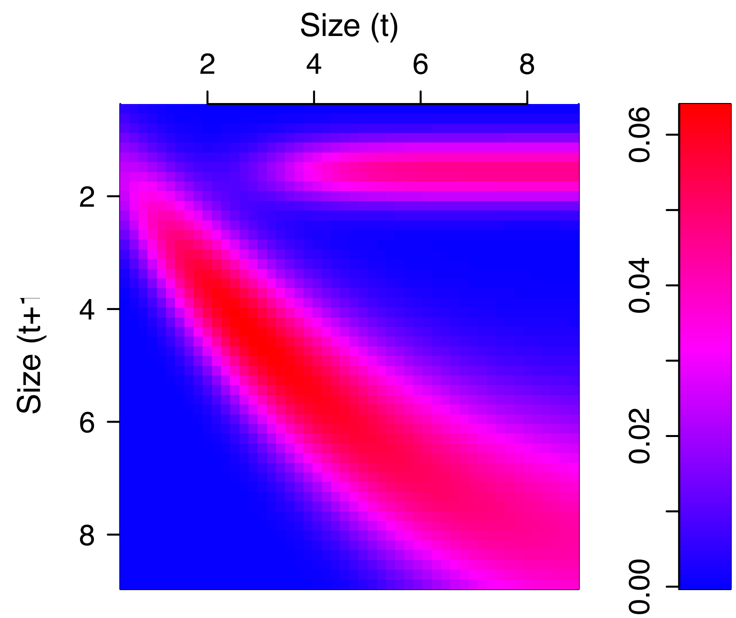


Matrix models and IPMs arrive at matrices for different reasons

Workflow



Life History
Data
Vital Rate Regressions
IPM Kernel
Analysis



Size (t)
2
4
6
8
Size (t+
2
4
6
8
0.00
0.02
0.04
0.06

Workflow

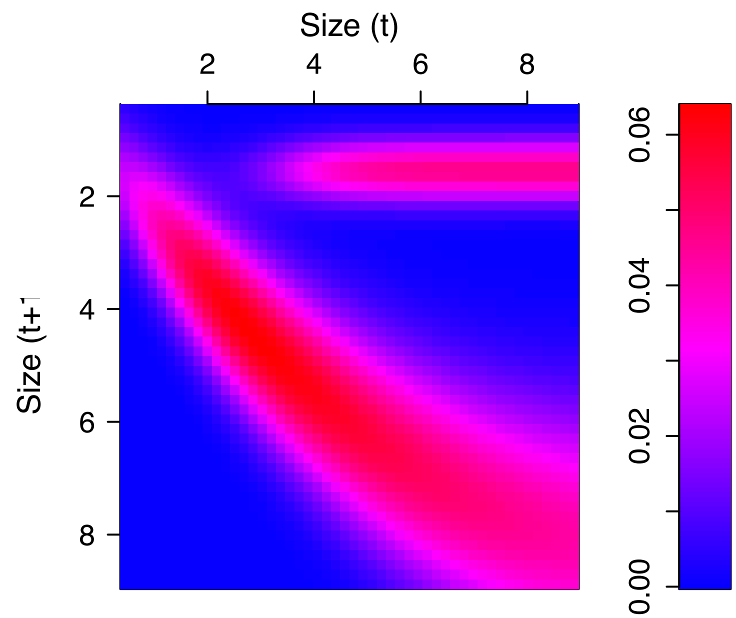
Life History

Data

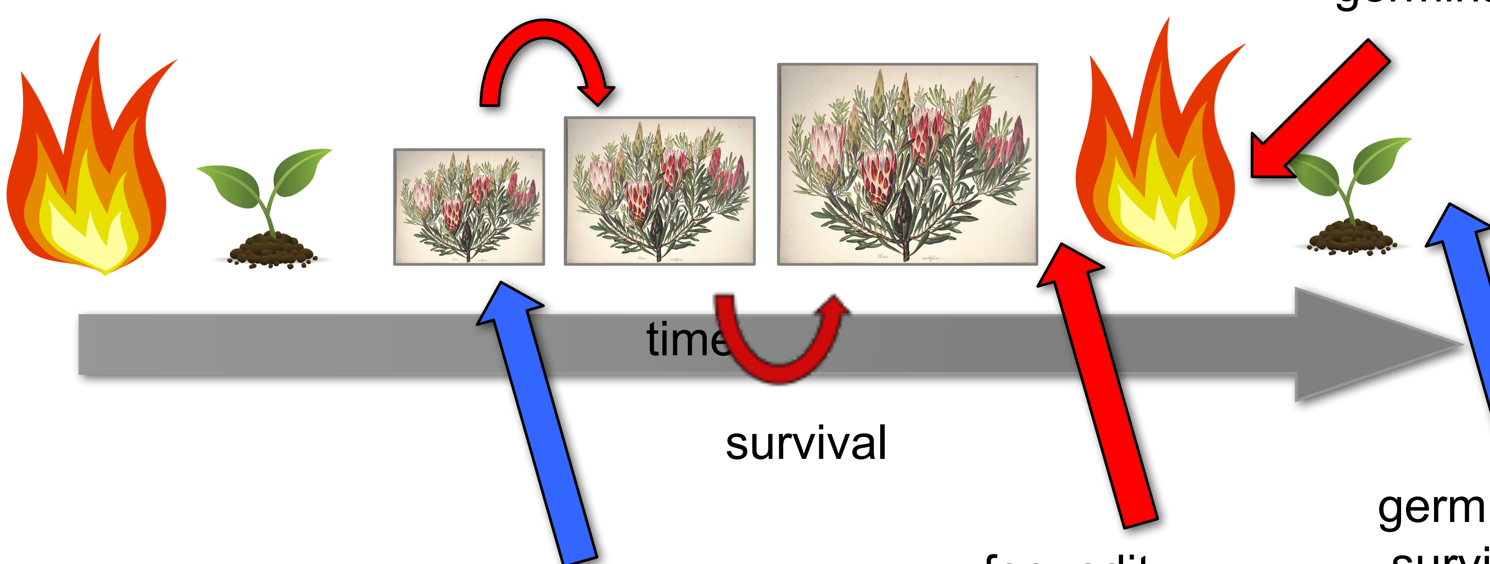
Vital Rate Regressions

IPM Kernel

Analysis

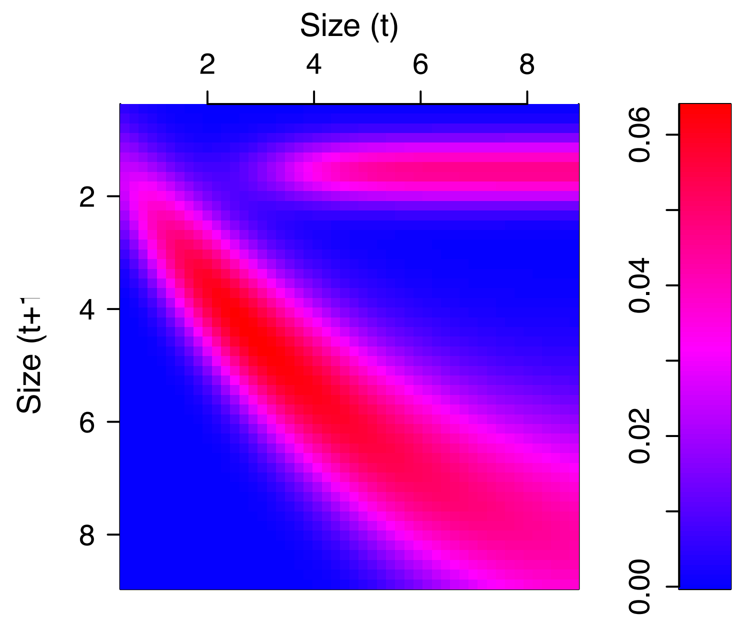


Life history

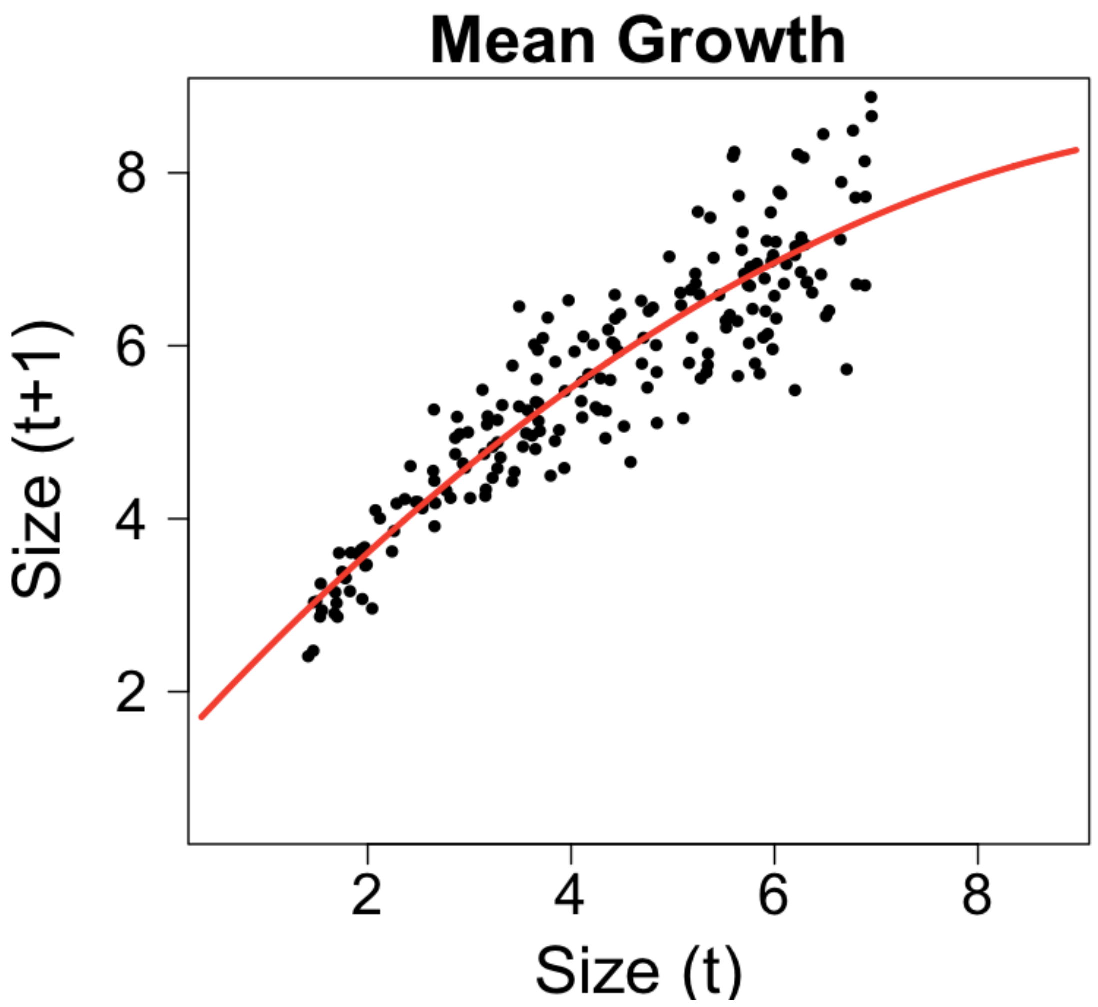


Workflow

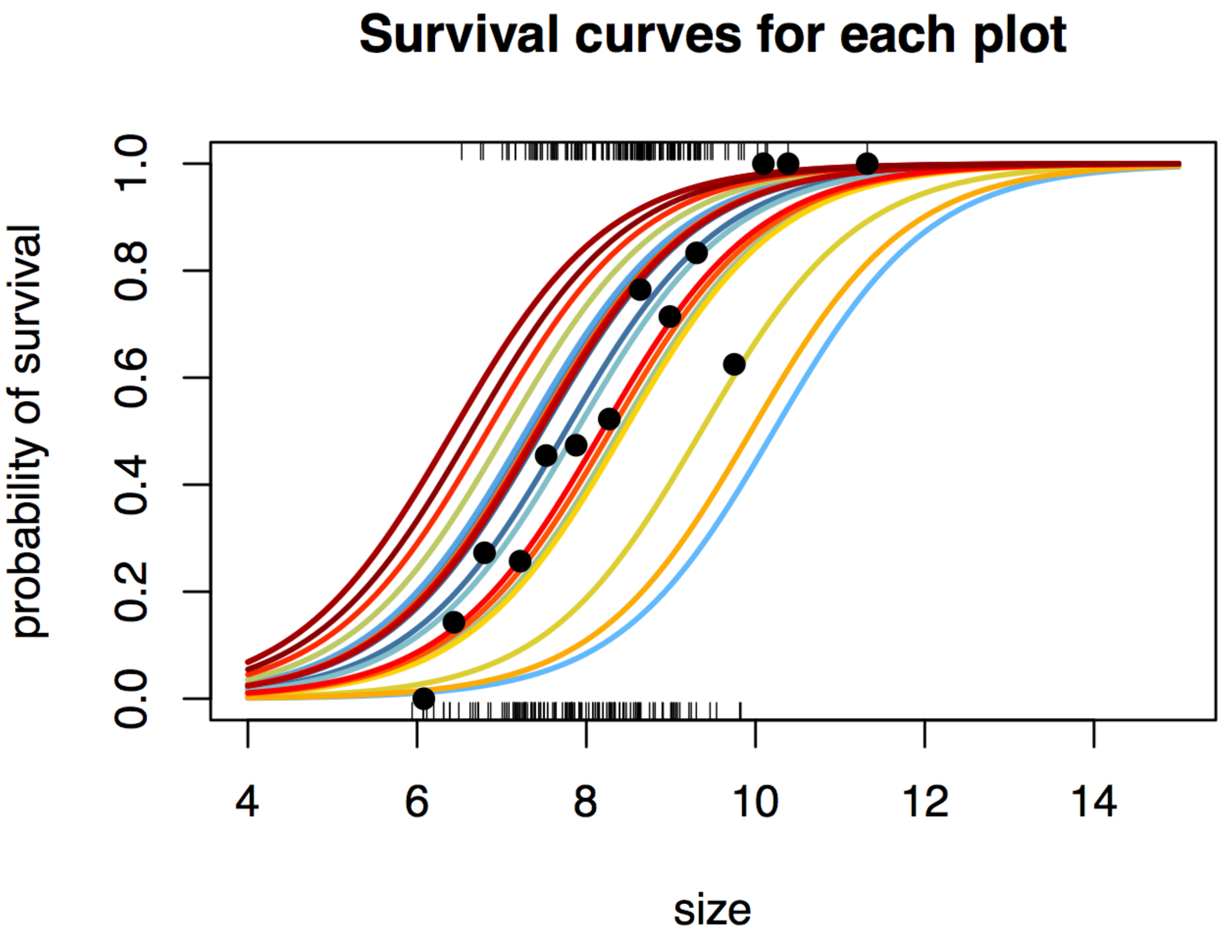
- Life History
- **Data**
- Vital Rate Regressions
- IPM Kernel
- Analysis



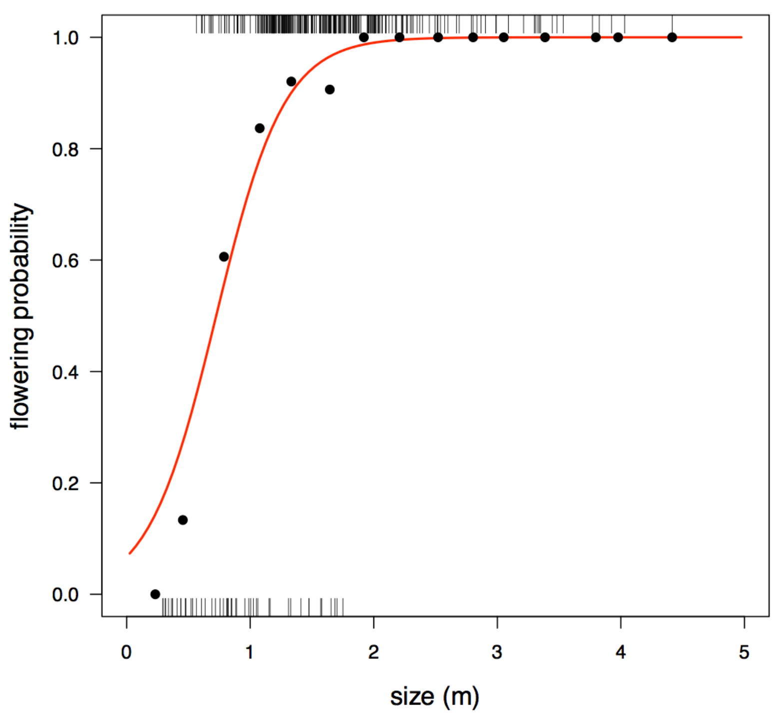
Data: Growth

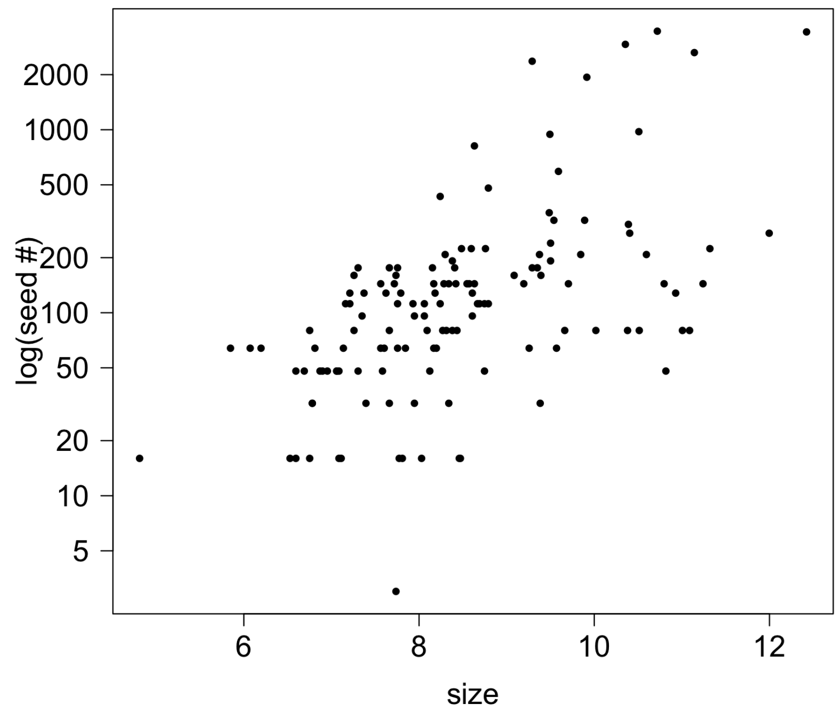


Data: Survival



Data: Fecundity





Germination probability

Workflow

Life History

↓

Data

↓

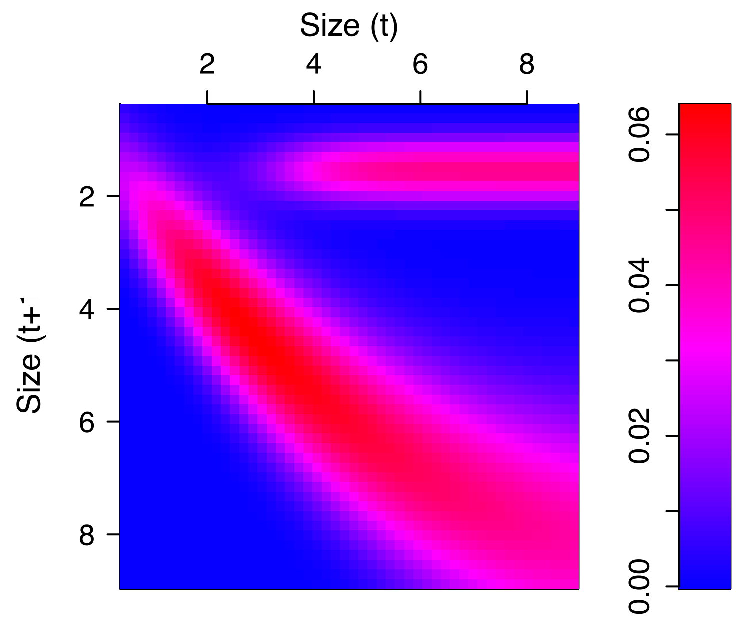
Vital Rate Regressions

↓

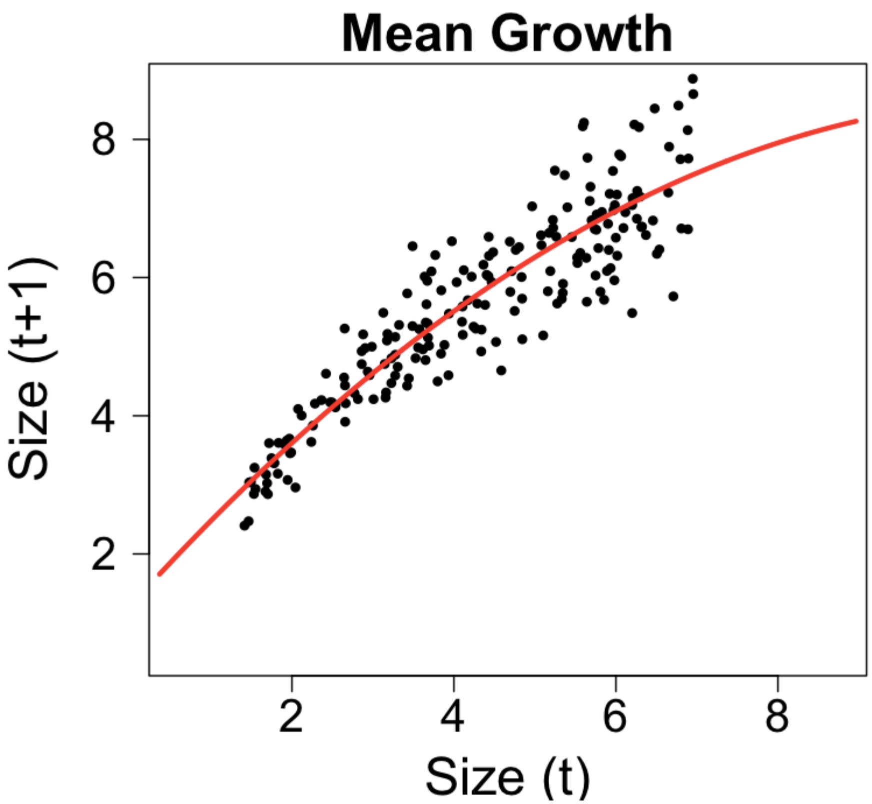
IPM Kernel

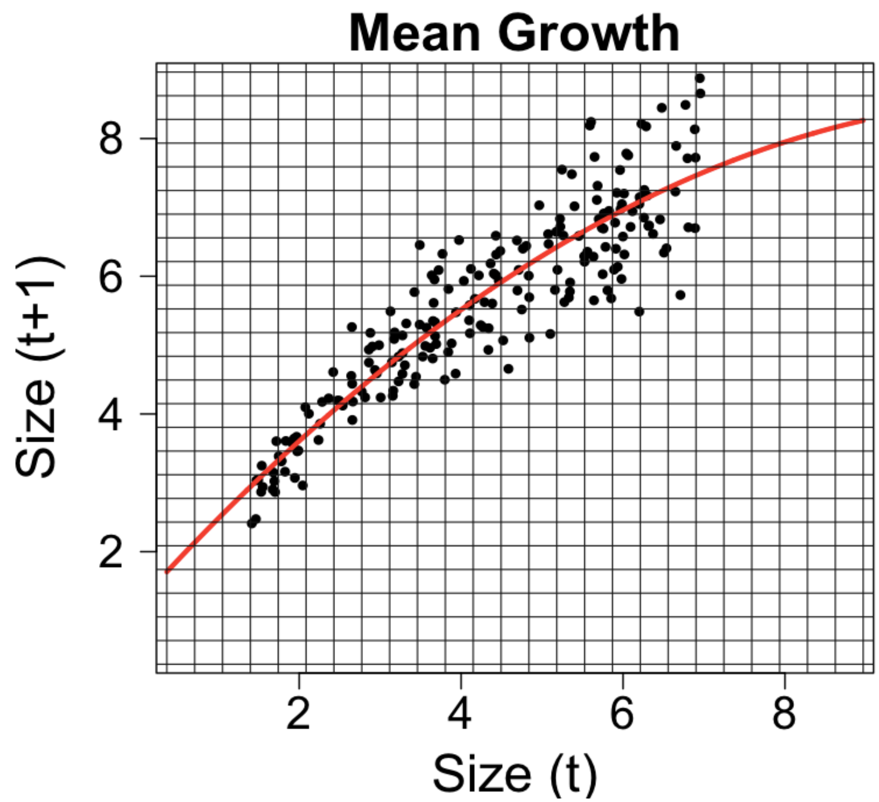
↓

Analysis



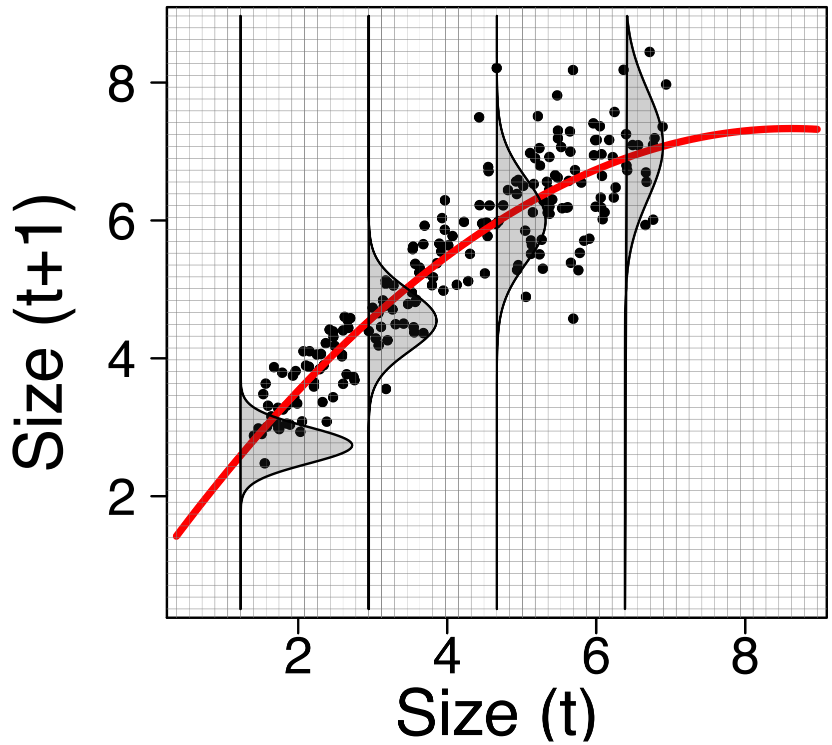
Vital Rate Regression: Growth

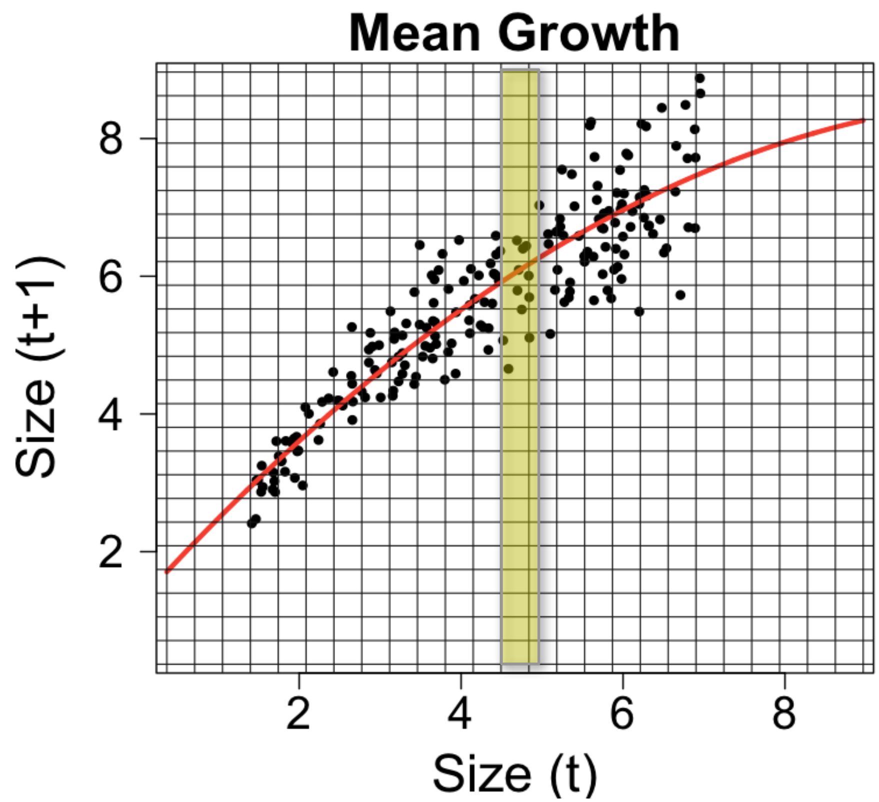




$$\text{mean} = b_0 + b_1 size + b_2 size^2$$

Vital Rate Regression: Growth

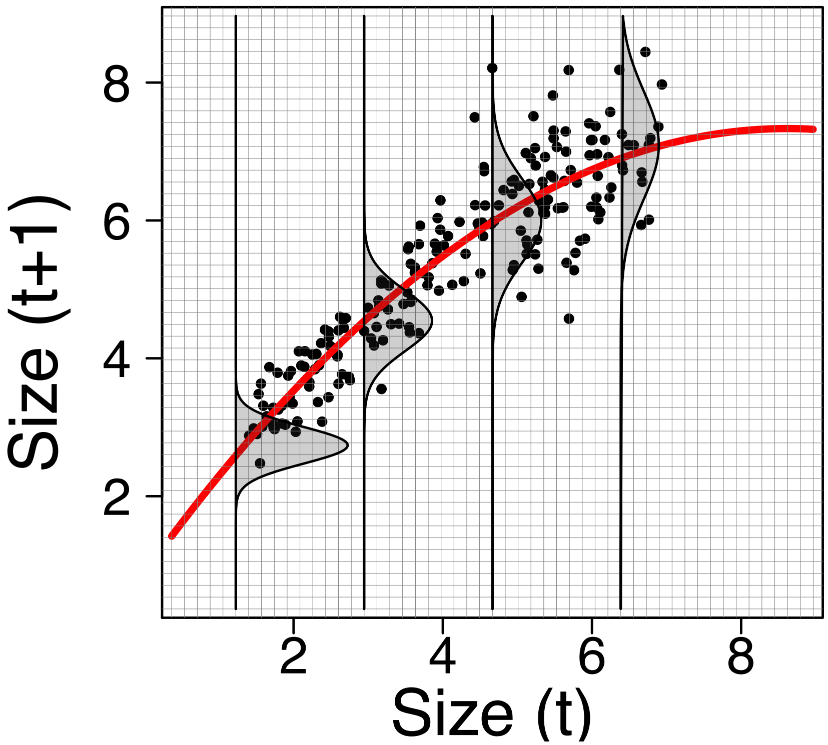


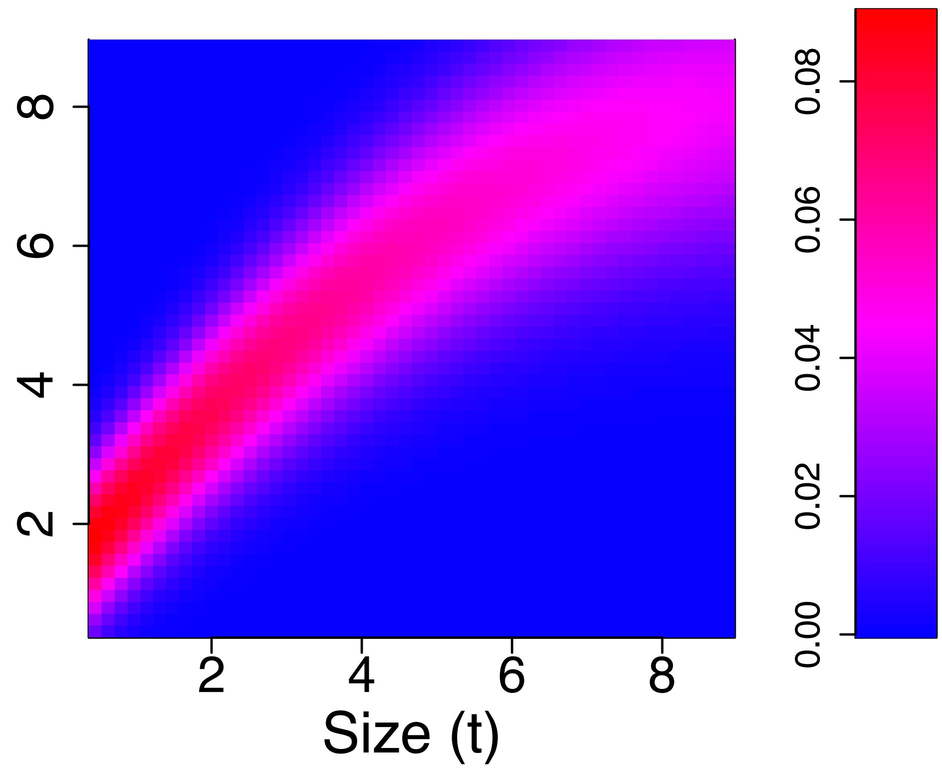


$$\text{mean} = b_0 + b_1 size + b_2 size^2$$

$$\text{variance} = b_3 + b_4 size$$

Vital Rate Regression: Growth





$$\text{mean} = b_0 + b_1 size + b_2 size^2$$

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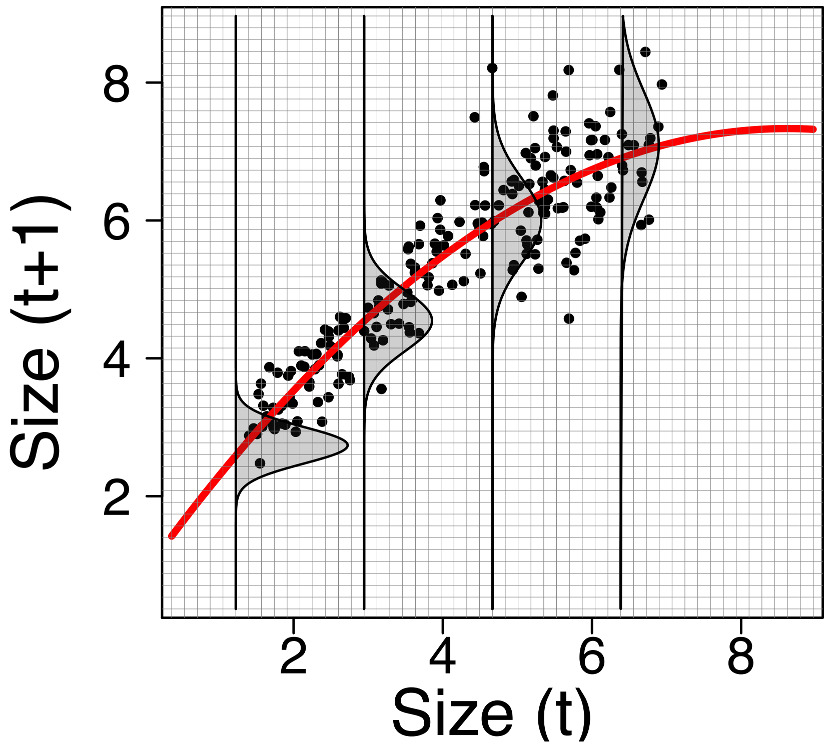
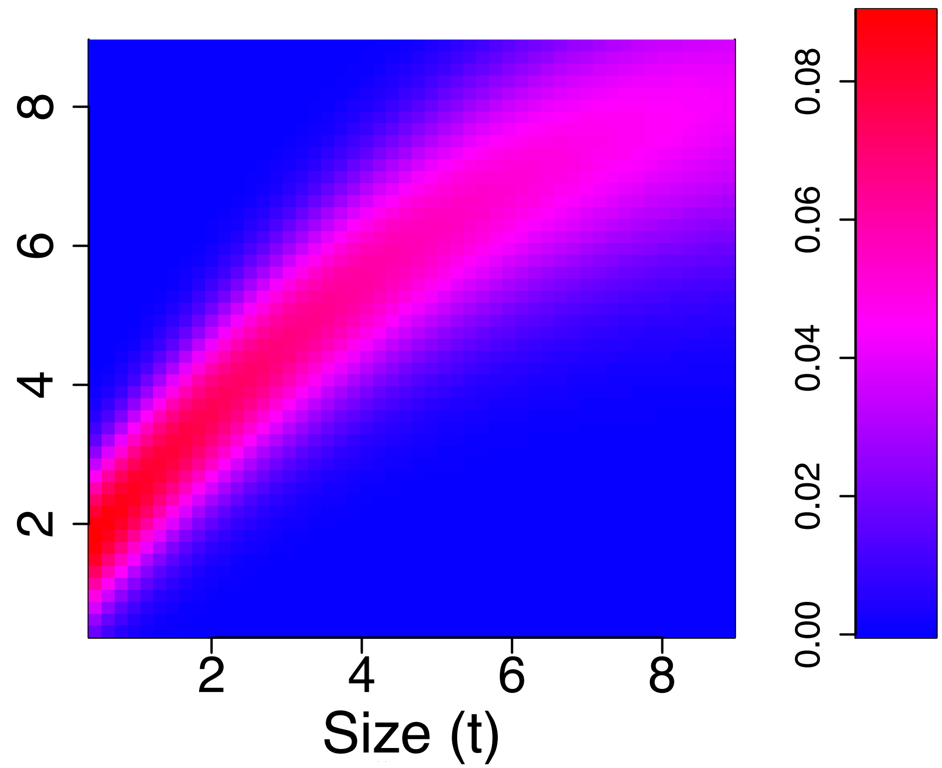
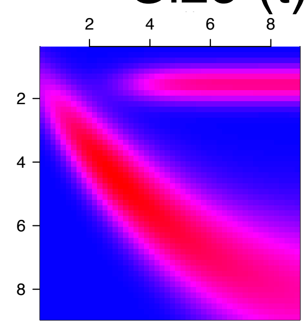
Vital Rate Regression: Growth



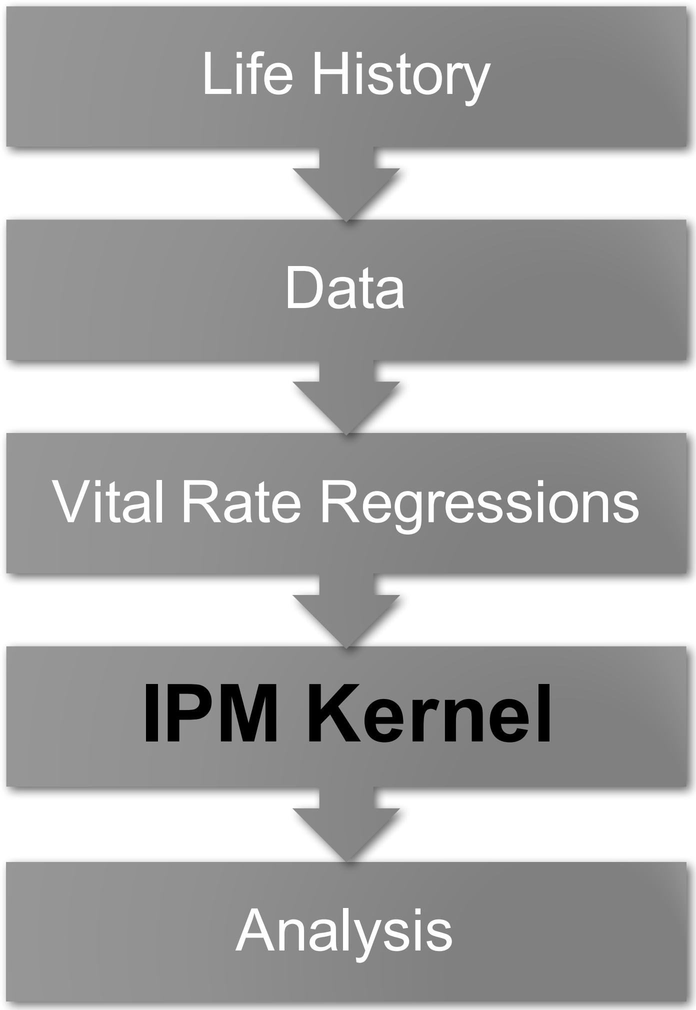


$$g(x,y) = \frac{1}{\sqrt{2\pi\sigma(x)^2}}\exp\left(\frac{(y-\mu(x))^2}{2\sigma(x)^2}\right)$$



Full kernel

Workflow


Life History
Data
Vital Rate Regressions
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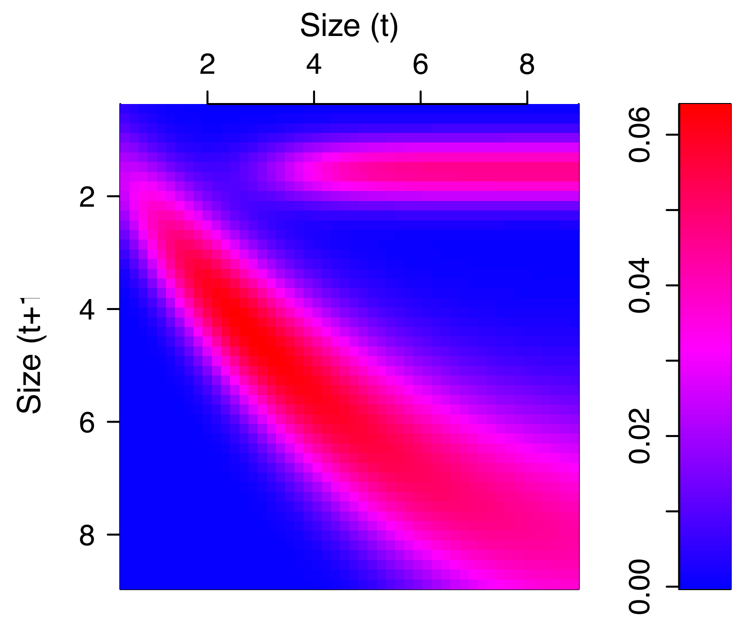
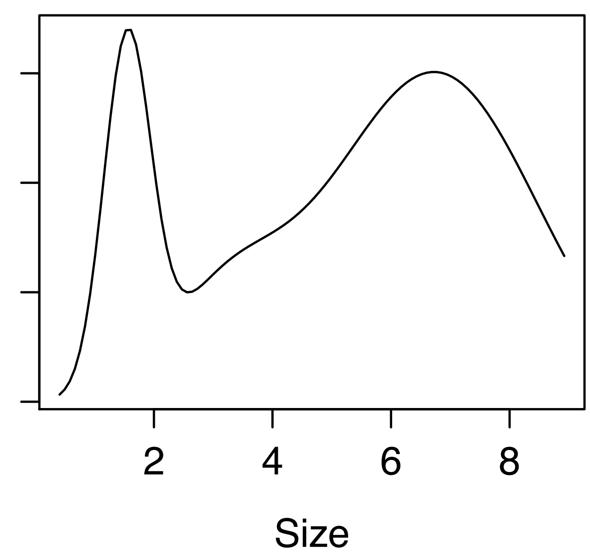

Size (t)
2
4
6
8
Size (t+1
2
4
6
8
0.00
0.02
0.04
0.06

The model

- t = time
- x = size at t
- y = size at t+1
- $n_t(x)$ = size distribution at t
- $n_{t+1}(y)$ = size distribution at t+1

- K(x,y) = full kernel
- P(x,y) = growth/survival kernel
- F(x,y) = fecundity kernel

Number of individuals of each size



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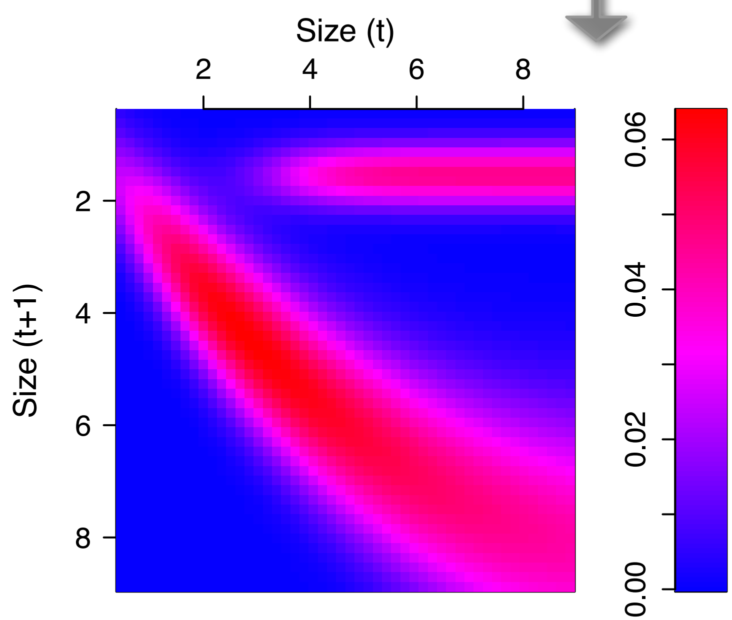

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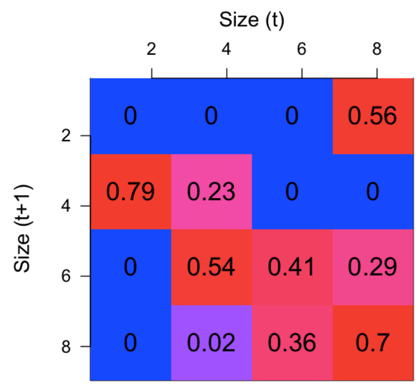
$$\mathbf{n}_{t+1} \quad = \quad \mathbf{A} \quad \mathbf{n}_t \qquad\qquad (Matrix)$$

$$n_{t+1}(y) = \int_{\substack{all \\ sizes}} K(y,x) \; n_t(x)\, dx \qquad\qquad (IPM)$$

The model



$$\begin{pmatrix} 50 \\ 23 \\ 14 \\ 23 \end{pmatrix} = \begin{pmatrix} 18 \\ 13 \\ 14 \\ 48 \end{pmatrix}$$

- K(x,y) = full kernel
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$$\mathbf{n}_{t+1} = \mathbf{A} \quad \mathbf{n}_t \qquad (Matrix)$$

$$n_{t+1}(y) = \int_{\substack{all\\sizes}} K(y,x) \; n_t(x)\,dx \qquad (IPM)$$

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$$\mathbf{n}_{t+1} = \mathbf{A} \quad \mathbf{n}_t \qquad (Matrix)$$

$$n_{t+1}(y) = \int_{\substack{all \\ sizes}} K(y,x) \; n_t(x)\, dx \qquad (IPM)$$

$$n_{t+1}(y) = \int_{\substack{all \\ sizes}} \left[P(x,y) + F(x,y)\right] n_t(x)\, dx$$

The model

- t = time
- x = size at t
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$$n_{t+1}(y) = \int_{\substack{all\\sizes}} \left[P(x,y) + F(x,y)\right] n_t(x)\,dx$$

$$size(y)_{t+1} = \int_{\substack{all\\sizes}} \left[growth(size\ x \rightarrow y) + offspring(size\ x \rightarrow y)\right] size(x)_t\,dx$$

We need functions for…

- Growth
- Survival
- Reproduction

We have the option of splitting these in to finer detail if the data are available and the life history requires it

Life History

$$n(y,t+1) = \int_{\Omega} \left[P(x,y) + F(x,y) \right] n(x,t)\, dx$$

Example 1: Long-lived perennial plant

P(x,y) = (survival probability at size x) * (growth from x to y)
= s(x) * g(x,y)

Life History

$$n(y,t+1) = \int_{\Omega} \left[P(x,y) + F(x,y) \right] n(x,t)\, dx$$

Example 1: Long-lived perennial plant

P(x,y) = (survival probability at size x) * (growth from x to y)
= s(x) * g(x,y)

F(x,y) = (mean # seeds of size x parent) *
(establishment probability)
(probability of size y offspring from size x parent)
= $f_{seeds}(x) * p_{estab} * f_{recruit}(y)$

Life History

$$n(y,t+1) = \int_{\Omega} \left[P(x,y) + F(x,y)\right] n(x,t)\, dx$$

Example 1: Long-lived perennial plant

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Life History

$$n(y,t+1) = \int_{\Omega} \left[P(x,y) + F(x,y) \right] n(x,t)\, dx$$

Example 1: Long-lived perennial plant

P(x,y) = (survival probability at size x) * (growth from x to y)

$= \boxed{s(x)} * \boxed{g(x,y)}$

F(x,y) = (mean # seeds of size x parent) *

(establishment probability)

(probability of size y offspring from size x parent)

$= \boxed{f_{seeds}(x) * p_{estab}} * \boxed{f_{recruit}(y)}$

Workflow

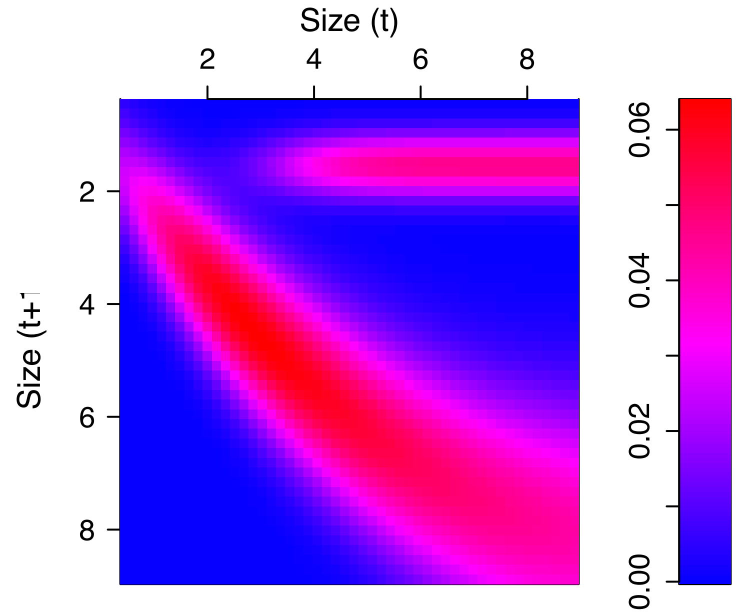
Life History

Data

Vital Rate Regressions

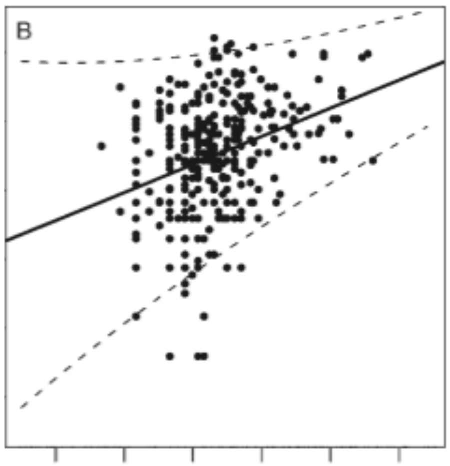
IPM Kernel

Analysis

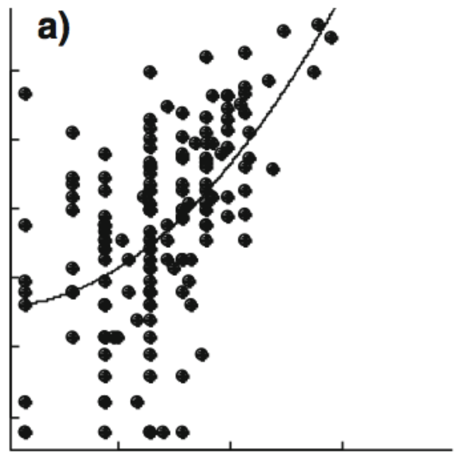


Vital Rate Regression: Growth – g(x,y)

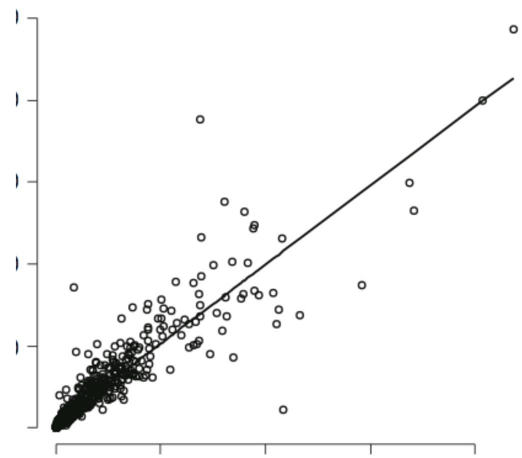
Jongejans et al. 2011



Metcalf et al. 2008

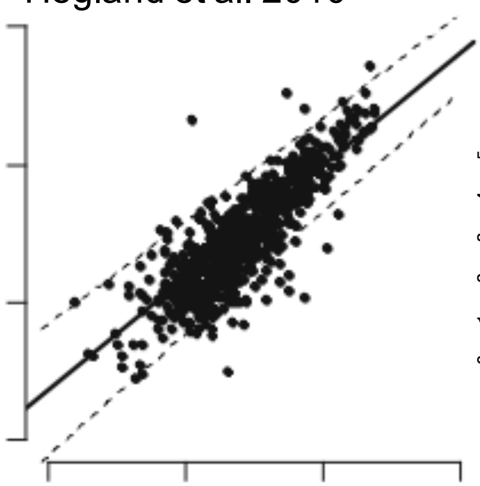


Ferrer-Cervantes et al. 2012

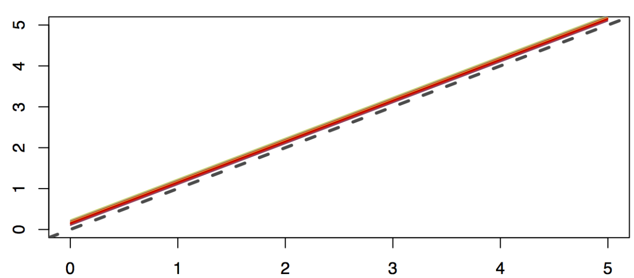


Size (t+1)

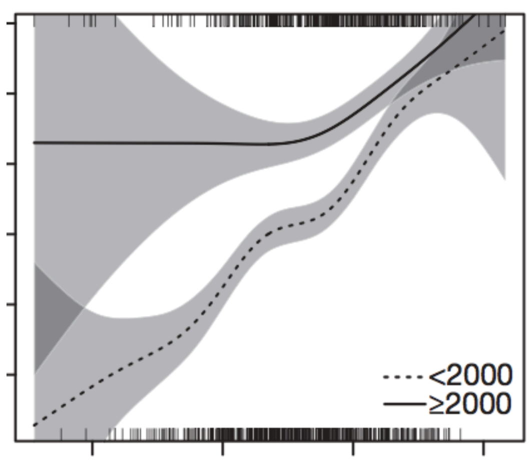
Hegland et al. 2010



Merow et al. 2014



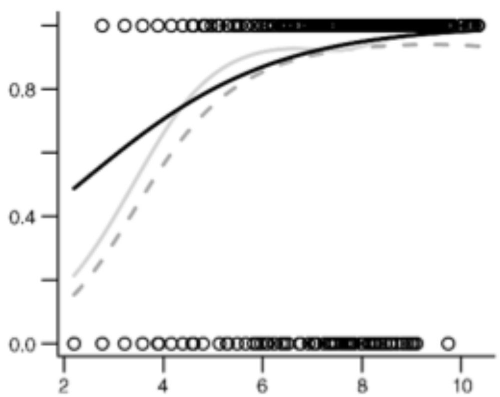
Ozgul et al. 2010



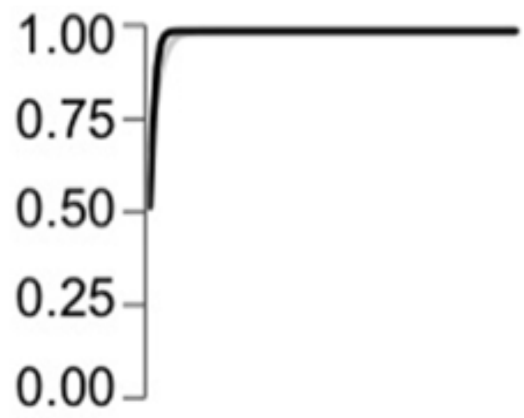
Size (t)

Vital Rate Regression: Survival – s(x)

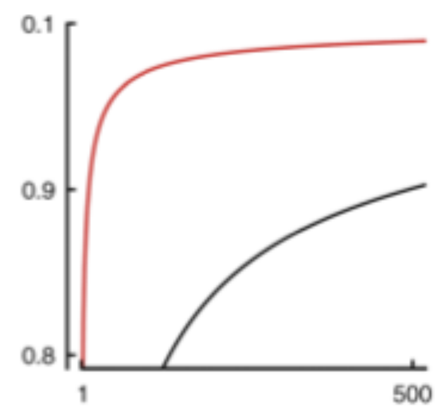
Dahlgren et al. 2011



Salguero-Gomez et al. 2012

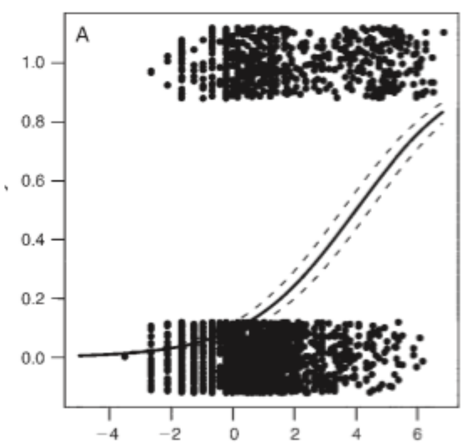


Metcalf et al. 2009

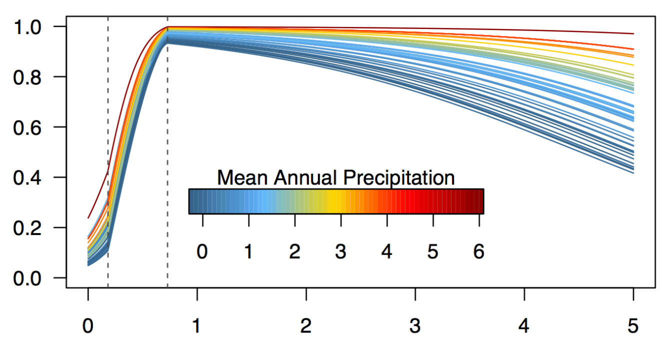


Survival Probability

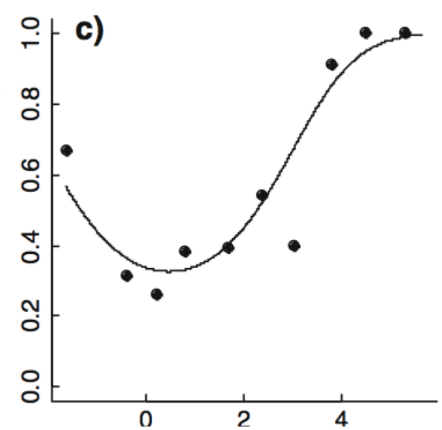
Jongejans et al. 2011



Merow et al. 2014

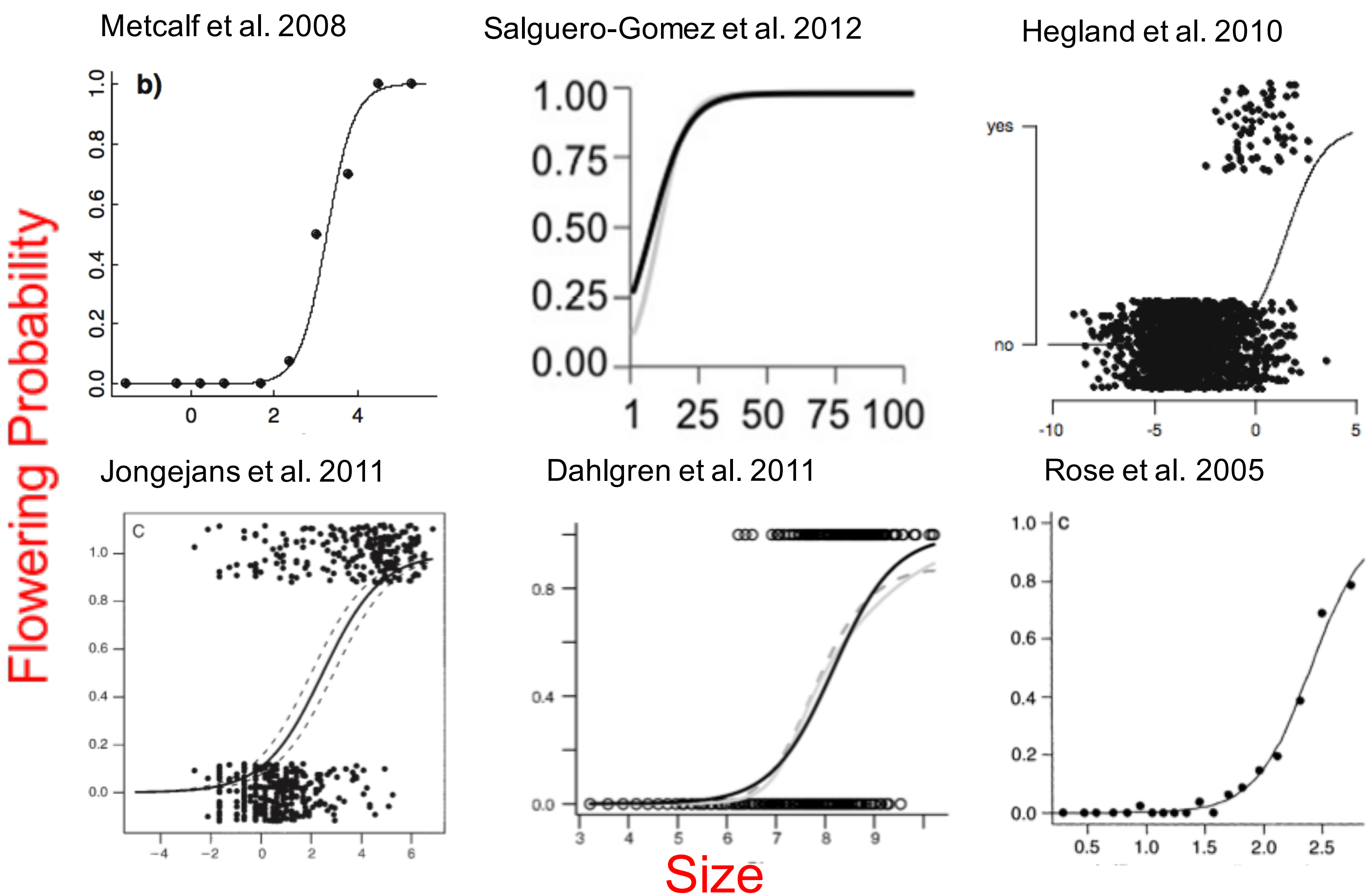


Metcalf et al. 2008

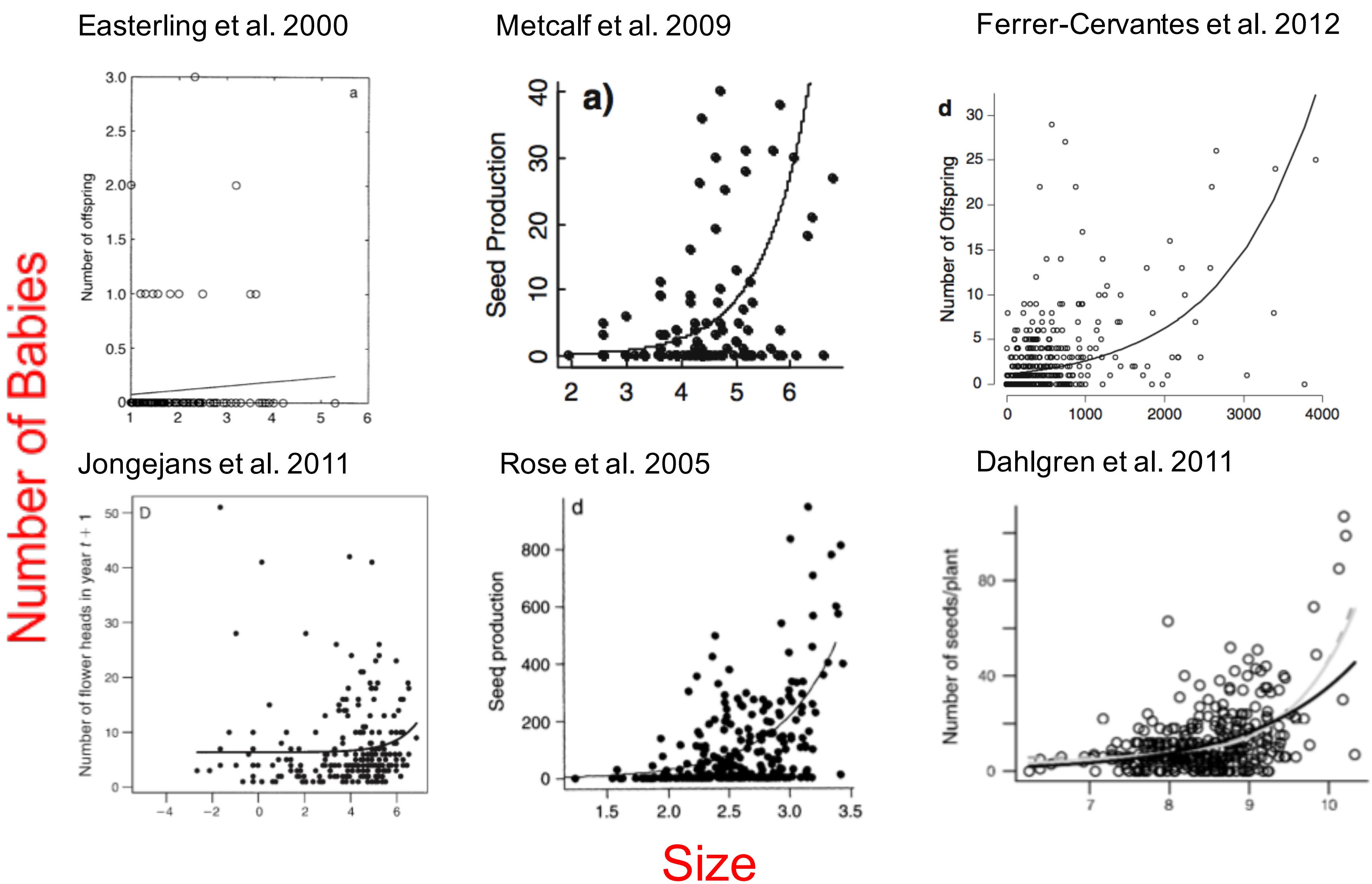


Size

Vital Rate Regression: Flowering – $p_{flower}(x)$



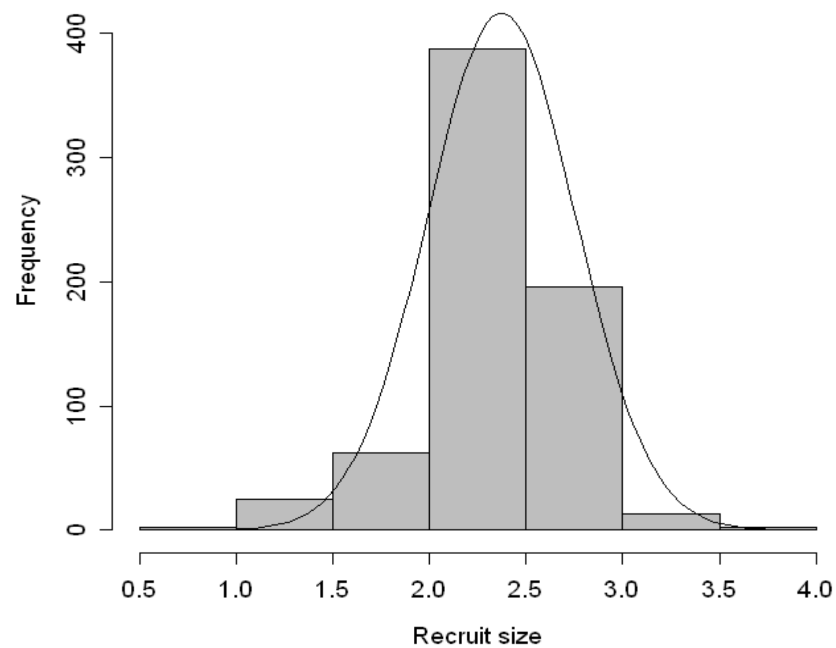
Vital Rate Regression: Fecundity – $f_{seeds}(x)$



Vital Rate Regression: Fecundity – $f_{recruit}(x,y)$

Usually…

$$f_{recruit}(y) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{(y-\mu)^2}{2\sigma^2}\right)$$



Vital Rate Regression: Fecundity – $f_{recruit}(x,y)$

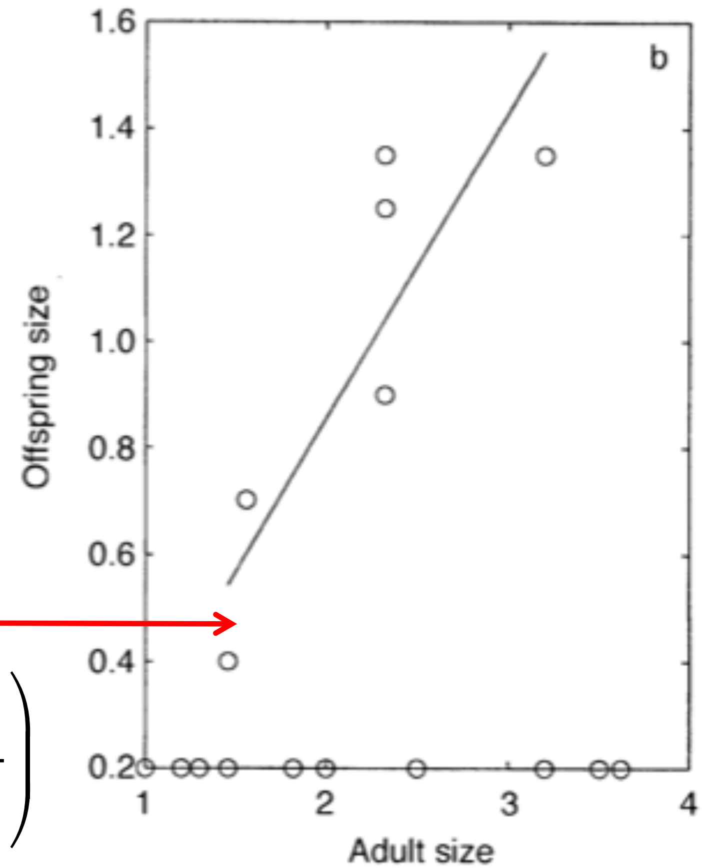
Usually…

$$f_{recruit}(y) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{(y-\mu)^2}{2\sigma^2}\right)$$

but sometimes…

$$\mu(x) = ax + b$$

$$f_{recruit}(x,y) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{(y-(ax+b))^2}{2\sigma^2}\right)$$



Easterling et al. 2000

Workflow

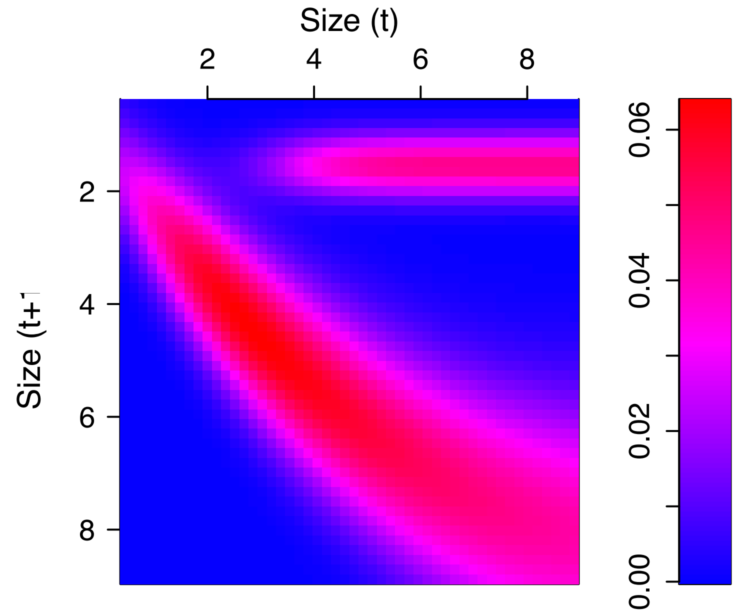
Life History

Data

Vital Rate Regressions

IPM Kernel

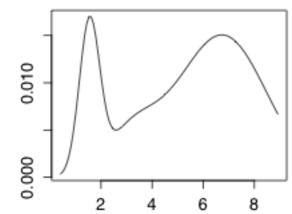
Analysis



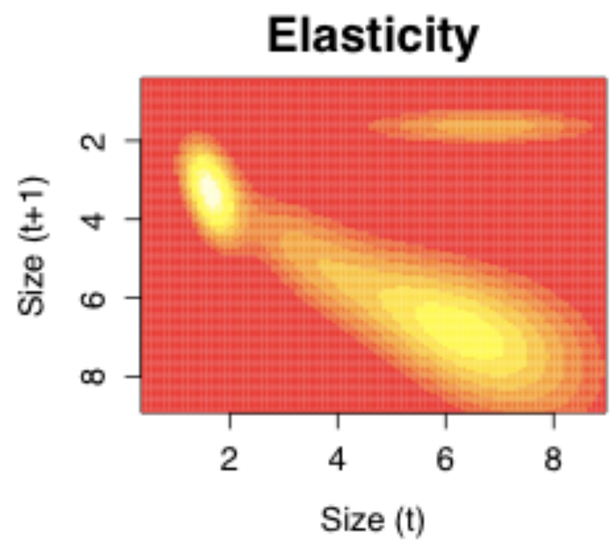
Analysis

- Want the same things from IPMs as from matrix models
  - Eigenvalues
  - Eigenfunction (vectors)

λ



- Can do all the same analyses with IPMs as matrix models
  - Elasticity/sensitivity
  - Forward projections
  - Stochastic dynamics
  - Life table response experiments
  - Passage time, Life expectancy
  - Etc…



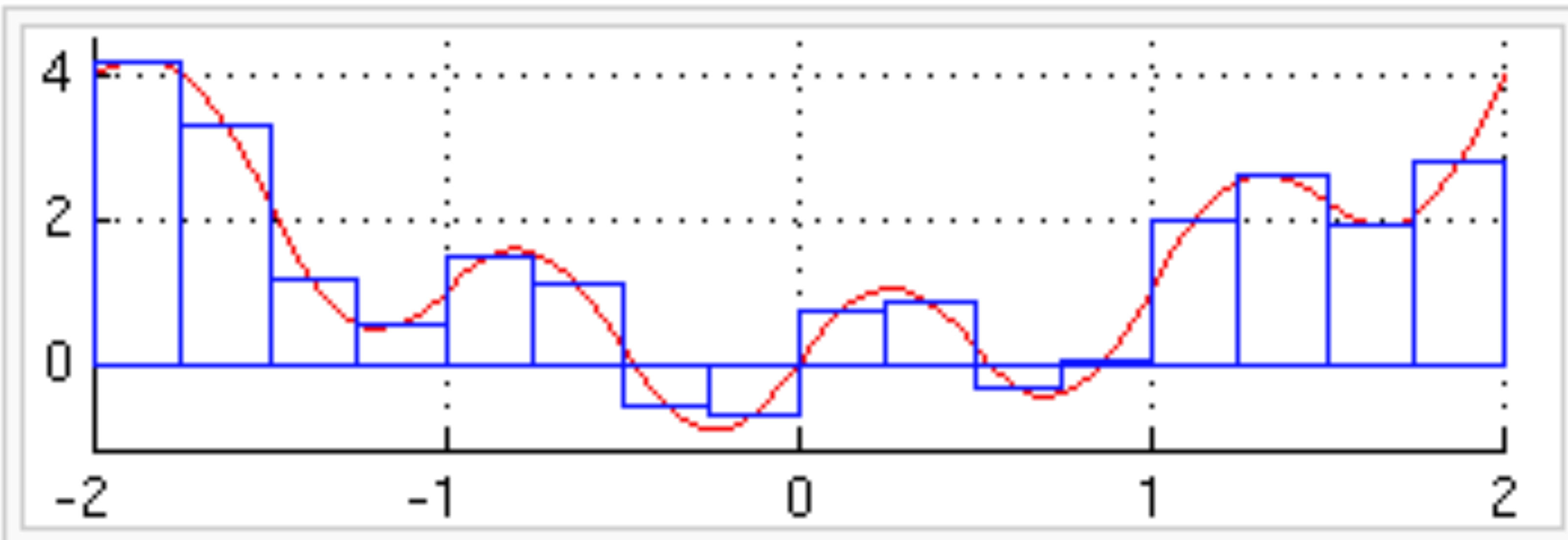
Full kernel function

$$size(y)_{t+1} = \int_{all\ sizes} \left[growth(size\ x \to y) + offspring(size\ x \to y) \right] size(x)_t\, dx$$

$$n_{t+1}(y) = \int_{\Omega} \begin{bmatrix} \mathrm{logit}(a_s x + b_s) * \dfrac{1}{\sqrt{2\pi (a_{g\sigma} x + b_{g\sigma})^2}} \exp\left(\dfrac{(x - (a_{g\mu} x + b_{g\mu}))}{2(a_{g\sigma} x + b_{g\sigma})^2} \right) + \\ \exp(a_{f\#} x + b_{f\#}) * \dfrac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\dfrac{(x - (a_f x + b_f))^2}{2o^2} \right) \end{bmatrix} n_t(x)\, dx$$

Numerical integration

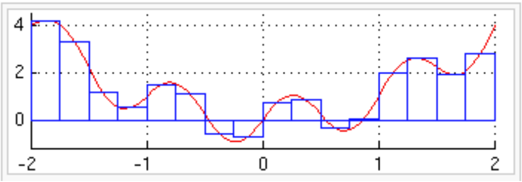
Midpoint rule

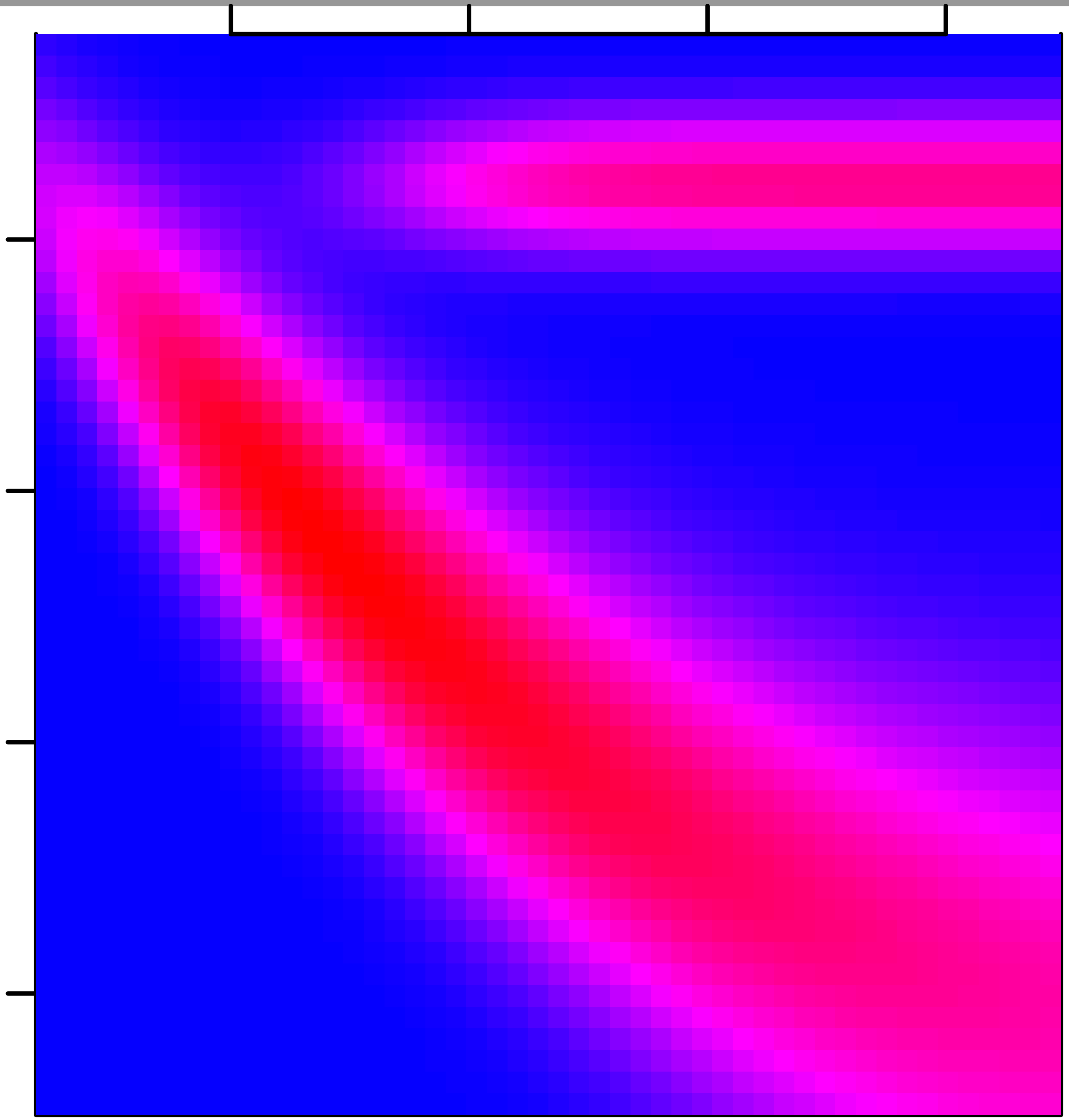


IPMs discretize for numerical integration

Numerical integration

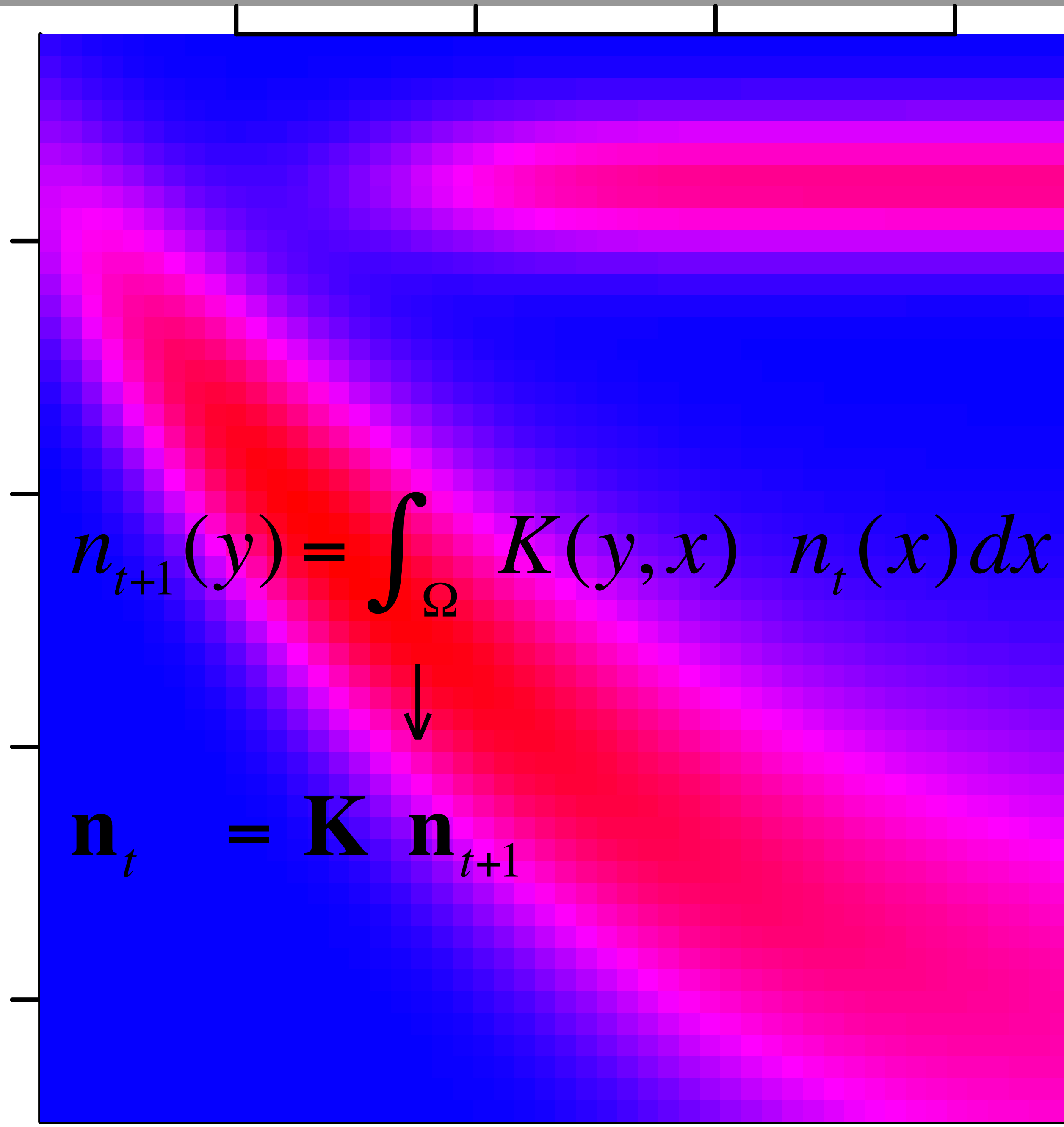
Evaluate kernel at midpoint of each cell to obtain a large matrix





Numerical integration

Evaluate kernel at midpoint of each cell to obtain a large matrix



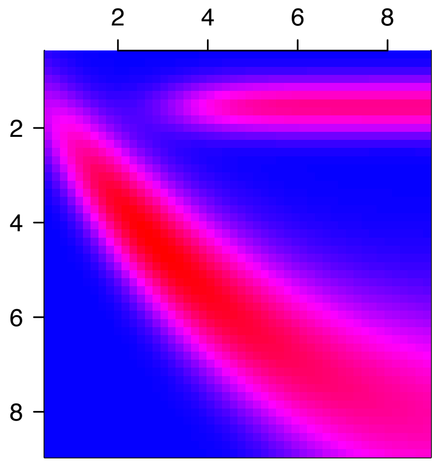
$$n_{t+1}(y) = \int_{\Omega} K(y,x) \; n_t(x)\,dx$$

$$\downarrow$$

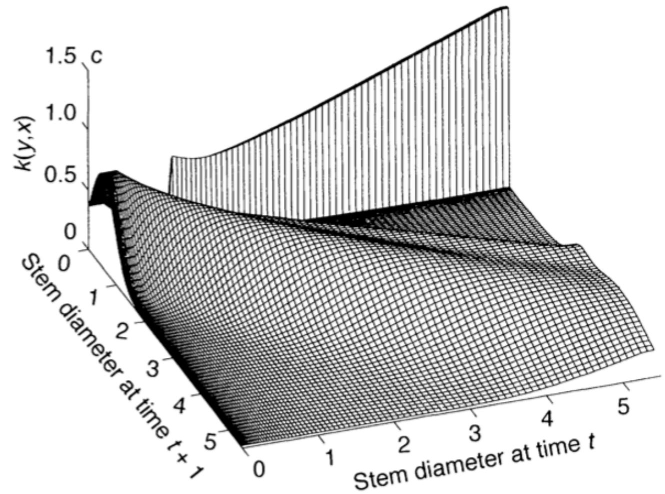
$$\mathbf{n}_t = \mathbf{K} \; \mathbf{n}_{t+1}$$

Full kernel function

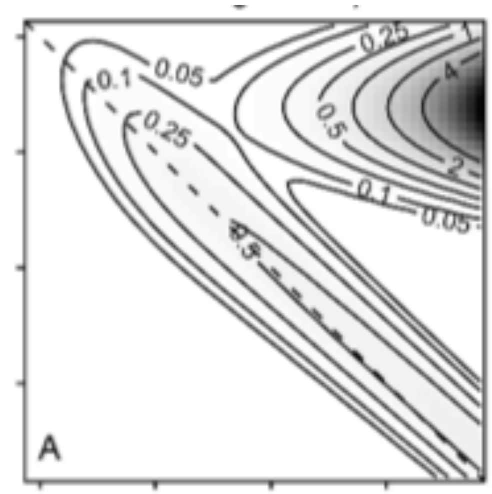
~Nicolé et al. 2011



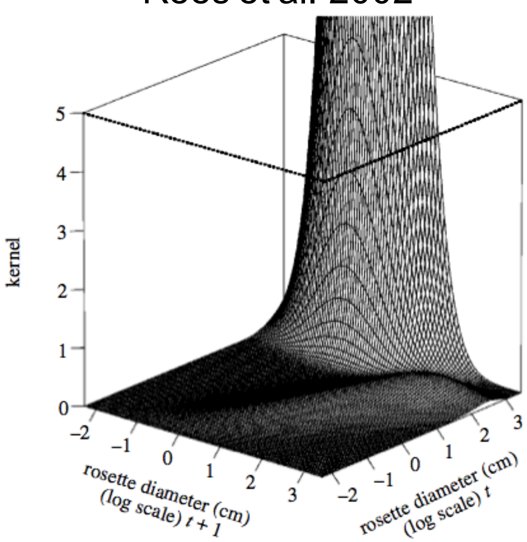
Easterling et al. 2000



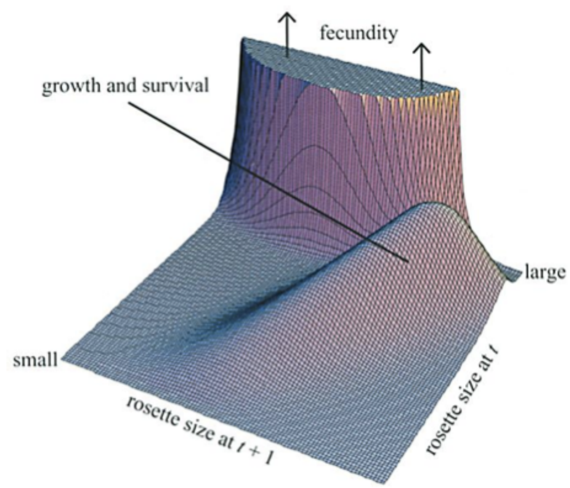
Dalgliesh et al. 2011



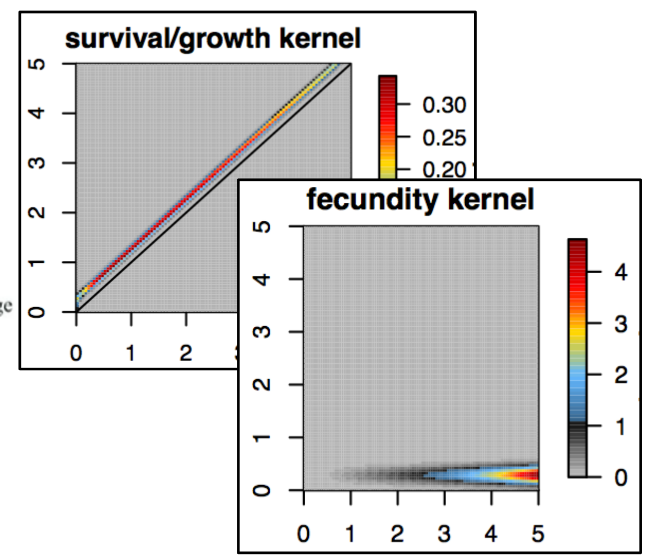
Rees et al. 2002



Godfray et al. 2002

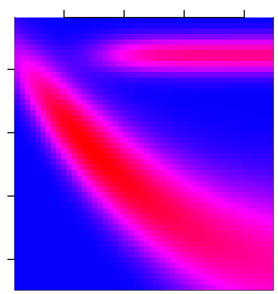


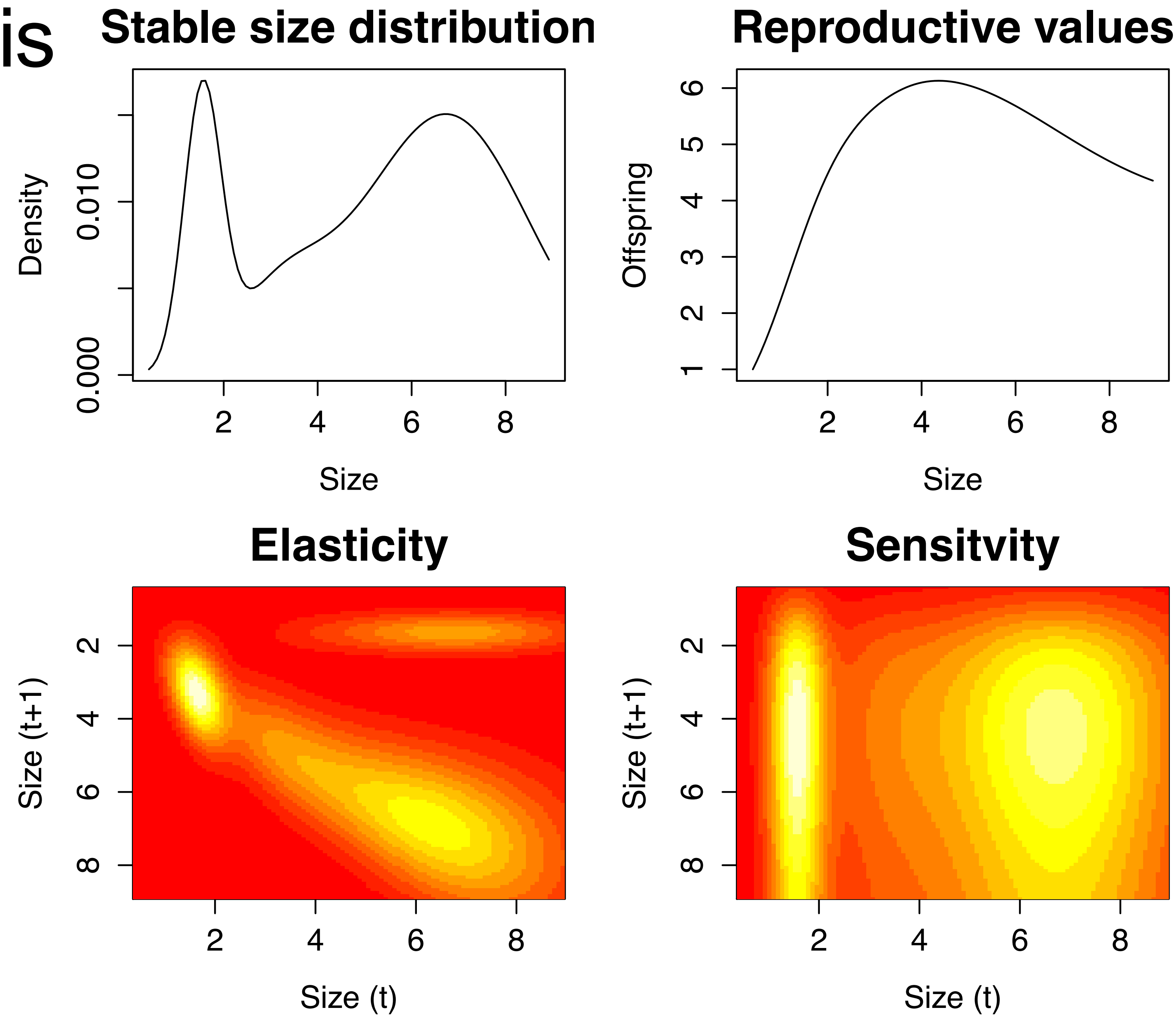
Merow et al. 2014



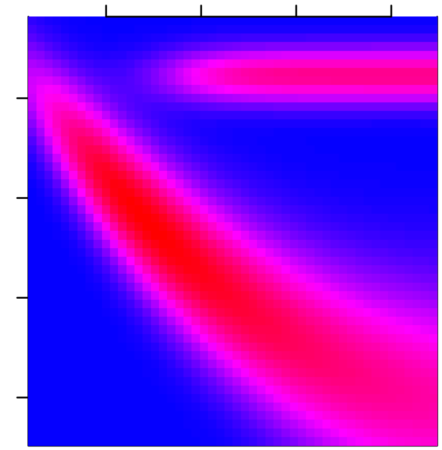
Analysis

Kernel





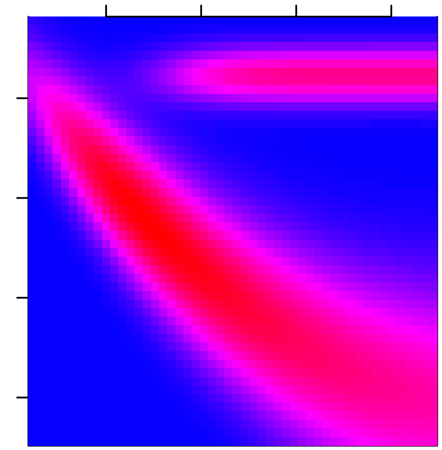
Summary - Why IPMs?



Process-based demography

- Continuous stages
- Heterogeneity among individuals
- Decompose life history to desired level of detail
- Built on regressions and matrices

Summary - Why IPMs?



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Questions?