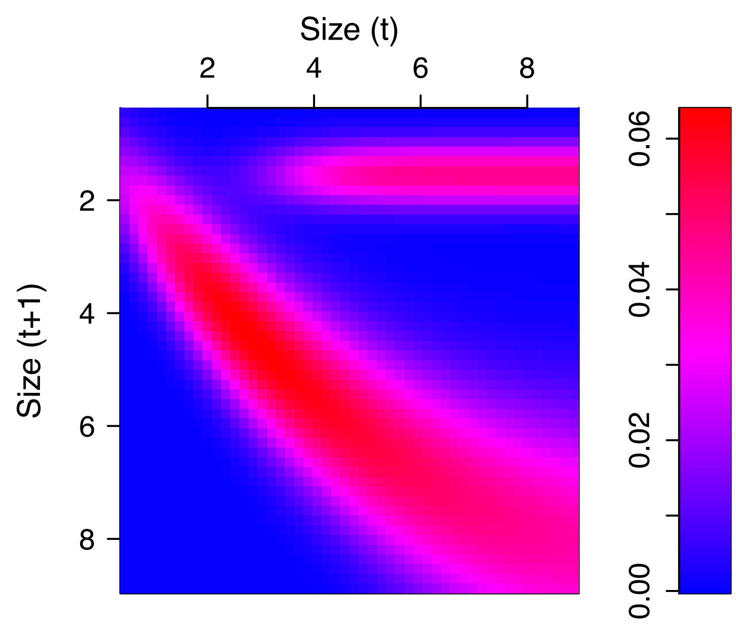
AN INTRODUCTION TO INTEGRAL PROJECTION MODELS (IPMS)

Cory Merow



Methods in Ecology and Evolution

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REVIEW

Advancing population ecology with integral projection models: a practical guide

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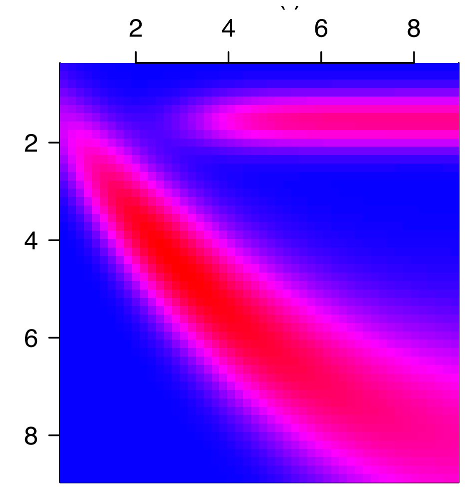
IPMs

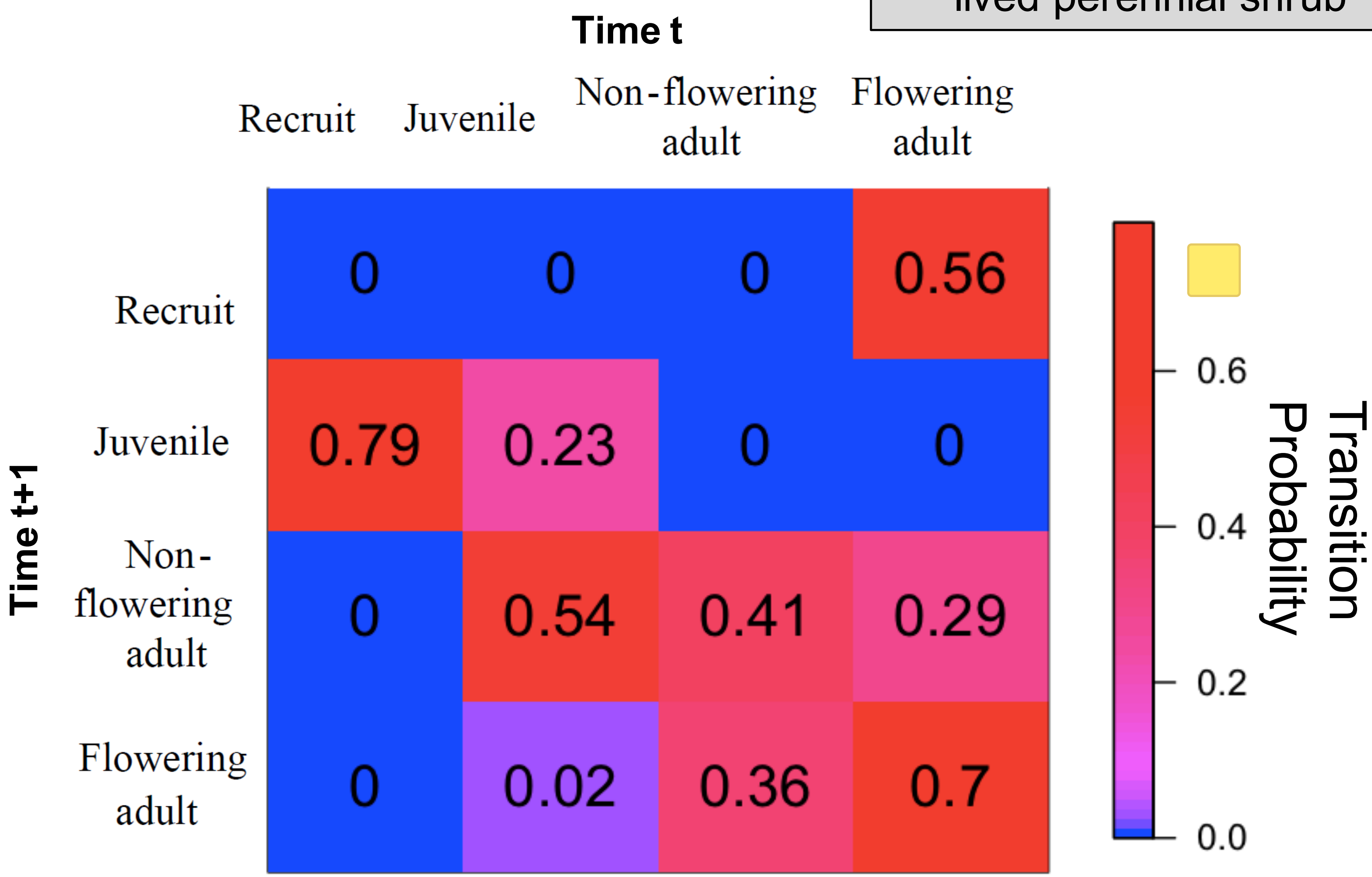
Process-based demography:

- 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



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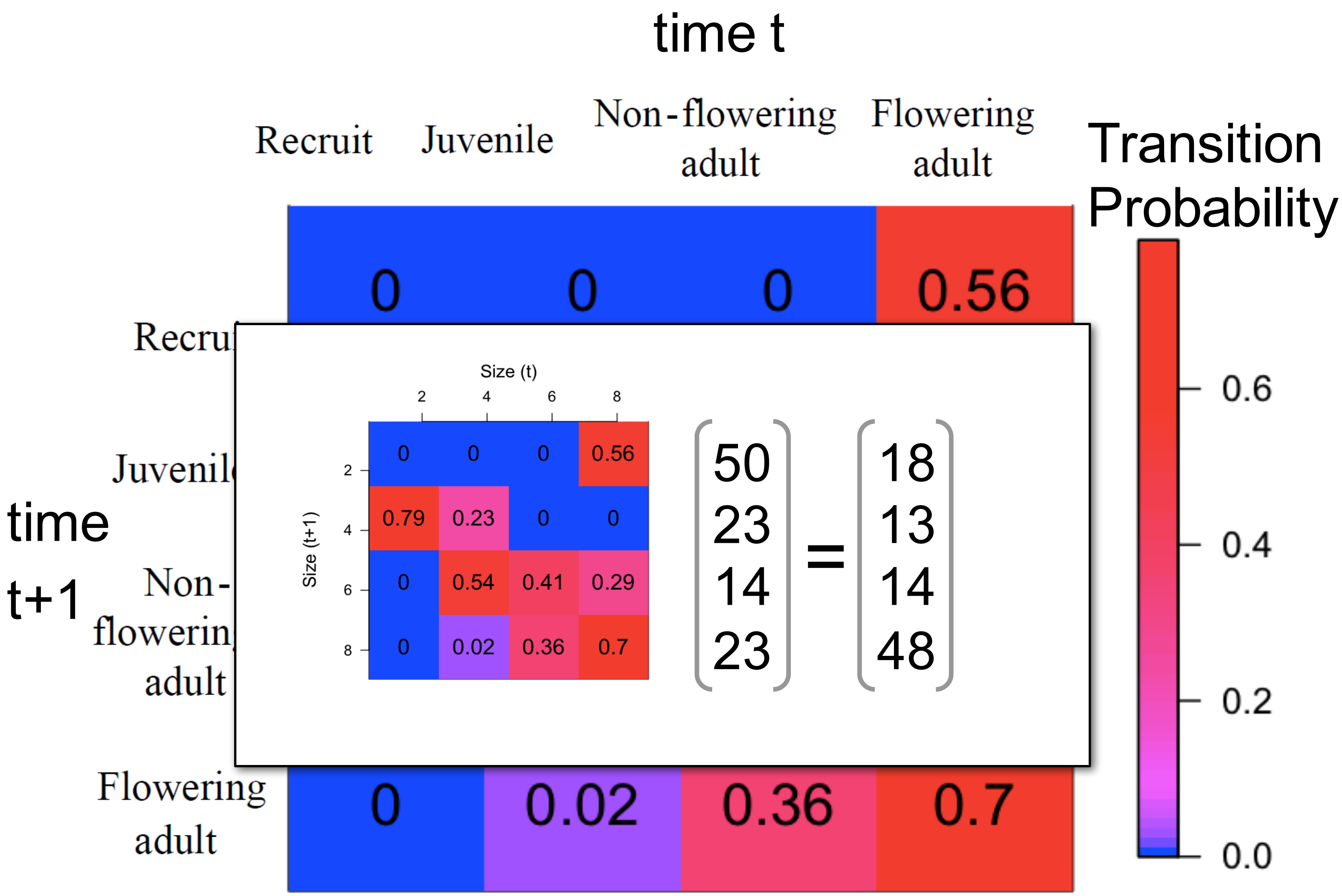

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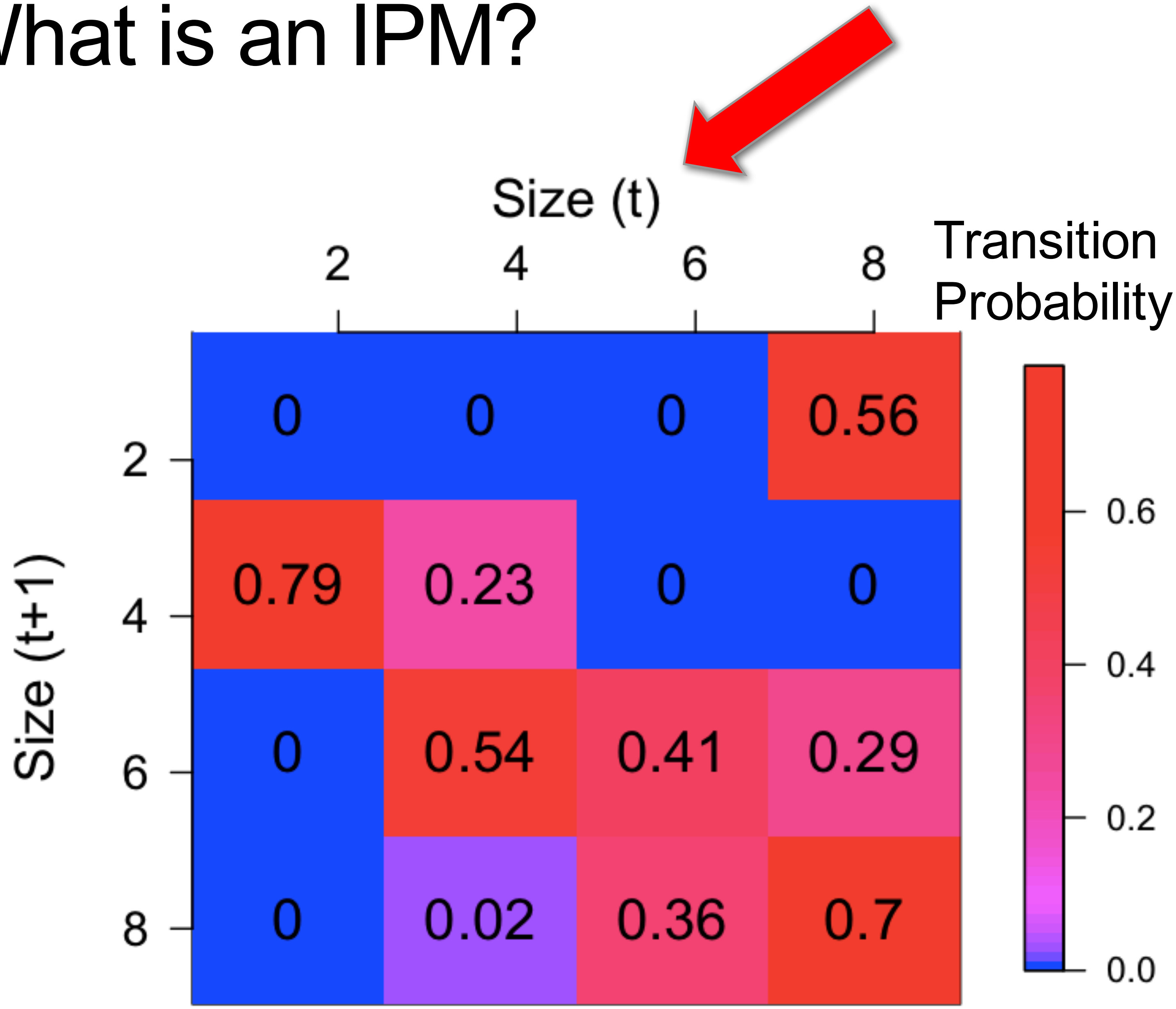

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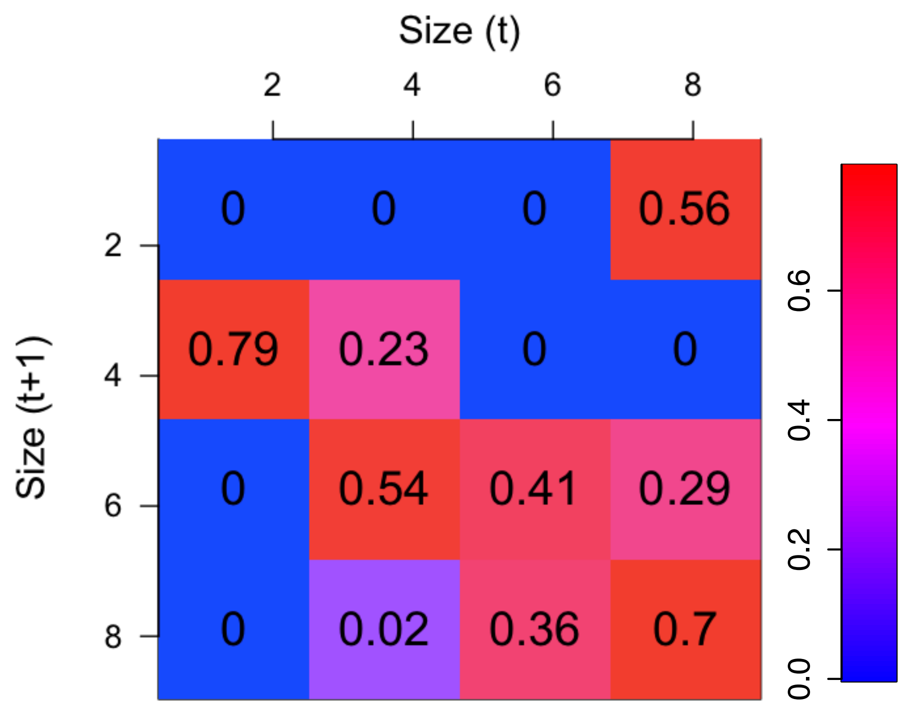
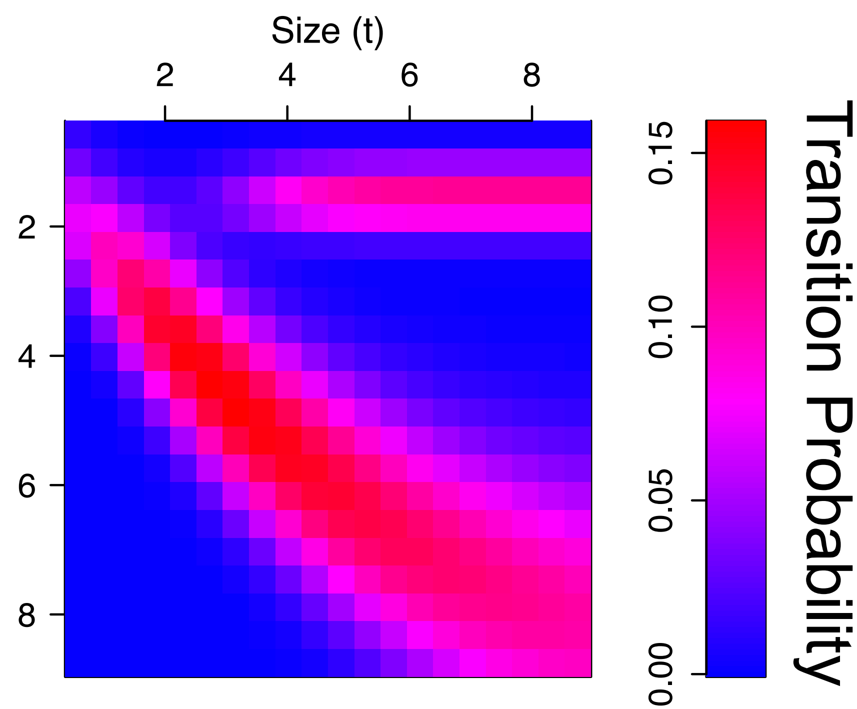
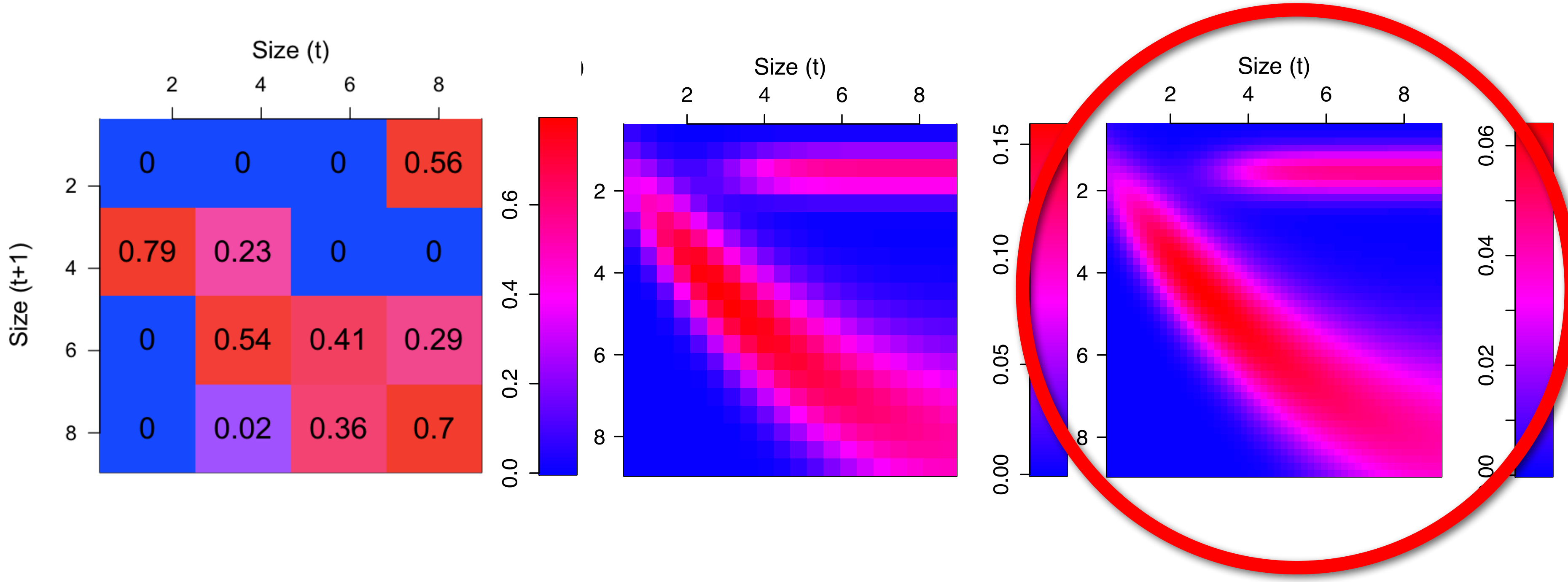




More stages = more heterogeneity among individuals

What is an IPM?



Matrix models and IPMs arrive at matrices for different reasons

Workflow

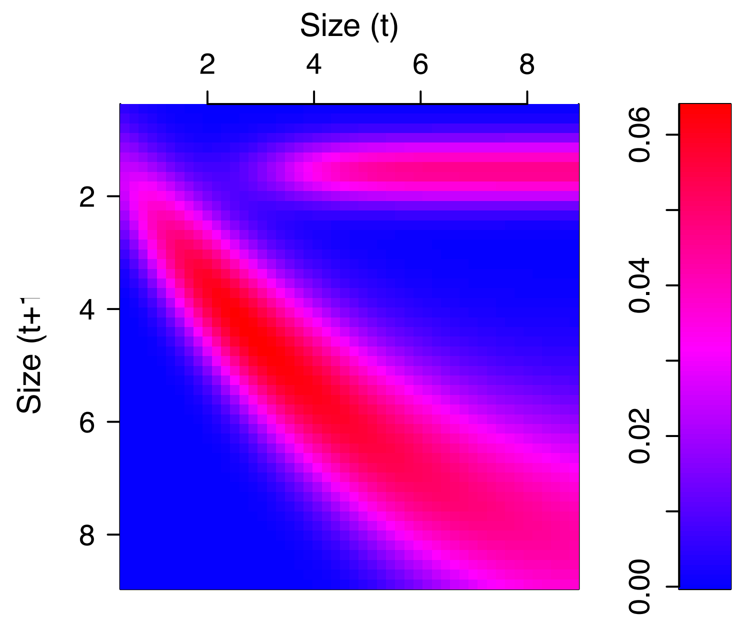
Life History

Data

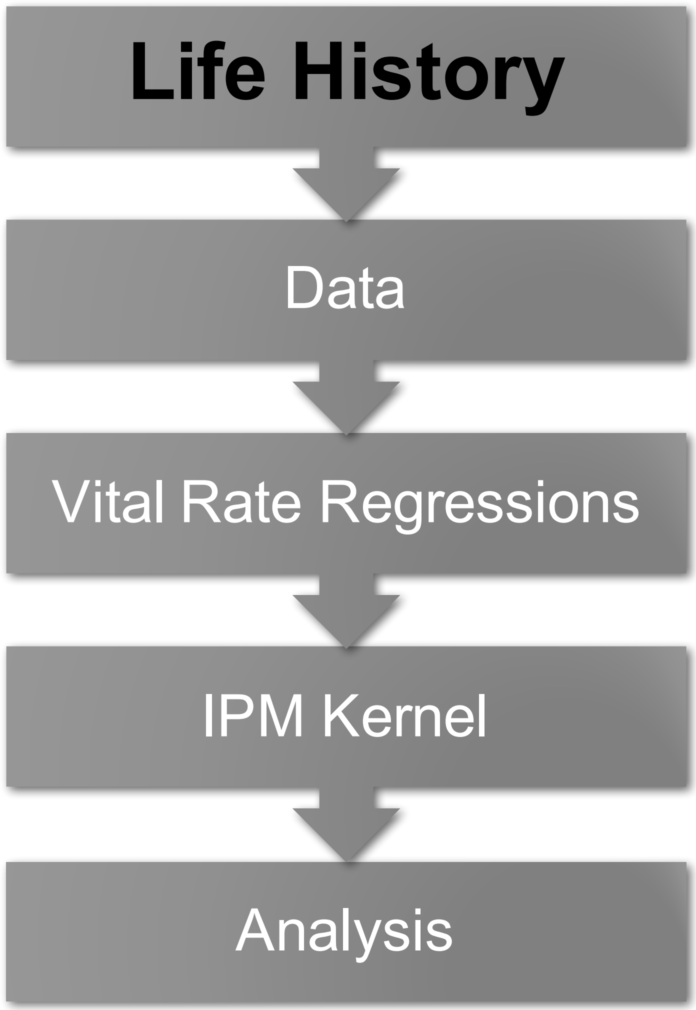
Vital Rate Regressions

IPM Kernel

Analysis



Workflow



Life History
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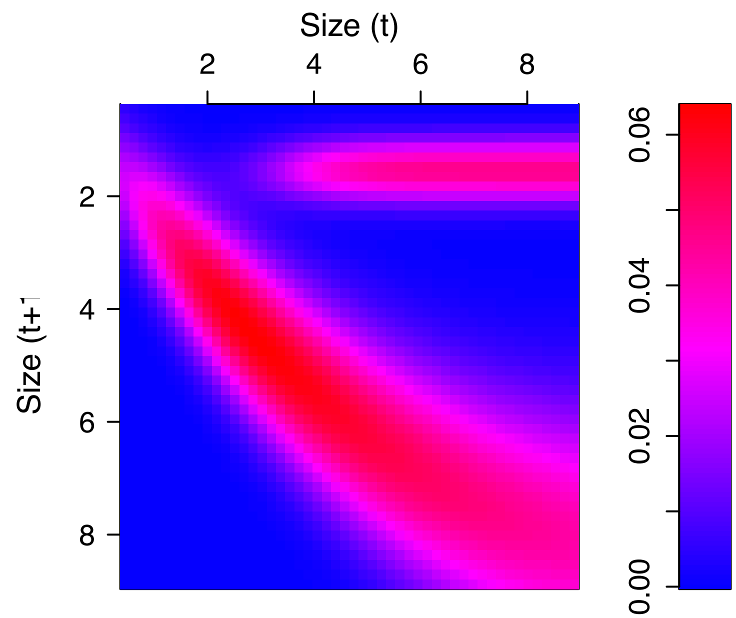
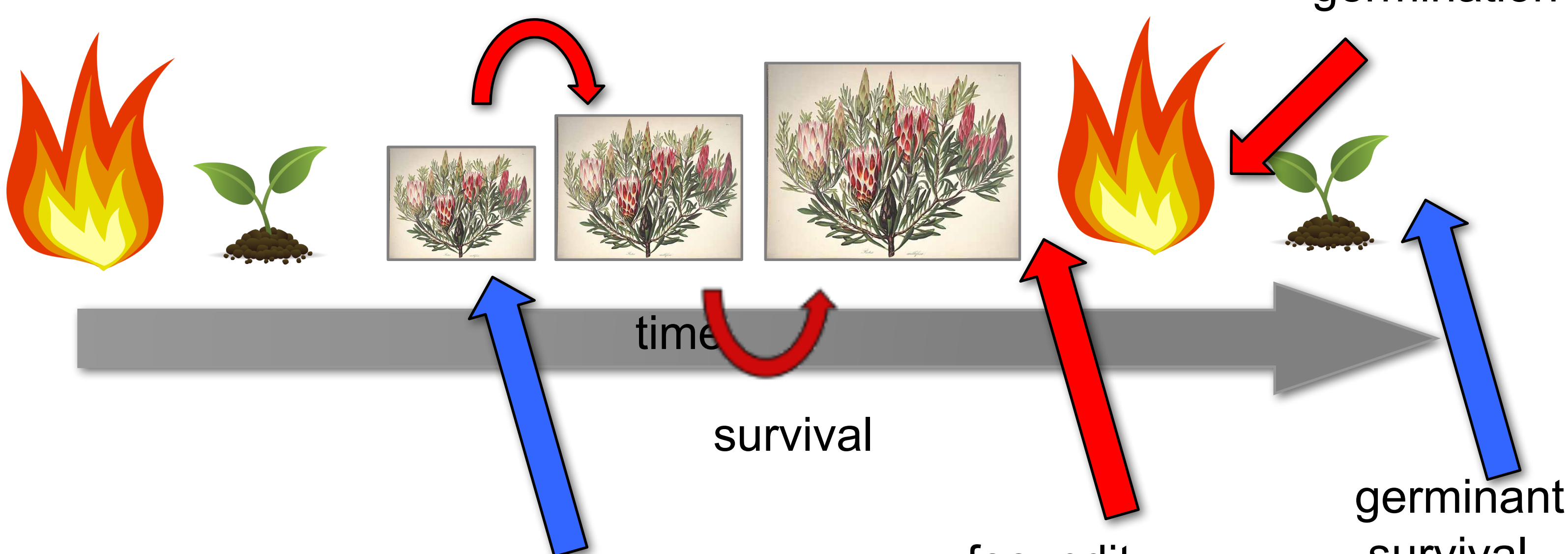


Size (t)
2
4
6
8
Size (t+
2
4
6
8
0.00
0.02
0.04
0.06

Life history



Workflow

Life History

↓

Data

↓

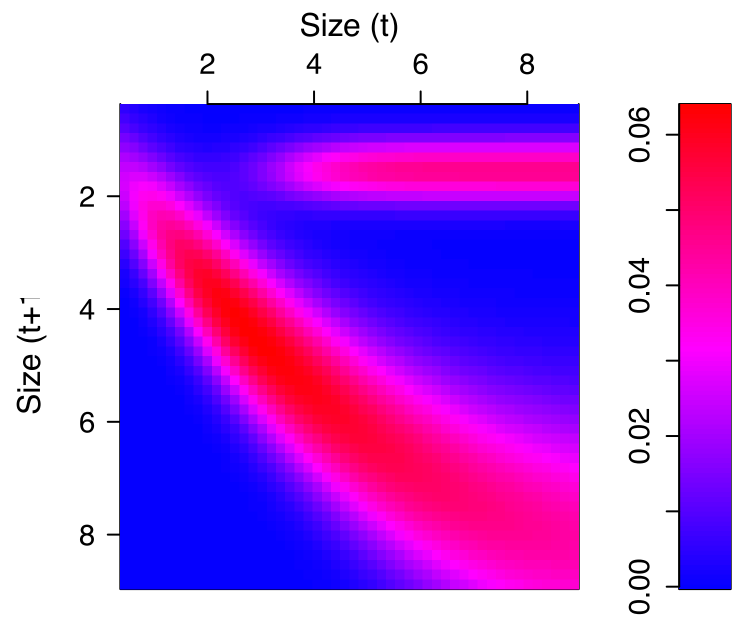
Vital Rate Regressions

↓

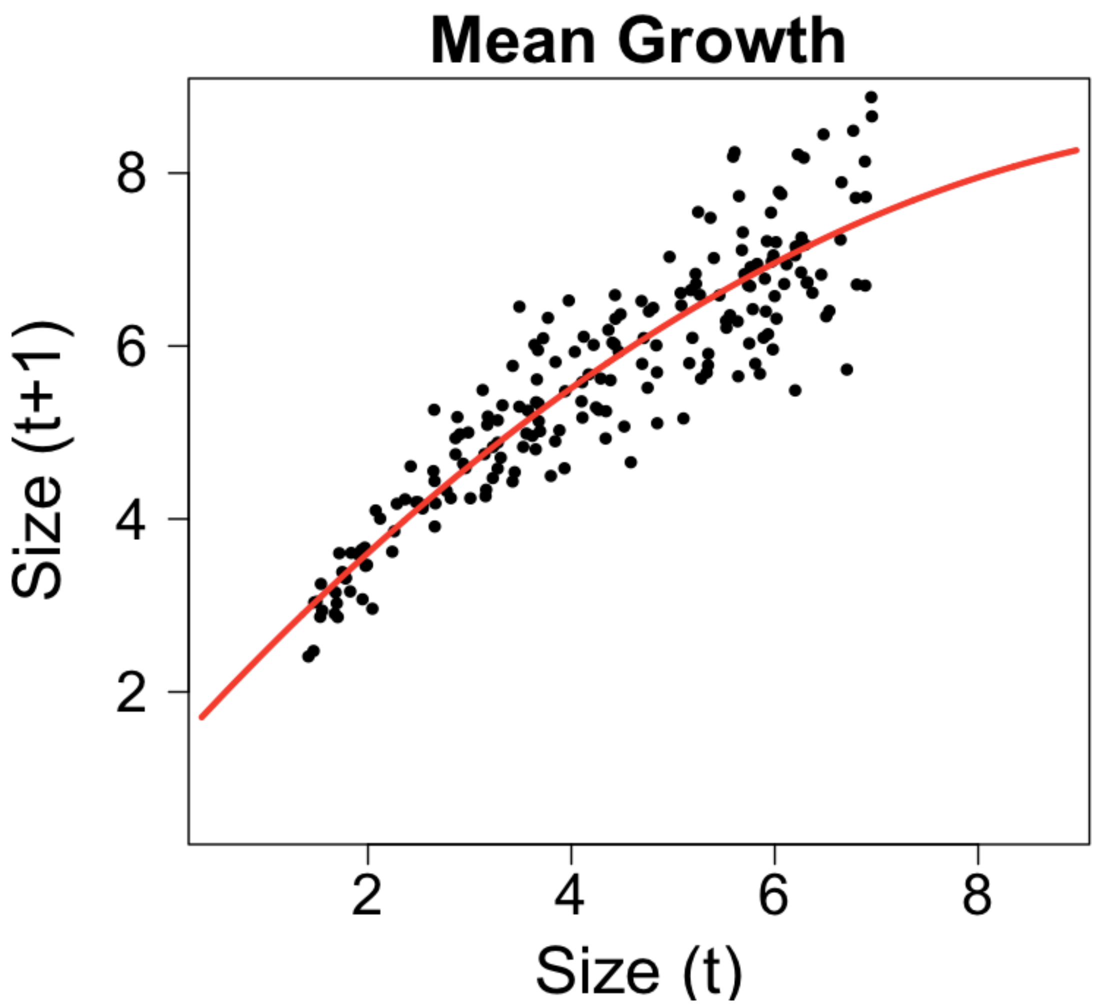
IPM Kernel

↓

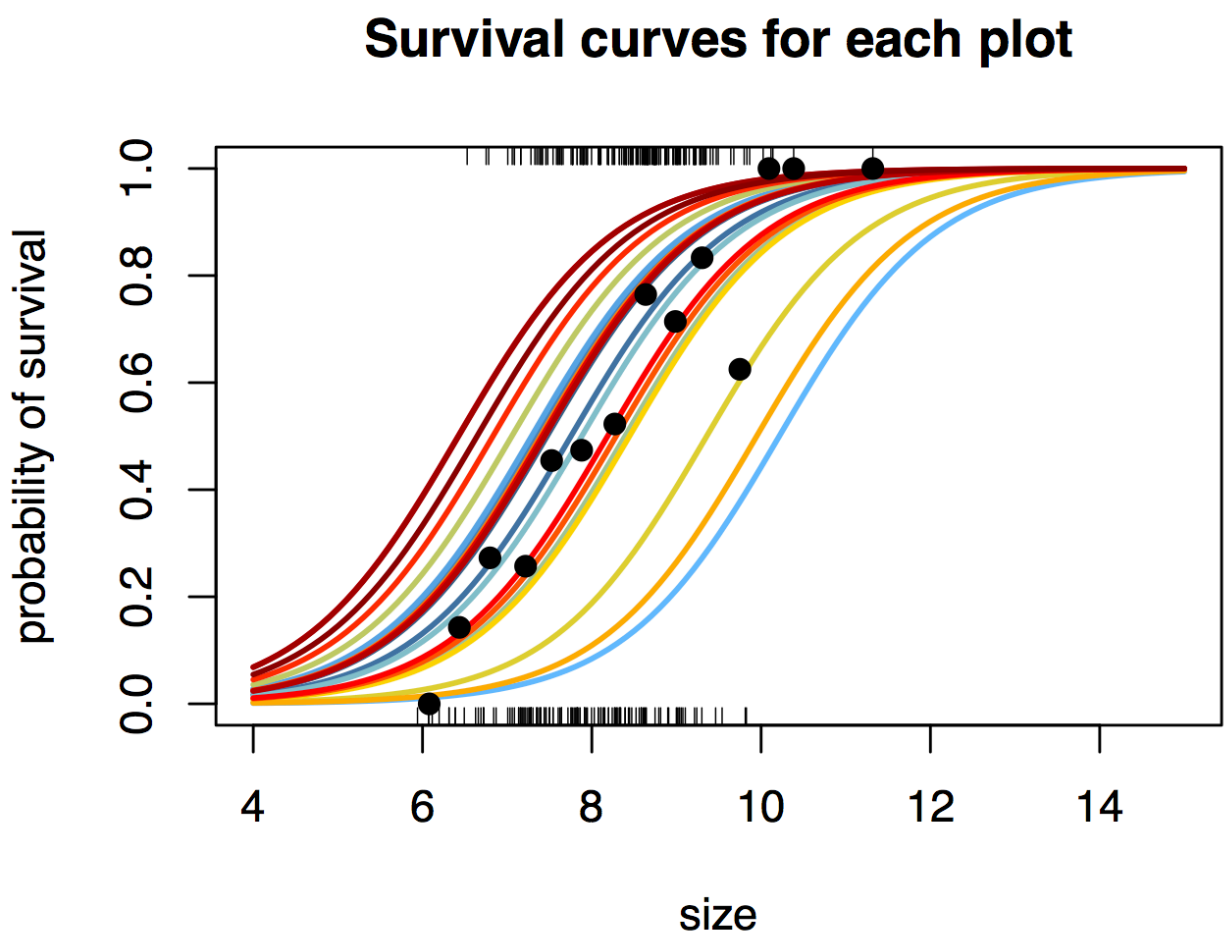
Analysis



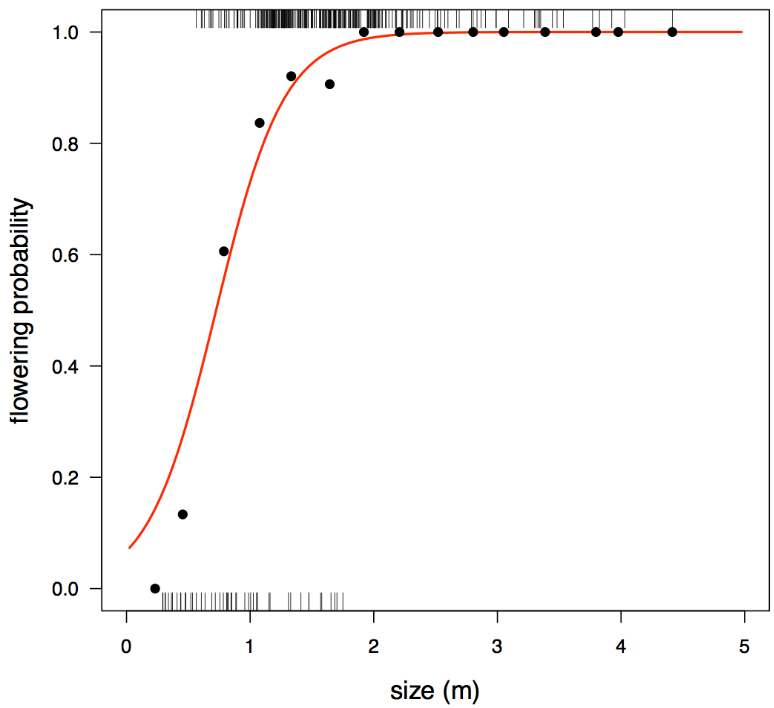
Data: Growth

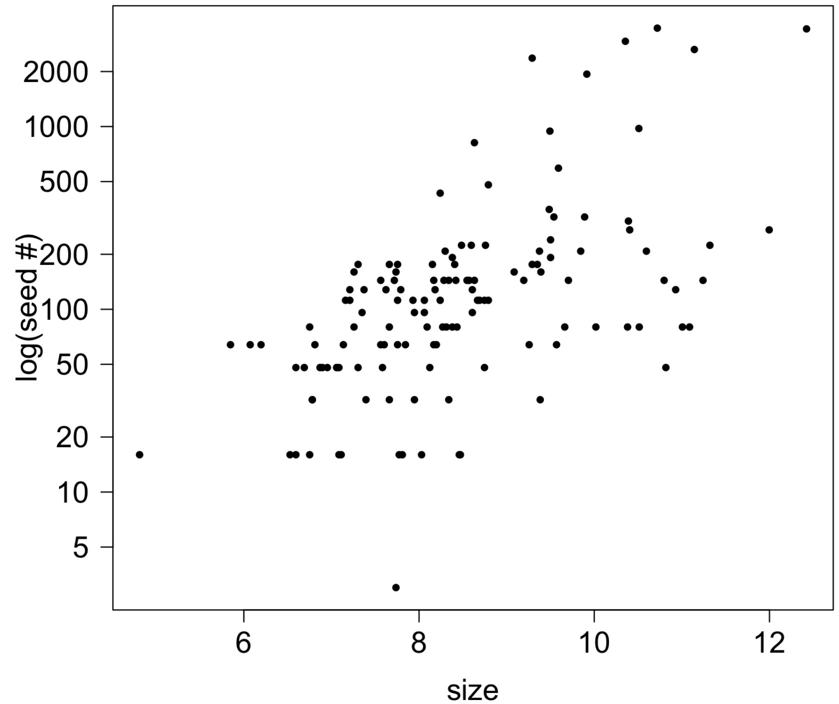


Data: Survival



Data: Fecundity





Germination probability

Workflow

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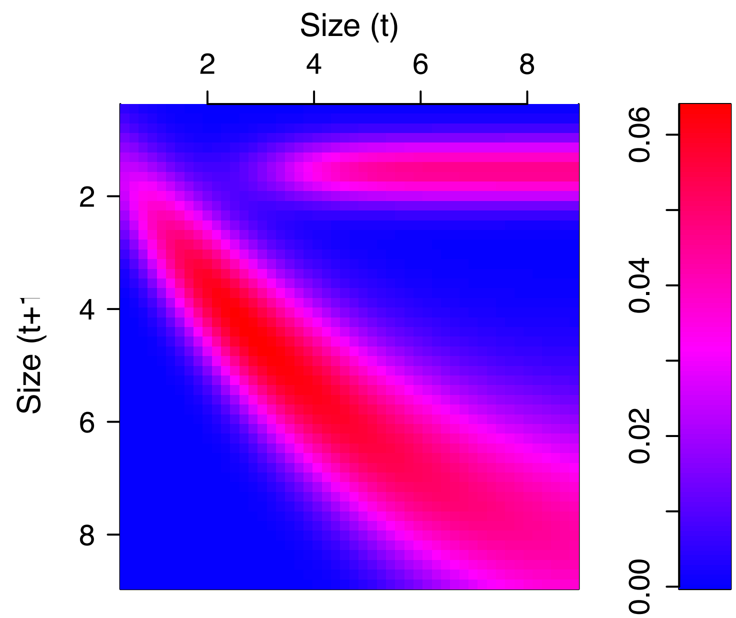
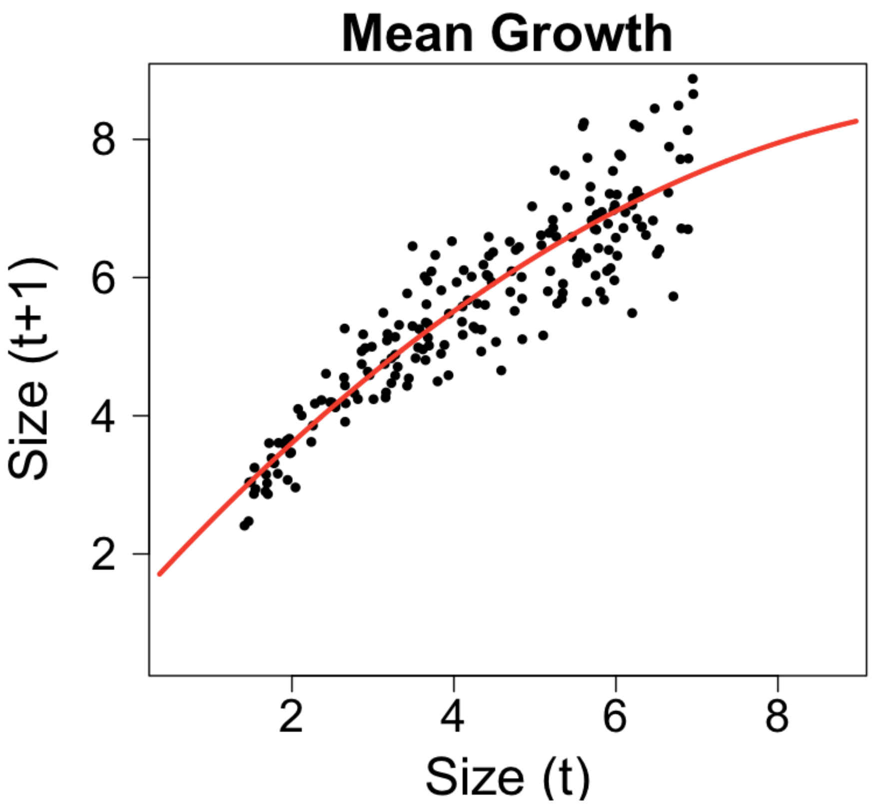
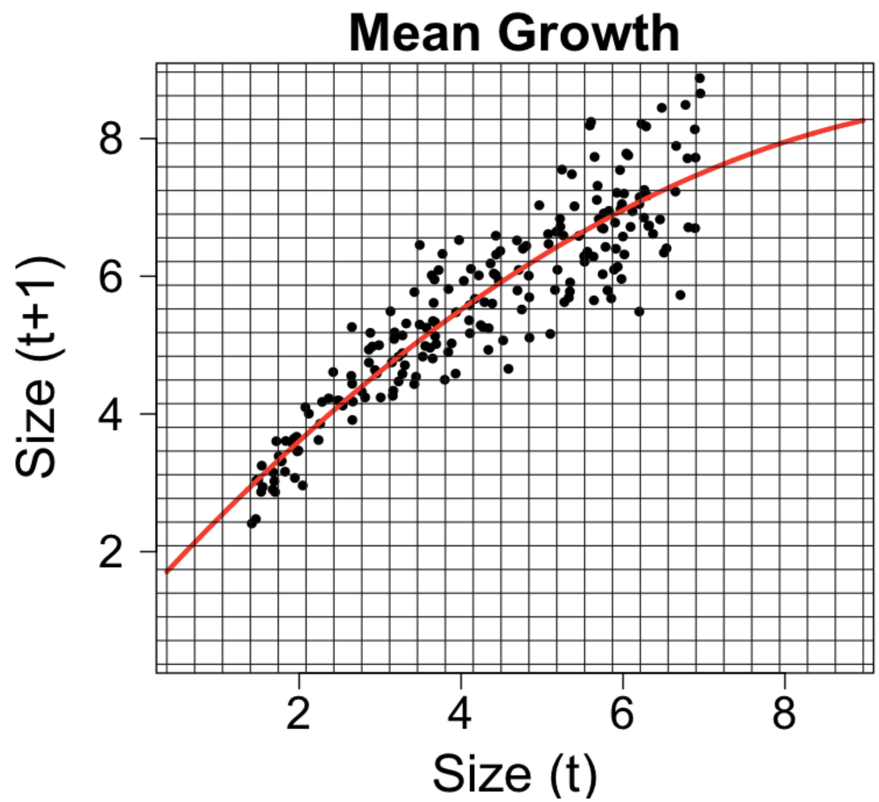


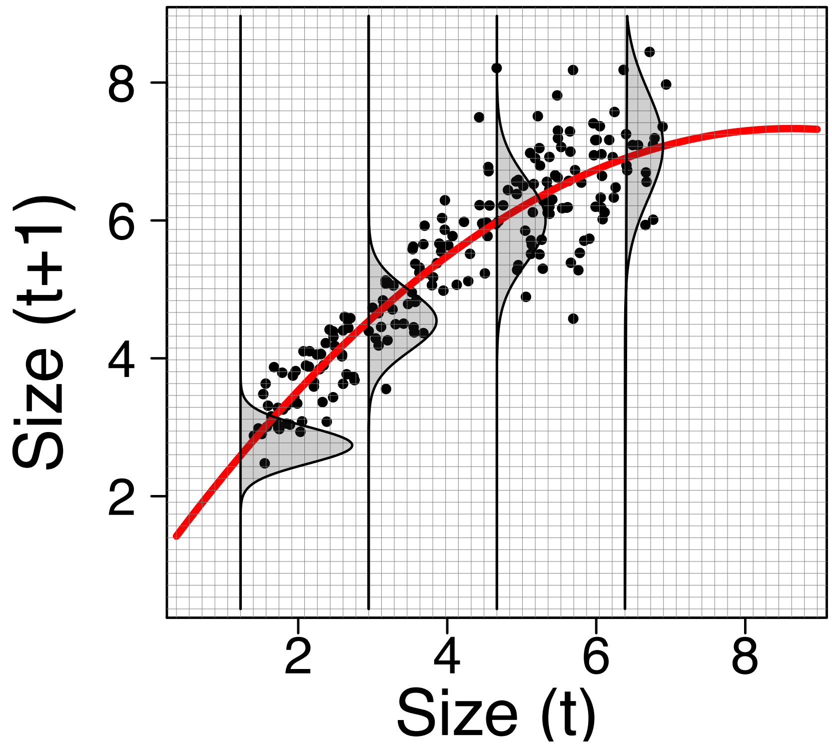
Vital Rate Regression: Growth

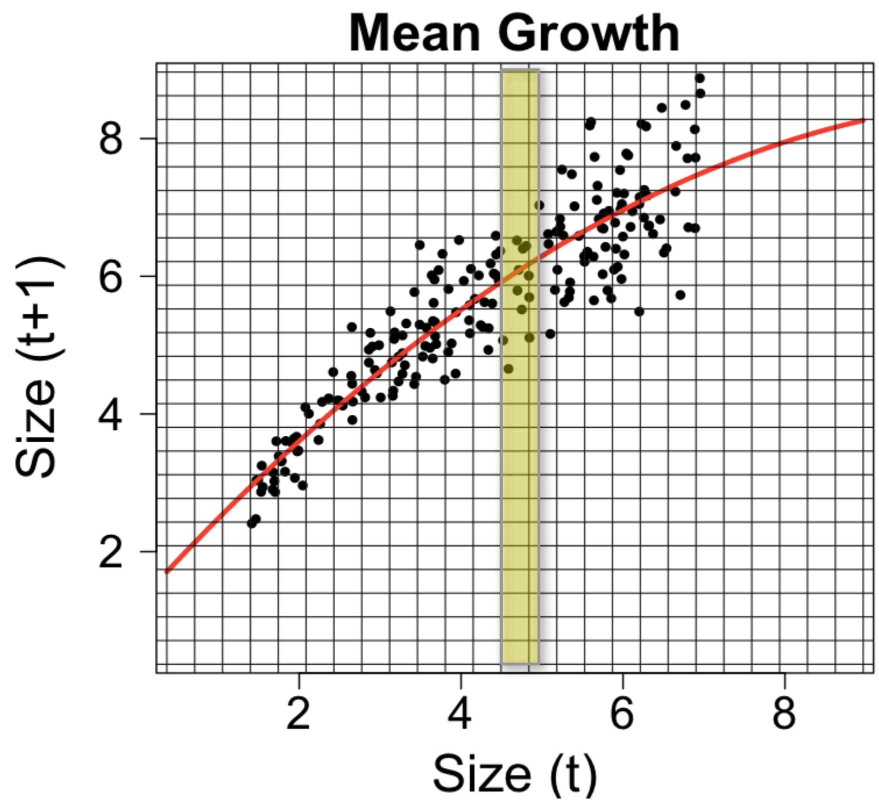




$$\text{mean} = b_0 + b_1 size + b_2 size^2$$

Vital Rate Regression: Growth

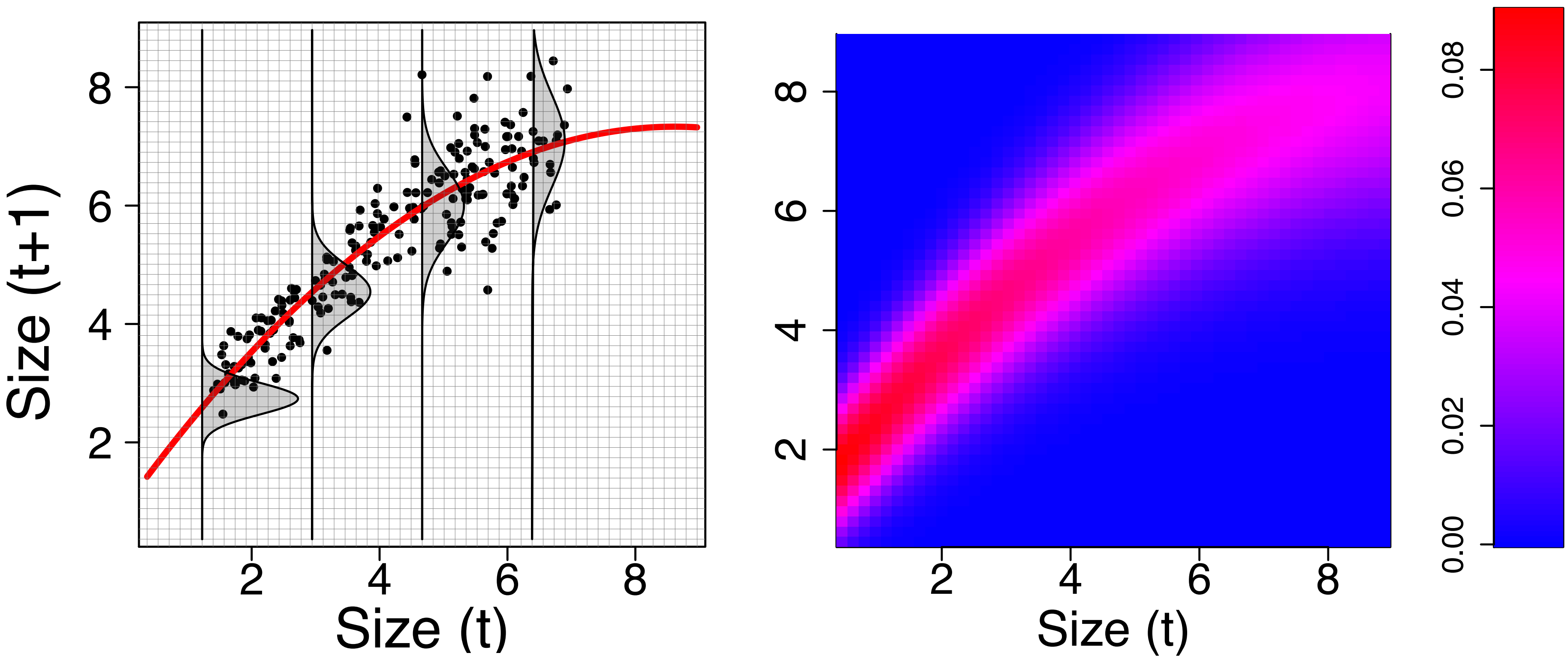




$$\text{mean} = b_0 + b_1 size + b_2 size^2$$

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

Vital Rate Regression: Growth



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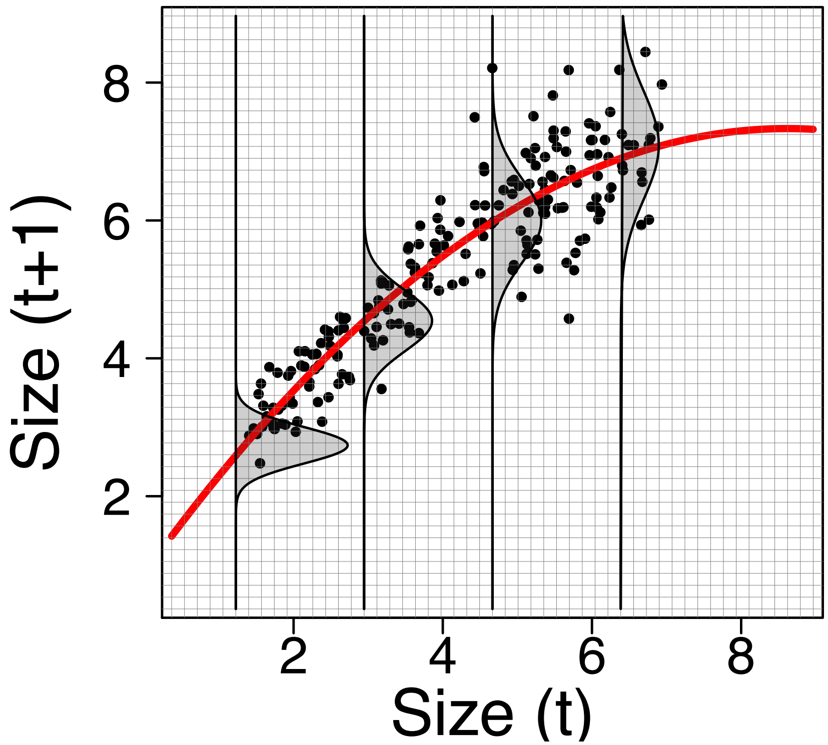
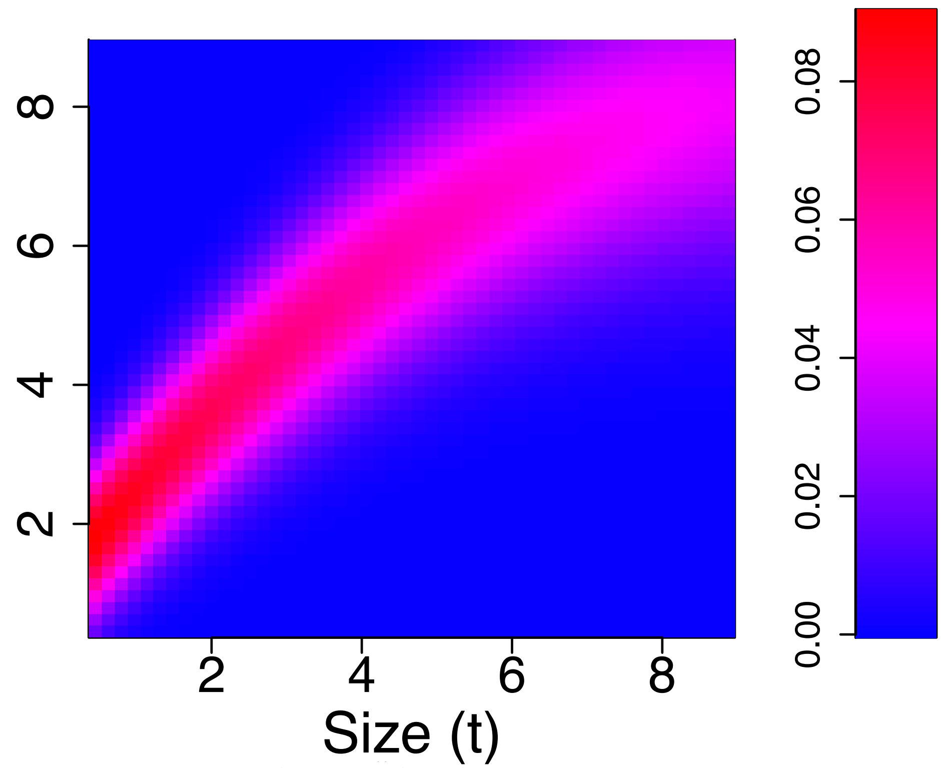
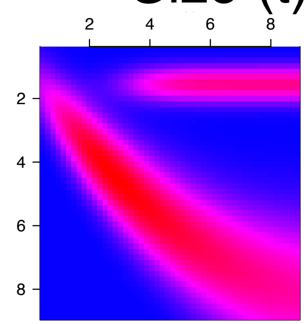
Vital Rate Regression: Growth



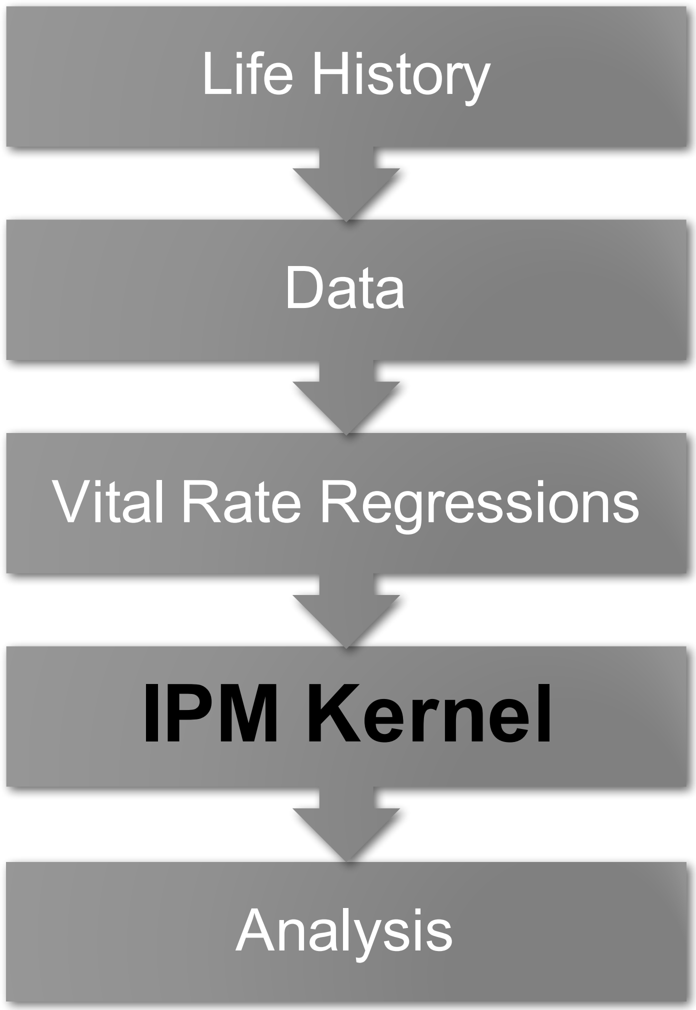


$$g(x,y)=\frac{1}{\sqrt{2\pi\sigma(x)^2}}\exp\left(\frac{(y-\mu(x))^2}{2\sigma(x)^2}\right)$$



Full kernel

Workflow


Life History
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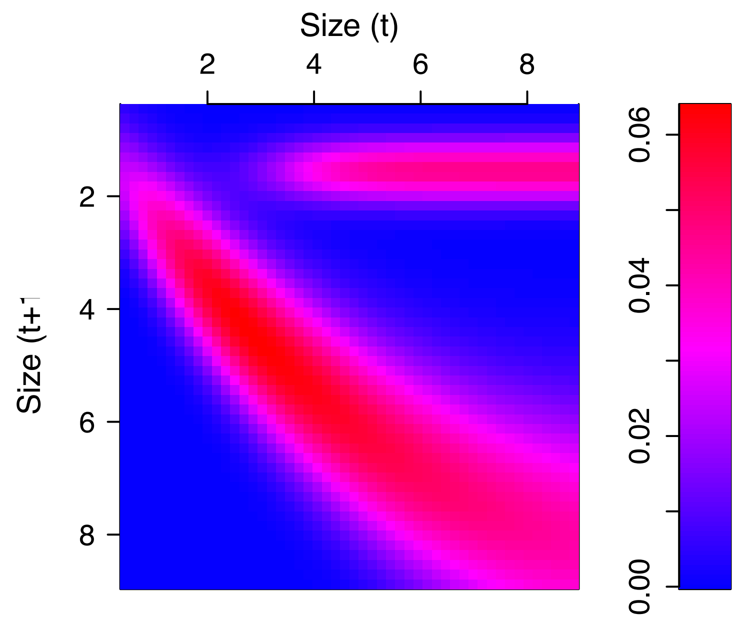
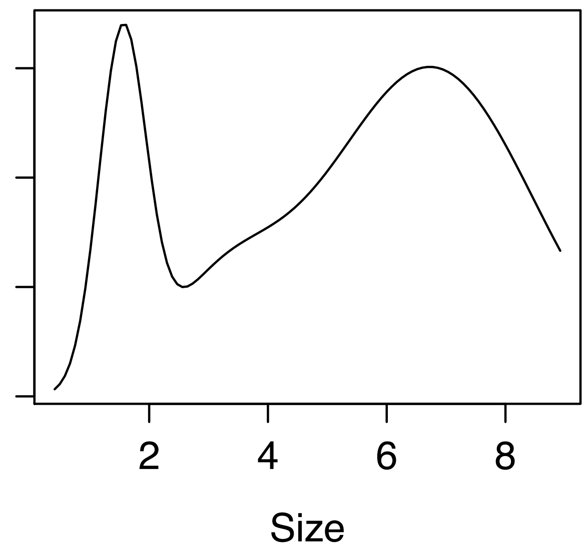

Size (t)
2
4
6
8
Size (t+
2
4
6
8
0.00
0.02
0.04
0.06

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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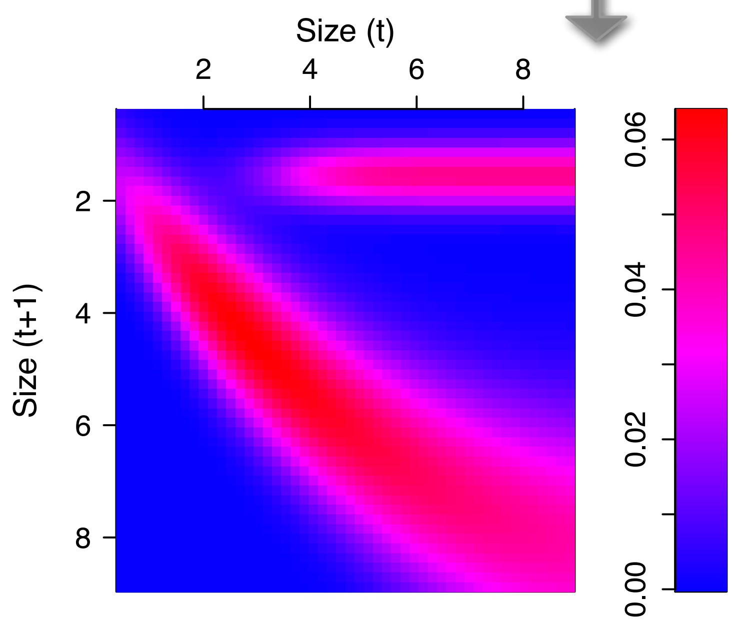

The model

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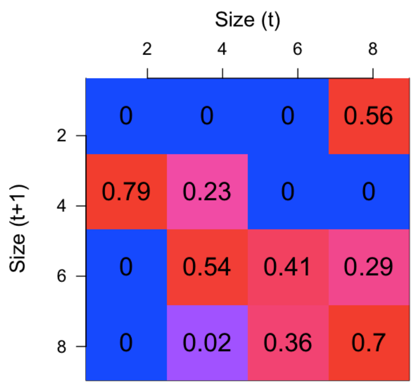
$$\mathbf{n}_{t+1} = \mathbf{A} \quad \mathbf{n}_t \qquad (Matrix)$$

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

The model



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

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

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

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

The model

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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
- y = size at t+1
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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

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

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Life History

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

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

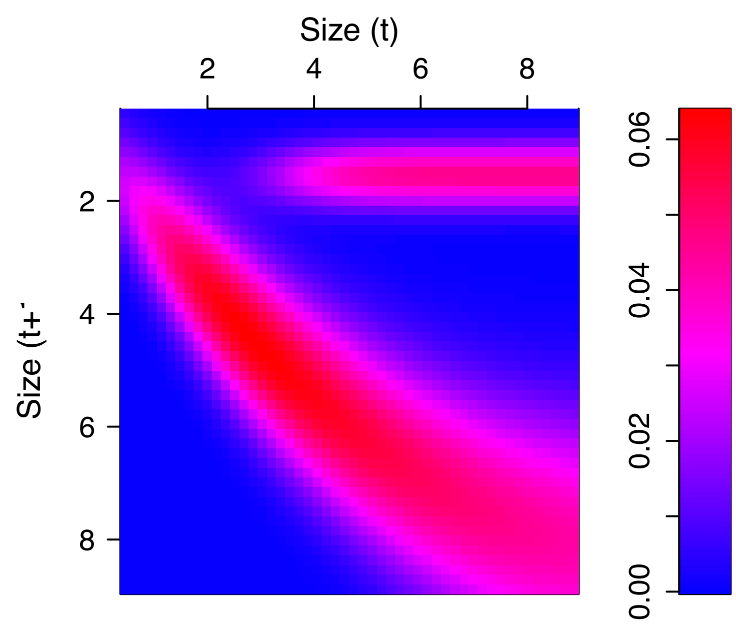
Life History

Data

Vital Rate Regressions

IPM Kernel

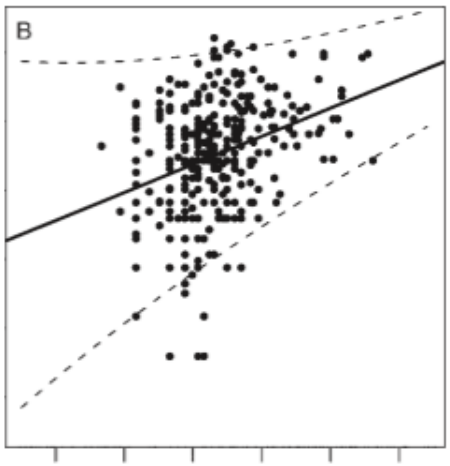
Analysis



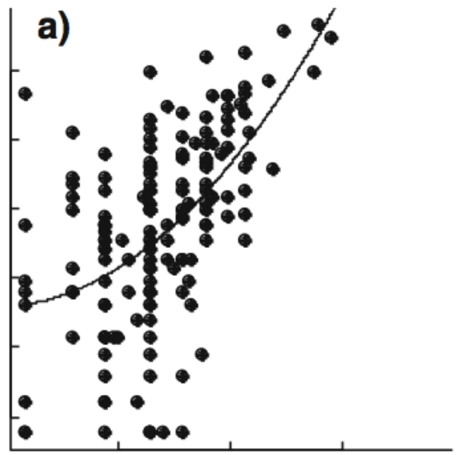
Vital Rate Regression: Growth – g(x,y)

Size (t+1)

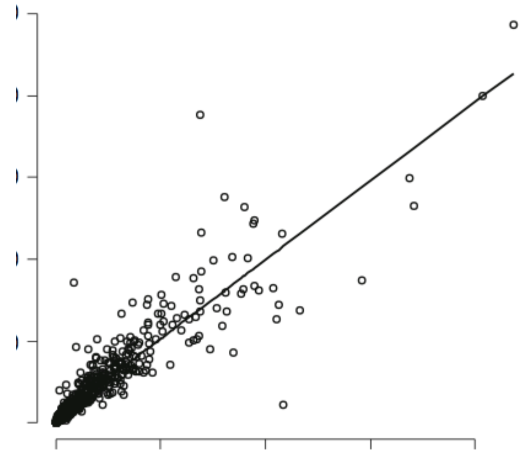
Jongejans et al. 2011



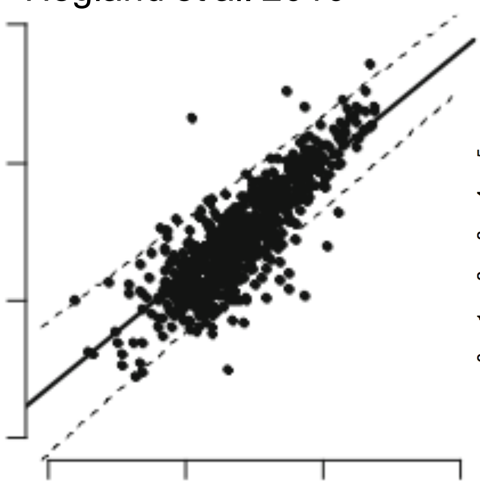
Metcalf et al. 2008



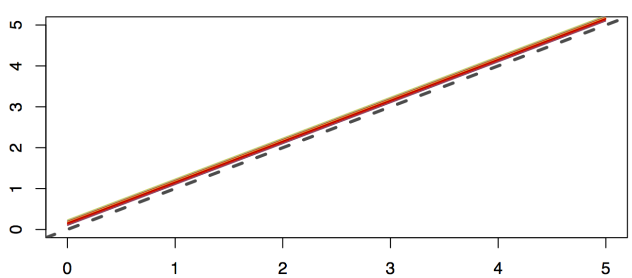
Ferrer-Cervantes et al. 2012



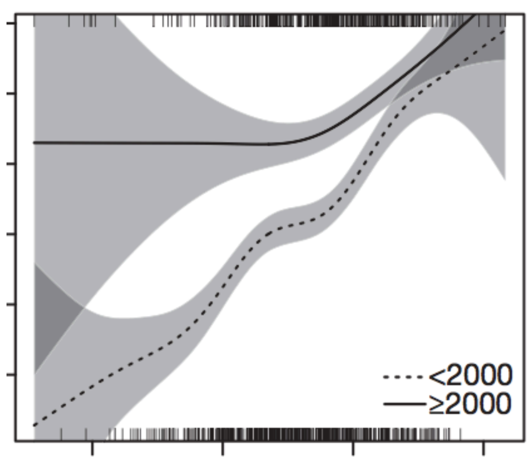
Hegland et al. 2010



Merow et al. 2014



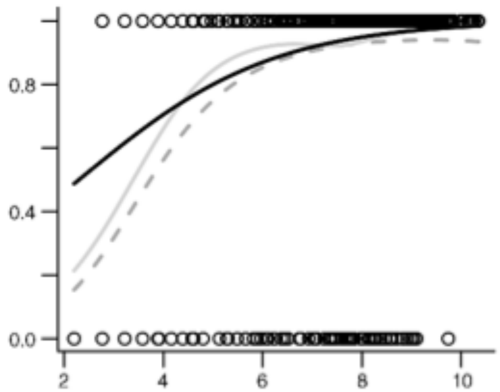
Ozgul et al. 2010



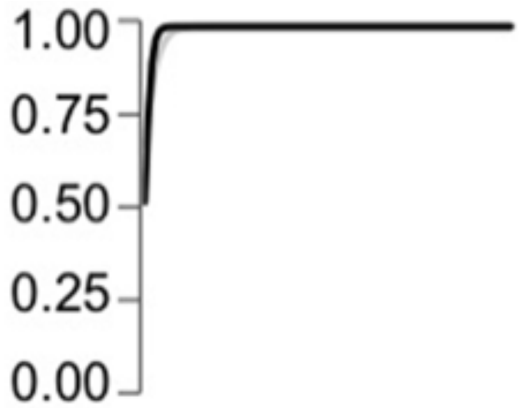
Size (t)

Vital Rate Regression: Survival – s(x)

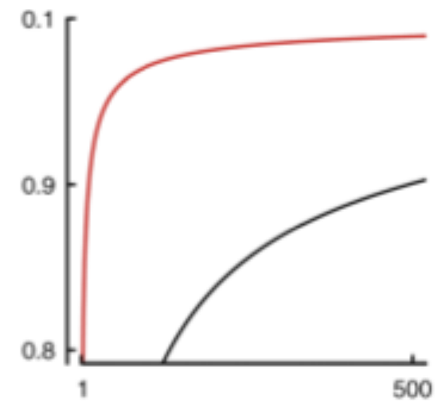
Dahlgren et al. 2011



Salguero-Gomez et al. 2012

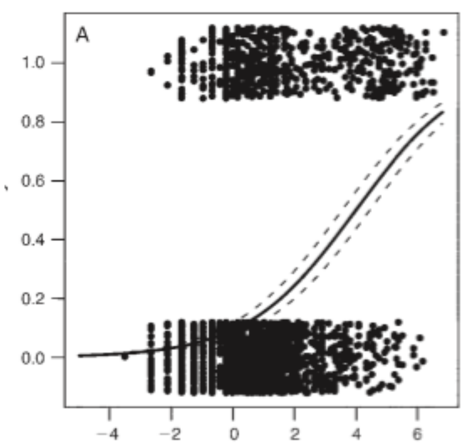


Metcalf et al. 2009

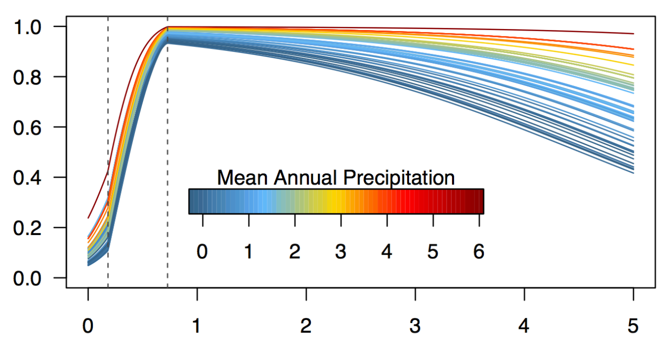


Survival Probability

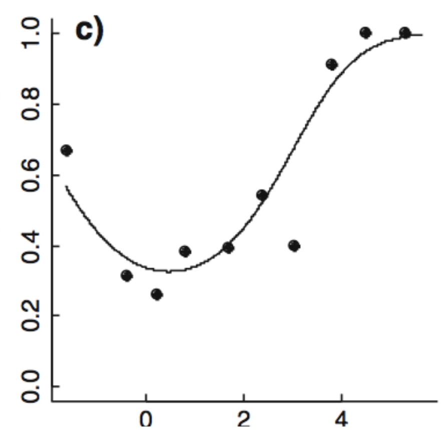
Jongejans et al. 2011



Merow et al. 2014

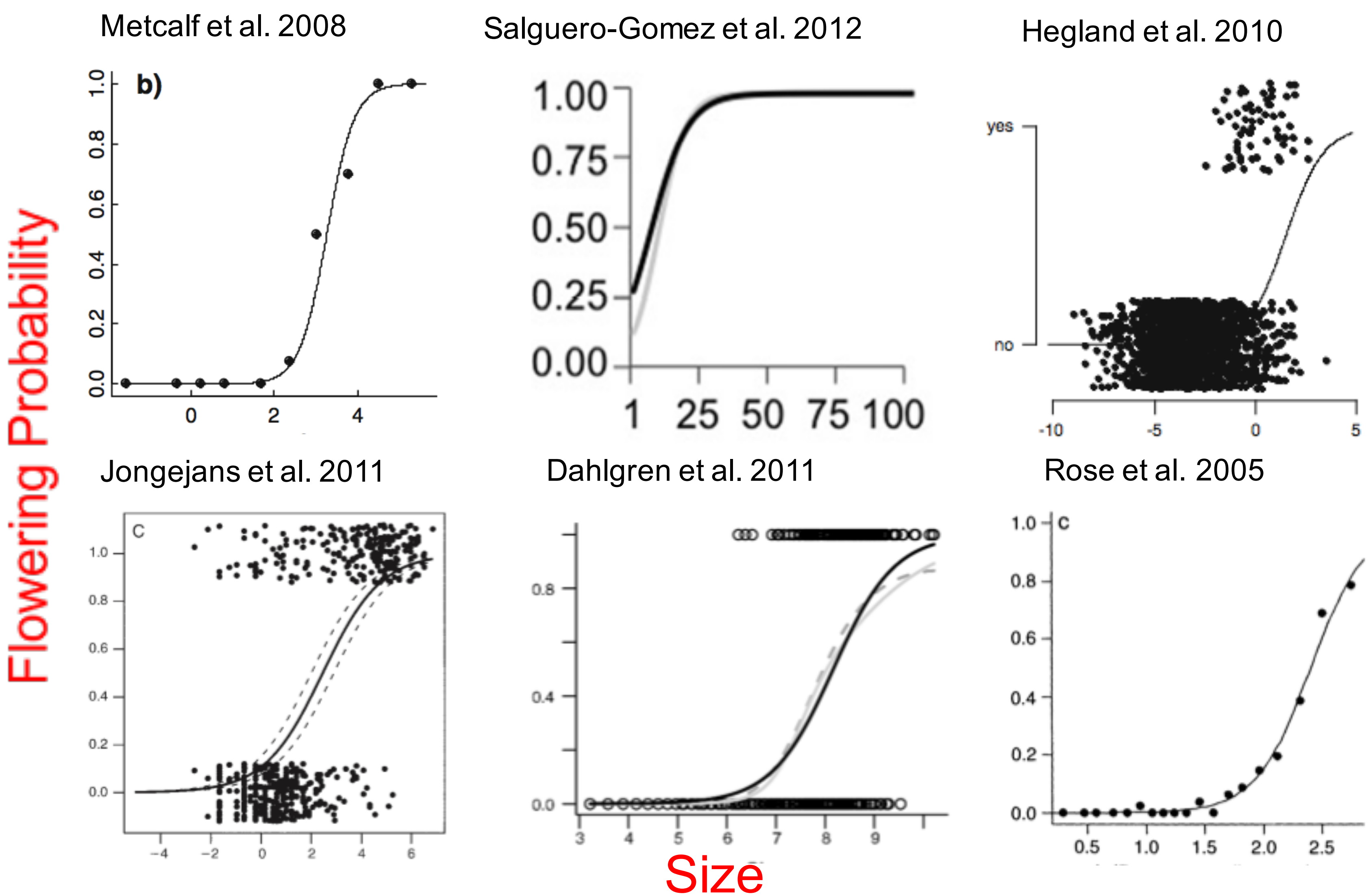


Metcalf et al. 2008



Size

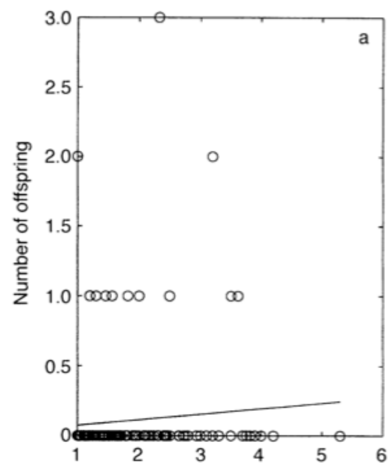
Vital Rate Regression: Flowering – $p_{flower}(x)$



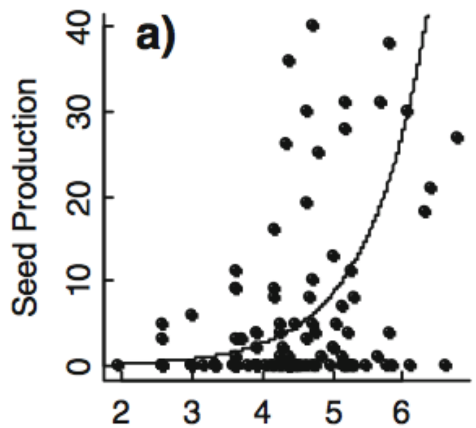
Vital Rate Regression: Fecundity – $f_{seeds}(x)$

Number of Babies

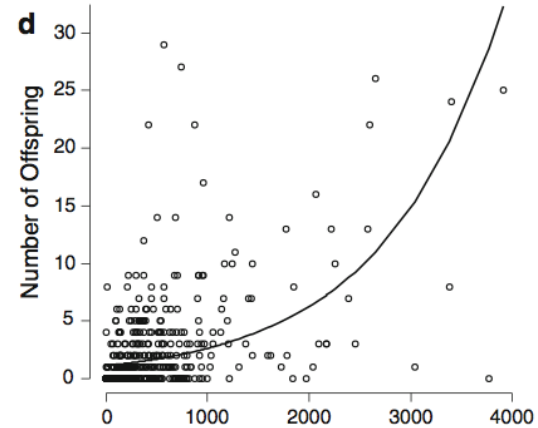
Easterling et al. 2000



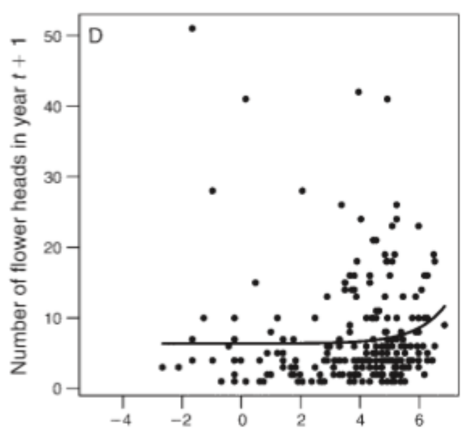
Metcalf et al. 2009



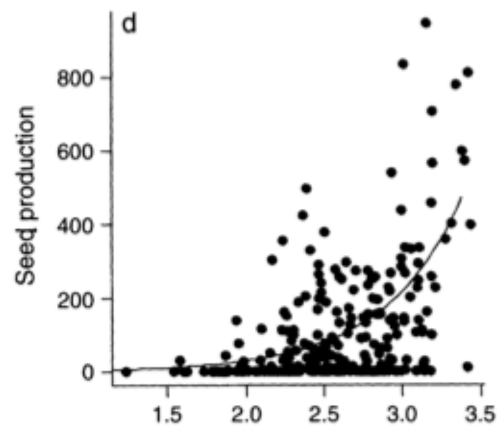
Ferrer-Cervantes et al. 2012



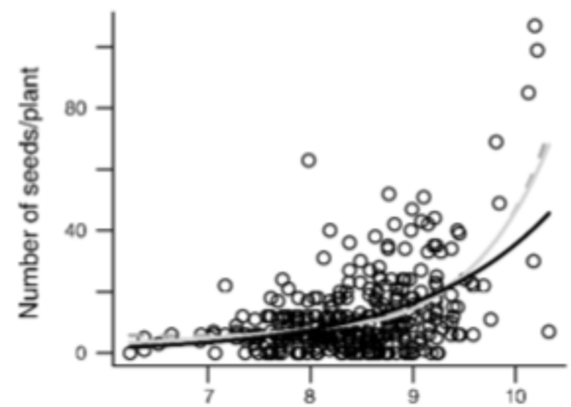
Jongejans et al. 2011



Rose et al. 2005



Dahlgren et al. 2011

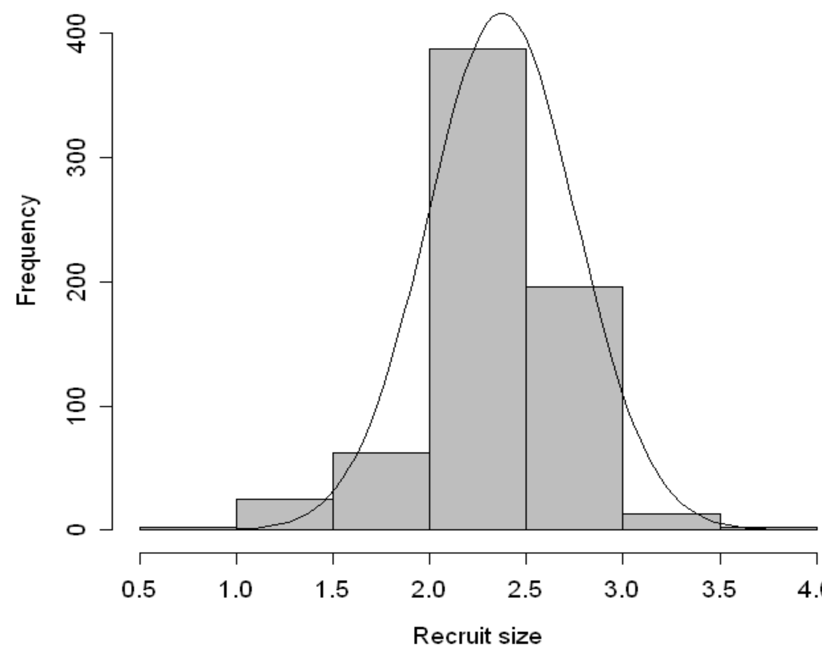


Size

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 – $f_{recruit}(x,y)$

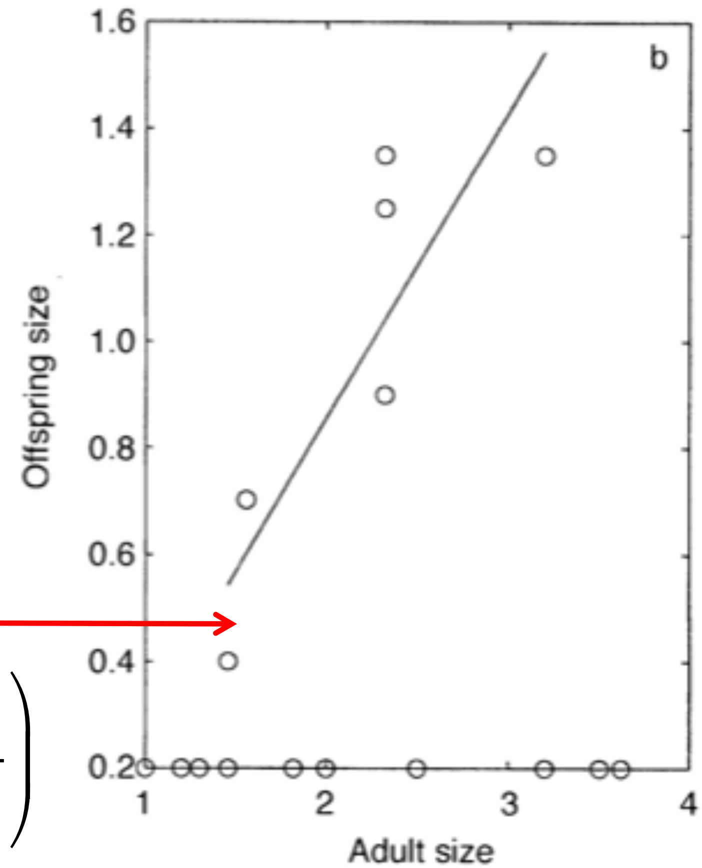
Usually…

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

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

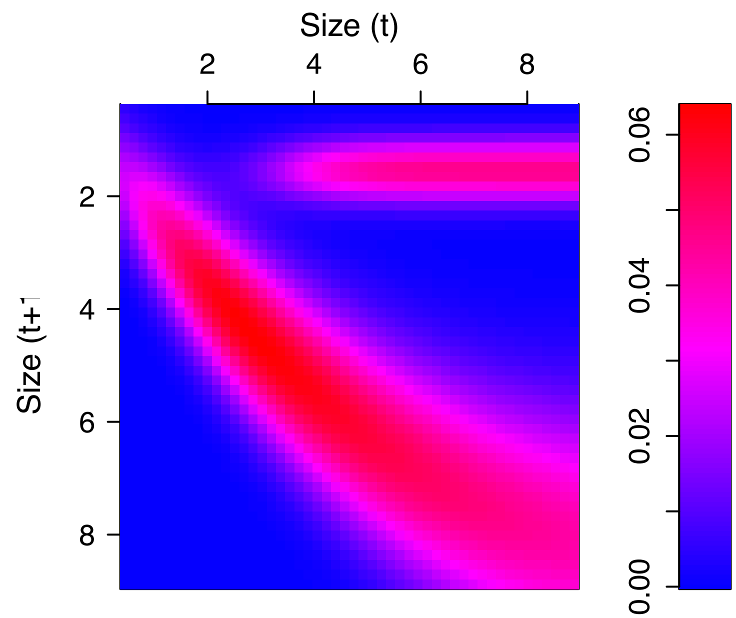
Life History

Data

Vital Rate Regressions

IPM Kernel

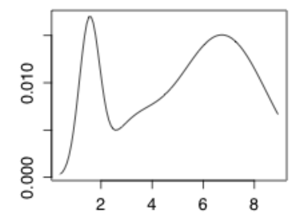
Analysis



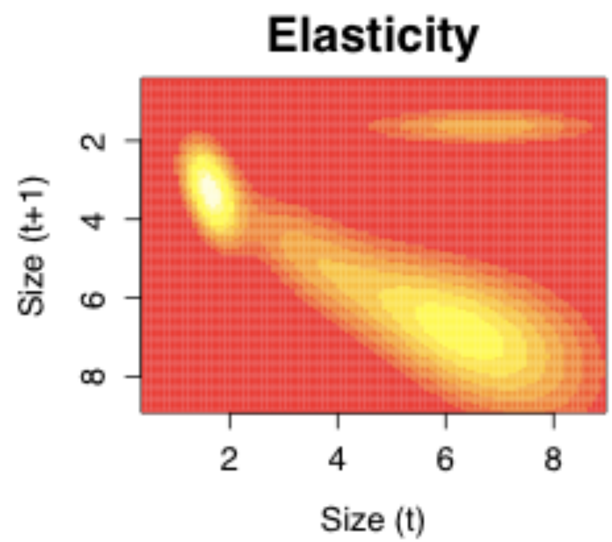
Analysis

- 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…



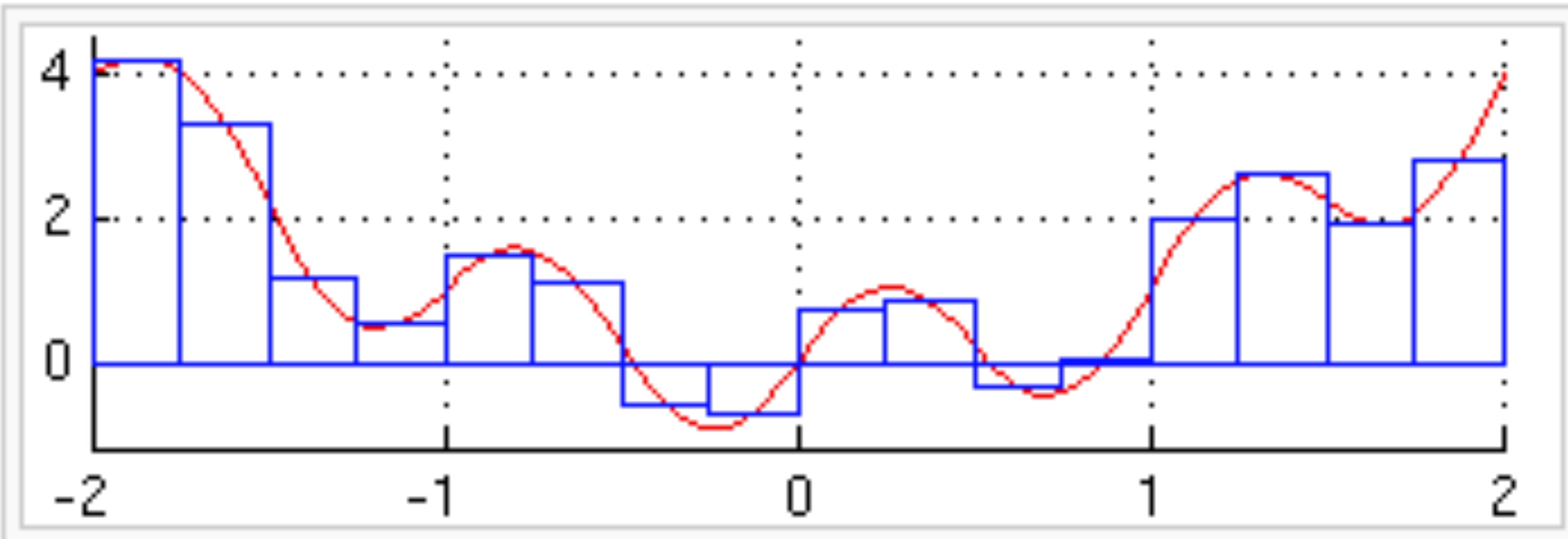
Full kernel function

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

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

Numerical integration

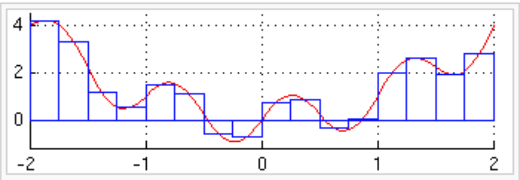
Midpoint rule

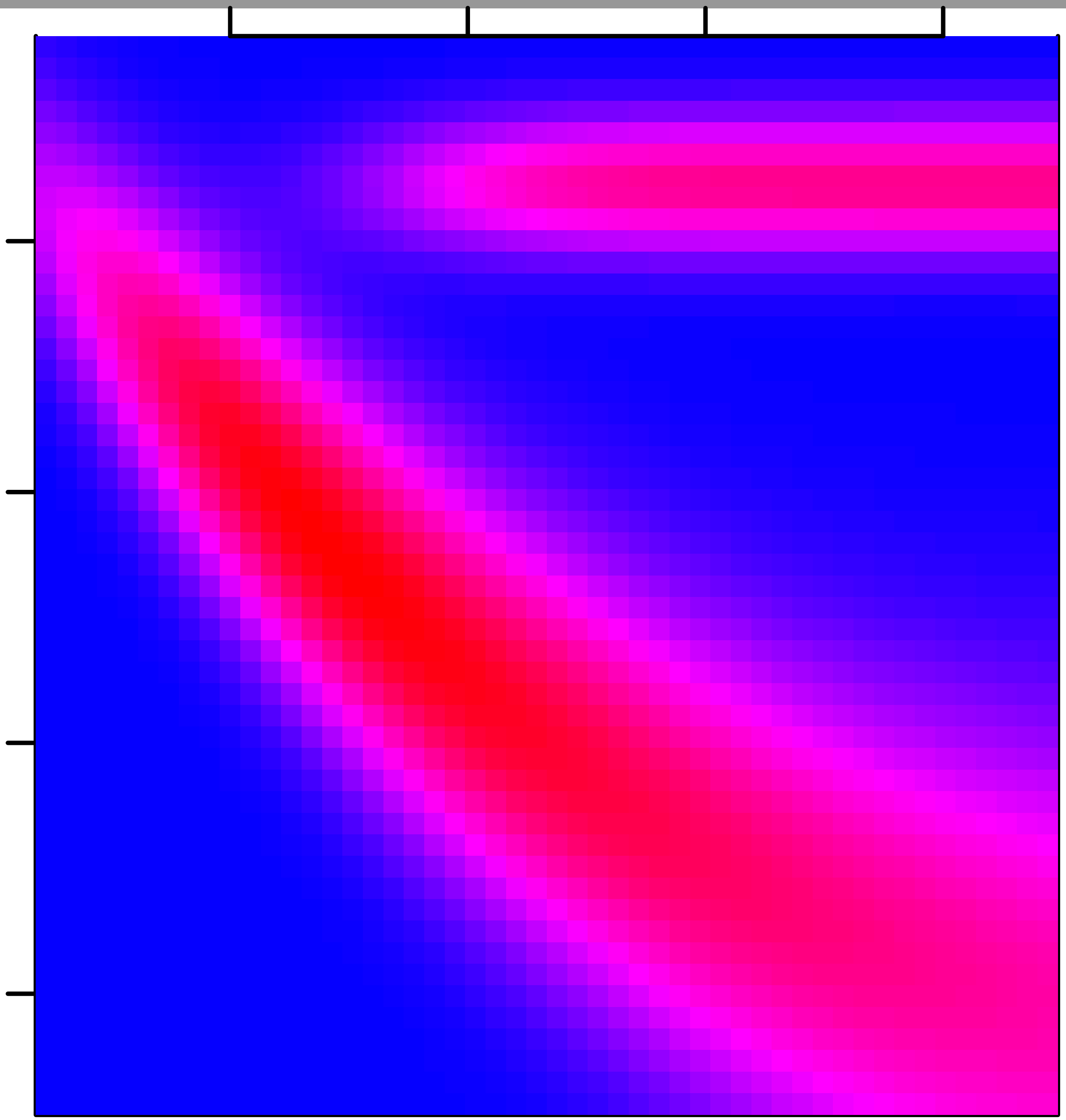


IPMs discretize for numerical integration

Numerical integration

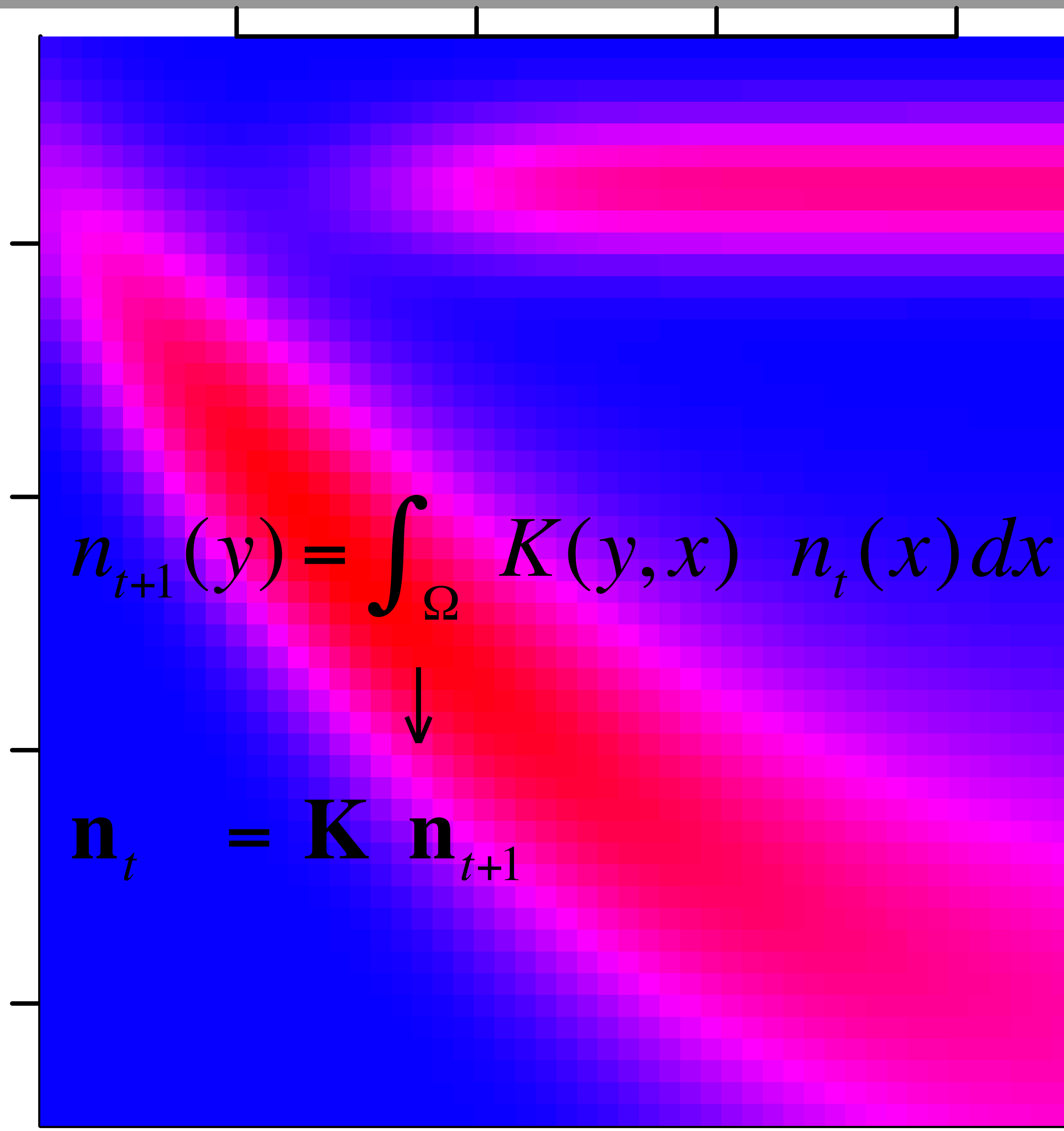
Evaluate kernel at midpoint of each cell to obtain a large matrix





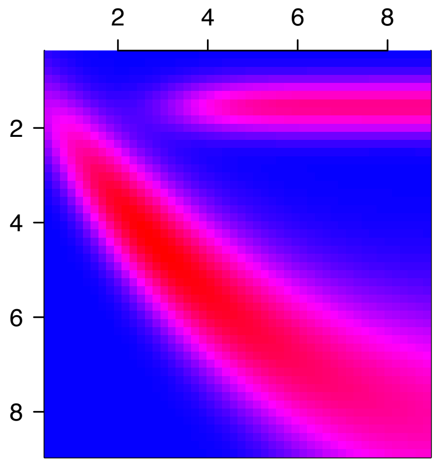
Numerical integration

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

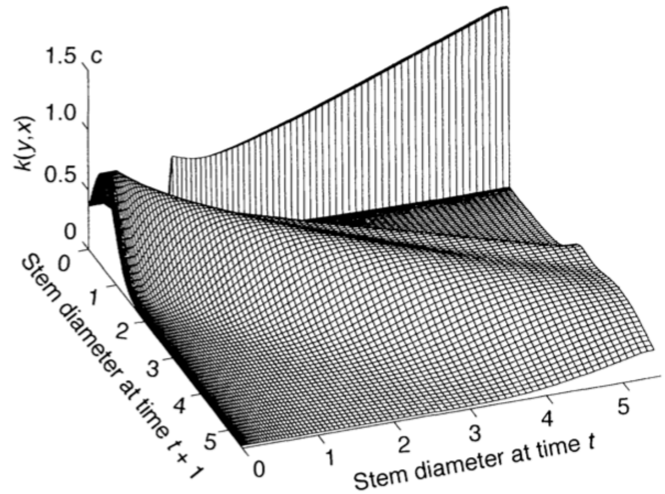


Full kernel function

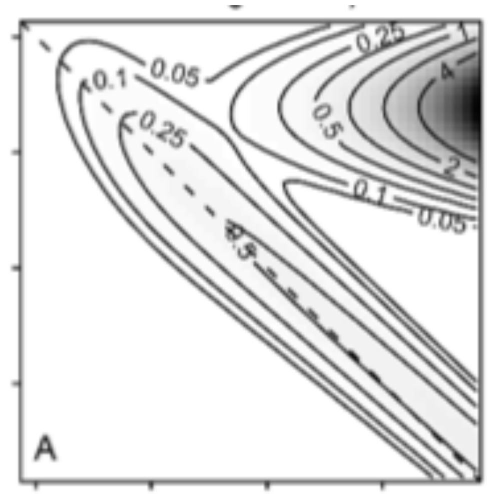
~Nicolé et al. 2011



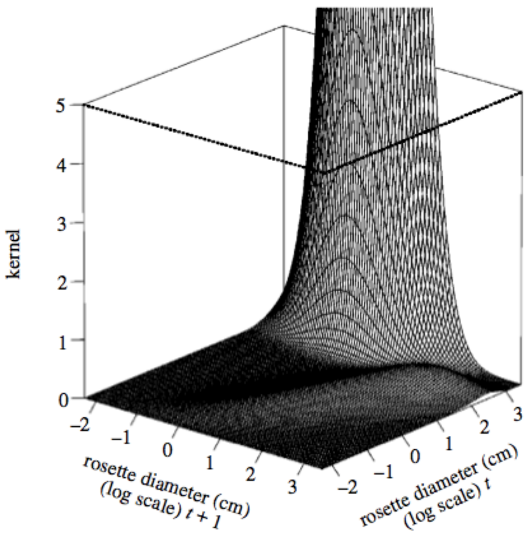
Easterling et al. 2000



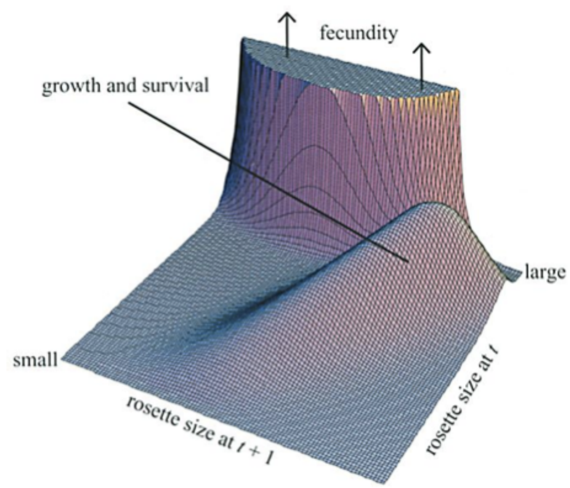
Dalgliesh et al. 2011



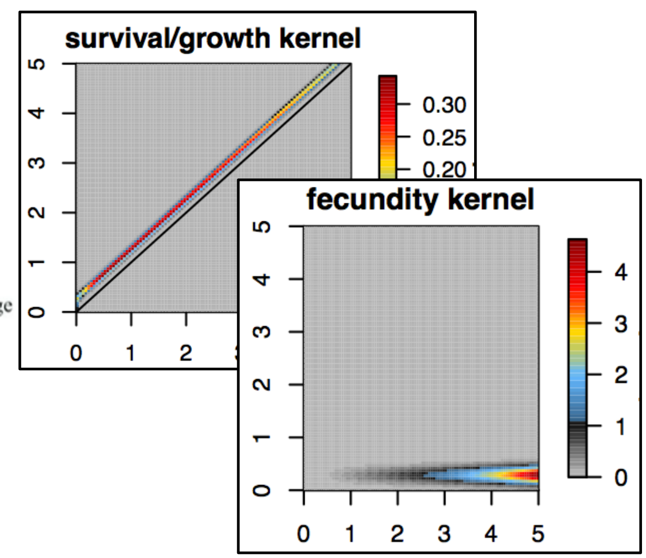
Rees et al. 2002



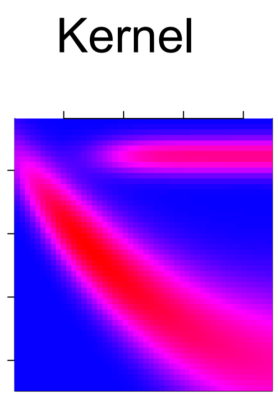
Godfray et al. 2002

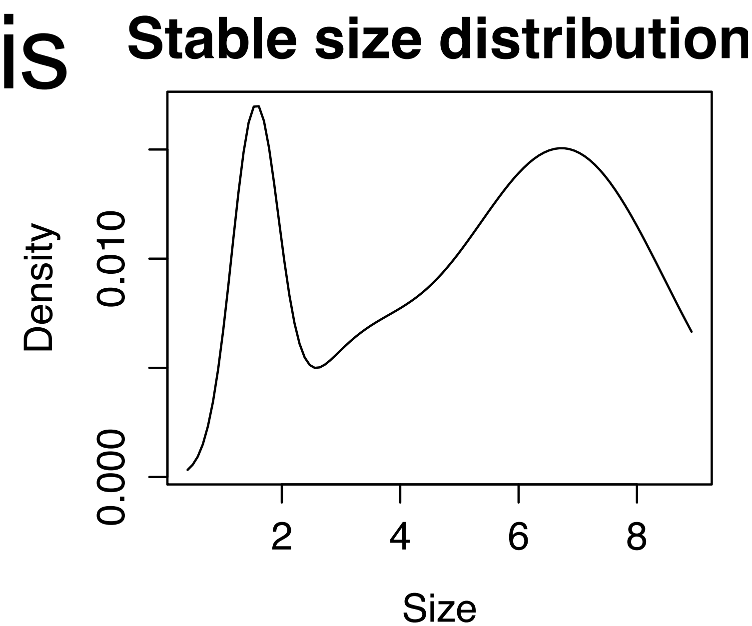


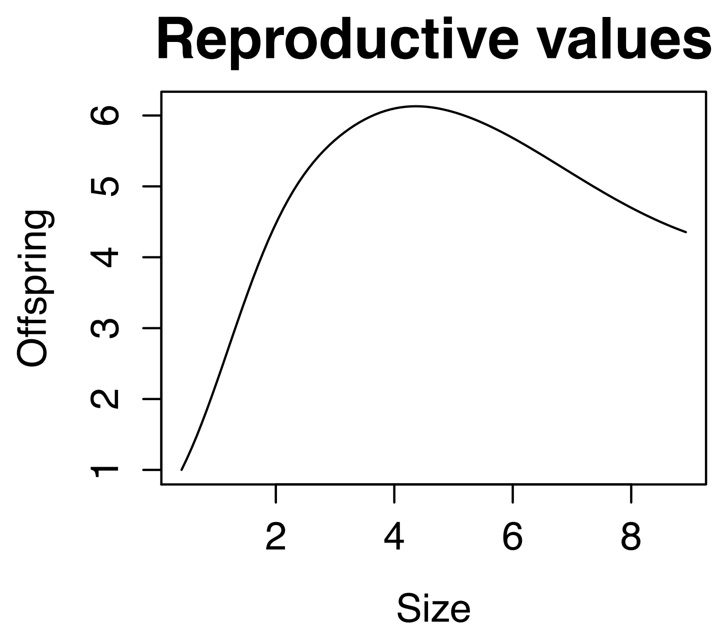
Merow et al. 2014

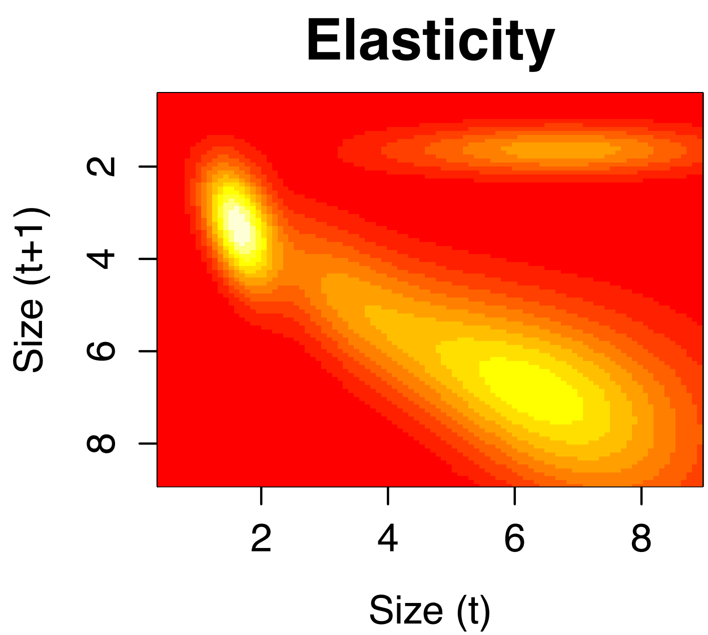


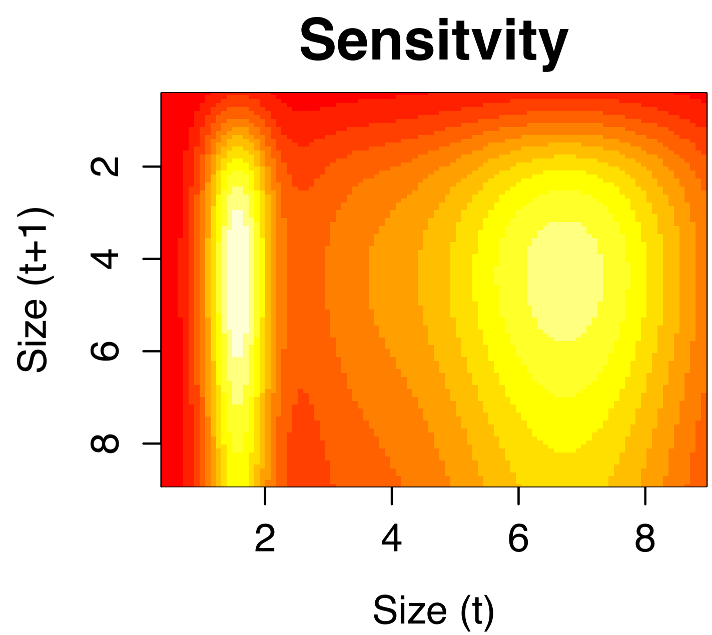
Analysis


Kernel

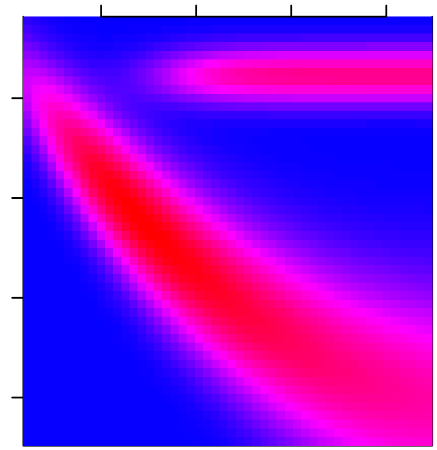

Stable size distribution
Density
0.000
0.010
2
4
6
8
Size


Reproductive values
Offspring
1
2
3
4
5
6
2
4
6
8
Size


Elasticity
Size (t+1)
2
4
6
8
2
4
6
8
Size (t)


Sensitvity
Size (t+1)
2
4
6
8
2
4
6
8
Size (t)

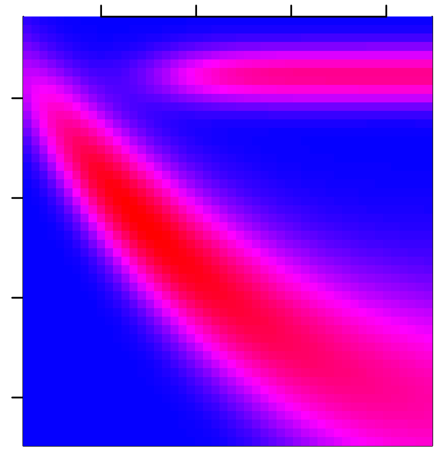
Summary - Why IPMs?



Process-based demography

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

Summary - Why IPMs?



Process-based demography

- Continuous stages
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Questions?