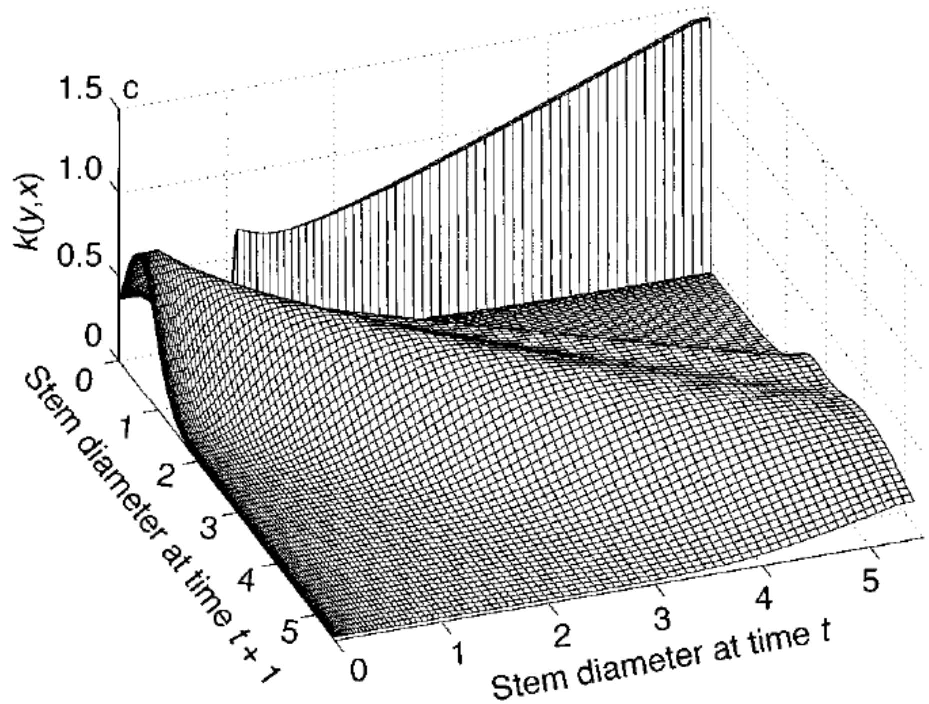
Basics of plant population modelling and its application



Pieter Zuidema, Pieter.zuidema@wur.nl

Programme

Monday**: Matrix models**

Tuesday**: Integral Projection Models: construction**
Plus first paper discussion

Wednesday**: Integral Projection Models: output**
Plus: second paper discussion

Thursday**: Integral Projection Models: more applications**
Plus: preparing presentations

Friday**: Presentations**

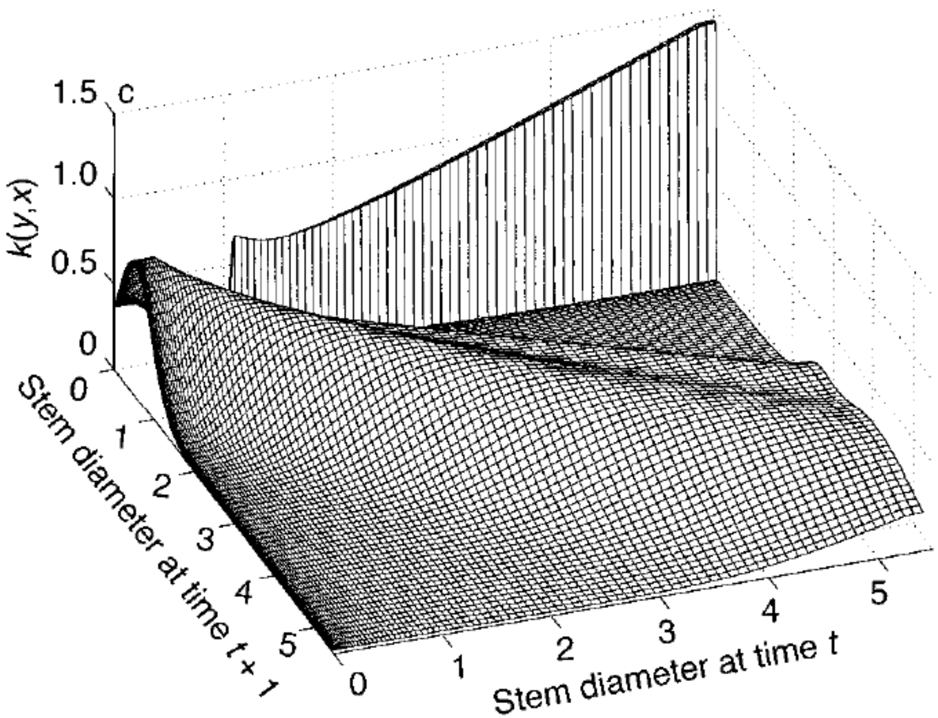
Programme

Tuesday February 11th: Integral Projection Models: construction

9-10.30	Lectures: introduction IPMs & their construction
10.30-12	Exercises: IPM construction
12	Lunch
2-3	Discuss results of exercises
3-3.30	Read/refresh paper
3.30-4.30	Discuss paper in subgroups
4.30-5	Share with all what you discussed

Lecture: Background & construction IPMs

- What are IPMs?
- Why IPMs?
- Differences with matrix models
- Model construction
- Intro ipmr

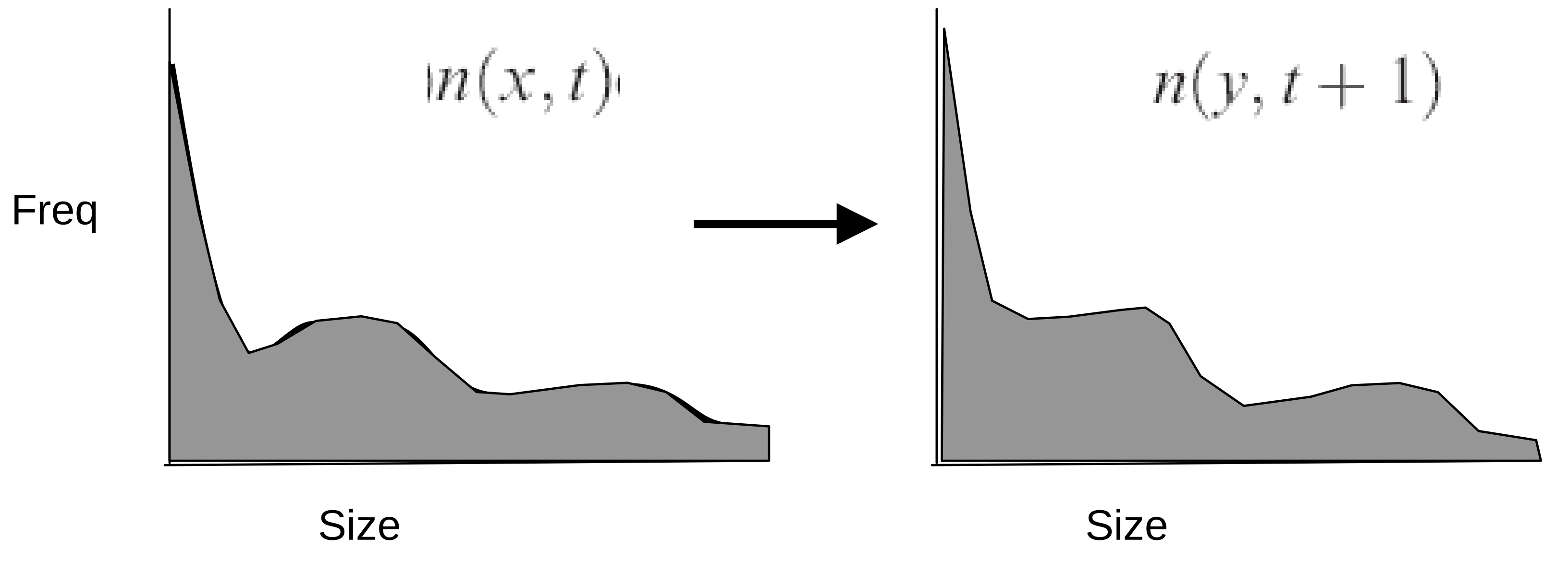


Integral Projection Models

Demographic models that simulate the **continuous** distribution of a population over **discrete** timesteps.

Integral Projection Models

Model continuous population structure in discrete time



Integral Projection Models

Projection: $$n(y, t+1) = \int_L^U K(y, x) n(x, t) \mathrm{d}x$$

- t = time
- x = size at t
- y = size at t+1
- n(x,t) = size distribution at t
- n(y,t+1) = size distribution at t+1

- K(x,y) = full kernel

Probability densities

Integral Projection Models

Projection:

$$n(y, t+1) = \int_L^U K(y,x) n(x,t) \mathrm{d}x$$

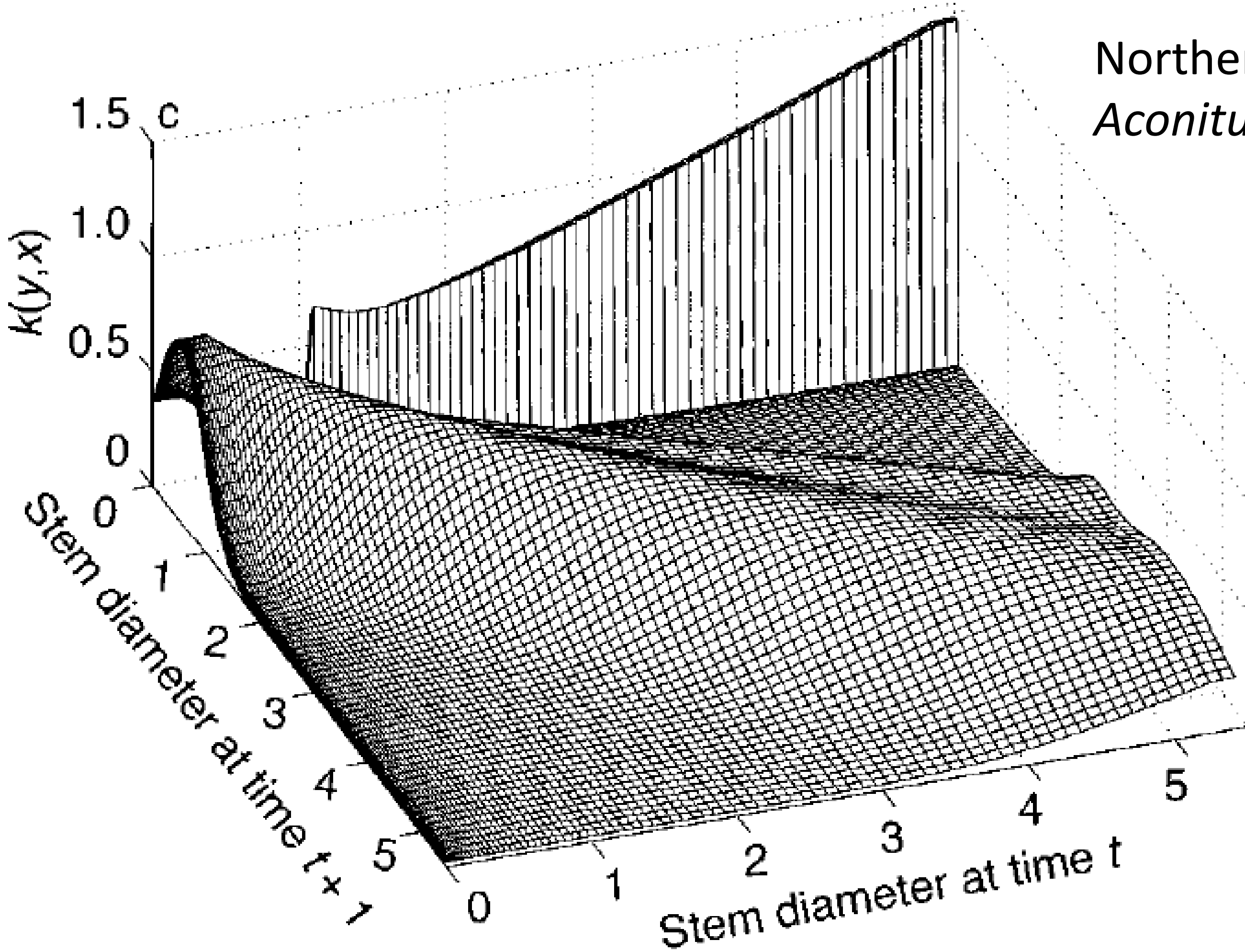
Kernel: $K\,(y,x) = P\,(y,x) + F\,(y,x)$

- t = time
- x = size at t
- y = size at t+1
- n(x,t) = size distribution at t
- n(y,t+1) = size distribution at t+1

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

Probability densities

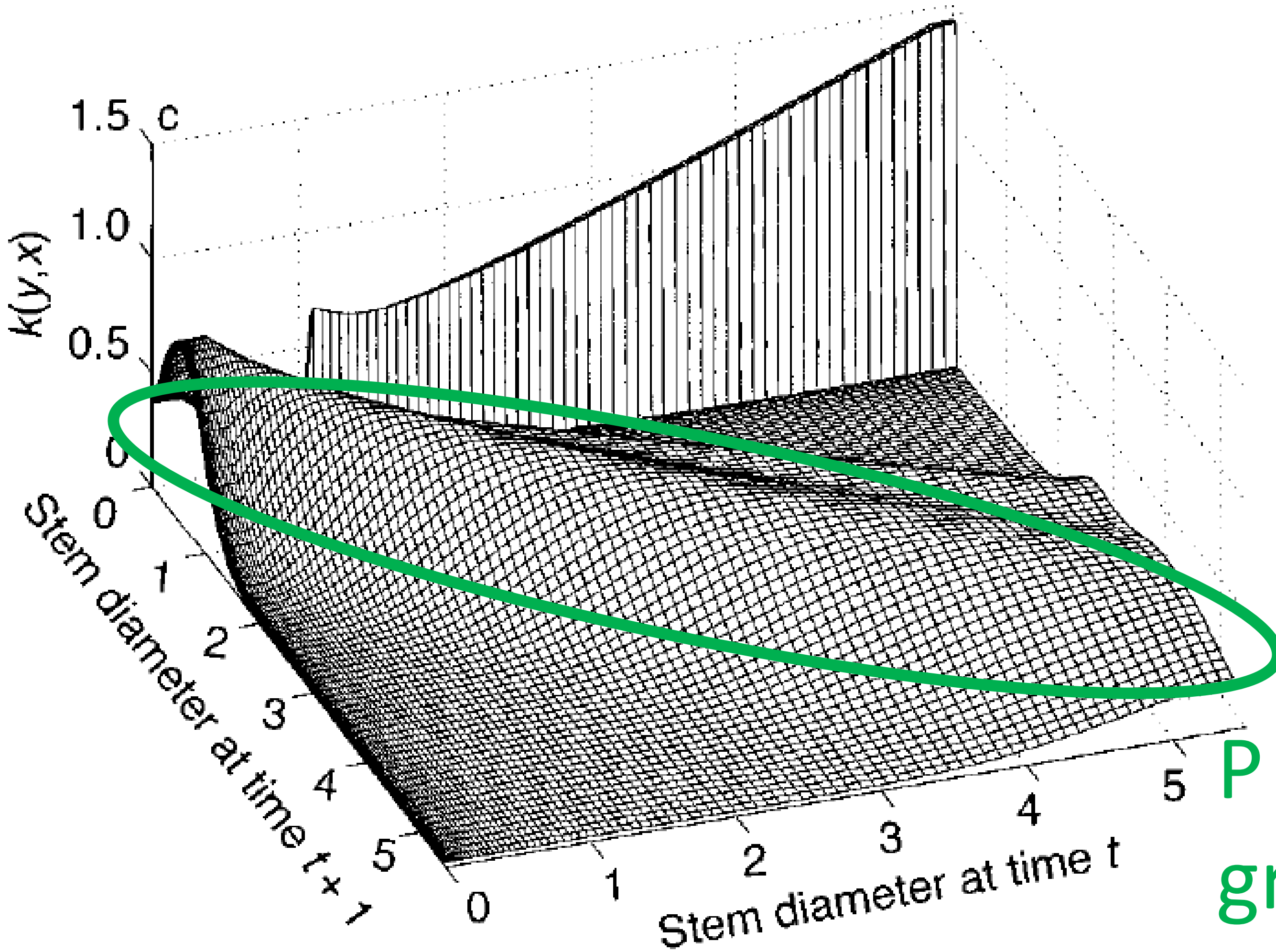
Integral Projection Models



Northern monkshood
Aconitum noveboracense

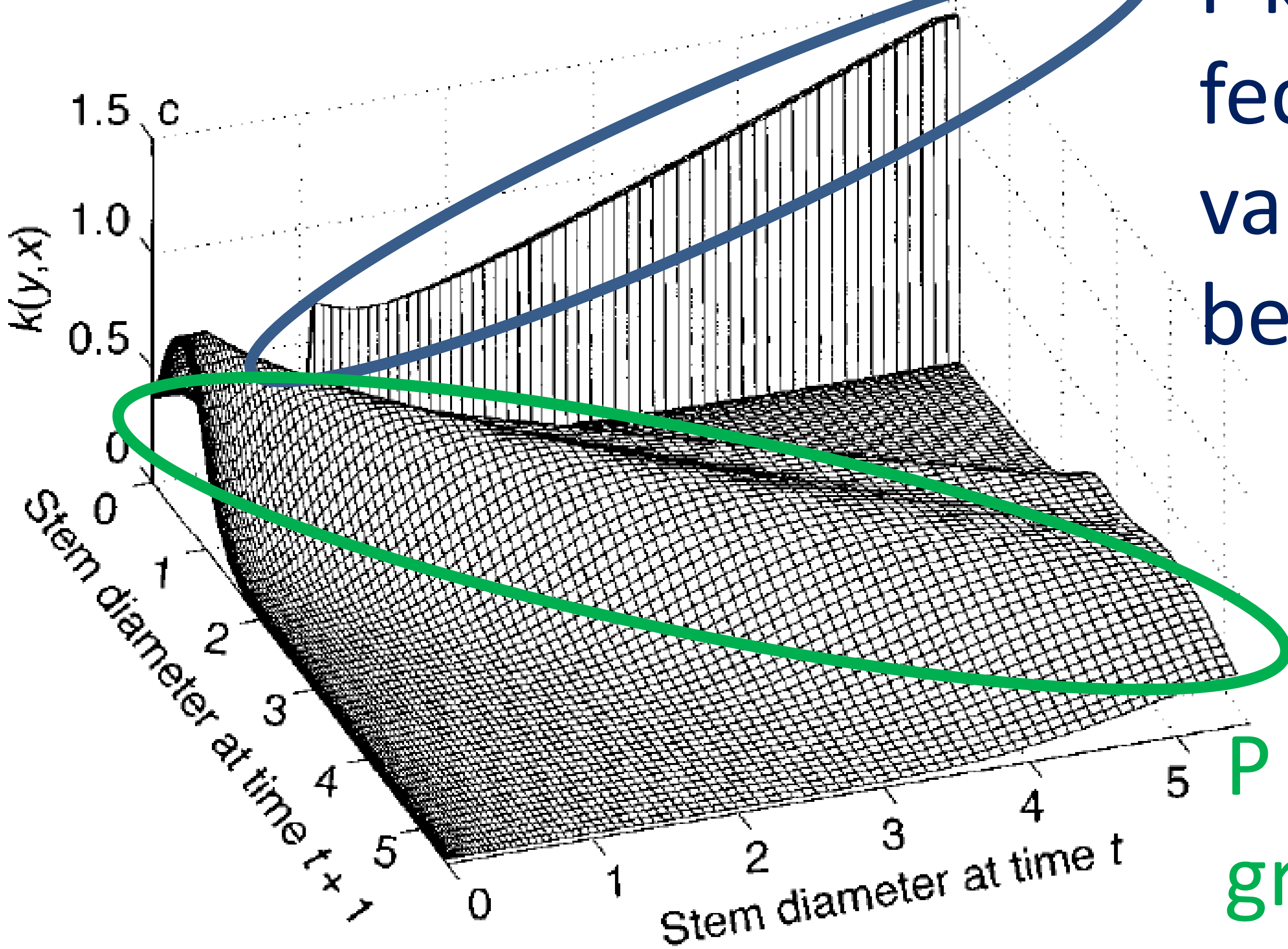
Easterling, Ellner & Dixon 2000, *Ecology*

Integral Projection Models



P kernel: growth and survival; 0-1

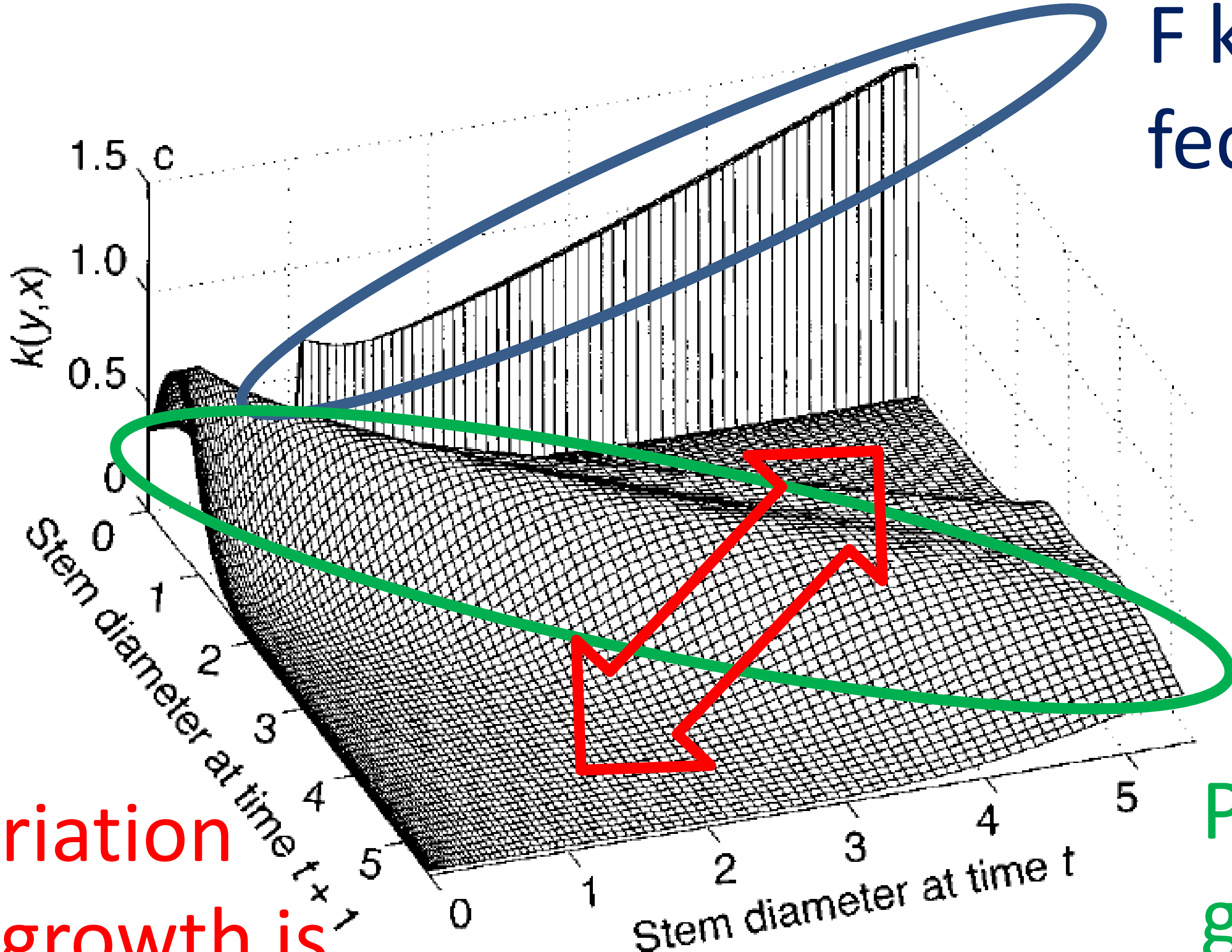
Integral Projection Models



F kernel: fecundity; value can be >1

P kernel: growth and survival; 0-1

Integral Projection Models



F kernel: fecundity

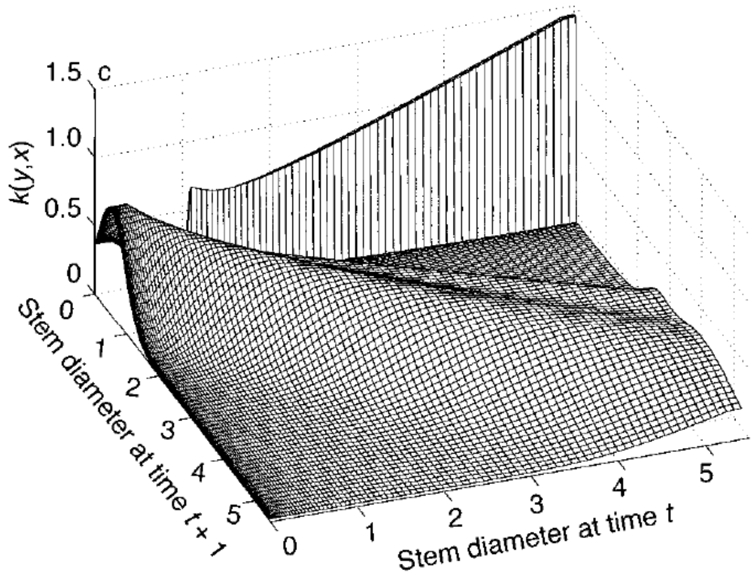
P kernel: growth and survival

Variation in growth is included

Integral Projection Models

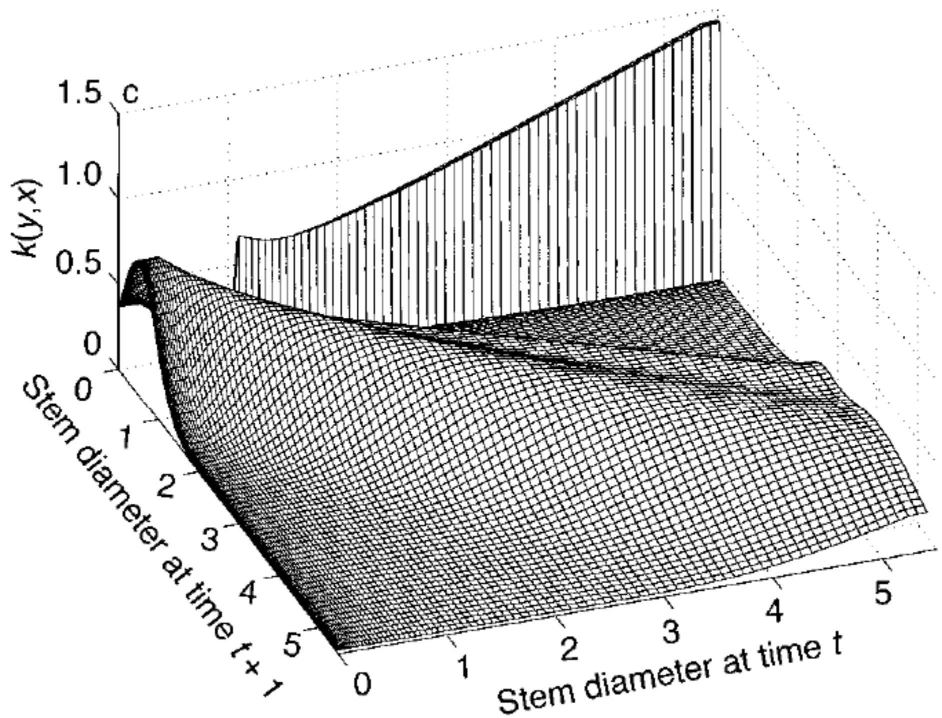
- Kernel is discretized
- Large number of categories (=mesh), such that category number does not affect output
- Then:

  n(t+1) = Kmatrix * n(t)
- Use matrix model tools



Lecture: Background & construction IPMs

- What are IPMs?
- Why IPMs?
- Differences with matrix models
- Model construction
- Intro ipmr

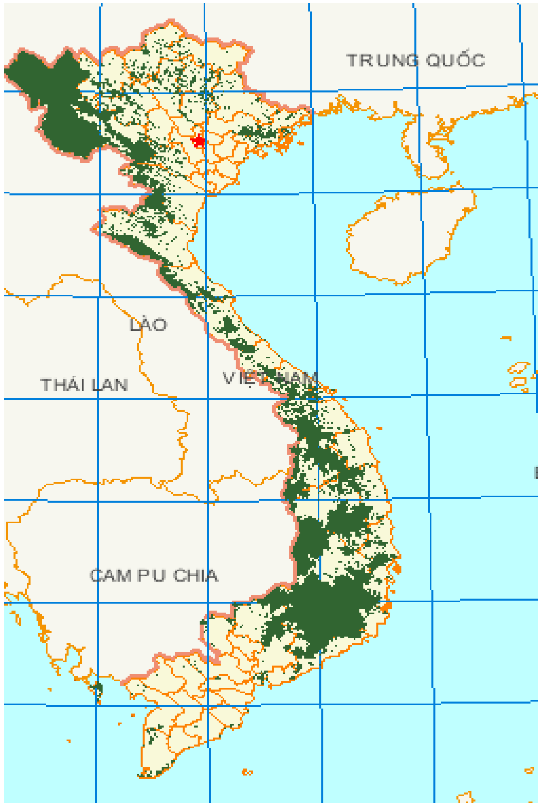


Why IPMs?

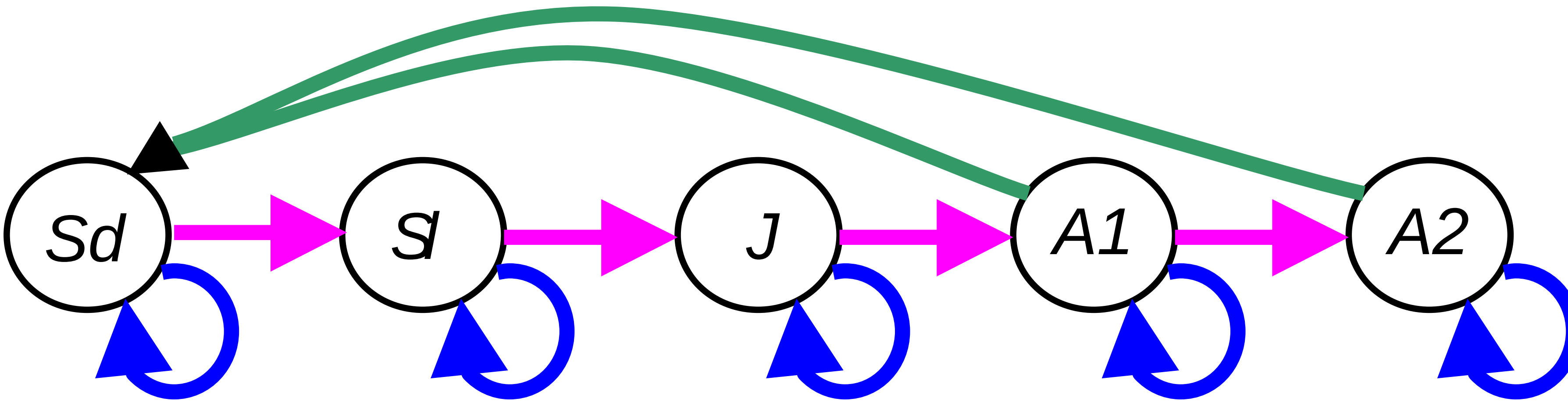
1. <u>Eliminate effect of category width</u>
2. Incorporate growth variation among individuals
3. Flexible model with few parameters

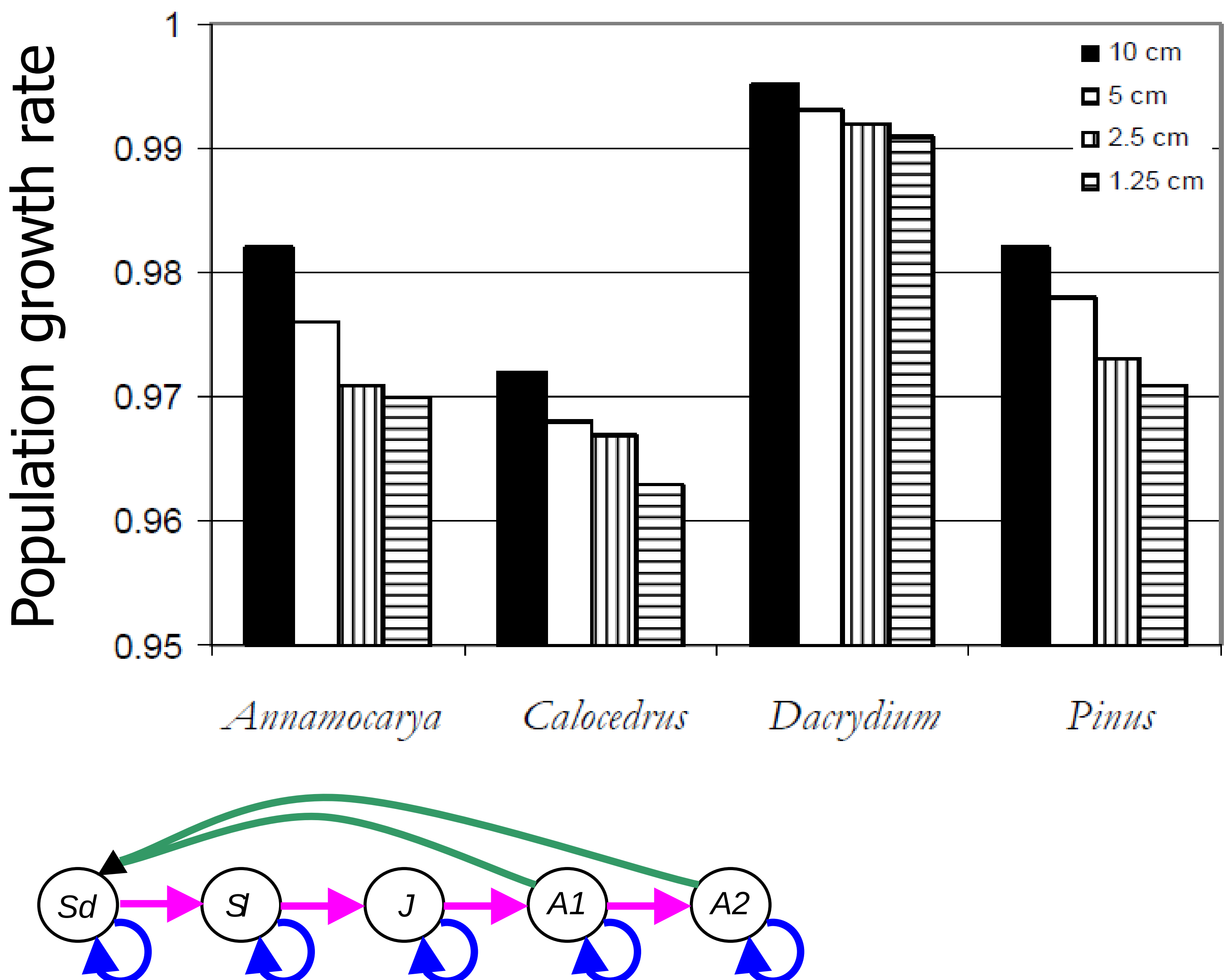
Vietnamese tree species

- Threatened species
- Last known populations
- 200-400 individuals sampled

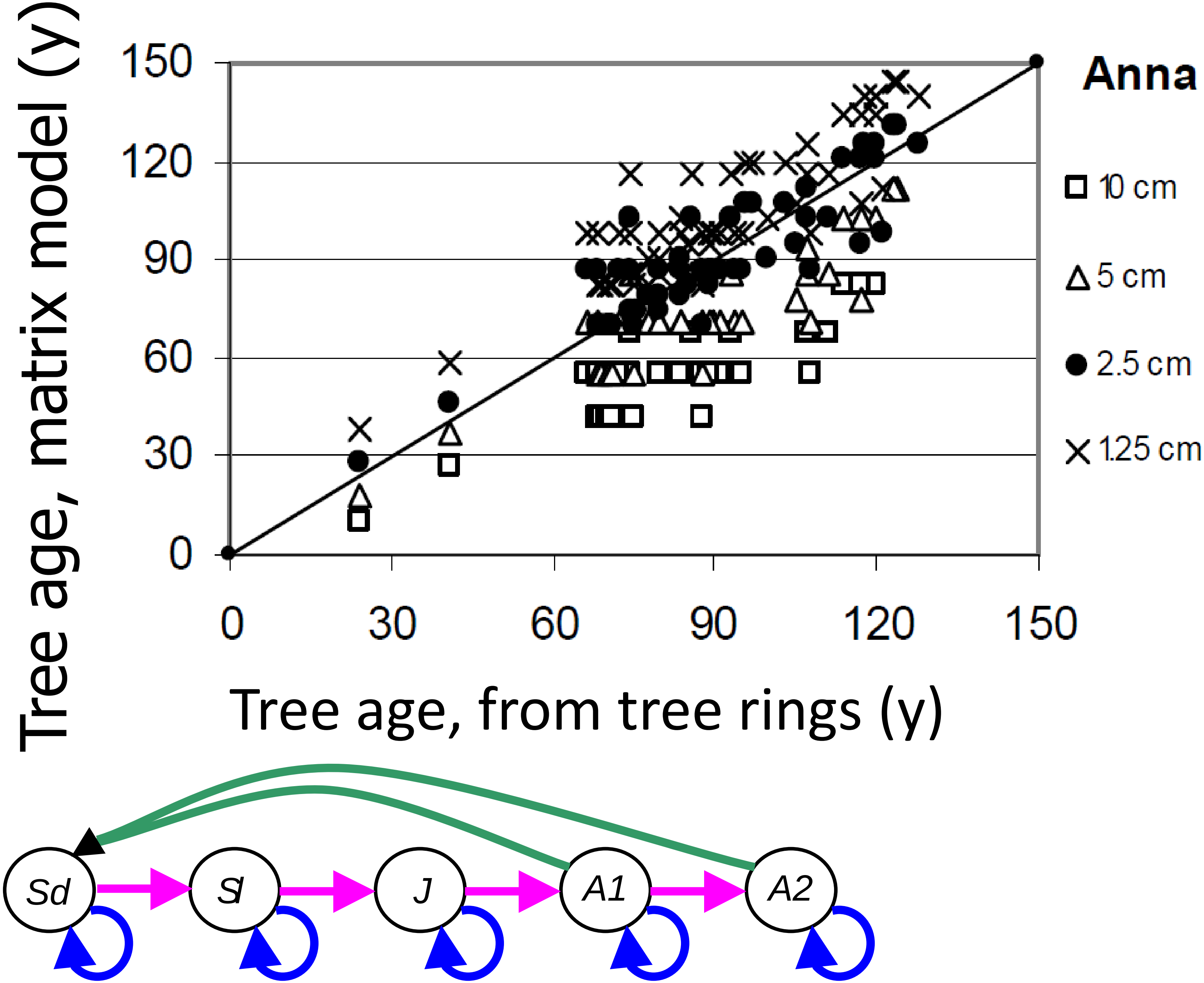


How many categories?



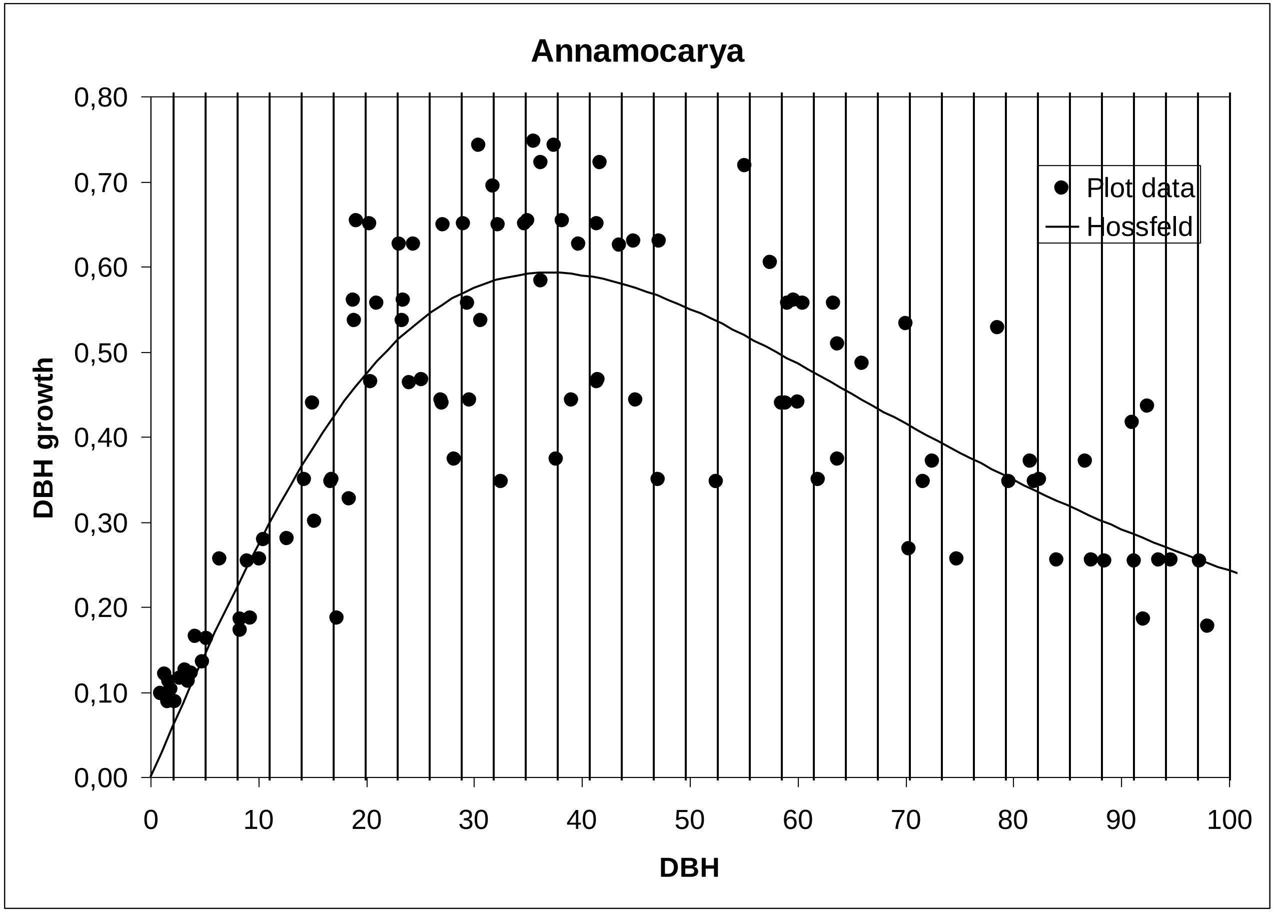


Chien 2006, *thesis*

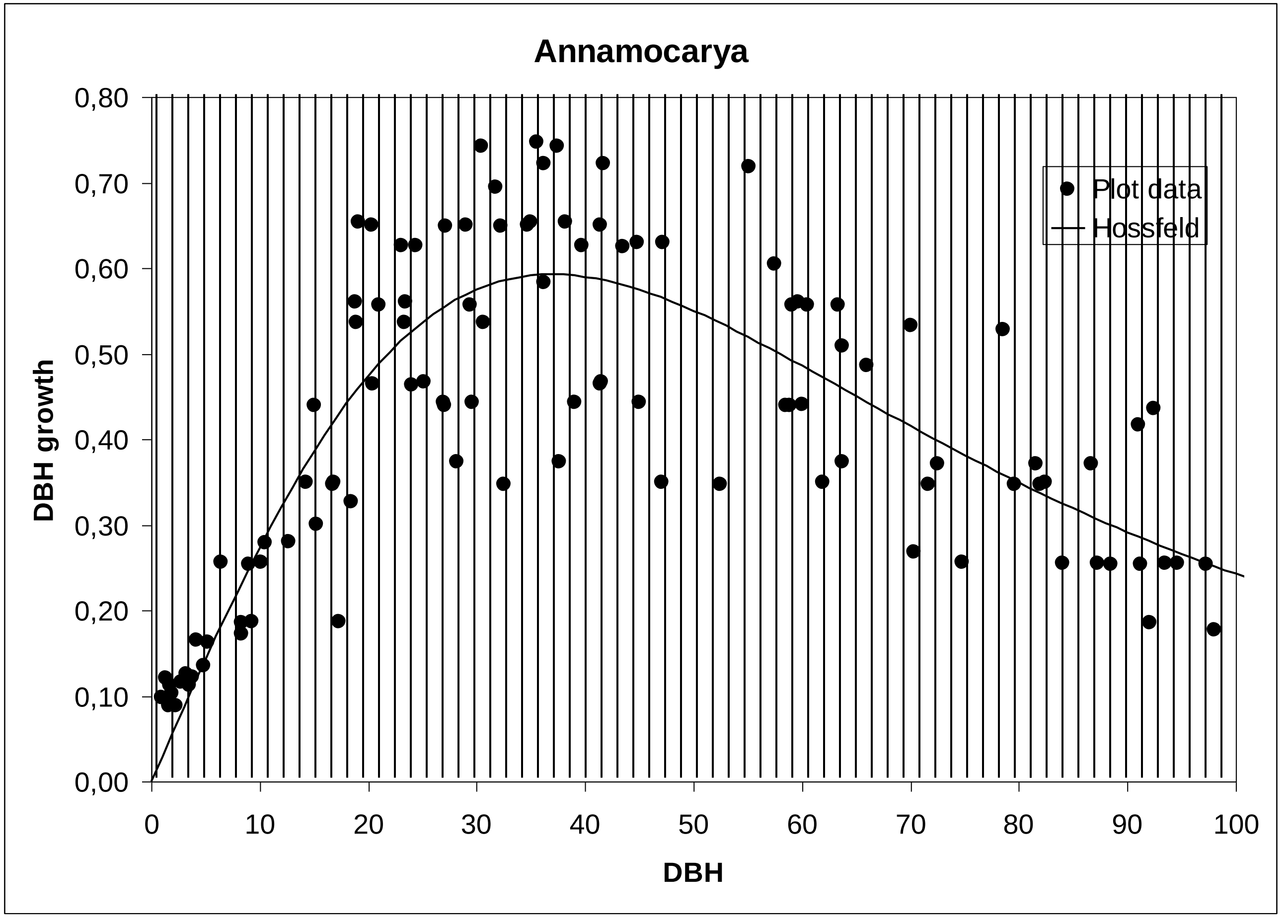


Chien 2006, *thesis*

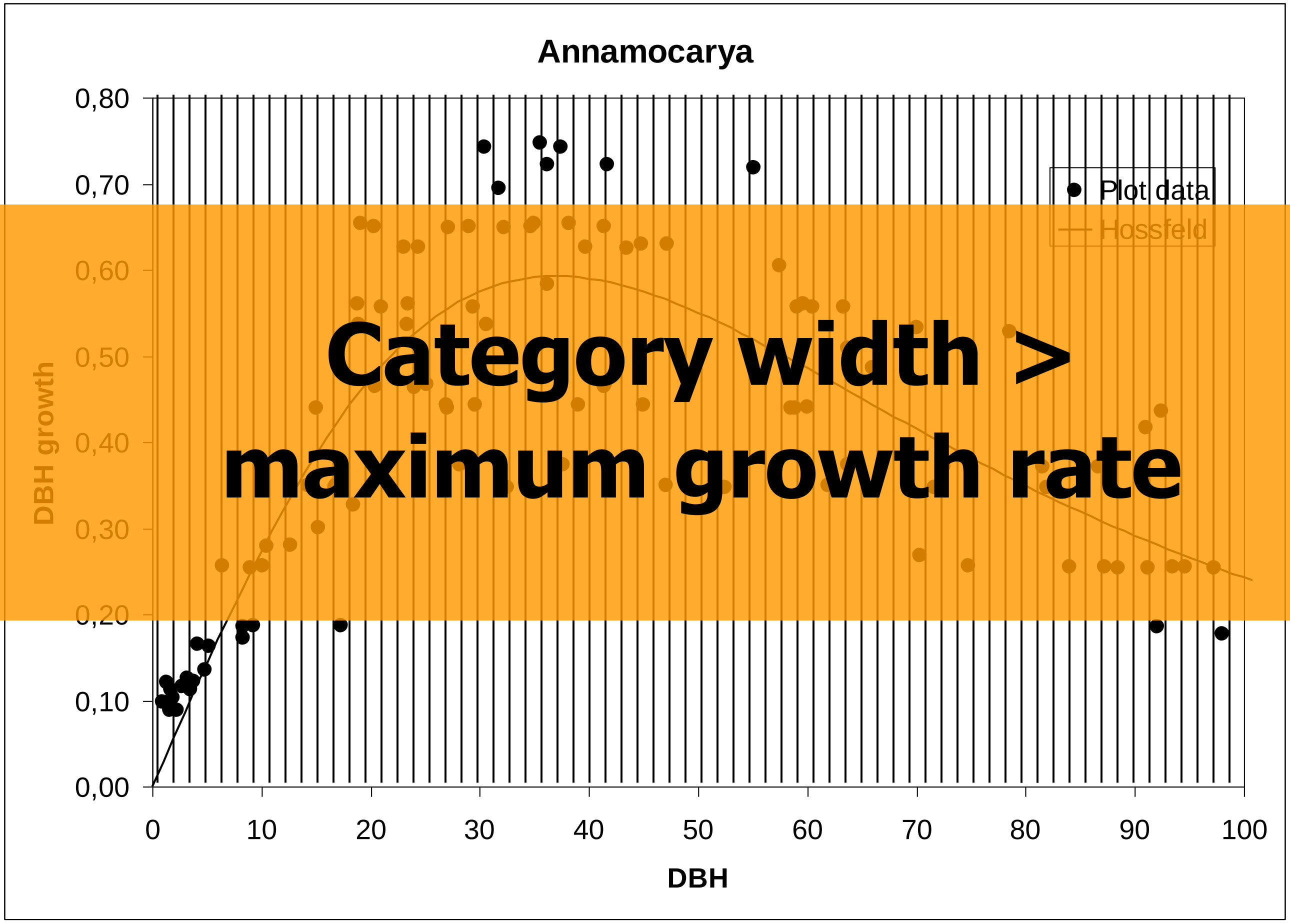
Solution? More categories



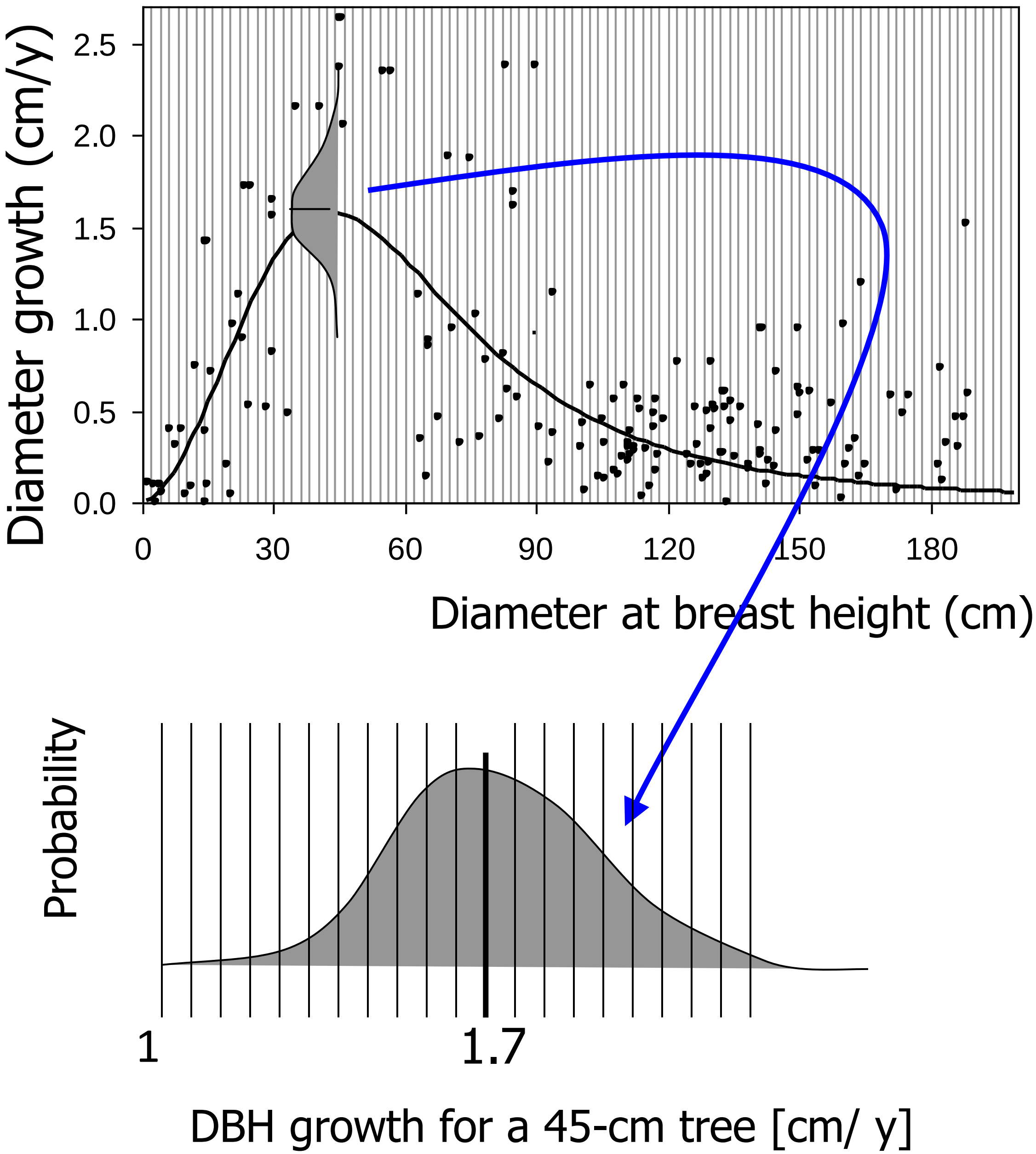
Solution? More categories



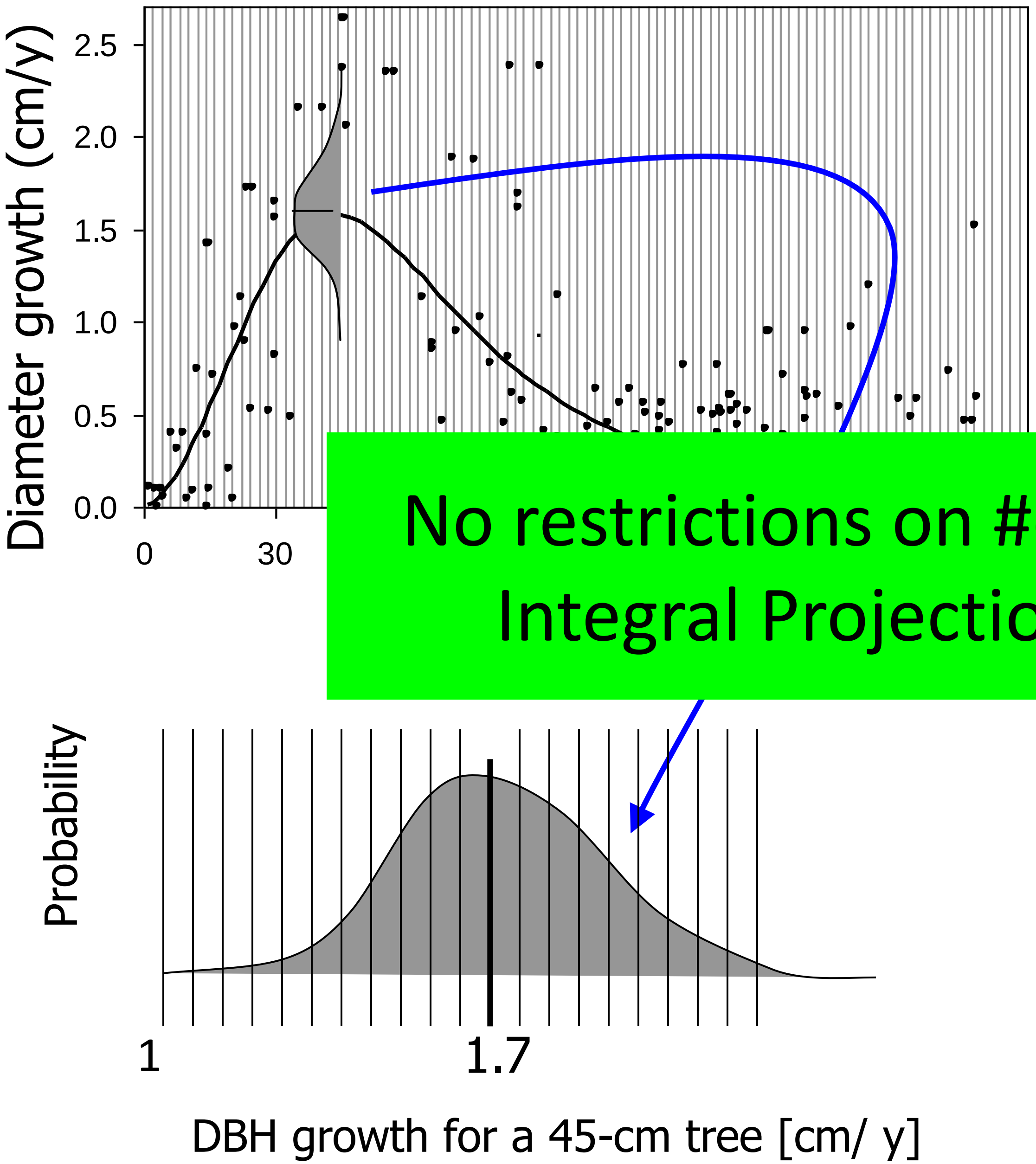
Solution? More categories



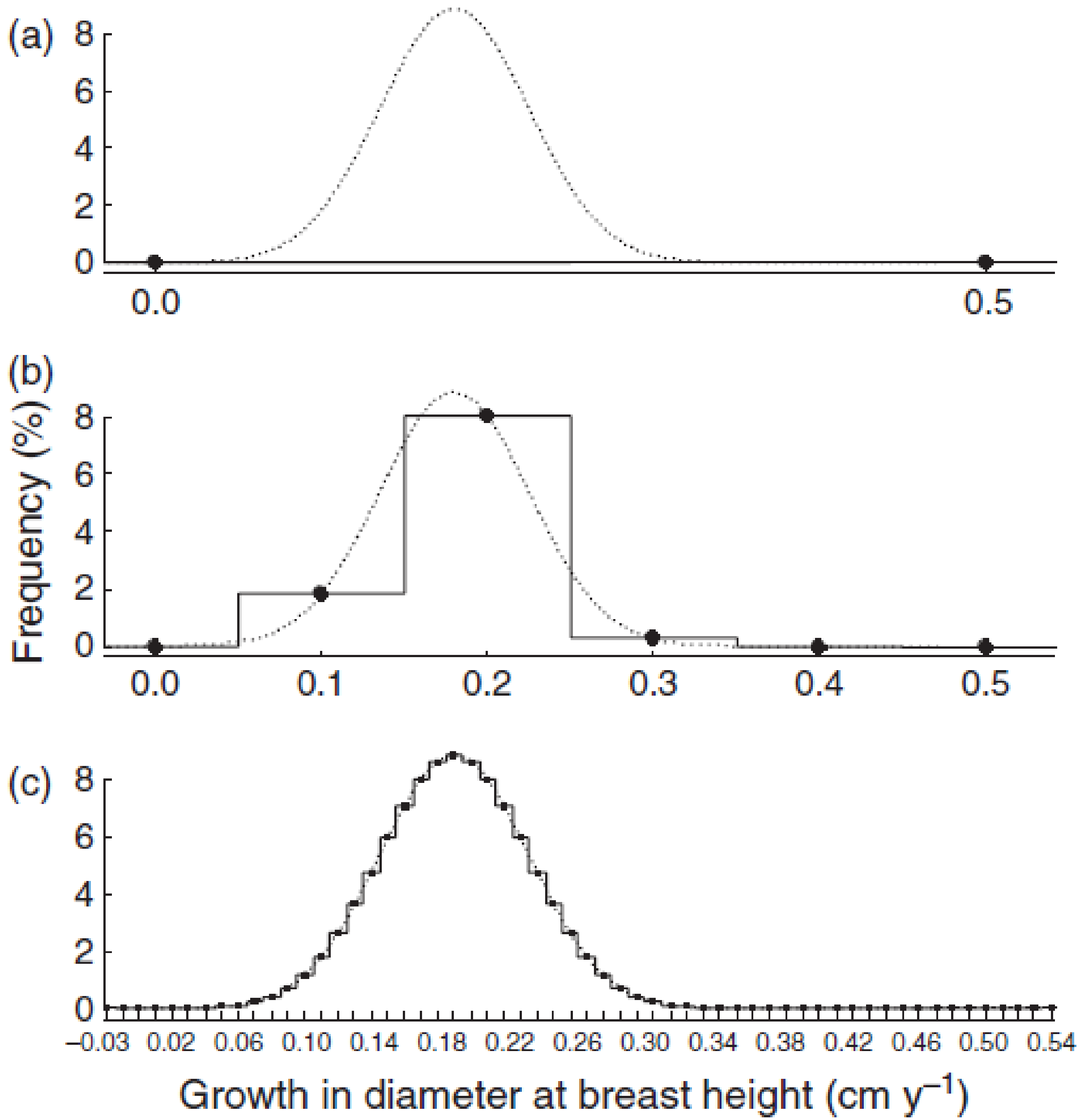
Category width > maximum growth rate



Diameter growth (cm/y)
0.0
0.5
1.0
1.5
2.0
2.5
0
30
60
90
120
150
180
Diameter at breast height (cm)
Probability
1
1.7
DBH growth for a 45-cm tree [cm/ y]

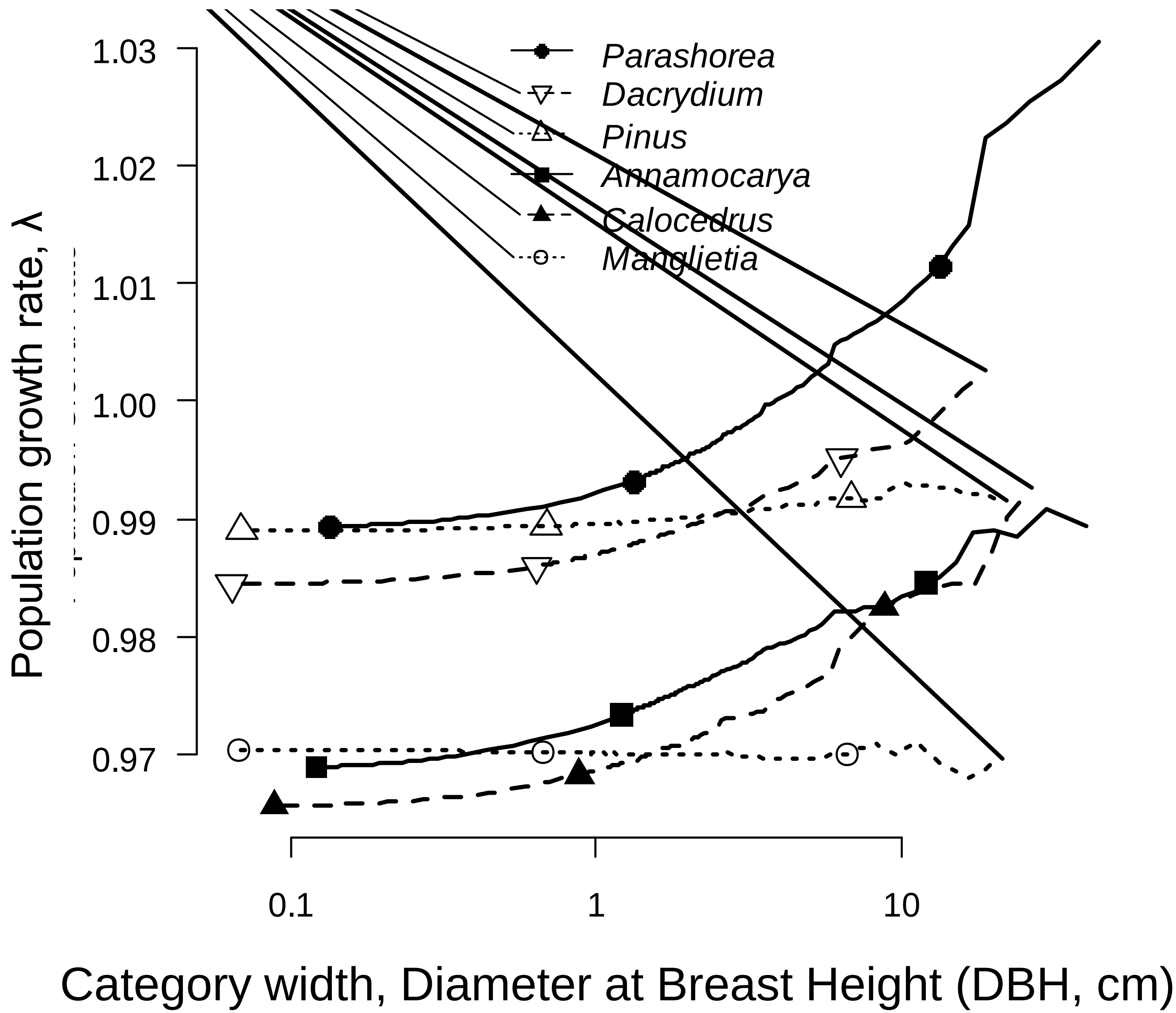


No restrictions on #categories in Integral Projection Models



Zuidema et al. 2010 *J Ecol*

No restrictions on #categories in IPMs

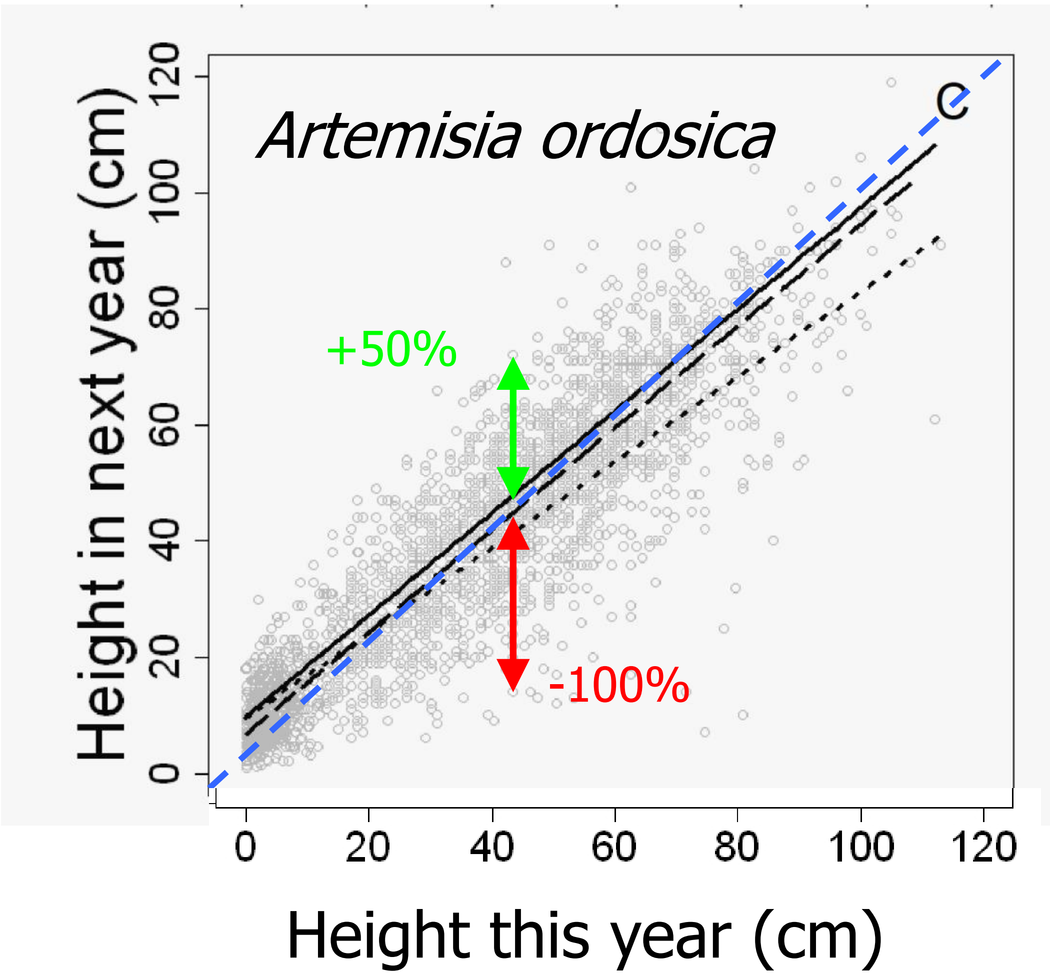


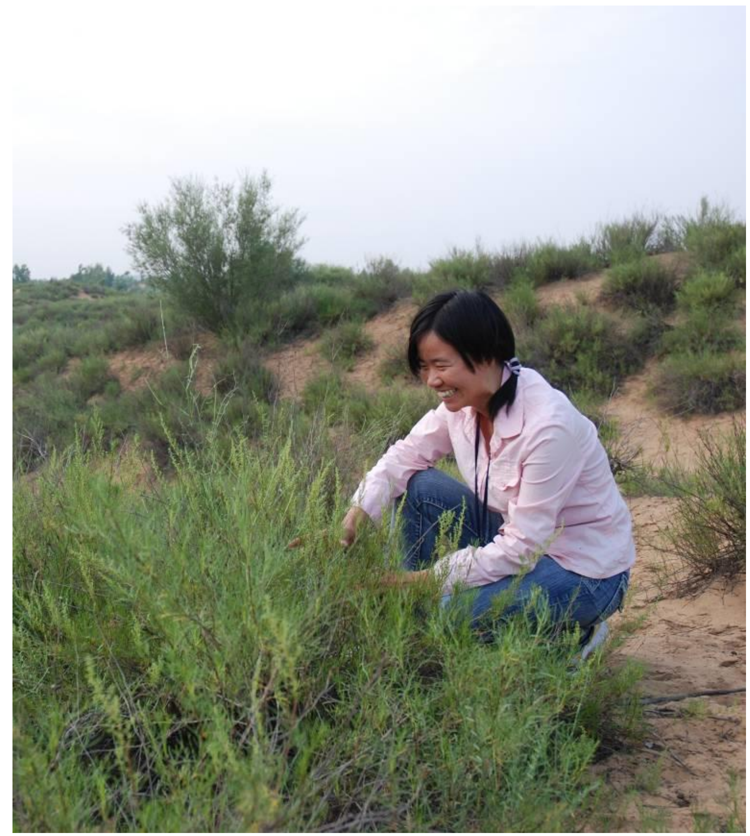
Zuidema et al. 2010 *J Ecol*

Why IPMs?

1. Eliminate effect of category width
2. <u>Incorporate growth variation among individuals</u>
3. Flexible model with few parameters

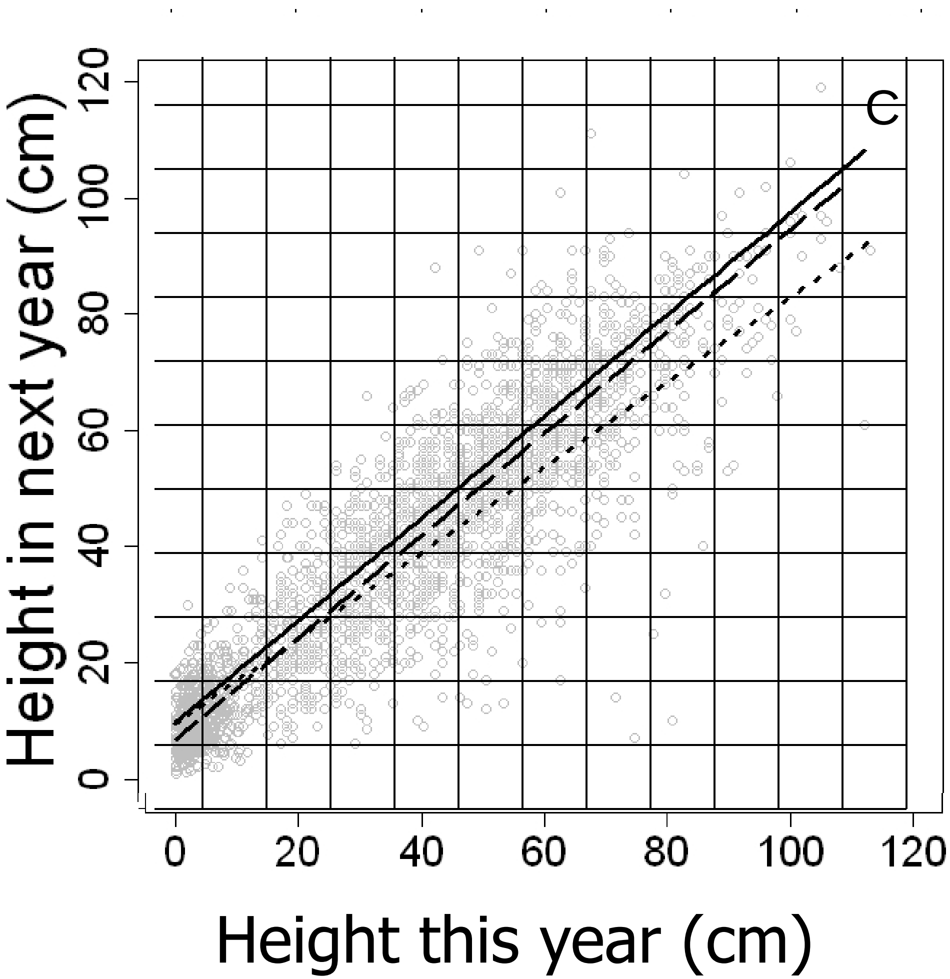
Strong and relevant growth variation





Li et al. 2011 *J Ecology*

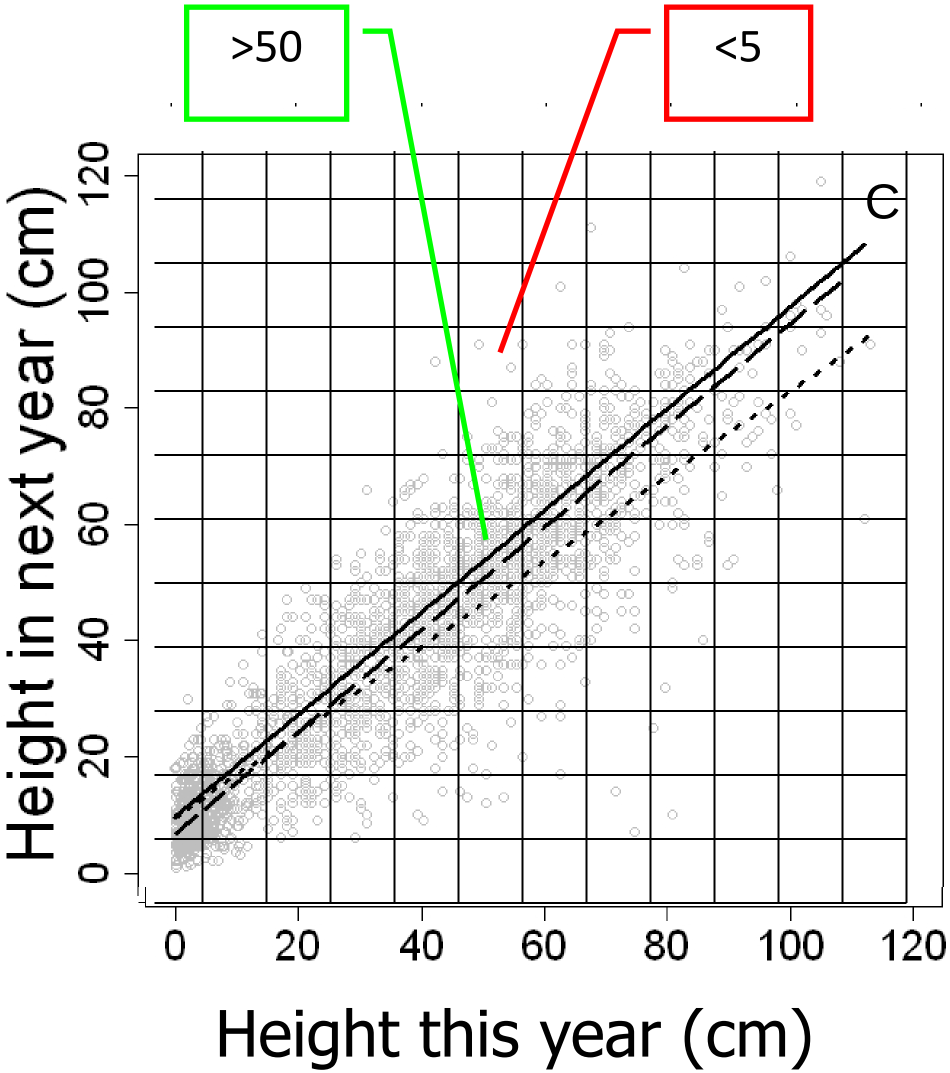
Growth variation in matrix models



- Variation can be incorporated:
- Observed transitions

Li et al. 2011 *J Ecology*

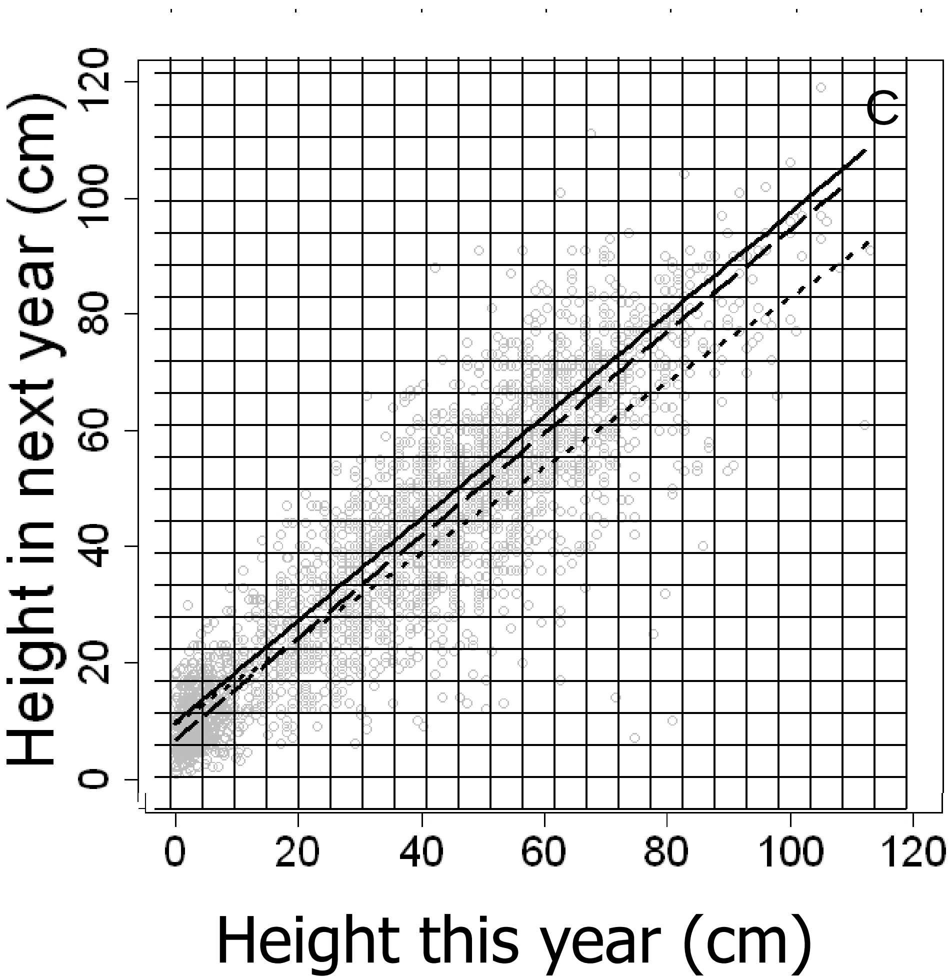
Growth variation in matrix models



- Variation can be incorporated:
- Observed transitions
- Only with sufficient observations

Li et al. 2011 *J Ecology*

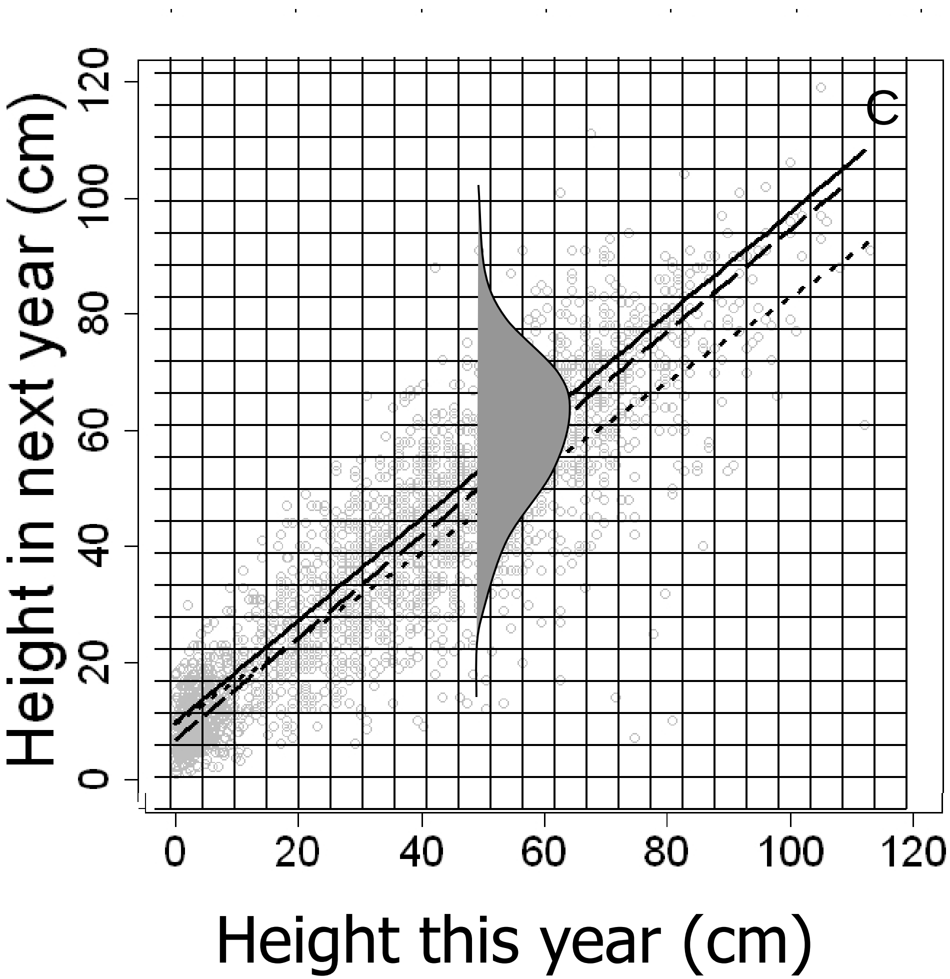
Growth variation in matrix models



- Variation can be incorporated:
- Observed transitions
- Only with sufficient observations
- More categories would be better

Li et al. 2011 *J Ecology*

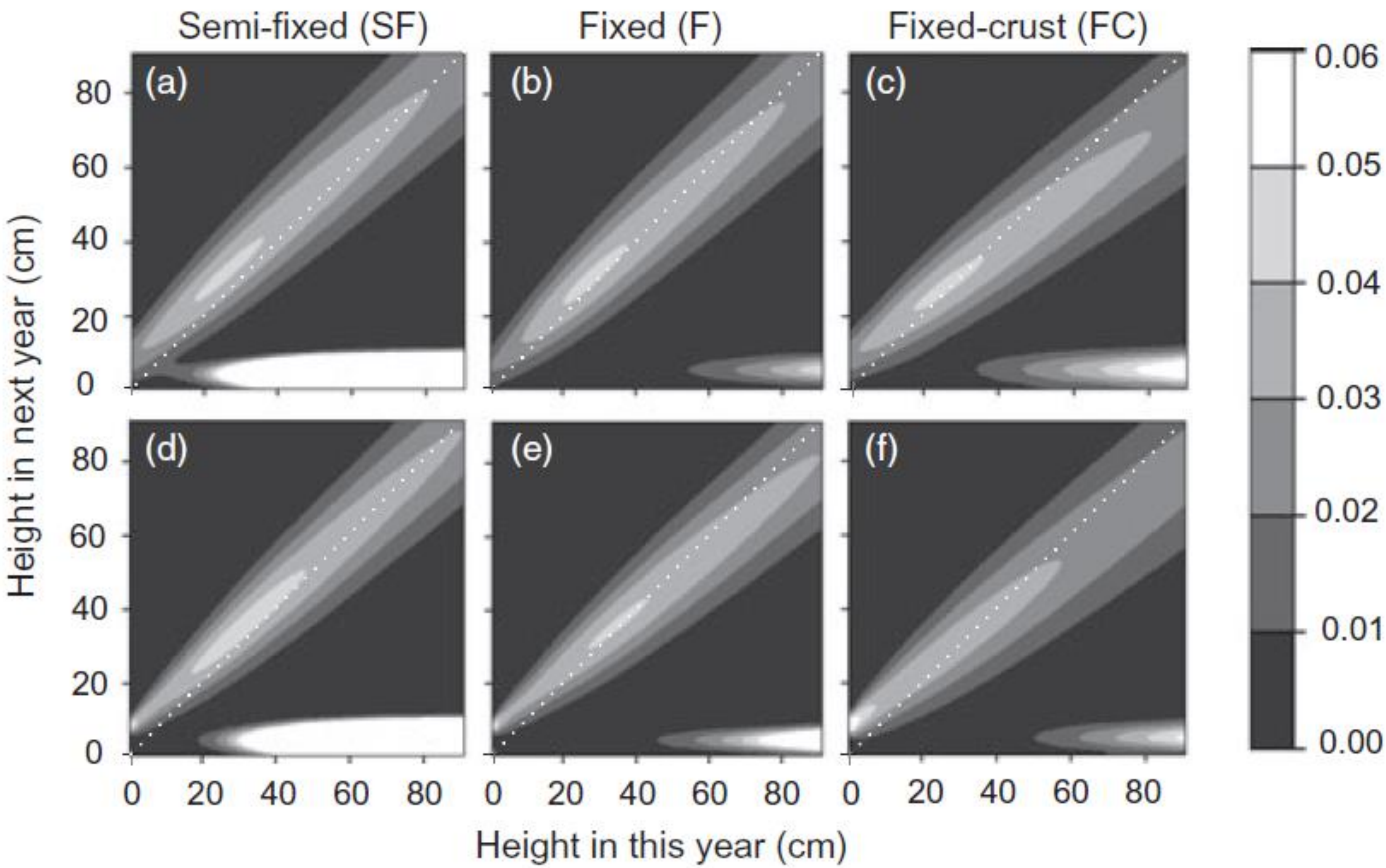
Growth variation in IPMs



- Variation explicitly included
- No consequences for accuracy

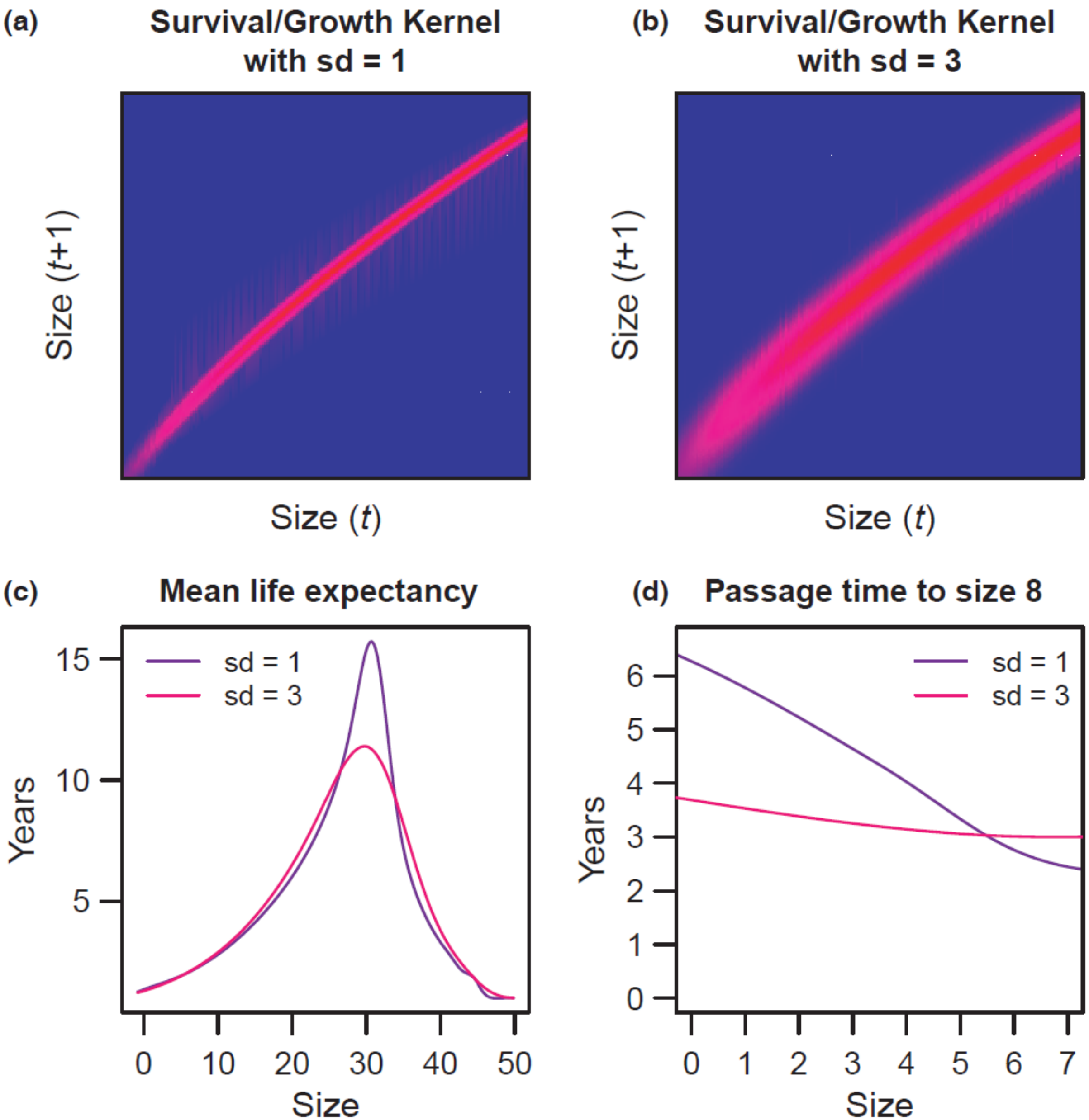
Li et al. 2011 *J Ecology*

Growth variation in IPMs



Li et al. 2011 *J Ecology*

Impact of growth variation



Merow et al. 2014 *Meth Ecology Evolution*

Why IPMs?

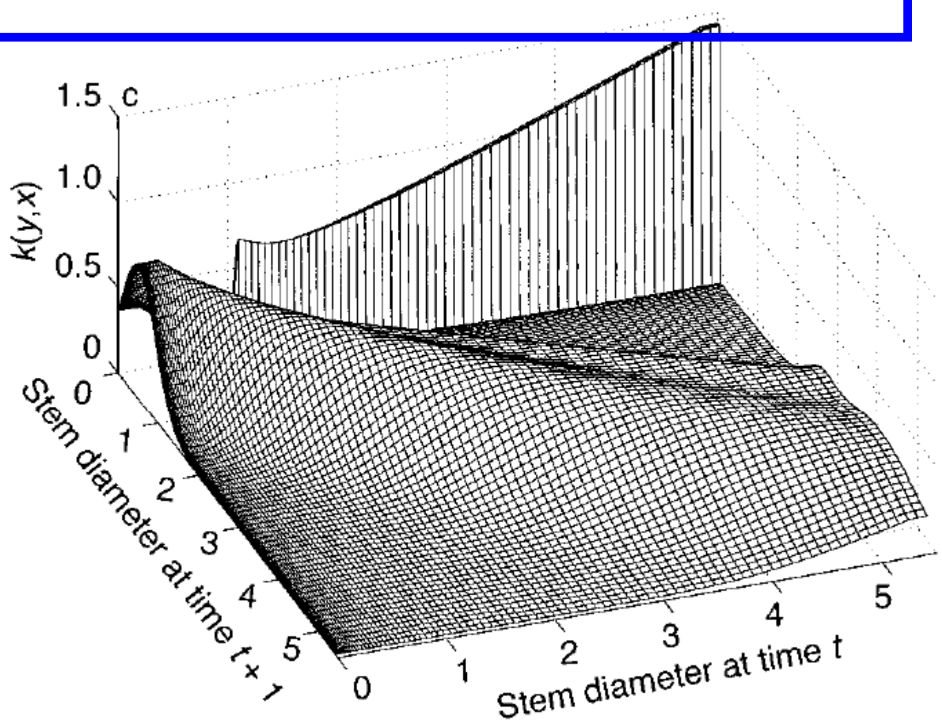
1. Eliminate effect of category width
2. Incorporate growth variation among individuals
3. <u>Flexible model with few parameters</u>

Flexible model & few params

1. Limited # of regressions => few parameters
2. Borrow strength across life classes, treatments or environments
3. Direct and clear link between statistics & model parameterization & output

Lecture: Background & construction IPMs

- What are IPMs?
- Why IPMs?
- Differences with matrix models
- Model construction
- Intro ipmr

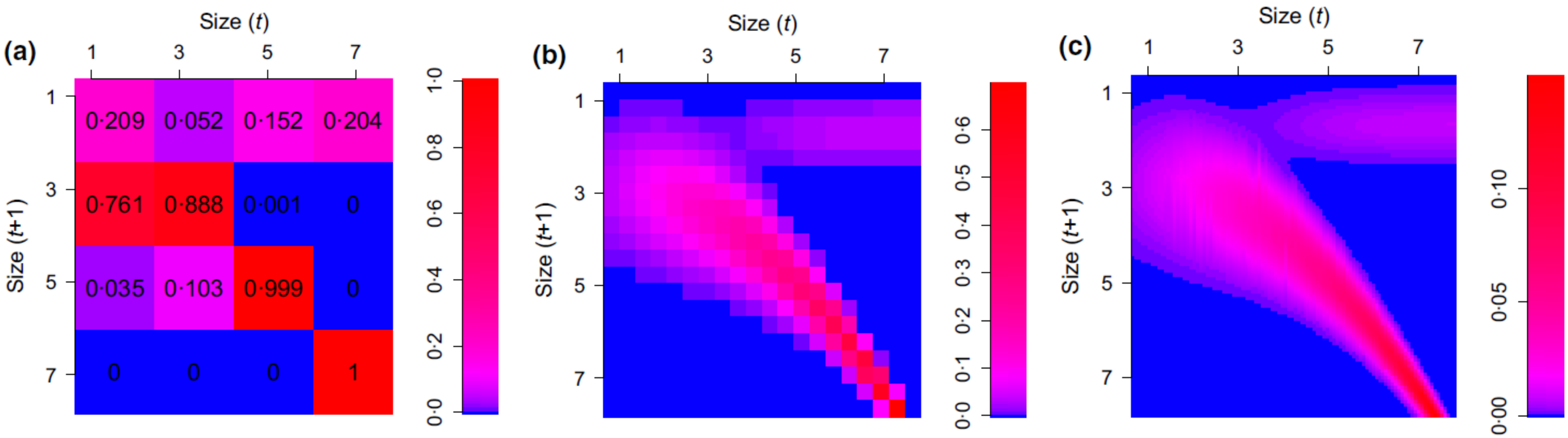


Matrix models vs IPMs

IPMs:

1. Explicitly incorporate growth variation among individuals
2. Have (many) more classes
3. Are based on statistical analyses of vital rates
4. Are more flexible in terms of categories and statistical models applied
5. Use fewer parameters (generally)

Matrix models vs IPMs



Merow et al. 2014 *Meth Ecology Evolution*

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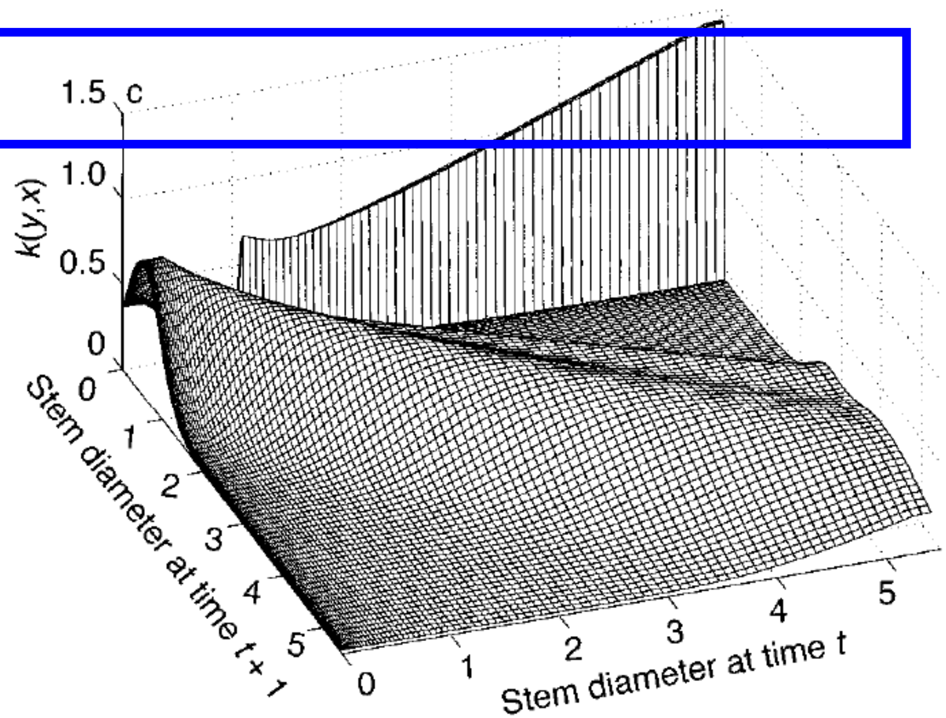
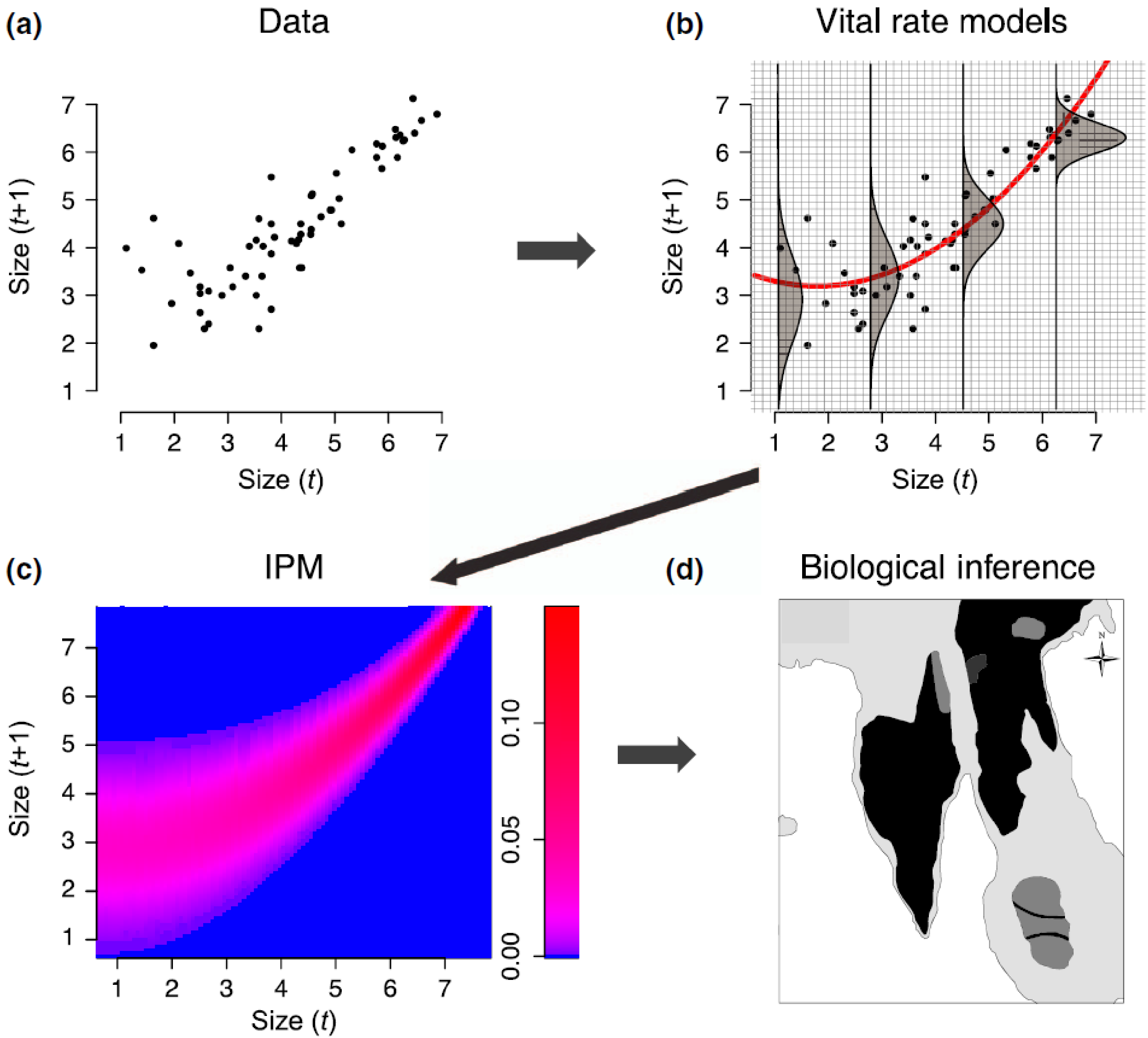
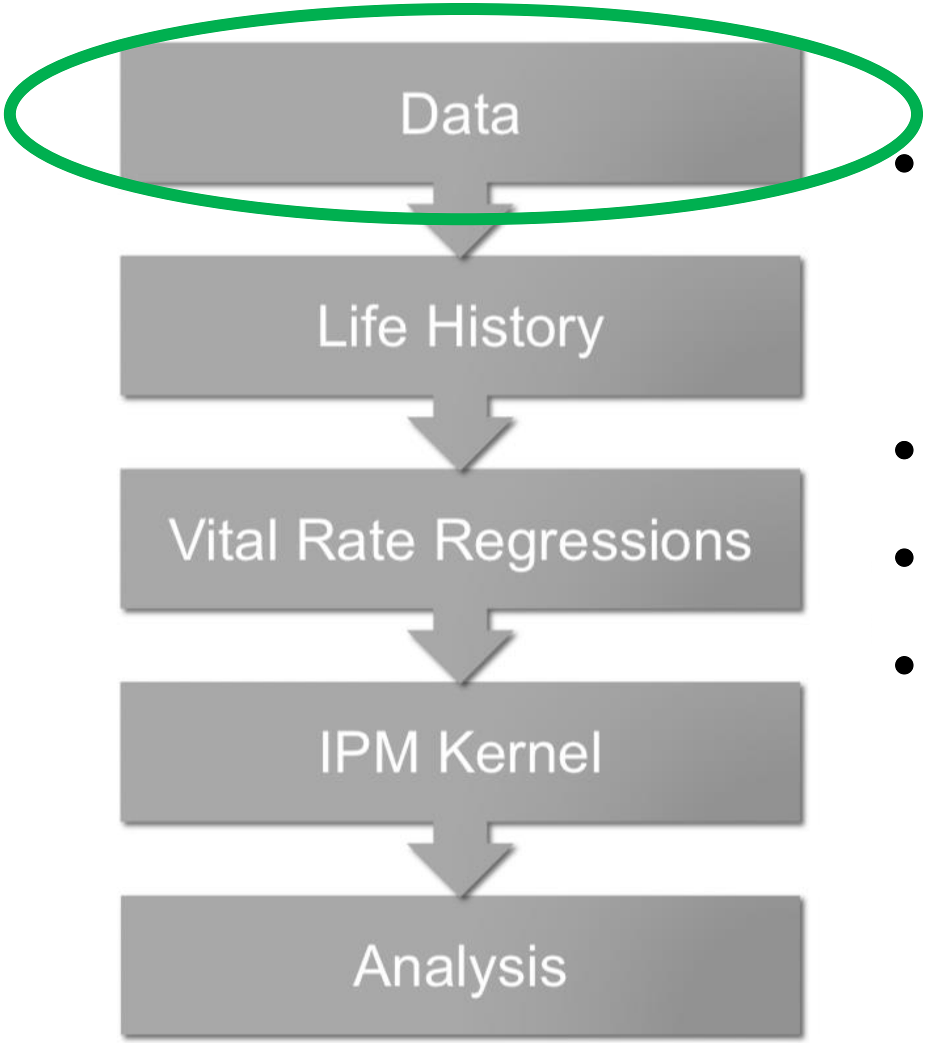




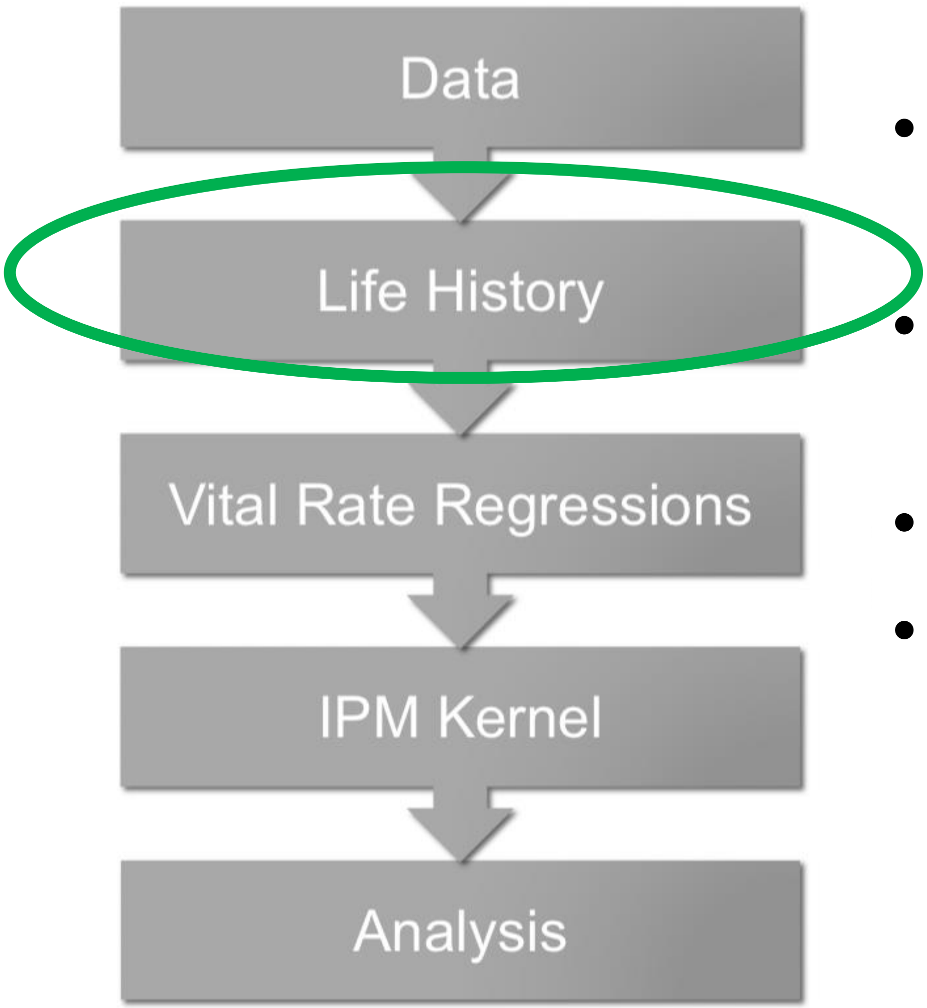
Merow et al. 2014 *Meth Ecology Evolution*

Model construction



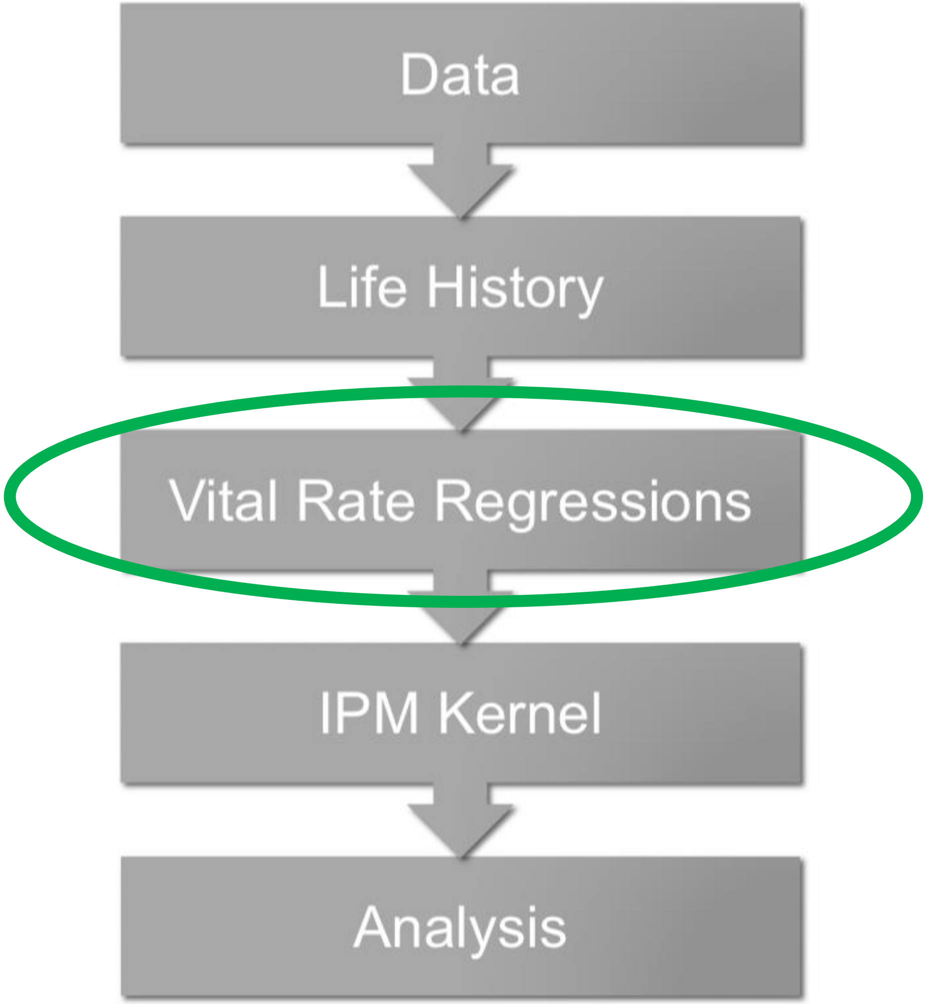
- Repeated measurements on individuals
- Within a population
- For 1-many years
- Info on survival, growth and recruitment

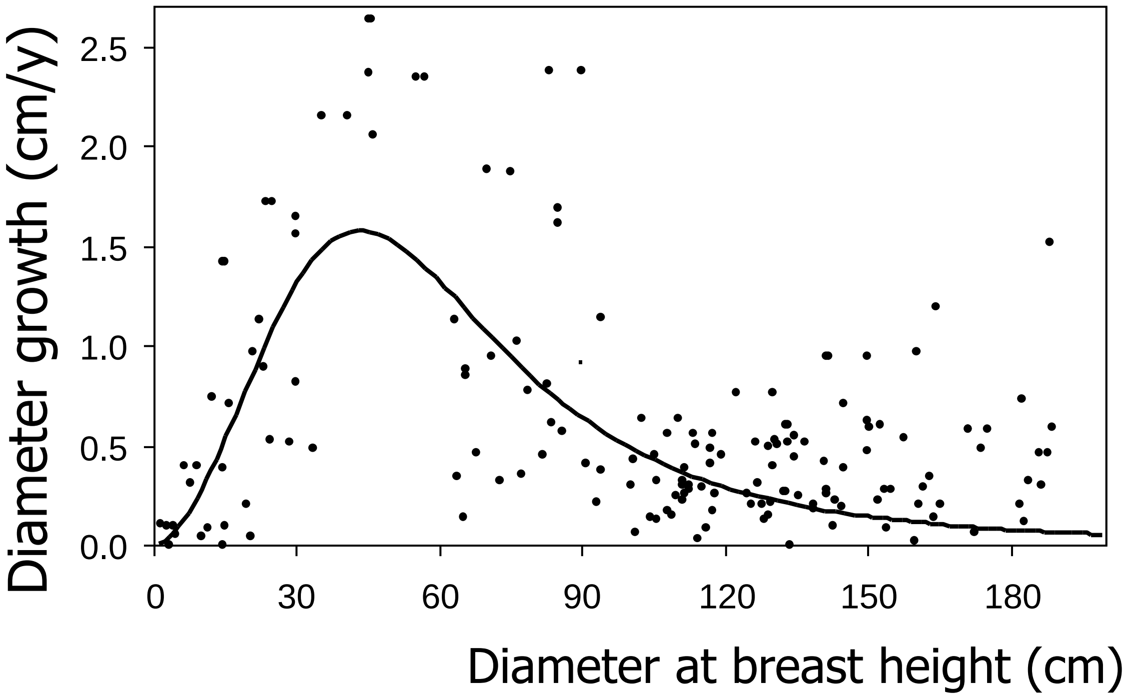
Model construction



- Only sexual reproduction?
- Also vegetative (clonal) reproduction?
- How to describe size?
- What co-variates to include?
  - Habitat
  - Climate, etc

Model construction

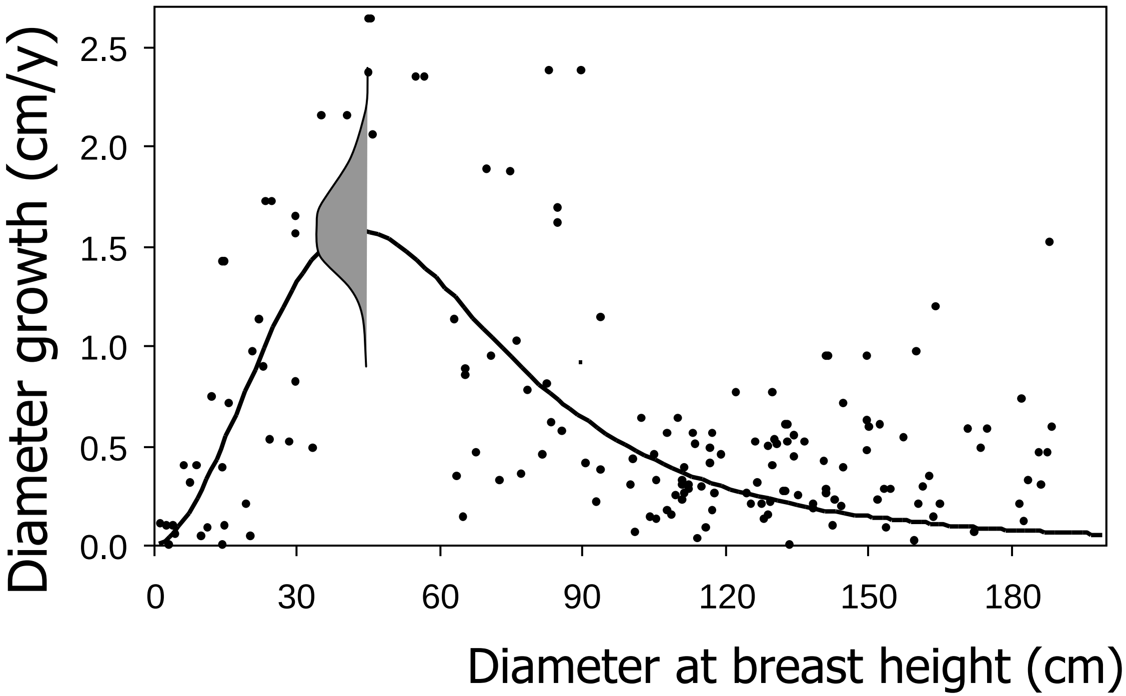




Vital rate regression: growth

<u>Integral Proj models</u>

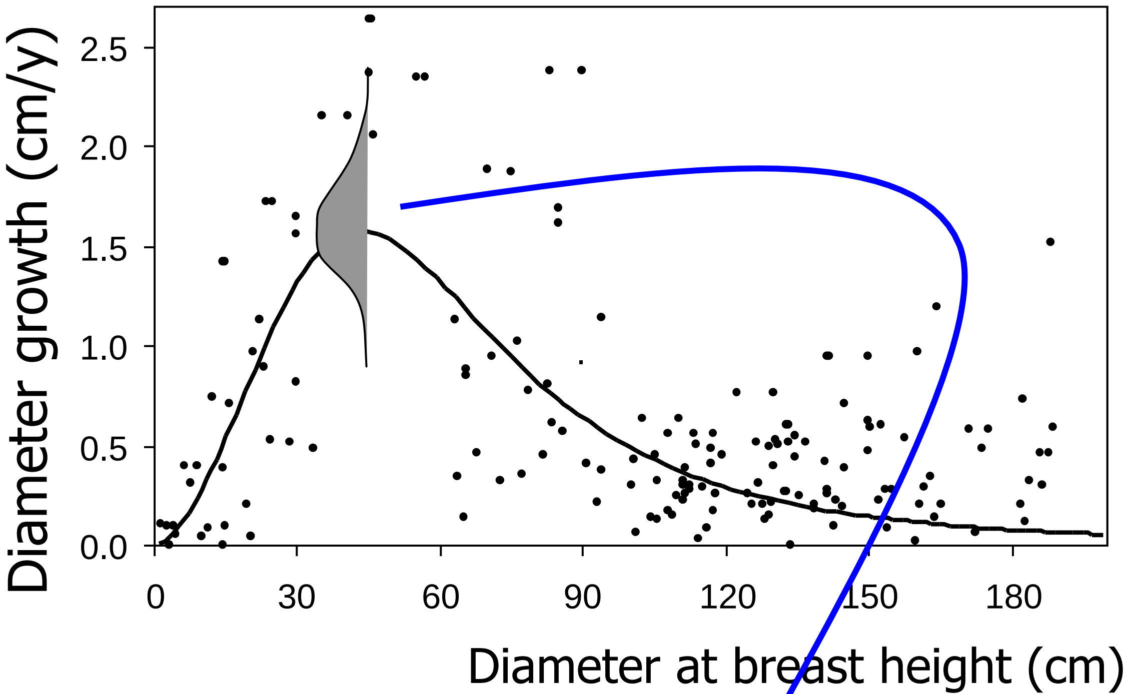
- Establish relations



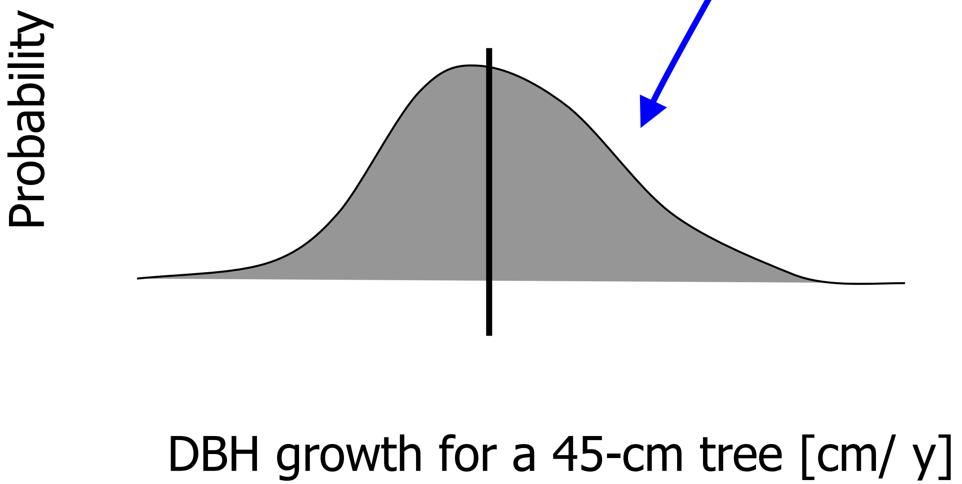
Vital rate regression: growth

Integral Proj models

- Establish relations
- Residuals distr



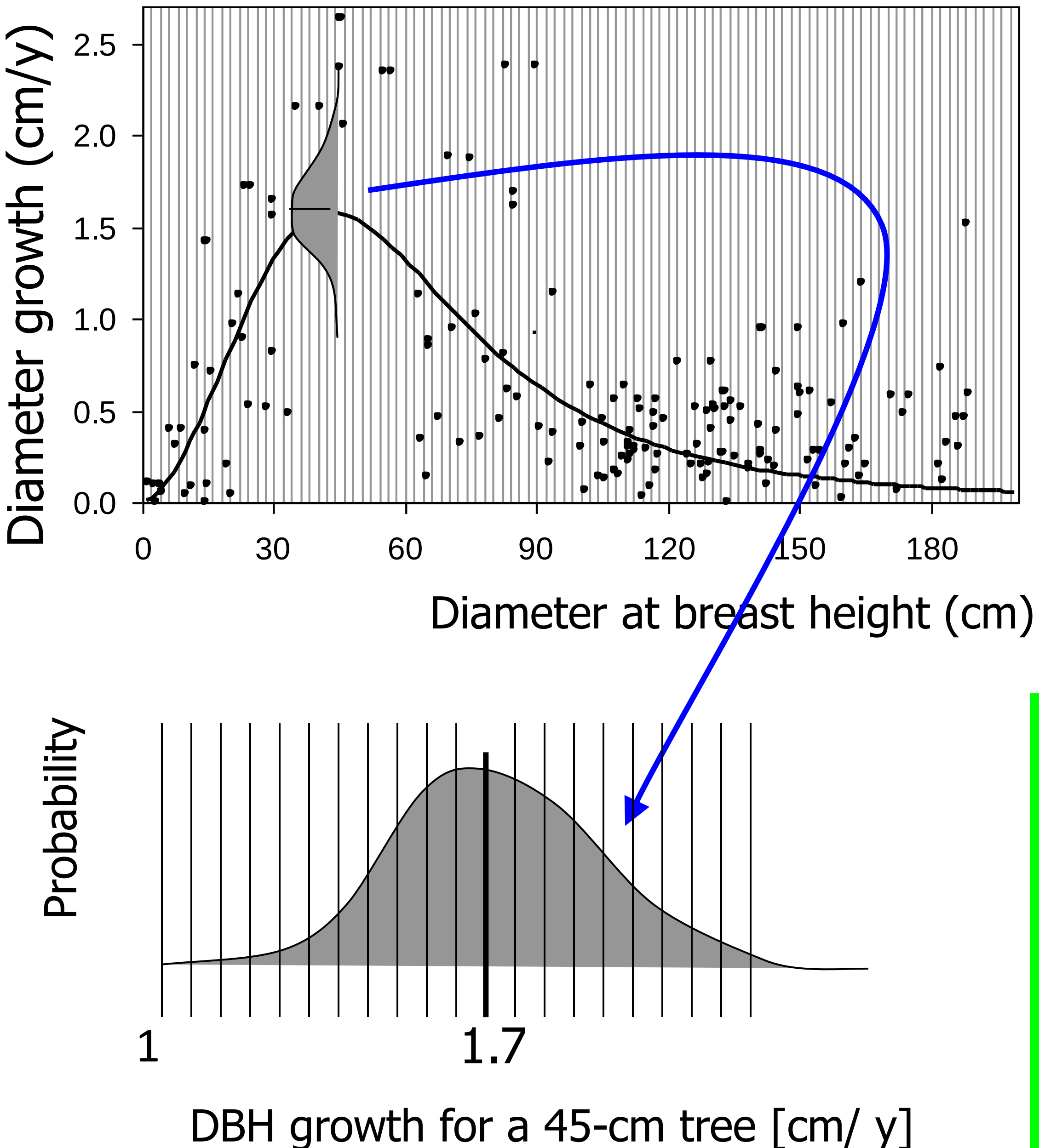
Vital rate regression: growth



Integral Proj models

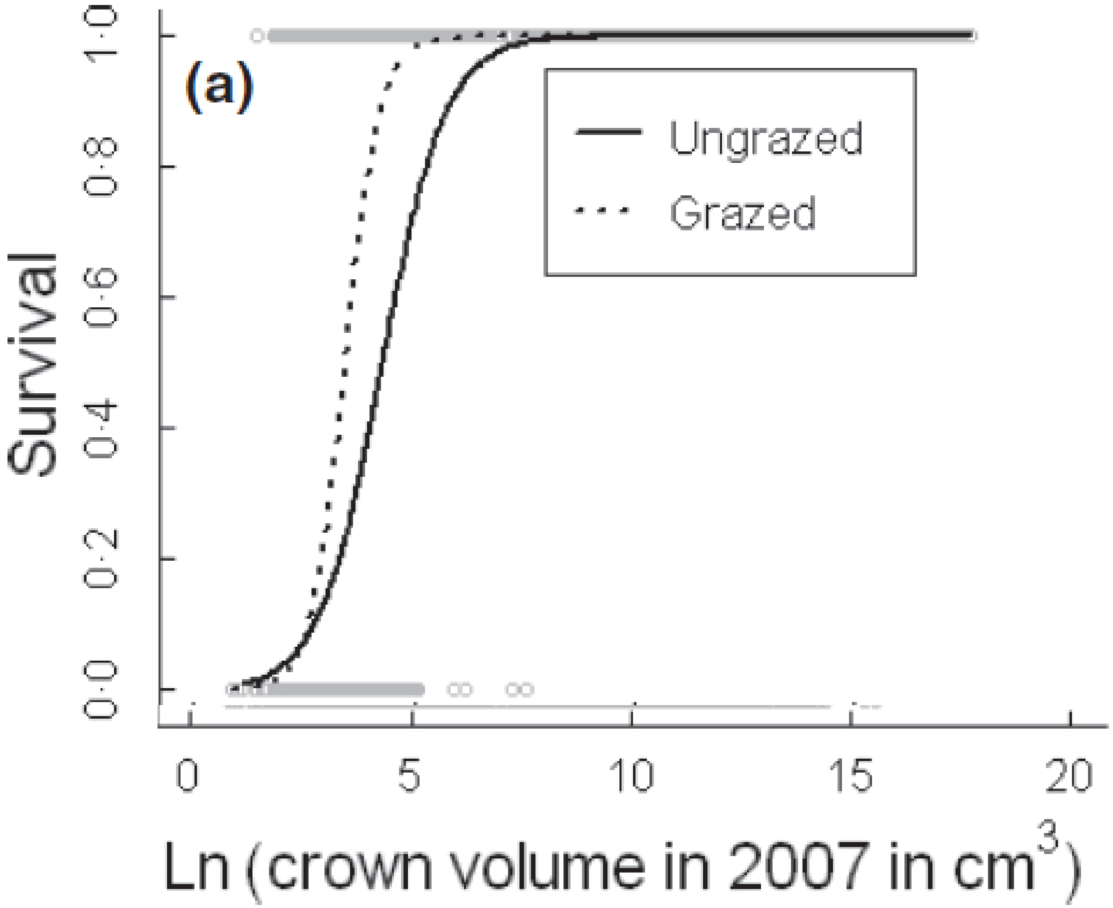
- Establish relations
- Residuals distr

Vital rate regression: growth



Integral Proj models

- Establish relations
- Residuals distr
- Calculate chance from x to y

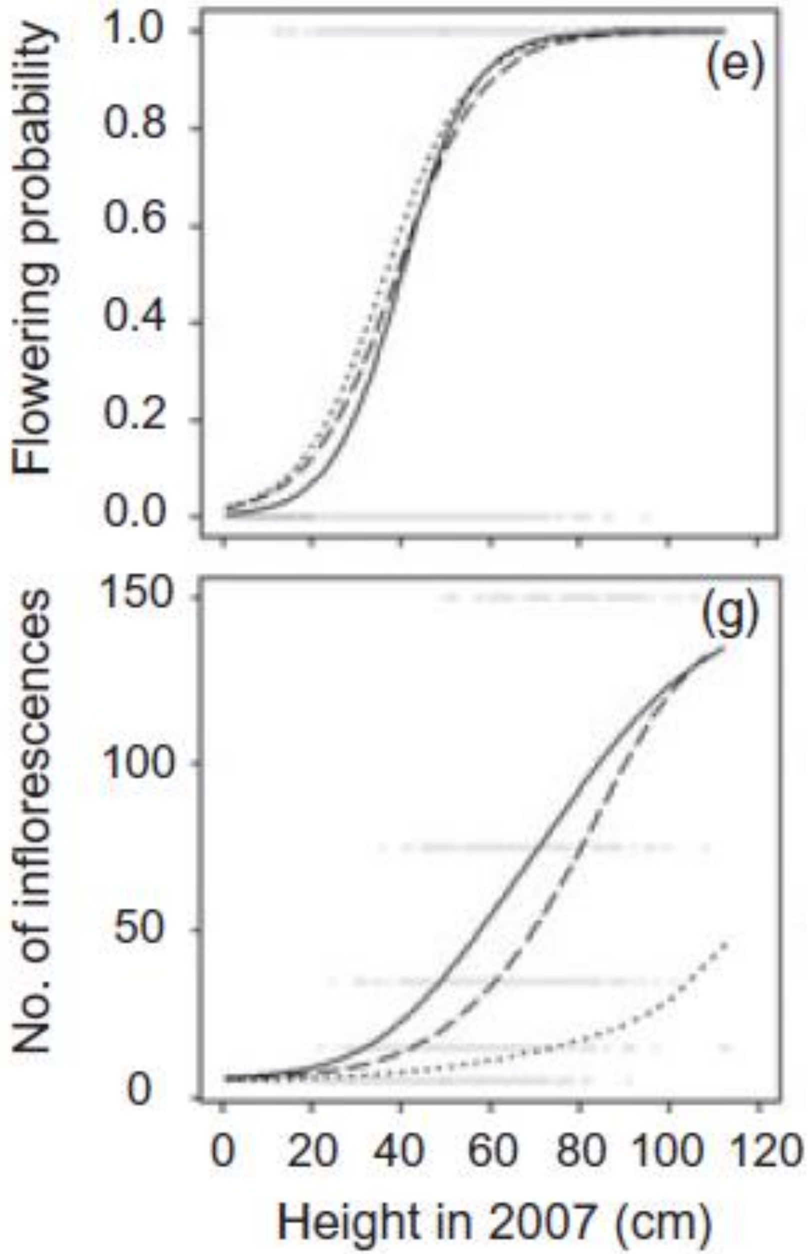


Vital rate regression: survival

Li et al. 2013 *J Applied Ecology*

<u>Integral Proj models</u>

- Establish relations



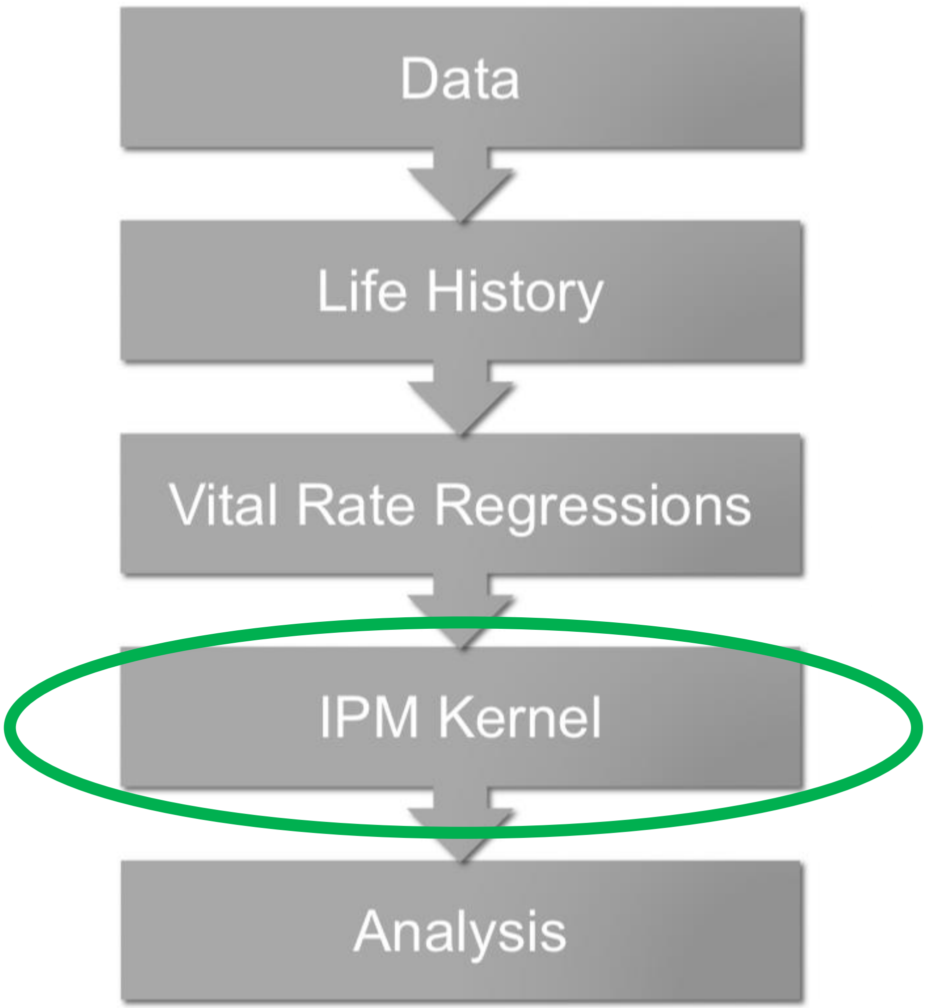
Li et al. 2011 *J Ecology*

Vital rate regression: reproduction

<u>Integral Proj models</u>

- Establish relations
- For reproductive probability
- For reproductive output

Model construction



Establish P part of Kernel

Projection:
$$n(y, t+1) = \int_L^U K(y, x) n(x, t) \mathrm{d}x$$

Kernel: $K(y,x) = P(y,x) + F(y,x)$

For each x (t) & for chosen category width

1. Multiply survival of x-sized individual
2. With probability for a surviving x-sized individual to grow to each possible y (y can be > or < than x)

Establish F part of Kernel

Projection:

$$n(y, t+1) = \int_L^U K(y,x)\,n(x,t)\,\mathrm{d}x$$

Kernel: $K\,(y,x) = P\,(y,x) + F\,(y,x)$

For each x (t) & for chosen category width

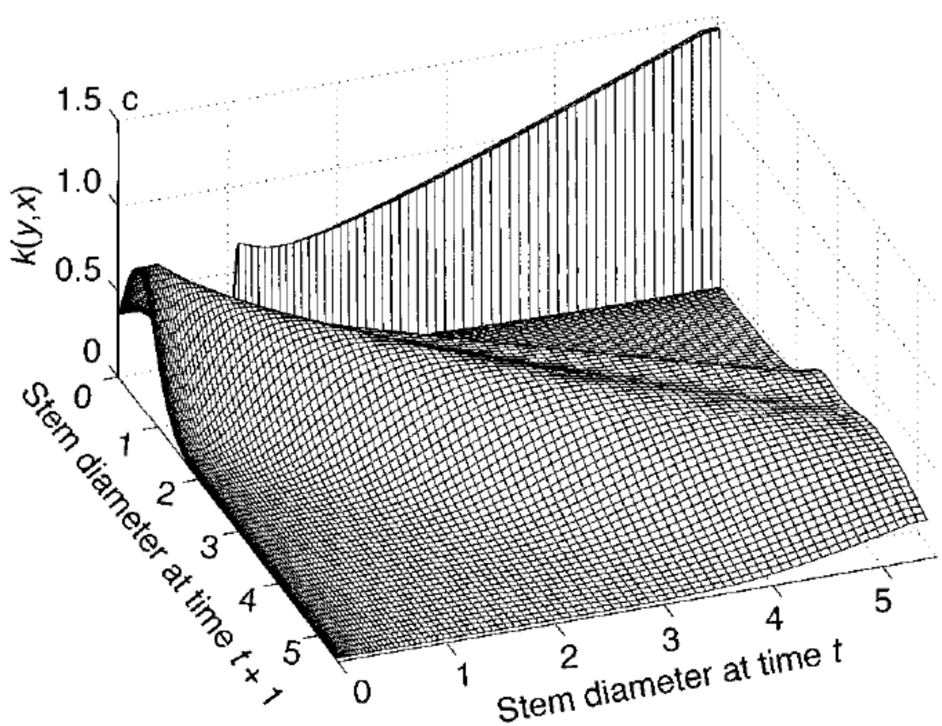
1. Multiply probability of reproduction for size x
2. With number of seeds produced per year for size x (if available)
3. With recruits per seed produced (or with recruits per reproductive individual, if 2 is not available)

Calculate K

Projection:

$$n(y, t+1) = \int_{L}^{U} K(y, x) n(x, t) \mathrm{d}x$$

Kernel: $K\,(y,x) = P\,(y,x) + F\,(y,x)$



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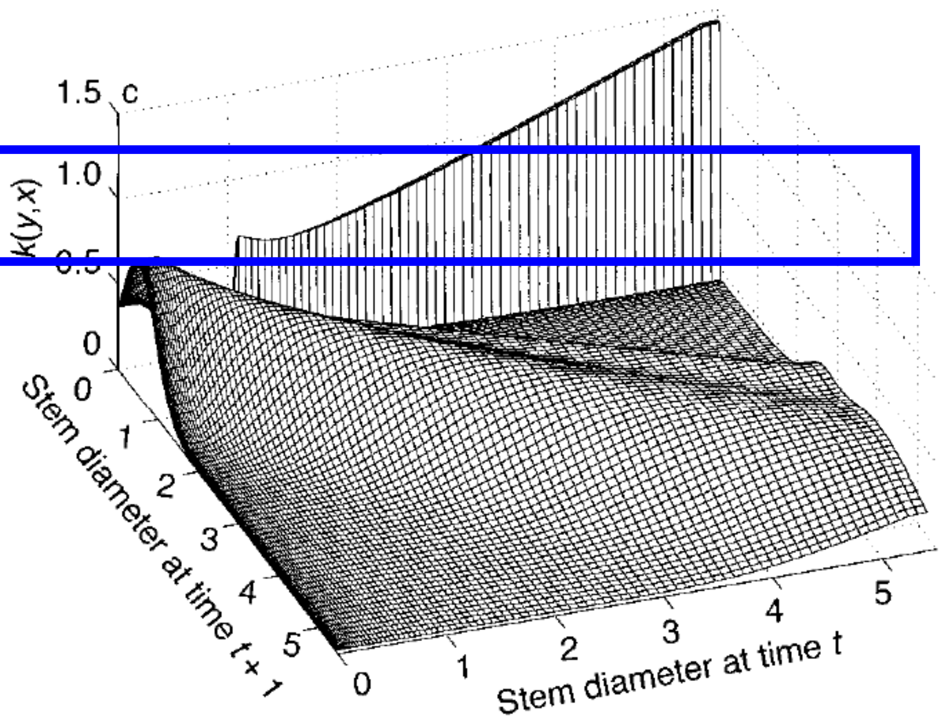
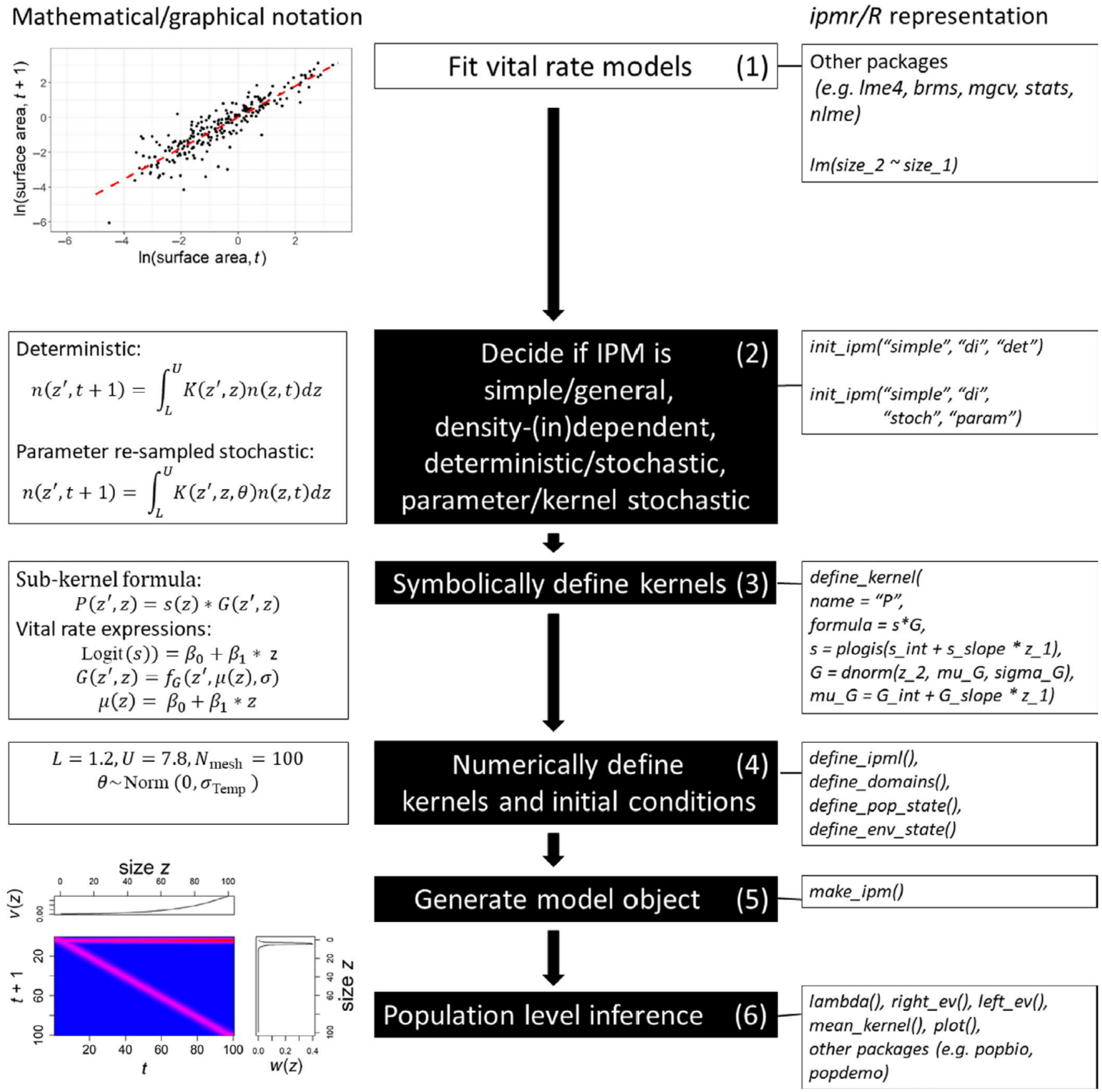


Intro ipmr

- Performs:
  - Kernel building
  - Discretization
  - Some model simulations
- Can include treatments, variation, stochasticity
- Quite flexible
- In this course, we will keep it quite simple in exercises, but if you want…. (!)

Intro ipmr

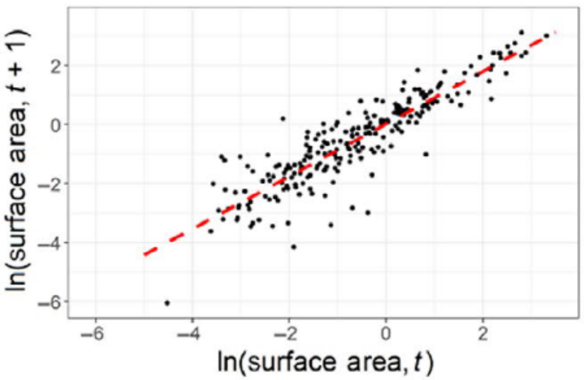


Levin et al. 2021 *Meth Ecology Evolution*

Intro ipmr

Mathematical/graphical notation

ipmr/R representation



Fit vital rate models (1)

Other packages
(e.g. lme4, brms, mgcv, stats, nlme)

lm(size_2 ~ size_1)

Deterministic:

$$n(z', t+1) = \int_L^U K(z', z) n(z, t) dz$$

Parameter re-sampled stochastic:

$$n(z', t+1) = \int_L^U K(z', z, \theta) n(z, t) dz$$

Decide if IPM is simple/general, density-(in)dependent, deterministic/stochastic, parameter/kernel stochastic (2)

init_ipm("simple", "di", "det")

init_ipm("simple", "di", "stoch", "param")

Levin et al. 2021 *Meth Ecology Evolution*

Intro ipmr

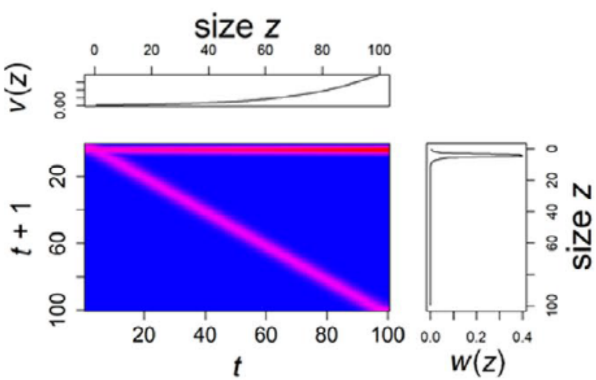
Sub-kernel formula:

$$P(z', z) = s(z) * G(z', z)$$

Vital rate expressions:

$$\mathrm{Logit}(s)) = \beta_0 + \beta_1 * \mathrm{z}$$
$$G(z', z) = f_G(z', \mu(z), \sigma)$$
$$\mu(z) = \beta_0 + \beta_1 * z$$

$$L = 1.2, U = 7.8, N_{\mathrm{mesh}} = 100$$
$$\theta \sim \mathrm{Norm}\,(0, \sigma_{\mathrm{Temp}})$$



Symbolically define kernels (3)

define_kernel(
name = "P",
*formula = s*G,*
*s = plogis(s_int + s_slope * z_1),*
G = dnorm(z_2, mu_G, sigma_G),
*mu_G = G_int + G_slope * z_1)*

Numerically define kernels and initial conditions (4)

define_ipml(),
define_domains(),
define_pop_state(),
define_env_state()

Generate model object (5)

make_ipm()

Population level inference (6)

lambda(), right_ev(), left_ev(),
mean_kernel(), plot(),
other packages (e.g. popbio, popdemo)

Levin et al. 2021 *Meth Ecology Evolution*

Downside of ipmr

- Requires growth part of kernel to be in the form:

  size_next ~ a*size + …

- For many organisms a form like:

  growth ~ a*size + b*size^2 + …

  would be more logical
- In our exercises, we therefore use curve fitting (function nls) to model

  size_next ~ size + some_growth_equation

Terms IPM

- Vital rates = rates of growth, survival, reproduction, germination
- Kernel = the function that describes the transitions among sizes, based on vital rate regressions
- P Kernel = the function describing transitions among sizes based on survival and growth
- F Kernel = the function describing transitions among sizes based on fecundity and size distribution of recruits
- Discretization = the change in P and F kernels from continuous functions to large matrices containing transition probabilities