Spatial population dynamics and control

Broad overview

- Aspects of stochasticity at a single location (with Brett Melbourne)
- Stochastic spatial spread (with Brett Melbourne)
- Control of invasive species (with Caz Taylor, Richard Hall, Julie Blackwood, Chris Costello, Rebecca Epanchin-Niell plus others for experimental/field aspects)

New stochastic Ricker models: extinction risk could be higher

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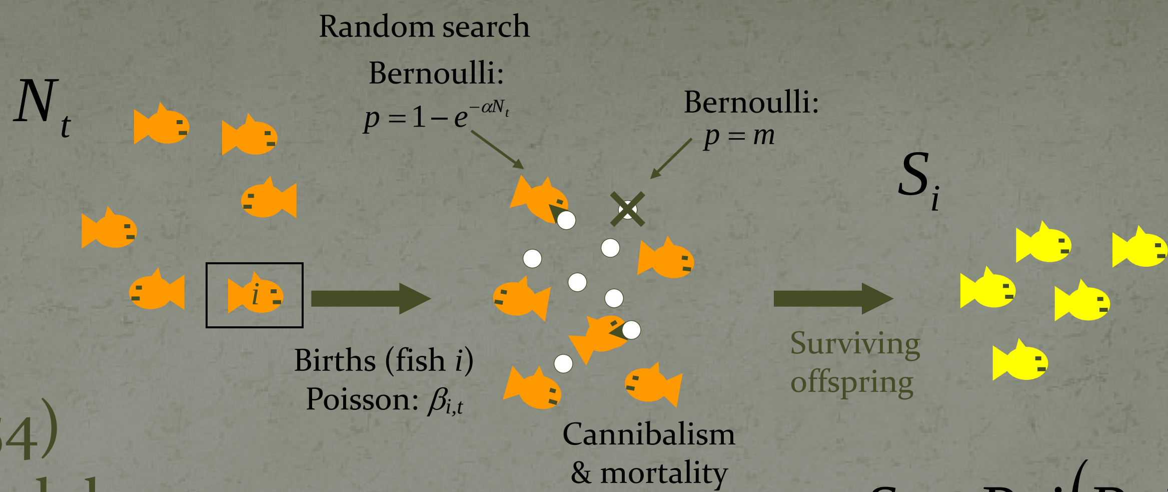
Extinction

- Deterministic and stochastic causes
- Demographic stochasticity *
  - random births & deaths: within-individual scale
- Environmental stochasticity *
  - random births & deaths: population scale
- Demographic heterogeneity
  - vital rates (birth/death): between-individual scale
- Sex ratio stochasticity
  - random: male or female?

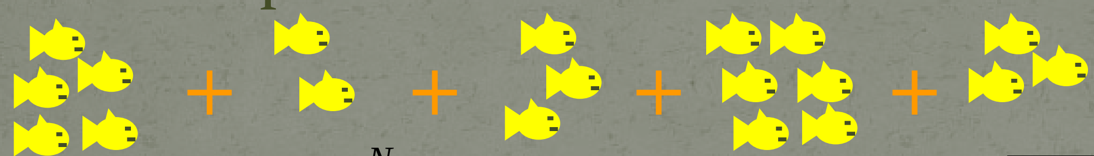


Ricker (1954) Fisheries model

$$S_i \sim \text{Poi}\left(R\, e^{-\alpha N_t}\right)$$

$$R = \beta\left(1 - m\right)$$

Sum up survivors over all adults

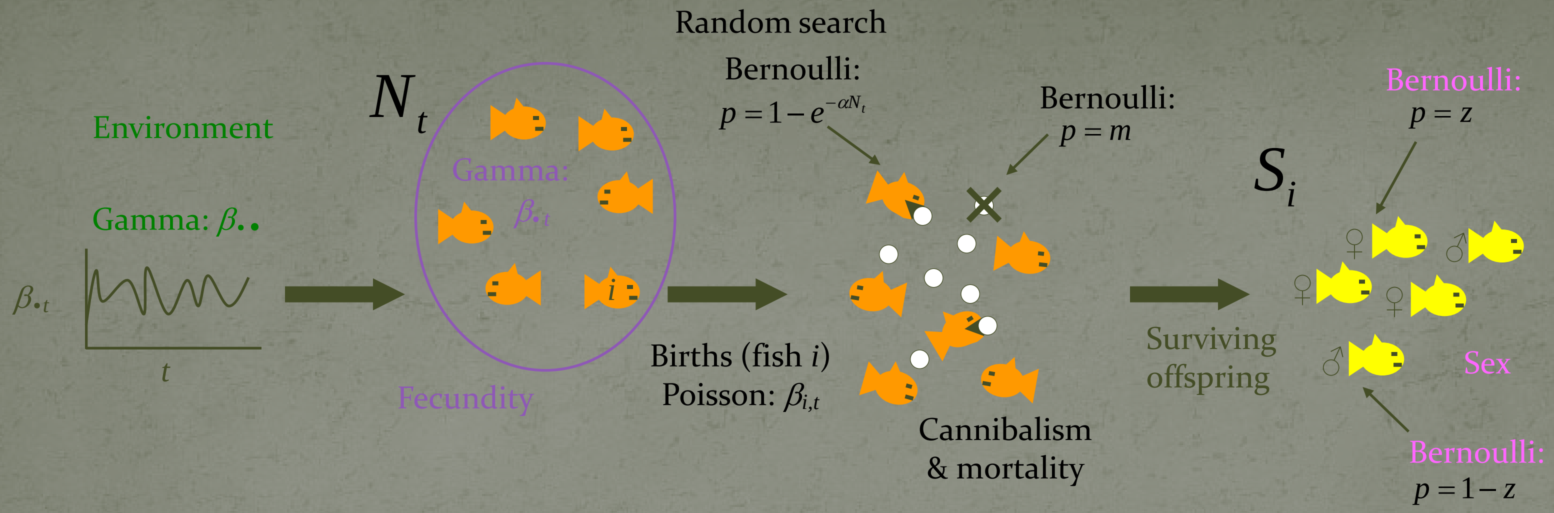


$$N_{t+1} = \sum_{i}^{N_t} S_i \sim \text{Poi}\left(N_t R\, e^{-\alpha N_t}\right)$$

Poisson Ricker

(sum of Poissons is Poisson)

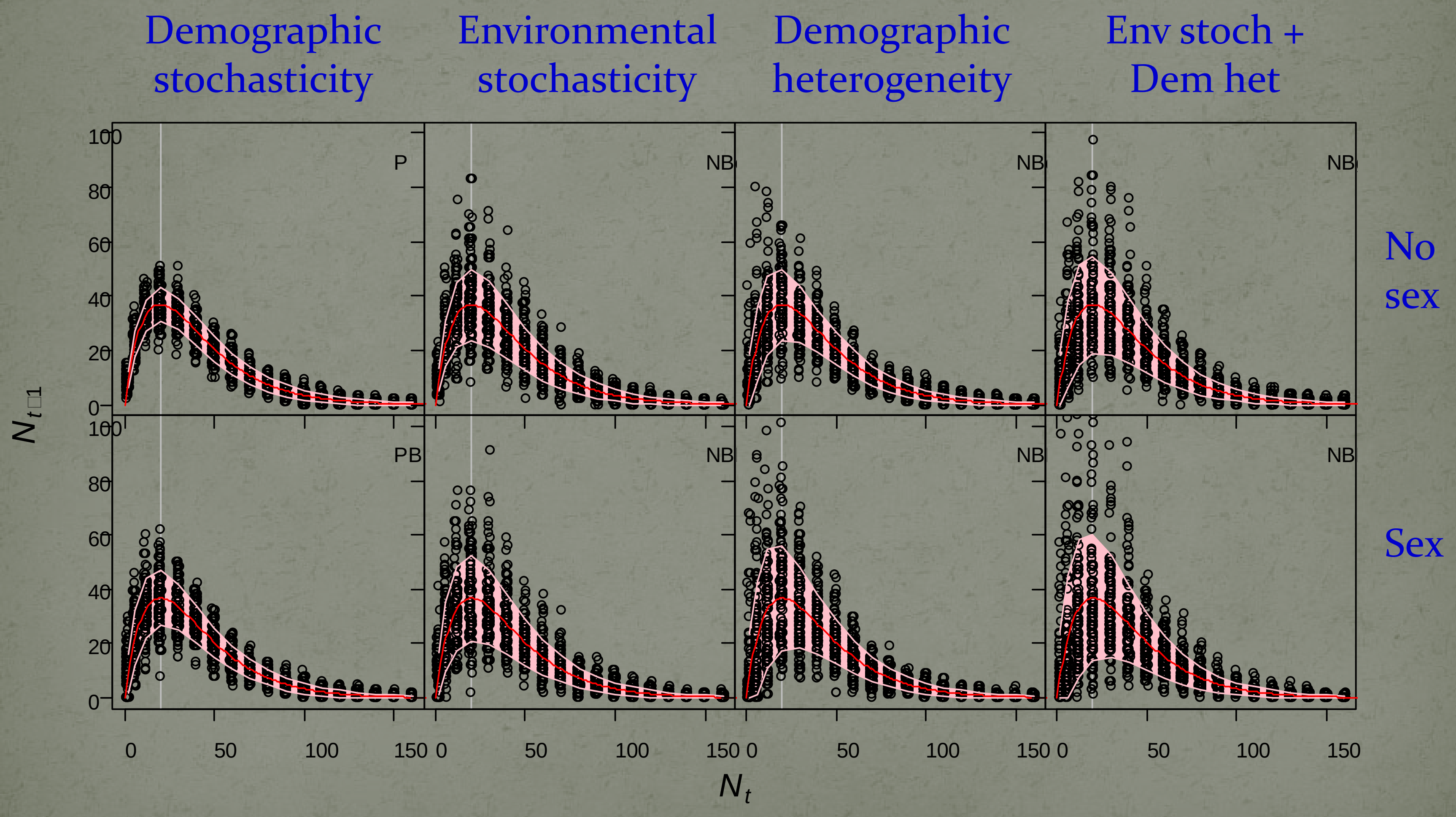
Model for demographic stochasticity



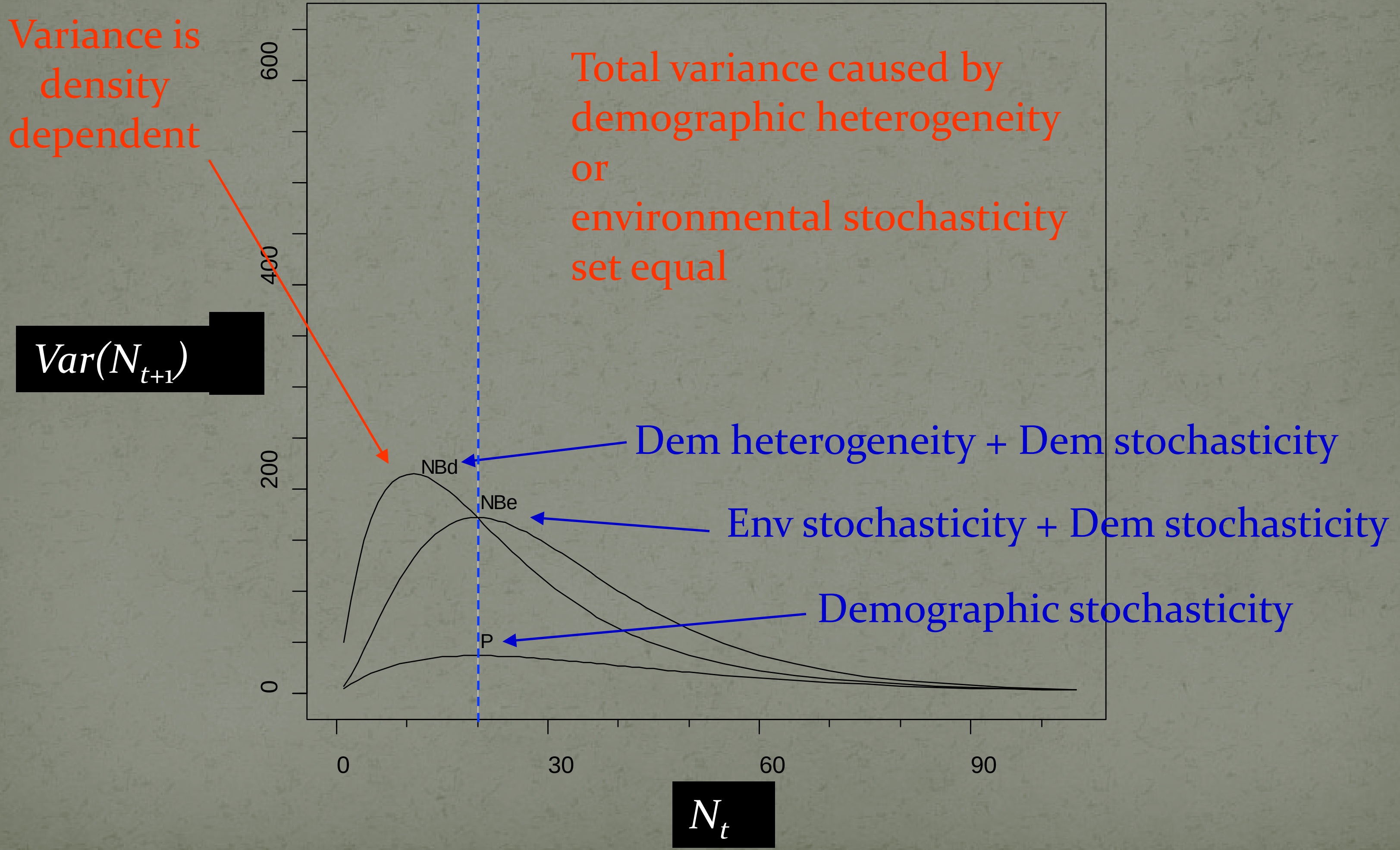
Demographic stochasticity	Environmental stochasticity	Demographic heterogeneity	Sex	Model	Abbr.
●				Poisson	P
●	●			Neg bin-environmental	NBe
●		●		Neg bin-demographic	NBd
●	●	●		Neg bin-gamma	NBg
●			●	Poisson-binomial	PB
●	●		●	Neg bin-binomial-environmental	NBBe
●		●	●	Neg bin-binomial-demographic	NBBd
●	●	●	●	Neg bin-binomial-gamma	NBBg

All models have mean: $N_{t+1} = N_t R e^{-\alpha N_t}$

Stochastic production functions



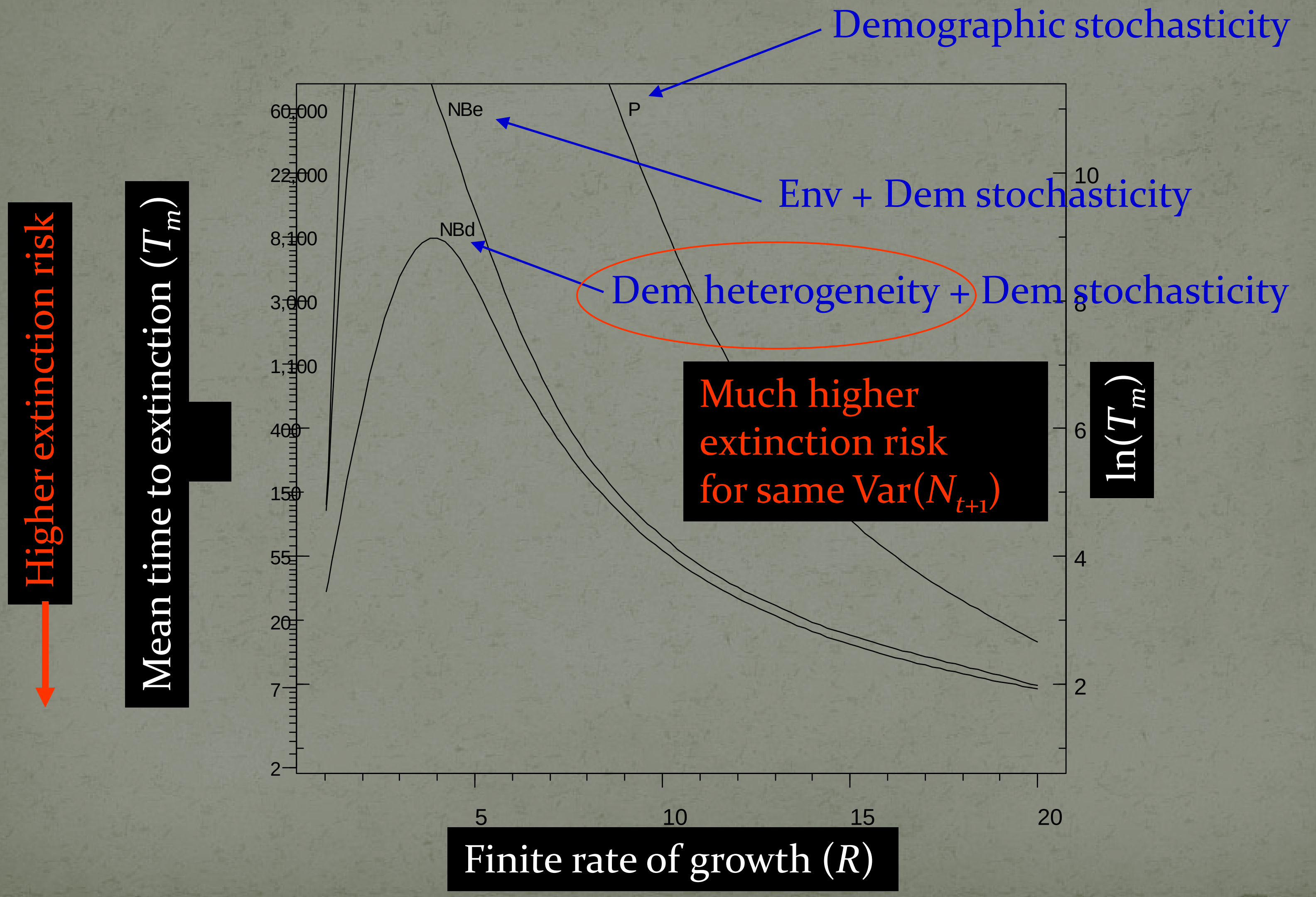
Variance in N_{t+1}



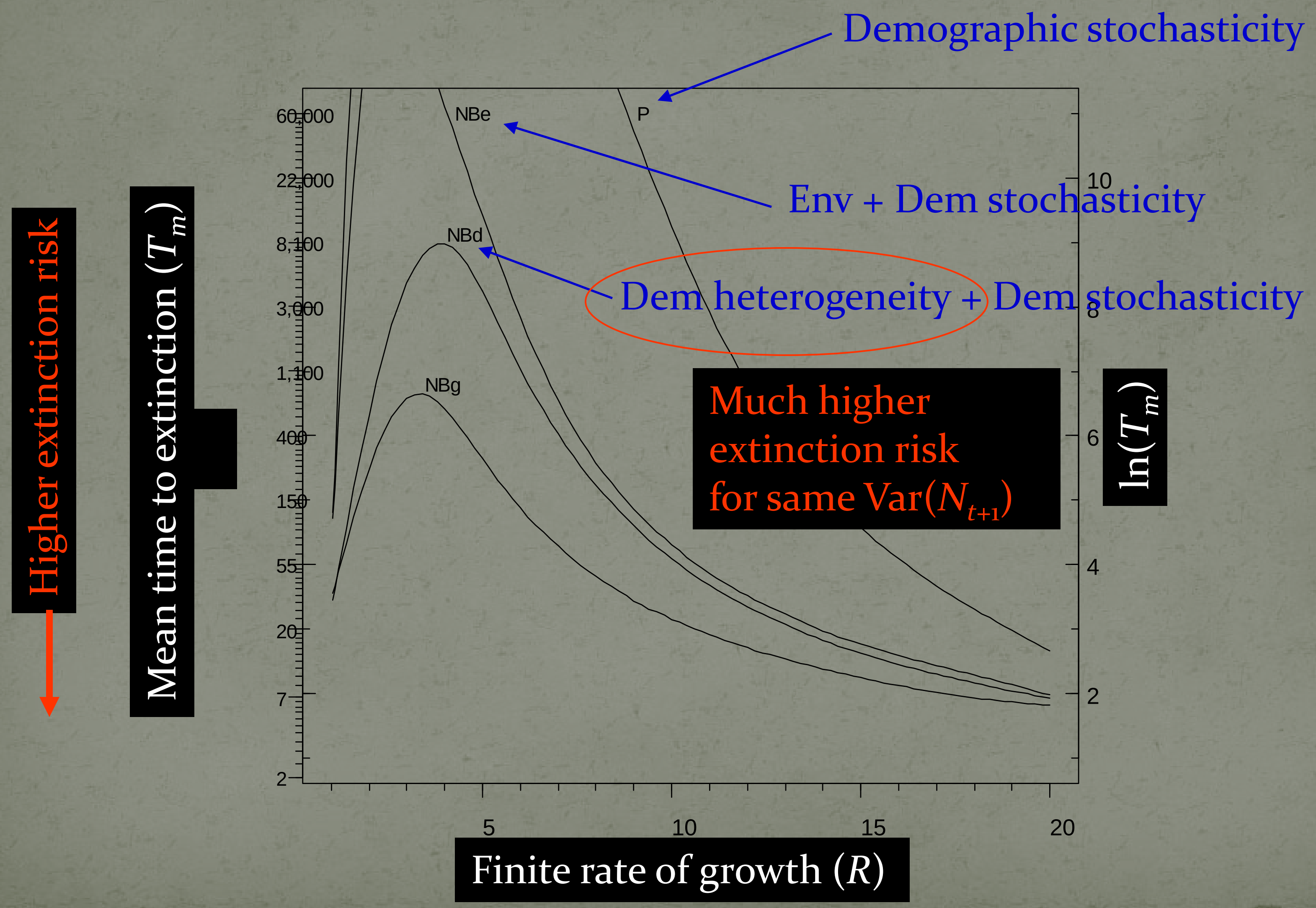
Extinction times

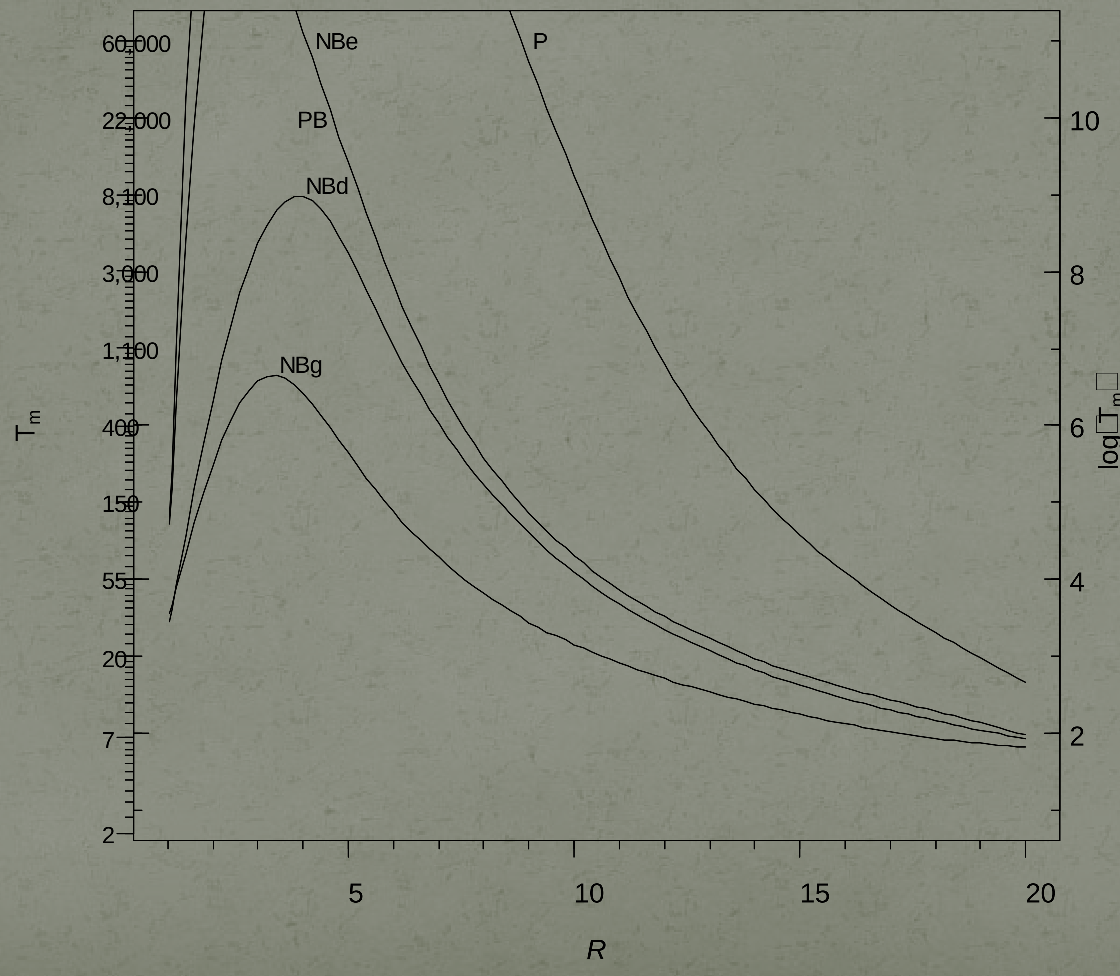
- Intrinsic mean time to extinction (Grimm & Wissel 2004, Oikos 105: 501-511)

Extinction times



Extinction times





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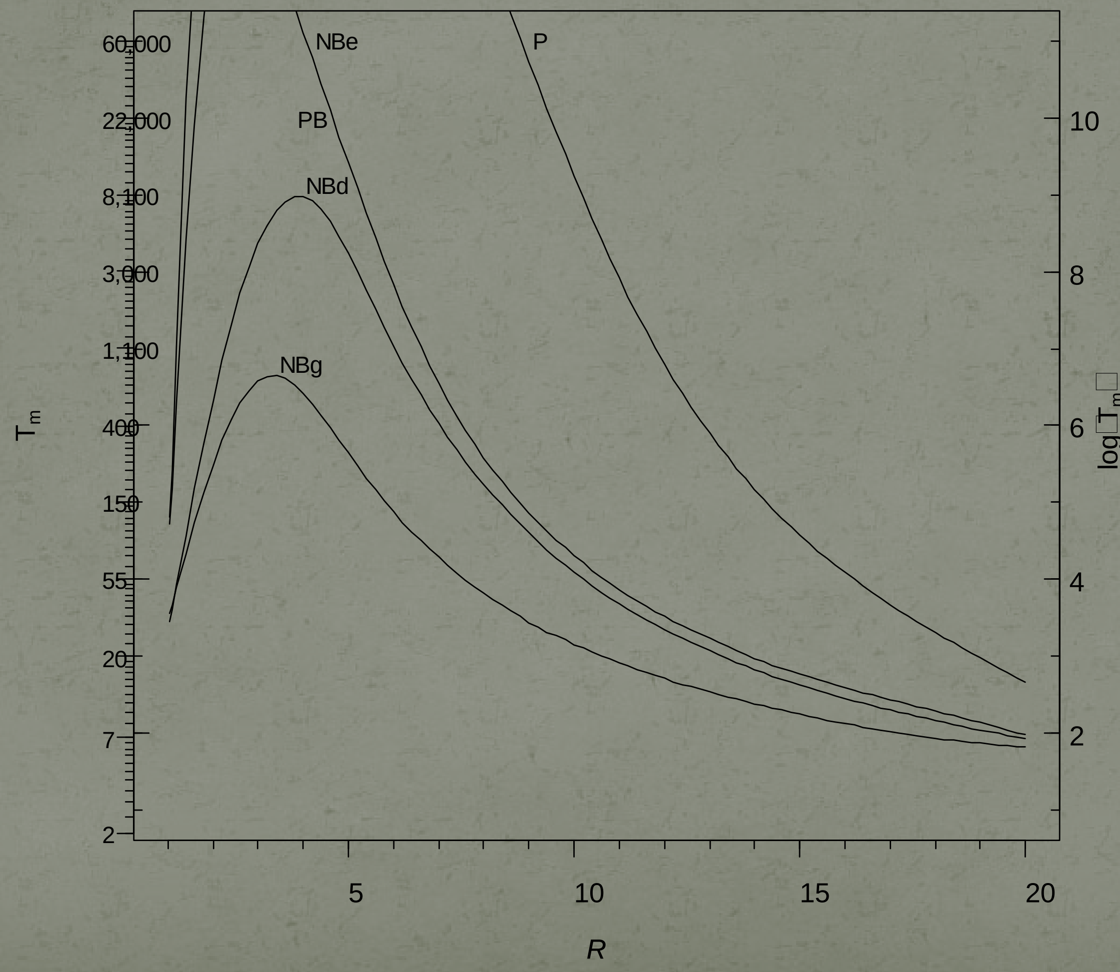
T_m
log T_m



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NBg
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10
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20
R
log T_m

Fitting models to data

Likelihoods:

Poisson Ricker (demographic stochasticity)

$$\Pr\left(N_{t+1} = n_{t+1} \mid \theta, N_t = n_t\right) = \frac{e^{-\mu}\mu^{n_{t+1}}}{n_{t+1}!}, \quad \mu = n_t R e^{-\alpha n_t}$$

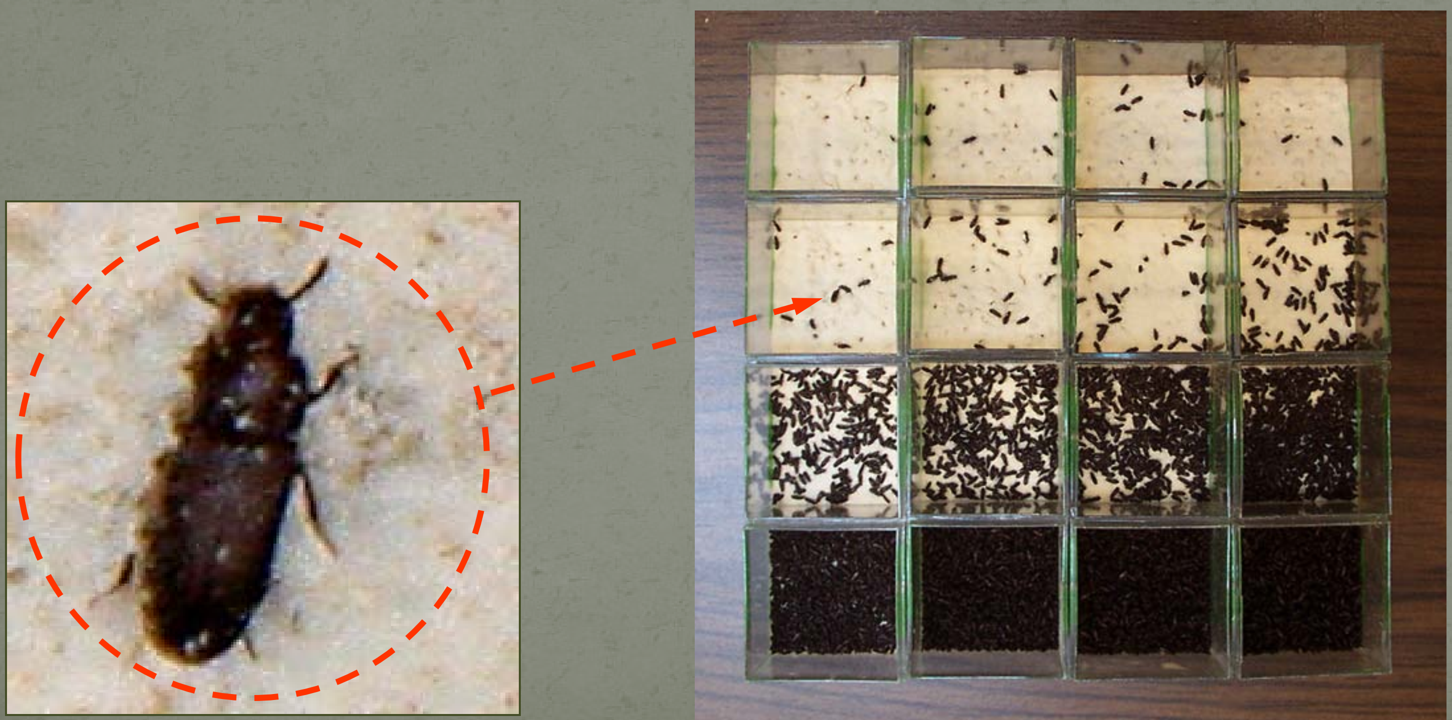
NBBg Ricker (all sources of stochasticity)

$$\int_{R_E=0}^{\infty} G(R_E) \sum_{F=0}^{n_t} \binom{n_t}{F} z^F (1-z)^{n_t-F} \binom{n_{t+1} + Fk_D - 1}{Fk_D - 1} \left(\frac{\lambda}{Fk_D + \lambda}\right)^{n_{t+1}} \left(\frac{Fk_D}{Fk_D + \lambda}\right)^{Fk_D}$$

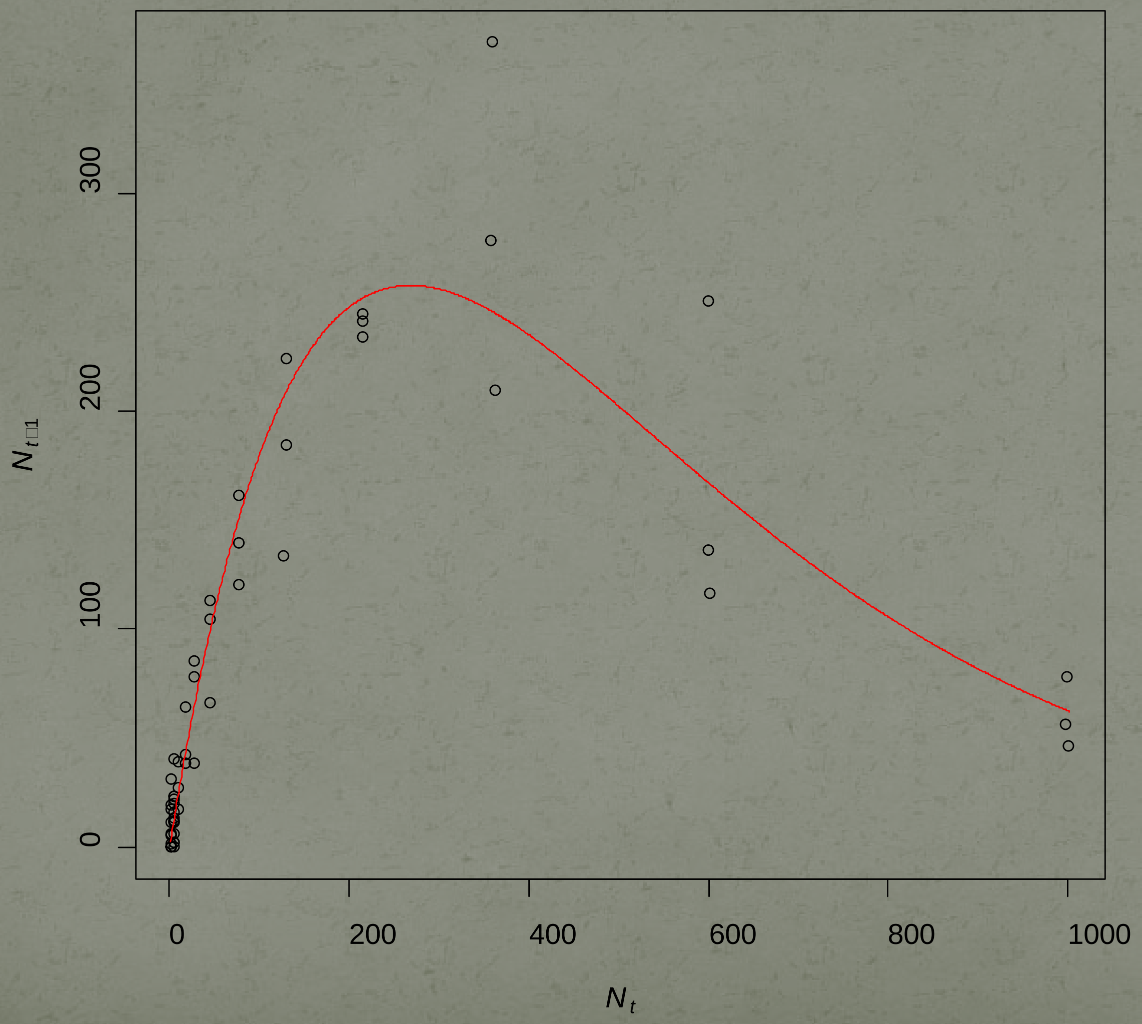
$$G(R_E) = R_E^{k_E - 1} \exp\left(-\tfrac{R_E k_E}{R}\right)\left(\tfrac{k_E}{R}\right)^{k_E} \frac{1}{\Gamma(k_E)}, \quad \lambda = F\,\tfrac{R_E}{z}\,e^{-\alpha n_t}$$

Experiment

- *Tribolium castaneum* (red flour beetle)
- Same life history as Ricker's fish
- Cannibalism



Experimental data



Model comparison

Demographic heterogeneity

Environmental stochasticity

Model	R	α	k_D	k_E	ΔAIC
Poisson (dem stoch)	2.5	0.0036			336
Negative binomial (dem het)	2.6	0.0037	0.15		18
Negative binomial (env stoch)	2.7	0.0038		2.0	56
Negative binomial-gamma	2.6	0.0037	0.26	29.2	5
Poisson-binomial (sex)	2.7	0.0038			87
NB-binomial (dem het)	2.6	0.0037	0.39		17
NB-binomial (env stoch)	2.8	0.0038		13.1	10
NB-binomial-gamma (all)	2.6	0.0037	1.15	26.6	0

Demographic heterogeneity mistaken for environmental stochasticity

Small k value = big variance

Conclusion

- Many species could be at much higher risk than we thought!
- … because simpler models can wrongly conclude that environmental stochasticity dominates, whereas demographic variance has higher extinction risk (for the same variance in abundance)
- Important to include all stochasticity

Melbourne B. A. & Hastings A. (2008).

Extinction risk depends strongly on factors contributing to stochasticity.

Nature 454: 100-103.

Assistants
Michelle Gibson, Dylan Hodgkiss, Claire Koenig, Tom McCabe, Devan Paulus, David Smith, Nancy Tcheou, Roselia Villalobos, Motoki Wu

NSF DEB 0516150

Stochastic dynamics of invasive spread

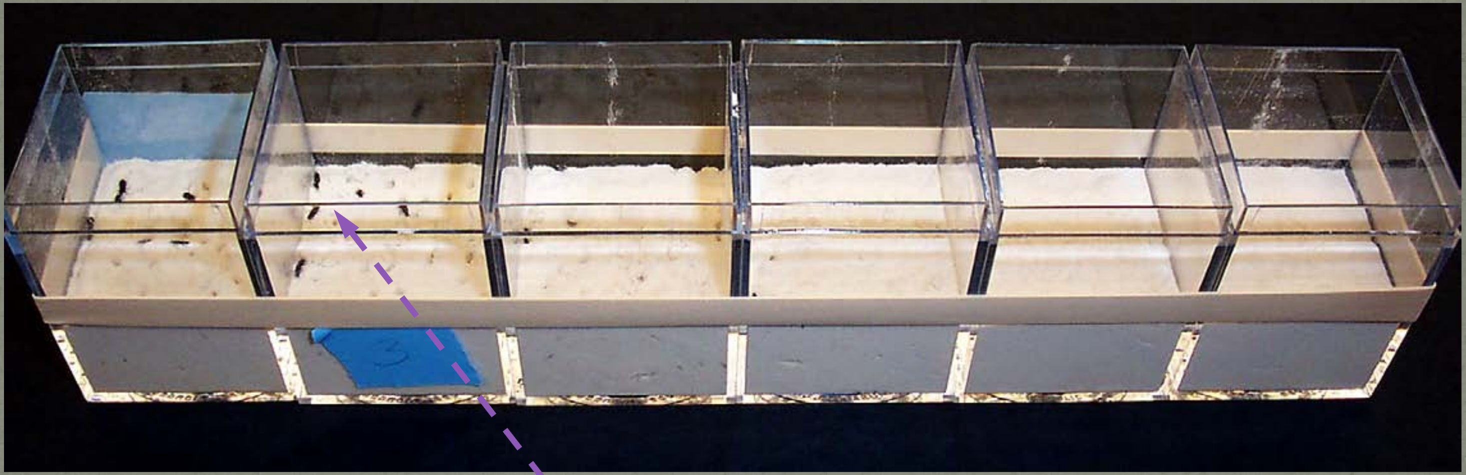
Brett Melbourne & Alan Hastings
University of California, Davis

Stochastic spread

- Stochasticity (→ variance in speed)
  - Population growth & dispersal
  - Demographic, environmental, genetic
- Repeat an invasion: different
  - Nature: one realization
- Real invasions can't be repeated
  - Many times, identical conditions
  - Laboratory microcosms

Experiment

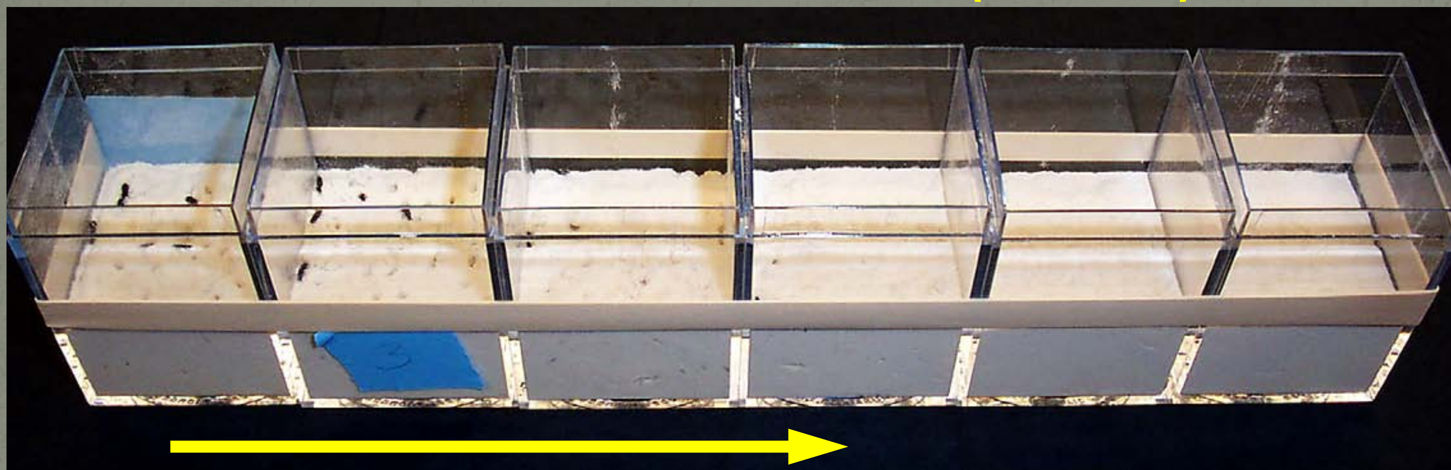
4 cm

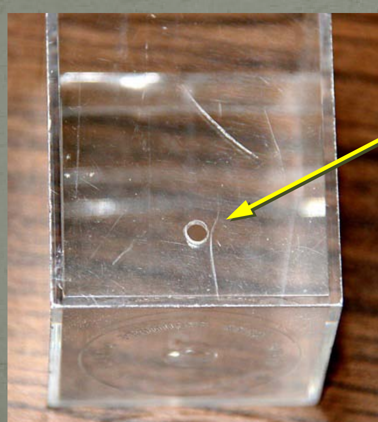


Flour beetle: *Tribolium castaneum*

Experiment

4 cm





Hole

Tunnel

Lifecycle in laboratory

- Discrete time (35 day cycle)

Lifecycle in laboratory

- Discrete time (35 day cycle)

  1) Adults lay eggs (24 hr)

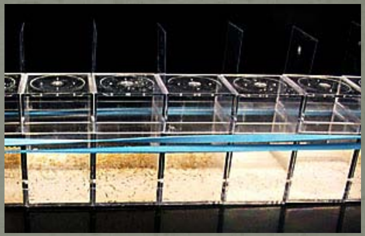
  - Fences installed; adults removed

Lifecycle in laboratory

- Discrete time (35 day cycle)

  1) Adults lay eggs (24 hr)
  - Fences installed; adults removed

  2) Larvae grow
  - Adults emerge (ca day 30)



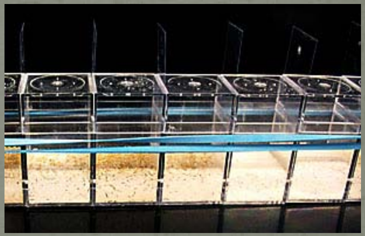
Lifecycle in laboratory

- Discrete time (35 day cycle)

  1) Adults lay eggs (24 hr)
  - Fences installed; adults removed

  2) Larvae grow
  - Adults emerge (ca day 30)

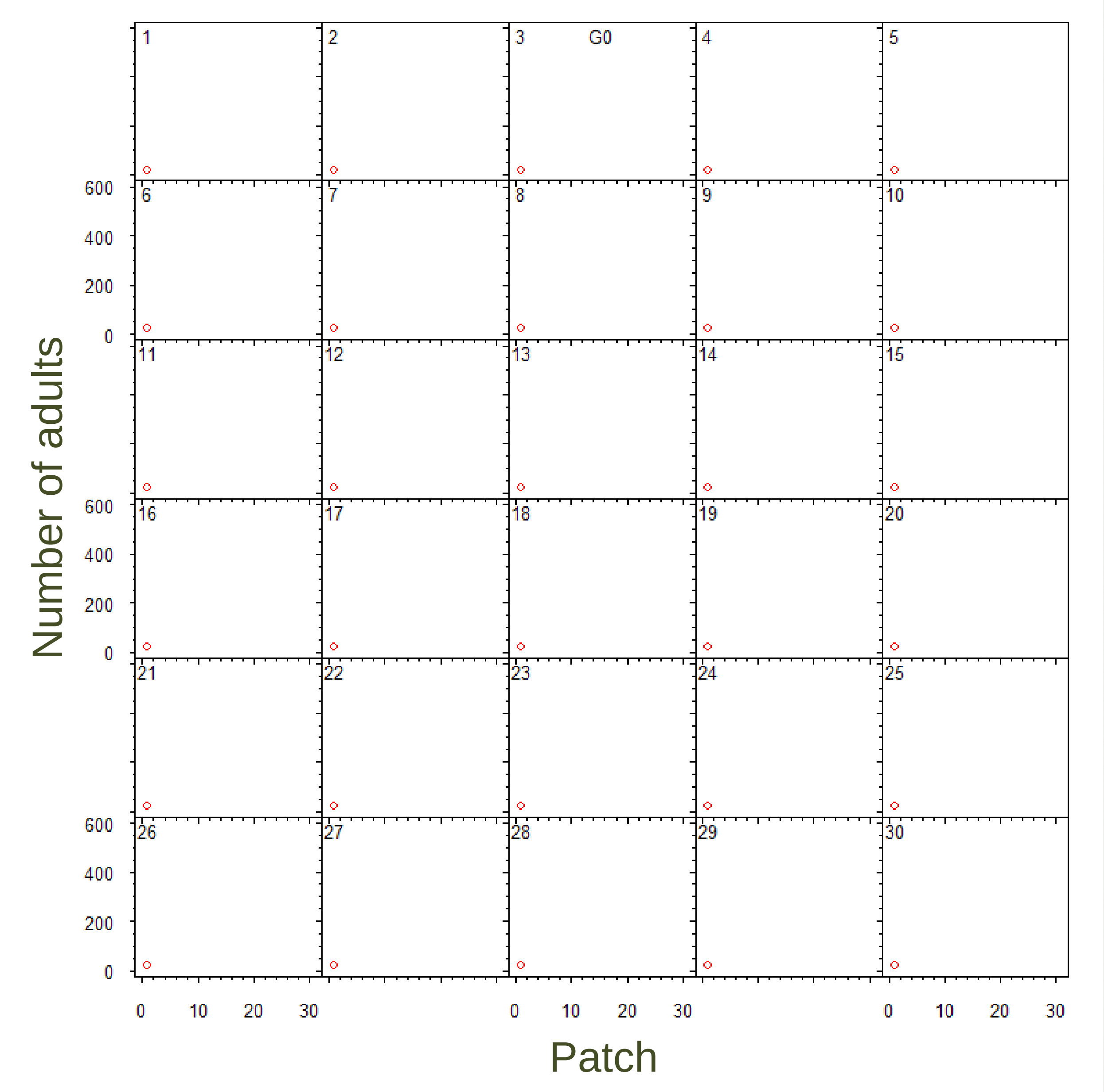
  3) Adults disperse (48 hr)
  - Census after dispersal



Experiment

- 30 landscapes
- Constant environment
- 13 generations

Spatio-temporal dynamics



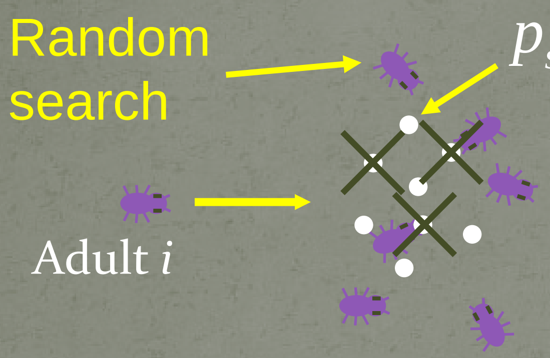
Mechanistic stochastic models

- Individual based derivation
- Predict mean, variance, & prob dist

$$N_x(t+1) = \text{growth} + \text{migration}$$

Growth (birth, surv) in a patch

Survive cannibalism & DI mortality



$$p_s = (1-m)e^{-\alpha N_x(t)}$$

Bernoulli

$$\text{eggs}_i \sim \text{Poi}(\beta)$$

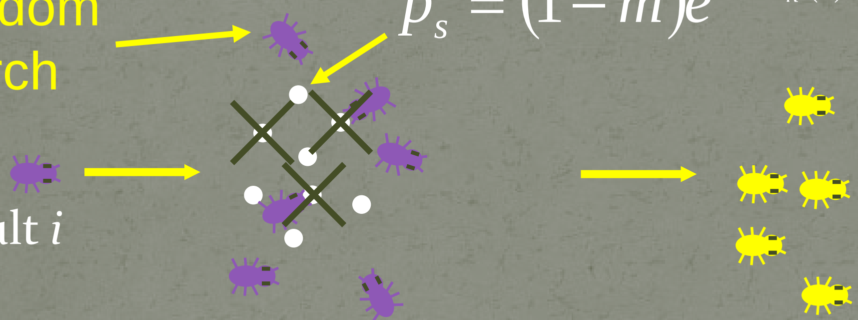
Growth (birth, surv) in a patch

Survive cannibalism & DI mortality

Random search

$$p_s = (1-m)e^{-\alpha N_x(t)}$$

Bernoulli



Adult i

$$S_i \sim \mathrm{Poi}\left(R\, e^{-\alpha N_x(t)}\right)$$

$$R = \beta(1-m)$$

$$\mathrm{eggs}_i \sim \mathrm{Poi}(\beta)$$

Patch scale:

$$N_x(t+1) = \sum_i^{N_x(t)} S_i \sim \mathrm{Poi}\left(N_x(t) R e^{-\alpha N_x(t)}\right)$$

Sum up survivors over all adults

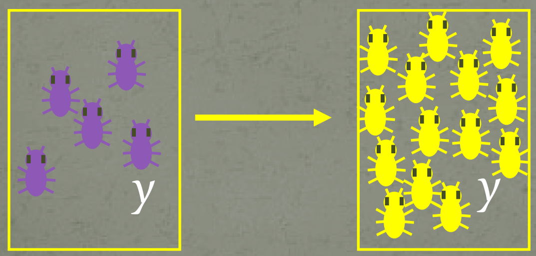
Poisson Ricker

Stochastic Ricker models

Model	Dem stoch (*Birth*, *Surv*)	Sex	Env stoch	Dem het
Poisson				
Neg bin				
Neg bin (Density Dep.)				
Neg bin-gamma				
Poisson-binomial				
Neg bin-binomial				
Neg bin-binomial (DD)				
Neg bin-binomial-gamma				

Stochastic spatial model

Patch scale growth



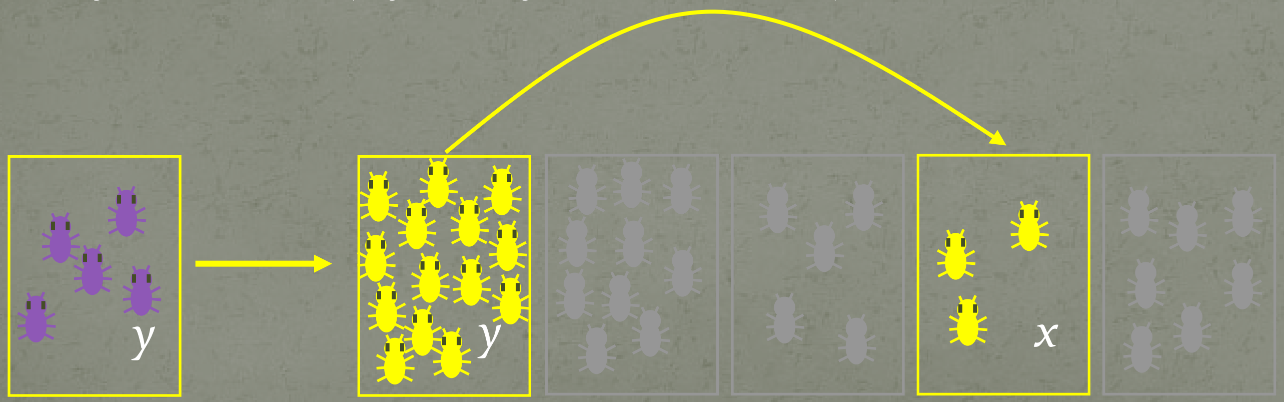
Number surviving is a random variable: stochastic Ricker

$$N_y(t) \qquad\qquad N_y(t+h) \sim \mathrm{Poi}\left(N_y(t) R\, e^{-\alpha N_y(t)}\right)$$

Stochastic spatial model

Migration from patch *y* to *x*

$$M_{y \to x} \sim \mathrm{Poi}\left(p_{y \to x} N_y(t) R e^{-\alpha N_y(t)}\right)$$



$$N_y(t) \qquad N_y(t+h) \sim \mathrm{Poi}\left(N_y(t) R e^{-\alpha N_y(t)}\right)$$

Stochastic spatial model

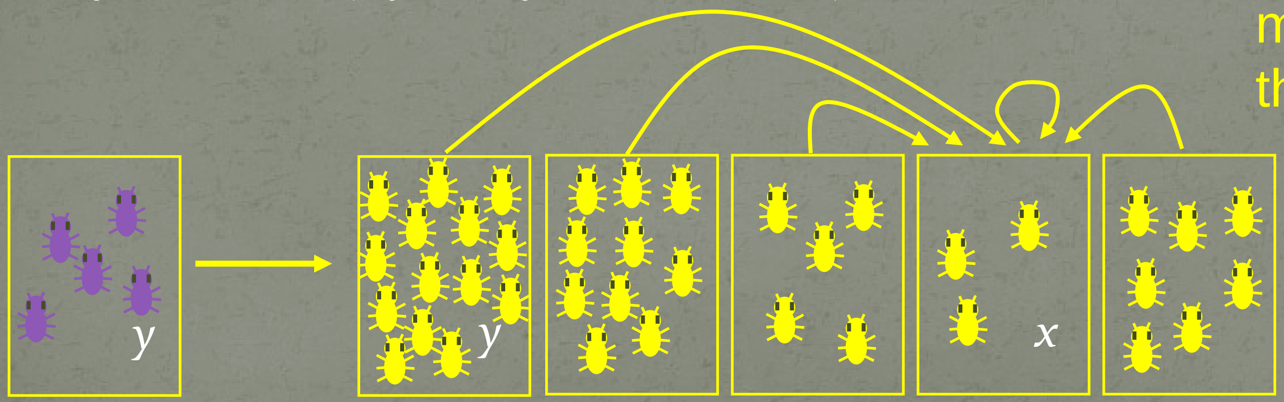
Landscape scale

Sum contributions from all patches

$$N_x(t+1) = \sum_y M_{y\to x} \sim \mathrm{Poi}\left(\sum_y p_{y\to x} N_y(t) R\, e^{-\alpha N_y(t)} \right)$$

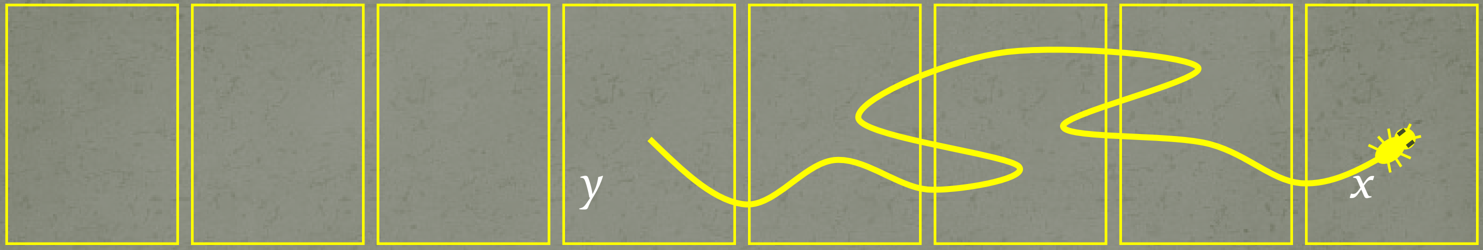
$$M_{y\to x} \sim \mathrm{Poi}\left(p_{y\to x} N_y(t) R\, e^{-\alpha N_y(t)} \right)$$

Other Ricker models work the same way



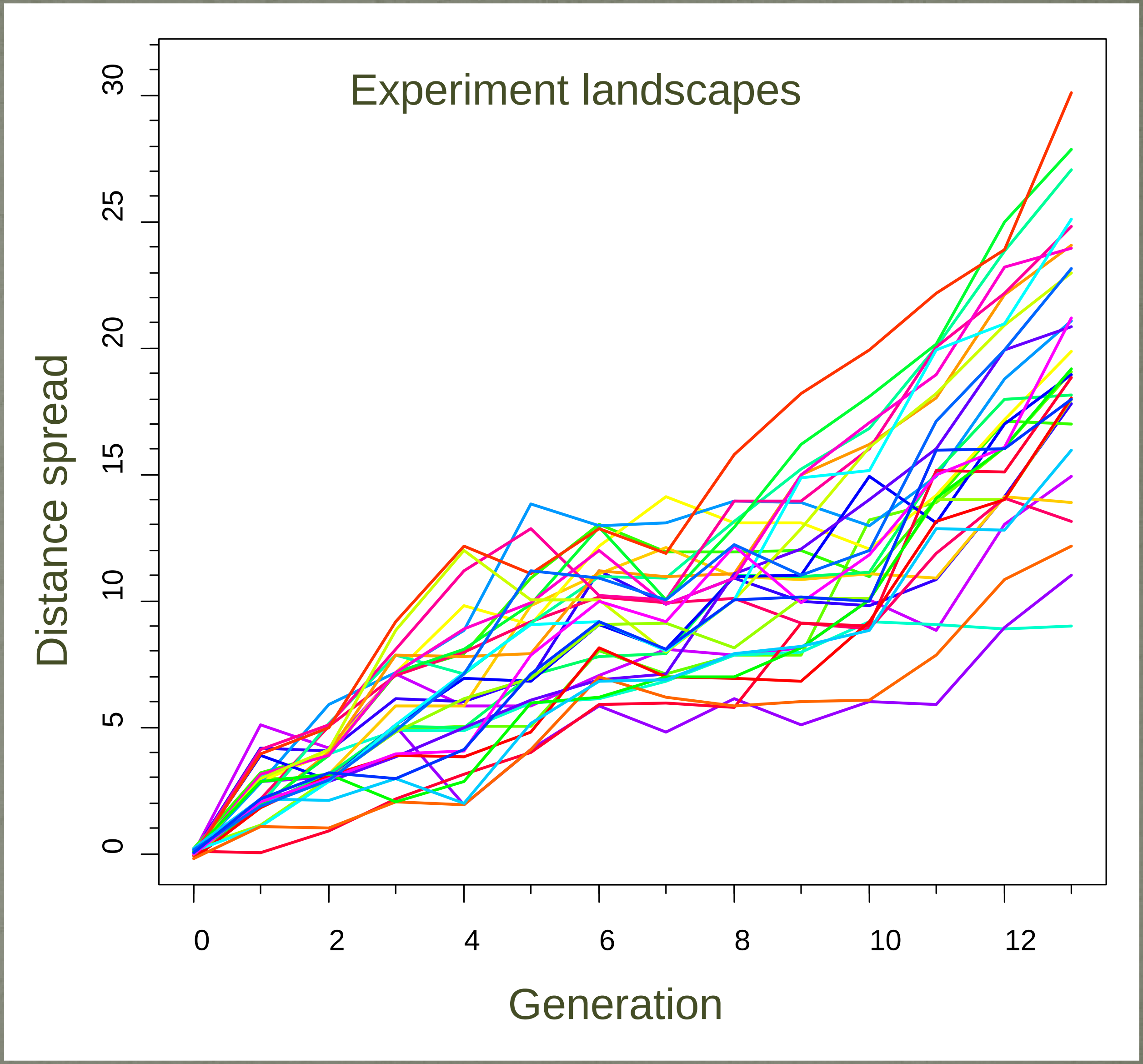
$$N_y(t) \qquad N_y(t+h) \sim \mathrm{Poi}\left(N_y(t) R\, e^{-\alpha N_y(t)} \right)$$

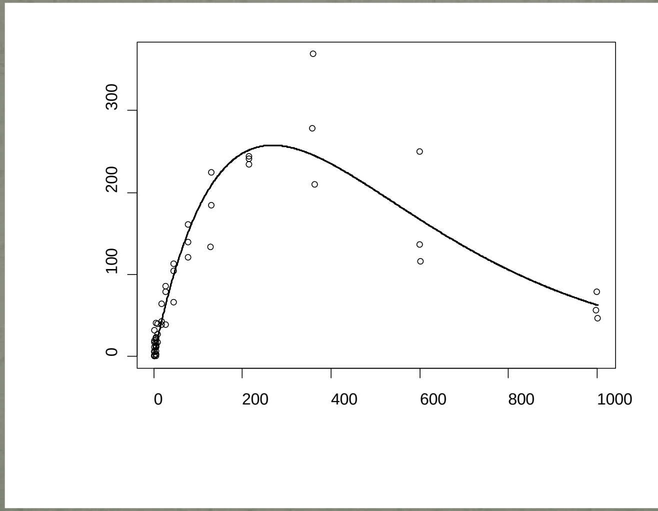
$p_{y \to x}$ (individuals)



- Poisson diffusion
  - individuals have same *D*
- Poisson-gamma diffusion
  - individuals have different *D*
  - longer tail

Variance in spread rates



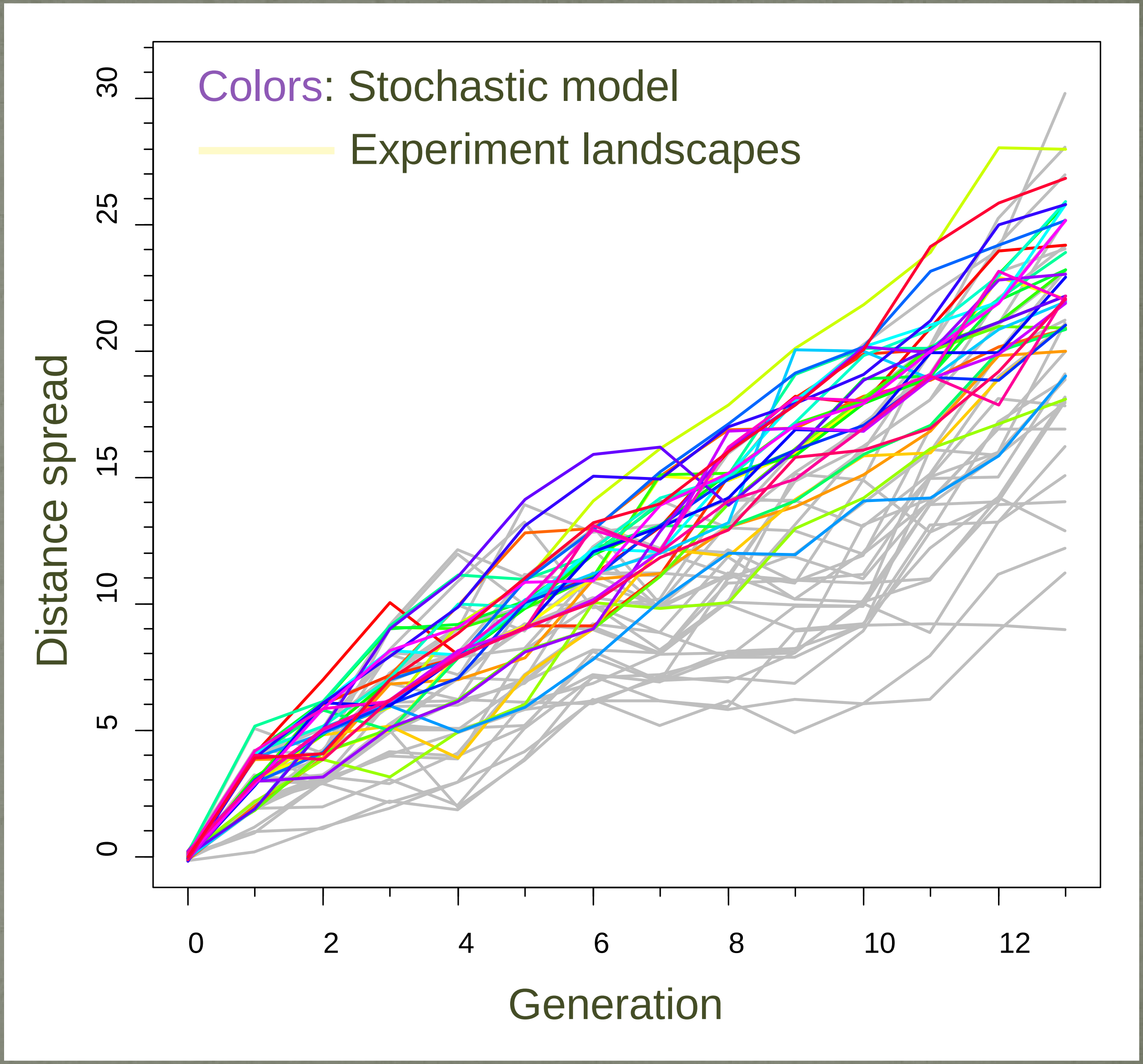


0
100
200
300
0
200
400
600
800
1000

Variance in spread rates

Stochastic model

Dem stoch
Sex
Env stoch
Dem het
Pois diffusion



Founder effects?

Landscapes started with 20 individuals

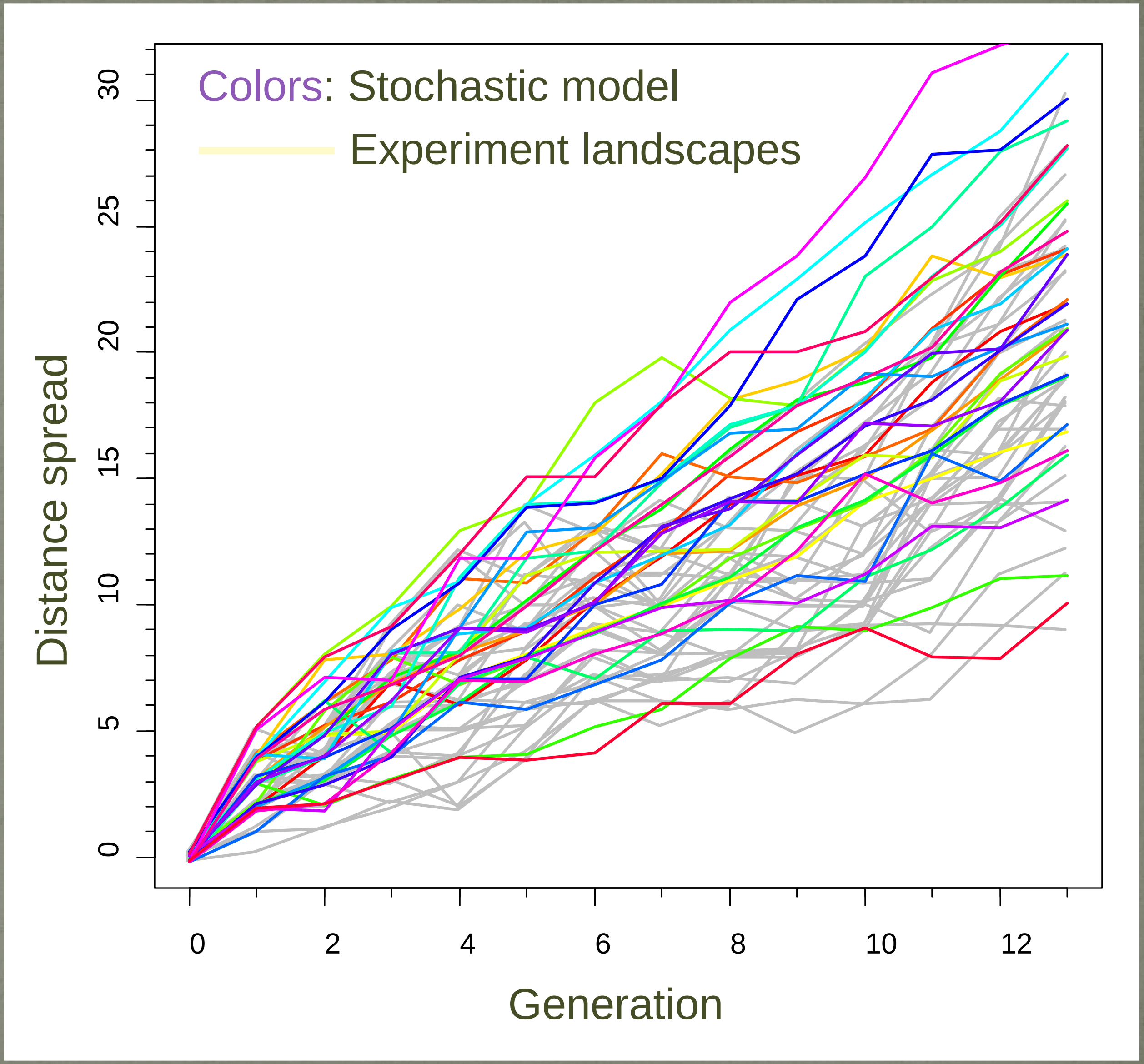
Stochastic spatial model fit

R, α, D common

R, α, D unique

Variance in spread rates

Stochastic process + founder effects



Conclusion

- Variance in spread rates between multiple realizations very high
- Not entirely explained by stochastic population processes
- Founder effects seem to be important – test experimentally

Acknowledgments

Assistants:

Claire Koenig
David Smith
Roselia Villalobos
Motoki Wu.

NSF Biological Invasions IGERT
DGE 0114432

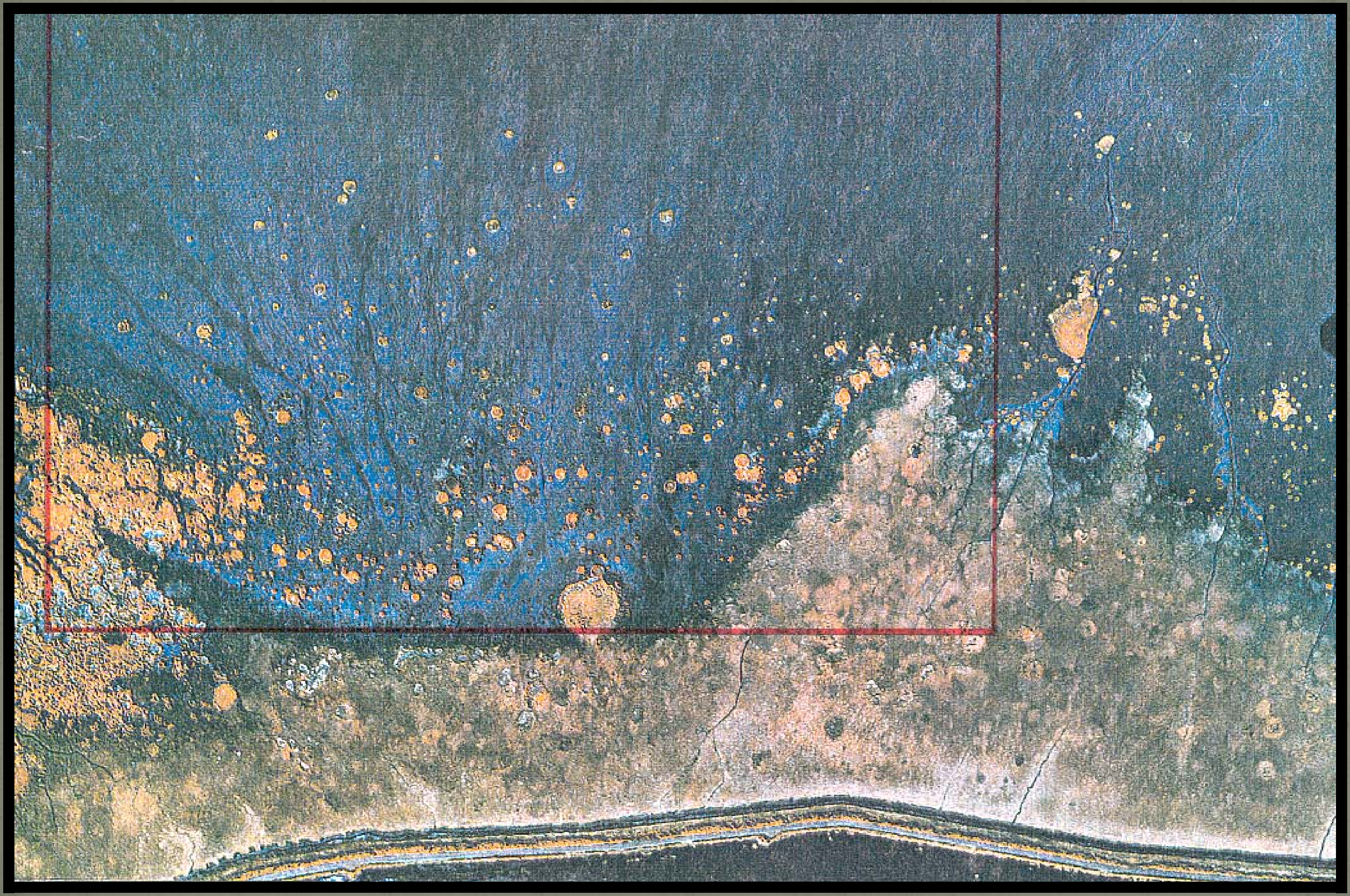
NSF DEB 0516150

Problem

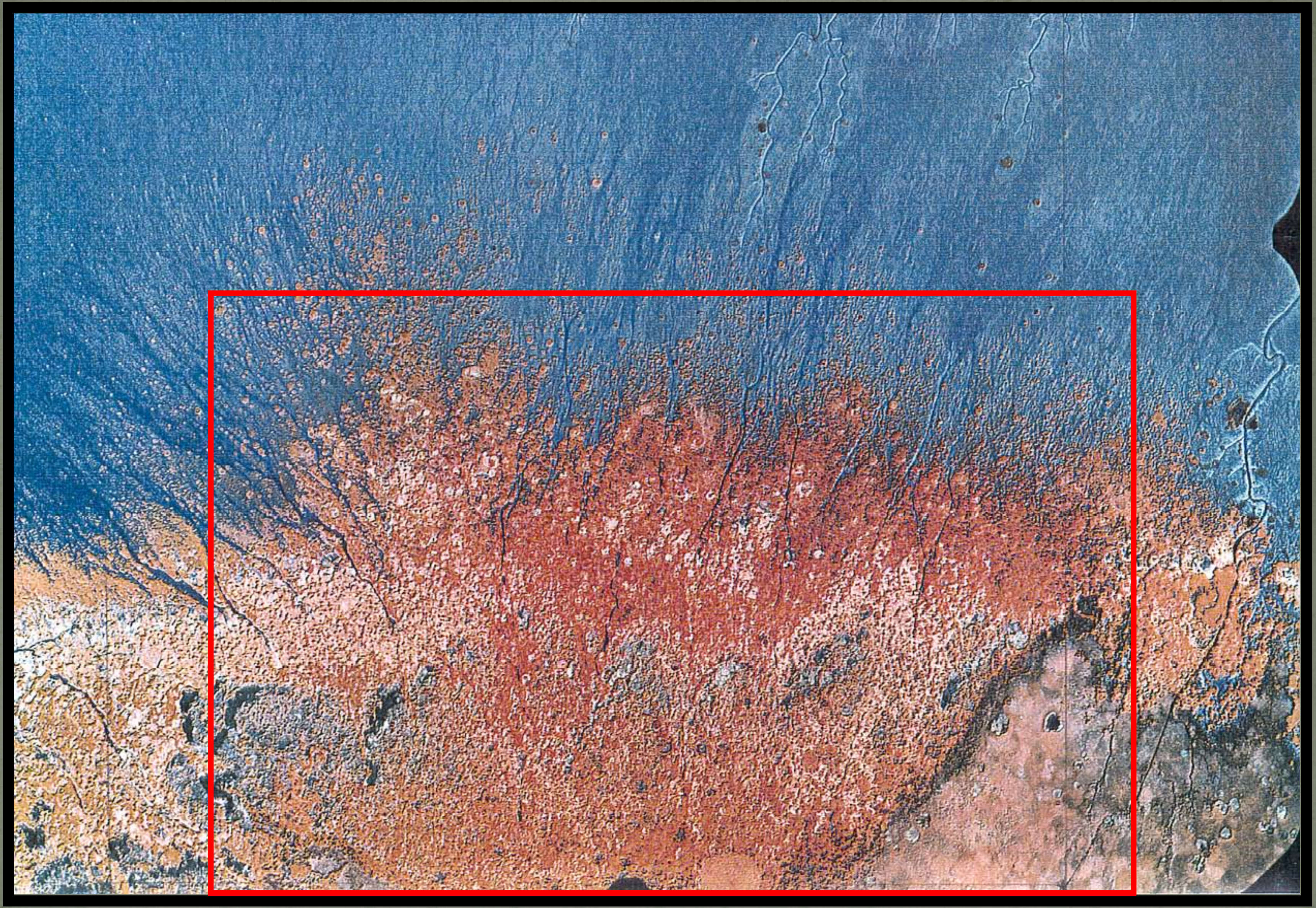
- *Spartina alterniflora*
- Native to eastern US (and Gulf)
- Invasive in western U.S.
- 2 sites
  - S.F. Bay – replacing native
  - Willapa Bay – invading bare ground


Seattle
WASHINGTON
Willapa Bay
Portland
OREGON
CALIFORNIA
NEVADA

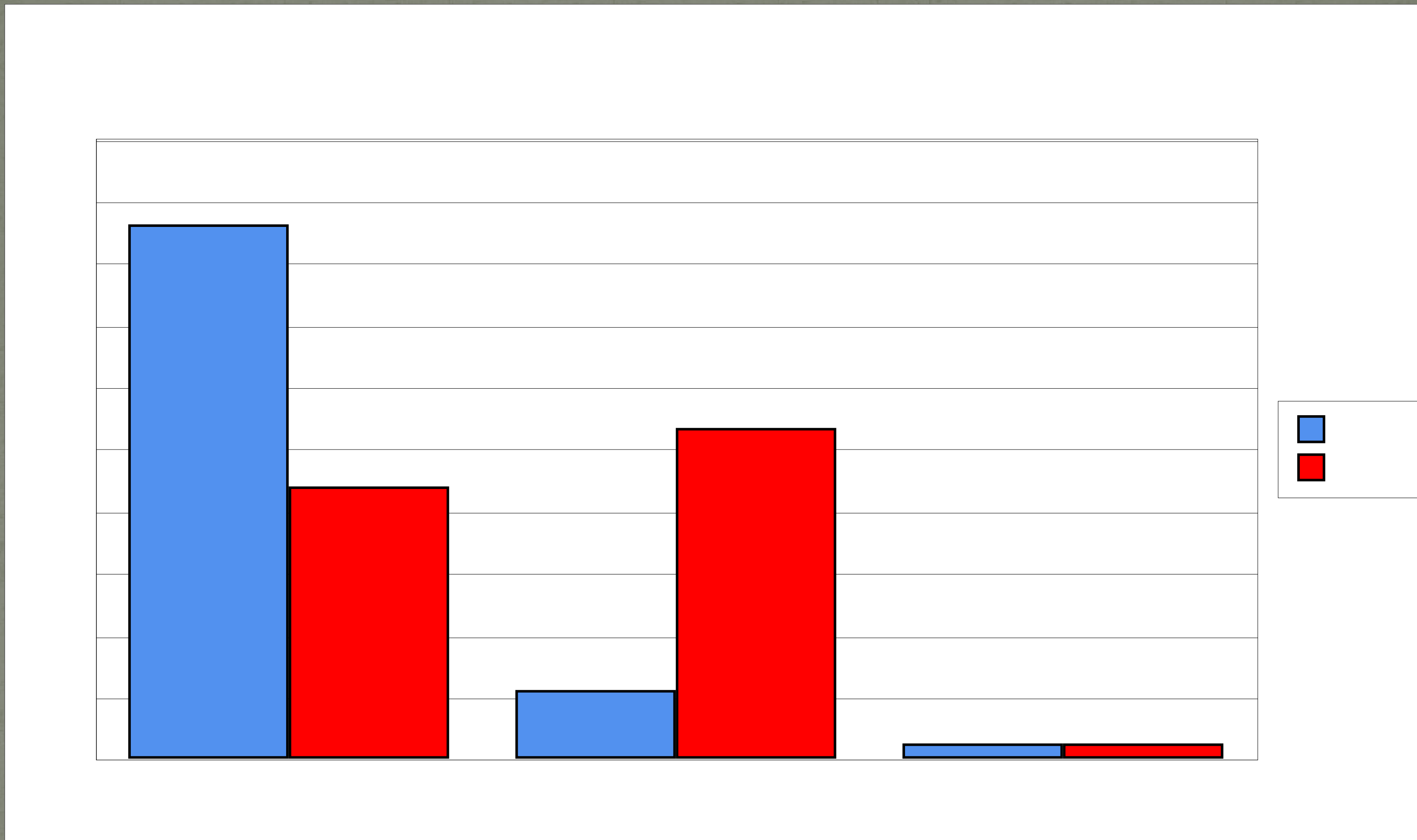

U.S. FISH & WILDLIFE SERVICE
DEPARTMENT OF THE INTERIOR
Willapa National Wildlife Refuge



Aerial photos courtesy of Washington State DNR



Aerial photos courtesy of Washington State DNR



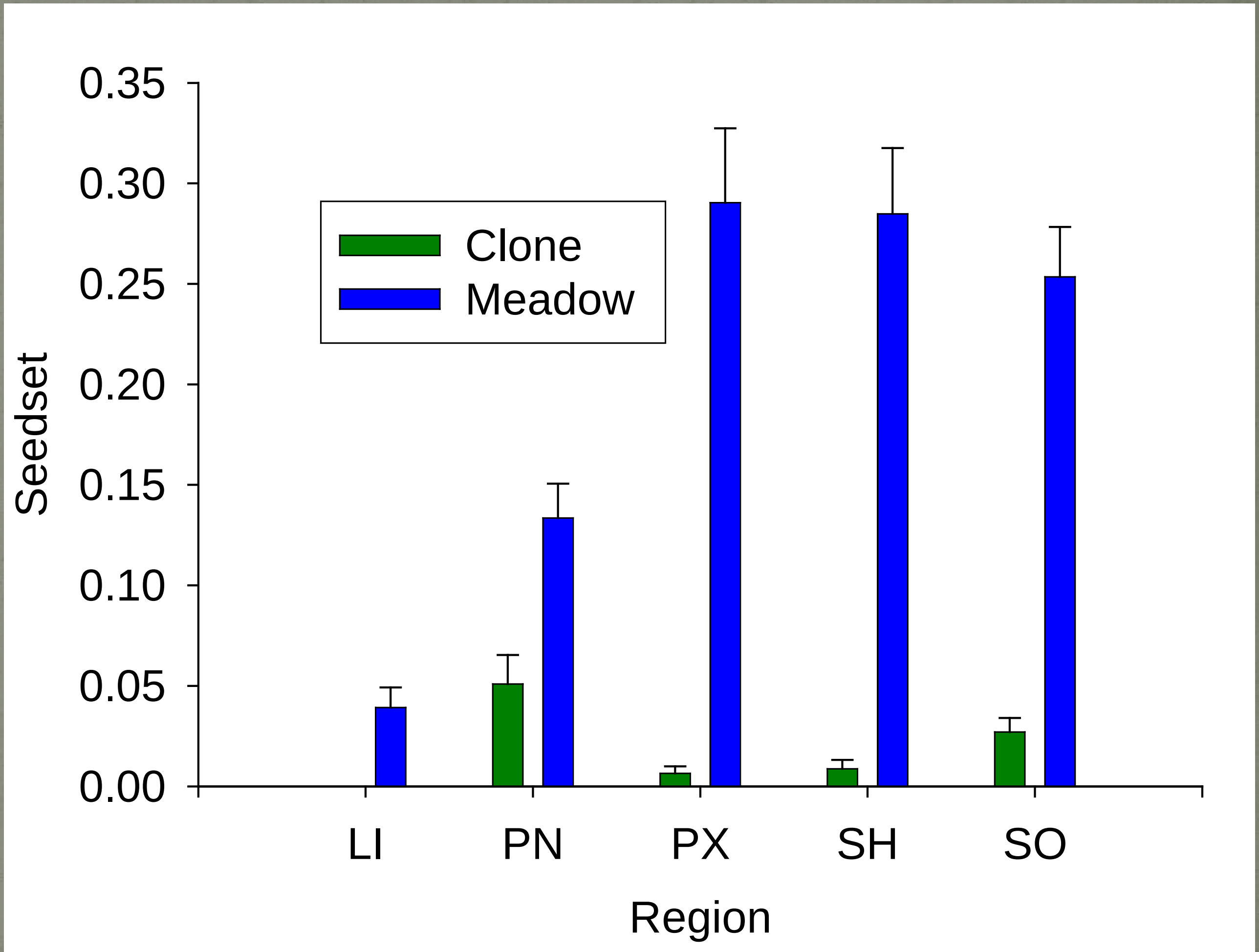
Models

- Spatially-explicit Stochastic Simulation
  - Consequences of an Allee effect
  - Compare to analytic model to justify use of latter in designing control strategies

- Analytical Non Spatial Model
  - Finding Optimal Control Strategies

Field Results: Allee effect

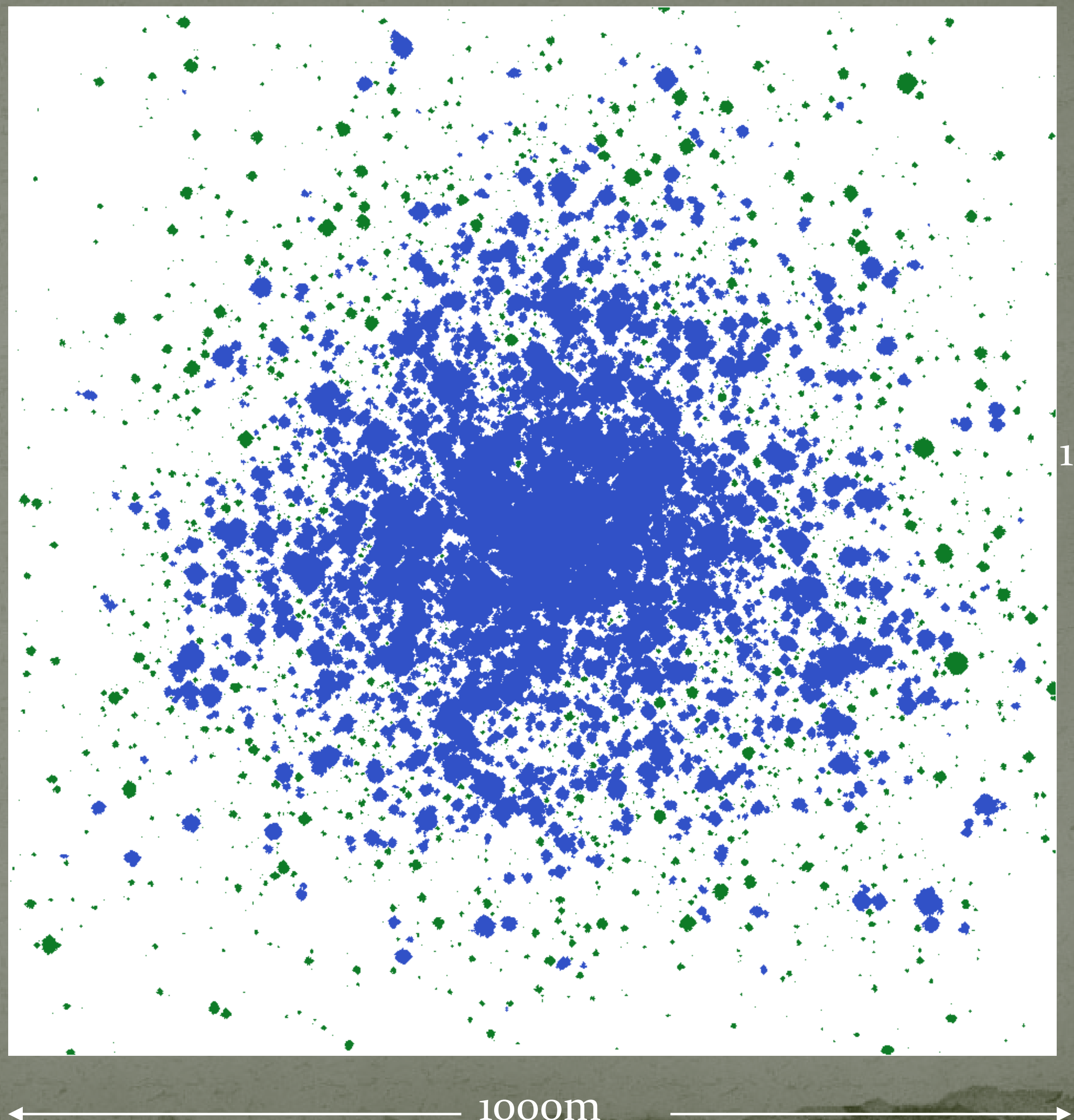
Low density plants set < 10 X the seed



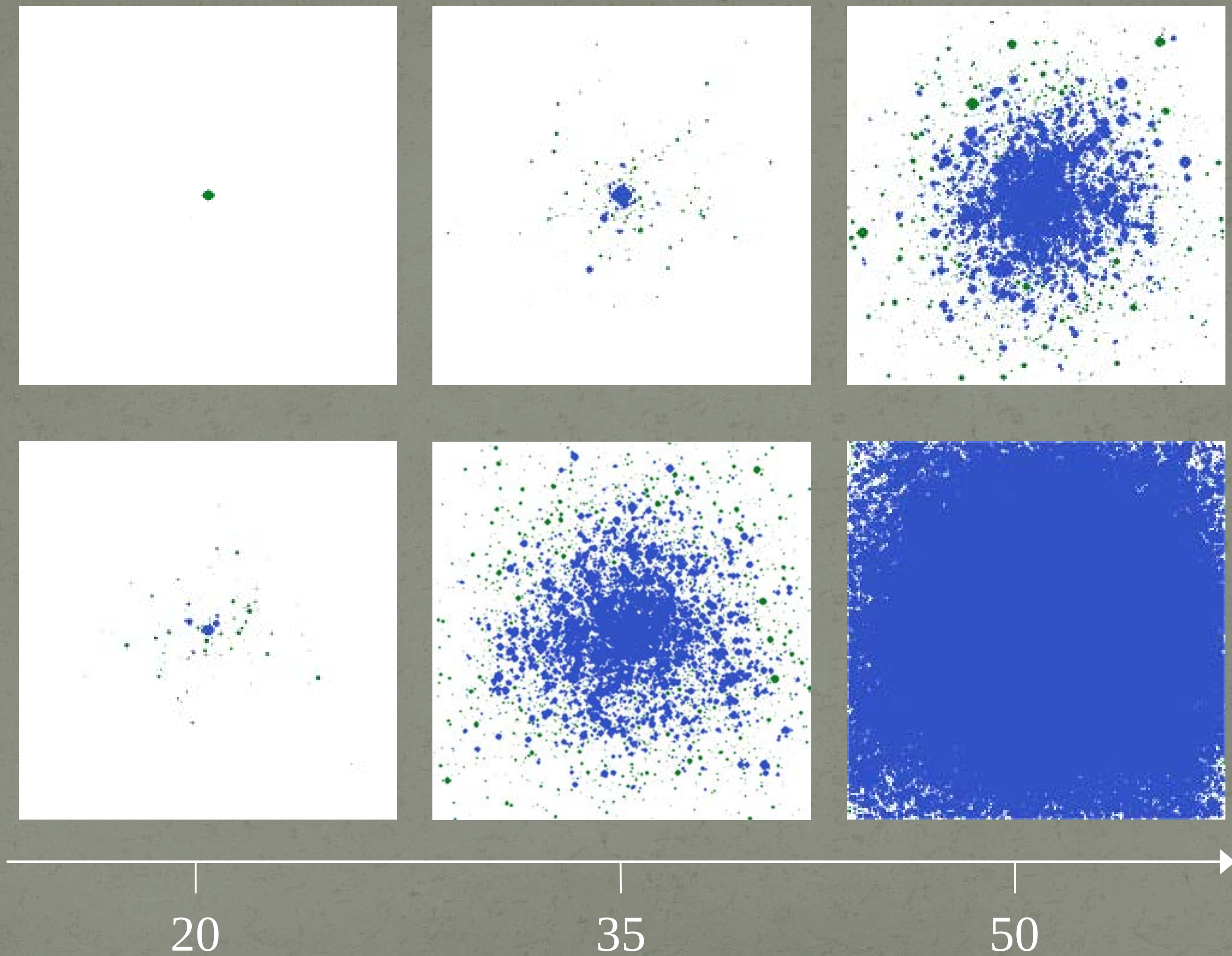
Davis, Taylor, Civille and Strong. 2004 Journal of Ecology 92

Spatially-explicit simulation model

- One square km
- Parameterized from
  - GIS maps (Civille)
  - Field data (Davis, Taylor, Civille, Grevstad)
- Run for 100 years, time step 1 year
- Clones have low seed production
- Meadows have high seed production



Allee Effect Slows Invasion



Taylor, Davis, Civille, Grevstad and Hastings. Ecology *2004*

Analytical Non-spatial Model

Seedling Area $_{+1} = \quad + $

Clone Area $_{+1} = \quad + (1 - \eta)$

Meadow Area $_{+1} = \eta \quad + $

Parameters are dependent on density and numbers of individuals.

: FECUNDITY OF CLONES

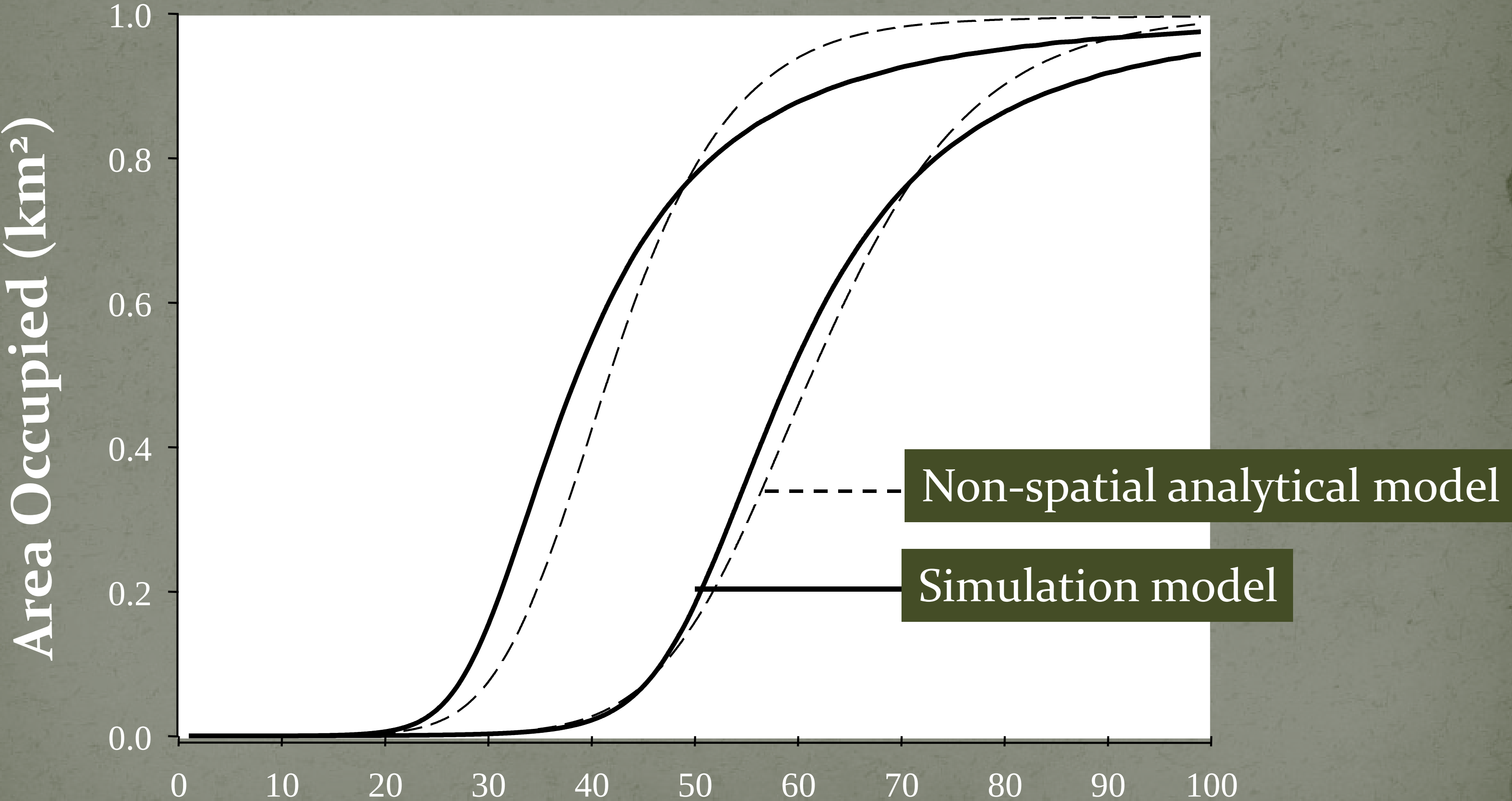
: FECUNDITY OF MEADOWS

: GROWTH RATE OF CLONES

: GROWTH RATE OF MEADOWS

η : MERGE RATE OF CLONES INTO MEADOWS

Analytical model predicts same dynamics as simulation model



Control of *Spartina*




2003 Control

Control questions

- How much *Spartina* needs to be removed every year to eradicate invasion within 10 years

- Is it better to prioritize removal of *fast growing* but *low seed producing* clones or is it better to prioritize removal of *slow-growing* but *high seed producing* meadows?

Control Strategy

- T_t < MAX = Total area removed in year t
- $0 \leq X_t \leq 1$ = fraction of T_t that was meadows
- $0 \leq (1 - X_t) \leq 1$ = fraction of T_t that was clones

$$_{+1} = \quad + (1-\eta) \quad - (1- \quad)$$

$$_{+1} = \eta \quad + \quad -$$

Control Objectives

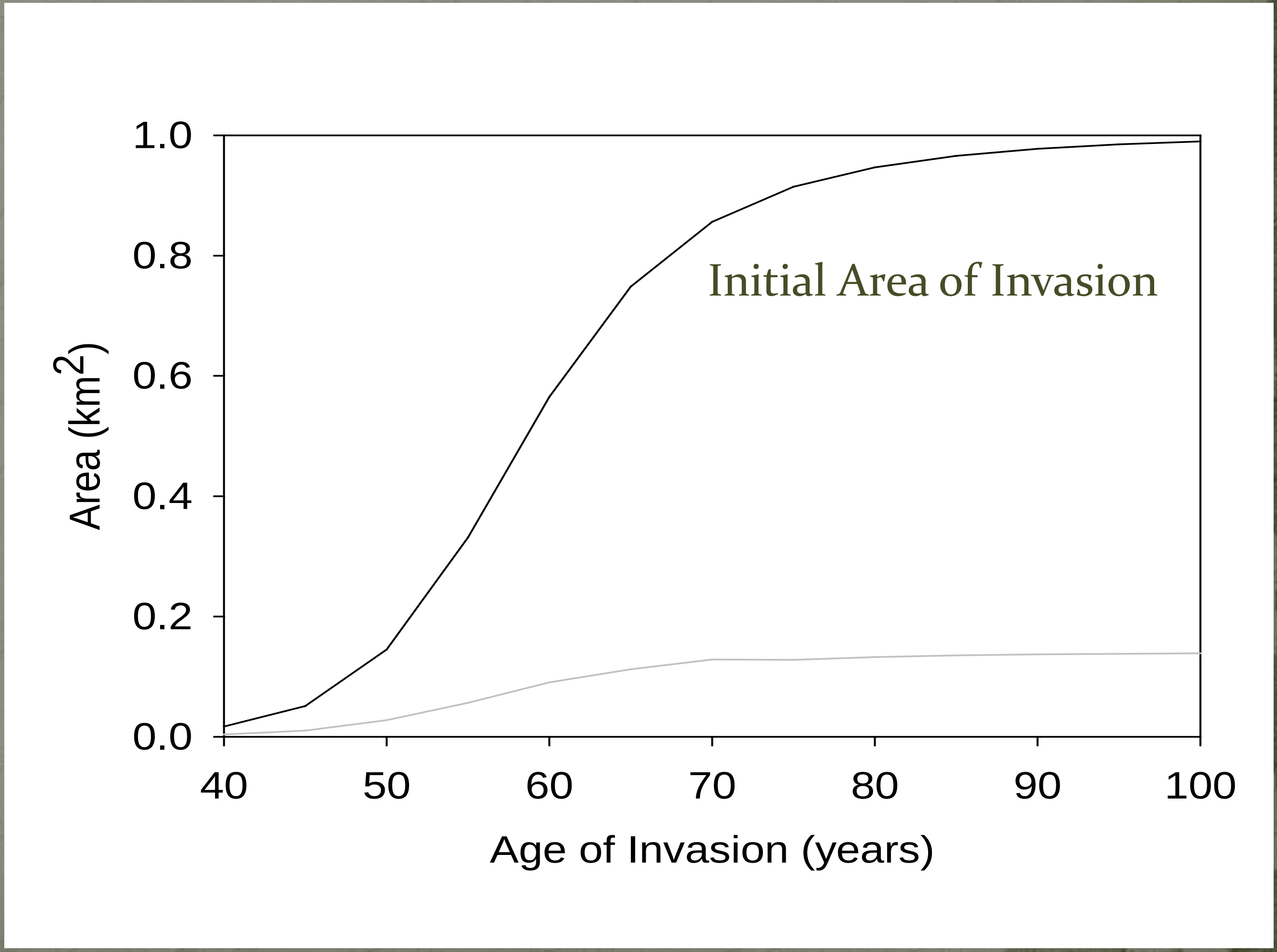
1. Eradicate invasion in one square km region within 10 years
2. Minimize Cost X Risk of colonizing other sites

Total area removed in 10 years

Total seed production during 10 years

Minimum Removal needed to Eradicate within 10 years

Equivalent of 15-20% of initial invasion has to be removed annually

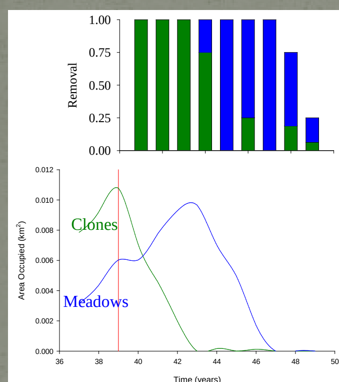


Taylor and Hastings. Journal of Applied Ecology *2004*

Optimal Control Strategies

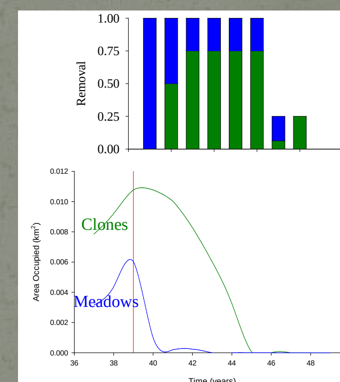
Low Budget

Clones First



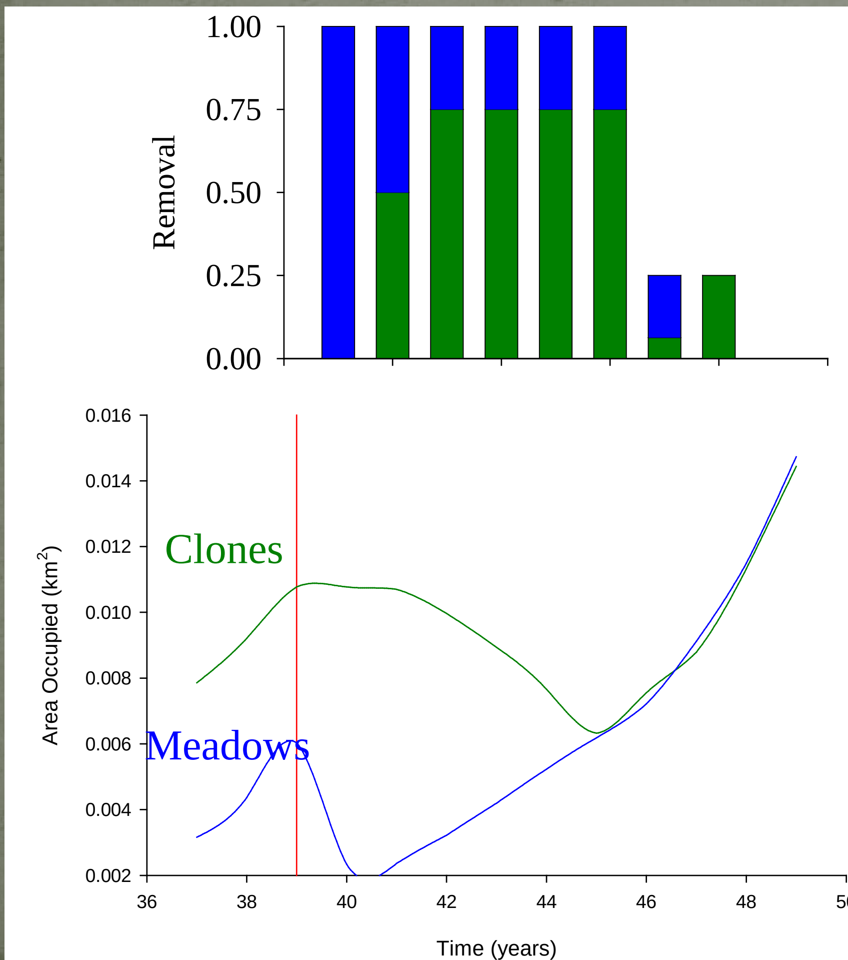
High Budget

Meadows First

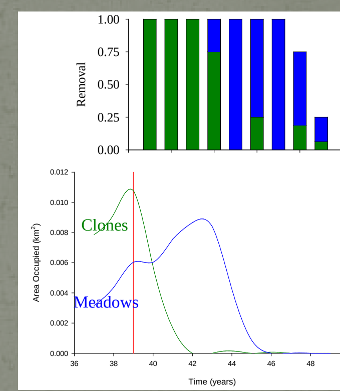


Switch Control Strategies

Low Budget
Meadow First

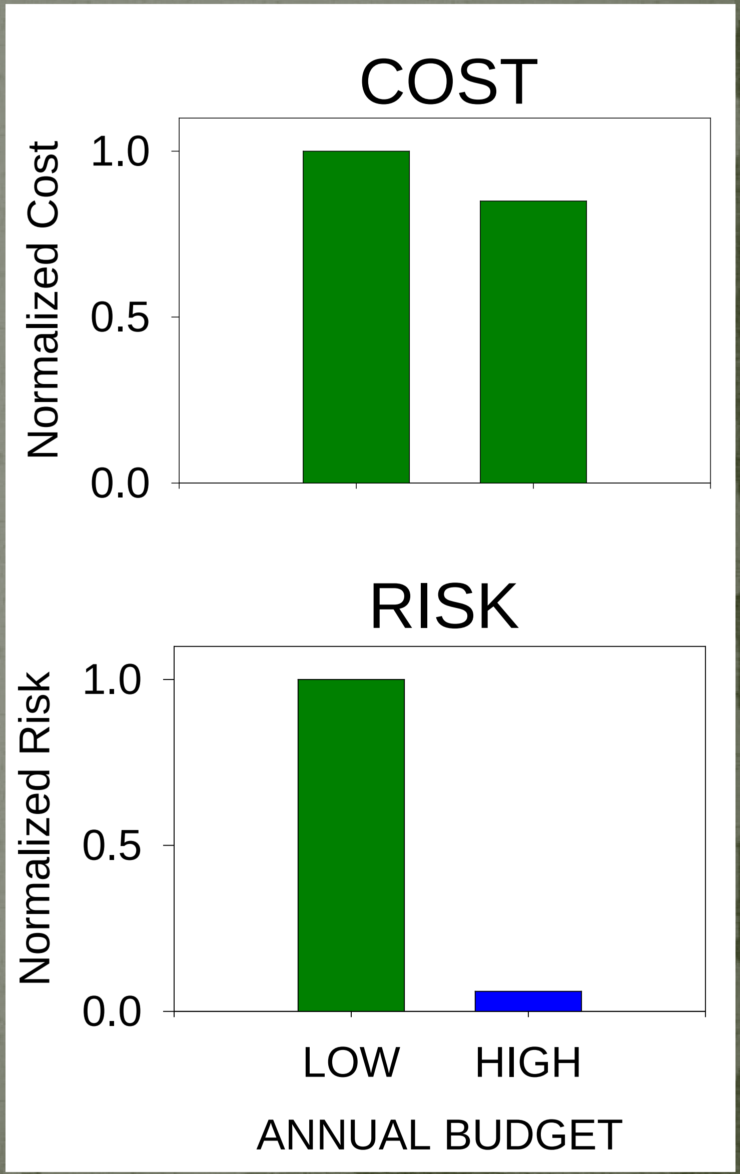


High Budget
Clones First



Summary

	Low Budget	High Budget
Minimize Cost Only	Clones First	Clones First
Minimize Risk Only	Clones First	Meadows First
Minimize Cost and Risk	Clones First	Meadows First
No Allee Effect	Clones First	Clones First



Linear control model

- Density independent
- Three classes – seedlings,juveniles and adults
  - Express model in terms of area occupied
- If the model were nonlinear this would become a dynamic programming problem –
  - Difficult numerical problem – cannot really get a solution
  - So, can we simplify in this case?

(Hastings, Hall and Taylor, TPB in press)

$$N_{t+1} = LN_t,$$

$$N_{t+1} = L(N_t - H_{t+1}).$$

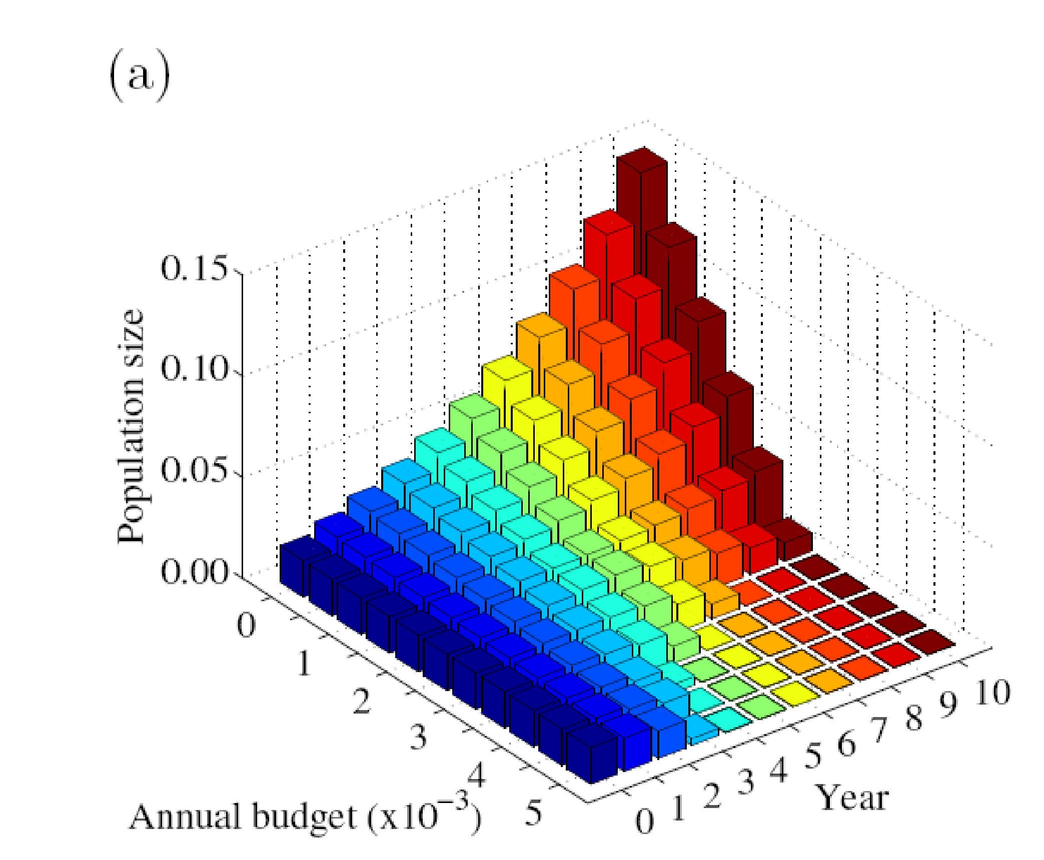
$$N_T = L^T N_0 - \sum_{i=1}^{T} L^{T+1-i} H_i,$$

Population = size without control – contribution of removed

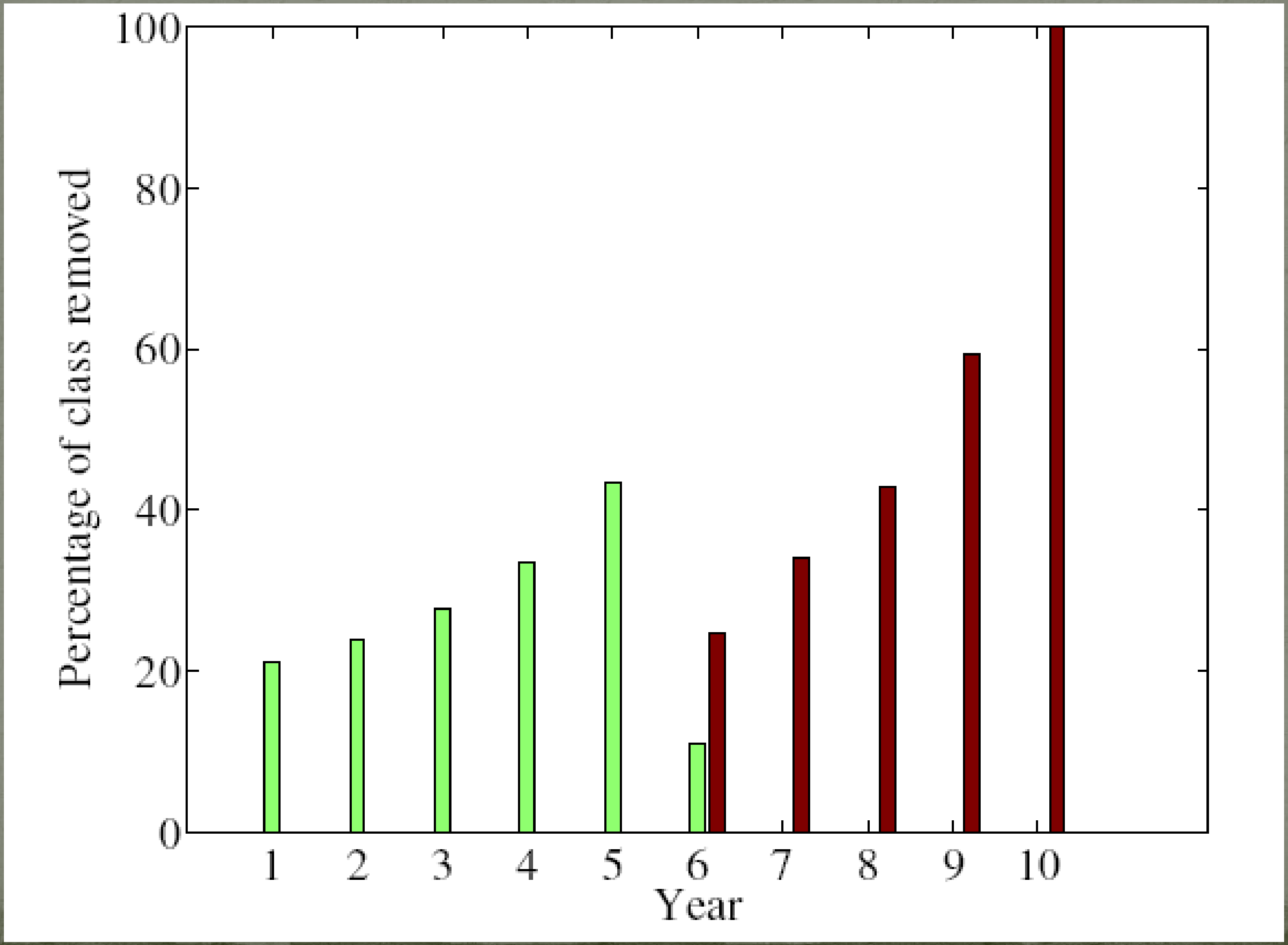
What classes should be removed?

- One year ahead?
  - The class that contributes the most area (normalized by 'cost') should be removed first
- "Infinitely" far ahead?
  - The class that has the highest reproductive values (normalized by 'cost') should be removed first
- Therefore do intermediate case, finite time horizon, which becomes a linear programming problem (from previous slide)

Population size as a function of time and the annual budget allocated to control, when the objective is to minimize the population within 10 years subject to budget
constraint.



The fraction of each stage class (green for isolates, red for meadows) removed
by control in each year under the optimal control strategy.



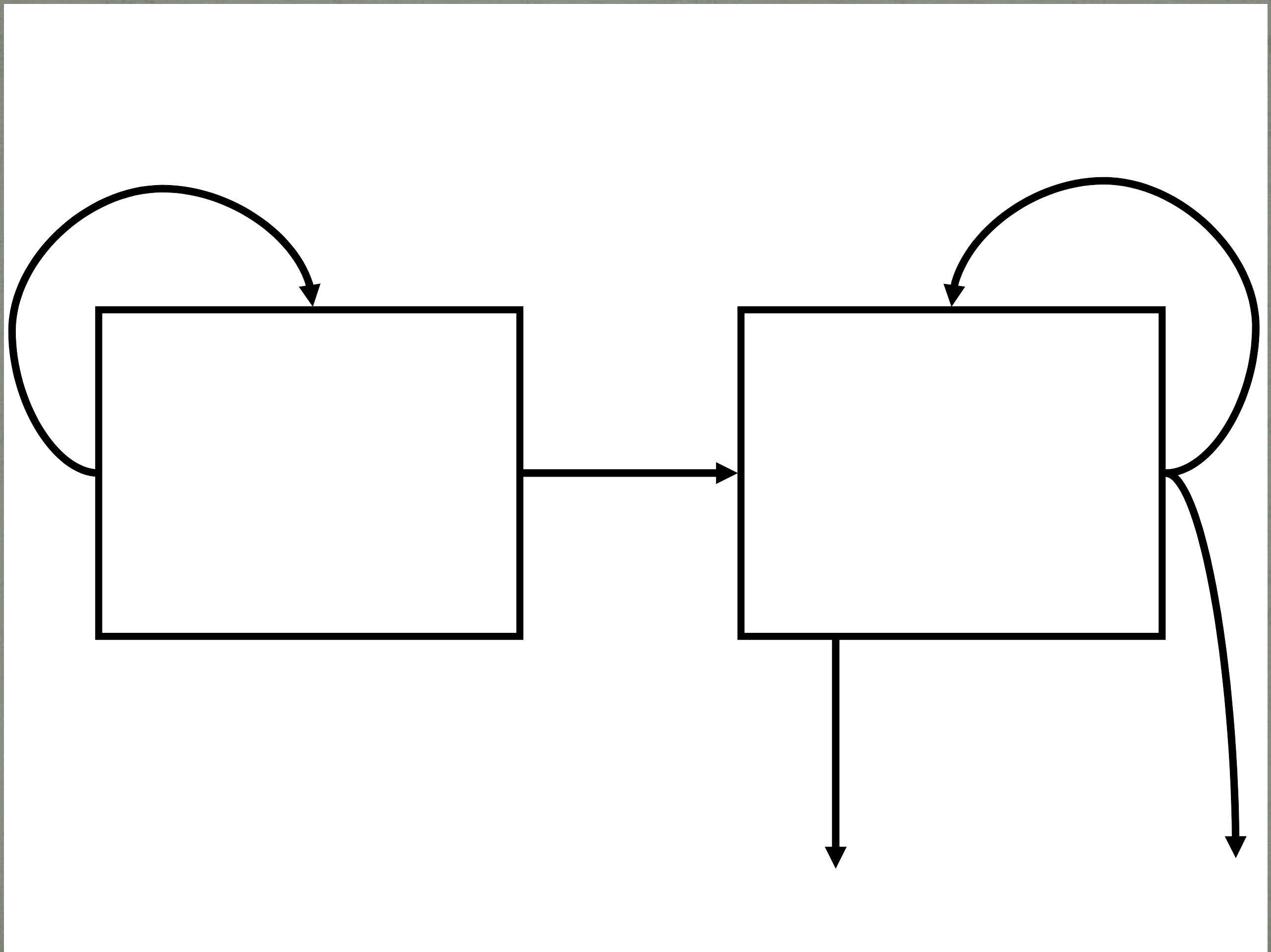
Initial conclusions

- Optimal approach is time dependent
  - May be much more effective
- Cost of waiting
  - Overall cost of control can be much less when started earlier
- Since a LP problem solution is always at a vertex – focus on a single class unless budget large enough to remove an entire class, then add one more class

‘Easy’ extensions

- Dependence on habitat
- Spatial extent
- Dependence on tidal height

Damage (Hall and Hastings, JTB)

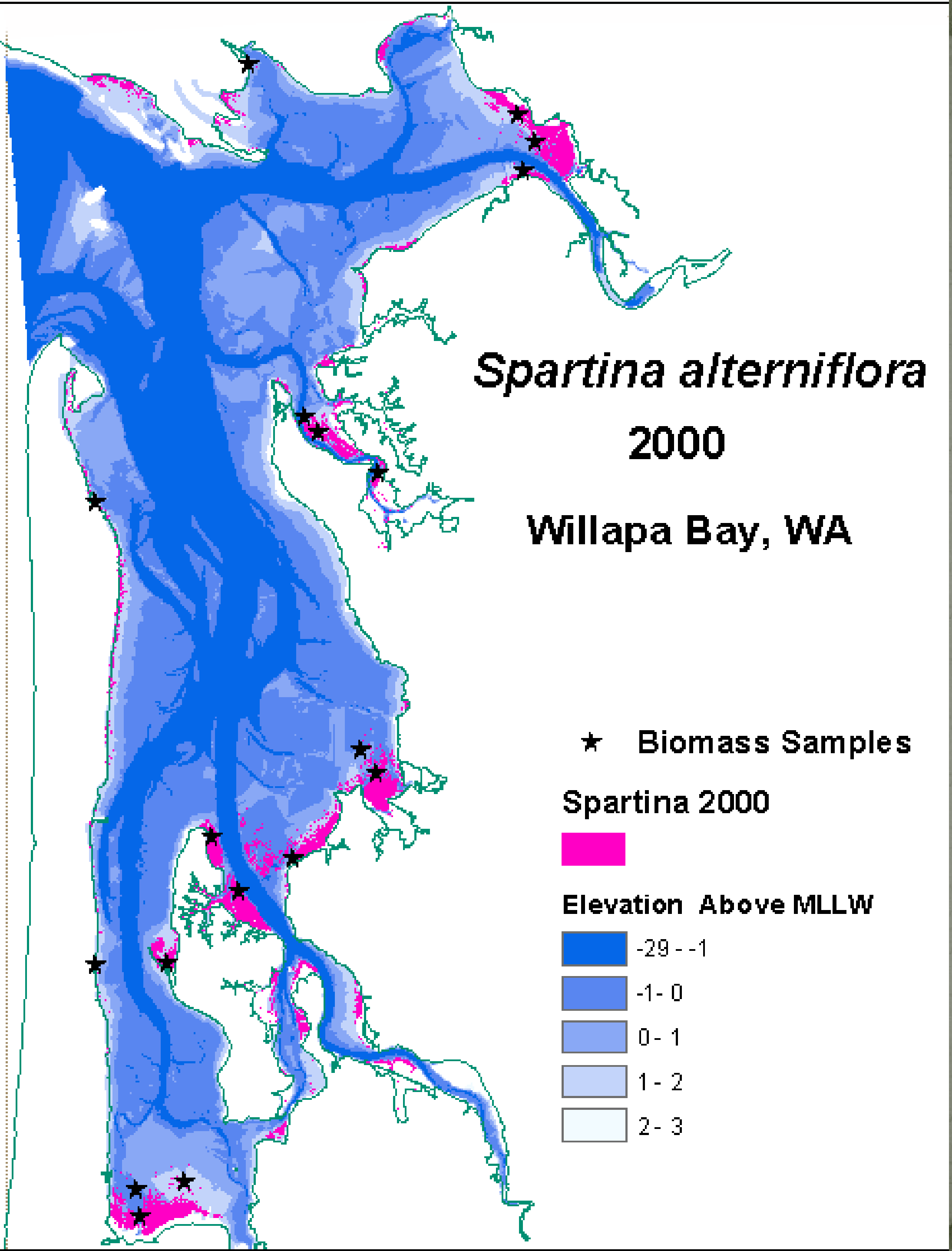


Conclusions

- Allee effect slows down invasion considerably
- Best control strategy is to remove clones first if budget is low or if minimizing for cost only
- If minimizing for risk and budget is high, removing meadows first is best strategy
- Meadow first strategy is risky especially if budgets for future years are unpredictable.

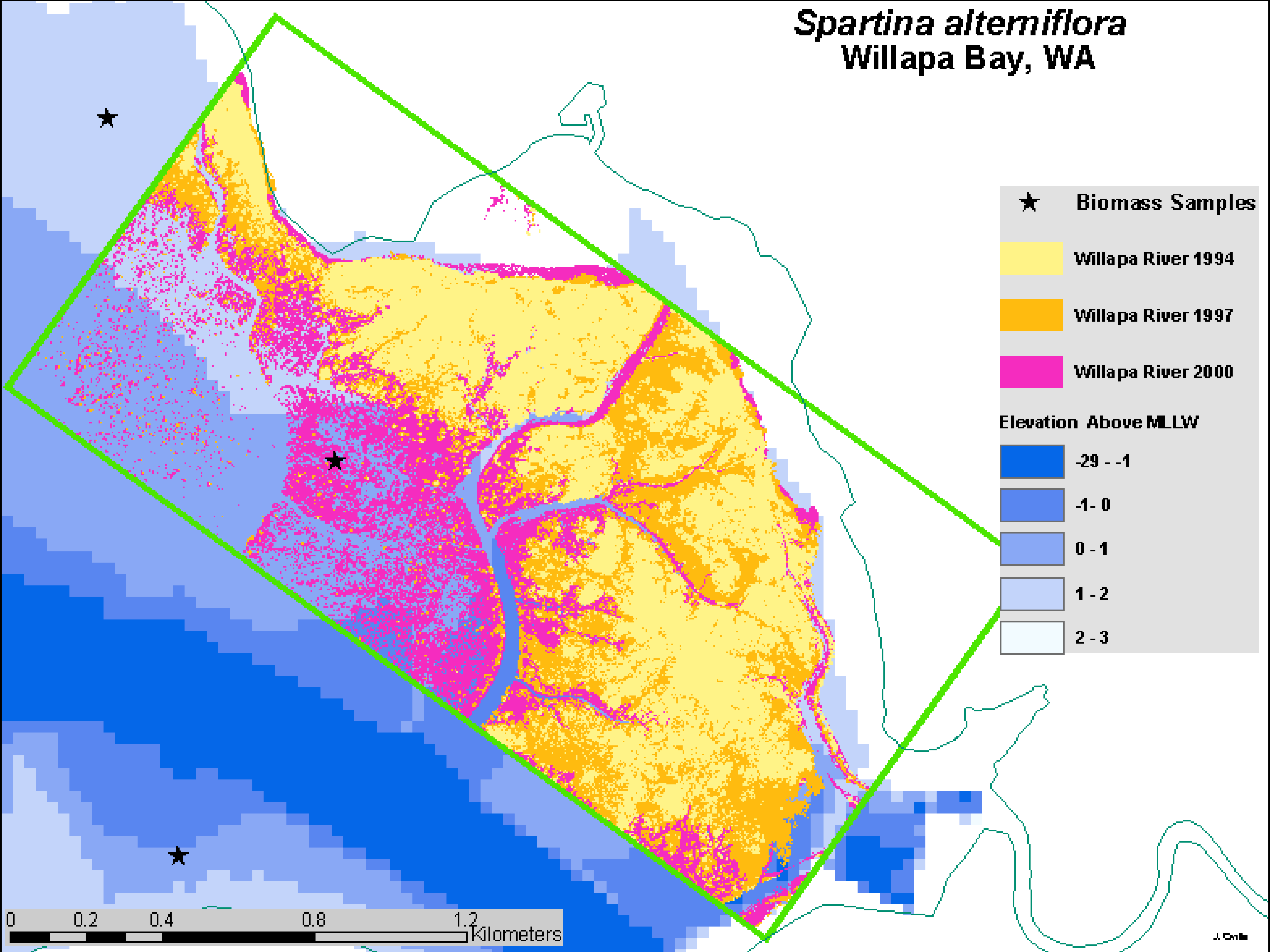
Where's the data?

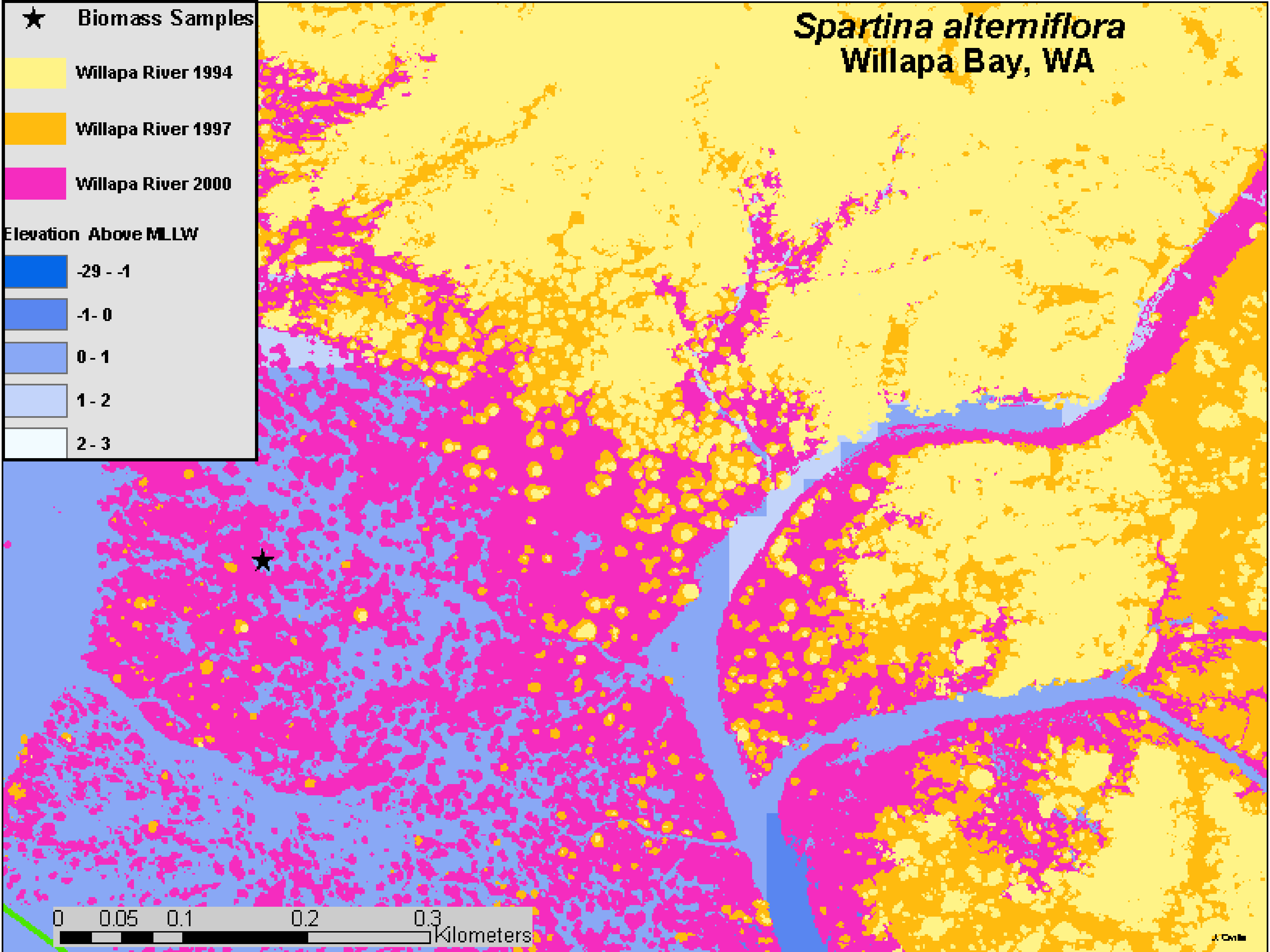
- Willapa Bay
  - Analysis of aerial photographs
- SF Bay
  - Remote sensing data


Spartina alterniflora
2000
Willapa Bay, WA
Biomass Samples
Spartina 2000
Elevation Above MLLW
-29 - -1
-1- 0
0 - 1
1 - 2
2 - 3

Approach in Willapa Bay

- Initial steps
  - (orthorectify, etc.)
- With aid of GIS software, identify clones
  - By hand
- Match up successive years


Spartina alterniflora
Willapa Bay, WA
Biomass Samples
Willapa River 1994
Willapa River 1997
Willapa River 2000
Elevation Above MLLW
-29 - -1
-1 - 0
0 - 1
1 - 2
2 - 3
0
0.2
0.4
0.8
1.2
Kilometers

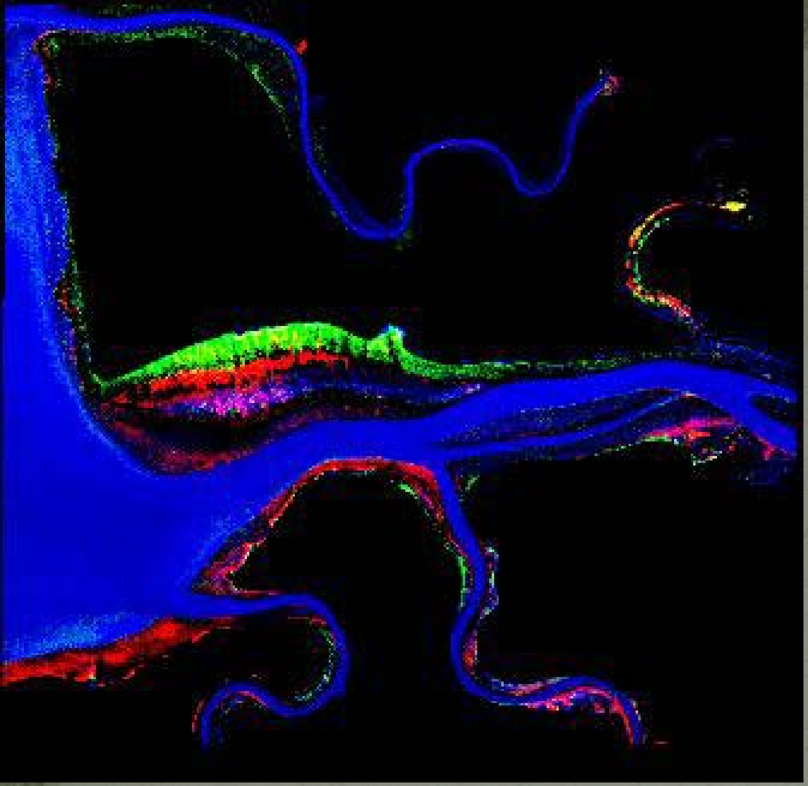

Biomass Samples
Willapa River 1994
Willapa River 1997
Willapa River 2000
Elevation Above MLLW
-29 - -1
-1 - 0
0 - 1
1 - 2
2 - 3
Spartina alterniflora
Willapa Bay, WA
0 0.05 0.1 0.2 0.3
Kilometers


San Francisco Estuary Invasive Spartina Project
Coastal Conservancy
Distribution of Invasive Spartina Populations by Species, 2000 - 2001 Survey
S. alterniflora / hybrid
S. alterniflora / hybrid
S. densiflora
S. patens
S. anglica
Oakland
San Francisco
Funding Provided By:
CALFED BAY-DELTA PROGRAM

Approach in SF Bay

- Low resolution, high bandwidth data
- Identify components by 'spectral signature'
  - Ground truthing
  - Choose number of components to identify
    - Mud
    - Water
    - Spartina
    - Other vegetation

(Rosso, P. H., Ustin, S. L. & (2005) International Journal of Remote Sensing 26: 5169 – 5191)



Picture is an Aviris image (pixel size, 17x17 m approx.) of Coyote Creek area marsh, in the southern tip of San Francisco Bay. Image is from August 1999.

Colors indicate the percentage of each component, Spartina (red), Salicornia (green) and water (blue), present at each pixel as determined by a spectral unmixing approach. The unmixing was done on the basis of eight endmembers (reference spectra). Five plant species, water and open mud.

Comparison of approaches

- Willapa
  - High resolution, low bandwidth
  - High accuracy
  - Labor intensive
  - Data expensive
  - Works well with invasion into bare mud
- SF Bay
  - Low resolution, high bandwidth
  - Lower accuracy
  - After difficult initial steps, easier to implement
  - Can handle multiple types