University of Miami, Everything Disperses to Miami, December 14, 2012

Spread of fleshy-fruited exotic shrubs when dispersal is structured by dispersers that vary over time

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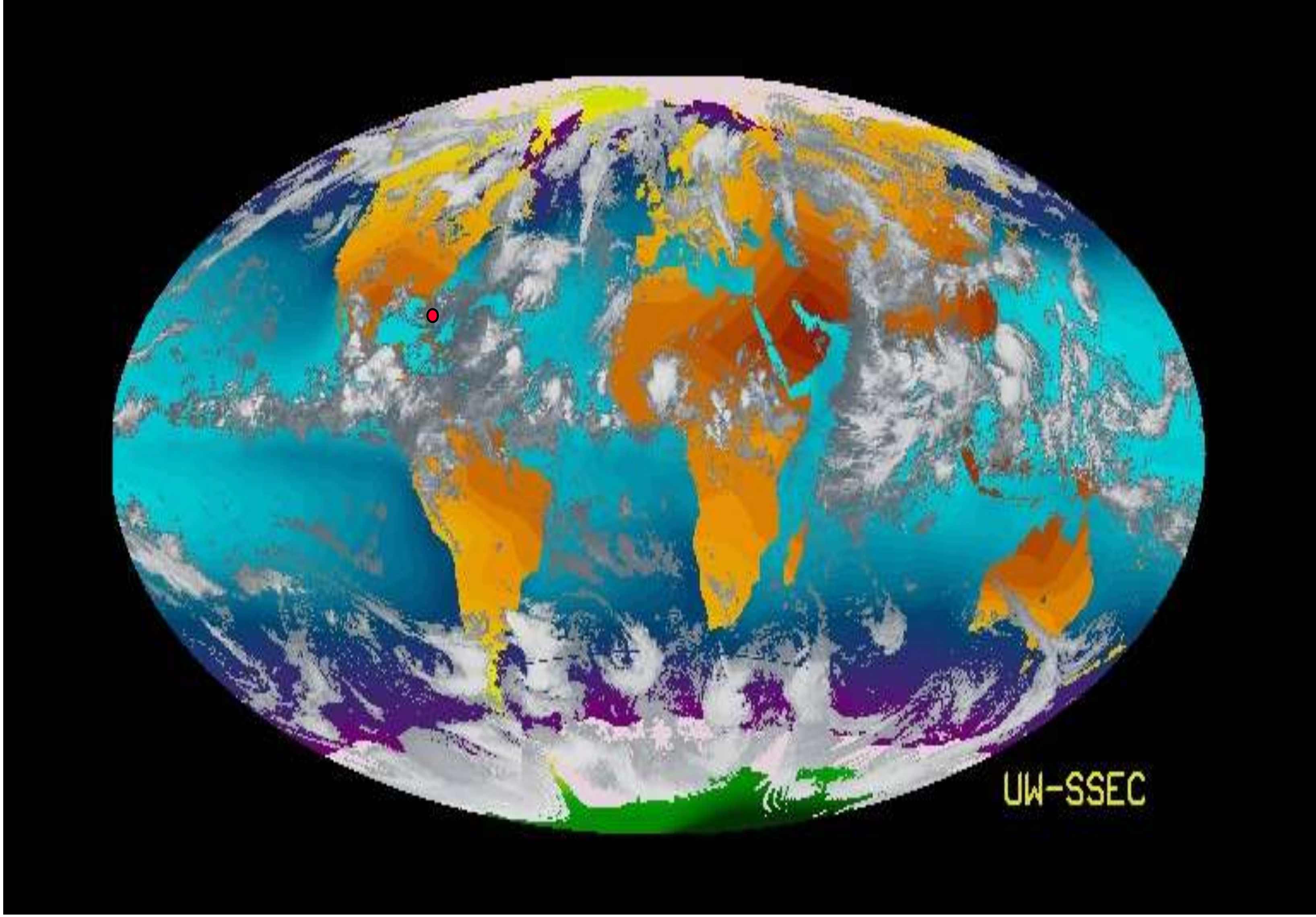


…Welcome to life under our little subtropical patch of clouds

Latitude:
Subtropical 26° N

Temperature:
Cool mo: 26° C
Hot mo: 33° C

Substrate:
Oolitic limestone

Rainfall:
Wet mo: 230 mm
Dry mo: 33 mm

Floods, fires, hurricanes, The Army Corps of Engineers


Seedlings seen at point *x*
at a certain time,
where did they come from?
- Seeds are produced
- travel
- germinate

Main issues

- How do different animals contribute to population spread?

- How would permanent changes in disperser assemblages affect population spread?

- How does temporal variation in disperser assemblage affect population spread?

Two population processes

- population change in numbers
- population change in space occupied

Two types of dynamic models in a structured world

- population change in numbers
  - Population projection matrix
- population change in space occupied
  - Dispersal kernels

    for each dispersing stage

Two population parameters in a structured constant world

- λ
- **projection matrix analysis** of a matrix of growth, survival and reproduction
- c*, wavespeed
- analysis of **integrodifference equation model** based on analysis of a matrix that combines growth, survival and reproduction with movement

Neubert and Caswell 2000

Two population parameters in a structured random world

- λ_s
- **Population projection with temporal variation** = random matrix product analysis

Tuljapurkar 1982, 1990

- c^*_s, wavespeed
- analysis of **integrodifference equation model with temporal variation** = random matrix product analysis

Ellner and Schreiber 2012

Stage-Structured Integrodifference Model with Temporal Variation

$$\mathbf{n}(x,t+1) = \int_{-\infty}^{\infty} [\mathbf{K}_{(t)}(x-y) \circ \mathbf{B}_{(n,t)}] \; \mathbf{n}(y,t)dy$$

Population at location x at t+1

=

Matrix of movement across space From y to x

Population projection matrix at location y

Population at location y at t

Model

s is a wave shape parameter, (try more than one to look for the one of interest, s_s^*)

Population Projection Matrix at low density

$B_{(0,t)}$

$H(s,t)$

Hadamard Product Matrix of Demography & Dispersal

c^*_s = stochastic wave speed, from the random matrix product of the H's

Matrix of moment generating functions

$M(s,t)$

s_s^* is the value corresponding to c^*_s

$$c^*_s = \min\left[\frac{1}{s^*}\ln \rho_s(s^*)\right]$$

Matrix of Dispersal Kernels

$K_{(t)}$

ρ_s is the stochastic growth rate from random matrix product of the H's

λ_s is the stochastic growth rate from the random matrix product of B's

Ardisia elliptica (Myrsinaceae)

- Tropical understory shrub
- Native to SE Asia
- Naturalized in Hawaii, Southern Florida, Okinawa and Jamaica.
- Can survive and reproduce under low light levels
- Tolerate high densities

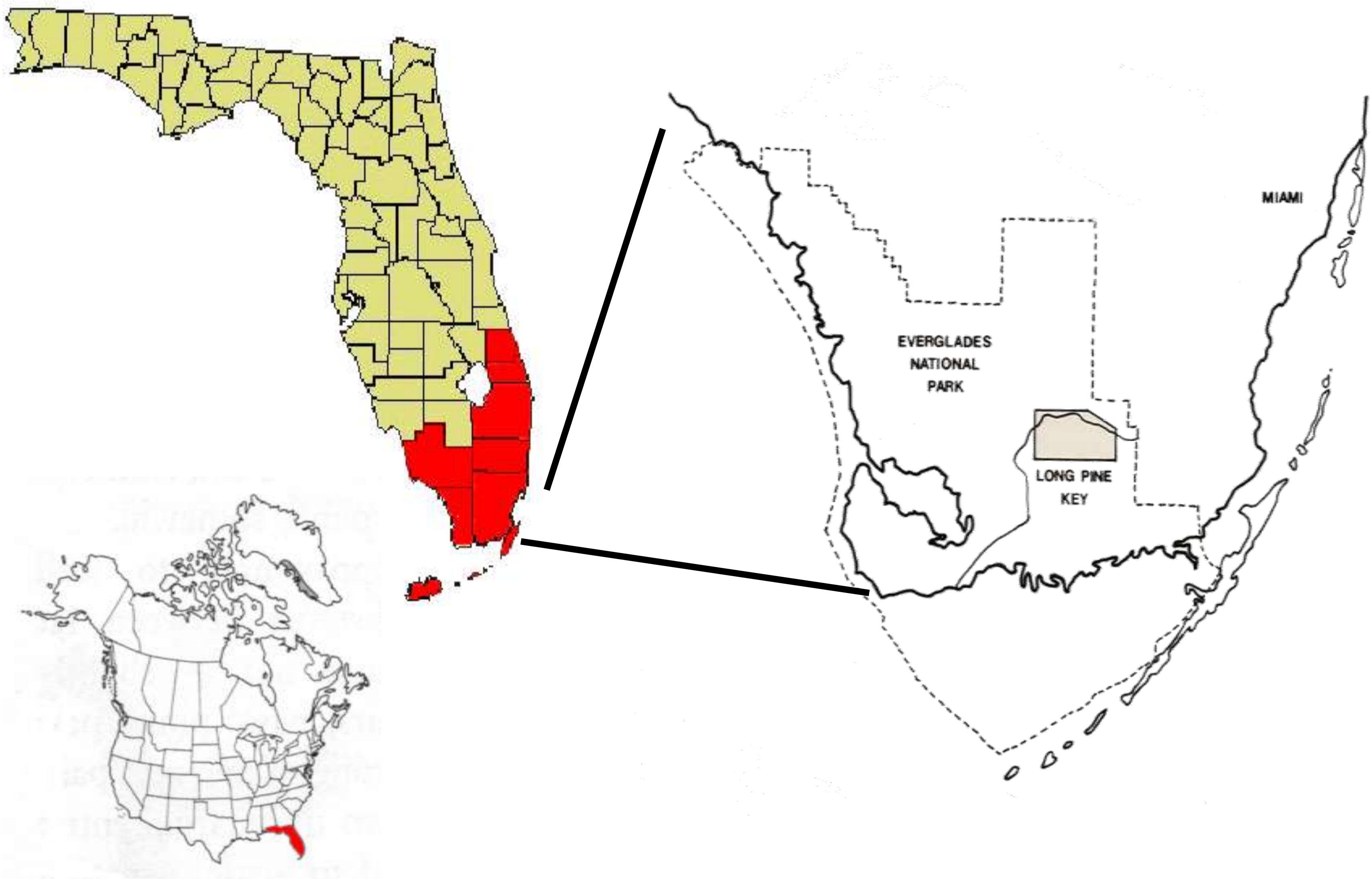
Biotic Dispersal

Eastern Grey Catbird
Dumetella carolinensis

Common Raccoon
Procyon lotor

American Robin
Turdus migratorius

Study Location:
Everglades National Park, Florida



Everglades National Park

Courtesy South Florida Water Management District

Population projection matrix with structured dispersal

(An unstructured, composite model collapses all seeds into one stage)

							Time *t*					
		Drpoped Seed	Raccoon Seed	Cat Bird Seed	Robin Seed	SG Seedling	Small Juvenile	Medium Juvenile	Large Juvenile	Pre Repro-ductive	Small Adult	Large Adult
	DS	0	0	0	0	0	0	0	12.20	36.59	52.62	90.03
	RacS	0	0	0	0	0	0	0	0.69	2.08	2.99	5.12
	CatS	0	0	0	0	0	0	0	16.01	48.03	69.08	118.18
	RobS	0	0	0	0	0	0	0	0.00	0.00	0.00	0.00
Time	SG	0.15	0.15	0.15	0.15	0.312	0	0	0	0	0	0
t + 1	SJ	0	0	0	0	0.624	0.738	0.034	0	0	0	0
	MJ	0	0	0	0	0	0.24	0.517	0	0	0	0
	LJ	0	0	0	0	0	0.004	0.172	0.167	0	0	0
	PR	0	0	0	0	0	0.009	0.276	0.5	0	0	0
	SA	0	0	0	0	0	0	0	0.333	1	0.7	0.017
	LA	0	0	0	0	0	0	0	0	0	0.3	0.978

"*Schinus* Thicket population of 1999"

low density abandoned farmland site, 5.4 individuals m^{-2}

Adpated from Koop and Horvitz 2005 (Ecology 86:2661-2672),

Matrix of moment-generating functions, from matrix of dispersal kernels

(An unstructured, composite model collapses all seeds into one stage)

							Time *t*					
		Drpoped Seed	Raccoon Seed	Cat Bird Seed	Robin Seed	SG Seedling	Small Juvenile	Medium Juvenile	Large Juvenile	Pre Repro-ductive	Small Adult	Large Adult
	DS	1	1	1	1	1	1	1	1	1	1	1
	RacS	1	1	1	1	1	1	1	*m1(s)*	*m1(s)*	*m1(s)*	*m1(s)*
	CatS	1	1	1	1	1	1	1	*m2(s)*	*m2(s)*	*m2(s)*	*m2(s)*
	RobS	1	1	1	1	1	1	1	*m3(s)*	*m3(s)*	*m3(s)*	*m3(s)*
Time	SG	1	1	1	1	1	1	1	1	1	1	1
t + 1	SJ	1	1	1	1	1	1	1	1	1	1	1
	MJ	1	1	1	1	1	1	1	1	1	1	1
	LJ	1	1	1	1	1	1	1	1	1	1	1
	PR	1	1	1	1	1	1	1	1	1	1	1
	SA	1	1	1	1	1	1	1	1	1	1	1
	LA	1	1	1	1	1	1	1	1	1	1	1

the Gaussian dispersal kernel (which fit our data),

has moment generating function

$m(s)=\exp(\ ((\alpha * s)/2)\ \hat{}\ 2)$,

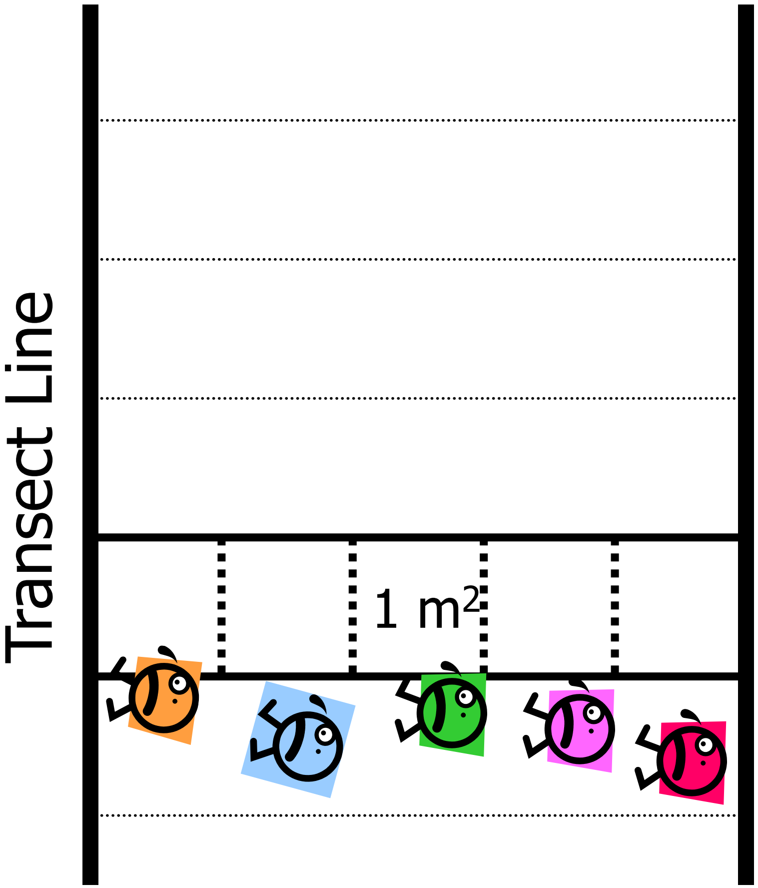
α is related to mean dispersal distance

and is estimated from data

Inverse modeling method…

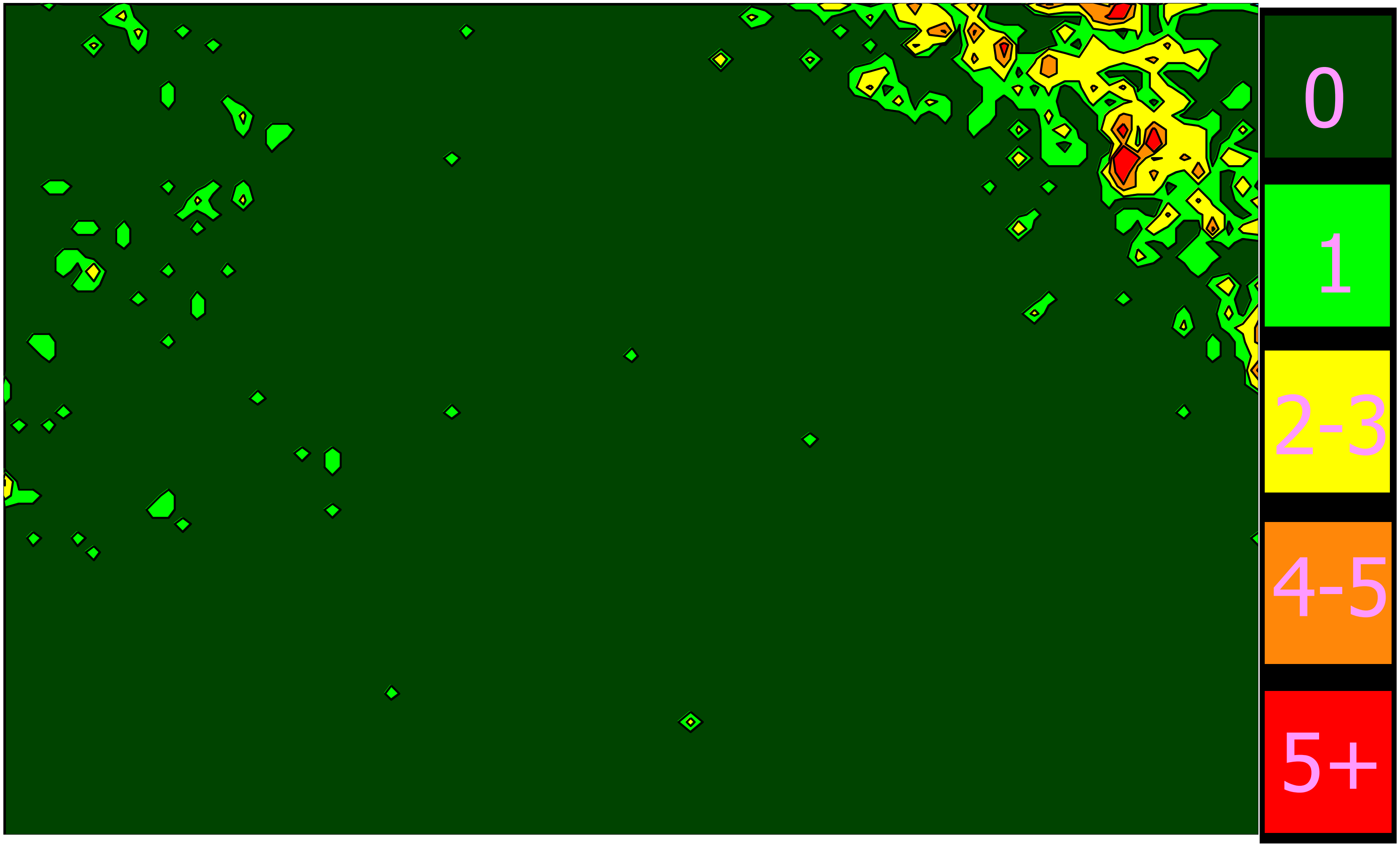
- Jim Clark:
  - Developed a program that takes account of locations of adults and of seedlings
  - And estimates dispersal kernel parameters

Estimating the Dispersal Kernel: spatially referenced counts of adults and seedlings

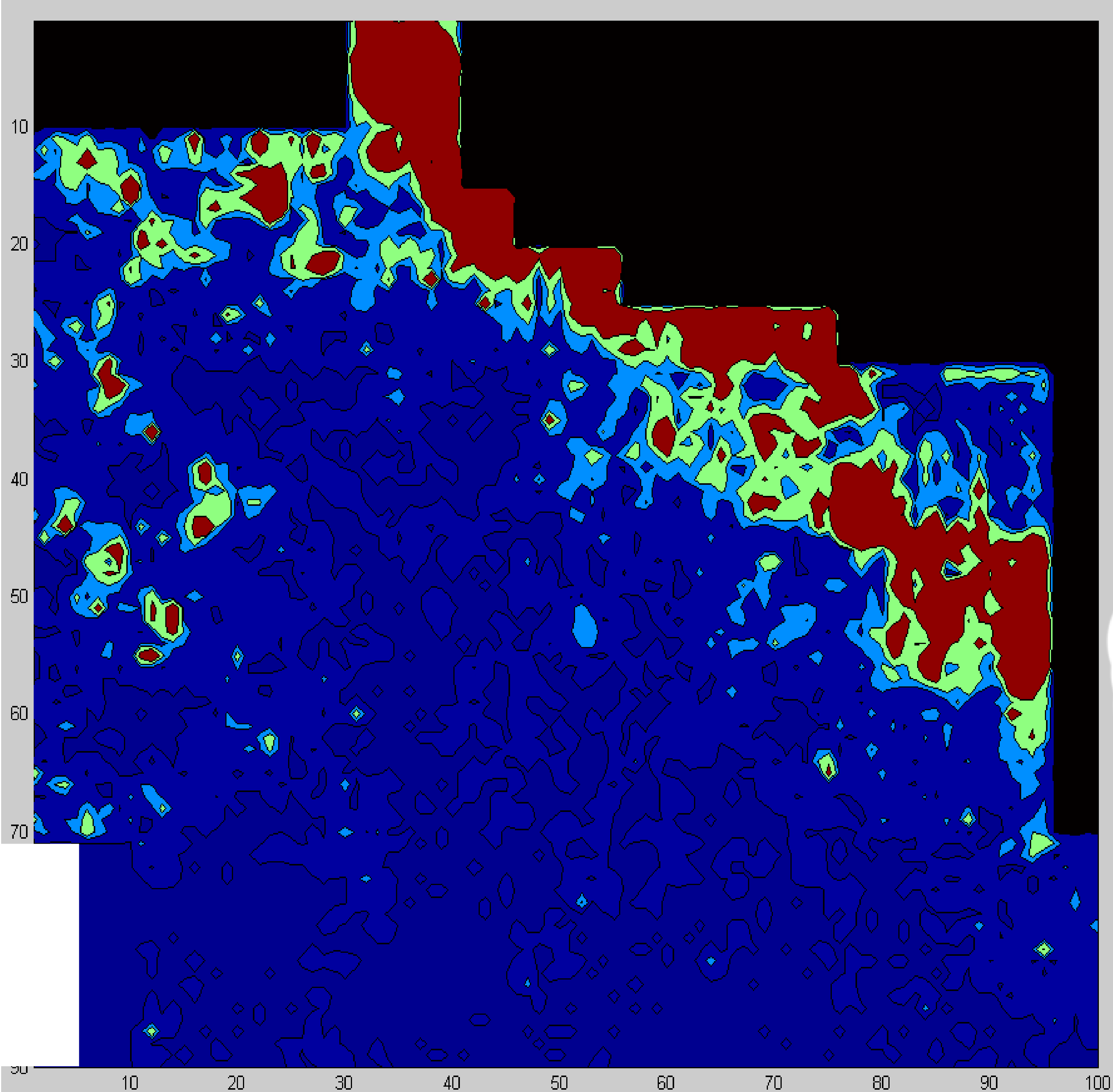


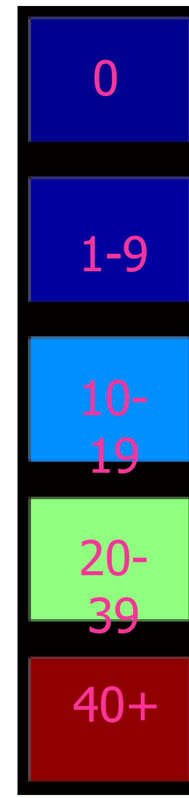
- Mapped individuals (app. 100m X 90m)
- Grid size was 1 m^2
- Classified plants into 5 stage classes
  - Seedlings, Juveniles, Pre-Reproductives, Small Adults, & Large Adults

All Adults



All Inds





Dispersal kernels from field data

Bird Dispersed
(Isolated Seedlings)

We mapped ALL individuals in 100 x 90 m grid

Composite	**48,703 seedlings**
Gravity	**20,543 seedlings**
Catbird	**27,019 seedlings**
Raccoon	**1,141 seedlings**

Mammal Dispersed
(Seedlings in clusters)

Gaussian dispersal kernel parameter α estimated for composite, catbirds and raccoons

$$K(r_{ij}) = \frac{1}{\pi\alpha^2}\exp\left[-\left(\frac{r_{ij}}{\alpha}\right)^2\right]$$

$$\bar{r} = \alpha\sqrt{\pi}\Big/2$$

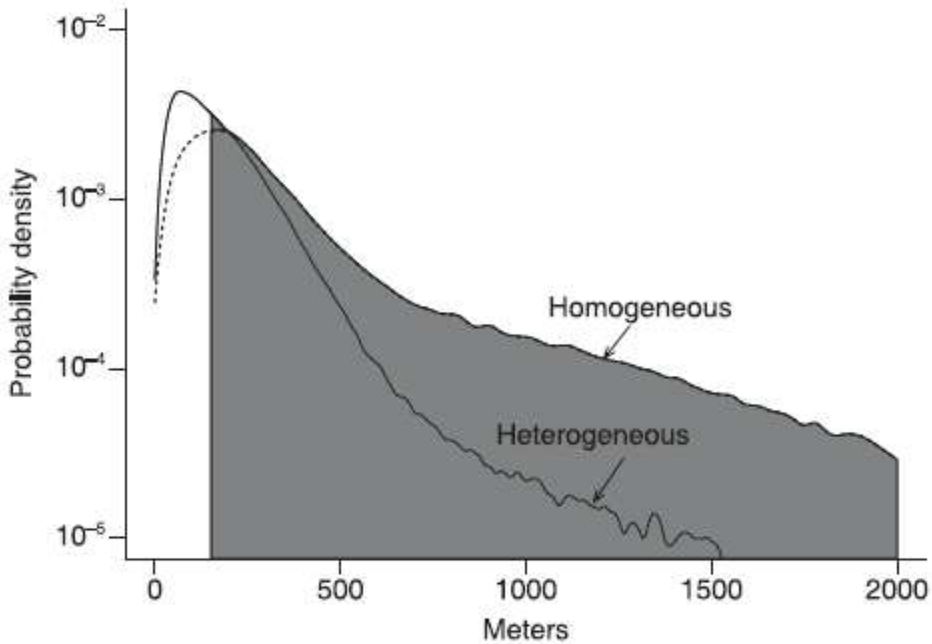
Composite vs Disperser-specific Dispersal Kernel parameters

	Composite	Raccoon	Catbird
α	15.3	77.0	18.5
mean dispersal distance, m	13.6	68.2	16.4

Robin dispersal kernel parameter based loosely on related bluebirds

Non- Gaussian mode between 70 and 170 m

We guesstimated a Gaussian mean of ~133 m

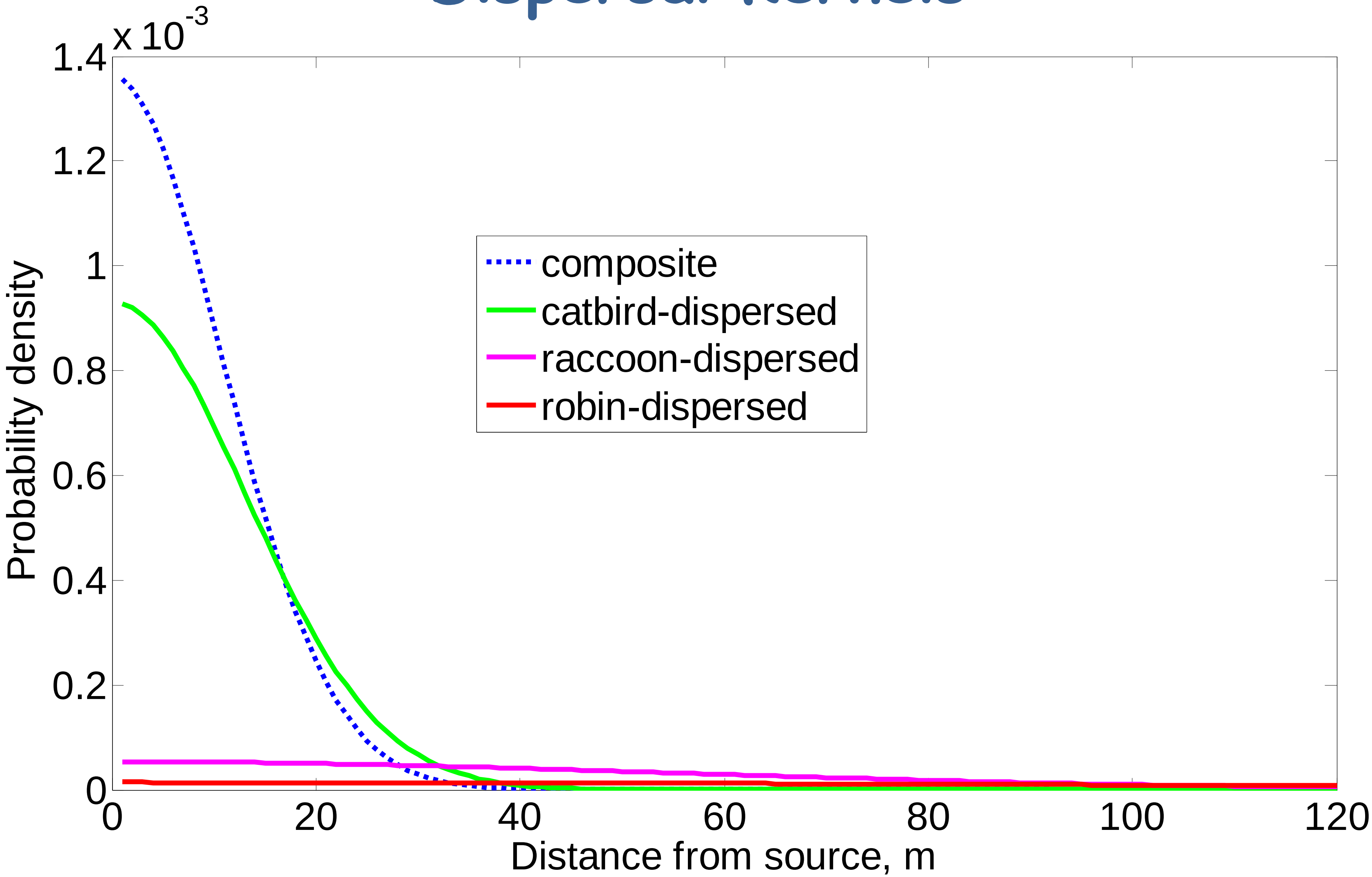


Levey *et al*. 2008

Composite vs Disperser-specific Dispersal Kernel parameters

	Composite	Raccoon	Catbird	Robin
α	15.3	77.0	18.5	150.0
mean dispersal distance, m	13.6	68.2	16.4	132.9

Composite vs Disperser-specific Dispersal Kernels



s is a wave shape parameter,
(try more than one to look
for the one of interest, *s**)

Model

Population Projection Matrix at low density

$B_{(0)}$

$H(s)$

Hadamard Product Matrix of Demography & Dispersal

c*
wave speed,
from the
dominant eigenvalue
of H

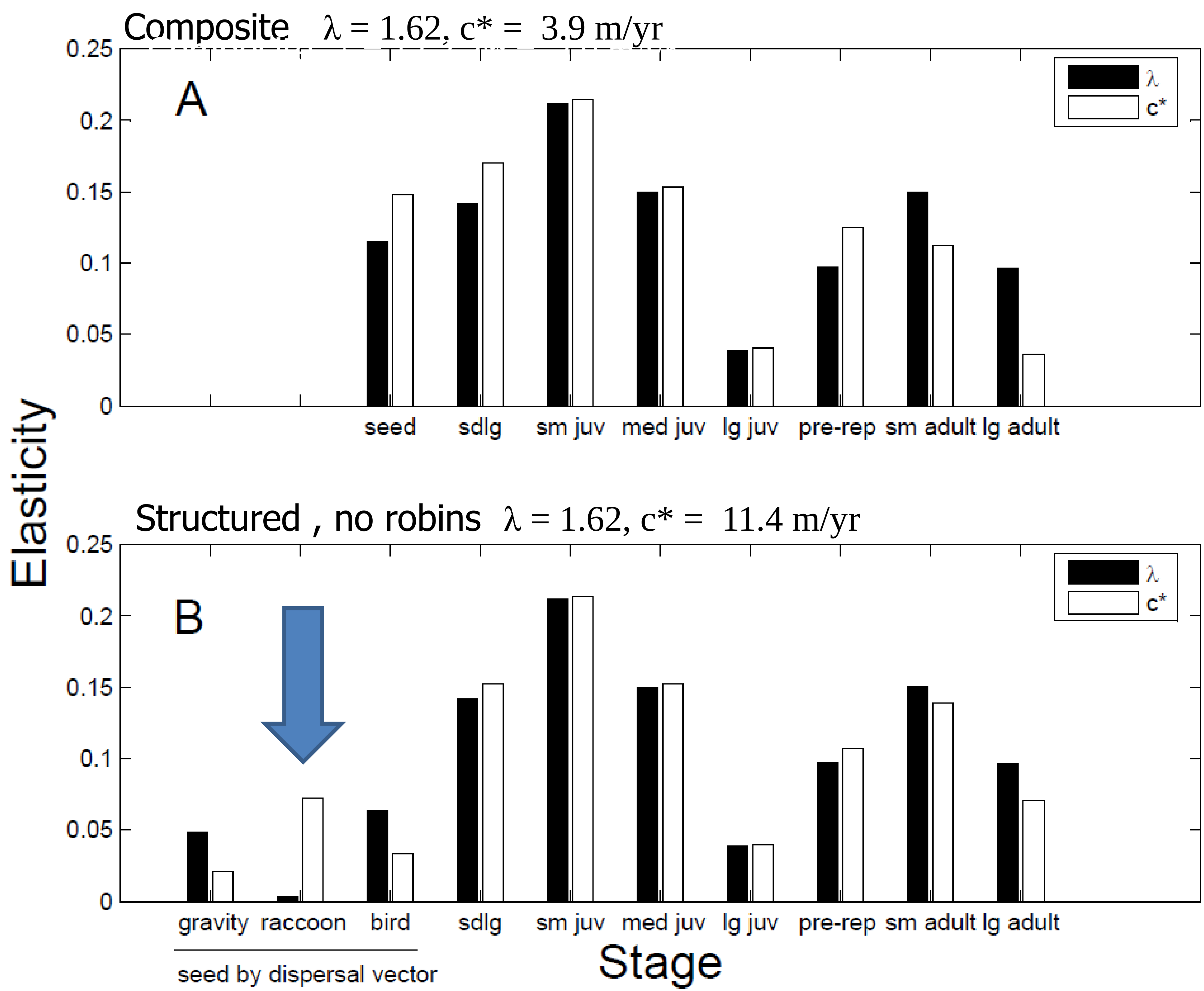
Matrix of moment generating functions

$M(s)$

M is a function of α , m(s)=exp(((α*s)/2) ^2)
we have unstructured composite α
& structured: α catbirds, α raccoons, α robins

Matrix of Dispersal Kernels

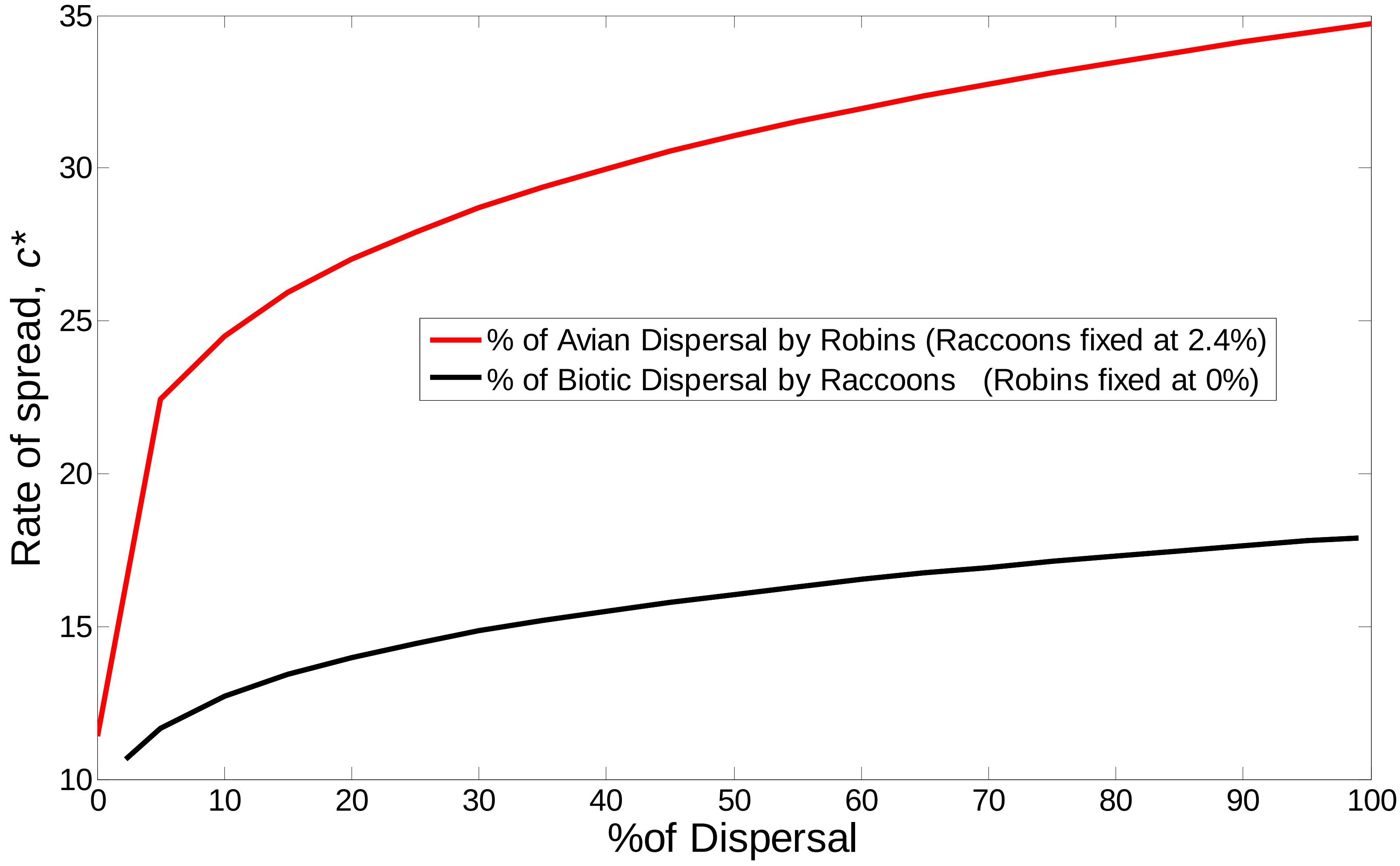
K


Composite λ = 1.62, c* = 3.9 m/yr
A
λ
c*
0.25
0.2
0.15
0.1
0.05
0
seed sdlg sm juv med juv lg juv pre-rep sm adult lg adult
Elasticity
Structured , no robins λ = 1.62, c* = 11.4 m/yr
B
λ
c*
0.25
0.2
0.15
0.1
0.05
0
gravity raccoon bird sdlg sm juv med juv lg juv pre-rep sm adult lg adult
seed by dispersal vector
Stage

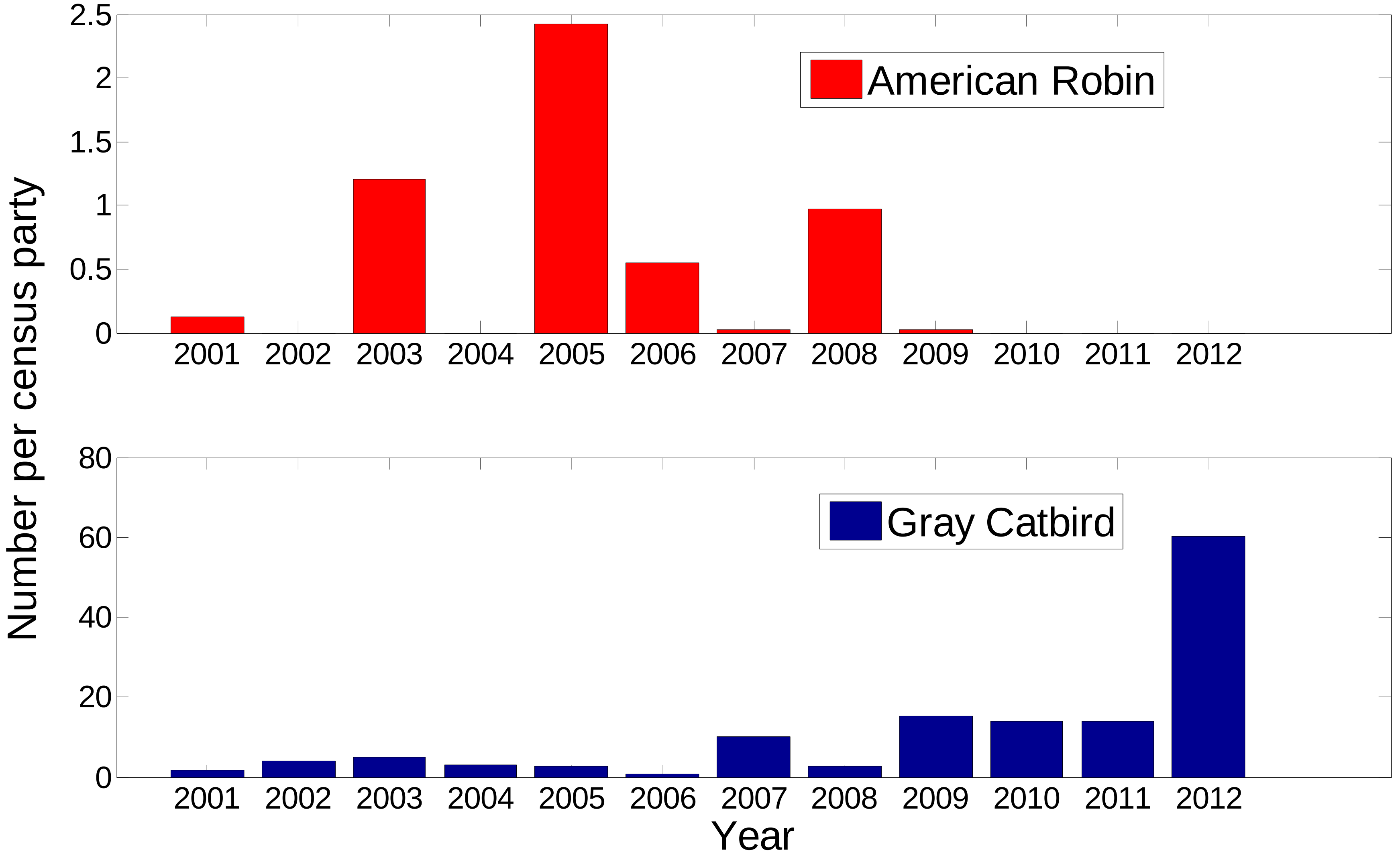
Main issues

- How do different animals contribute to population spread?
- How would permanent changes in disperser assemblages affect population spread?
- How does temporal variation in disperser assemblage affect population spread?

Simulation: effects on *c** of permanent changes in biotic dispersal



Christmas Bird Count : Long Pine Key, Everglades National Park, Florida



Main issues

- How do different animals contribute to population spread?
- How would permanent changes in disperser assemblages affect population spread?
- How does temporal variation in disperser assemblage affect population spread?

Transitions among years with differing amounts of robins based on Christmas Bird Count : Long Pine Key, Everglades National Park, Florida

			Time t	
		No robins	Robins	More robins
Time	No robins	0.57	0.9999	0.05
$t + 1$	Robins	0.29	0.0001	0.95
	More robins	0.14	0	0

Robins =10% of avian dispersed seeds taken by robins
More robins = 30% of avian dispersed seeds taken by robins

Model

s is a wave shape parameter, (try more than one to look for the one of interest, s_s*)

Population Projection Matrix at low density

$B_{(0,t)}$

$H(s, t)$

Hadamard Product Matrix of Demography & Dispersal

c^*_s = stochastic wave speed, from the random matrix product of the H's

s_s* is the value corresponding to c^*_s

Matrix of moment generating functions

$M(s)$

M is a function of α , m(s)=exp(((α*s)/2) ^2)
we have
α catbirds, α raccoons, α robins

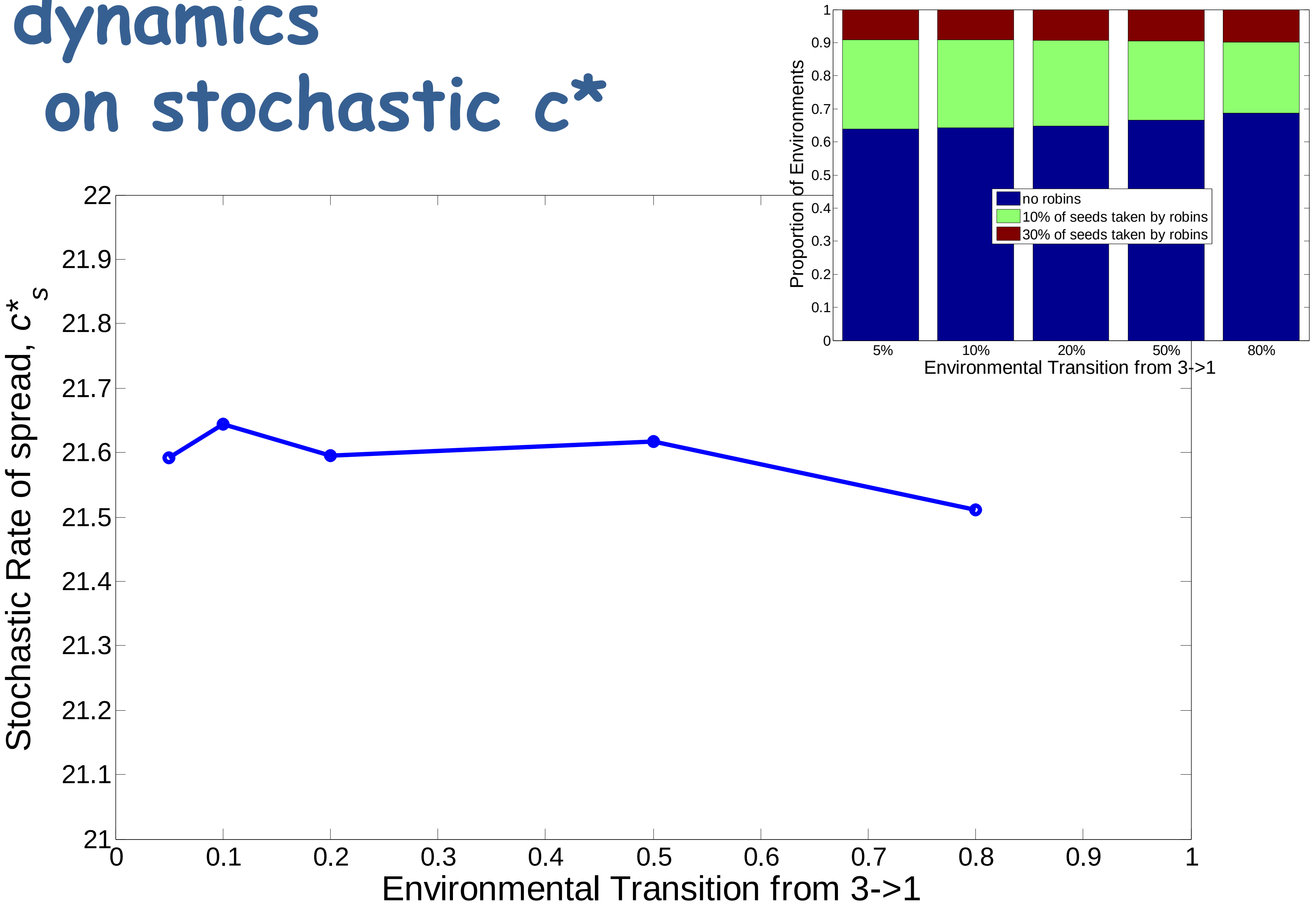
Matrix of Dispersal Kernels

K

ρ_s is the stochastic growth rate from random matrix product of the H's

λ_s is the stochastic growth rate from the random matrix product of B's

Effect of changes in environmental dynamics on stochastic c*



Comparison of wavespeeds among dispersal models

Model	Rate of spread, m/yr
Constant composite (ignore disperser structure)	3.9
Constant disperser structured (many catbirds, no robins, few raccoons)	11.4
Constant disperser structured (no robins, shift from catbird to raccoon)	17.9
Constant disperser structured (shift from catbirds to robins, few raccoons)	34.7
Time varying disperser structured (occassional robins)	21.6

Note: Population growth rate was the same for all models, $\lambda = 1.6244$, $\lambda_s = 1.6244$

Conclusions

- Structured dispersal matters

- Ignoring it underestimates the influence of rare long-distance dispersers

- Temporal variability causes distinct effects from within year

Future: Kelley Erickson will be working on stochastic spread of exotics vs natives

Schinus terebinthifolius
Brazilian Pepper
Invasive

Ilex cassine
Dahoon Holly
Native

Thanks!

- Everglades National Park for research permits (No: 1999125 and 2000107)
- NCEAS "Demography and Dispersal Synthesis Working Group" (2001-2002)
- Hal Caswell, Mike Neubert, James Clark, Janneke HilleRisLambers, Brian Beckage for inspiration and code
- "Ecology-236" students at Umiami
- Ellner, Schreiber for stochastic wavespeed inspiration and model

Extra slides in case of questions.

Model

s is a wave shape parameter, (try more than one to look for the one of interest, s_s*)

Population Projection Matrix at low density $B_{(0,t)}$

Matrix of Dispersal Kernels $K_{(t)}$

Matrix of moment generating functions $M(s,t)$

Hadamard Product Matrix of Demography & Dispersal $H(s,t)$

c^*_s = stochastic wave speed, from the random matrix product of the H's

s_s* is the value corresponding to c^*_s

$$c^*_s = \min\left[\frac{1}{s^*}\ln\rho_s(s^*)\right]$$

ρ_s is stochastic growth rate from random matrix product of the H's

λ_s is the stochastic growth rate from the random matrix product of B's

The dispersal kernel is created from the spatially referenced counts by a statistical model

$$\text{seedlings}_j = \frac{\beta}{\pi\alpha^2} \sum_{i=1}^{\text{n adults}} b_i \exp\left[-\left(\frac{r_{ij}}{\alpha} \right)^2 \right]$$

b_i = size of each adult (where size predicts reproduction)

α = Dispersion parameter estimated by statistical model

β = scaling parameter estimated by statistical model (turns probability density into numbers of seedlings)

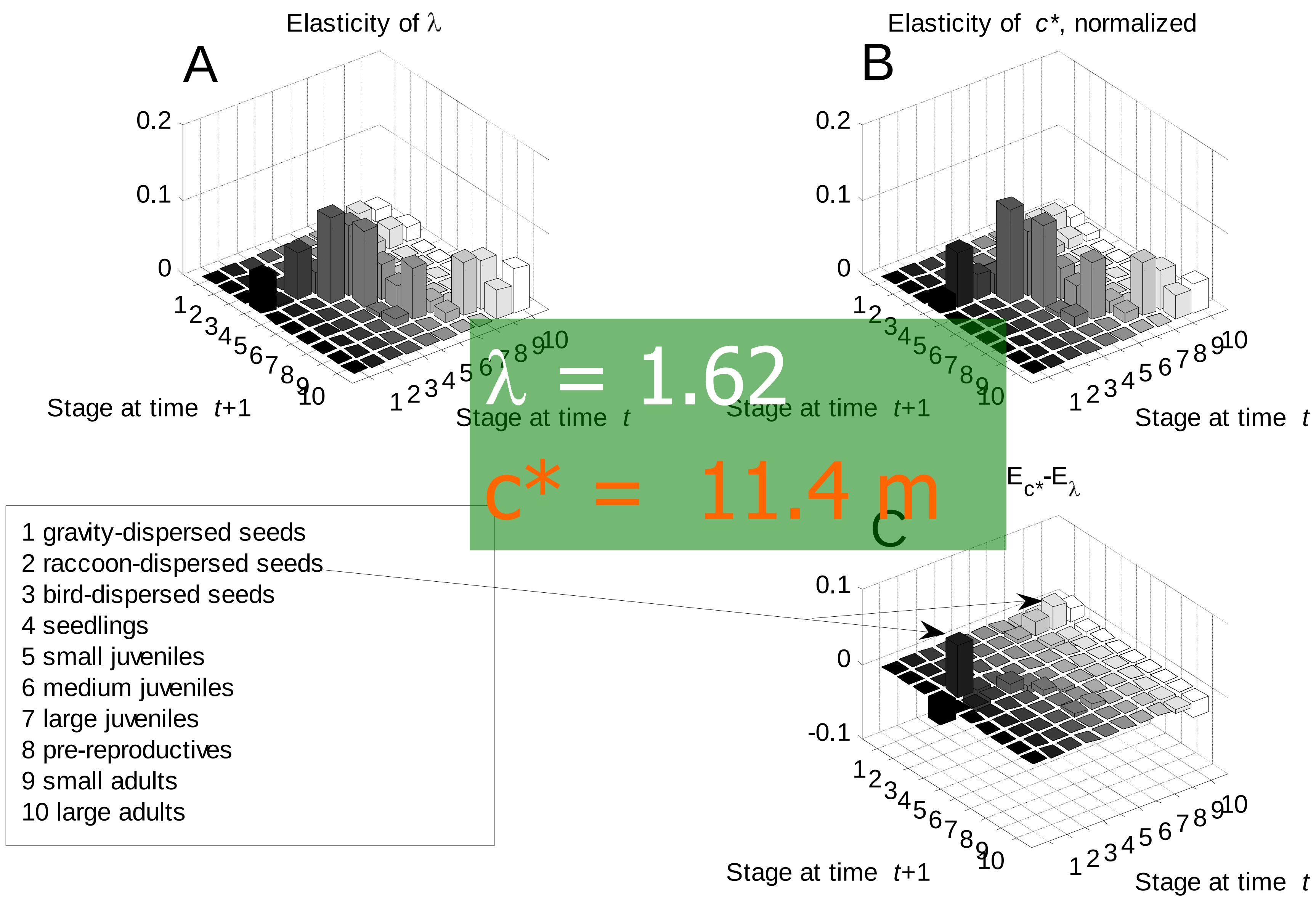
Moment generating function

For the Gaussian dispersal kernel,
the moment generating function is:

$$m(s)=\exp(\ ((\alpha*s)/2)\ \hat{}2)$$

α = Dispersion parameter estimated from data by statistical model

s = Waveshape parameter found by trial and error,



Elasticity of λ
A
0.2
0.1
0
Stage at time t+1
Stage at time t
Elasticity of c*, normalized
B
E_{c*}-E_{λ}
C
-0.1
1 gravity-dispersed seeds
2 raccoon-dispersed seeds
3 bird-dispersed seeds
4 seedlings
5 small juveniles
6 medium juveniles
7 large juveniles
8 pre-reproductives
9 small adults
10 large adults
λ = 1.62
c* = 11.4 m