Investigating seed dispersal and natural enemy attack with wavelet variances and moment methods

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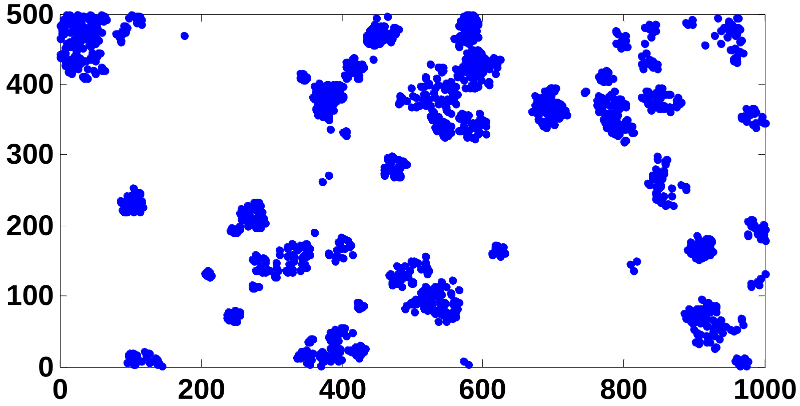
Heterogeneous spatial patterns are ubiquitous in ecology

Rinorea silvatica



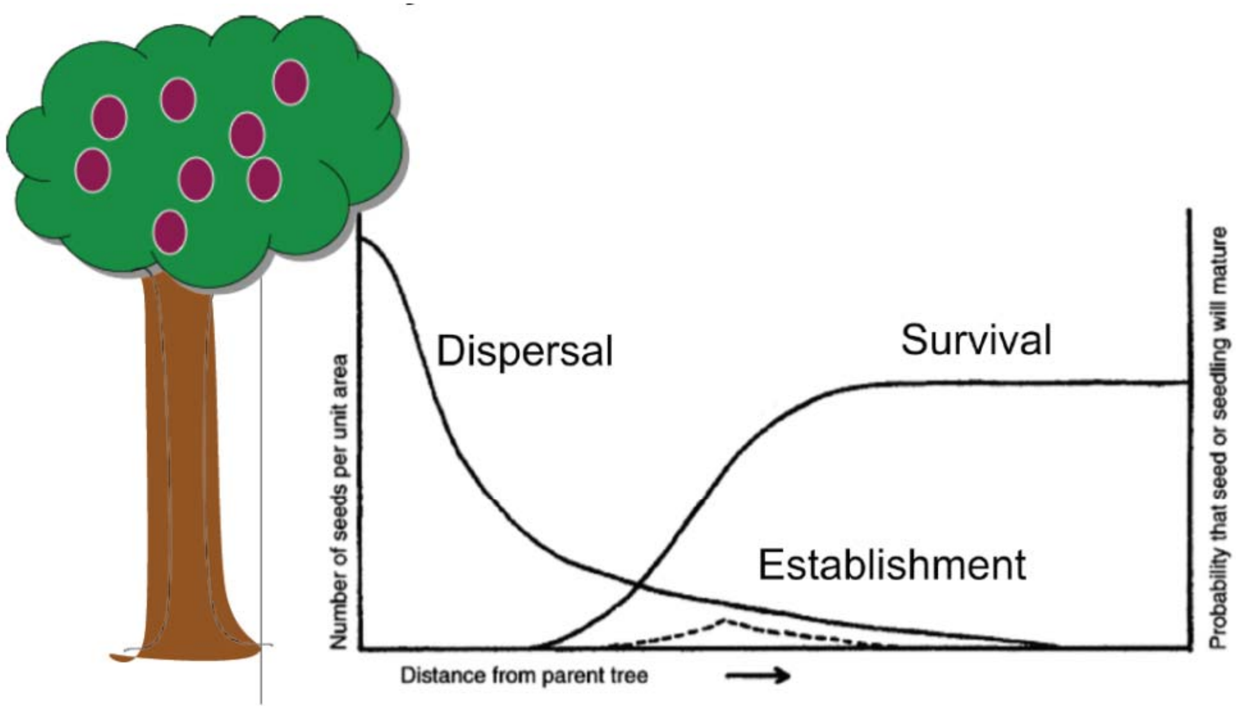
Due to multiple processes, including local dispersal, neighborhood competition, and habitat heterogeneity.

Spatial processes are integral to population and community dynamics

Connell 1971:

"The mechanism I suggest is that each tree species has host-specific enemies which attack it and any of its offspring which are close to the parent. The healthy parent tree supports a large population of these enemies without itself being killed, but the seedlings, whose growth is suppressed in the heavy shade, succumb to the attack of insects and other enemies which come from the parent tree itself or the soil below it."

Janzen 1970:



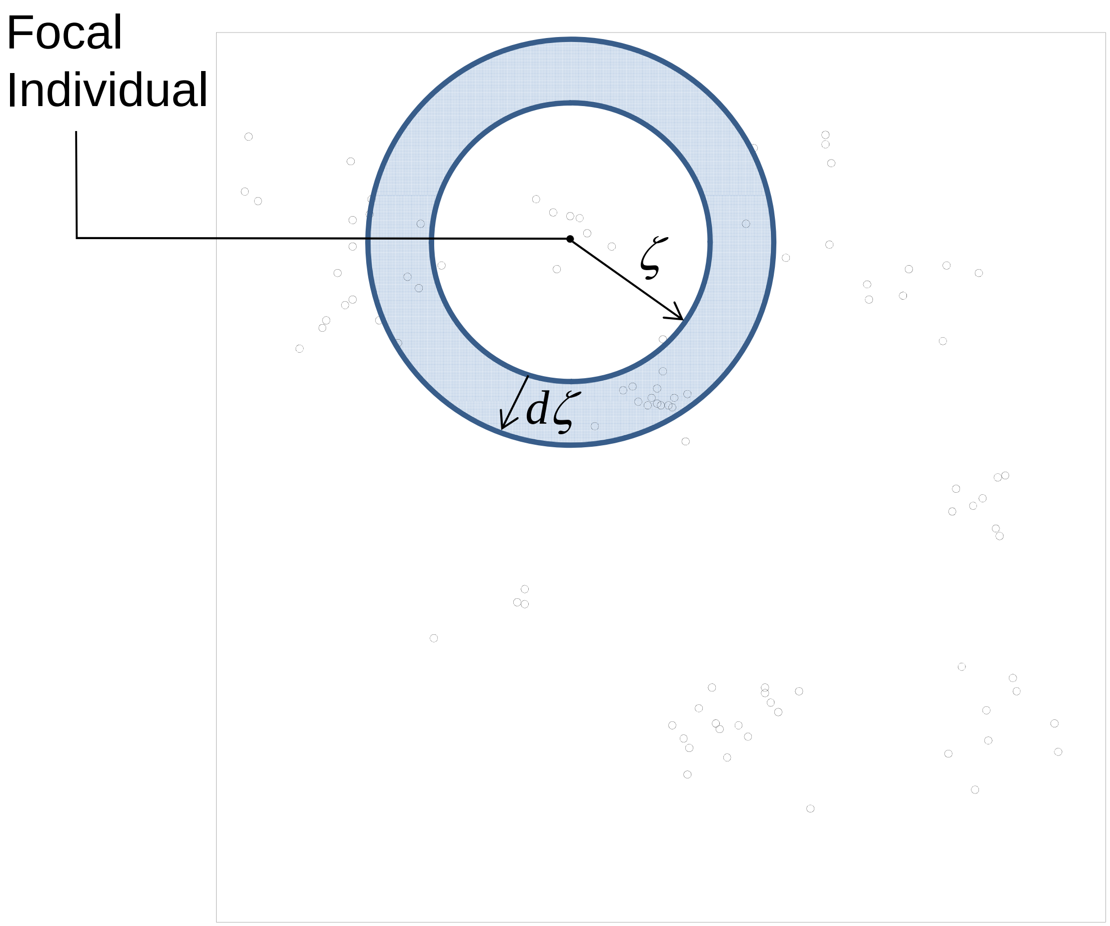
Talk outline

- Wavelet variances introduced
- Estimating seed dispersal and density-dependence parameters from observed patterns
  - Deriving expected wavelet variances from models using moment methods
  - Estimating model parameters from spatial patterns
- Investigating how seed dispersal and natural enemy parameters influence population dynamics

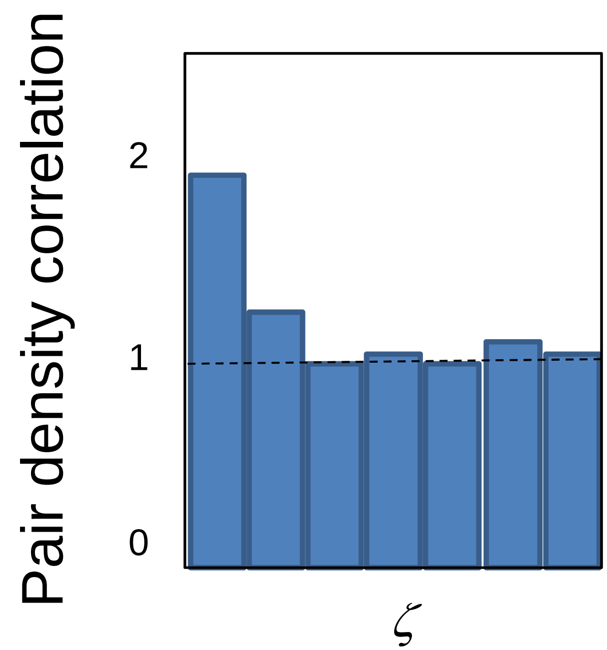
Measuring aggregation:
Pair density correlation

$$C(\zeta)=\frac{1}{A}\int N(x)\big(N(x+\zeta)-\delta(\zeta)\big)\,dx$$

2nd moment



$$C(\zeta)=\frac{1}{A}\sum_{i=1}^{N_{tot}}\frac{N_i}{2\pi\zeta\, d\zeta}$$



From pair density correlation to wavelet variance

Apply Fourier transforms:

$$\hat{N}(\omega) = \int N(x) e^{-i\omega x} dx$$

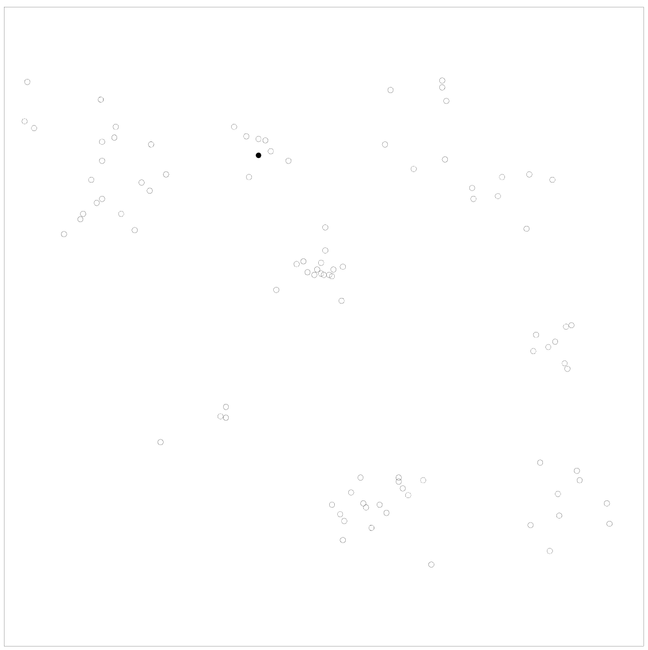
$$\tilde{C}(\omega) = \left|\tilde{N}(\omega)\right|^2 - N$$

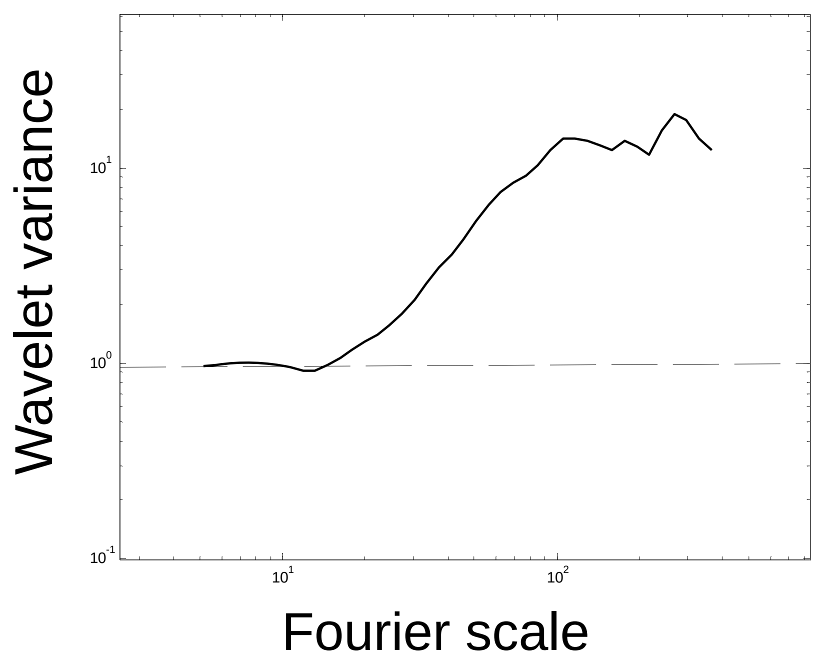
Apply wavelet filters:

$$\mathrm{H}_0(\omega) = \left|\hat{\psi}_0\left(\omega\right)\right|^2$$

To obtain the normalized wavelet variance:

$$\nu^2(\lambda) = \frac{1}{N} \int \hat{C}(\omega) \mathrm{H}(\lambda\omega) d\omega + 1$$

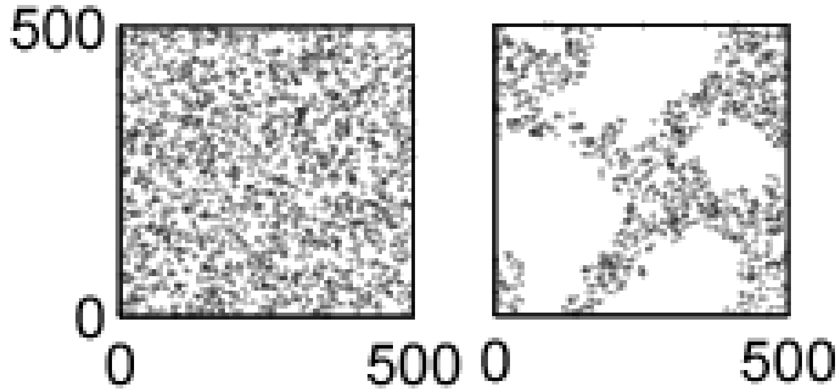


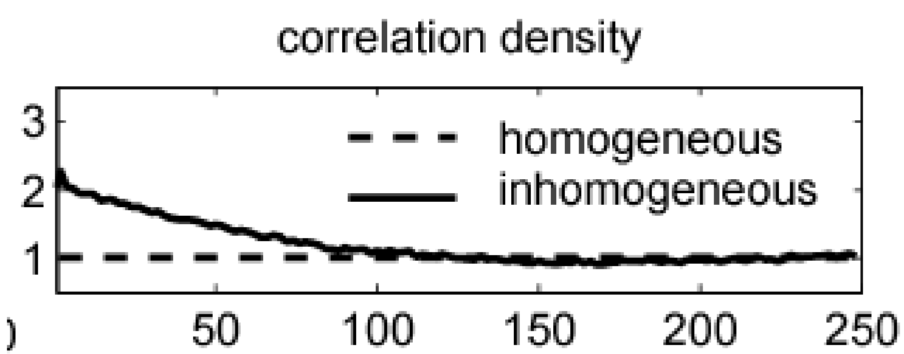


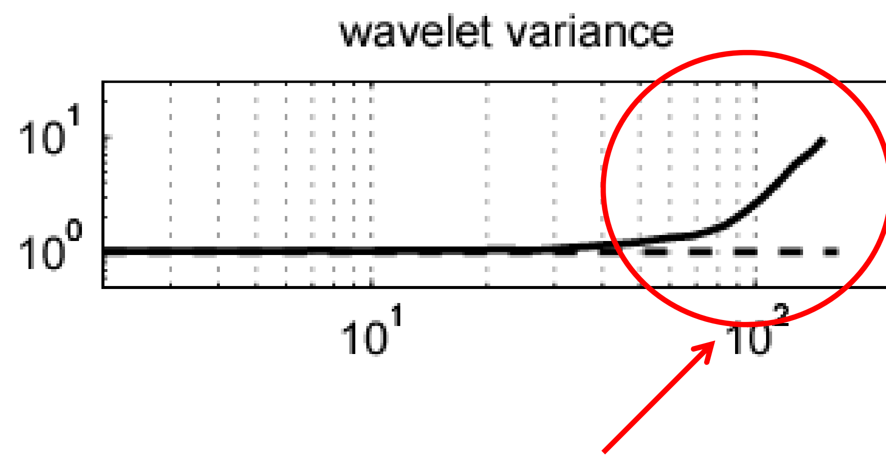
Wavelet variances vs. pair correlation densities

Homogenous vs. inhomogenous habitat

Poisson process (global dispersal)







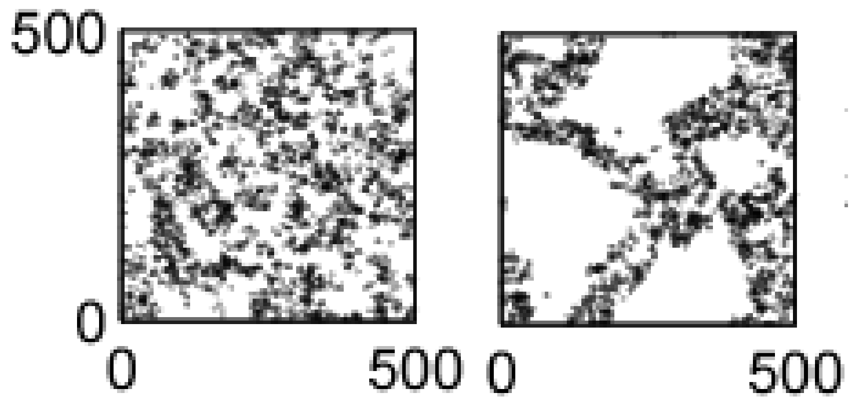
Detto & Muller-Landau, in press, *Am Nat*

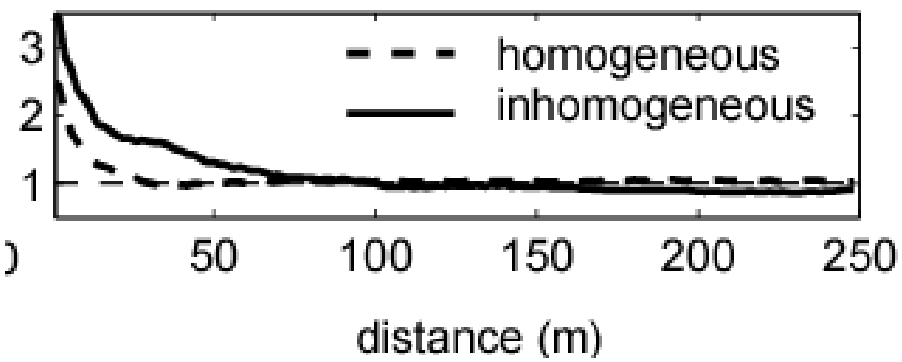
Differences reflecting habitat emerge at the (large) scales of habitat variation

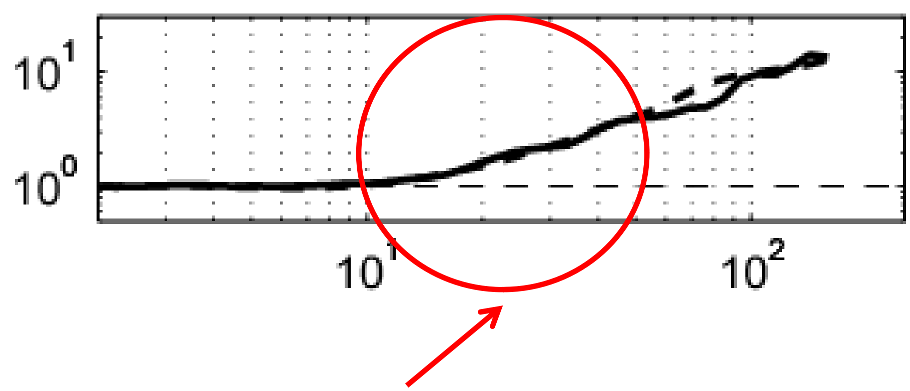
Wavelet variances vs. pair correlation densities

Homogenous vs. inhomogenous habitat

Local dispersal



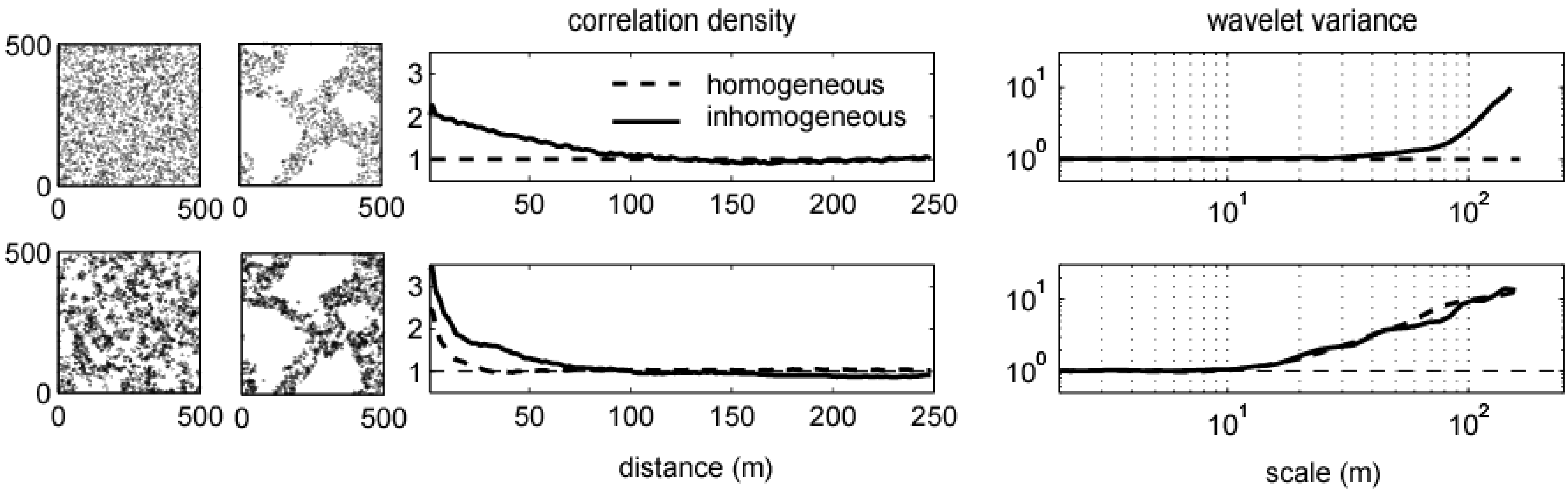




Detto & Muller-Landau, in press, *Am Nat*

Small-scale structure related to dispersal is the same in both cases

Wavelet variances vs. pair correlation densities



Detto & Muller-Landau,
in press, *Am Nat*

Deriving expected wavelet variances from individual-based, spatially explicit models using moment methods

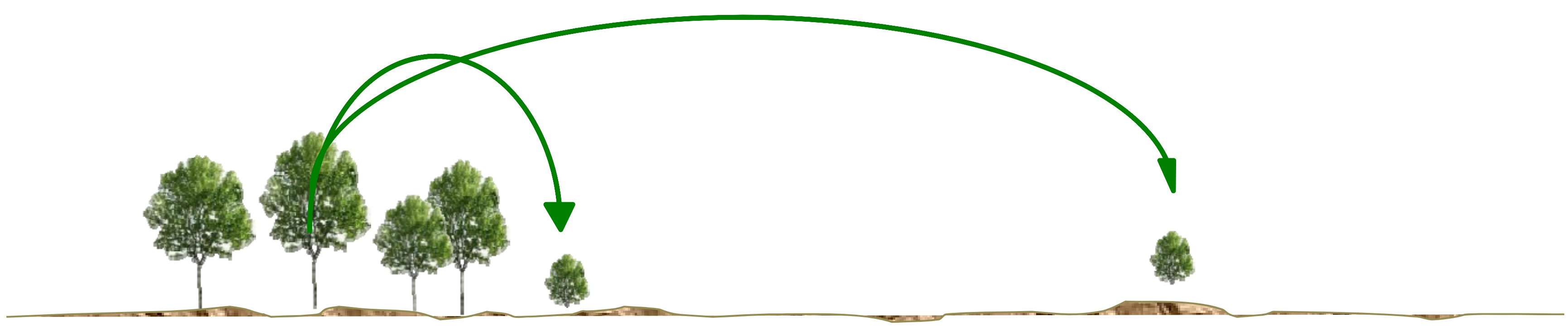
Detto & Muller-Landau,
in press, *Am Nat*

Model 1: An individual-based, model with local dispersal
Model formulation

reproduction — mortality

$$\frac{dN(x,t)}{dt} = \boxed{f\int D(x-x')N(x',t)dx'} - \boxed{mN(x,t)}$$

$N(x,t)$	Population density in space and time
f	Reproductive rate
$D(x)$	Dispersal kernel
m	Density independent mortality rate



Model 1: an individual-based, model with local dispersal

Steady-state solution for the wavelet variance

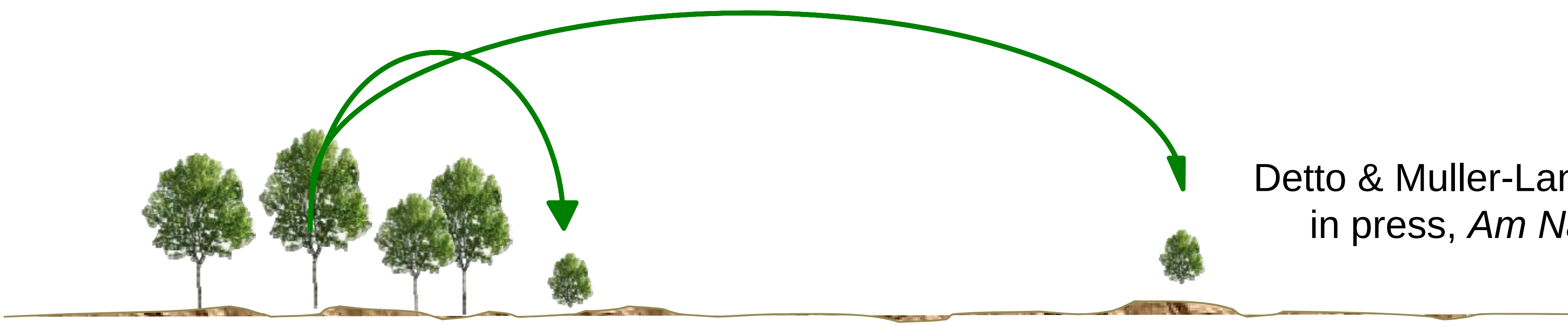
reproduction — mortality

$$\frac{dN(x,t)}{dt} = \boxed{f\int D(x-x')N(x',t)dx'} - \boxed{mN(x,t)}$$

The steady-state solution:

f=m and $\tilde{C}(\omega) = \frac{N\tilde{D}(\omega)}{1-\tilde{D}(\omega)}$ Pair correlation density

$$\nu_{\mathrm{I}}^2(\lambda) = \left(1-\tilde{D}(\lambda,\lambda_D)\right)^{-1}$$ Wavelet variance

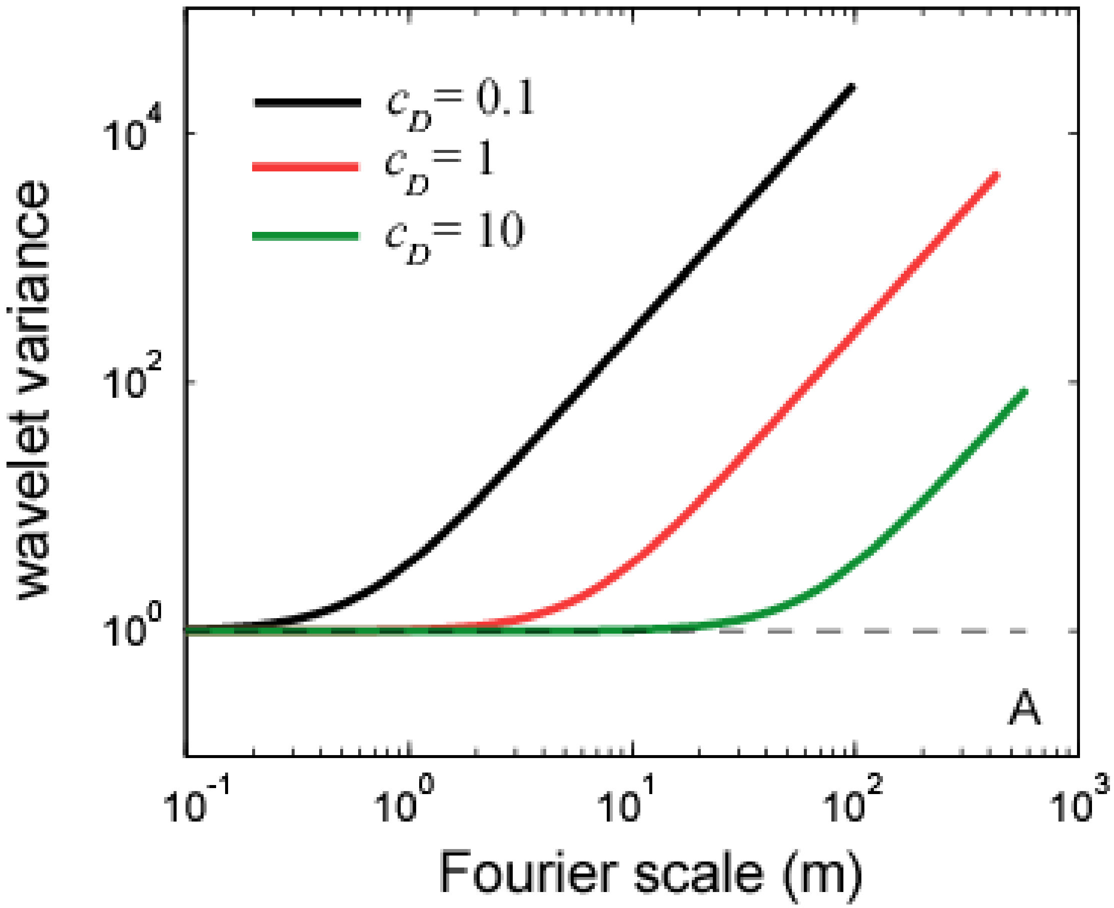


Detto & Muller-Landau, in press, *Am Nat*

Model 1: An individual-based, model with local dispersal

Relationship of dispersal parameter to wavelet variance

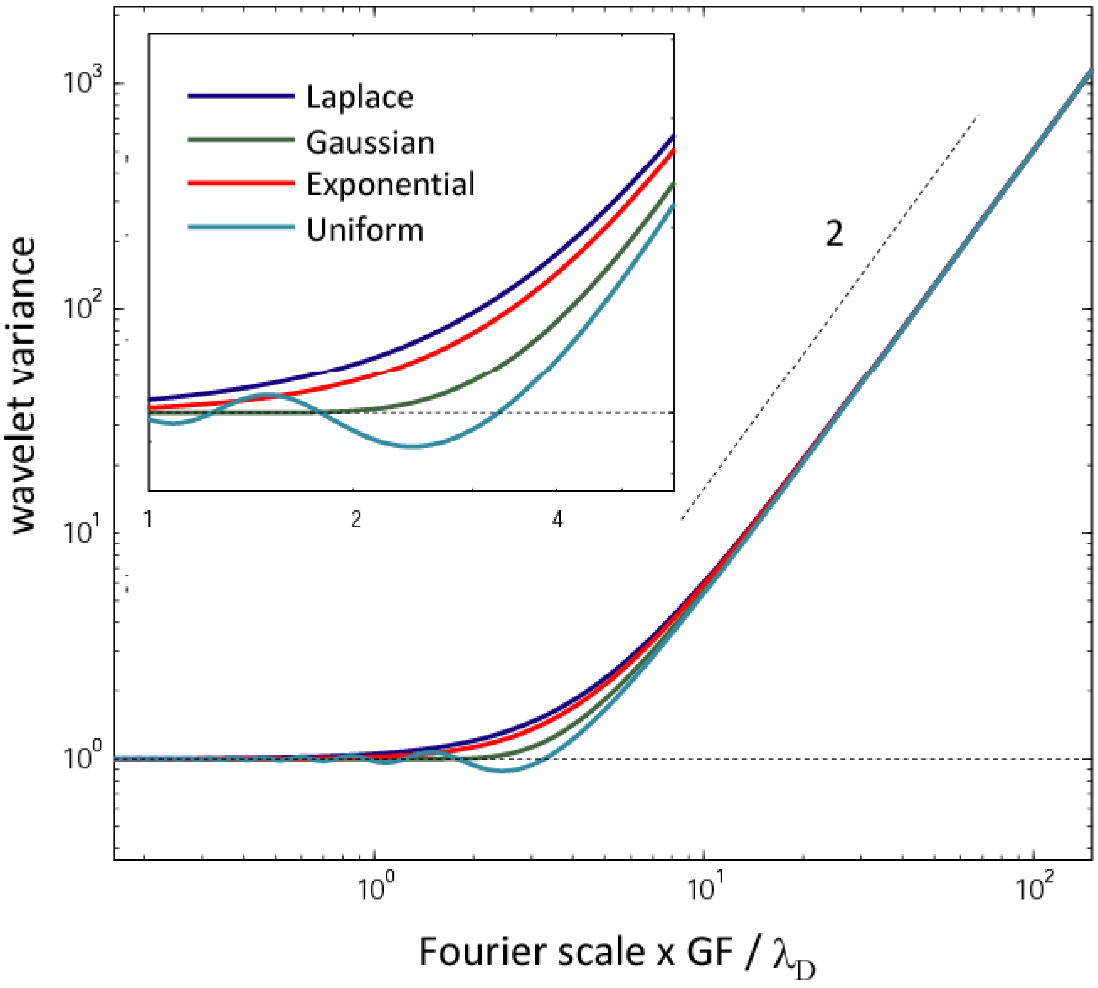
$$\nu^2(\lambda) = \frac{1}{1 - \hat{D}(\lambda, \lambda_D)}$$



Detto & Muller-Landau, in press, *Am Nat*

Model 1: An individual-based, model with local dispersal
Differences among dispersal kernels

$$\nu^2(\lambda) = \frac{1}{1 - \hat{D}(\lambda, \lambda_D)}$$



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Model 2: Local dispersal and conspecific inhibition

Model formulation

reproduction

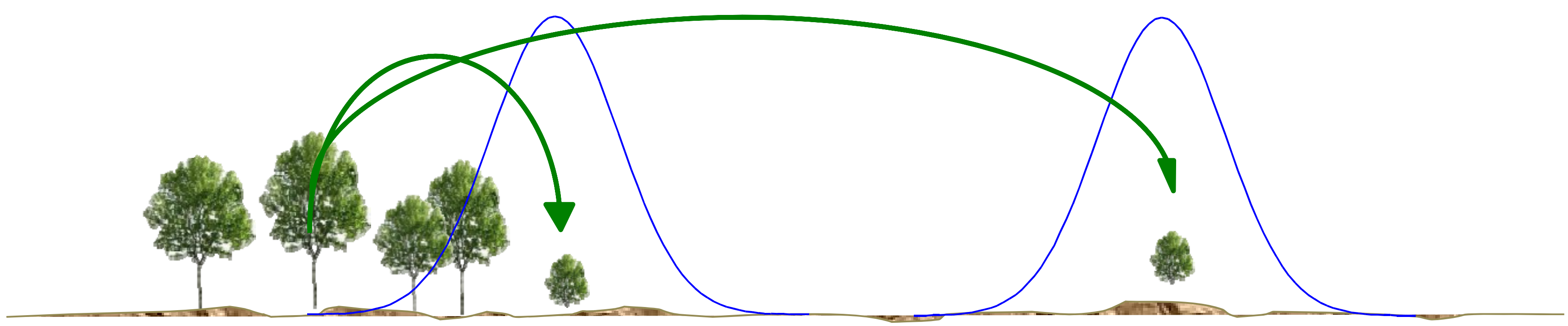
Density-dependent establishment

Density-indepenent mortality

$$\frac{dN(x,t)}{dt} = f\int D(x-x')N(x',t)\left(1-\frac{m'}{f}\int K(x-x'')N(x'',t)dx''\right)dx' - mN(x,t)$$

m' Density-dependent establishment rate

$K(x)$ Establishment kernel



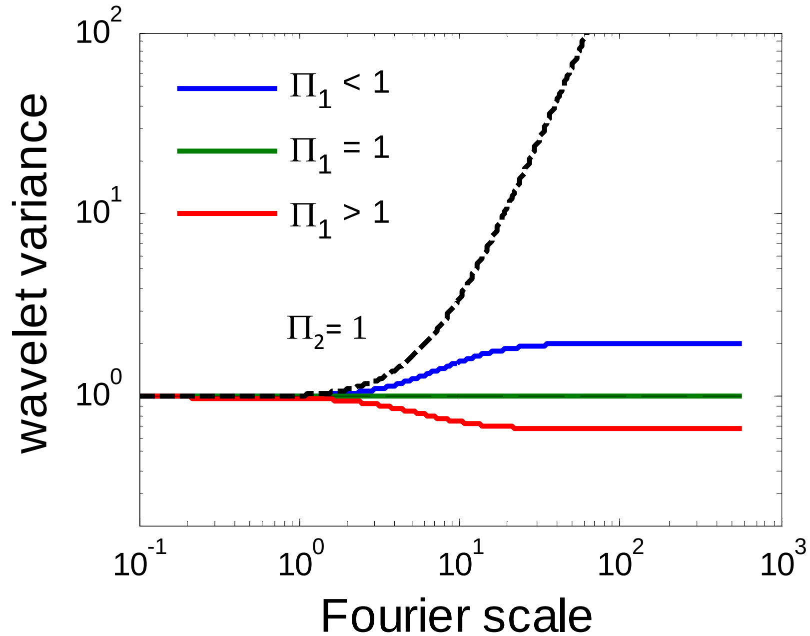
Model 2: Local dispersal and conspecific inhibition: *Steady state wavelet variance*

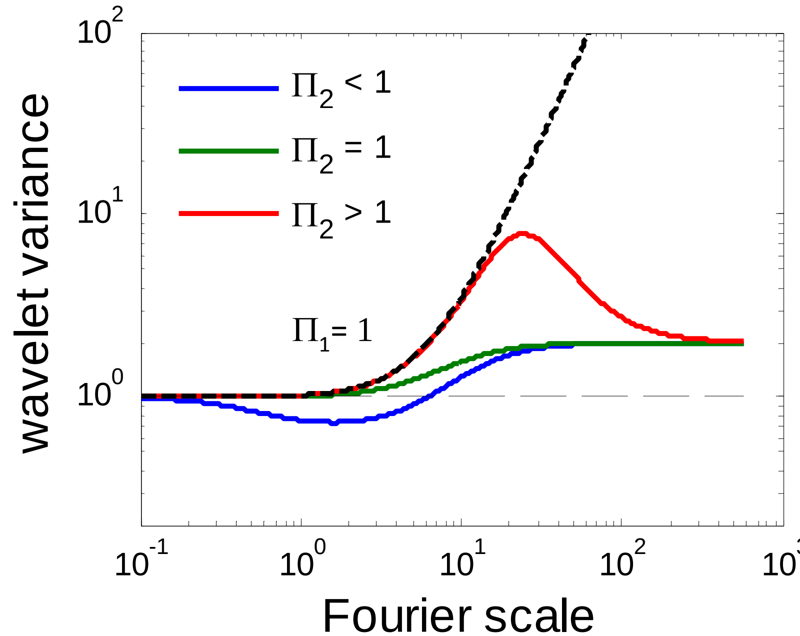
$$n_{\mathrm{II}}^2(\lambda) \approx \frac{1}{1 - \hat{D}(\lambda, \lambda_D) + \Pi_1 \hat{K}(\lambda, \lambda_K)}$$

Approximate solution from closing the third moment.

$\Pi_1 = (f\text{-}m)/m$ density dependent effect

$\Pi_2 = \lambda_D/\lambda_K$ scaling of dispersal to density dependence

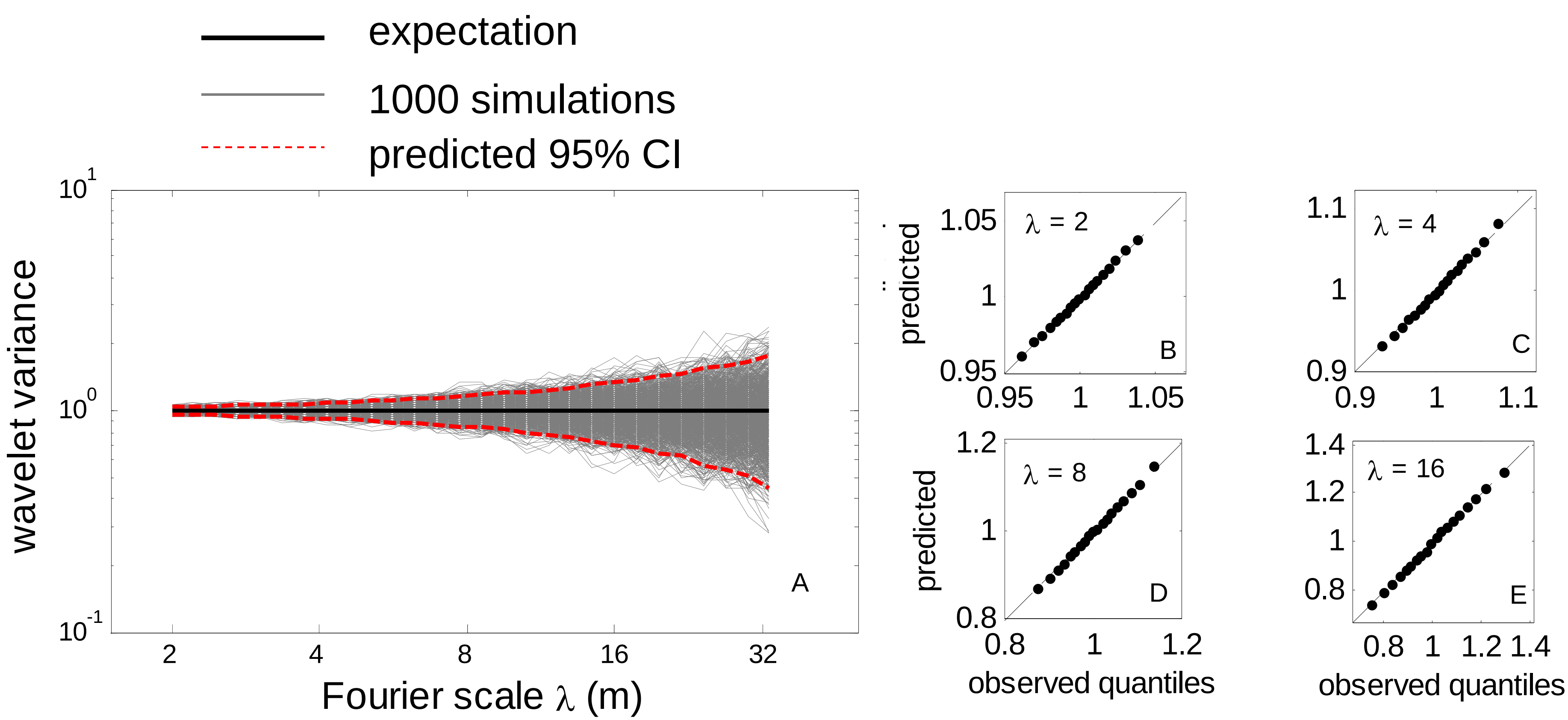




Detto & Muller-Landau, in press, *Am Nat*

Estimating process parameters from spatial patterns using moment methods and wavelets

Statistical properties of the wavelet variances
1. Expectations under complete spatial randomness

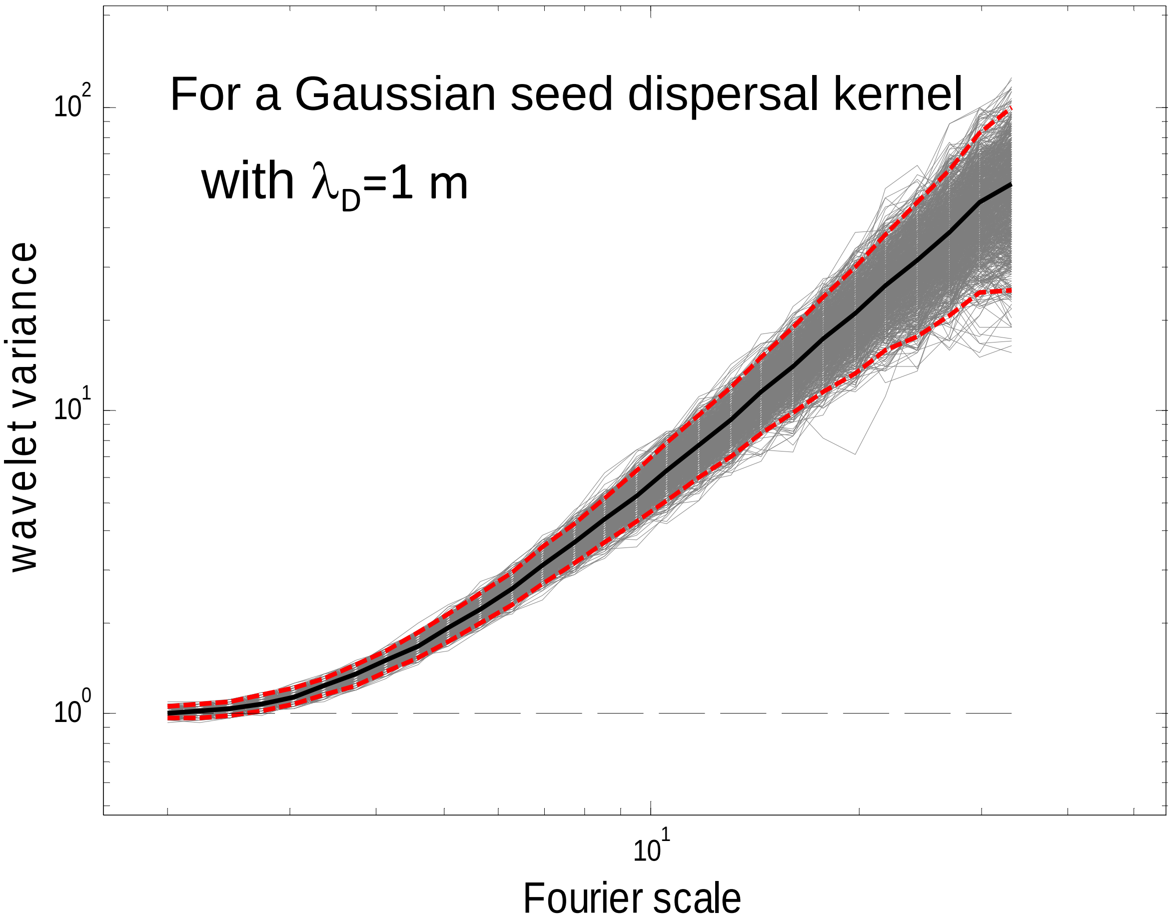


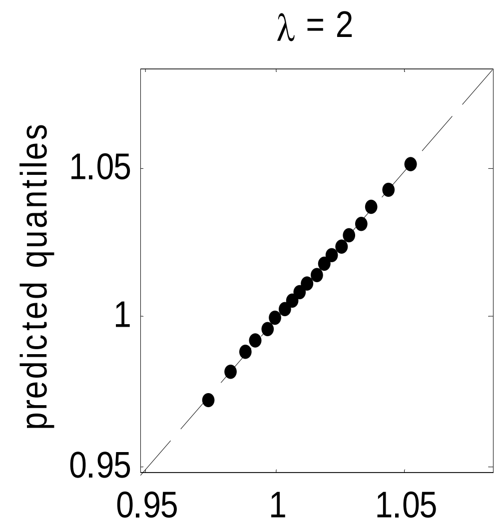
This provides a basis for statistical tests of the null hypothesis of complete spatial randomness.

Detto & Muller-Landau, in press, *Am Nat*

Statistical properties of the wavelet variances

2. Expectations under nonrandom processes

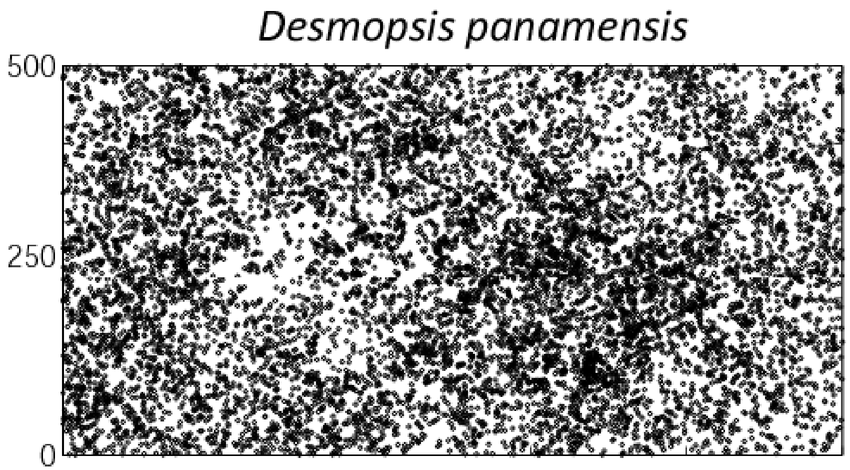




This provides a basis for estimating model parameters using maximum likelihood.

Detto & Muller-Landau, in press, *Am Nat*

Model fitting results – example 1



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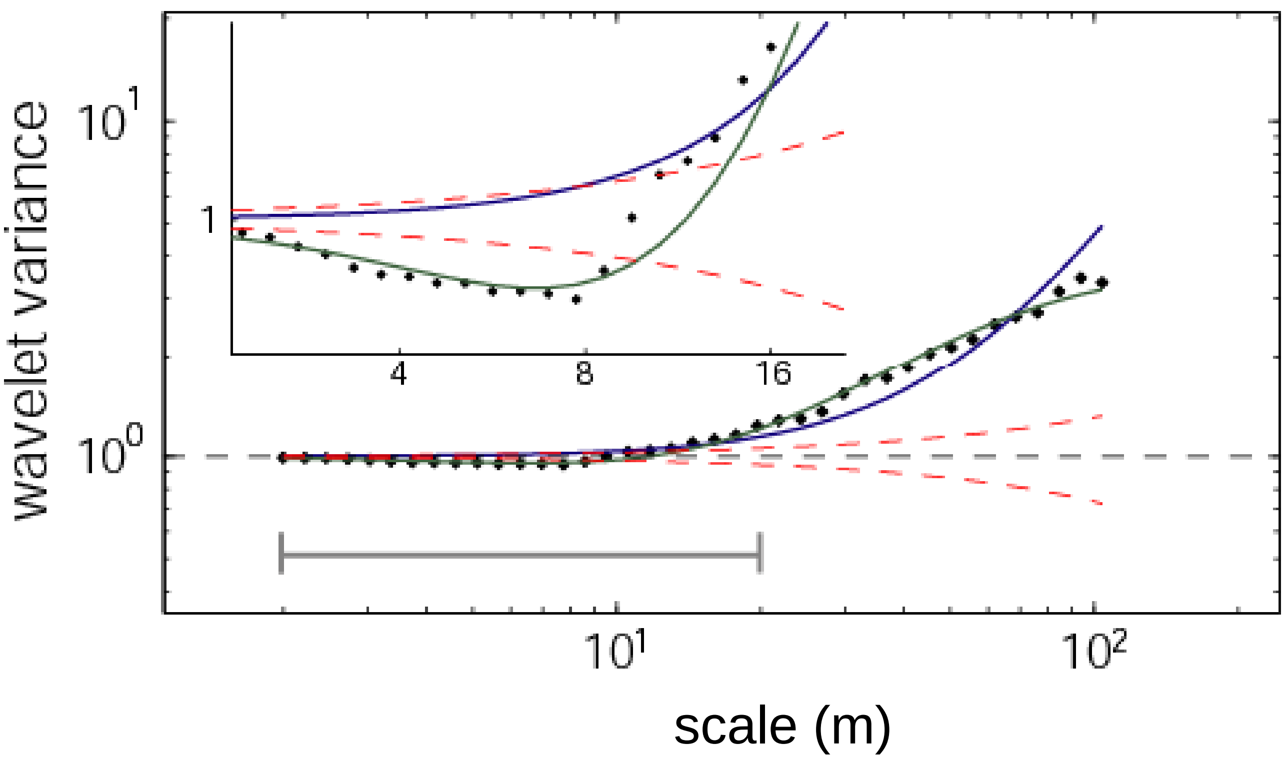


N = 230 (#ha^{-1})

$c_{D(I)} = 8.03\ (0.42)$

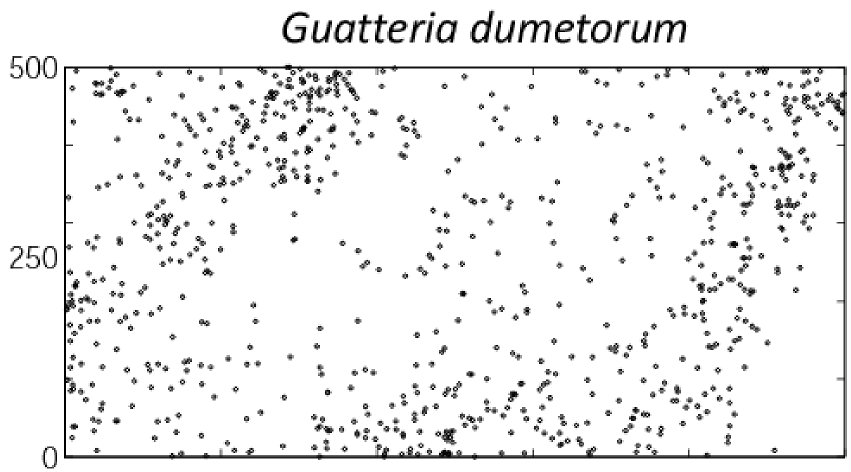
$c_{D(II)} = 3.26\ (1.80)$

$c_{K(II)} = 1.24\ (1.11)$

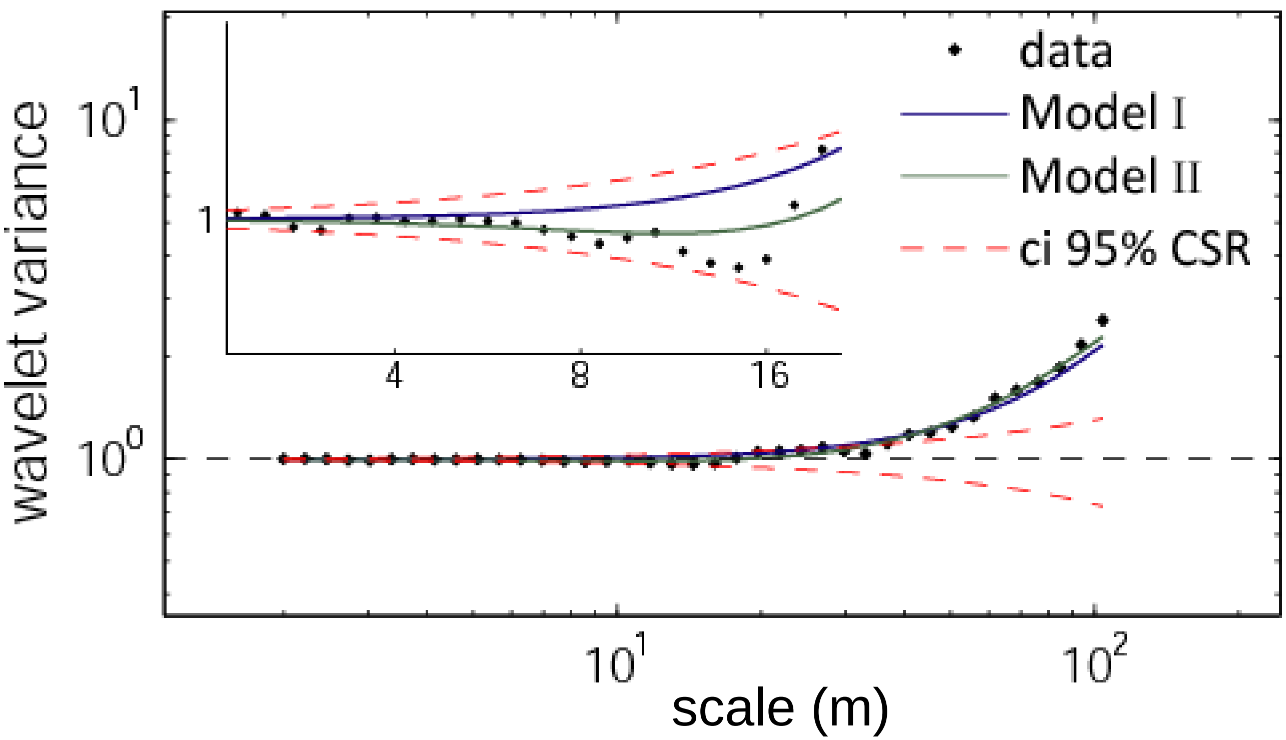
$\Pi_1 = 0.34\ (0.58)$

$\Delta AIC_{II\text{-}I} = -98$

Model fitting results – example 2



Detto & Muller-Landau, in press, *Am Nat*



N = 24 (#ha^{-1})

$c_{D(I)}$ = 15.38 (2.12)

$c_{D(II)}$ = 12.02 (3.4)
$c_{K(II)}$ = 2.44 (1.5)
Π_1 = 0.08 (0.29)

$\Delta AIC_{II\text{-}I}$ = -3

- Advantages of wavelet variances
  - require only static data
  - separate processes operating at different scales
  - analytically tractable, thus can be linked to models

- Ongoing work
  - Characterize interspecific variation
  - Analyze spatiotemporal patterns
  - Models for heterogeneous environments
  - Multi-species models

Detto and Muller-Landau

Talk outline

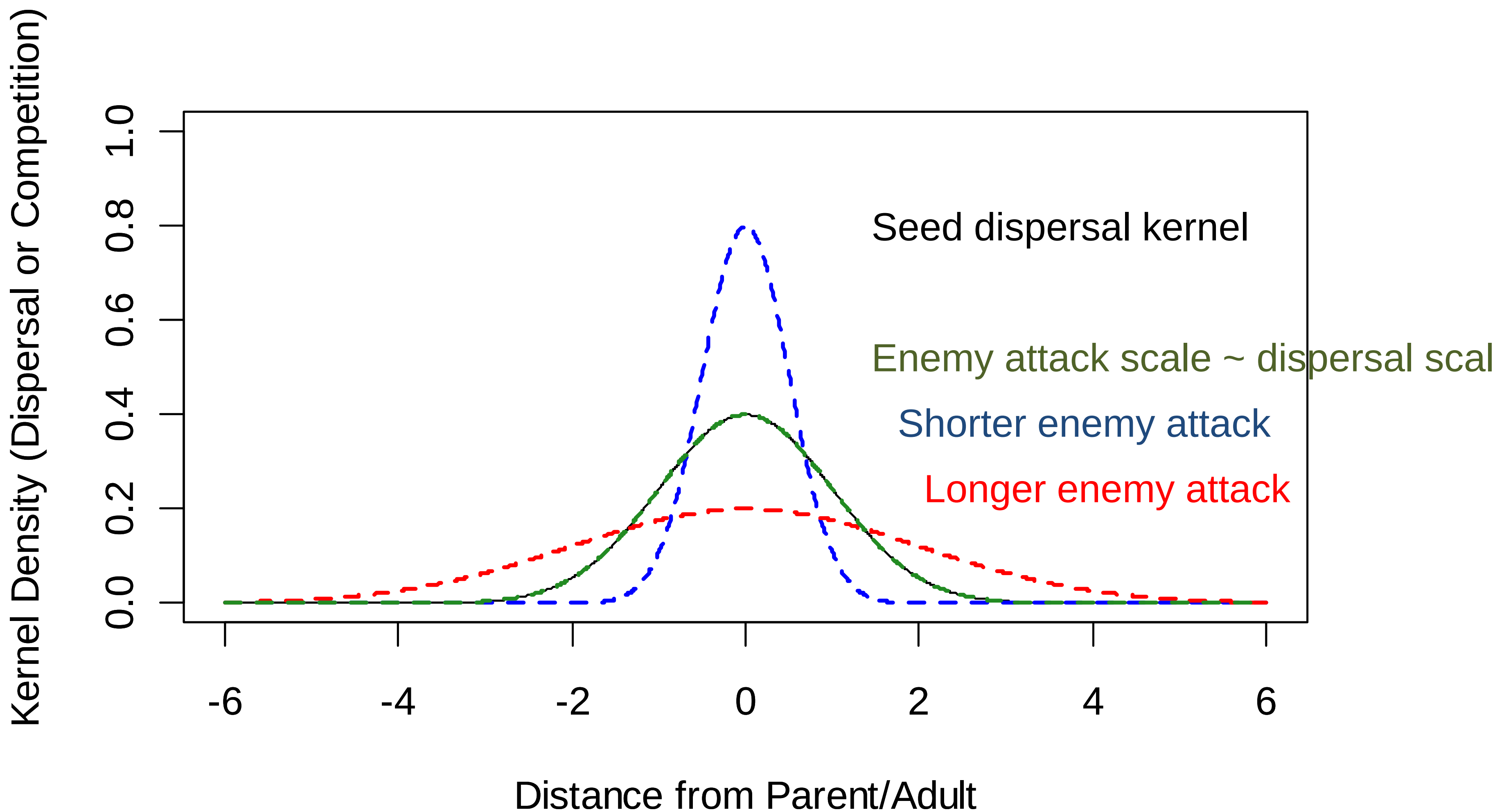
- Wavelet variances introduced
- Estimating seed dispersal and density-dependence parameters from observed patterns
  - Deriving expected wavelet variances from models
  - Estimating model parameters from spatial patterns
- **Investigating how seed dispersal and natural enemy parameters influence population dynamics**

When do specialized natural enemies contribute most strongly to stabilization?

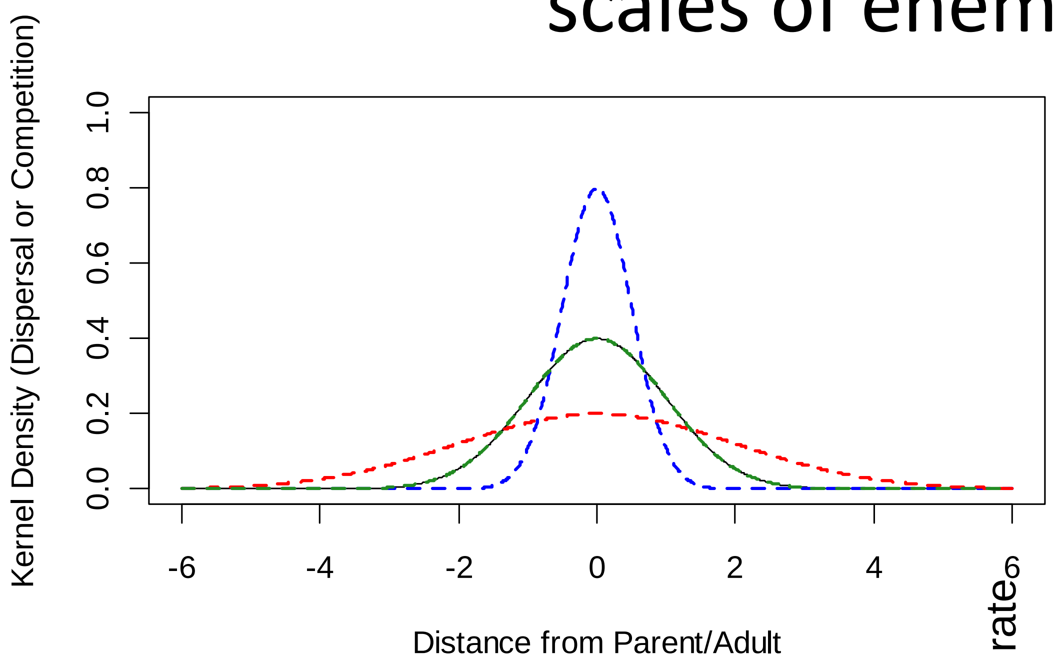
Janzen emphasized local distance- and density-dependence, and subsequent studies have focused on quantifying this, especially the extreme cases of overcompensation and overdispersion.

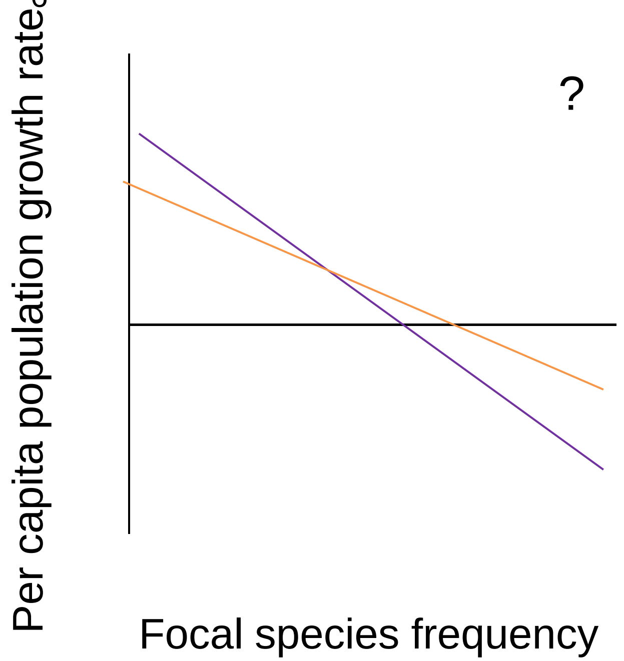
But are natural enemies that attack locally the ones that contribute most strongly to stabilization?

How is the strength of stabilization affected by the spatial scales of seed dispersal and enemy attack?



Will stabilization be stronger at shorter or longer scales of enemy attack?





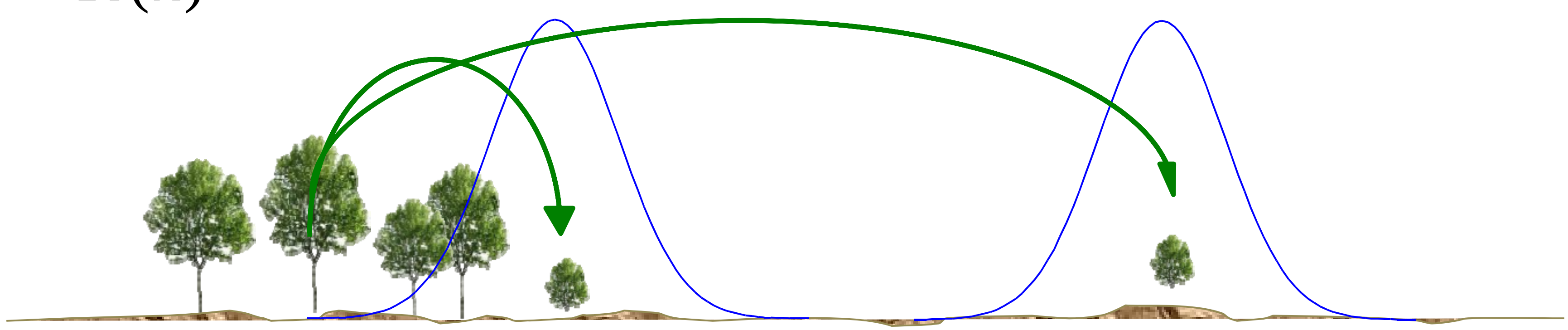
Methods – a spatial logistic model:

individual-based, spatially explicit, continuous

reproduction — density-independent mortality — density-dependent mortality

$$\frac{dN(x,t)}{dt} = \underbrace{f\int D(x-x')N(x',t)\,dx'}_{\text{reproduction}} - \underbrace{mN(x,t)}_{\text{density-independent mortality}} - \underbrace{m'N(x,t)\int K(x-x'')N(x'',t)\,dx''}_{\text{density-dependent mortality}}$$

$N(x,t)$	Population density in space and time
f	Reproductive rate
$D(x)$	Dispersal kernel
m	Density independent mortality rate
m'	Density-dependent mortality rate
$K(x)$	Conspecific “competition” kernel representing enemy attack



Moment methods for the spatial logistic model

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Results: Effects on the spatial structure

[Unpublished results omitted from posted pdf]

Results: Effects on strength of stabilization

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Results: Effects on invasion growth rate

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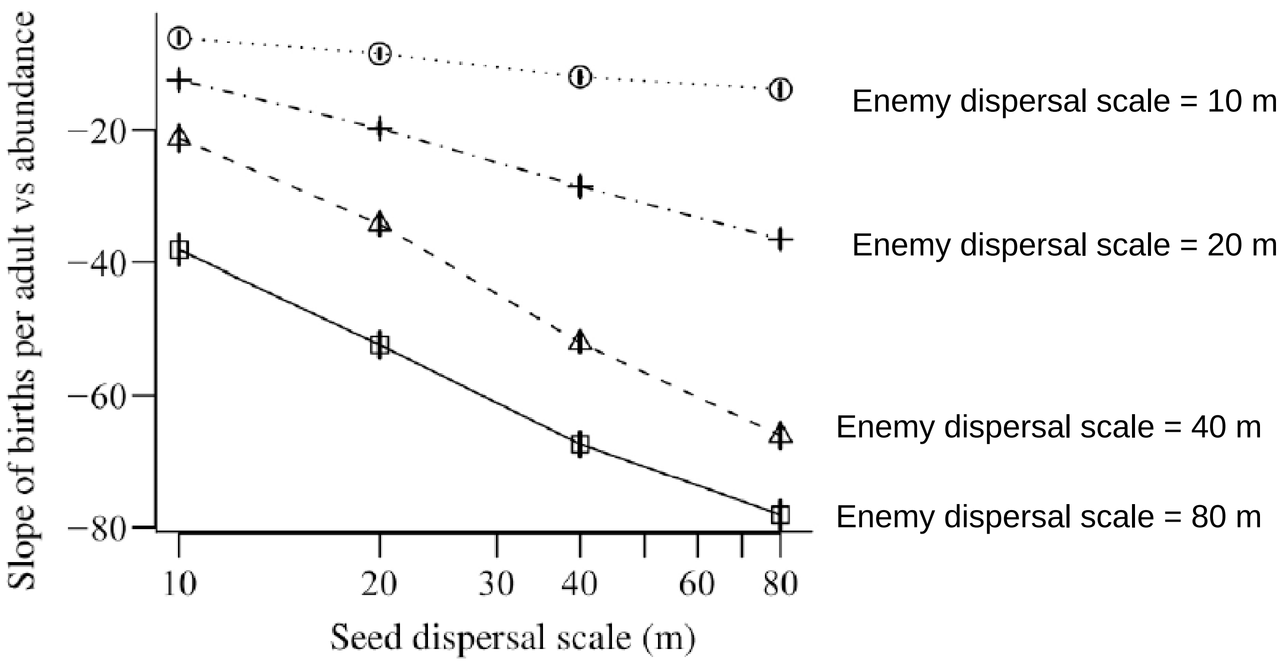
These results are consistent with previous simulation results for spatially explicit community models

In a discrete space simulation model



Muller-Landau & Adler 2007

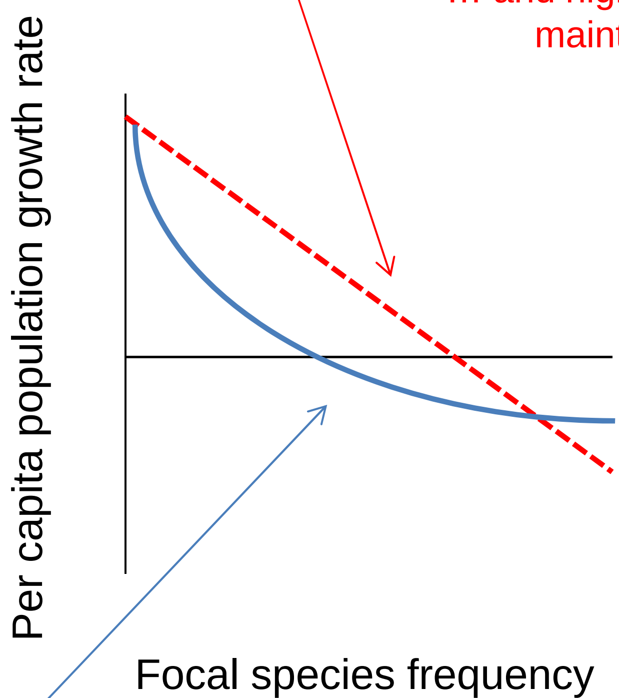
Adler & Muller-Landau 2005 *Ecology Letters* found parallel results for species diversity in a continuous space simulation model.

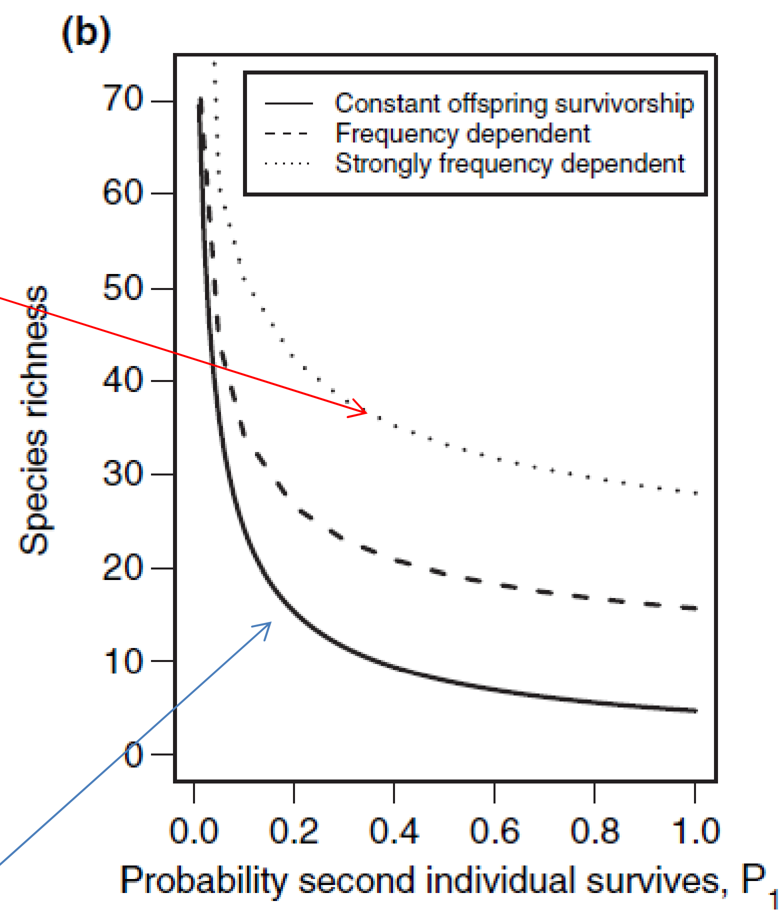
What explains these results?

The shape of the curve relating per capita success to focal species abundance.

Long-distance attack results in a steady decline, providing stronger stabilization...

… and higher diversity maintained.





Local dispersal and attack results in an initial fast decline and then a slow decline, providing less protection from extinction...

… and lower diversity maintained.

Adler & Muller-Landau 2005 *Ecology Letters*

Summary

Matteo Detto

- Wavelet variances provide a key tool for investigating spatial patterns, one that separates influences operating at different spatial scales and is analytically tractable.

- Moment methods can provide analytical solutions or approximations of wavelet variances expected under different spatially-explicit, individual-based ecological process models.
- We provide a statistical framework for testing the null hypothesis of complete spatial randomness and for fitting ecological process models from spatial patterns using wavelet variances.

Detto & Muller-Landau, in press, *Am Nat*

- Specialized natural enemies that attack over long distances from adult plants (relative to seed dispersal distances) contribute *more strongly* to stabilizing plant populations and promoting species coexistence than do those that disperse over short distances.
- Ongoing/future work examines spatiotemporal patterns, habitat heterogeneity, and interspecific interactions.