Estimating environmental heterogeneity from spatial dynamics data

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IISC

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Outline

1. Introduction
2. Endogenous vs exogenous: qualitative
   - Explanations for spatial patterns
3. Endogenous vs exogenous: quantitative
   - Spatial synchrony
   - Pines
4. Conclusions

What do ecologists want?

- *Explicit* questions: explain observed patterns
- *Implicit* questions: explain outcomes of ecological interactions: persistence, coexistence, trait evolution, etc..

- *Qualitative* answers: presence/absence, persistence/extinction, coexistence/exclusion
- *Quantitative* answers: how many? how quickly? scale(s) of pattern?

- *Deductive* (forward) models: model $\rightarrow$ outcome
- *Inductive* (inverse) models: data $\rightarrow$ model

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Typical examples

- Can spatial pattern allow coexistence of similar species?
- Is a particular example of coexistence spatially mediated?

- Do endogenous or exogenous drivers produce spatial clustering?
- What drives spatial clustering in a particular case?

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Typical models

- Stochastic spatial point processes: continuous time & space, point individuals
- Usually assume isotropy and translational invariance
- Population structure and environmental heterogeneity both described by *correlation functions*

e.g. *spatial logistic*:

- constant *per capita* fecundity f
- dispersal kernel $D(r)$
- death rate increases with local density: $\mu = \mu_0 + \alpha \int U(x-y)N(y)\,dy$

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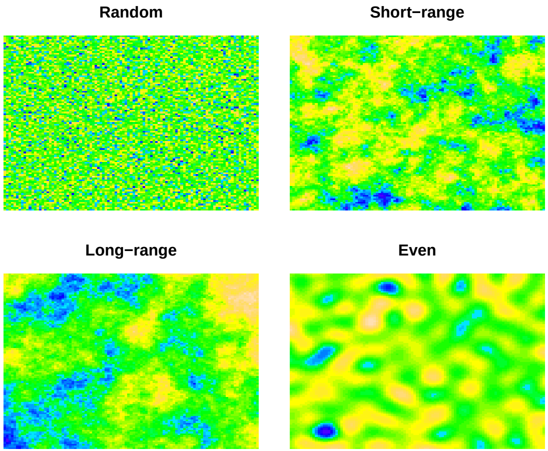
Spatial correlation



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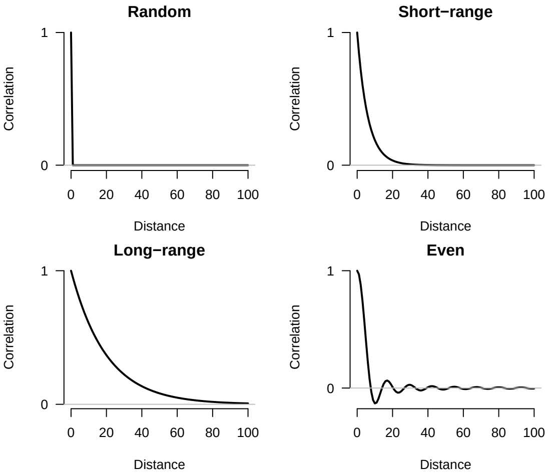
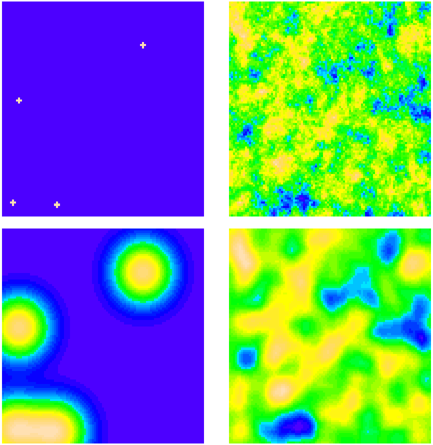


Spatial convolution

- distance-dependent spatial interactions
  (dispersal, competition, pollen flow . . .)
- blurs out landscape according to scale of kernel
- relatively straightforward math
- easily described by *power spectra*:
  transformation of spatial correlation information



Outline

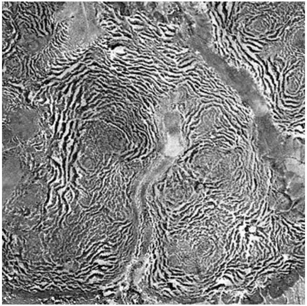
Templates

- assume habitat map reflects underlying spatial pattern more or less exactly: low diffusion (but > 0), high growth rate

photo: Henry Horn

Nonlinear (deterministic) pattern formation

- *Turing instabilities*: unstable spatial modes of nonlinear systems
- in ecology: tiger bush, spruce waves, predator-prey spirals (Rohani et al., 1997)
- requires *no* noise, just initial perturbation



tiger bush (Wikipedia)

Demographic noise-driven pattern

- Demographic stochasticity appears in correlation equations
- Drives pattern in homogeneous, stable systems (e.g. competition)
- Effects could be weak:
  - depend on scale of interaction neighborhood (Bolker, 1999): small if effective # neighbors > 10-20?
  - effects depend on $R = f/\mu$:
    for equal scale of dispersal & competition,
    no clumping if $R > 2$ (Bolker & Pacala, 1999)
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General (environmental) noise-driven pattern

Most general case: space(-time) noise $\xi(x, t, N(t))$

- Scale may be > 0 (non-white in space and time)
- Amplitude may scale differently from $\sqrt{N}$
- Space-time correlations:
    - separable (Snyder & Chesson, 2004) ?
    - model correlations as their own sub-processes North et al. (2011)

Descriptions other than correlation functions? (Endler, 1986)

Summary: what do we need?

- Lots of interesting questions, but perhaps existing methods are good enough for ecologists?
- Importance of stochastic dynamics at various scales:
  - Is demographic (endogenous) noise really that important?
  - Perhaps a more traditional separation of scales (individual, patch, site, ...) is enough?
- **How do we estimate the (effects of) heterogeneity?**

Outline

Spatial synchrony

- Eastern spruce budworm, *Choristeroneura fumiferna*
- non-spatial dynamics: plant quality, climate, enemies (Kendall et al., 1999)?
- What generates large-scale spatial synchrony?
  - *Moran effect*: large-scale weather patterns
  - *Dispersal coupling*: movement of larvae

Correlation equations: *via* continuous eqns

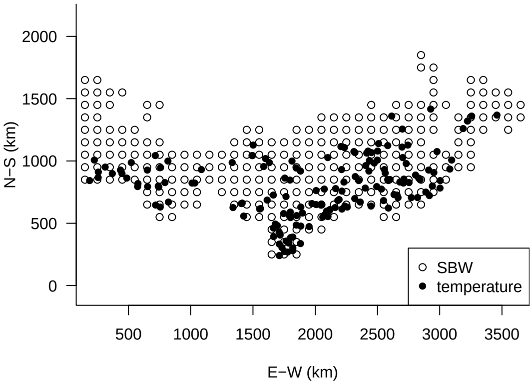
cf. Lande et al. (1999), Engen et al. 2002:

$$\frac{\partial N(\mathbf{x},t)}{\partial t} = \underbrace{F(N(\mathbf{x},t),E(\mathbf{x},t))}_{\text{pop. growth}} - \underbrace{mN(\mathbf{x})}_{\text{emigration}} + \underbrace{m\int D(\mathbf{y},\mathbf{x})N(\mathbf{y})\,d\mathbf{y}}_{\text{immigration}}$$

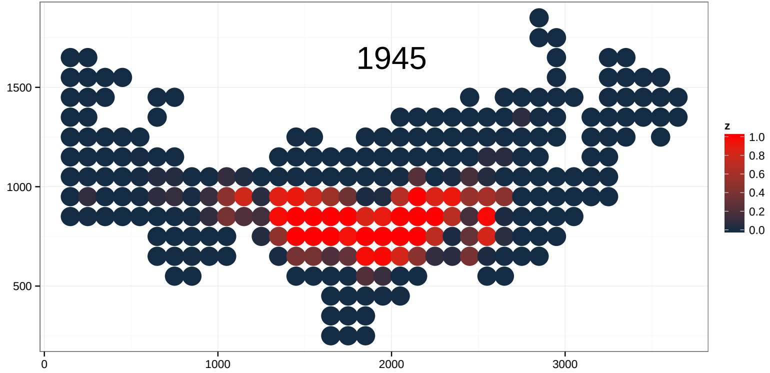
$$\frac{\partial n}{\partial t} \approx \underbrace{-rn(\mathbf{x},t)}_{\text{regulation}} + \underbrace{m(D*n-n)}_{\text{redistribution}} + \underbrace{\sigma_E^2 e(\mathbf{x},t)}_{\text{noise}}$$

$$2(r+m)c^* = m(D*c^*) + \sigma_E^2 \mathrm{Cor}(e)$$

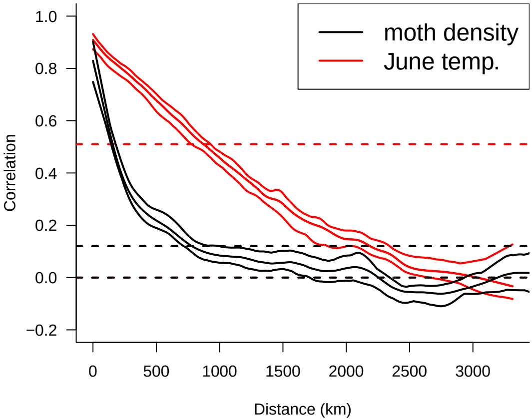
Moth sampling locations



Moth dynamics



Spatial correlations of moth data



Spatial logistic: solution

At equilibrium, the power spectrum of the population densities obeys

$$\tilde{S} = \left|\left(\tilde{N}^*\right)\right|^2 = \frac{\sigma_E^2 \tilde{e}}{2(r + m(1 - \tilde{D}))}$$

where ˜ denotes the Fourier transform. Therefore:

$$\sigma_P^2(p) = \sigma_E^2 + \frac{m}{r}\sigma_D^2$$

(Lande et al. 1999) where σ_X represents the standard deviation of the autocorrelation function

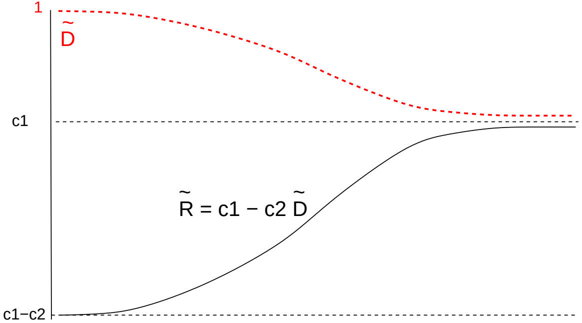
Spectral ratios

To factor out dispersal, calculate the *spectral ratio*:

$$\tilde{R} = \frac{\tilde{e}}{\tilde{S}} = \frac{2}{\sigma_E^2}(r + m(1 - \tilde{D})) = c_1 - c_2 \tilde{D}$$

Deconvolve the effects of environmental variability from the population pattern ...

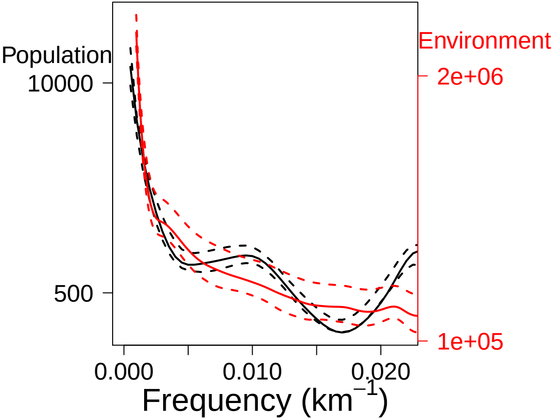
Reconstructing the dispersal curve



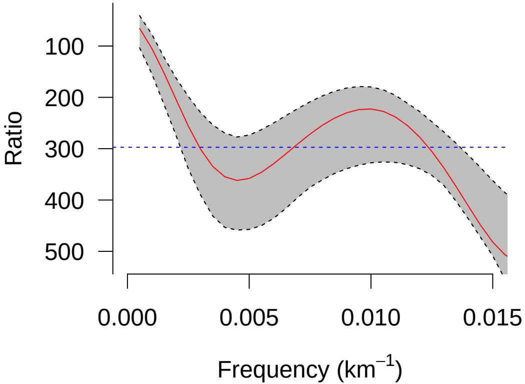
We know the limits $\tilde{D}(0) = 1$, $\tilde{D}(\infty) \to 1$: thus

$$\tilde{D}_{\text{est}}(\omega) = \frac{\tilde{R}(\infty) - \tilde{R}(\omega)}{\tilde{R}(\infty) - \tilde{R}(0)}$$

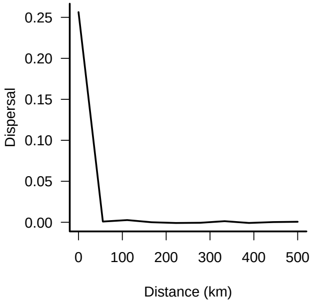
Moth data: spectra



Moth data: spectral ratios



(Putative) moth dispersal curve



- Reconstructed moth dispersal kernel $\approx 50\text{km}$
- Consistent with natural history

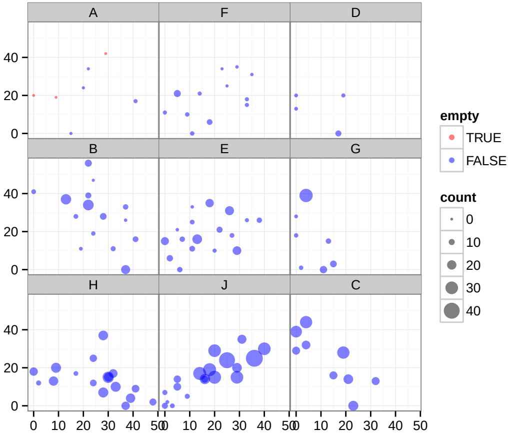
Outline

Pines

- Slash pine, *Pinus elliottii*
- Data on seed distribution, seedling distribution, but not collected on the same quadrats
- Sampling scheme highly irregular; sparse data

Wikipedia

Seed data


A
F
D
B
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empty
TRUE
FALSE
count
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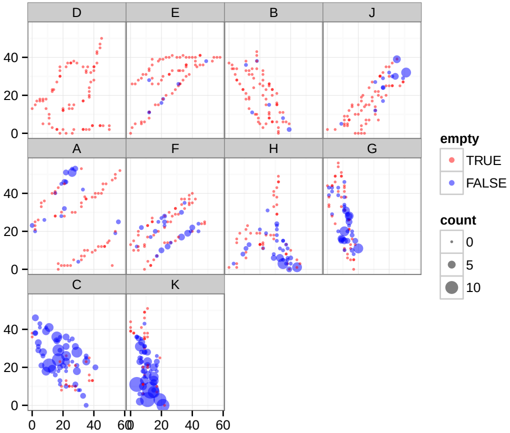
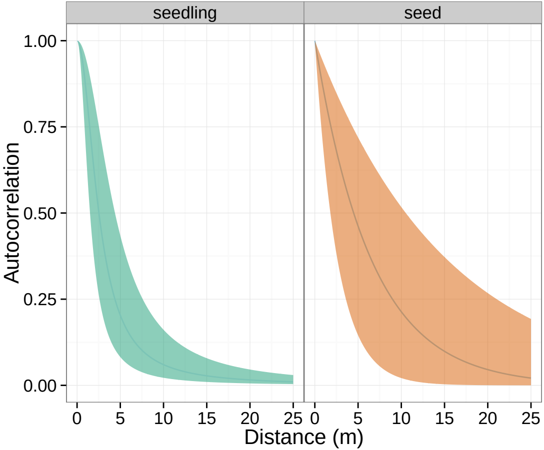
10
20
30
40

Sapling data



Correlation functions



Analytical framework (2)

- assume *cross-covariance* $C_{EN} = 0$
  no correlation between seeds and environment,
  e.g. long-distance dispersal
- $$C_{SS}(r) = \bar{N}^2 C_{EE}(r) + \bar{E}^2 C_{NN}(r)$$
  (where $\bar{N}$=mean seed density, , $\bar{E}$=mean establishment probability)
- or (switch to correlation c)
  $$C_{SS} \propto \frac{\sigma^2 E}{\bar{E}^2} c_{EE} + \frac{\sigma_N^2}{\bar{N}^2} c_{NN}$$
- ...a weighted mixture of the two correlation functions

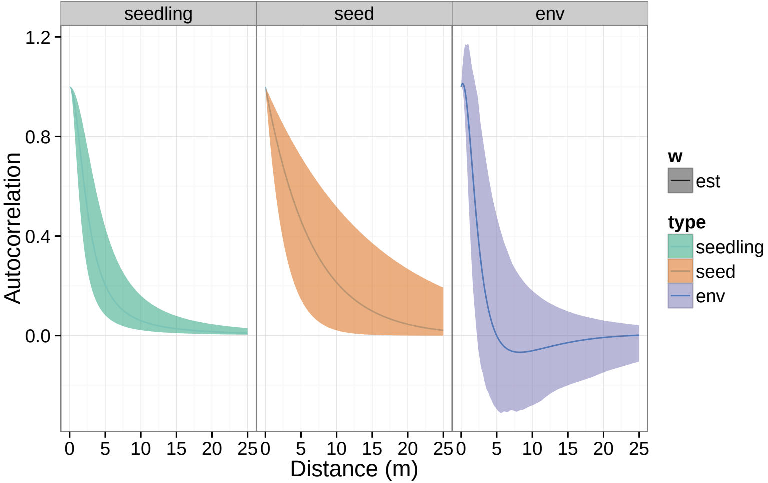
Solving for c_{EE}

Therefore,

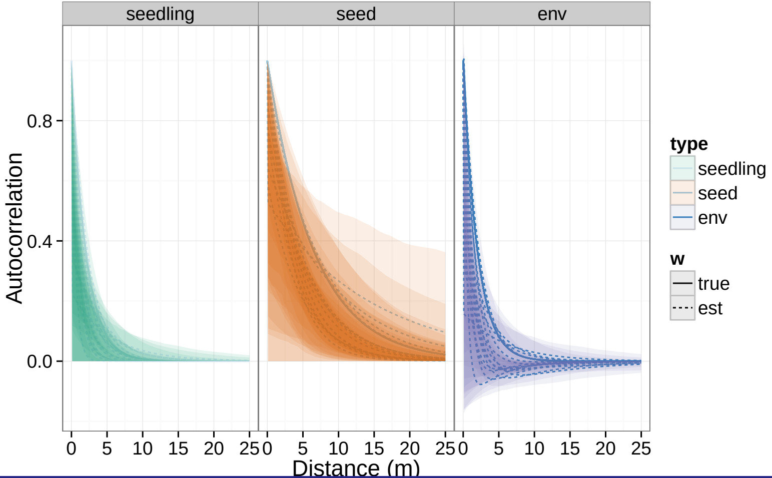
$$c_{EE} \propto \sigma_S^2 c_{SS} - \bar{E}^2 \sigma_N^2 c_{NN}$$

Can we really use this?

Results: observed/inferred correlation equations



Simulation results



Caveats/assumptions

- Assumes linearization/moment truncation
- Assumes isotropy/homogeneity
- Estimating spectra of small, irregular, noisy data sets is difficult (!)
- Advantages vs. direct estimation (e.g. via MCMC) ?

Goals

- Simple, light-weight (!!), non-parametric (??) approach to spatial estimation
- leverage "unreasonable effectiveness" of linearization (Gurney & Nisbet, 1998)
- Use all available information:
  - snapshots, before/after, time/series
  - non-matching spatial samples

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