The dynamics of spatially-extended populations

Statistics and theory for spatial correlation functions

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Spatial autocorrelation (e.g. Fortin & Legendre 1989, Legendre 1993)
(= spatial 'self-similarity')

Variable N measured at locations i, j:

Spatial autocorrelation: $\rho_{ij} = (N_i - \overline{N})(N_j - \overline{N}) / \sigma_N^2$

'Classical' statistical inference → *not correct*

Theoretical ecology: → *critical quantity* ✔

Ecological processes leave detailed signatures in the spatial autocorrelation and cross-correlation functions

Part 1) Theory & Moment equations

Simplest case - single species & dispersal (Spatial ‘BIDE’)

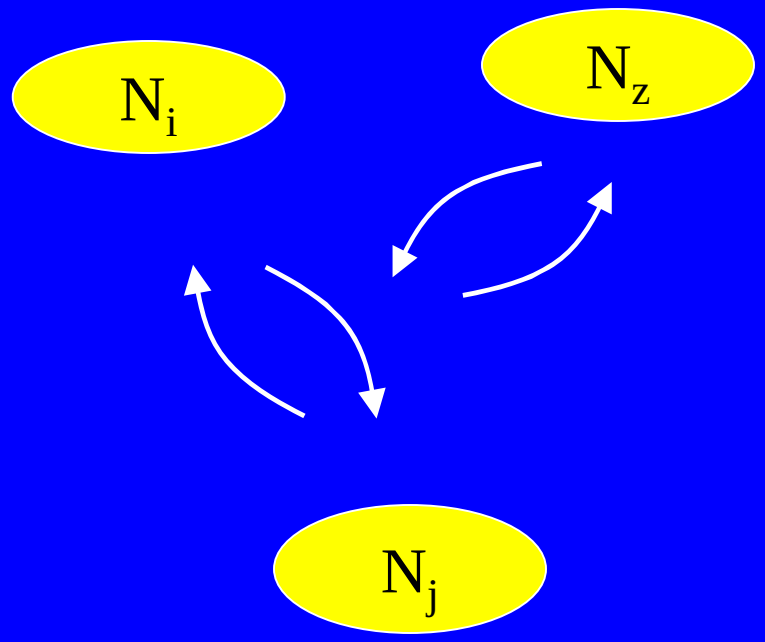
Changes in autocorrelation in locations {i, j}

Depends on:
- Birth
- Death

- migration between i and j

- emigration from i *not to j*
  from j *not* to i

- immigration from *not*-j to i
  from *not*-i to j



Moment equations for dynamics and dispersal:

$$\frac{dN_i}{dt} = \underbrace{N_i R(N_i)}_{\text{Local pop dyn}} - \underbrace{pN_i + p\int K(d_{iz})N_z dz}_{\text{Movement}} + \underbrace{\sigma_R \frac{dB_i}{dt}}_{\text{Noise}}$$

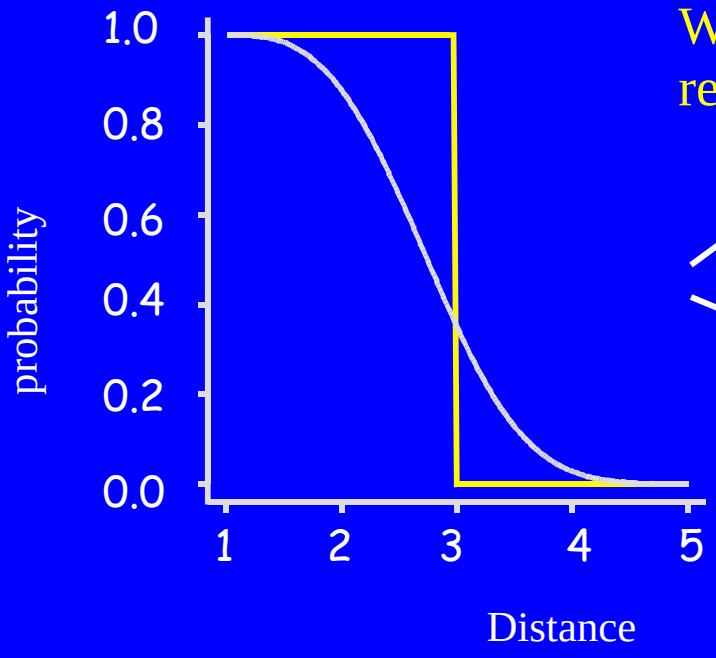
$$\frac{dC(d)}{dt} = 2R(\overline{N}) + 2\overline{N}R'(\overline{N})C(d) - pC(d) + p(K * C)(d) + \sigma_R^2 \delta(d)$$

$C(d)$	Covariance at distance d	$K(d)$	Dispersal kernel
N_i	Number at i	σ_R	Magnitude of environmental stochasticity
$R(N)$	Density-dependent growth	$\delta(d)$	Environmental correlation function
p	Dispersal probability	$K * C$	Convolution of K(d) and C(d)

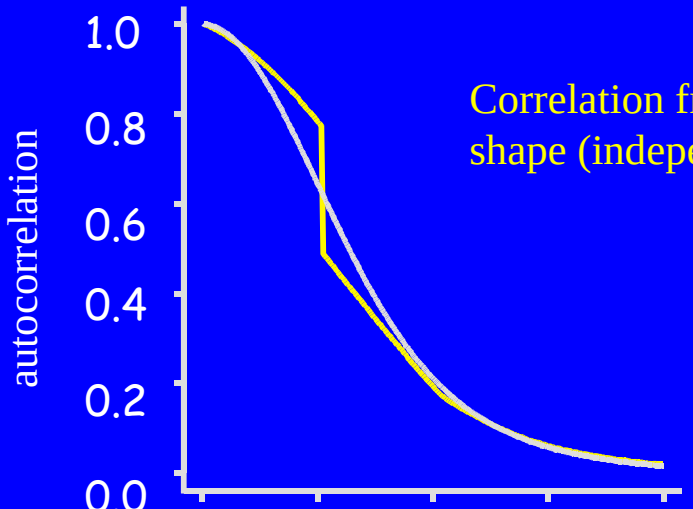
$\frac{dB_i}{dt}$ Derivative of Brownian motion (cf stochastic ODE's)

Bjornstad and Bolker (2000) Proc R Soc Lond B. 267: 1787-1794

Dispersal induced autocorrelation:

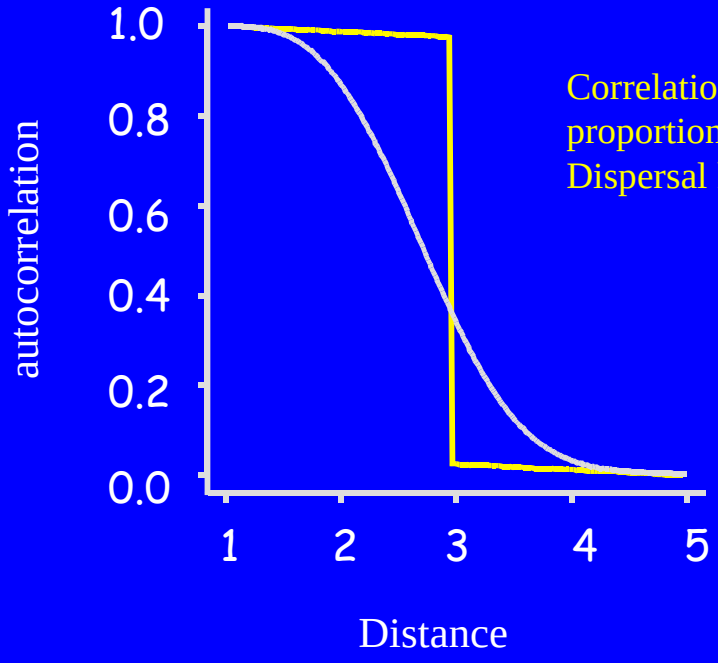


Weak regulation



Correlation fn takes invariant shape (independent of kernel)

Strong regulation



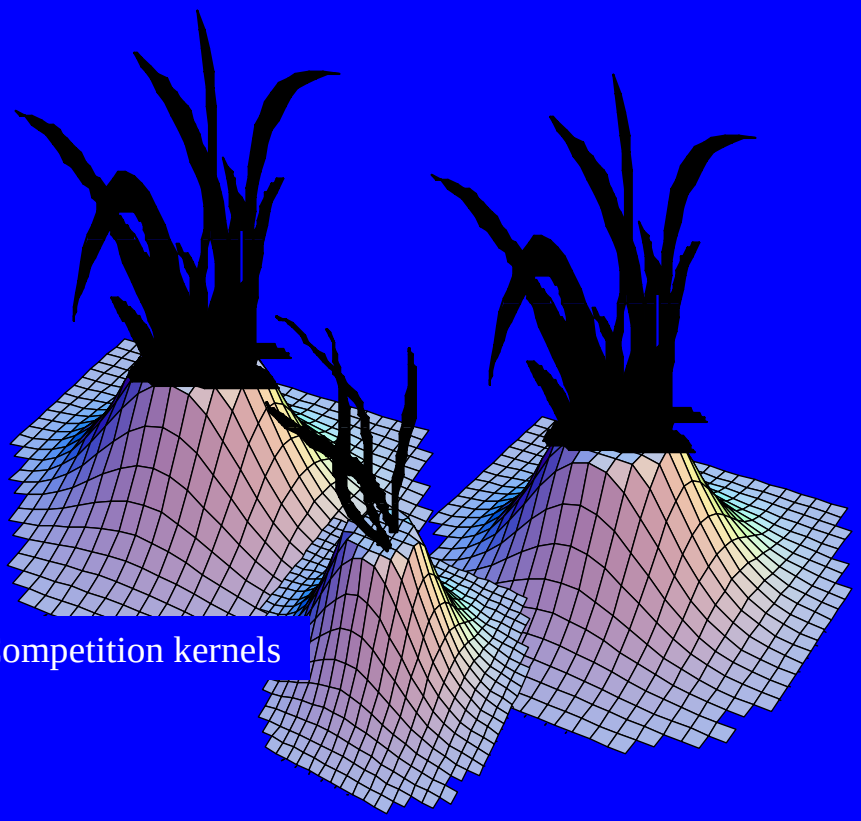
Correlation fn proportional to Dispersal kernel

Gaussian

Tophat

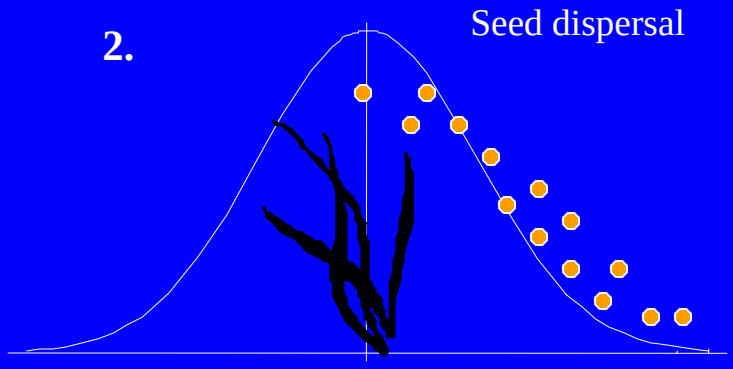
What about interspecific processes: (1) spatial competition

1.



Competition kernels

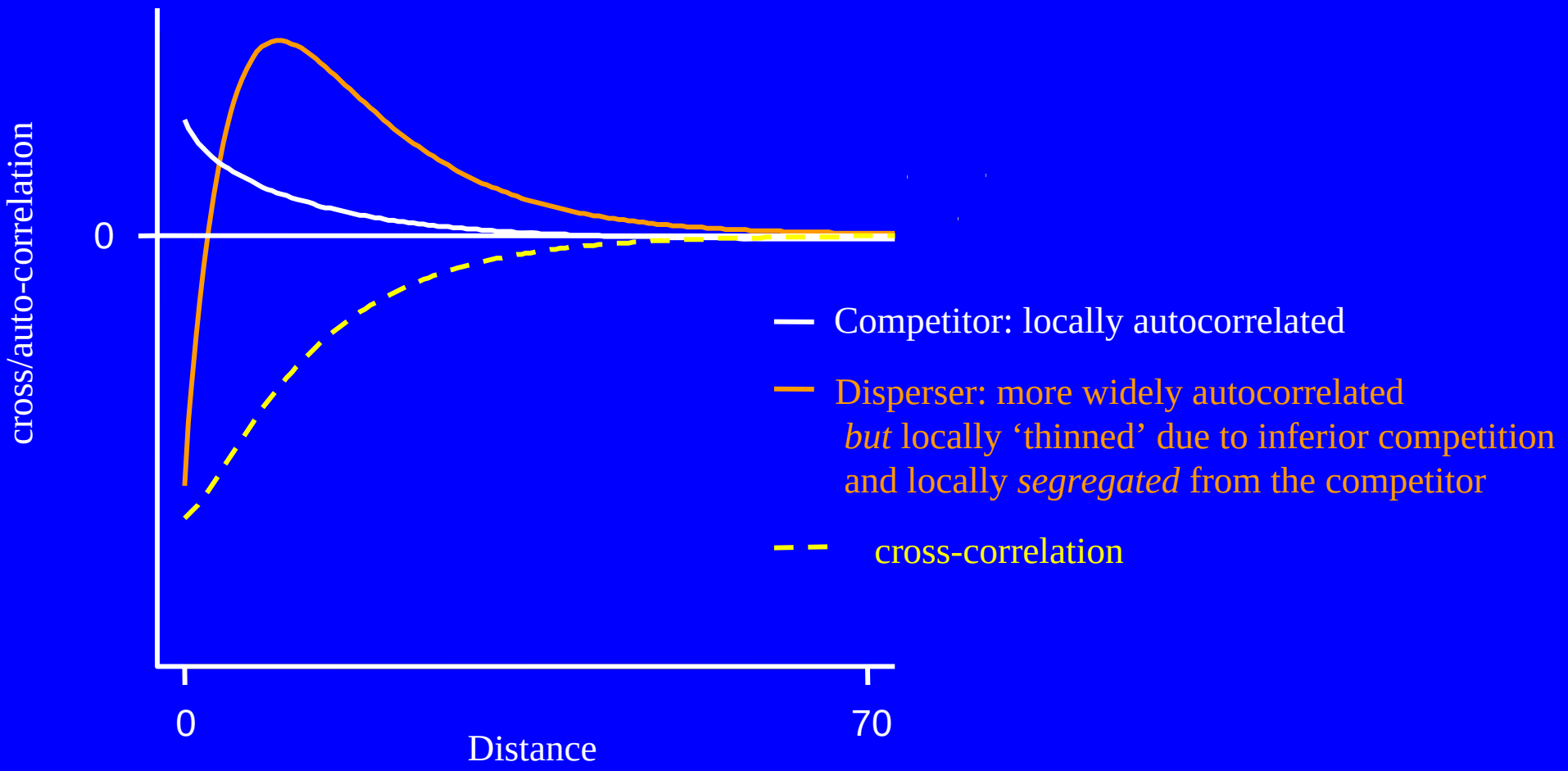
2.



Two spatial processes:
- Local competition (for light and nutrients)
- Seed dispersal

Predicted auto/cross- correlation:

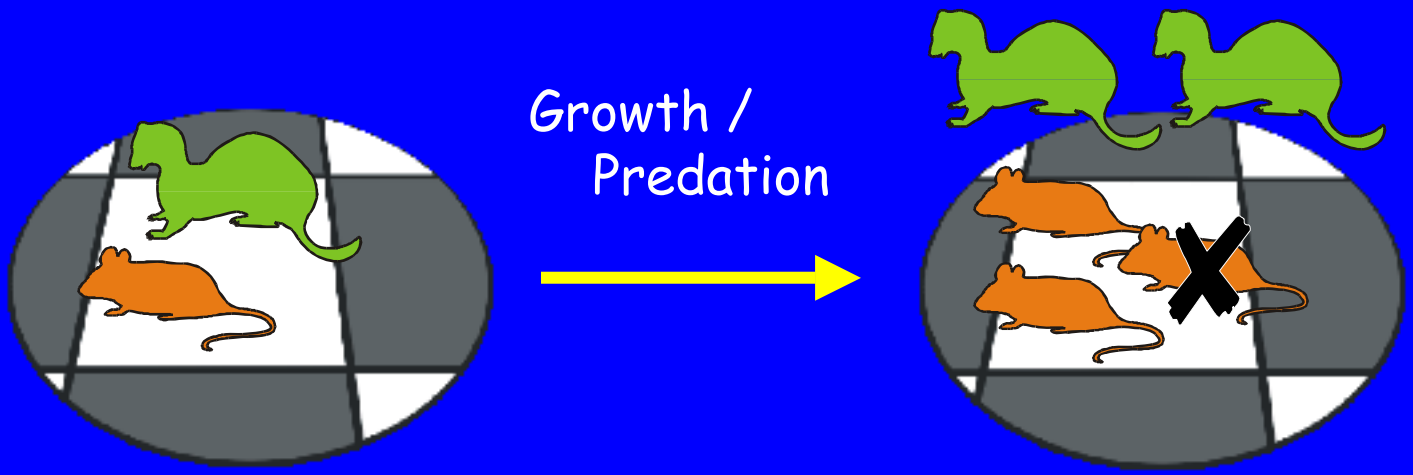
Eg competitively dominant (but weak disperser) vs mobile (but weak competitor)



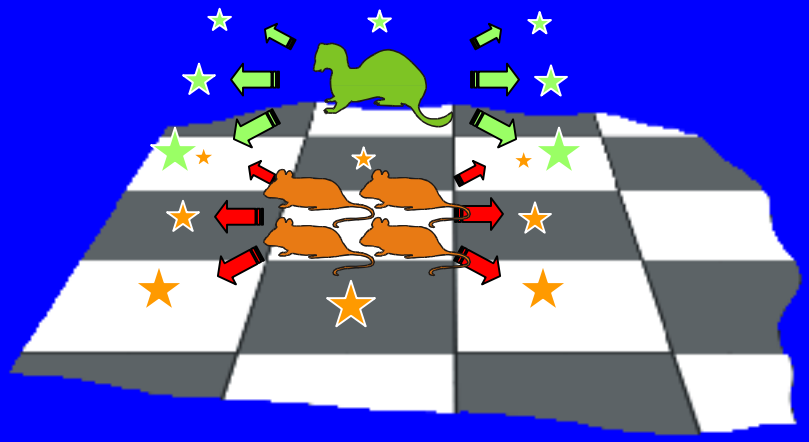
Seabloom et al. (2005) Ecological Monographs 75: 199-214

Interspecific processes: (2) predation

(2) predation

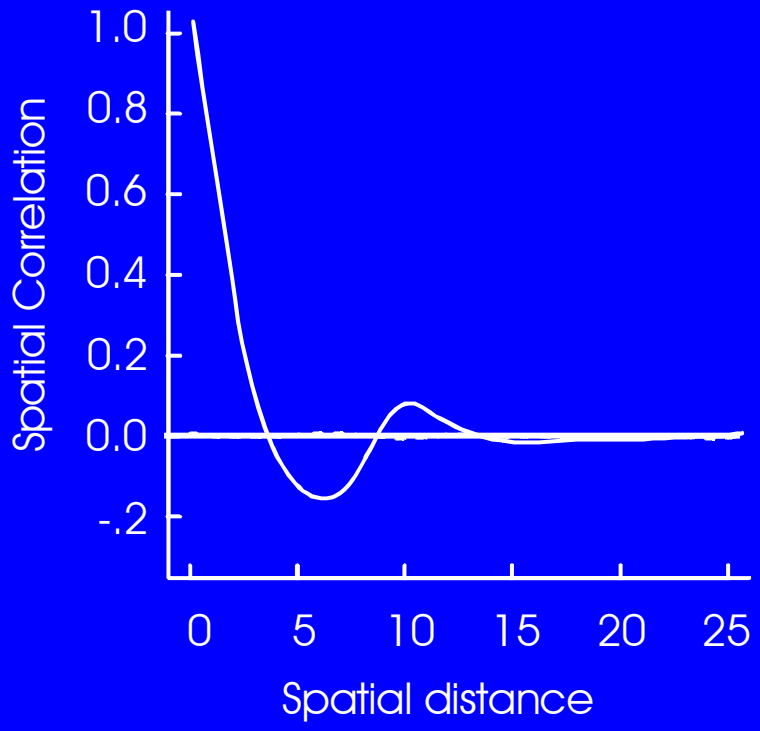


Redistribution

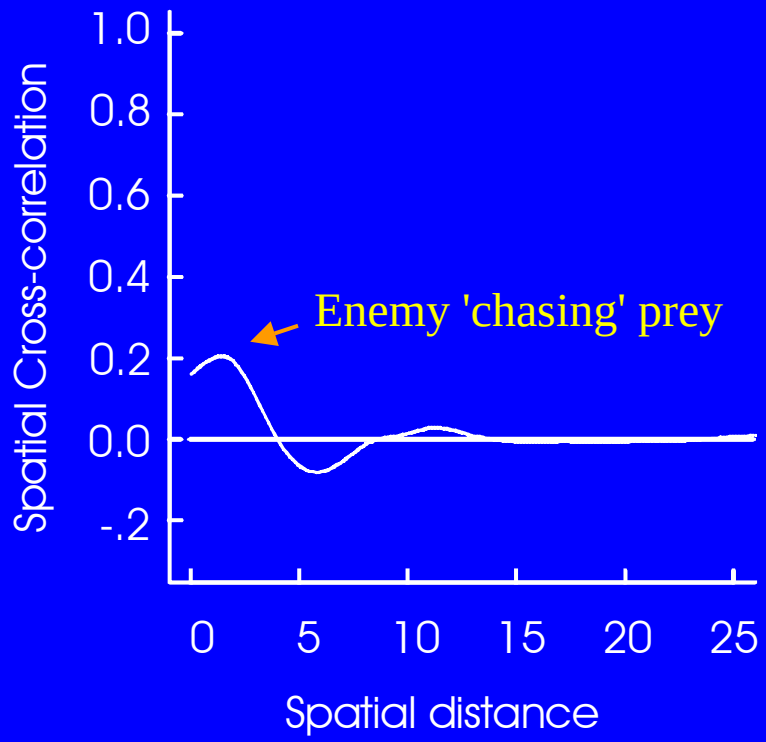


(Cross-)Correlation functions in predator-prey systems

Prey autocorrelation function



Cross-correlation fn



Cyclic correlation functions from traveling waves:
Predator population 'chasing' prey numerically in space & time

Bjornstad & Bascompte (2001) J Animal Ecology **70**:924-933.

Part 2) Statistical estimation

- Geostatistics offer numerous parametric models

  (eg Spherical, Exponential or Gaussian models)

  but these are not flexible enough

- The classical *nonparametric* method is the correlogram or variogram

  but these do not offer estimates of the *correlation functions*

The nonparametric spatial covariance functions

$$\tilde{\rho}(\delta) = \frac{\sum_{i=1}^{N}\sum_{j=i+1}^{N} G\left(\delta_{ij} / h\right)\rho_{ij}}{\sum_{i=1}^{N}\sum_{j=i+1}^{N} G\left(\delta_{ij} / h\right)}$$

where G is a kernel function with kernel bandwidth h

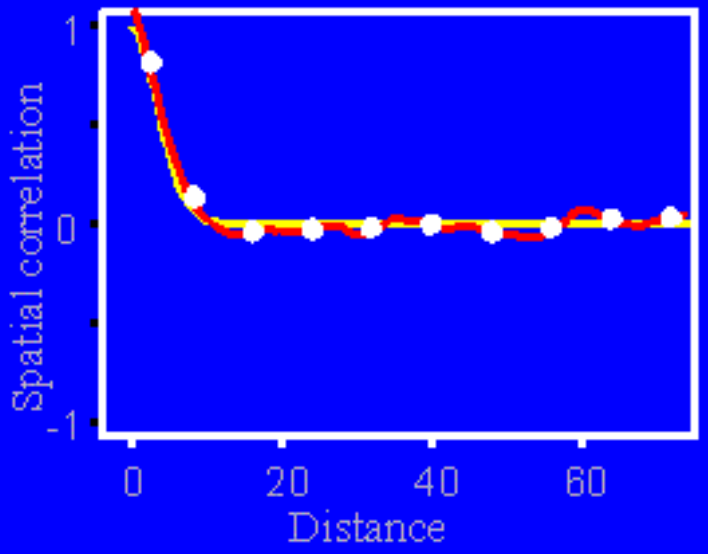
: A kernel regression of pairwise correlation, ρ_{ij} , on pariwise distance, δ_{ij} .

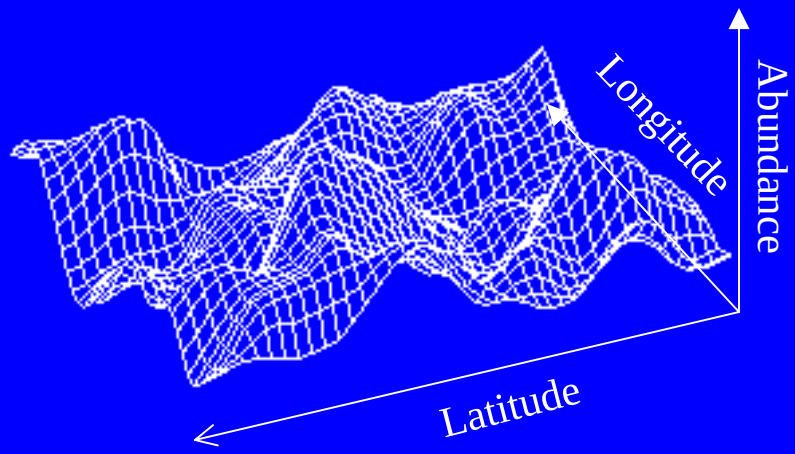
[But C-fns must obey additional constraints

Beuchners thm: Fourier filtering ensures positive semi-definiteness the resultant function **will be** a permissible correlation function]

Bjornstad & Falck (2001) Environmental and Ecological Statistics 8: 53-70

NCF – test using simulated data





— True correlation function

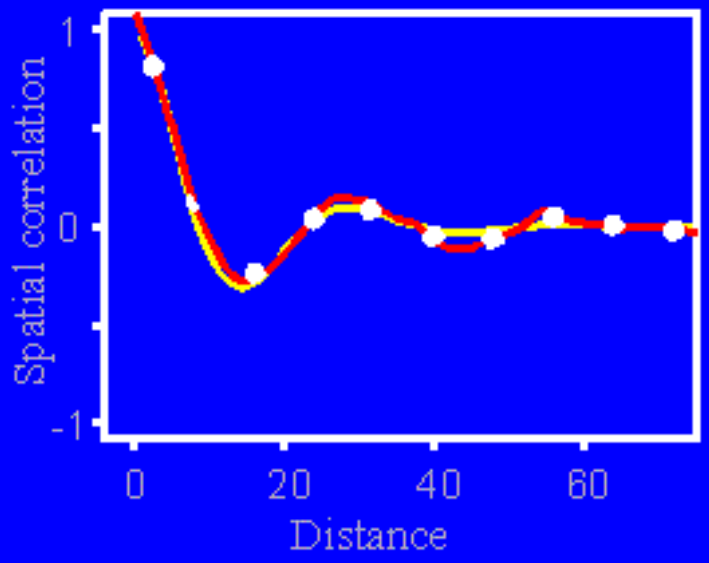
— NCF estimate

(• Spatial correlogram)

Estimation is based on 400 observations from simulated data

NCF – test using simulated data (2)

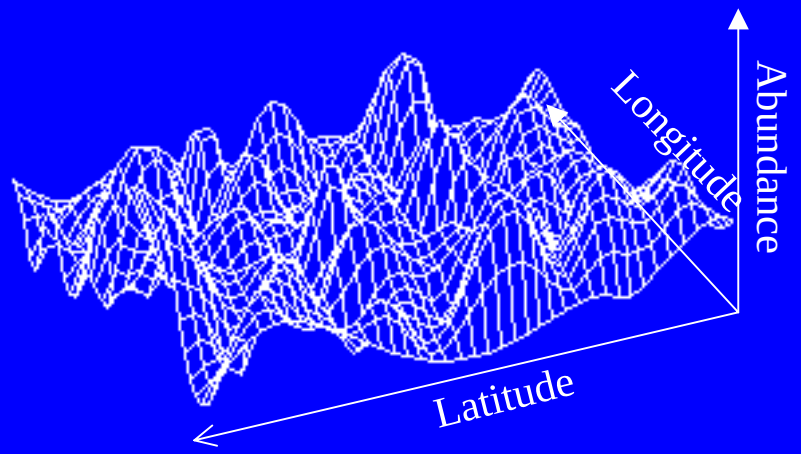
The nonparametric estimator applied to 'spatially cyclic' data



— True correlation function

— NCF estimate

(• Spatial correlogram)

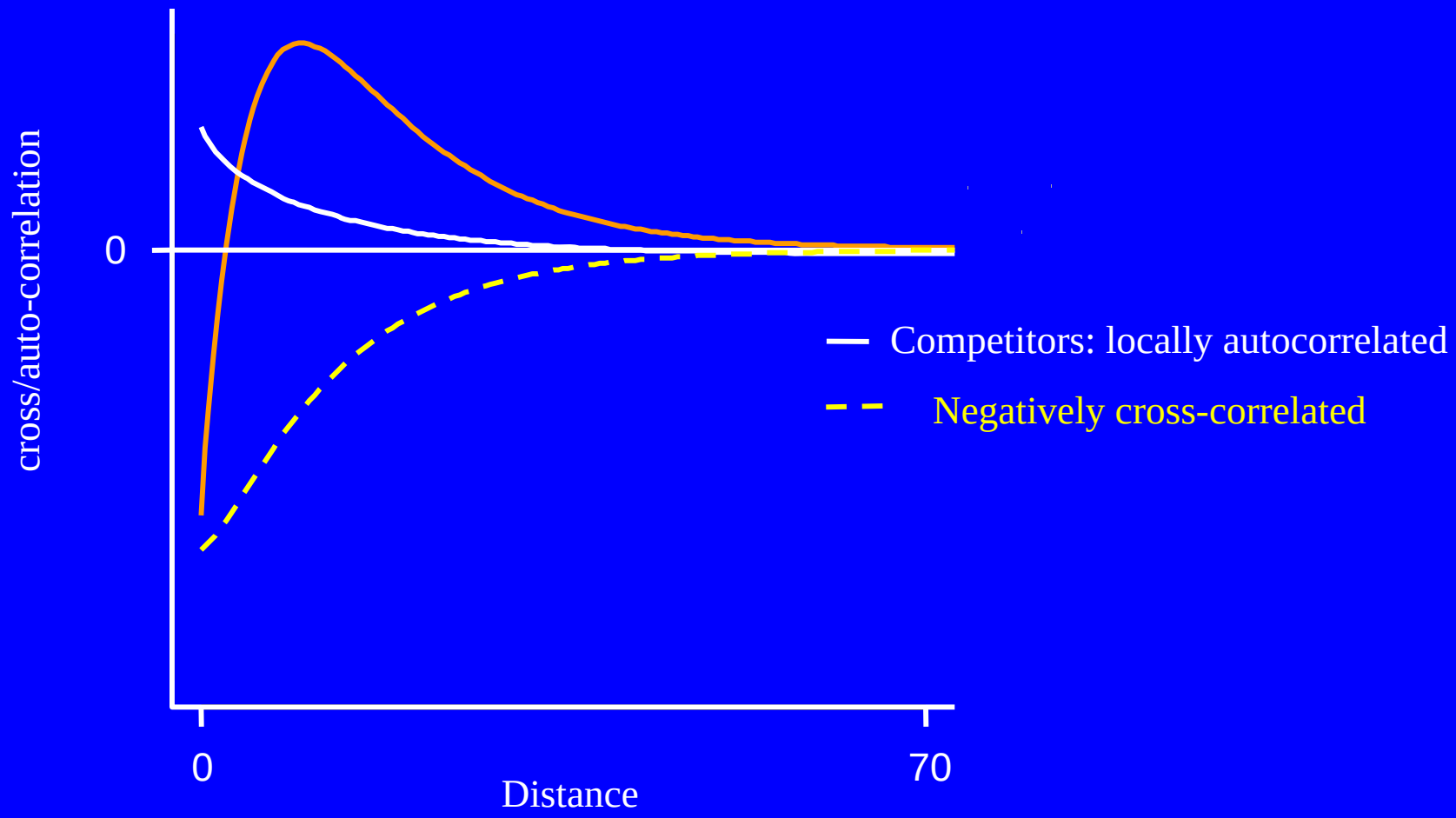


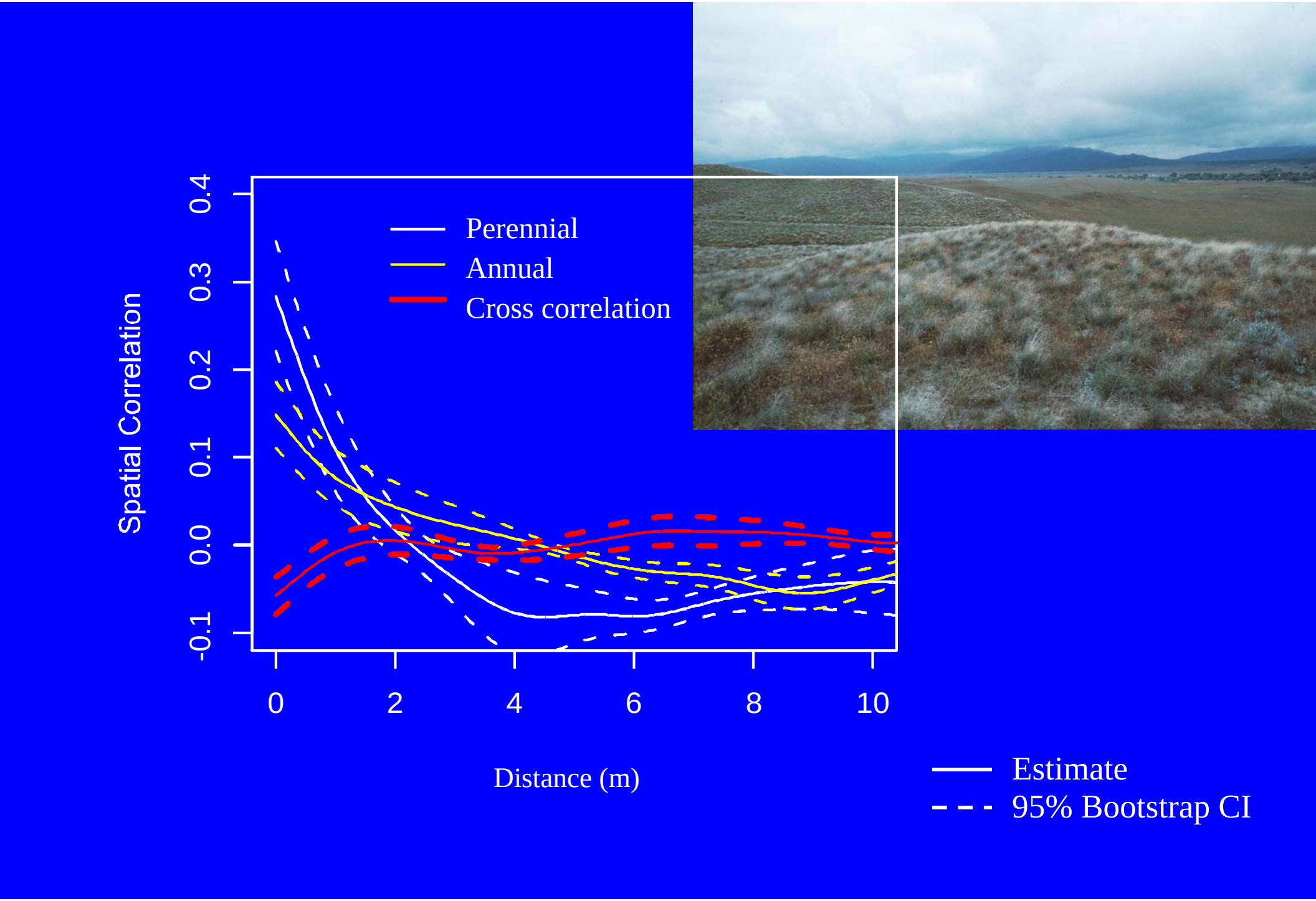
Part 3) DATA: spatial grass competition

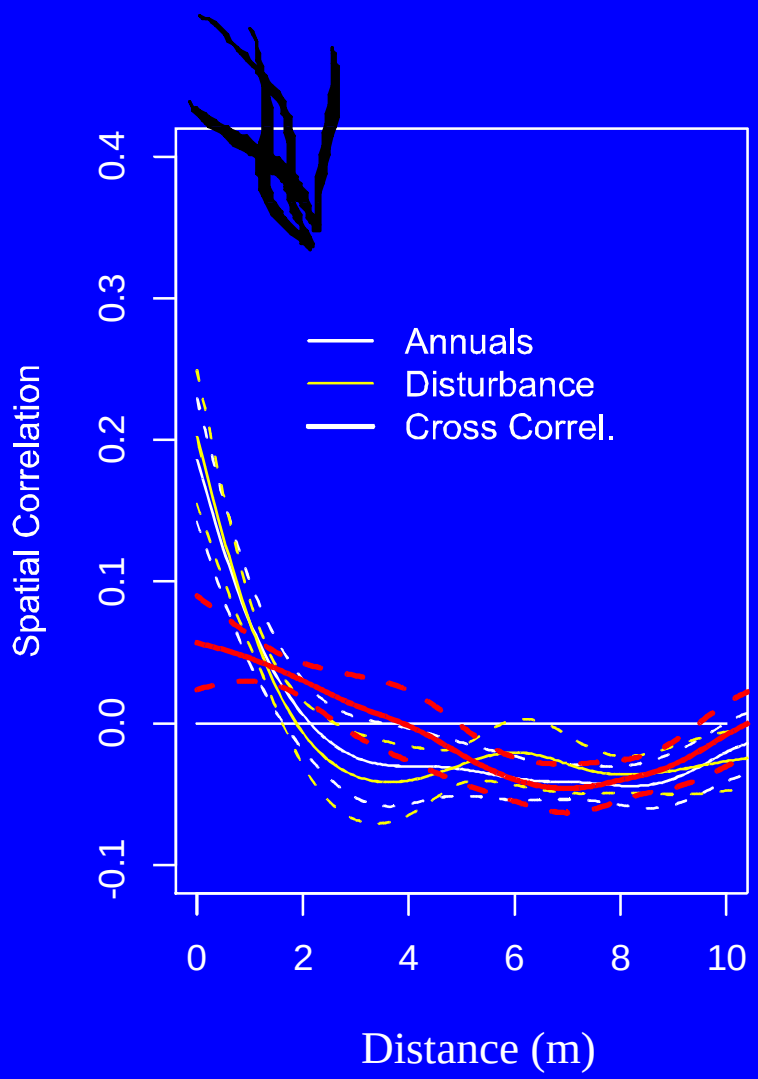
Spatial patterns in experimental grasslands

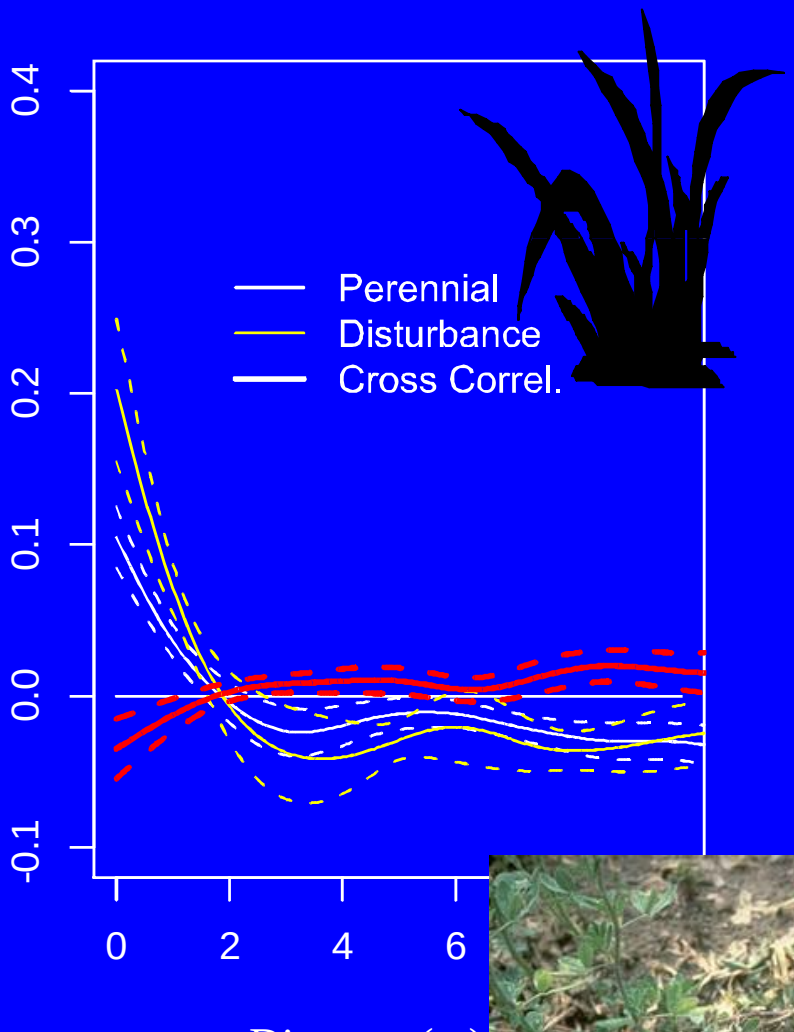
Sedgewick reserve,
S California

Recall prediction form theory:




Spatial Correlation
-0.1
0.0
0.1
0.2
0.3
0.4
0
2
4
6
8
10
Distance (m)
Perennial
Annual
Cross correlation
Estimate
95% Bootstrap CI





Seabloom et al. (2005) Ecological Monographs 75: 199-214

Conclusions:

- Ecological processes leave detailed spatial signatures
- Spatial autocorrelation and cross-correlation functions is a meeting ground for ecological theory and data
- Moment equations offer detailed predictions
- The nonparametric correlation function offers statistical estimates

- R-package and reprints on http://asi23.ent.psu.edu (Bjornstad)
- Details on Moment equations on http://www.zoo.ufl.edu/bolker/ (Bolker)
- Data repository http://science.oregonstate.edu/~seabloom/ (Seabloom)