Process and pattern in spatial epidemics: correlation equations, dynamics, and estimation

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Outline

- Spatial scales and modeling frameworks
- Results from simple (SI) and SIR epidemics
- R_0 from spatial epidemics
- Thoughts on heterogeneity and estimation

Grass in distress

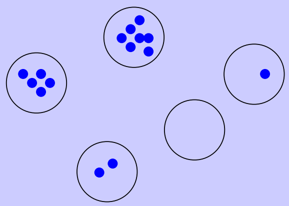
Patchy epidemics

- Spatial scales of epidemics: from foci to pandemics
- Explore *within-field* epidemics, where spatial heterogeneity is *endogenous* (although host population may be patchy)
- Multiple foci: caused by spore showers, long-tailed dispersal kernels, multiple dispersal modes
- Wind/splash/soil-dispersed disease, typically fungal pathogens

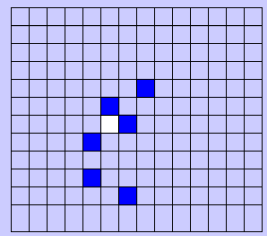
Focal epidemics

- Wave speed of isolated disease focus: generalizes Fisher equation (etc.): van den Bosch, Zadoks, Zawolek 1988-1994
- Flexible dispersal kernel, latent period, infectious period
- Experimental results: van den Bosch & Zadoks, Minogue & Fry, Gilligan
- Shortcomings: invasion phase only, single-focus

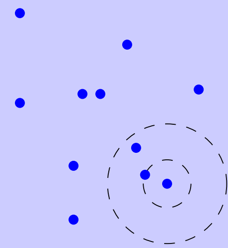
Spatial ecology: models



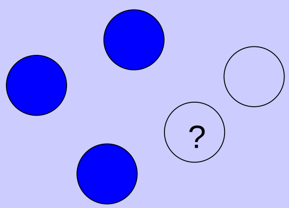
patch/metapopulation



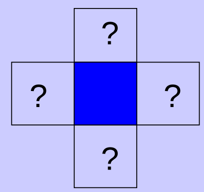
lattice



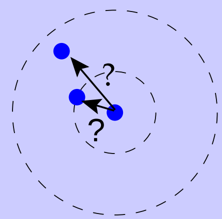
point process/IBM



patch occupancy models
("classical" metapops)



pair
approximation



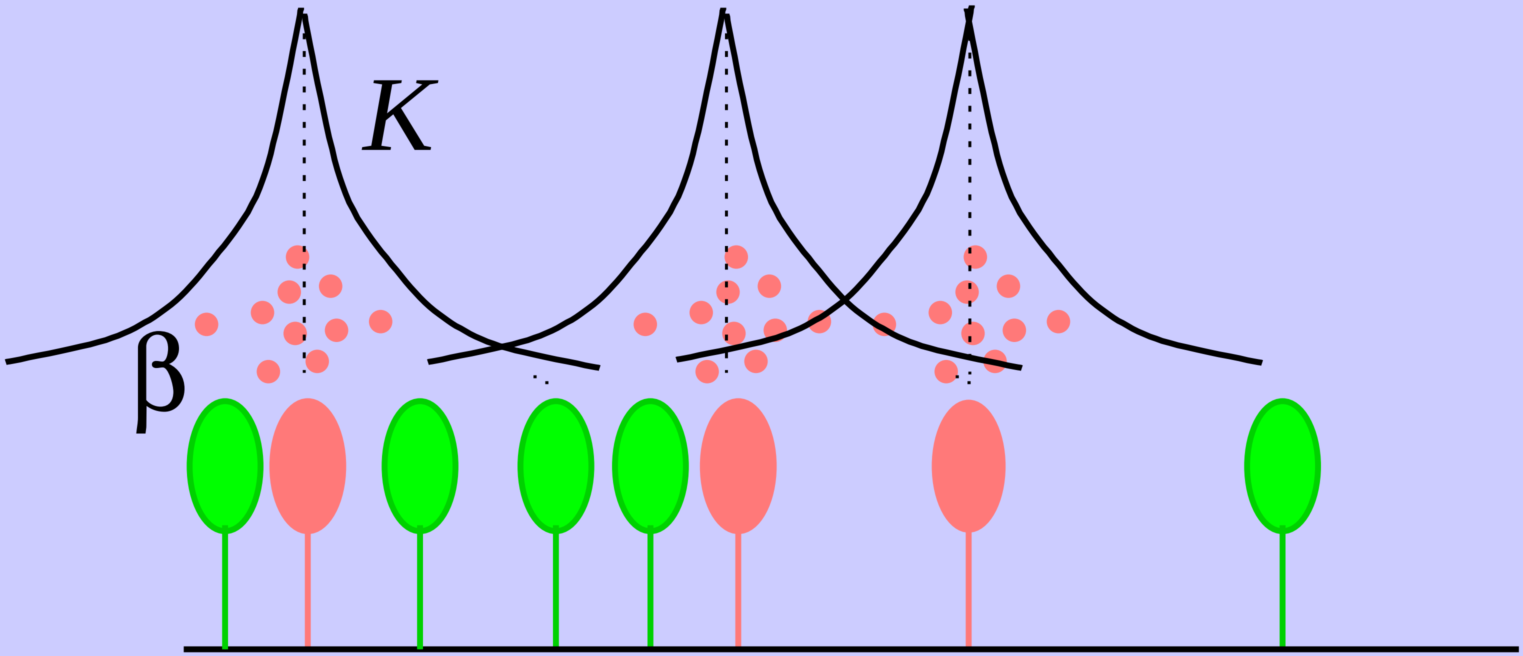
spatial
moment
equations

Simple epidemic models

Model for short-term, within-field epidemics (static host population):

- *contact rate* β: combined rate of spore production, infection probability

- *spore dispersal kernel* $\mathcal{K}(r)$: probability of a spore travelling a distance r from an infected to a healthy plant

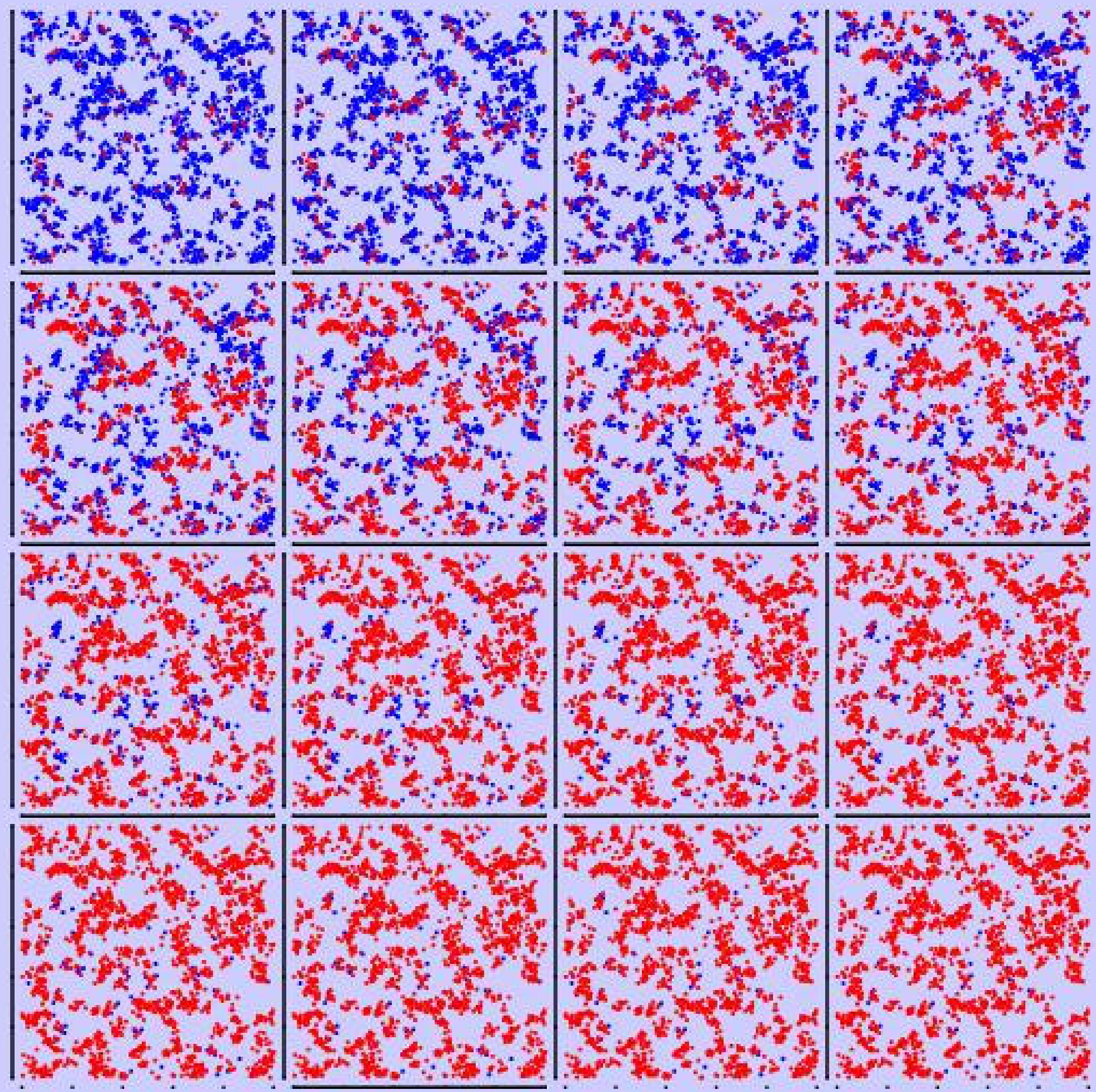

K
β

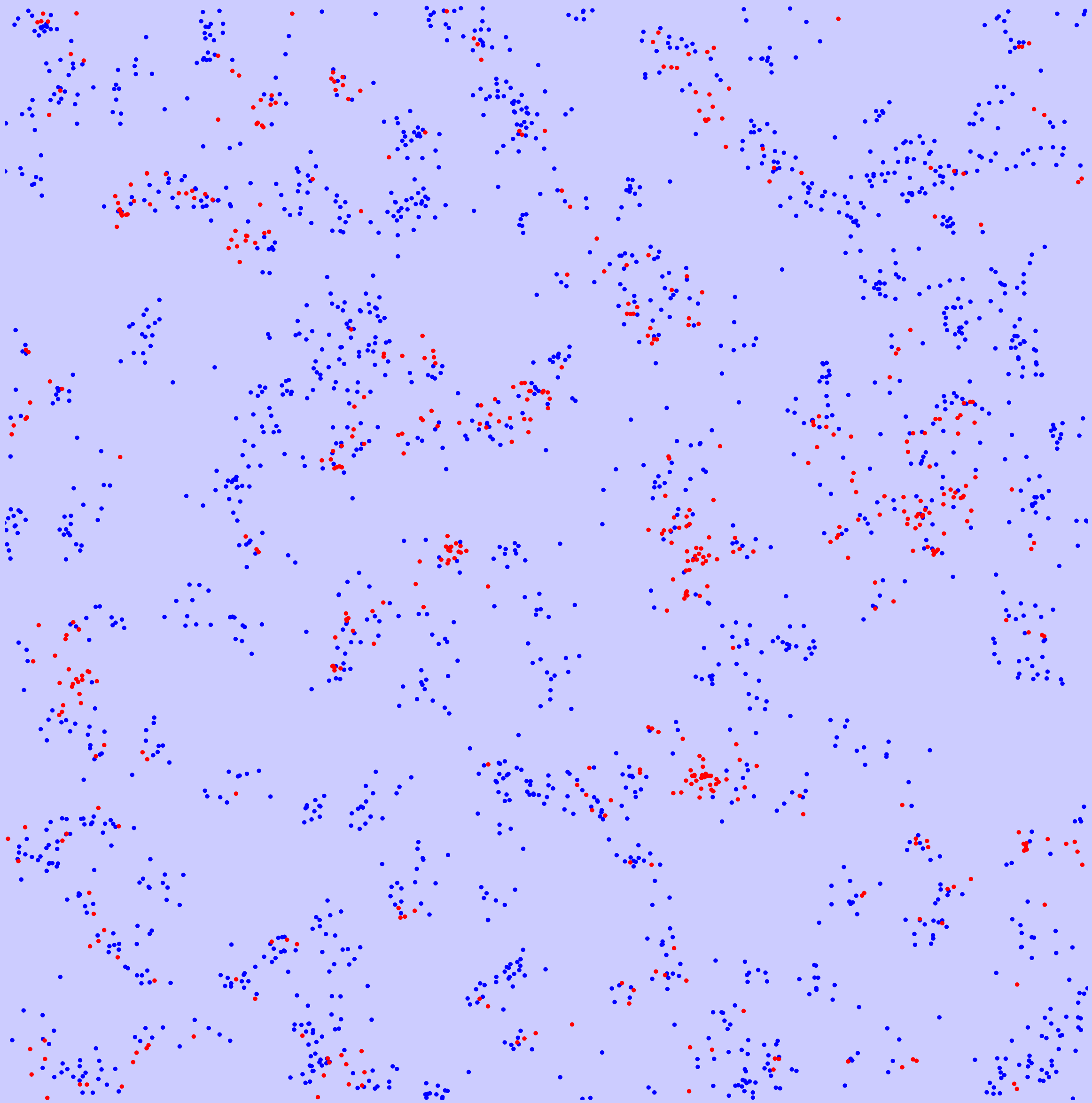
Point-process equations

$$\lambda(\mathbf{x}) = \beta \sum_{j=1}^{N_i} U(|\mathbf{x} - \mathbf{y}_j|) = \beta \int_\Omega U(|\mathbf{x} - \mathbf{y}|) I(\mathbf{y})\, d\mathbf{y}$$

Overall infection rate:

$$\Lambda = \sum_{j=1}^{N_s} \lambda(\mathbf{s}_j) = \int_\Omega \lambda(\mathbf{x}) S(\mathbf{x})\, d\mathbf{x},$$





Neighborhood density & spatial covariance

Local or *neighborhood densities* drive the epidemic.

Quadrat sampling gives means, variances, covariance: $n + \frac{s^2}{n}$ estimates the n.d. of plants near other plants.

Neighbourhood density of infected plants around uninfected plants $= \bar{I} + \frac{c_{SI}}{S}$.

Neighbourhood densities are *dynamic*.

Moment equations

- Define *spatial covariance*

- Using stochastic equation for rates (from simulator)
  - Mean: derive expected change in population density
  - Covariance: derive expected change in *spatial covariance*
  - Close moments

- Analyze spatial population dynamics

Spatial covariance

$$c_{ij}(|\mathbf{x}-\mathbf{y}|) = \langle (n_i(\mathbf{x}) - \bar{n}_i) \cdot (n_j(\mathbf{y}) - \bar{n}_j) \rangle$$

- Standard spatial/geostatistical measure
- Estimable from data
- Connection with analytic models

Moment equations

Describe the change in the densities of infected (I) and uninfected (susceptible, S) plants in terms of the spatial covariances:

$$\begin{aligned}\dot{I} = \text{infection rate} &= \beta(SI + \bar{c}_{SI}) \\ &= \beta S \left(I + \frac{\bar{c}_{SI}}{S} \right) \\ &= \beta S[\text{neighbourhood density of } I|S]\end{aligned} \tag{1}$$

where $\bar{c}_{SI}$ is the *average covariance*, $\int \mathcal{K}(r) c_{SI}(r)\, dr$.

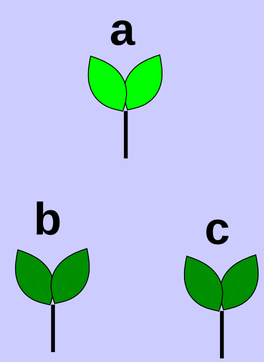
Moment closure

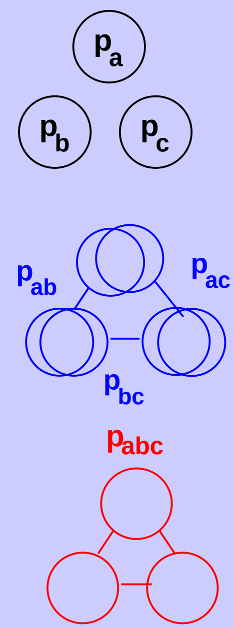
What about *higher moments*? **Closure rules**

- non-spatial/independent:
  $p_{abc} = p_a p_b p_c$

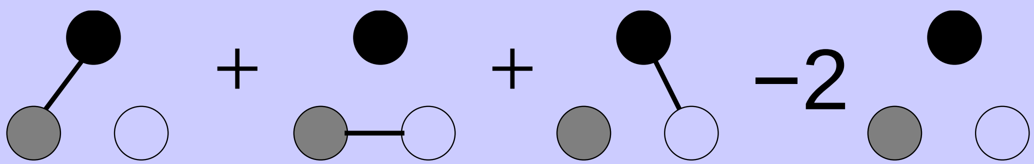
- power-1: $p_{abc} = (p_a p_{bc} + p_b p_{ac} + p_c p_{ab} - 2 p_a p_b p_c$

- power-2:
  $p_{abc} = \left(\frac{p_{ab} p_{ac}}{p_a} + \ldots \right) /3$

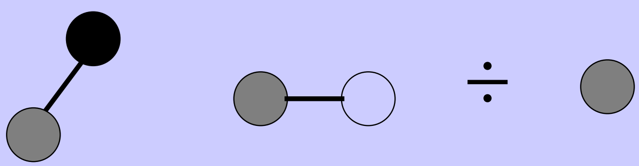




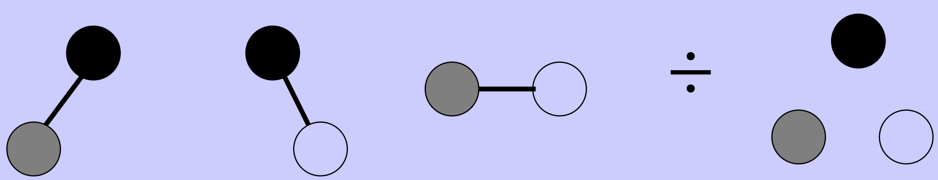
Closure rules, cont.



power−1



power−2a



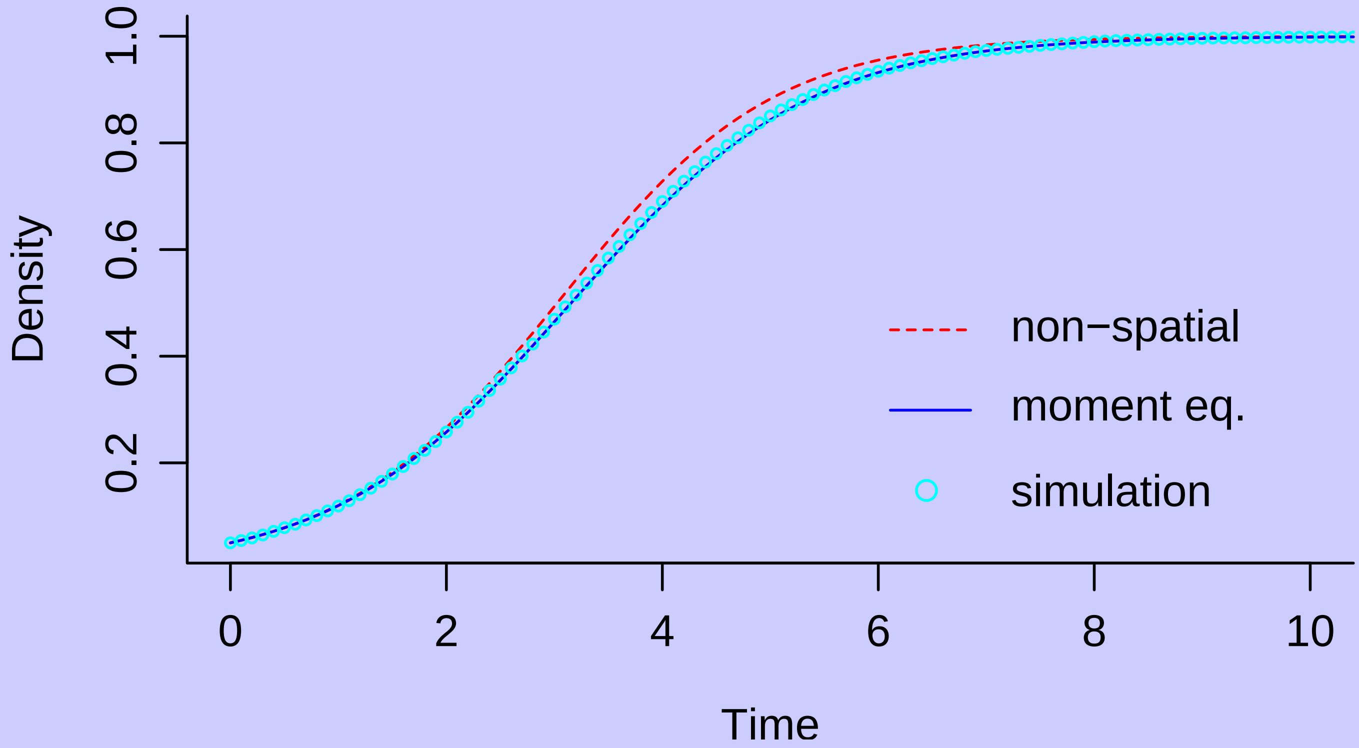
power−3

Moment equations: covariance equations

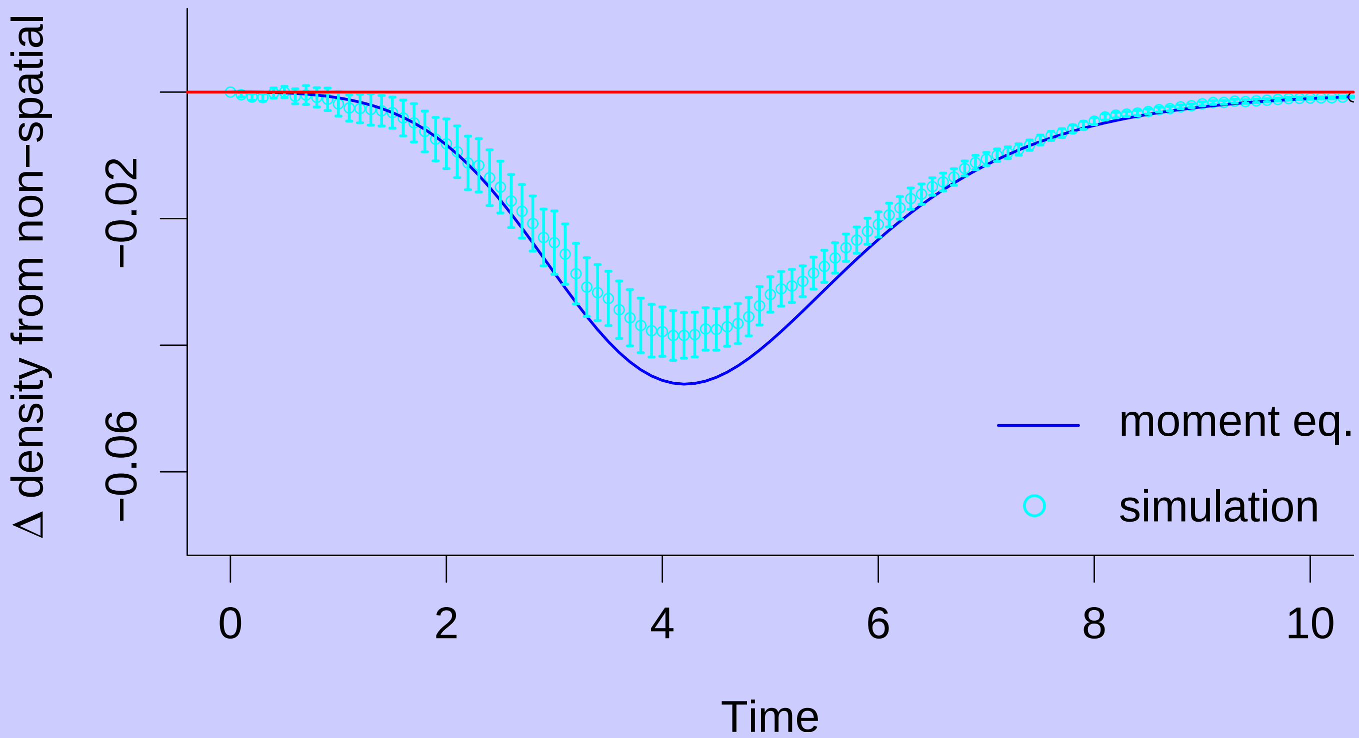
$$\frac{\partial c_{SI}(r)}{\partial t} = \beta\Big[\bar{S}(U * c_{SI})(r) + \bar{I}c_{SS}(r) \\ - \bar{I}c_{SI}(r) - \bar{S}(U * c_{II})(r) - \bar{S}\bar{I}U(r)\Big]$$

$$\frac{\partial c_{II}(r)}{\partial t} = 2\beta\Big[\bar{I}c_{SI}(r) + \bar{S}(U * c_{II})(r) + \bar{S}\bar{I}U(r)\Big]$$

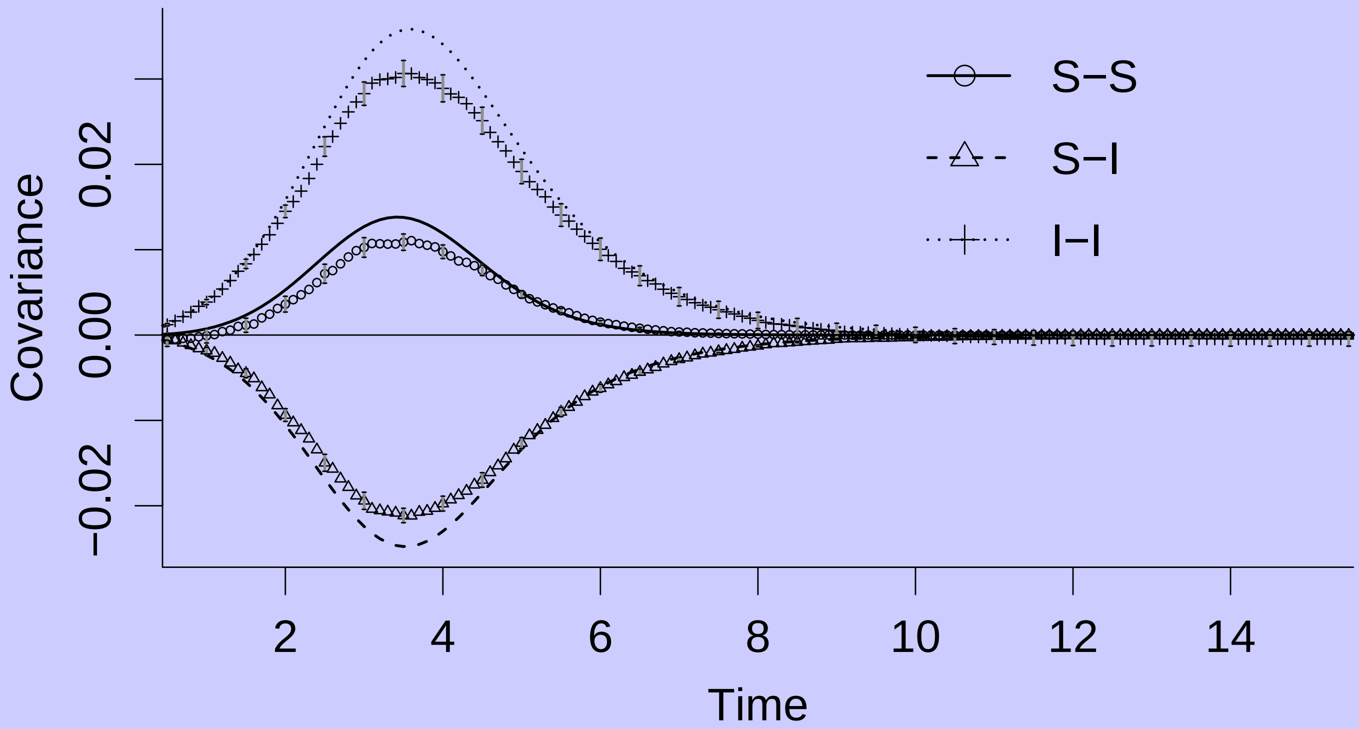
Density dynamics



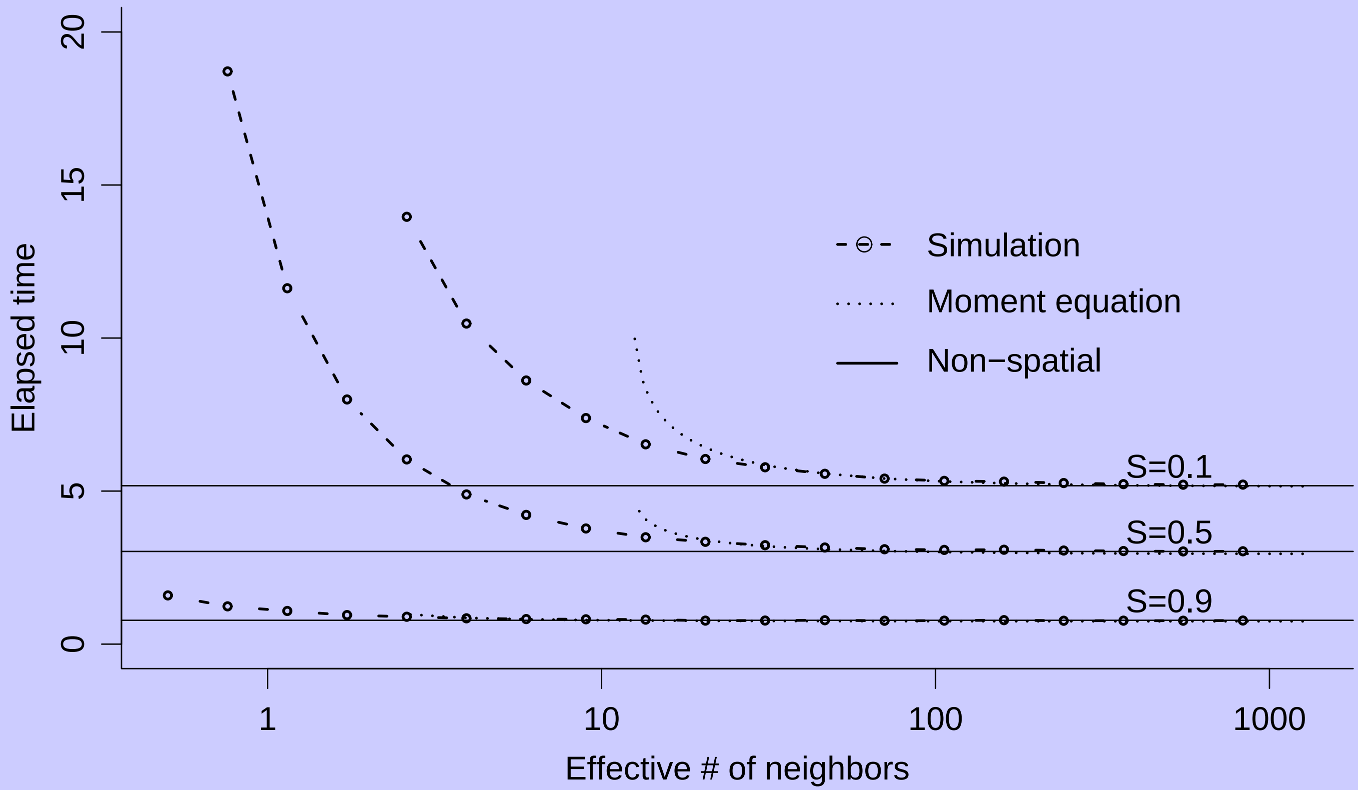
Deviation from mean-field



Covariance dynamics (Poisson hosts)



Epidemic trajectories (Poisson hosts)



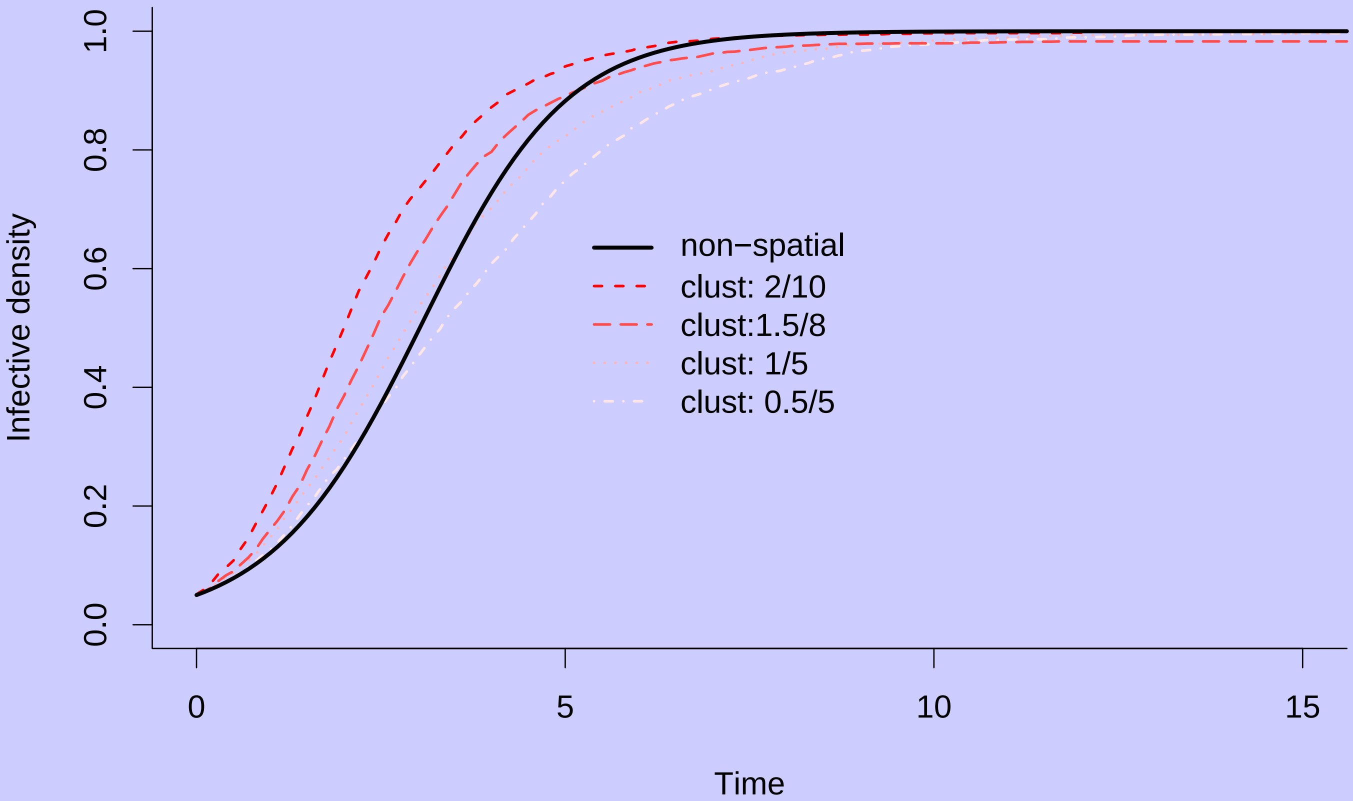
Patchy host distributions

- Realistic complication:
  - plant demography (local dispersal)
  - environmental heterogeneity
  - distribution of *susceptible* hosts (small-scale pop. genetics)
  - result of previous epidemics
- Model as a *Poisson cluster process*

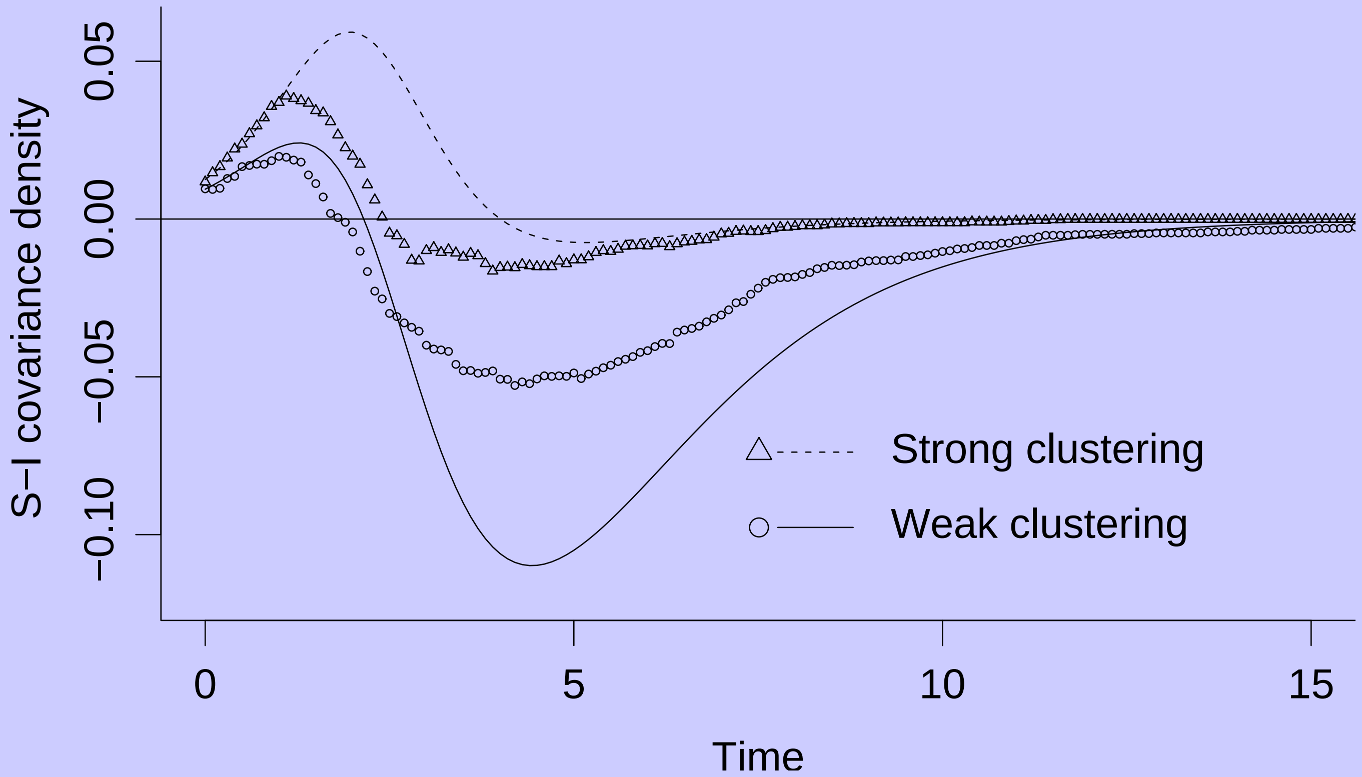
A familiar result

Host heterogeneity initially *accelerates* epidemic, proportional to $1 + \dfrac{\text{variance}}{\text{mean}^2} = 1 + (\text{coeff. of variation})^2$ (*before* buildup of covariance etc.)

Simple epidemic (clustered hosts)



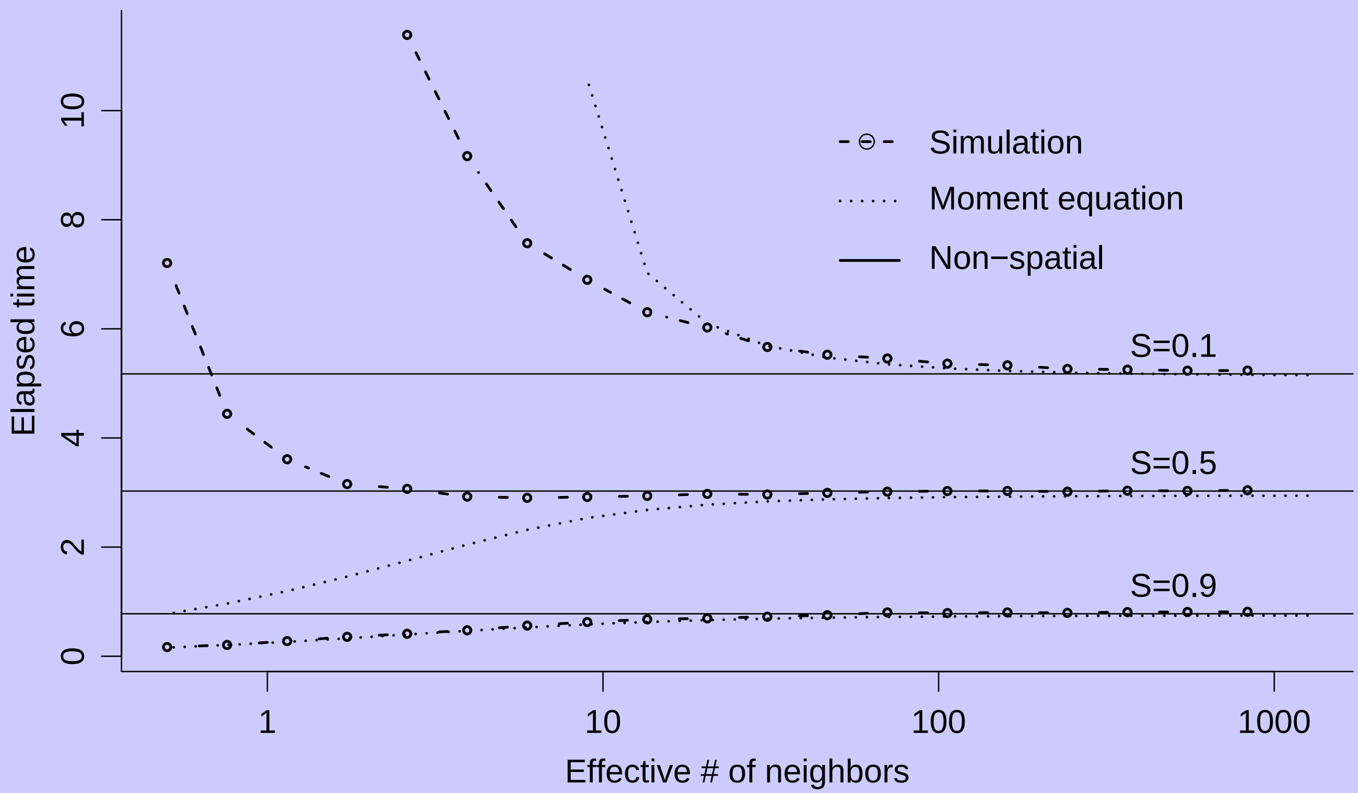
Covariance dynamics (clustered hosts)



Conclusion so far

Infective patchiness (c_{II}) builds up over time; this patchiness, and associated spatial association/segregation between susceptibles and infectives (c_{SI}), initially *accelerates* but then *decelerates* the epidemic ("burn-out" of clusters).

Epidemic trajectories (clustered hosts)

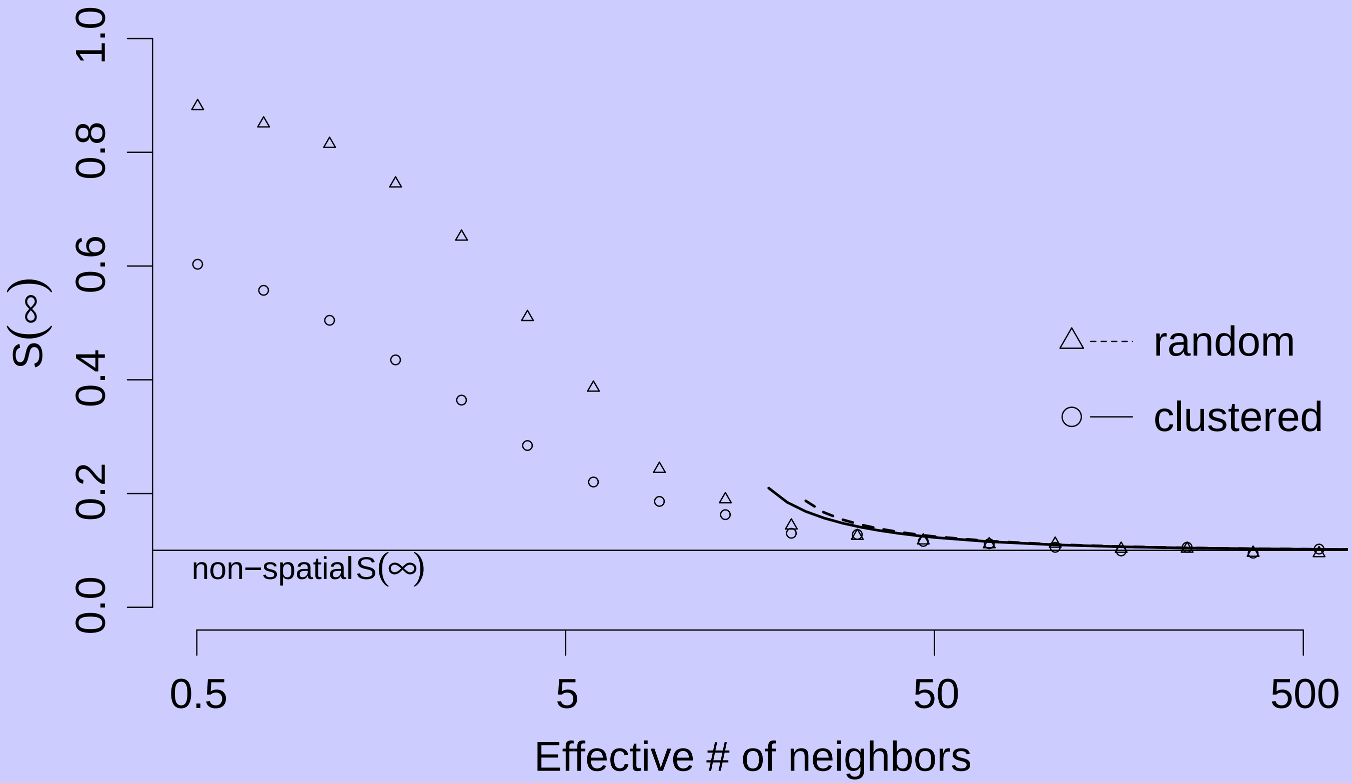


SIR models

- (Standard) Susceptible/Infective/Removed: allow for recovery or death

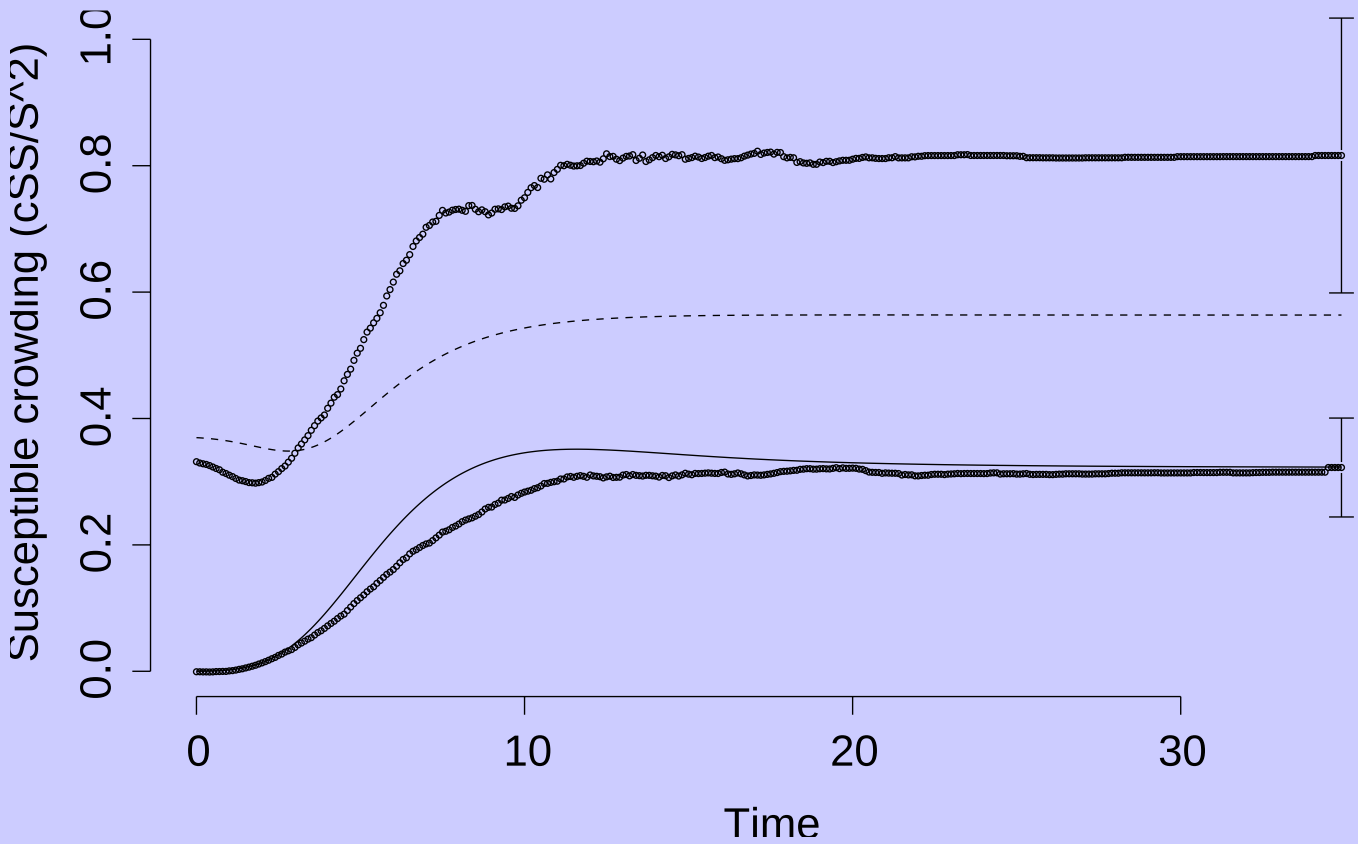
- Allows much larger effects of space (even in random-hosts case) than the simple epidemic

Final sizes

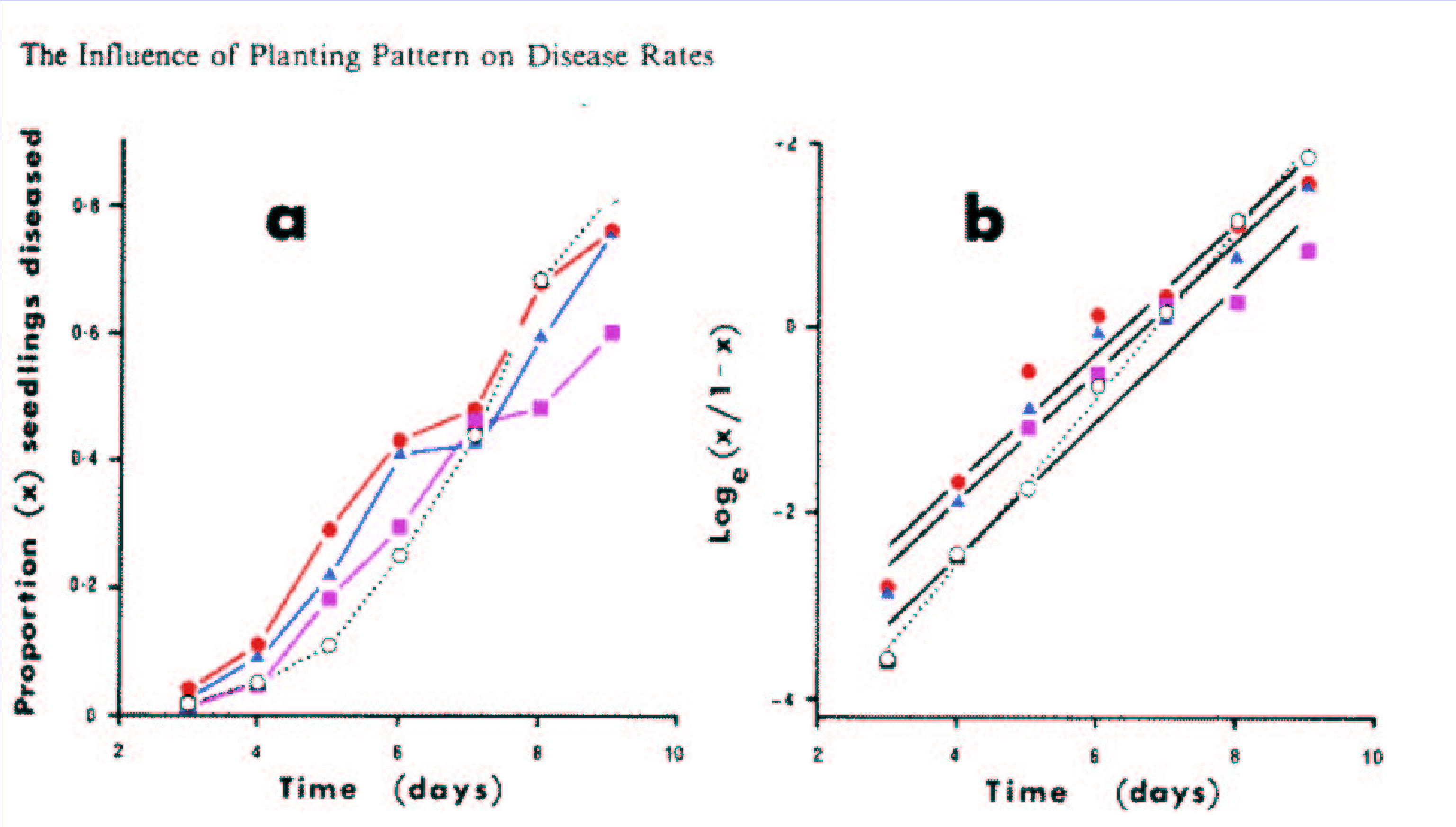


S(∞)
0.0
0.2
0.4
0.6
0.8
1.0
non−spatial S(∞)
random
clustered
0.5
5
50
500
Effective # of neighbors

Post-epidemic patterns



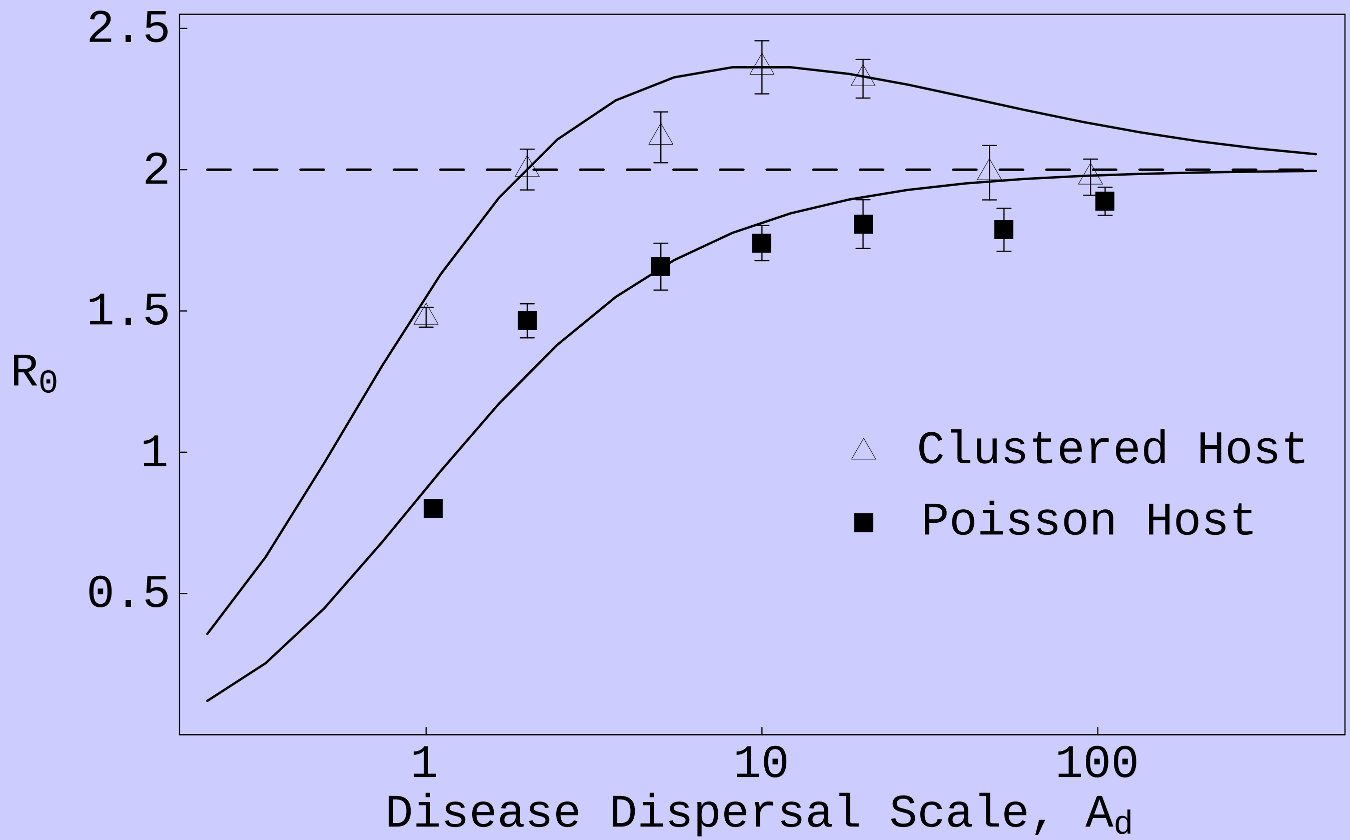
Reality? (Burdon and Chilvers exp.)



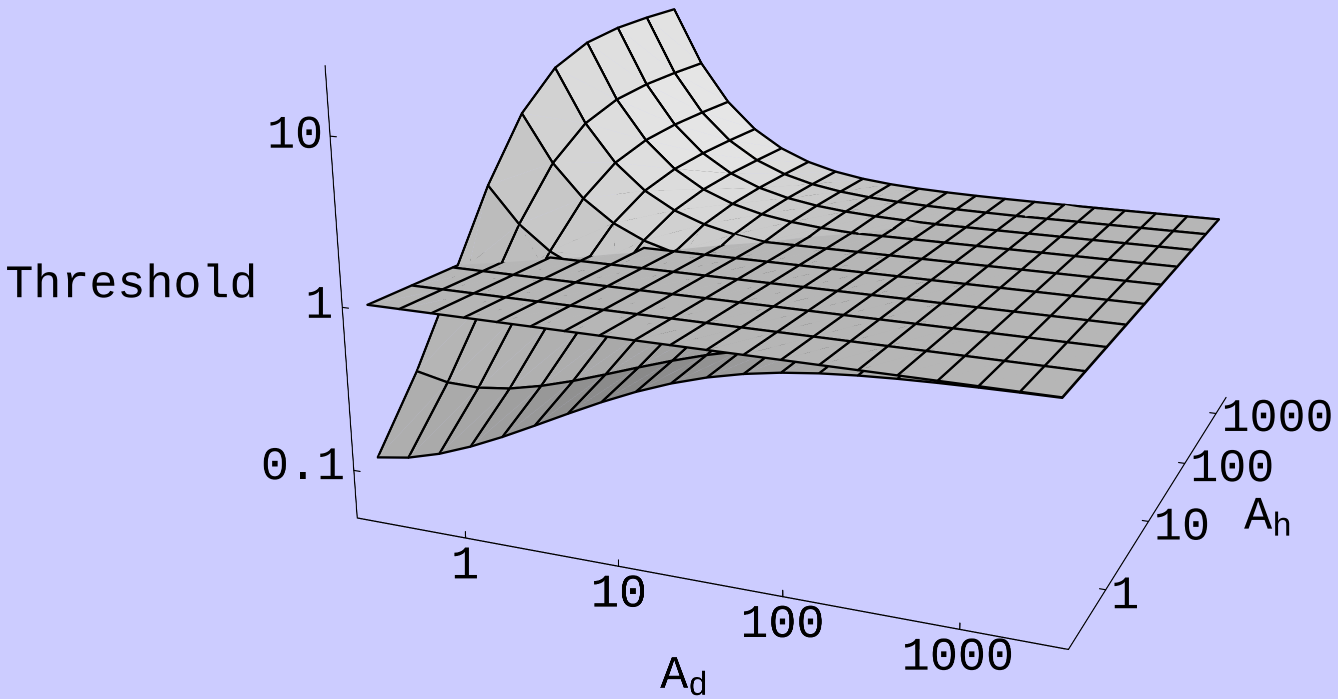
Results on R_0 (David Brown)

- Change closure rule to power-2 asymmetric (accounts for I-S-I structure)
- Analytic simplicity decreases (but wasn't great to begin with)
- Quasi-equilibrium state exists — can estimate eigenvectors numerically

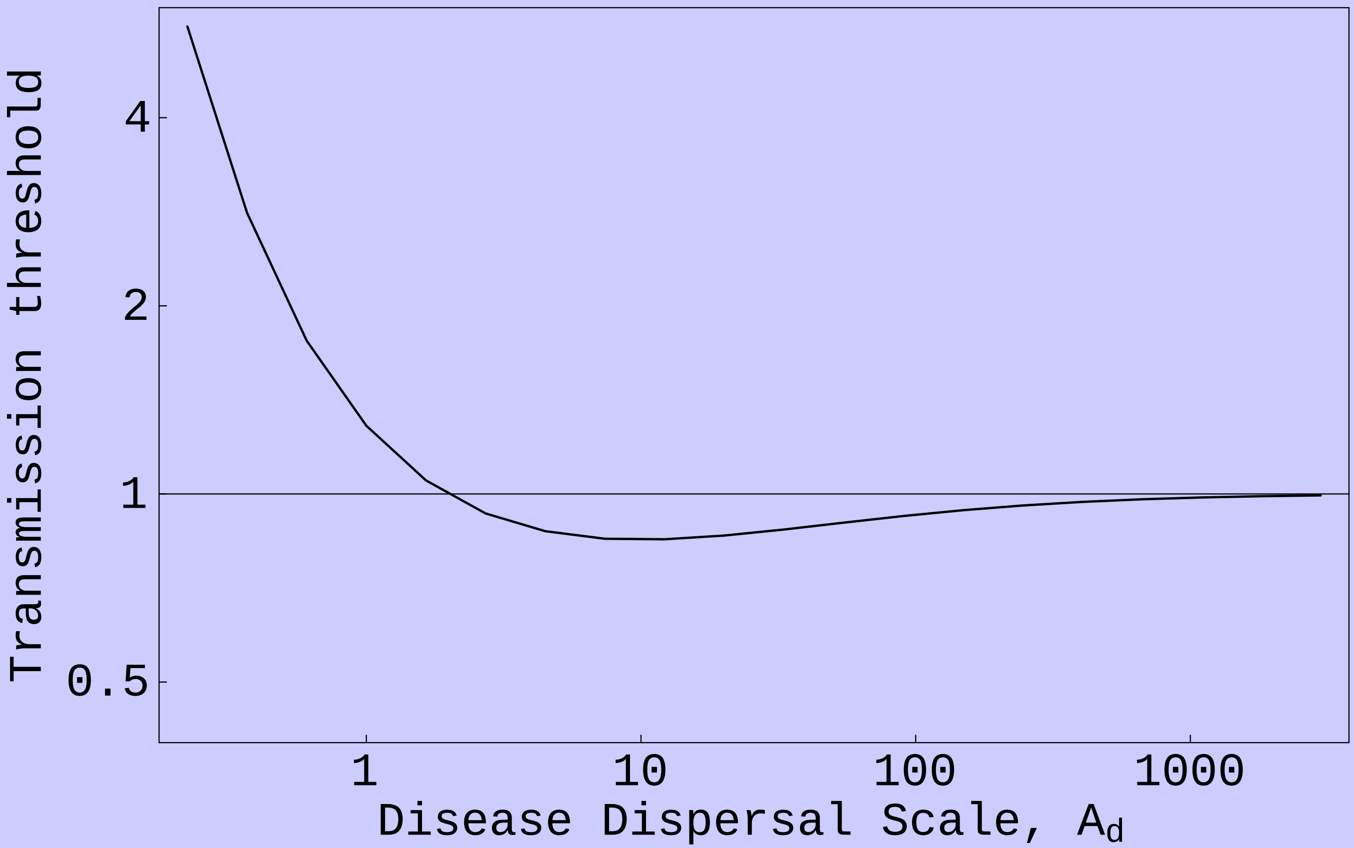
R_0, simulation vs moment equations



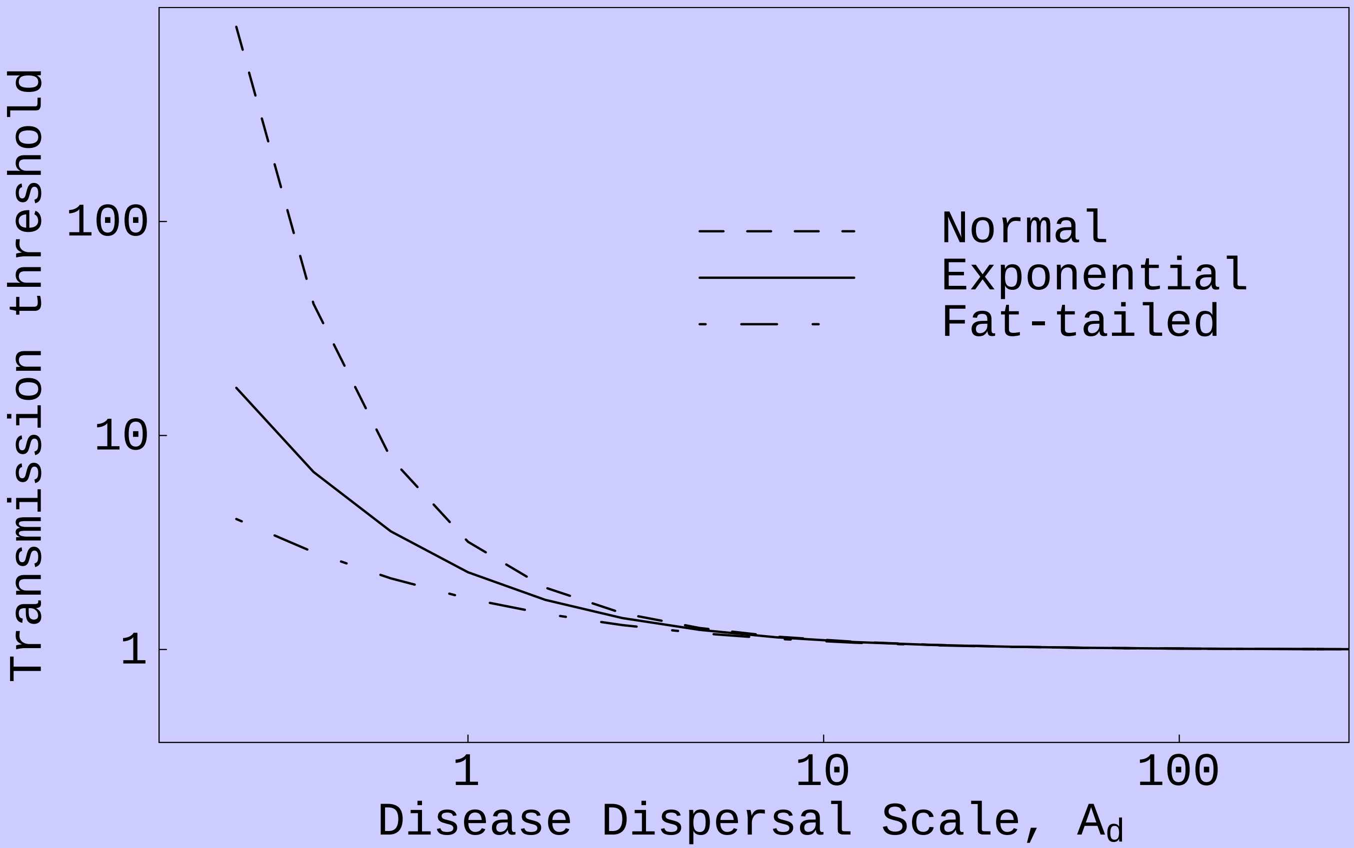
R_0 (m. eq.) dependence on scales



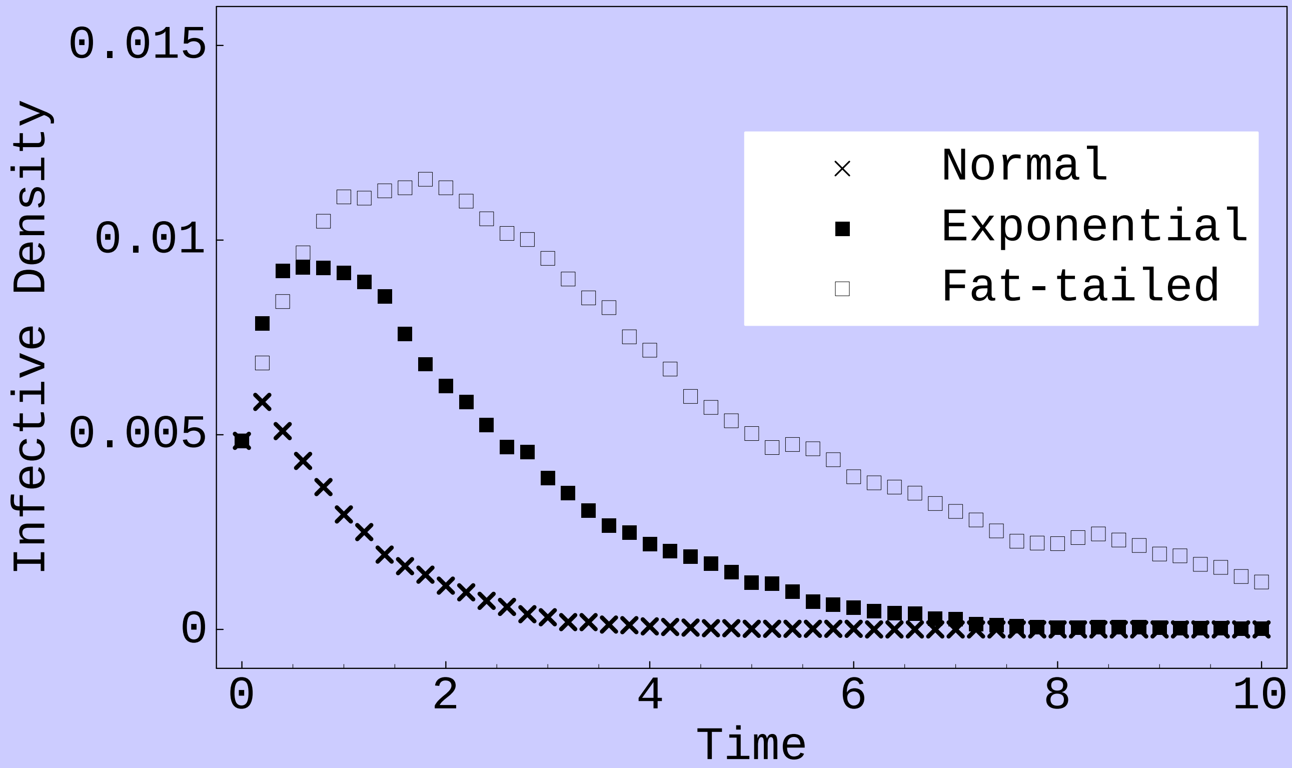
R_0 for clustered hosts ($A_h = 20$)



Effects of kernel shape



Effects of kernel shape: 2



Heterogeneity and estimation

- Introduce heterogeneity (in recovery, susceptibility, infectivity)
- Classical *pattern vs. process* problem
- Separate by *deconvolution*

Ingredients for correlation estimation

- Methods for estimating correlations/spatial power spectra (e.g. spatial ARMA)

- Equations for expected spectra:
  - Via moment equations
  - Via stochastic PDEs (Lande, Saether, Engen)

- Equate equilibria or changes in correlation with observations: e.g. $\tilde{N} = \frac{\tilde{E}}{m+\tilde{D}}$ in logistic case

What are moment equations good for?

- Simple descriptions of spatial dynamics, especially including multiple scales/shapes (cf. pair approximations)
- Replacement for stochastic simulations (with fancier closures: Filipe)
- Linking spatial (non-grid) data with spatial models

Open questions

- Formal framework missing (Barton, Etheridge, & DePaulis)
- Modeling: analysis vs. flexibility vs. realism
- Simple models can focus on only one aspect at a time (invasion phase, wave edge, etc.)
- Extensions of moment equations: more species, etc. (requires biological foundations)
- Connections between different frameworks:

Acknowledgements

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