Can Mathematical Ecology Help Explain How Plants Compete for Space? (and more)

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Outline

I Spatial ecology

II Spatial competition and moment equations

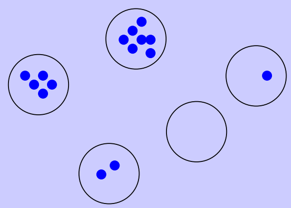
III Moment equations: other applications

IV Conclusions: other people's data

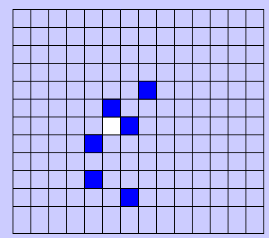
I. Spatial ecology: why?

	Explicit	Implicit
Competition	Spatial patterns of plant distributions in competitive communities	Persistence, coexistence, and diversity
Epidemics	Focal spread, patterns left by epidemics	Invasion thresholds and epidemic curves in spatial settings
Population ecology	Spatial patterns of habitat use, synchrony	Population survival under habitat degradation

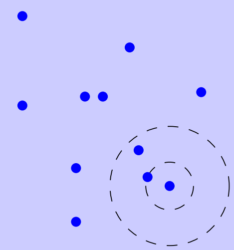
Spatial ecology: models



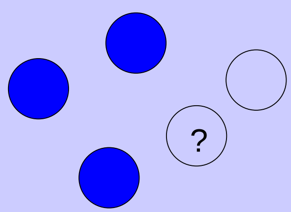
patch/metapopulation



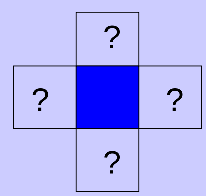
lattice



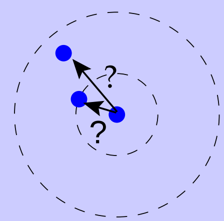
point process/IBM



patch occupancy models
("classical" metapops)



pair
approximation



spatial
moment
equations

II: Spatial competition

- Competition-colonization trade-offs in continuous space
- Moment equations
- Beyond competition-colonization

Diversity & spatial heterogeneity in plant communities

- The *paradox of diversity*: why are there so many species?
- Plants: one trophic level, few limiting resources, sessile
- Coexistence via spatial/temporal heterogeneity: gradients or patches, exogenous or endogenous
- *Competition-colonization tradeoffs* or similar explanations

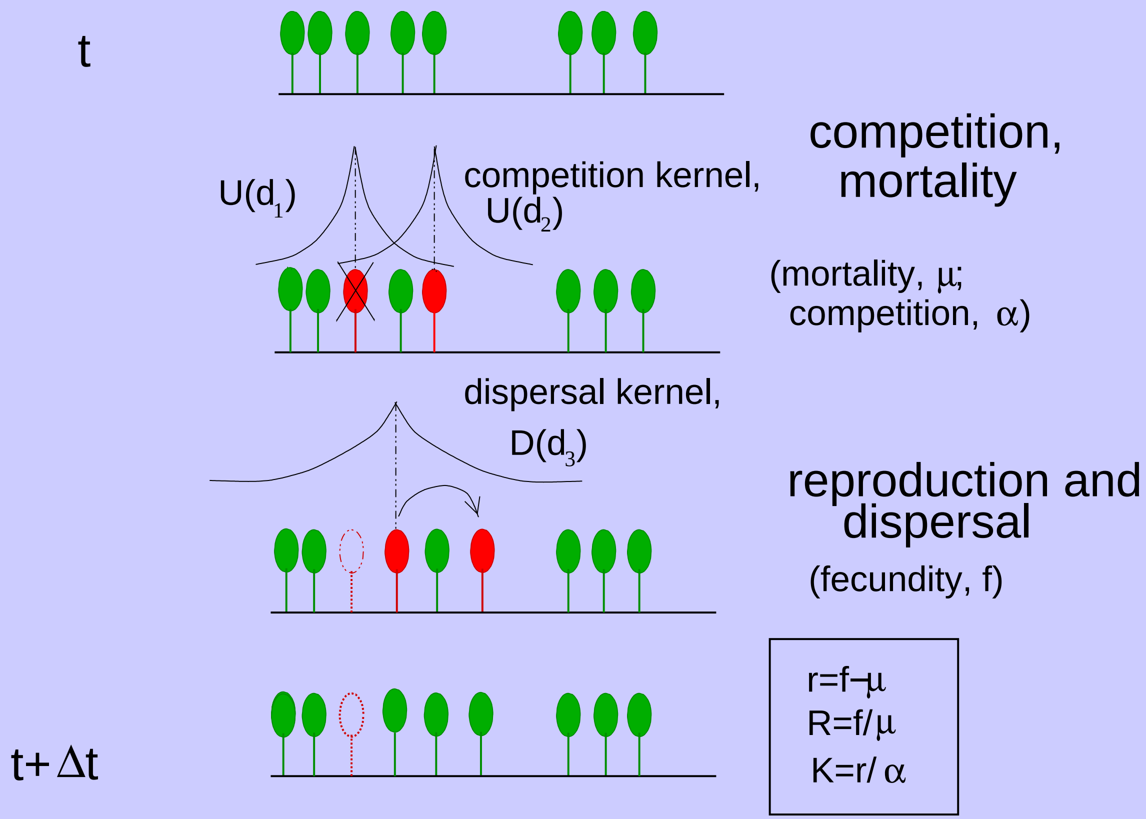
Spatial plant competition: strategies

- Colonization (ruderal)
- Exploitation (successional niche, competitive)

} r-selected, weedy, fugitive, early successional, guerrilla, high-R^*

- Tolerance (competitive, late-successional dominant, K-selected, phalanx, low-R^*)

Model: cartoon



Model: stochastic processes

Event	Result	Rate
birth	$N(\mathbf{x}) \rightarrow N(\mathbf{x}) + 1$	$\int_\Omega f N(\mathbf{y}) D(\lvert\mathbf{y} - \mathbf{x}\rvert) \omega d\mathbf{y}$
death	$N(\mathbf{x}) \rightarrow N(\mathbf{x}) - 1$	$N(\mathbf{x}) \left(\mu + \alpha \int_\Omega N(\mathbf{y}) U(\lvert\mathbf{y} - \mathbf{x}\rvert) d\mathbf{y}\right)$

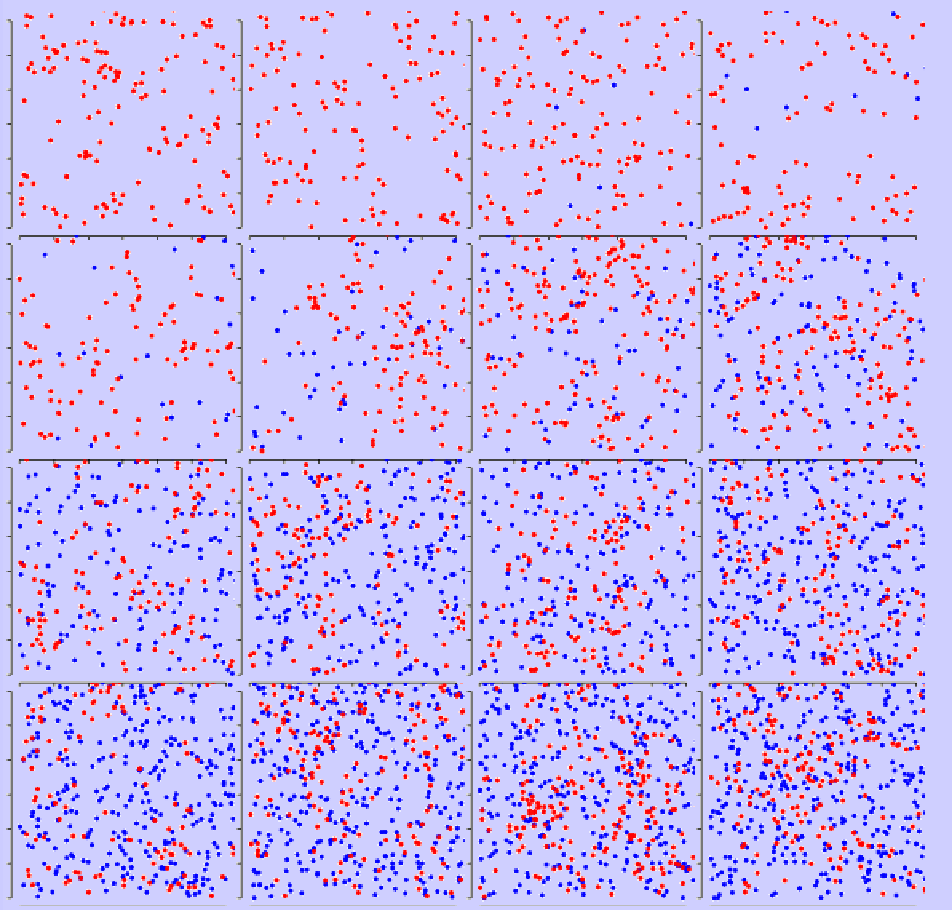
Competition-colonization trade-offs in a simulator

Many different models of CC share similar mechanisms.

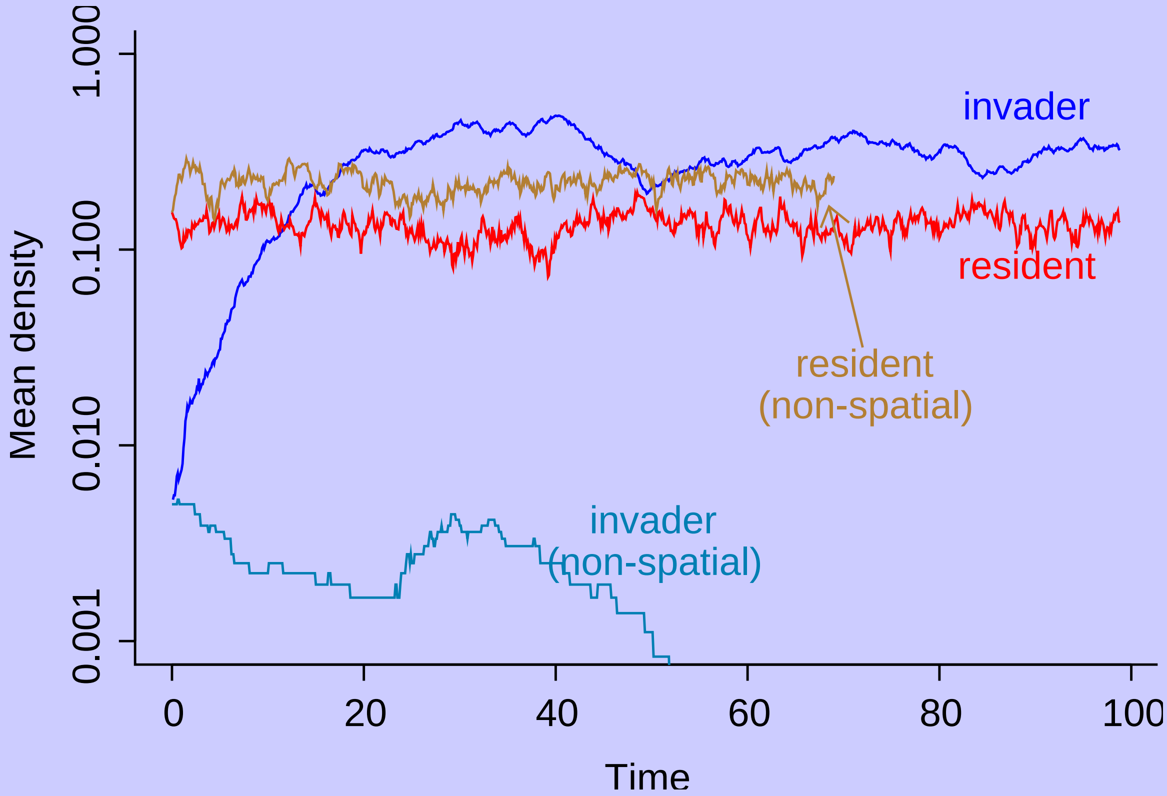
- One species competes better, the other colonizes better (disperses farther/higher fecundity)

- For CC, the better competitor must leave *open space* in the environment in monoculture

Competition-colonization: invasion sequence



Competition-colonization: invasion dynamics



Moment equations: beyond competition-colonization

- Define *spatial covariance*

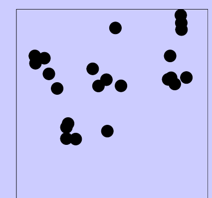
- Using stochastic equation for rates (from simulator)
  - Mean: derive expected change in population density
  - Covariance: derive expected change in *spatial covariance*
  - Close the system—*truncate* higher moments

- Analyze spatial population dynamics

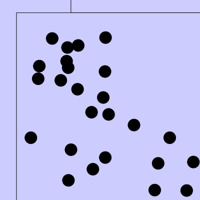
Spatial covariance

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

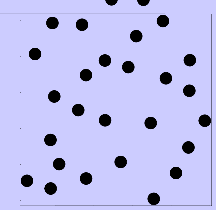
Positive covariance $\Longleftrightarrow$ clustering/association



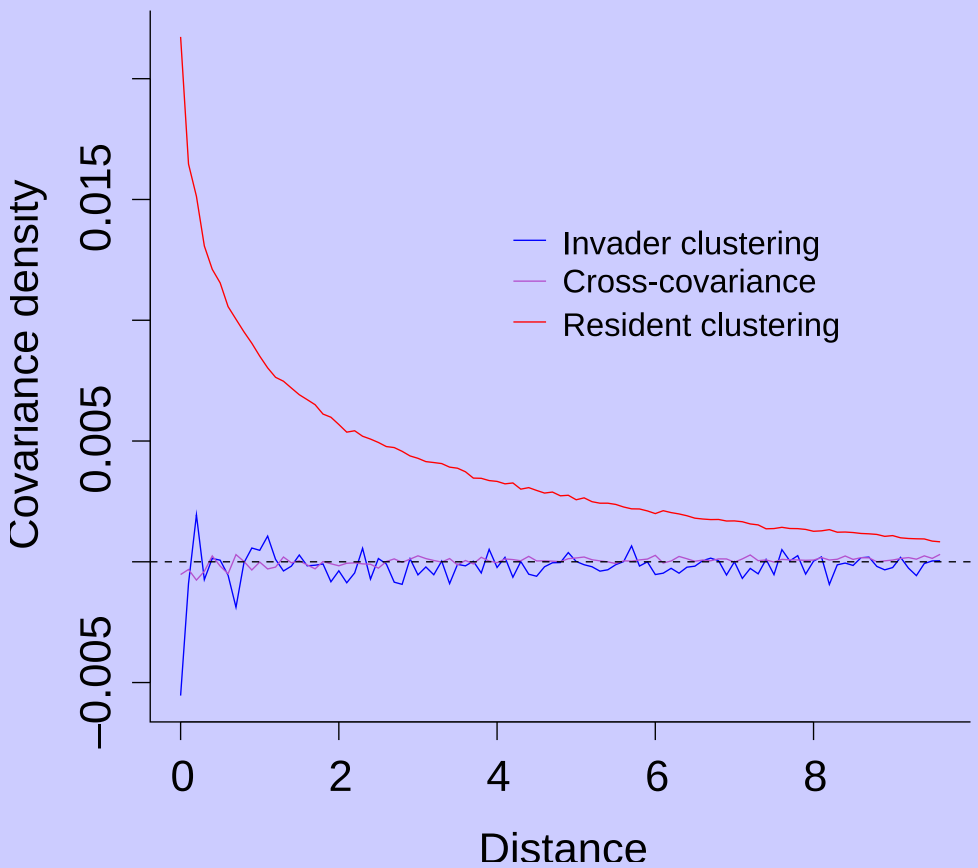
Zero covariance $\Longleftrightarrow$ random (Poisson)



Negative covariance $\Longleftrightarrow$ evenness/segregation



Spatial covariance



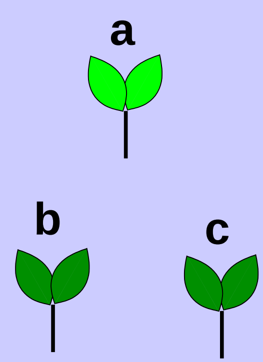
Moment closure

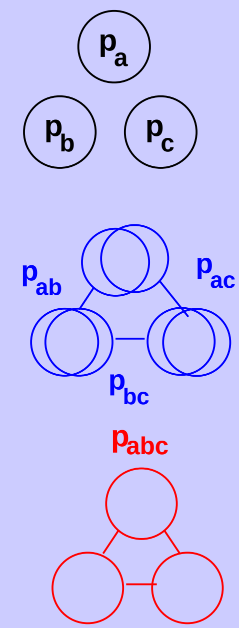
What about *higher moments*? **Closure rules**

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

- power-1: $p_{abc} =$
  $(p_a p_{bc} + p_b p_{ac} + p_c p_{ab})/3$

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





Moment equations: mean density

$$\frac{dn_i}{dt} = r_i n_i \left[1 - \frac{\overbrace{(n_i + \overbrace{\bar{c}_{ii}/n_i}^{\text{clustering}})}^{\text{neighborhood density}} + \alpha_{ij} \overbrace{(n_j + \overbrace{\bar{c}_{ij}/n_i}^{\text{segregation}})}^{\text{neighborhood density}}}{K_i} \right]$$

[$\bar{c}_{ij}$ is the *weighted covariance*: $\bar{c}_{ij} \equiv \int U_{ij}(x) c_{ij}(x)\, dx$]

plus equations for the changes in covariances $c_{11}(r)$, $c_{12}(r)$, $c_{22}(r)$ over time.

Moment equations: cross-covariance

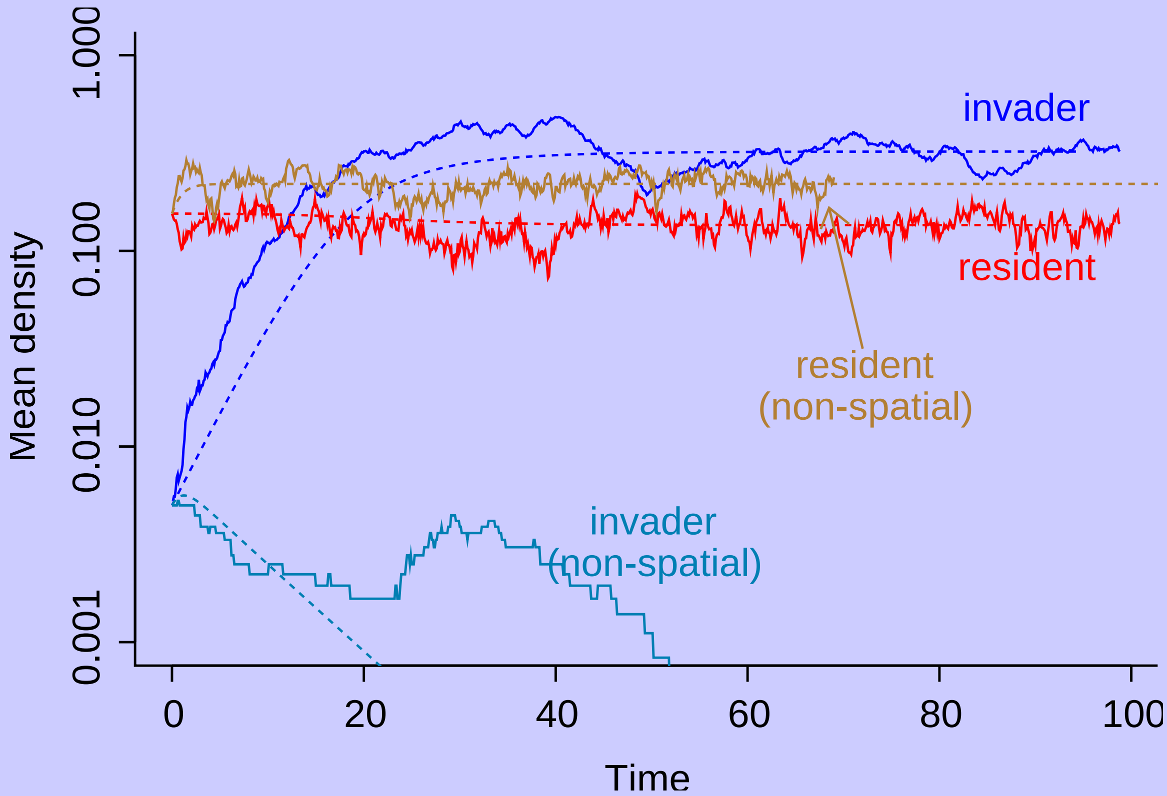
$$\frac{\partial c_{ij}(r)}{\partial t} = \underbrace{-(\mu'_i + \mu'_j)c_{ij}(r)}_{\text{random thinning}} + \underbrace{f_i(D_i * c_{ij})(r) + f_j(D_j * c_{ij})(r)}_{\text{clustering}}$$

$$- \sum_k \left[\alpha_{ik} \left(n_i(U_{ik} * c_{jk})(r) + n_k c_{ij}\right)\right]$$

$$- \sum_k \left[\alpha_{jk} \left(n_j(U_{jk} * c_{ik})(r) + n_k c_{ij}\right)\right]$$

$$\underbrace{\qquad\qquad - n_i n_j(\alpha_{ij}U_{ij}(r) + \alpha_{ji}U_{ji}(r))}_{\text{density-dependent thinning}}$$

Competition-colonization: predicted vs actual dynamics



Invasion criteria

Resident at equilibrium; invader at low density; spatial structure at *quasi-equilibrium*:

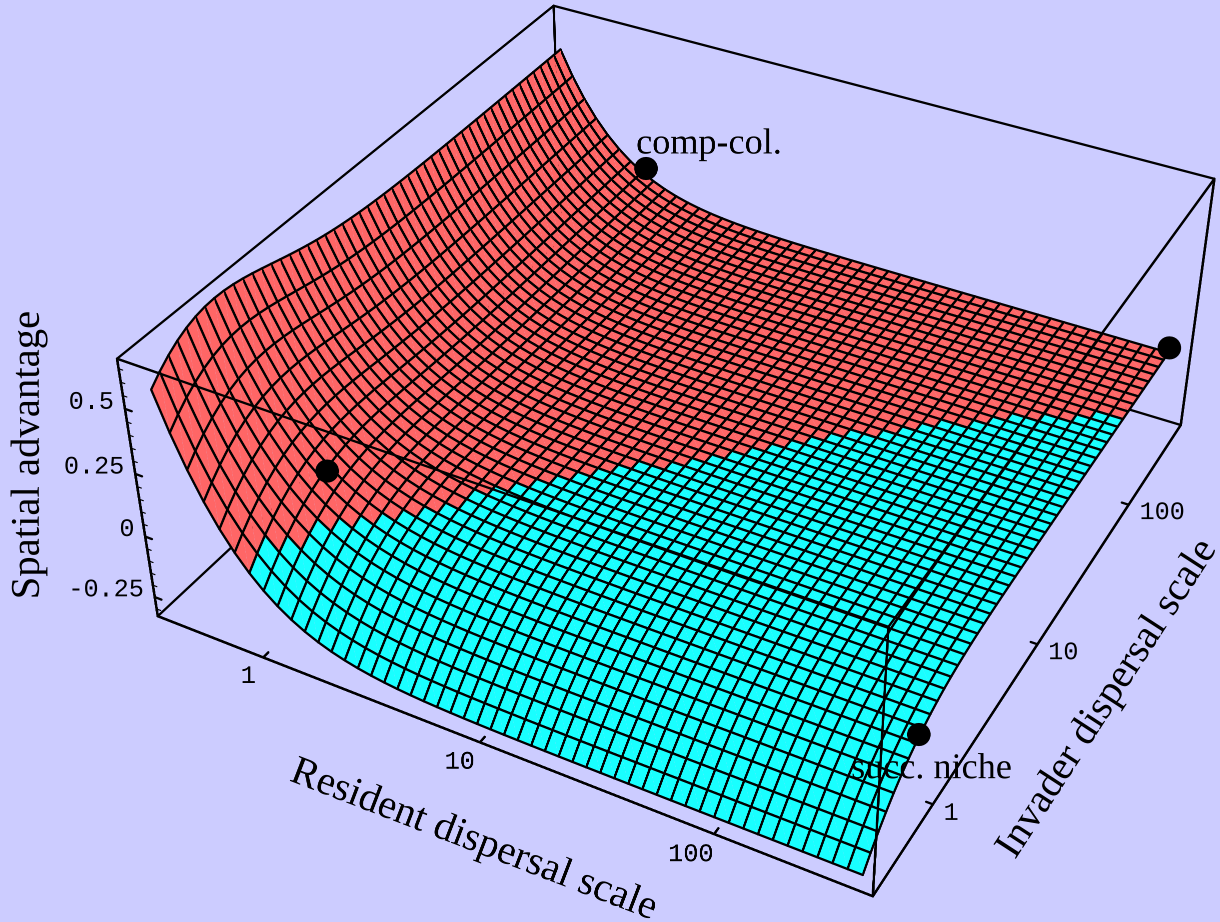
$$\text{invasion rate} = \underbrace{r_I \eta_{IR}}_{\text{non-spatial inv. rate}} - \underbrace{\alpha_{II} \frac{\bar{c}_{II}}{n_I}}_{\text{invader clustering}} + \underbrace{\alpha_{IR} \frac{\bar{c}_{RR}}{n_R}}_{\text{resident clustering}} + \underbrace{\alpha_{IR} \left(- \frac{\bar{c}_{IR}}{n_I} \right)}_{\text{spatial segregation}} > 0$$

Try to *partition* contributions to invasion speed from different strategies . . .

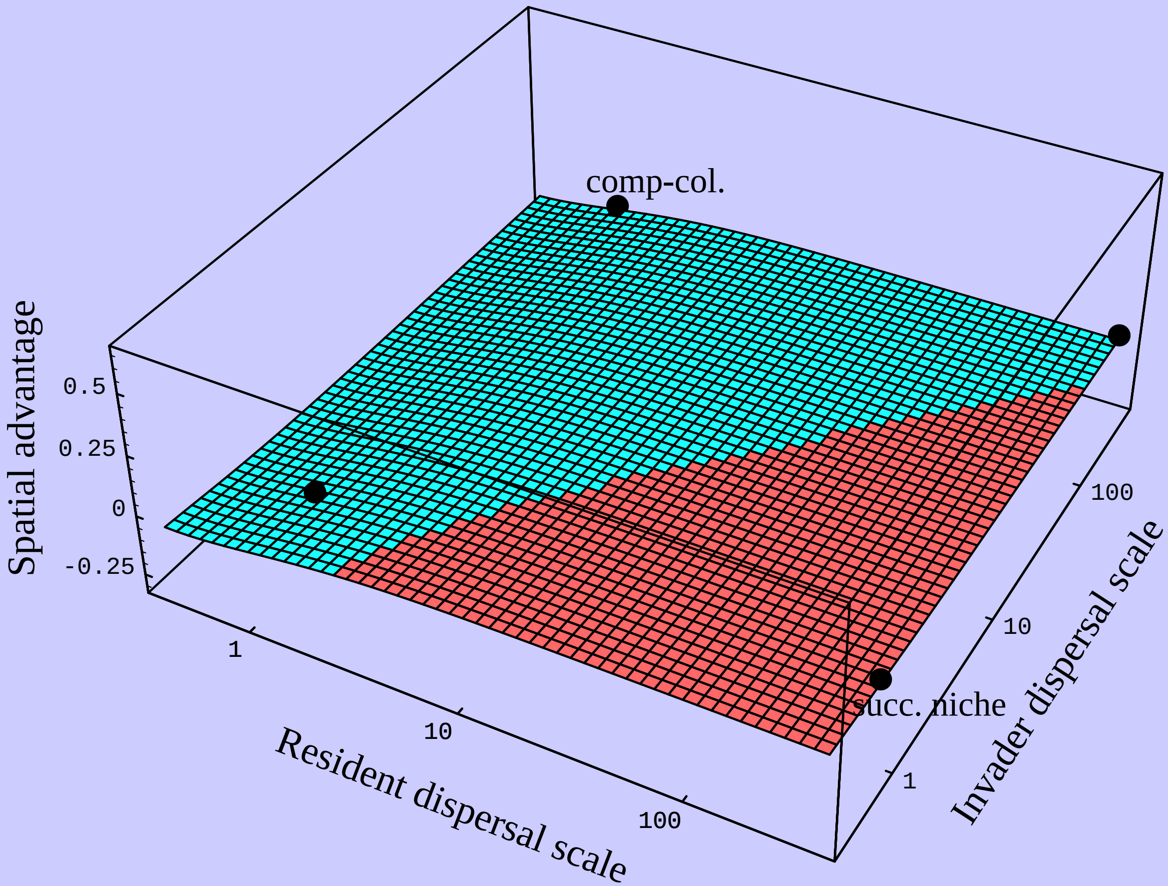
Intrinsic reproductive number: $R = \frac{f}{\mu}$

- appears in stochastic and spatial models
- determines *sensitivity to competition*: reduction in fecundity between empty habitat (R) and equilibrium density (1)
- large R helps in spatial competition—more offspring (even if most die) give better sampling of the environment

Low fecundity: $R_R = R_I = 1.2$



High fecundity: $R_R = R_I = 10$

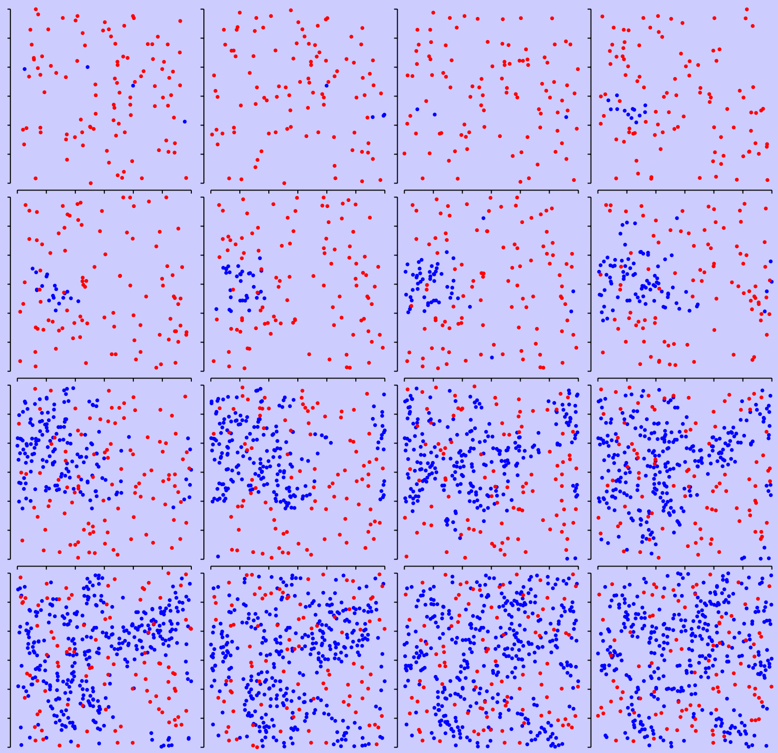


Short-dispersal strategies

Short dispersal can aid invasion/coexistence . . .

- Requires strong segregation and weak clustering (helps if both species have high R)
- Further partition strategies:
  - *Successional niche*: fast growth (high r), small individuals (large K)
  - *Phalanx strategy*: independent of r and K, but requires strong interspecific competition ('founder control" region)

Successional niche: invasion sequence



Are these strategies real?

Strategies are similar across model types: relative strength of strategies varies according to details

- Model-based tests of spatial coexistence
- Experimental tests of colonization limitation

How do we test for different strategies?

Experiments: comp-col. (CC) vs. successional niche (SN)

randomize sp. 1	randomize sp. 2	conclusion
—	2 ↑, 1 ↓	sp. 1 maintained by CC
1 ↑, 2 ↓	—	sp. 2 maintained by CC
1 ↓	—	sp. 1 maintained by SN
—	2 ↓	sp. 2 maintained by SN
1 ↓	2 ↓	phalanx/spatial segregation

Spatial competition: conclusions

- Spatial ecological dynamics as spatial covariance dynamics
- Strategies (CC, SN, phalanx) partition spatial variance
- Empirical work in progress: still don't know where/how spatial coexistence occurs

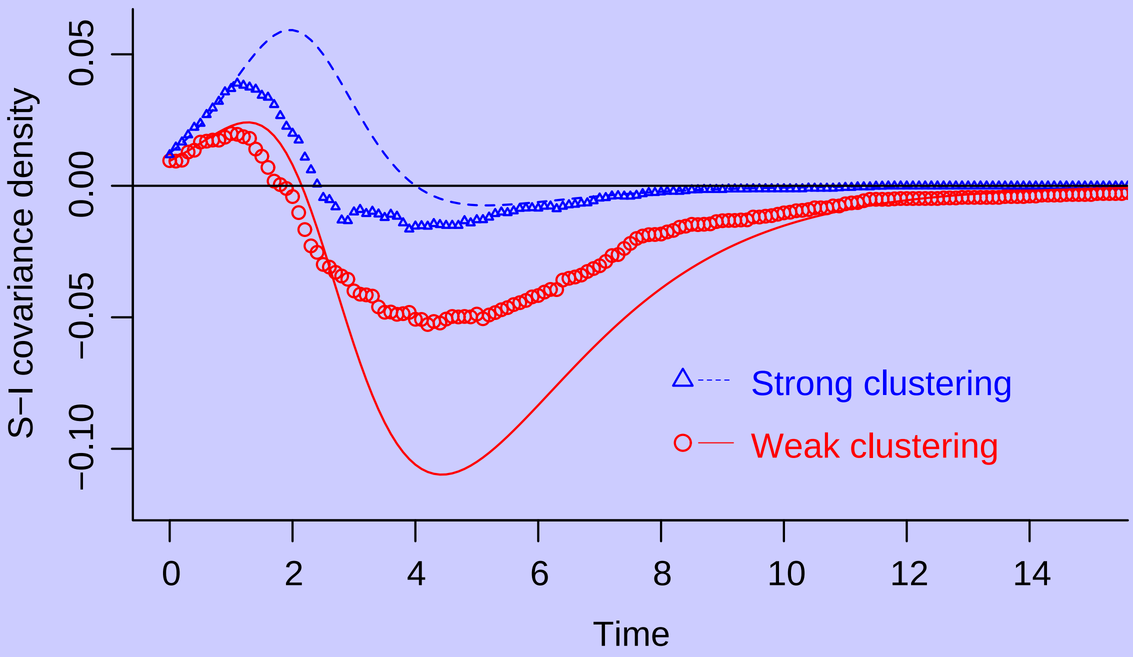
III. Moment equations: other applications

- Spatial epidemics
- Habitat degradation and refuge use
- Spatial synchrony

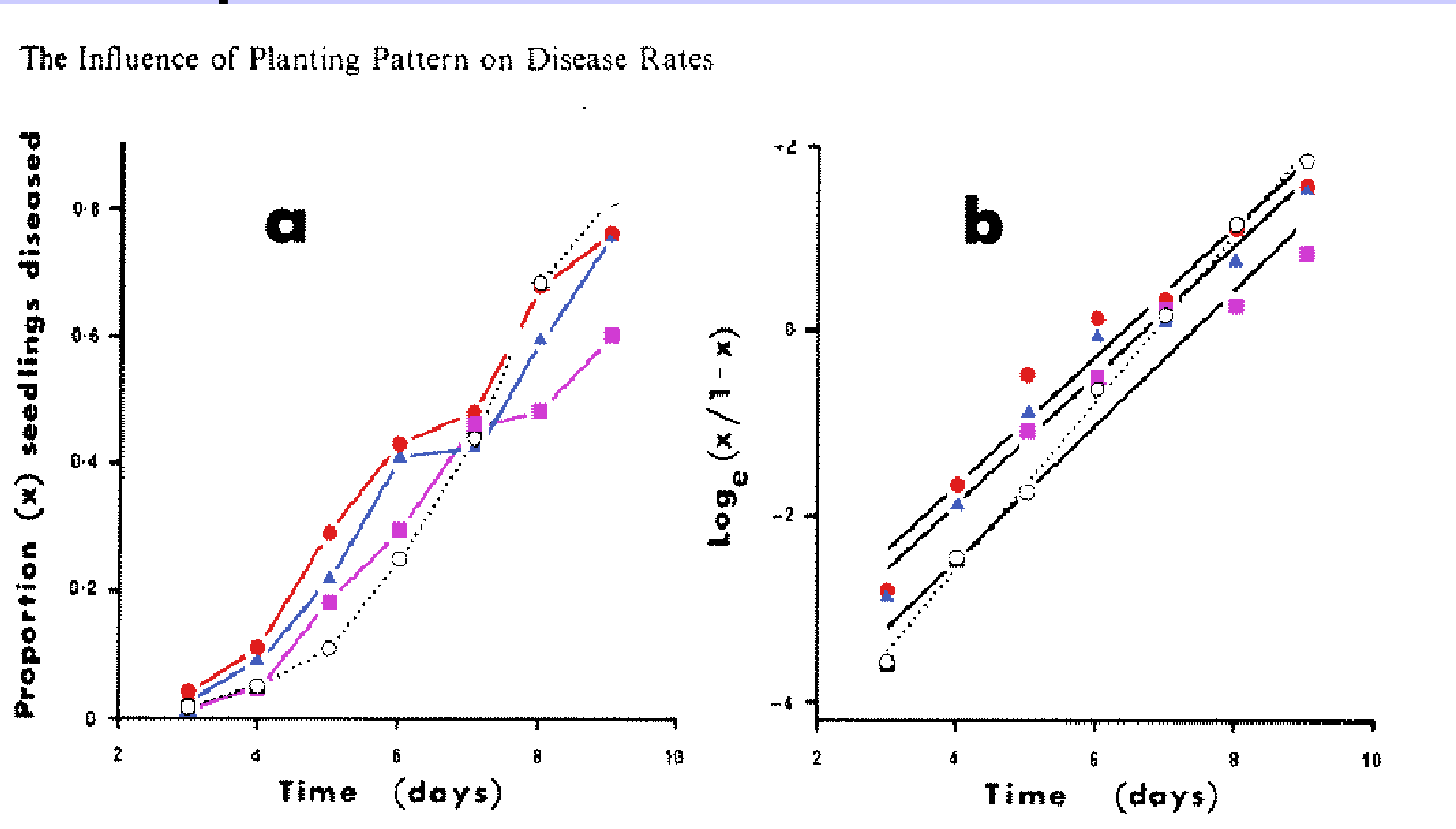
Spatial epidemics

- Within-field patchy epidemics: multiple foci
- How does host clustering affect spread?

Epidemics: susceptible-infective (SI) covariance



Experimental data: Burdon & Chilvers

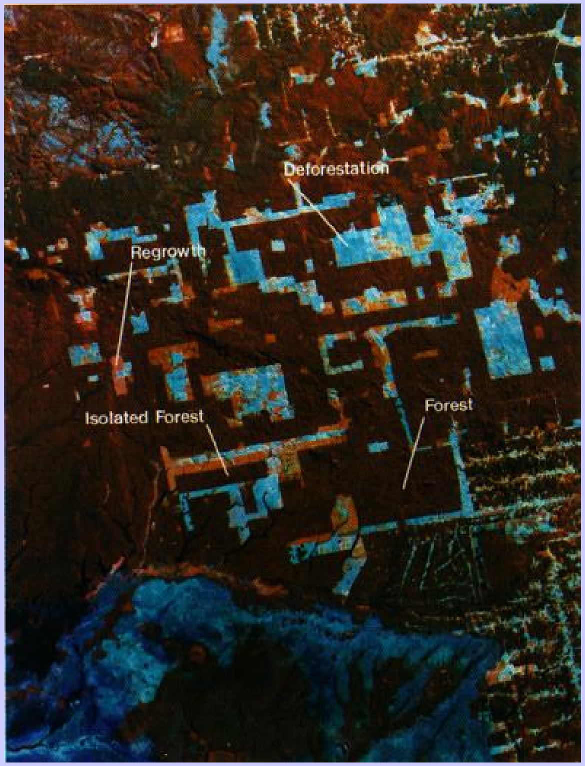


Spatial epidemics: conclusions

- Infective patchiness builds up over time; initially *accelerates* but then *decelerates* the epidemic ("burn-out" of clusters).

- (Brown) with Poisson-distributed hosts, local dispersal always increases the *epidemic threshold*; with clustered hosts, intermediate dispersal distance maximizes disease invasion

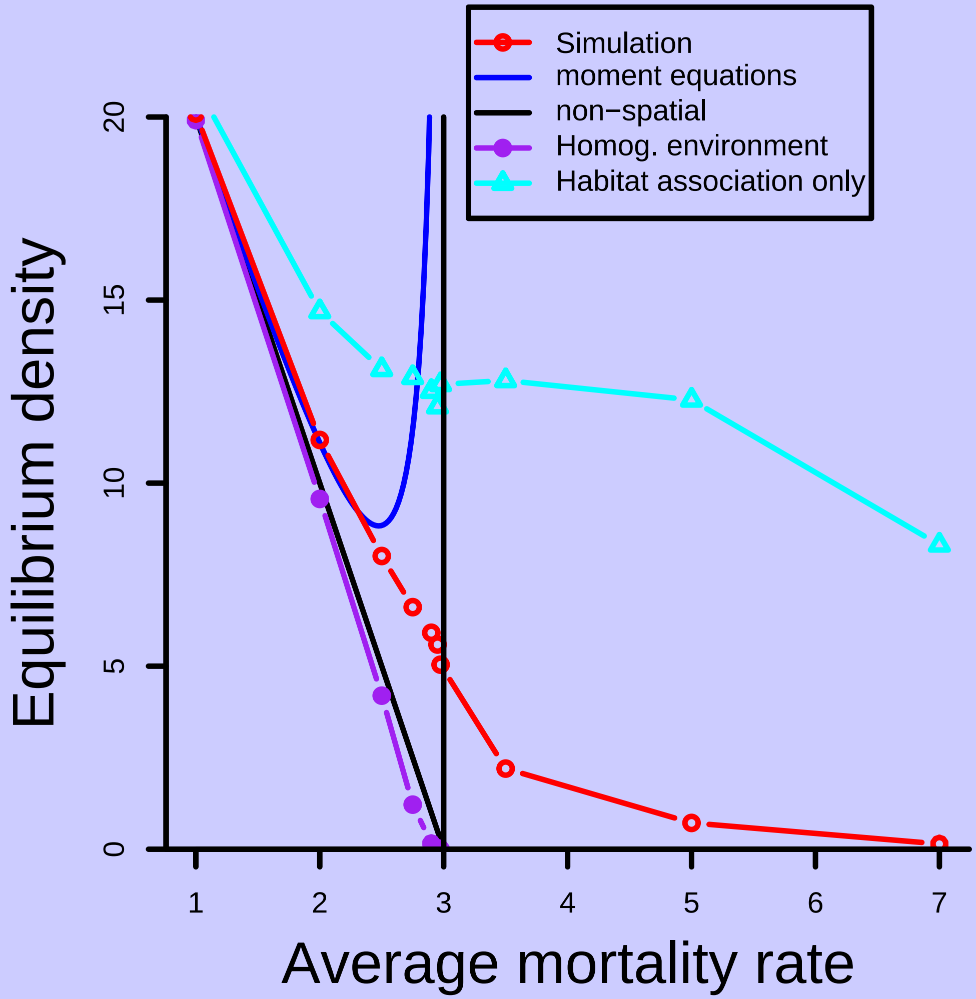
Refuge use



(Skole and Tucker *Science* 1991)

- Habitat destruction, degradation, and fragmentation
- How do spatial pattern and dispersal affect population viability?

Habitat degradation: results



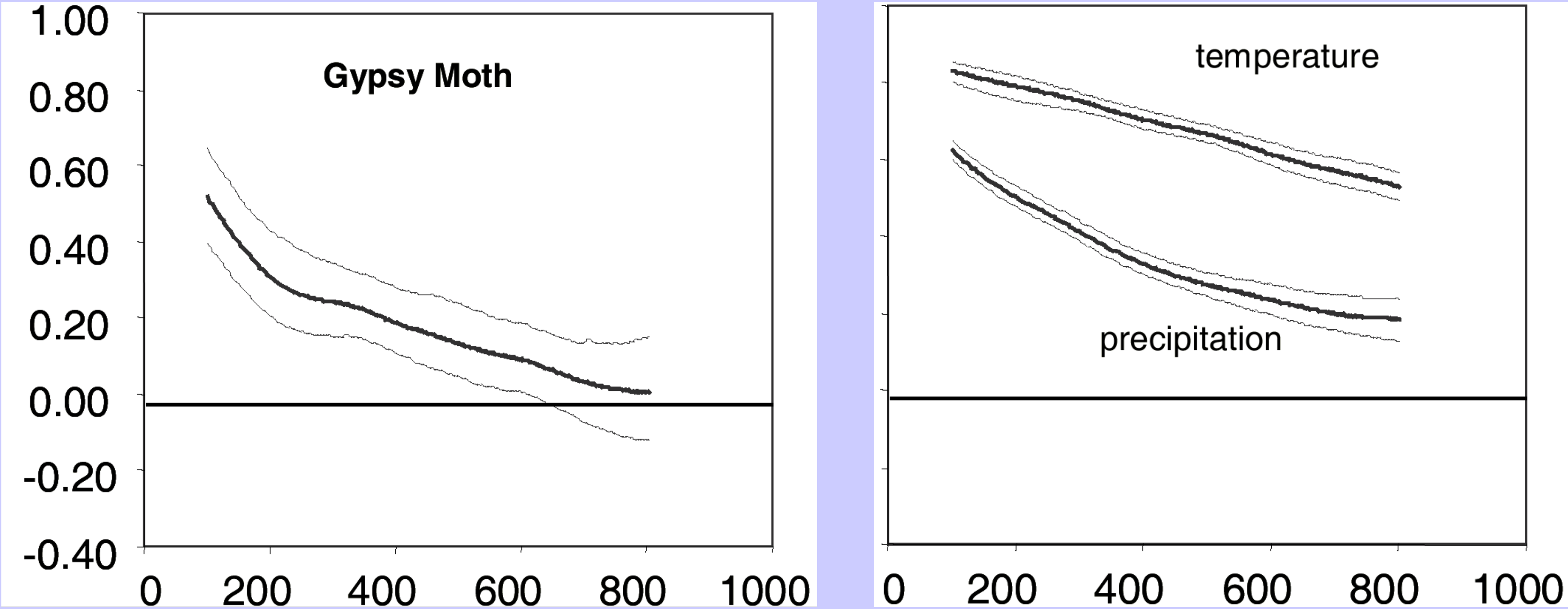
Refuge use: conclusions

- Short dispersal is *advantageous* (at first) in structured landscapes
- low-R species actually do better
- Caveats: fragmentation, temporal variation; need more detail for reliable predictions

Spatial synchrony

Large-scale synchronization in populations: why?

- *Moran effect*: spatial variation in (e.g.) weather drives spatial synchrony with the same pattern
- dispersal linkage
- nomadic predators



(Peltonen *et al.* 2002)

Deconvolution

Spatial pattern with dispersal and environmental variability:

$$\tilde{c}_{\mathsf{pop}} = \frac{\tilde{c}_{\mathsf{env}}}{\gamma + \tilde{D}}$$

- Separate exogenous and endogenous patterns by calculating spectra
- Very preliminary, but offers a way of *partitioning*

Conclusions

- Moment equations: a nice tool (with limitations)
- Reveal *generality* of spatial mechanisms, unify dynamics in patchy and continuous landscapes
- Many extensions: heterogeneity, different ecological settings; open mathematical questions?
- May bridge the gap between simulators and analytic theory

IV. Meta-ecology

- tools vs. questions
- qualitative vs. quantitative (statistical) questions
- theoretical ecologists: hosts, parasites, or mutualists?

Acknowledgements

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