Continuous-space models for (ecological) population dynamics

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Outline

Model classes

Space	Time	Populations	Stoch?	Model
discrete	discrete	discrete	no	cellular automaton
discrete	discrete	discrete	yes	probabilistic (stochastic) CA
discrete	discrete	continuous	maybe	coupled-map lattice
discrete	continuous	discrete	yes	interacting particle system $\approx$ pair approximation
continuous	discrete	continuous	maybe	integrodifference eq'ns
continuous	either	discrete	yes	spatial point process $\approx$ spatial moment equations
continuous	continuous	continuous	no	integrodifferential, partial differential (reaction-diffusion) eq'ns
continuous	continuous	continuous	yes	stochastic integro/ partial diff. eq'n

Model preferences: realism?

- **contiguous** (lattice/network) vs. **continuous** space: networks may or not be spatial
- What is special about space? (Bolker et al., 2003)
- PDEs, invasion waves (Fisher etc.)
- lattice models (IPS, CA/pair approximation): Durrett and Levin (1994)
- "realism": points or a square (or hexagonal) lattice? Connections to data . . .

Outline

1. Define the system (write **master equation**)
2. Write expectations of change in mean and pair densities
3. Assume spatial homogeneity
4. Expand products as covariances
5. Close moments
6. Take continuum limits
7. Analyze? Solve numerically?

Master equation

Define rates of a continuous-time stochastic process: patch size ω (small), positions $\mathbf{x}$, $\mathbf{y}$, time Δt (small): e.g. the **spatial logistic** (with environmental heterogeneity in mortality rate):

Event	$\delta N(x)$	Rate
birth	+1	$\sum_{\mathbf{y}\in\Omega} fN(\mathbf{y})\mathcal{D}(\mathbf{y},\mathbf{x})\omega$
death (dens-independent)	-1	$\mu(\mathbf{x})N(\mathbf{x})$
death (crowding)	-1	$N(\mathbf{x})\sum_{\mathbf{y}\in\Omega} \alpha N(\mathbf{y})\mathcal{U}(\mathbf{y},\mathbf{x})$

All **kernels** are symmetric (relax??) and normalized: $\sum_{\mathbf{y}\in\Omega} \mathcal{K}(\mathbf{y})\omega = 1$

Alternatives

- more rigorous derivations: start from point-process description, or rigorous patch description (Nevai, Barton et al. (2002), Ovaskainen and Cornell (2006), most of yesterday)
- movement (jump processes)
- disturbance (spatially correlated mortality)
- traits (marked point processes)

Difficulties

- multi-way interactions (e.g. twinning, indirect interactions)
- "velocity jump" processes
- density-dependent dispersal distance

Calculate expectations

Take expectations (1) over possible future outcomes, given starting conditions:

$$\overline{\Delta N} = \sum \text{rate}_i \cdot \delta_i$$

and (2) over all **configurations** with **current** summary statistics . . .

$$\langle \overline{\Delta N} \rangle = \left\langle \sum \text{rate}_i \cdot \delta_i \right\rangle$$

Challenges

- space-for-configuration substitution? ergodicity/homogeneity?
- non-homogeneous starting conditions?

Expected change in density

We get

$$\left\langle \overline{\frac{dN(\mathbf{x})}{dt}} \right\rangle = \left\langle \sum (\text{rate}_i \cdot \delta_i) \right\rangle$$

$$= f \sum_{\mathbf{y}} D(\mathbf{x}, \mathbf{y}) \langle N(\mathbf{y}) \rangle$$

$$- (\bar{\mu} + \alpha \langle N(\mathbf{x}) \rangle) \langle N(\mathbf{x}) \rangle$$

$$- \sum_{\mathbf{y}} \alpha U(\mathbf{x}, \mathbf{y}) \langle (N(\mathbf{x}) - \langle N(\mathbf{x}) \rangle)(N(\mathbf{y}) - \bar{N}(\mathbf{y})) \rangle$$

$$- \langle (\mu(\mathbf{x}) - \bar{\mu}) N(\mathbf{x}) \rangle$$

Expectations of pair changes

$$\left\langle \overline{\frac{dN(\mathbf{x})N(\mathbf{y})}{dt}} \right\rangle = f \sum_{\mathbf{y}} D(\mathbf{y},\mathbf{x}) \langle N(\mathbf{y})N(\mathbf{z}) \rangle - \langle \mu(\mathbf{x})N(\mathbf{x})N(\mathbf{y}) \rangle - \alpha \sum_{\mathbf{y}} \langle N(\mathbf{x})N(\mathbf{y})N(\mathbf{z}) \rangle$$

plus symmetric terms

Assume spatial homogeneity

Assume **second-order spatial homogeneity and isotropy**: i.e., that any $\langle f(\mathbf{x}, \mathbf{y}) \rangle$ depends only on $|\mathbf{x} - \mathbf{y}|$

Alternatives

- Gradients
- Distance from edge of wave ("pair-edge approximation":
- Habitat boundaries? (Finite spatial patches?)

Expand covariances

Convert expectations of products (second **central** moments) to covariances (**noncentral** moments):

$$\langle (N(\mathbf{x}) - \bar{N})(N(\mathbf{y}) - \bar{N}) \rangle \equiv C_{NN}(|\mathbf{x} - \mathbf{y}|)$$

Also have $C_{\mu N}$, $C_{\mu\mu}$ (assumed static); also higher central moments $M^3_{N,N,N}$ (etc.)

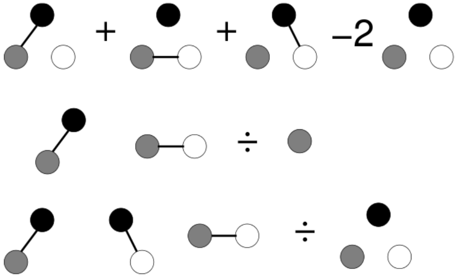
Alternatives:

- work with **central** moments instead
- scaled covariances (C/N), correlations (C/N^2)?
- multiplicative correlations (Keeling)

Moment closure

Power-1, -2, -3: e.g.

$$P(x,y,z) = P(x)P(yz)+P(y)P(xz)+P(x)P(yz)-2P(x)P(y)P(z)$$



Symmetric and asymmetric alternatives

Criteria for moment closure

- Analytical tractability (!)
- Invariance under relabeling (Murrell et al., 2004)
- Asymptotic convergence to mean-field
- Non-negativity (Murrell et al., 2004)
- Sensible **quasi-equilibrium** ($\lim_{N \to 0} C/N$) behavior

Invasion phases (digression)

- Early invasion: both local and global density $\ll 1$
- "Quasi-equilibrium": local structure established (invasion eigenvalue) [**stable manifold**]
- **Spread**: local structure at equilibrium, global structure out of equilibrium
- ...
- Equilibrium local and global structure

Mean should increase exponentially (non-spatial or spatial rate?), then quadratically ... may be hard to separate time scales (Mollison)
Edge approximations?

Continuum limits

$$n = \lim_{\omega \to 0} N/\omega$$

$$c = \lim_{\omega \to 0} C/(\omega^2)$$

- End up with important **singular** terms (Dirac δ): because individuals are discrete, $N(\mathbf{x})^2$ scales with ω rather than ω^2
- Could easily define other variance scaling (negative binomial?), in an **ad hoc** way ...
- Environmental variables (μ) scale as continuum rather than discrete variables (**intensive** vs. **extensive**)
- Moment equations on finite patches?

Analysis/solution

- Kernel choices: Laplacian, modified Bessel, "top hat" (Birch and Young, 2006; Ovaskainen and Cornell, 2006)): compact support works
- Dimensionality
- Parameter choices: length scale (competition vs dispersal vs environment), **effective neighborhood size**
- Fourier or Hankel transform often simplifies analysis (but again depends on closure)

electric monk: automatic moment equations

High-throughput math biology?

> *The Electric Monk was a labour-saving device, like a dishwasher or a video recorder. Dishwashers washed tedious dishes for you, thus saving you the bother of washing them yourself, video recorders watched tedious television for you, thus saving you the bother of looking at it yourself; Electric Monks believed things for you, thus saving you what was becoming an increasingly onerous task, that of believing all the things the world expected you to believe . . .*
>
> Douglas Adams, *Dirk Gently's Holistic Detective Agency*

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```
eqs = {
        {{n1[x]},{+1}, int[f1*Dk1[y-x]*n1[y],y]},
        {{n1[x]},{-1}, mu[x]*n1[x]},
        {{n1[x]},{-1}, a11*int[Uk[y-x]*n1[y],y]*n1[x]},
        {{mu[x]}, {0}, 0}  (* mu static *)
};
ContVarList={mu};
ceqs0 = resort[coveqs[DDMeqs1],3] //. intrules;
ceqs1 = closeM[noselfcomp[ceqs0,{Uk}],
              order->3,closure->power1,
              singm->True] //. intrules;
Expand[Simplify[implicitvar[ceqs1]]]
```

Power-1 closure

$$\frac{\partial c_{\mu n}}{\partial t} = f\mathcal{D} * c_{\mu n} - \mu c_{\mu n} - \alpha n\mathcal{U} * c_{\mu n} - \alpha n c_{\mu n} - n c_{\mu\mu}$$

$$\frac{1}{2}\frac{\partial c_{nn}}{\partial t} = f\mathcal{D} * c_{nn} - \mu c_{nn} - \alpha n\mathcal{U} * c_{nn} - \alpha n c_{nn} - n c_{\mu n} + f\mathcal{D}n - \alpha\mathcal{U}n^2$$

Analysis

- Power-1 closure gives **linear** covariance equations
- If n is close to mean-field eq., can compute equilibrium covariances
- Fourier transform of Laplacian $e^{-\lambda|x|}$ is $\frac{\lambda^2}{\lambda^2+q^2}$: ditto for Hankel transform of K_0. Simple algebra for rational functions of kernels (partial fractions)
- numerical solutions (may be faster in radially symmetric/Fourier space)

integro-PDE analogue

$$\frac{\partial n(x,t)}{\partial t} = f(D * n) - \mu(x)n(x) - \alpha n(x)^2$$

Try to simplify the equations by assuming (1) short-range kernels (changes kernels to diffusion operators), (2) local interactions: do we get to the naive reaction-diffusion equation? (Nevai)

Exploiting linearity

With $\mathbf{v} = (\tilde{c}_{\mu n}\tilde{c}_{nn})^T$ and $\phi = f\tilde{D} - \mu - \alpha n(\tilde{U}+1)$,

$$\frac{\partial \mathbf{v}}{\partial t} = \begin{pmatrix} \phi & 0 \\ -n & \phi \end{pmatrix} \mathbf{v} + \begin{pmatrix} -nc_{\mu\mu} \\ (f\tilde{D} - \alpha\tilde{U}n)n \end{pmatrix}$$

or

$$\tilde{c}^*_{\mu n}/n = c_{\mu\mu}/\phi$$
$$\tilde{c}^*_{nn}/n^2 = \frac{(f\tilde{D} - \alpha\tilde{U}n)}{n\phi} + \frac{c_{\mu\mu}}{\phi^2}$$

...defining a **spatial transfer function**.
Deconvolution??

Outline

What do ecologists want?

- general answers
- quantitative solutions (maybe)
- answers to open ecological questions
- simple analytical frameworks
- incorporation of environmental heterogeneity

not:

- rigorous proofs
- dependence on details
- complex algebra
- self-organization, changes in stability, complex dynamics for their own sake

Invasive species/epidemics/biocontrol

- Species invasion
  - Can species x invade environment y (i.e. grow when [globally] rare)?
  - How fast does the range of species x expand? Does range expansion decelerate, accelerate, or stabilize over time?
- What matters?
  - life history (birth/death rates)
  - competition
  - environmental variability (space & time)
  - demographic stochasticity (?)
  - evolution

Species coexistence

- What maintains **intra-guild** diversity?
  - Tradeoffs in space use ("competition-colonization tradeoffs")?
  - Other correlated tradeoffs in growth rate, fecundity, "competitive ability", dispersal in space & time (Snyder 2006)?
  - Is diversity enhanced by spatiotemporal heterogeneity? How? Under what conditions can organisms maintain/benefit from niche separation?
  - Janzen-Connell (positive frequency-dependent) models
  - Structured many-species models

Neutral theories

- Is the spatial/temporal pattern of species within guilds consistent with a **neutral** (symmetric, exchangeable) model? (urn models)
- What are the expected spatial/temporal/ rank-abundance distributions, and variations around those expectations, under various models (Chave and Leigh, 2002)? Can we quantify/ estimate parameters for divergence?

Community dynamics

- What is the expected spatial distribution of **natural enemies** and victims?
- How do enemies affect spatial patterning of victims?
- Feedbacks between spatiotemporal enemy-victim dynamics and overall densities . . . effects on species coexistence? (Adler and Muller-Landau, 2005) On population dynamics (cycles etc.)?
- Food webs and food web modules (apparent competition, etc.) in space
- Mutualism, parasitism, coevolution?

Trait dynamics

- Important in its own right, also as a different kind of space
- Vertical (height) structure: Picard and Franc (2001) (not really!)
- Size structure (Delius)
- Quantitative genetic models?

More . . .

- Advection terms/velocity-jump models
- Behavior (density-dependent? dispersal, foraging) (Marion)
- Zeros and local fade-out: Clark et al. (2001), Boerlijst. Probability of extinction on a finite patch? (Marion?)
- Discrete time

Connections with data

- Does knowing the **expected** correlation structure help us fit models? Do we need to derive the moments of the correlation structure itself?
- Is deconvolution possible? Easy?

Ecological questions: invasion

- Can a population grow when rare? (Is the "invasion eigenvalue" > 0? What is the value of R_0?) (Bound mean density away from zero?)
- How fast does a species invade a novel habitat (wave speed)? (Ellner et al., 1998; Lewis, 2000; Lewis and Pacala, 2000; Neubert and Caswell, 2000)
- Community dynamics: if N species have stable equilibria, can the $N+1^{\text{st}}$ species invade?
- **permanence**: are the dynamics bounded in the space where all species have positive density?
- invader growth rates under nonequilibrial resident dynamics?

Ecological questions: equilibria

- Does a non-trivial equilibrium exist?
- How do changes in parameters, qualitative changes to the model, affect stability?
- Transient dynamics . . .

Spatial models in ecology: goals

- capture qualitative (**quantitative?**) dynamics of (real) ecological communities
- desiderata ("good, cheap, fast: pick 2 out of 3":
  - analytical tractability
  - computational efficiency
  - realism:
    - stochasticity (demographic & environmental)
    - geometry of space and time

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