Diffusion approximation for a spatially realistic structured metapopulation model

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What is a metapopulation?
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- A Population inhabiting geographically separated habitat
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- Different patch sizes
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- A Population inhabiting geographically separated habitat
  - Different patch sizes
  - Spatial structure
  - Heterogenous landscape
Analytical Models

- Presence-absence
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- Homogenous patch sizes
Analytical Models

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- Homogenous patch sizes
- No spatial structure - homogenous mixing
Realistic Models

- Simulation models
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- Day and Possingham (1995)
  - Variability in patch size and position
  - Discrete-time Markov chain
Realistic Models

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  - Variability in patch size and position
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- But...
  - does not account for local population dynamics
  - computationally intensive ($2^k \times 2^k$ for a $k$-patch system)
My model

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- Variability in patch position and inter-patch landscape
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- Incorporates local population dynamics
- Analytically tractable
- Surprise surprise... a continuous-time Markov chain!
Why do we need such a model?

- Effect of relative patch sizes?
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- Reserve network design and decision theory
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- Patch abundance - local population dynamics?
The model - parameters

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- $\mu$ - per-individual death rate
- $e_i$ - $i$-th unit vector
The model - CTMC

We denote the population size at time $t$ by $n(t)$.
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$$Q = (q(i, j), i, j \in S),$$

so that $q(i, j)$ represents the rate of transition from state $i$ to state $j$, for $j \neq i$, and $q(i, i) = -q(i)$, where

$$q(i) := \sum_{j \neq i} q(i, j) (< \infty)$$

represents the total rate out of state $i$. 
The model - transition rates

Birth

\[ q(n, n + e_i) = b \frac{n_i}{N_i} (N_i - n_i), \quad \forall i \in K \]

Migration

\[ q(n, n - e_i + e_j) = \gamma_{ij} \frac{n_i}{N_j} (N_j - n_j), \quad \forall i \neq j, i, j \in K \]

Death

\[ q(n, n - e_i) = \mu n_i, \quad \forall i \in K \]

where \( K = \{1, \ldots, k\} \).
Density-dependence

**Definition:** A one-parameter family of Markov chains \( \{P_\nu, \nu > 0\} \) with state space \( S_\nu \subset \mathbb{Z}^D \) is called density dependent if there exists a set \( E \subseteq \mathbb{R}^D \) and a continuous function \( f : E \times \mathbb{Z}^D \rightarrow \mathbb{R} \), such that

\[
q_\nu(k, k + l) = \nu f \left( \frac{k}{\nu}, l \right), \quad l \neq 0.
\]

[Kurtz (1970)]
**Theorem:** Suppose that $f(x, l)$ is bounded for each $l$ and that $F$, where $F(x) = \sum_l lf(x, l)$, is Lipschitz continuous on $E$. Then, if

$$\lim_{\nu \to \infty} X_\nu(0) = x_0,$$

we have, for fixed $\tau > 0$ and for all $\epsilon > 0$, that

$$\lim_{\nu \to \infty} Pr \left( \sup_{t \leq \tau} |X_\nu(t) - X(t, x_0)| > \epsilon \right) = 0,$$

where $X(\cdot, x)$ is the unique trajectory satisfying

$$X(0, x) = x, \quad X(t, x) \in E, \quad 0 \leq t \leq \tau, \quad \frac{\partial}{\partial t} X(t, x) = F(X(t, x)).$$

[Kurtz (1970)]
Functional central limit theorem

\[ \sqrt{\nu} \left( X_\nu(t) - X(t, x_0) \right) \to \text{Gaussian Diffusion} \]

\[ \sqrt{\nu} \left( X_\nu(t) - x^* \right) \to N(0, \Sigma_t) \]

Long-term

\[ \mathbb{E}(X_\nu) \approx x^* \]

\[ \text{Var}(X_\nu) \approx \frac{1}{\nu} \Sigma \quad \text{where} \quad \Sigma = \lim_{t \to \infty} \Sigma_t. \]

[Kurtz (1971)]
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If we take the maximum population size of the metapopulation network, $N = \sum_{i=1}^{k} N_i$, as our index parameter.
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Density-dependence

If we take the maximum population size of the metapopulation network, \( N = \sum_{i=1}^{k} N_i \), as our index parameter and define \( X_i(t) = n_i(t)/N \) to be the population densities and the limiting proportion of patch carrying capacities to be \( \rho_i = \lim_{N \to \infty} N_i/N, i \in K = \{1, 2, \ldots, k\} \), we can define a continuous function \( f : E \times \mathbb{Z}^k \to \mathbb{R} \), where 
\[
E = \{X \in [0, \rho_1] \times \cdots \times [0, \rho_k]\},
\]
as follows:

\[
f(x, x + e_i) = b \frac{x_i}{\rho_i} (\rho_i - x_i), \quad \forall i \in K
\]

\[
f(x, x - e_i + e_j) = \gamma_{ij} \frac{x_i}{\rho_j} (\rho_j - x_j), \quad \forall i \neq j, i, j \in K
\]

\[
f(x, x - e_i) = \mu x_i, \quad \forall i \in K.
\]
Deterministic approximation

The functional law of large numbers gives us

$$\frac{dx}{dt} = F(x)$$

Therefore we have a system of $k$ differential equations with the $i$-th given by

$$\frac{dx_i}{dt} = \left( b - \mu - \sum_{j \neq i} \gamma_{ij} \right) x_i + \sum_{j \neq i} \gamma_{ij} x_j + \frac{x_i}{\rho_i} \left[ \sum_{j \neq i} \frac{\gamma_{ij}}{\rho_j} x_j (\rho_i - \rho_j) - bx_i \right]$$
Special case - 2 equal patches

\[
\frac{dx_1}{dt} = \left( b - \mu - \gamma - \frac{b}{\rho} x_1 \right) x_1 + \gamma x_2
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Fixed points and stability

Trivial fixed point: \((0, 0)\)
Stable if \(b - \mu < 0\), saddle if \(0 < b - \mu < 2\gamma\) and unstable if \(b - \mu > 2\gamma\).
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SL fixed point: \(\left( \frac{1}{2b}(b - \mu), \frac{1}{2b}(b - \mu) \right)\)
Unstable if \(b - \mu < -2\gamma\), saddle if \(-2\gamma < b - \mu < 0\) and stable if \(b - \mu > 0\).
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Another pair: Real and saddles if \( |b - \mu| > 2\gamma \).
Special case - 2 equal patches

Deterministic Trajectories and Gradient Field for $b=1, \mu=0.5$ and $\gamma=0.4$
Special case - 2 equal patches

Deterministic Trajectories and Gradient Field for $b=1, \mu=0.5$ and $\gamma=0.2$
Different patch sizes?

Deterministic Trajectories and Gradient Field with $b=1, \mu=0.5, \gamma=0.4$ and $\rho_1=0.3$. 
General stability analysis

The nonlinear system can be written in the linearised form

\[
\frac{d\mathbf{x}}{dt} = A\mathbf{x} + h(\mathbf{x})
\]

where

\[
A = \Gamma + (b - \mu)I
\]

in which \( \Gamma \) is a q-matrix with diagonal entries given by \(-\sum_{j \neq i} \gamma_{ij} \) and off-diagonal entries \( \gamma_{ij} \), and \( h(\mathbf{x}) \) consists of higher order terms such that \( ||h(\mathbf{x})|| = o(||\mathbf{x}||) \), as \( ||\mathbf{x}|| \to 0 \).
General stability analysis

Determine stability by considering the eigenvalues $\sigma$ of $A$

$$Ax = \sigma x$$

so we have

$$(b - \mu)x + \Gamma x = \sigma x$$

and therefore

$$\Gamma x = [\sigma - (b - \mu)]x$$

so finally we have

$$\sigma_i = \lambda_i + b - \mu$$

where $\lambda_i$ is the $i$-th eigenvalue of $\Gamma$. 
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where $\lambda_i$ is the $i$-th eigenvalue of $\Gamma$. Therefore, SL fixed point is always stable if

$$b > \mu.$$
One-dimensional summary

If the patches are close to homogenous in size, we can approximate the equilibrium mean population density by using the logistic model [Verhulst (1838)]

\[
\frac{dy}{dt} = by(1 - y) - \mu y
\]

with equilibrium \( y^* = \frac{1}{b}(b - \mu) \), which is stable if \( b > \mu \), where \( y = \sum_{i=1}^{k} x_i \).

The equilibrium density at each patch will then be given by

\[
x_i^* = \frac{1}{kb}(b - \mu), \quad i = \{1, 2, \ldots, k\}
\]
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- Full analysis of model - fixed points and stability
- Investigate effect of migration parameters and spatial structure
- Diffusion approximation - investigate the variances and covariances
- Listen to Michael’s talk and then have some pizza!
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