The behaviour of large metapopulations

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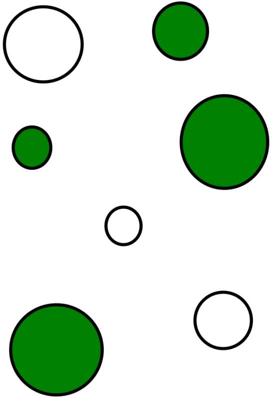
Joint work with P.K. Pollett

Overview of metapopulations

- A "population of populations" linked by migrating individuals.
- Local populations are located at disjoint habitat patches.
- Local populations frequently go extinct.
- Empty habitat patches may be colonised by migrating individuals from occupied patches.
- The aim is to understand regional persistence/extinction.



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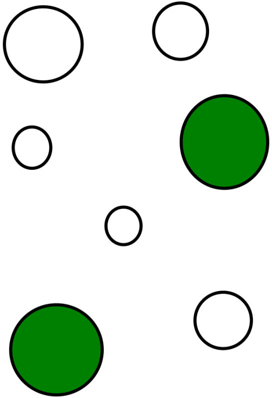

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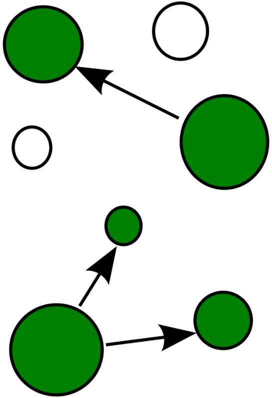

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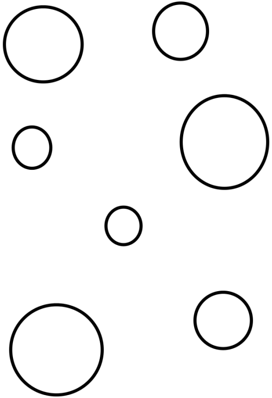

Hanski's metapopulation model

- Hanski's[1] incidence function metapopulation model has become one of the most widely used models in metapopulation ecology.
- This model employs the Presence – Absence assumption. Only the occupancy status of patches in the metapopulation is modelled, not the size of the local populations.
- Let $X_t^n = (X_{1,t}^n, \ldots, X_{n,t}^n)$ denote the state of an n–patch metapopulation at time t where

$$X_{i,t}^n = \begin{cases} 1, & \text{if patch } i \text{ is occupied at time } t, \\ 0, & \text{otherwise.} \end{cases}$$

- X_t^n is a discrete–time Markov chain on $\{0,1\}^n$.

[1] Hanski, I. (1994). A practical model of metapopulation dynamics. *J. Anim. Ecol.* **63,** 151-162.

Hanski's metapopulation model

- Conditional on X_t^n, the status of each patch at time $t+1$ is independent.
- Patch i is described by its location z_i, local extinction probability $1 - s_i$, and a weight related to the patch size A_i.
- Connectivity between patches is model by the function $D(z, \tilde{z})$. It describes how easy it is to move from a patch at $\tilde{z}$ to a patch at z.
- The transitional probabilities for Hanski's model is given by

$$\Pr\left(X_{i,t+1}^n = 1 \mid X_t^n\right) = s_i X_{i,t}^n + \left(1 - X_{i,t}^n\right) f\left(\sum_{j \neq i} A_j^b D(z_i, z_j) X_{j,t}^n\right),$$

where $f : [0, \infty) \mapsto [0, 1]$ and $b > 0$.

Simplifying assumptions

- $A_i = n^{-1/b}$.
- $z_i \in \Omega$ a compact subset of $\mathbb{R}^d$.
- $D(z, \tilde{z})$ is symmetric and defines a uniformly bounded and equicontinuous family of functions on Ω.
- f is increasing and twice differentiable.

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  Satisfied by many colonisation functions used in practice, e.g. $f(x) = 1 - \exp(-\beta x)$, $\beta > 0$.

Random measures

- Define the random measure σ_n on $[0,1] \times \Omega$ by

$$\int h(s,z)\sigma_n(ds,dz) := n^{-1} \sum_{i=1}^{n} h(s_i, z_i),$$

where $h \in C^+([0,1] \times \Omega)$.

- The sequence of random measures $\{\sigma_n\}_{n=1}^{\infty}$ converges in distribution to σ if for all $h \in C^+([0,1] \times \Omega)$

$$\int h(s,z)\sigma_n(ds,dz) \xrightarrow{d} \int h(s,z)\sigma(ds,dz).$$

- We will assume that $\sigma_n \xrightarrow{d} \sigma$ for some non-random measure σ.
- This assumption holds if, for example, $\{(s_i, z_i)\}_{n=1}^{\infty}$ is an iid sequence.

Point processes

- Define the random (counting) measure

$$\mu_{n,t}(B) := \# \left\{(s_i, z_i) \in B : X_{i,t}^n = 1\right\}$$

  for any bounded Borel set B.
- Let $\mathcal{V}$ be the class of real-valued Borel functions h on $\mathbb{R}^{d+1}$ with $1 - h$ vanishing off some bounded set and satisfying $0 \leq h(s,z) \leq 1$ for all $(s,z) \in \mathbb{R}^{d+1}$.
- The probability generating functional (p.g.fl.) of $\mu_{n,t}$ is

$$G_{n,t}[h] \quad = \quad \mathbb{E}\left(\prod_{i=1}^{n}\left(X_{i,t}^n h(s_i, z_i) + 1 - X_{i,t}^n\right)\right).$$

- Convergence of $\mu_{n,t}$ establish by proving convergence of the p.g.fl.s

Convergence

Theorem

Assume that $\mu_{n,0} \xrightarrow{d} \mu_0$ *with p.g.fl.* G_0 *and for all* $\alpha > 0$ $\sup_n \mathbb{E}\left(\exp\left(\alpha \sum_{i=1}^{n} X_{i,0}^{n}\right)\right) < \infty$. *Then* $\mu_{n,t} \xrightarrow{d} \mu_t$ *where* μ_t *has p.g.fl. given by*

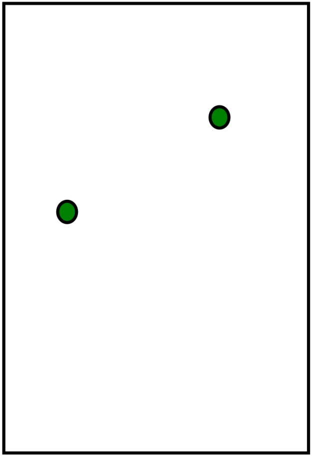
$$G_{t+1}[h] = G_t\left[G_1\left[h \mid (s,z)\right]\right], \quad \text{for any } h \in \mathcal{V},$$

and $G_1\left[h \mid (s,z)\right]$ *is given by*

$$(1 - s\,(1 - h(s,z)))\exp\left(-f'(0)\int D(\tilde{z}, z)\,(1 - h(\tilde{s}, \tilde{z}))\,\sigma(d\tilde{s}, d\tilde{z})\right).$$

Multiplicative population chains

- The limiting process is (marginally) a multiplicative population chain.
- A patch occupied at time t and located at z colonises unoccupied patches according to a Poisson process with intensity measure $f'(0)D(\cdot, z)\sigma$ at time $t+1$.
- A patch occupied at time t remains occupied at time $t+1$ with probability s.
- The collection of occupied patches at time $t+1$ is the superposition of these point processes.



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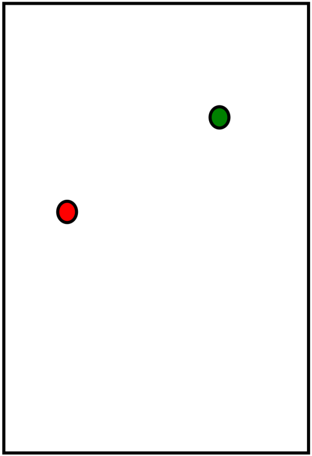

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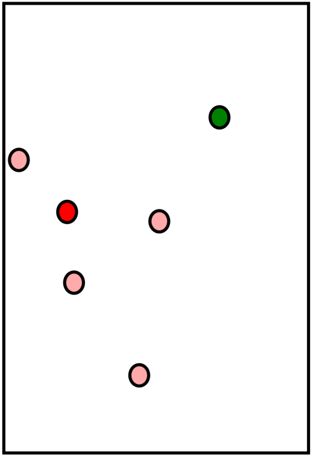

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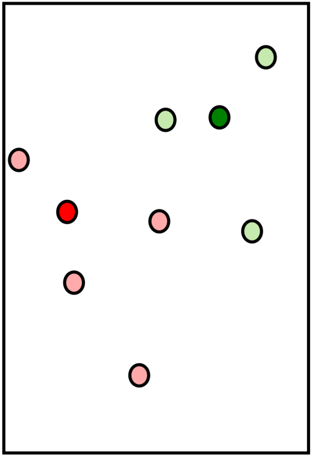

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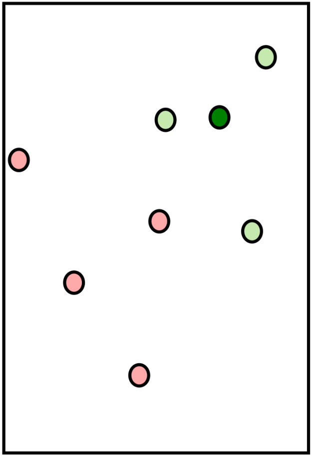

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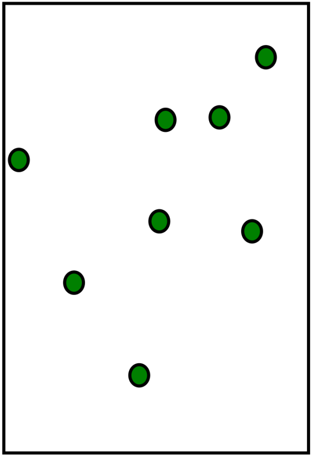

Probability of extinction

- What is the probability that the limiting process goes extinct in finite time?
- Moyal[2] showed that this is determined by the smallest fixed point h^* of $G_1\left[\cdot \mid (s,z)\right]$, that is, the smallest solution to

$$h = G_1\left[h \mid (s,z)\right], \quad h \in \mathcal{V}.$$

- $h^*(s,z)$ is the probability that the MPC goes extinct in finite time from an initial population consisting of a single occupied patch located at z with survival probability s.
- The function $h^* = 1$ for all (s,z) is always a solution. When does a smaller solution exist?

[2] Moyal, J.E. (1962) Multiplicative population chains, Proc. R. Soc. Lond. A, 266, 518–526.

Additional assumptions and notation

Our analysis requires some additional assumptions:

- For some $\epsilon > 0$, $\sigma([1-\epsilon, 1] \times \Omega) = 0$ and for every $z \in \Omega$ and every open neighbourhood N_z of z, $\sigma([0,1] \times N_z) > 0$.
- $D(z, \tilde{z}) > 0$ for all $z, \tilde{z} \in \Omega$.

Some additional notation is also required:

- Let $\mathcal{A} : C(\Omega) \mapsto C(\Omega)$ be the bounded linear operator

$$\mathcal{A}\phi(z) = f'(0) \int \frac{D(\tilde{z}, z)}{(1-\tilde{s})} \phi(\tilde{z}) \sigma(d\tilde{s}, d\tilde{z}), \quad \phi \in C(\Omega).$$

- Let $r(\mathcal{A})$ denote the spectral radius of $\mathcal{A}$.

Probability of extinction

Theorem

The limiting MPC goes extinct in finite time with probability one iff $r(\mathcal{A}) \leq 1$. If $r(\mathcal{A}) > 1$, the limiting MPC goes extinct in finite time with probability

$$G_0\left(\frac{(1-s)\,\psi^*(z)}{1-s\psi^*(z)}\right),$$

where ψ^* is the smallest nonnegative solution to

$$\psi(z) = \exp\left(-f'(0)\int D(\tilde{z},z)\left(\frac{1-\psi(\tilde{z})}{1-\tilde{s}\psi(\tilde{z})}\right)\sigma(d\tilde{s},d\tilde{z})\right).$$

Summary and future work

We have shown that:

- Under certain assumptions, Hanski's incidence function metapopulation model can be approximated by an MPC when the number of patches is large.
- Extinction in finite time is certain for the limiting process if $r(\mathcal{A}) \leq 1$. Otherwise, extinction in finite time occurs with probability less than one.

In our future work, we aim to:

- Relax some of the assumptions.
- Improve the convergence results.

The results given in this presentation will appear in the *Journal of Applied Probability*.