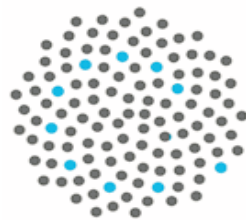


Point processes and patch survival in metapopulations

Phil Pollett

Department of Mathematics
The University of Queensland

<http://www.maths.uq.edu.au/~pkp>



AUSTRALIAN RESEARCH COUNCIL
Centre of Excellence for Mathematics
and Statistics of Complex Systems

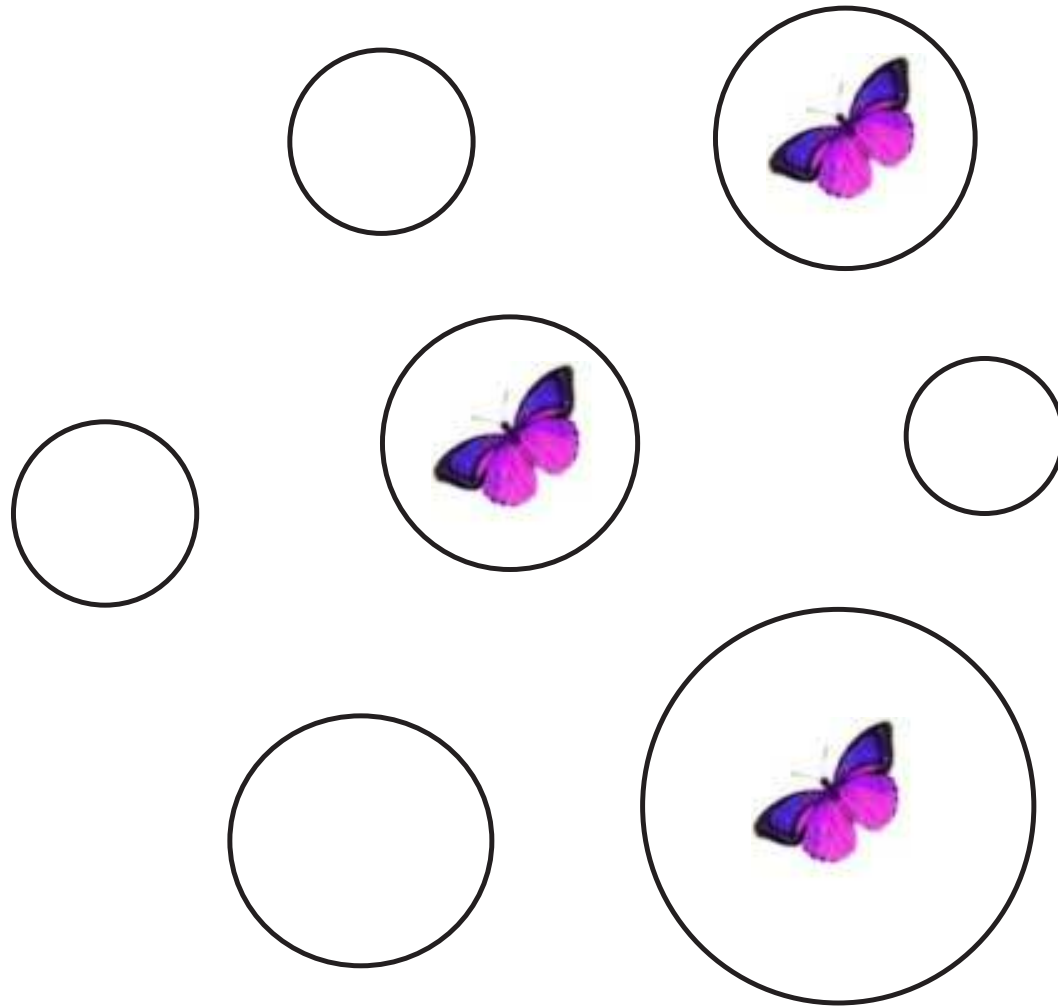
Ross McVinish
Department of Mathematics
University of Queensland



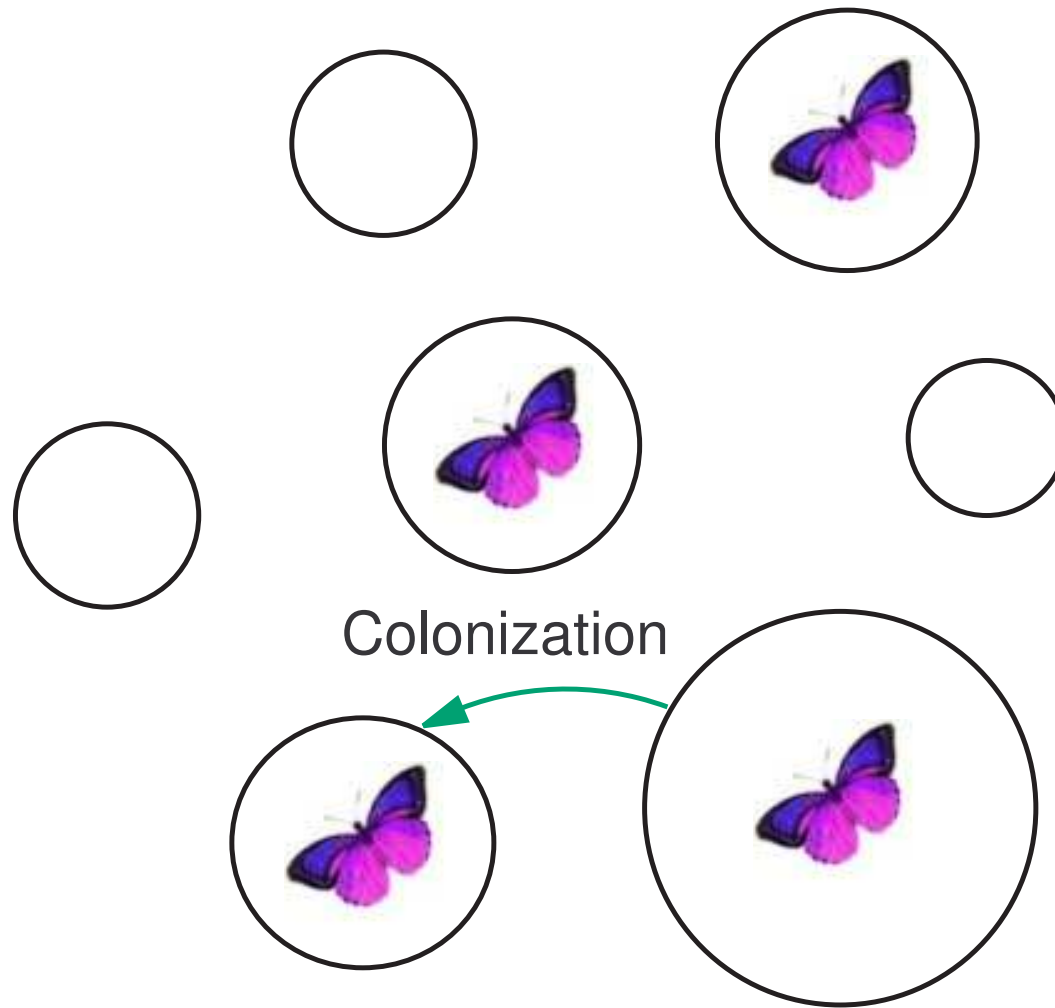
* McVinish, R. and Pollett, P.K. (2010) Limits of large metapopulations with patch dependent extinction probabilities. *Advances in Applied Probability* 42, 1172-1186.

* McVinish, R. and Pollett, P.K. (2011) The limiting behaviour of a mainland-island metapopulation. *Journal of Mathematical Biology*. To appear.

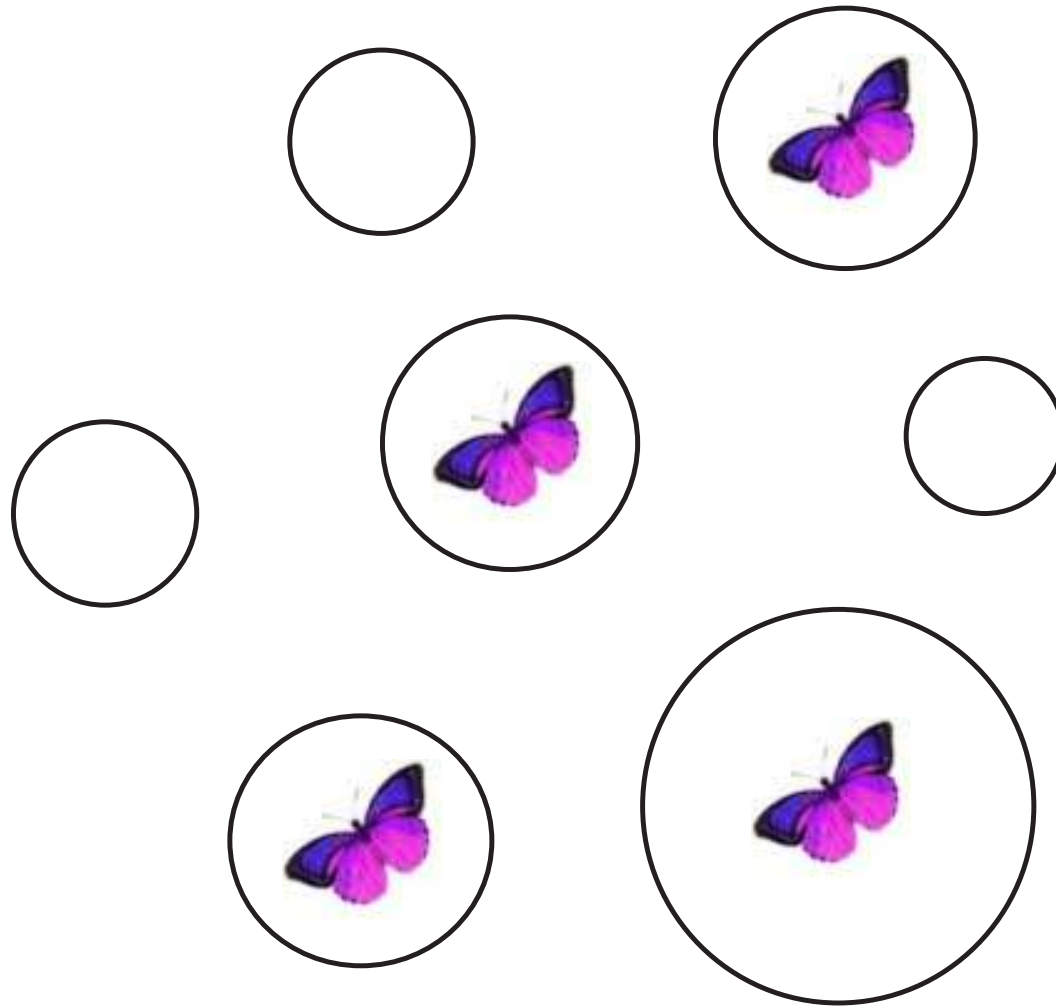
Metapopulations



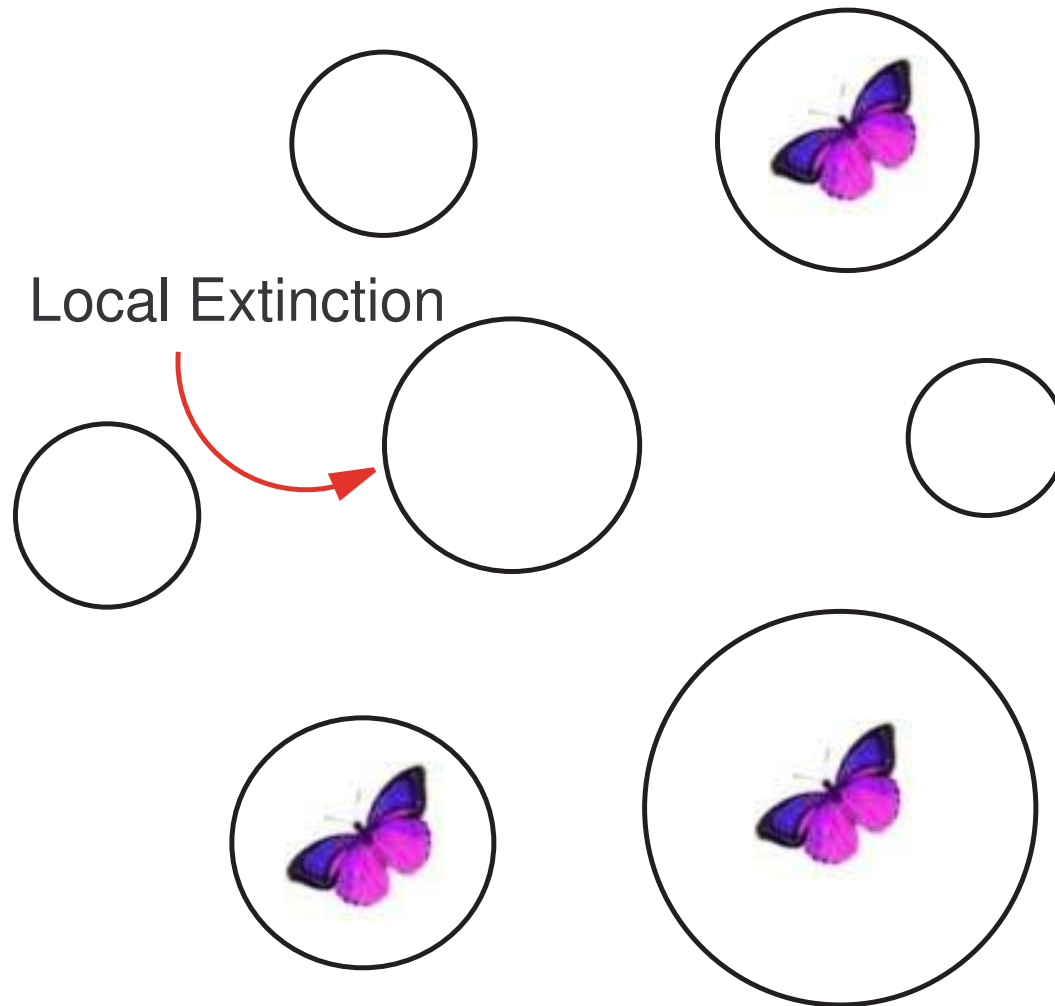
Metapopulations



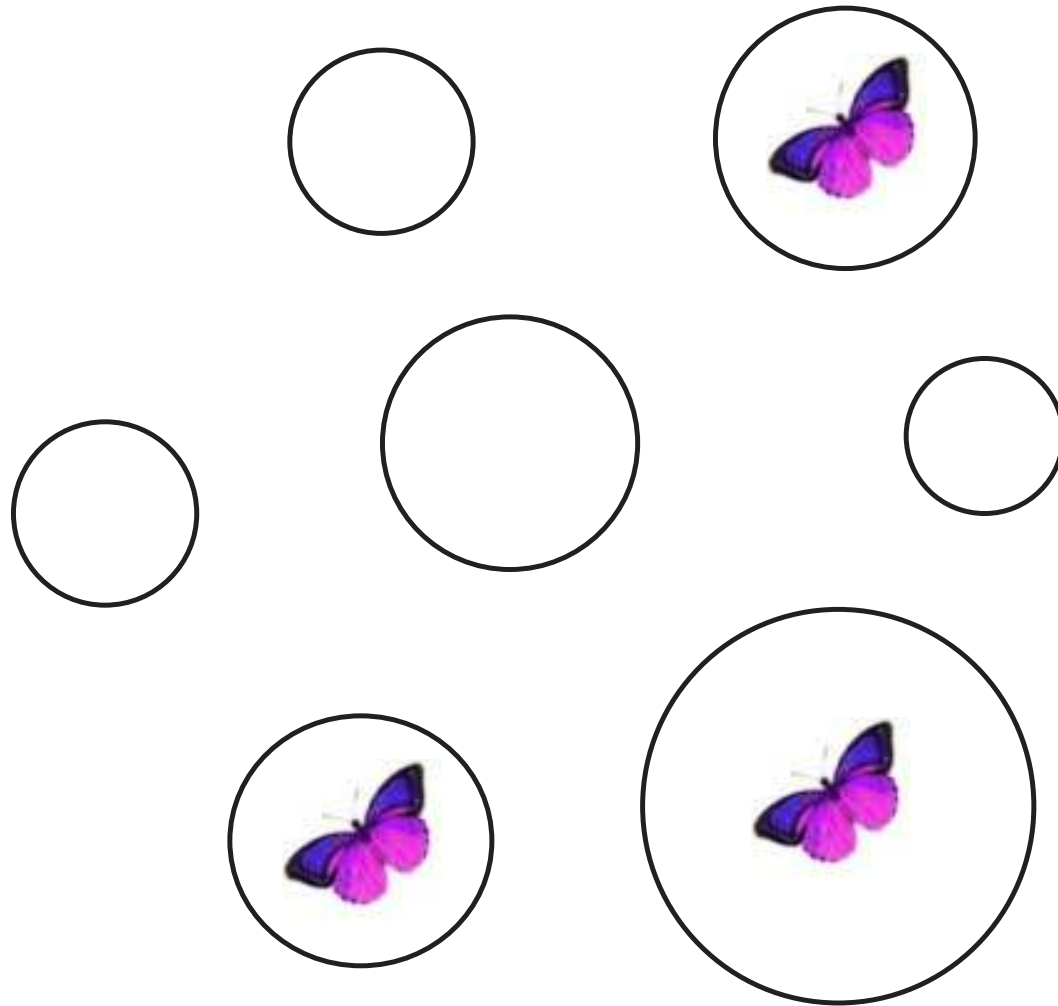
Metapopulations



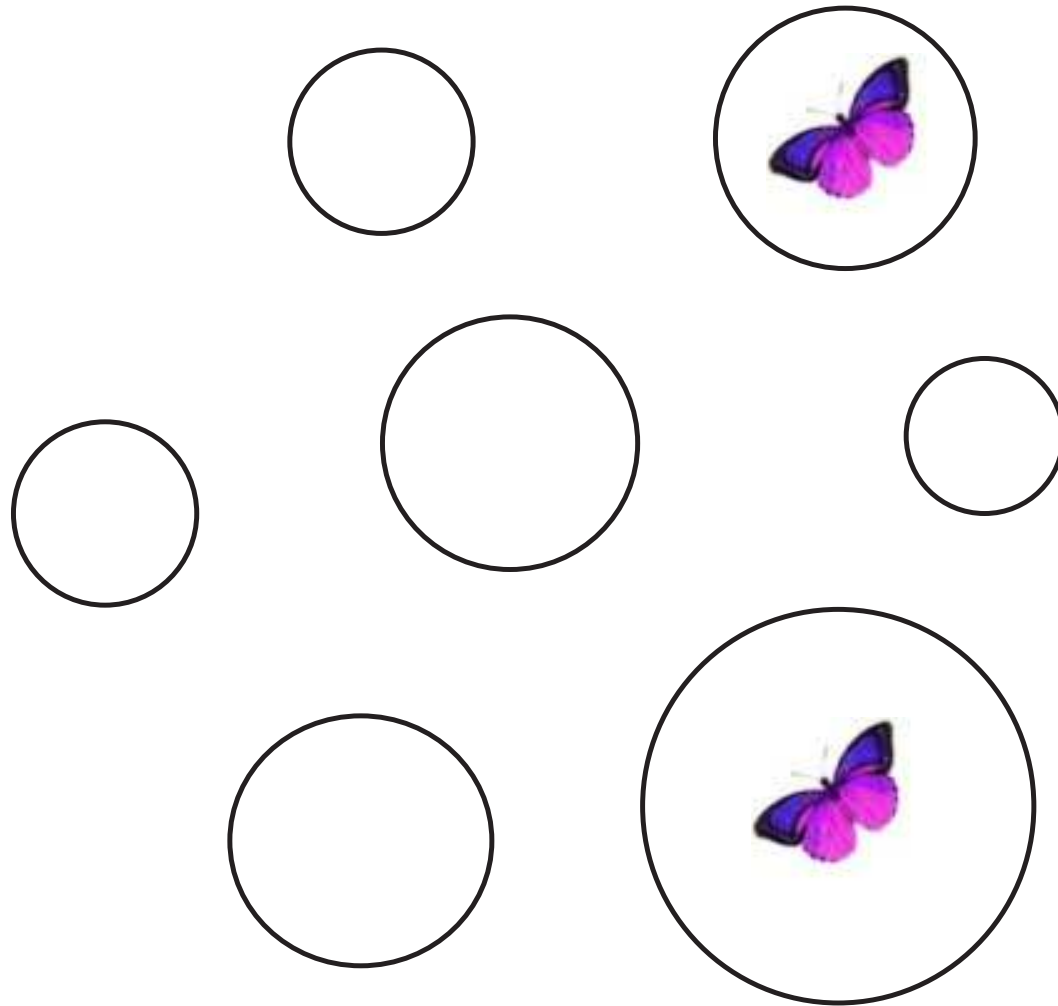
Metapopulations



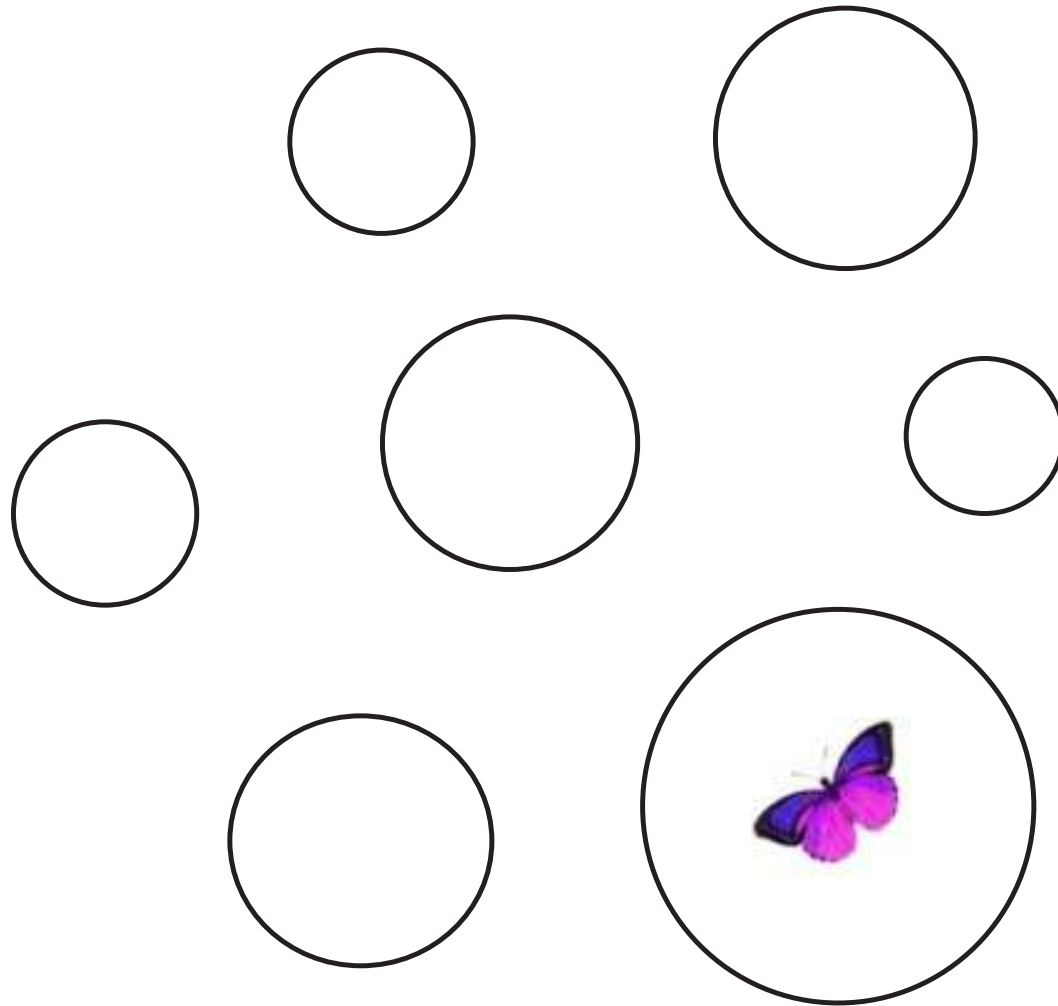
Metapopulations



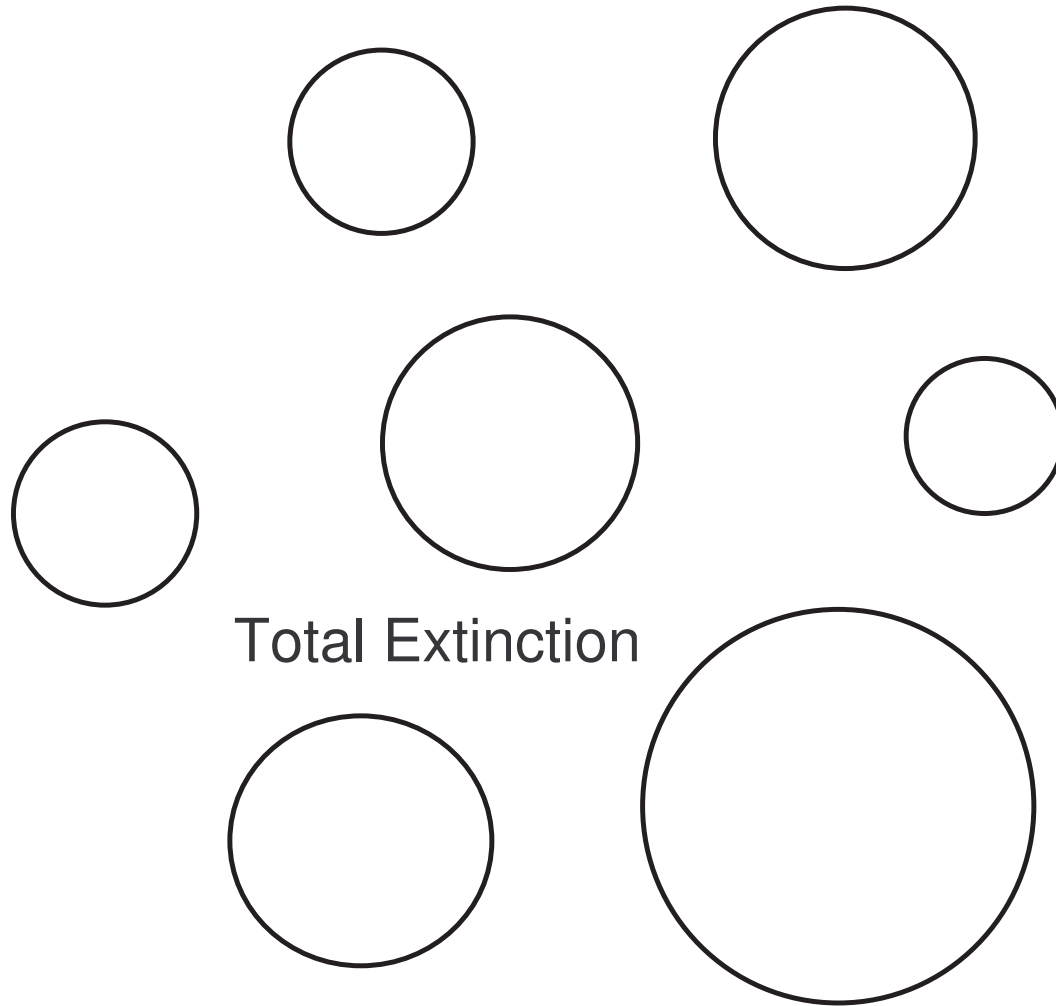
Metapopulations



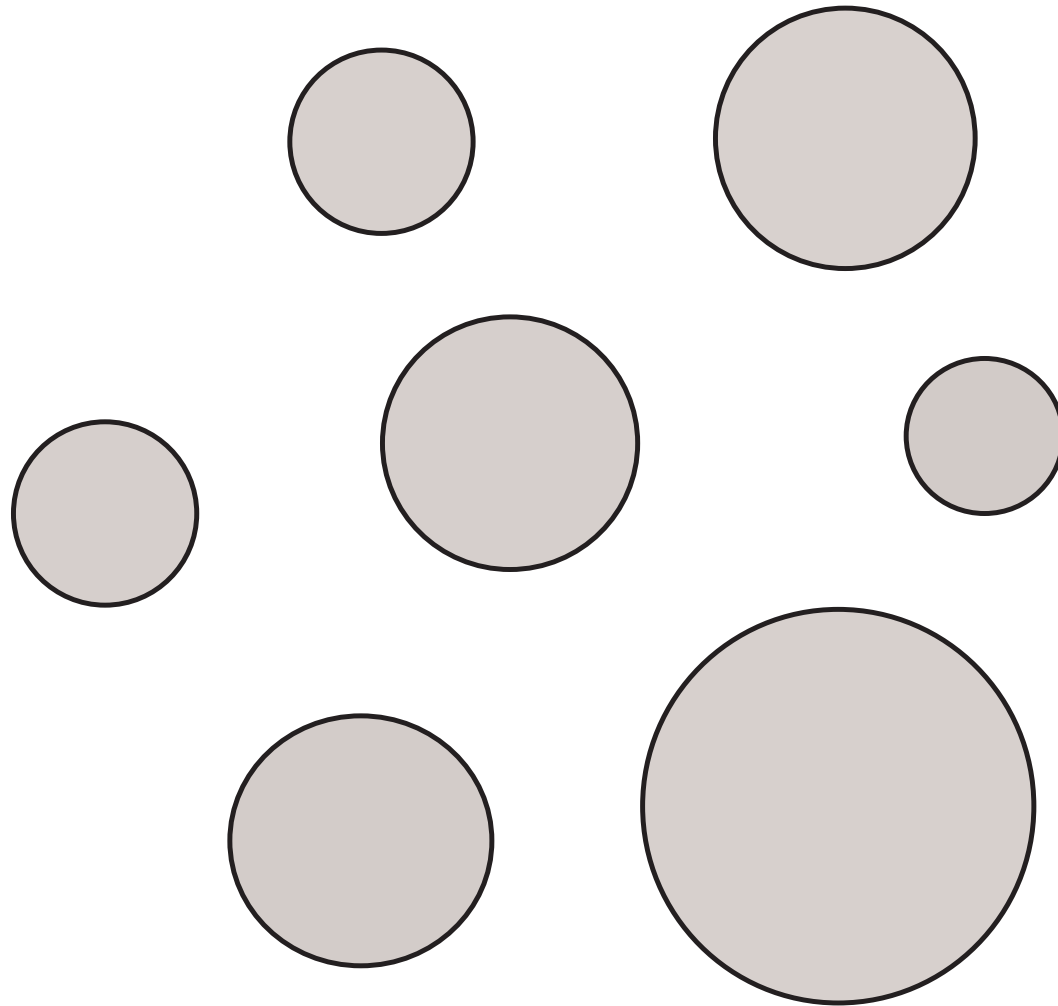
Metapopulations



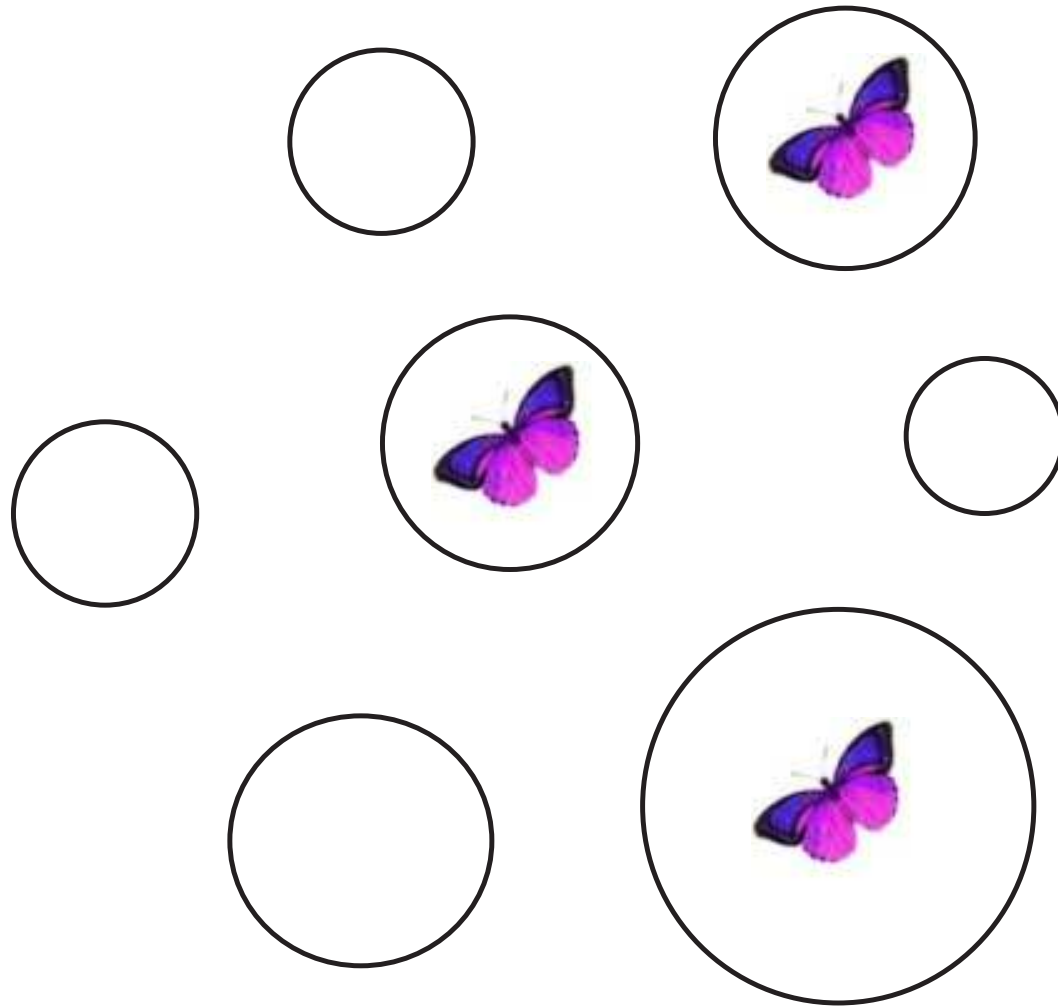
Metapopulations



Metapopulations



Metapopulations



A Stochastic Patch Occupancy Model (SPOM)

A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are n patches.

Let $X_t^{(n)} = (X_{1,t}^{(n)}, \dots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch i is occupied.

A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are n patches.

Let $X_t^{(n)} = (X_{1,t}^{(n)}, \dots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch i is occupied.

For each n , $(X_t^{(n)}, t = 0, 1, \dots)$ is assumed to be a Markov chain.

A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are n patches.

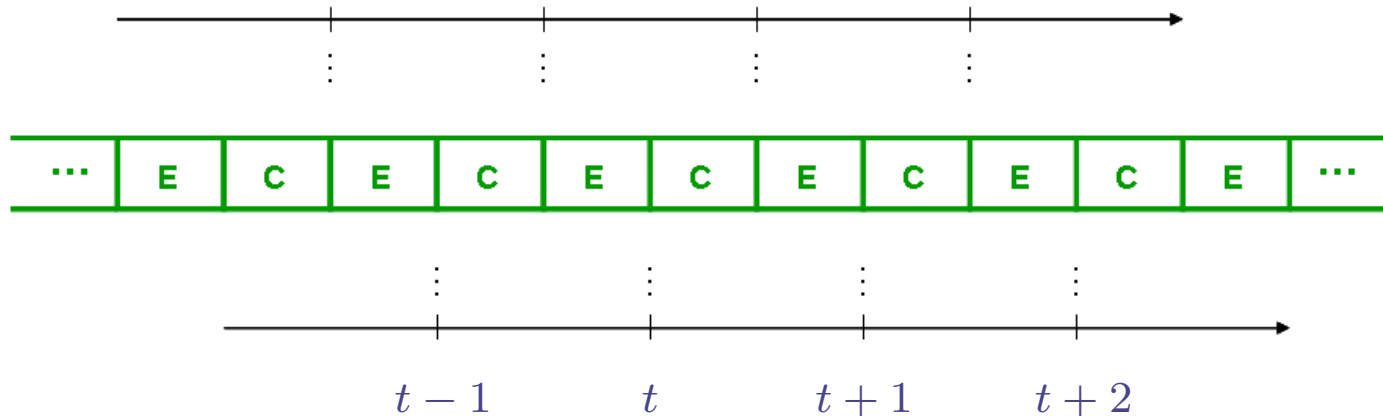
Let $X_t^{(n)} = (X_{1,t}^{(n)}, \dots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch i is occupied.

For each n , $(X_t^{(n)}, t = 0, 1, \dots)$ is assumed to be a Markov chain.

Colonization and extinction happen in distinct, successive phases.

SPOM - Phase structure

Colonization and extinction happen in distinct, successive phases.



We will assume that the population is *observed after successive extinction phases* (CE Model).

SPOM - Phase structure

Colonization and extinction happen in distinct, successive phases, as independent trials.

Colonization: unoccupied patches become occupied independently with probability $c(n^{-1} \sum_{i=1}^n X_{i,t}^{(n)})$, where $c : [0, 1] \rightarrow [0, 1]$ is continuous, increasing and concave.

SPOM - Phase structure

Colonization and extinction happen in distinct, successive phases, as independent trials.

Colonization: unoccupied patches become occupied independently with probability $c(n^{-1} \sum_{i=1}^n X_{i,t}^{(n)})$, where $c : [0, 1] \rightarrow [0, 1]$ is continuous, increasing and concave.

Extinction: occupied patch i remains occupied independently with probability s_i (fixed or random).

Thus, we have a *Chain Bernoulli* structure:

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \text{Bin}\left(X_{i,t}^{(n)} + \text{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right), s_i\right)$$

Thus, we have a *Chain Bernoulli* structure:

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \text{Bin}\left(X_{i,t}^{(n)} + \text{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right), s_i\right)$$

Thus, we have a *Chain Bernoulli* structure:

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \text{Bin}\left(X_{i,t}^{(n)} + \text{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right), s_i\right)$$

Thus, we have a *Chain Bernoulli* structure:

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \text{Bin}\left(X_{i,t}^{(n)} + \text{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right), s_i\right)$$

Thus, we have a *Chain Bernoulli* structure:

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \text{Bin}\left(X_{i,t}^{(n)} + \text{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right), s_i\right)$$

$n = 30, s_i \sim \text{Beta}(25.2, 19.8)$ ($\mathbb{E}s_i = 0.56$) and $c(x) = 0.7x$

0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0

$$c(x) = c\left(\frac{11}{30}\right) = 0.7 \times 0.3\dot{6} = 0.25\dot{6}$$

SPOM

$n = 30$, $s_i \sim \text{Beta}(25.2, 19.8)$ ($\mathbb{E}s_i = 0.56$) and $c(x) = 0.7x$

0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 0 0 1 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 0 0 0 1 0 1 0

$n = 30$, $s_i \sim \text{Beta}(25.2, 19.8)$ ($\mathbb{E}s_i = 0.56$) and $c(x) = 0.7x$

0 0 0 0 1 0 1 1 0 0 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0

SPOM

$n = 30$, $s_i \sim \text{Beta}(25.2, 19.8)$ ($\mathbb{E}s_i = 0.56$) and $c(x) = 0.7x$

	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0	
C	1	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	0	1	0
E	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0

$$c(x) = c\left(\frac{10}{30}\right) = 0.7 \times 0.\dot{3} = 0.2\dot{3}$$

SPOM

$n = 30$, $s_i \sim \text{Beta}(25.2, 19.8)$ ($\mathbb{E}s_i = 0.56$) and $c(x) = 0.7x$

```
0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0
E 0 0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 1 0 1 1 1 1 0 0 0 0 0 0 1 0
C 0 0 1 0 1 0 0 1 1 1 0 1 0 0 1 0 1 1 1 1 1 1 0 0 0 0 0 0 1 0
```


SPOM

$n = 30$, $s_i \sim \text{Beta}(25.2, 19.8)$ ($\mathbb{E}s_i = 0.56$) and $c(x) = 0.7x$

```
0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 0 1 1 1 0 1 0 1 0 0 0 1 0 0 0
C 1 0 0 0 1 1 1 1 0 1 0 1 0 0 0 0 1 1 1 1 1 1 1 0 0 0 1 0 1 0
E 0 0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 1 0 1 1 1 1 0 0 0 0 0 0 1 0
C 0 0 1 0 1 0 0 1 1 1 0 1 0 0 1 0 1 1 1 1 1 1 0 0 0 0 0 0 1 0
E 0 0 0 0 1 0 0 1 0 1 0 1 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 1 0
```


SPOM - Homogeneous case

In the *homogeneous case*, where $s_i = s$ (non-random) is the same for each i , the *number* $N_t^{(n)}$ of occupied patches at time t is Markovian.

It has the following *Chain Binomial* structure:

$$N_{t+1}^{(n)} \stackrel{d}{=} \mathbf{Bin}\left(N_t^{(n)} + \mathbf{Bin}\left(n - N_t^{(n)}, c\left(\frac{1}{n}N_t^{(n)}\right)\right), s\right)$$

A deterministic limit

Letting the initial number $N_0^{(n)}$ of occupied patches grow with $n \dots$

Theorem [BP] If $N_0^{(n)}/n \xrightarrow{p} x_0$ (a constant), then

$$N_t^{(n)}/n \xrightarrow{p} x_t, \quad \text{for all } t \geq 1,$$

with (x_t) determined by $x_{t+1} = f(x_t)$, where

$$f(x) = s(x + (1 - x)c(x)).$$

[BP] Buckley, F.M. and Pollett, P.K. (2010) Limit theorems for discrete-time metapopulation models. *Probability Surveys* 7, 53-83.

Stability

$x_{t+1} = f(x_t)$, where $f(x) = s(x + (1 - x)c(x))$.

Stationarity: $c(0) > 0$. There is a unique fixed point $x^* \in [0, 1]$. It satisfies $x^* \in (0, 1)$ and is stable.

Evanescence: $c(0) = 0$ and $1 + c'(0) \leq 1/s$. Now 0 is the unique fixed point in $[0, 1]$. It is stable.

Quasi stationarity: $c(0) = 0$ and $1 + c'(0) > 1/s$. There are two fixed points in $[0, 1]$: 0 (unstable) and $x^* \in (0, 1)$ (stable).

[Notice that $c(0) = 0$ implies that $c'(0) > 0$.]

Stability

$x_{t+1} = f(x_t)$, where $f(x) = s(x + (1 - x)c(x))$.

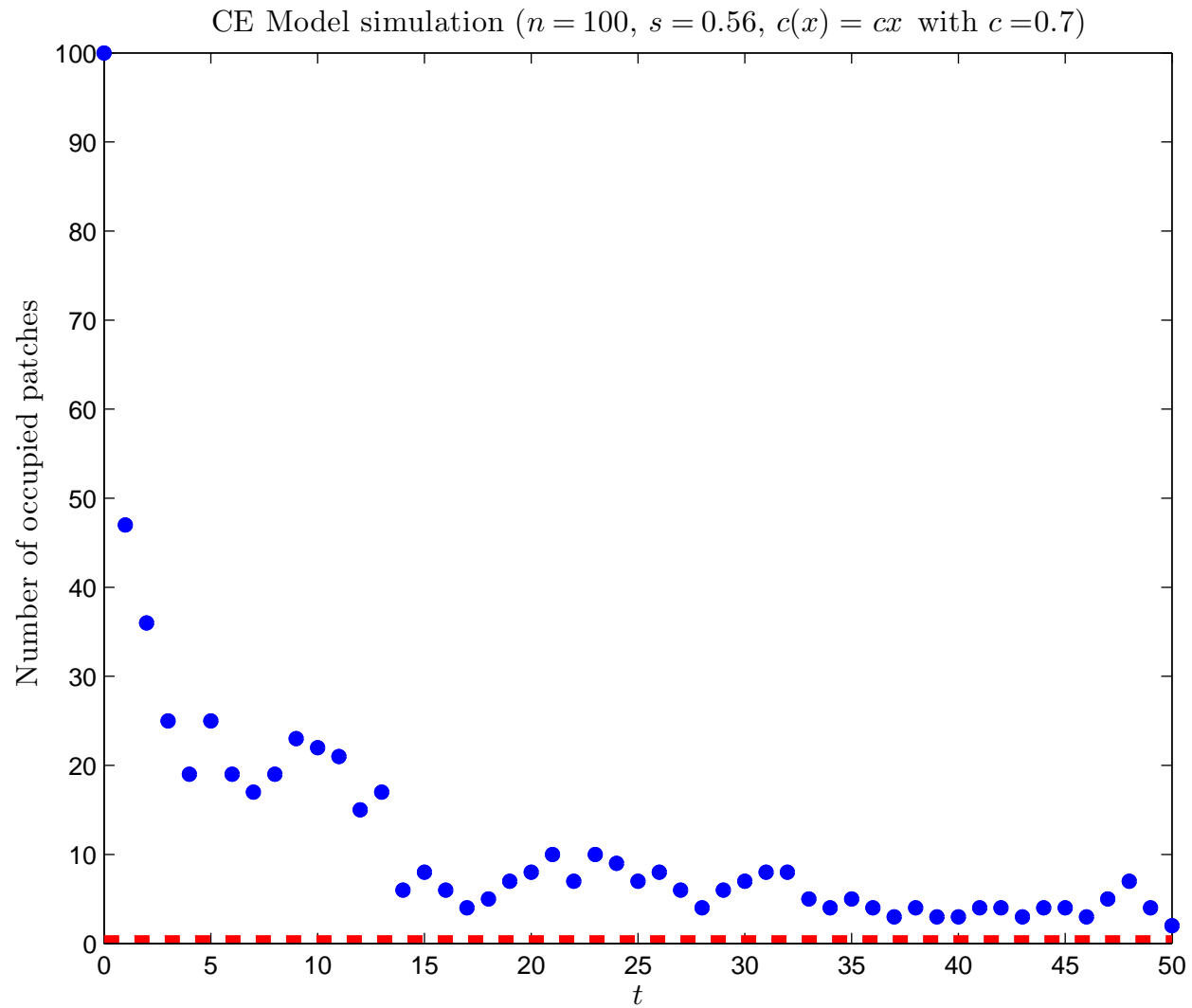
Stationarity: $c(0) > 0$. There is a unique fixed point $x^* \in [0, 1]$. It satisfies $x^* \in (0, 1)$ and is stable.

Evanescence: $c(0) = 0$ and $1 + c'(0) \leq 1/s$. Now 0 is the unique fixed point in $[0, 1]$. It is stable.

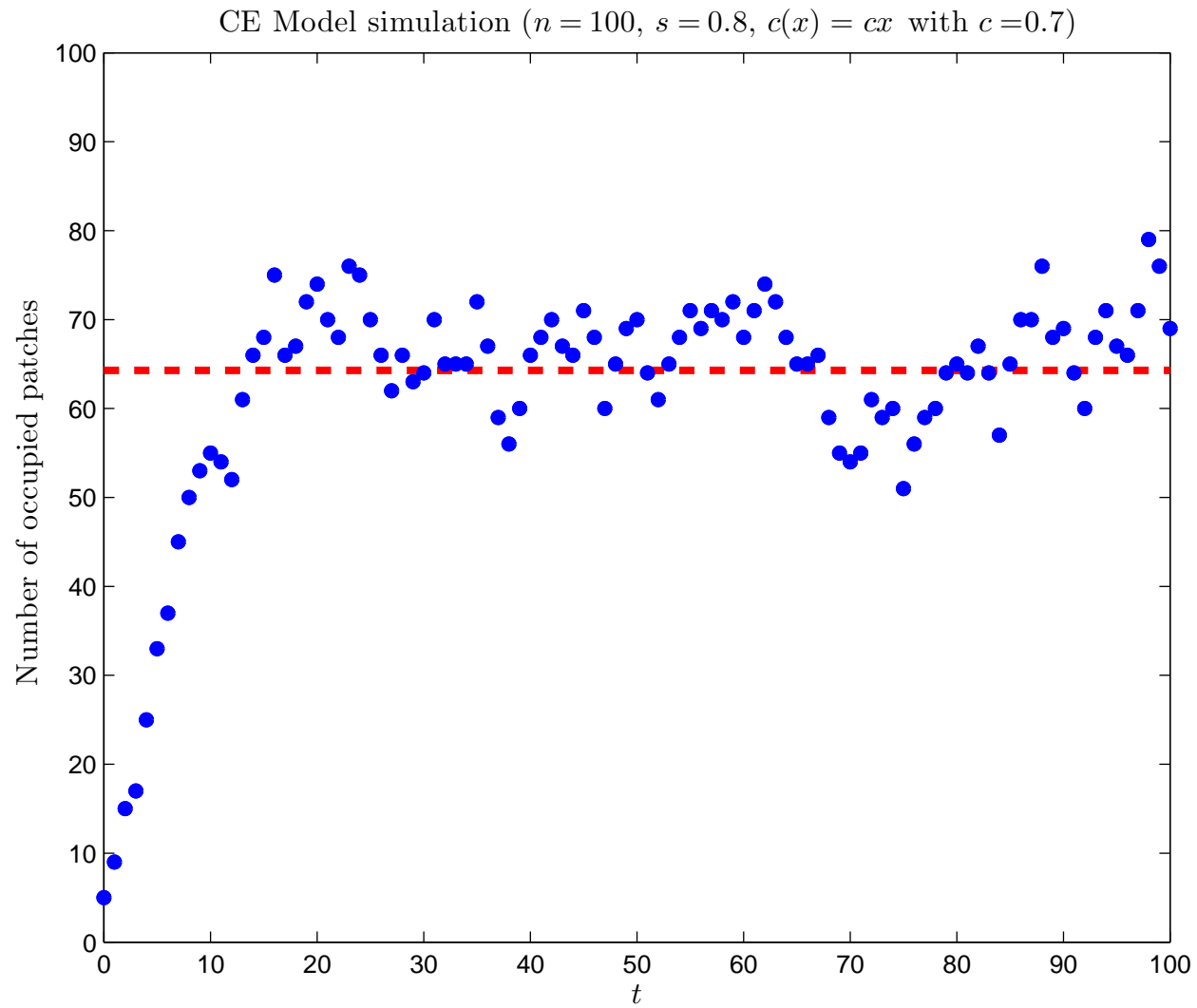
Quasi stationarity: $c(0) = 0$ and $1 + c'(0) > 1/s$. There are two fixed points in $[0, 1]$: 0 (unstable) and $x^* \in (0, 1)$ (stable).

[Notice that $c(0) = 0$ implies that $c'(0) > 0$.]

CE Model - Evanescence



CE Model - Quasi stationarity



SPOM - general case

Returning to the general case, where patch survival probabilities are *random* and *patch dependent*, and we keep track of which patches are occupied ...

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \text{Bin}\left(X_{i,t}^{(n)} + \text{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right), s_i\right).$$

SPOM - general case

Returning to the general case, where patch survival probabilities are *random* and *patch dependent*, and we keep track of which patches are occupied ...

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \text{Bin}\left(X_{i,t}^{(n)} + \text{Bin}\left(1 - X_{i,t}^{(n)}, c\left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)}\right)\right), s_i\right).$$

Assume now that $c(0) = 0$ and $c'(0) > 0$.

Recovery of a near-extinct population

Fix the initial configuration $X_0^{(n)}$ and let $n \rightarrow \infty$.

The aim is to determine conditions under which a metapopulation that is close to extinction may recover with positive probability.

Recovery of a near-extinct population

Fix the initial configuration $X_0^{(n)}$ and let $n \rightarrow \infty$.

The aim is to determine conditions under which a metapopulation that is close to extinction may recover with positive probability.

First notice that if c has a continuous second derivative near 0, then, for fixed m , $\text{Bin}(n - m, c(m/n)) \xrightarrow{d} \text{Poi}(\lambda m)$ as $n \rightarrow \infty$, where $\lambda = c'(0)$. So, if every patch had the same survival probability, then we might expect the number of occupied patches $N_t^{(n)}$ to converge to a Galton-Watson process (see [BP] for details).

Recovery of a near-extinct population

Treat the collection of patch survival probabilities of *occupied patches* at time t as a point process on $[0, 1)$.

Recovery of a near-extinct population

Treat the collection of patch survival probabilities of *occupied patches* at time t as a point process on $[0, 1)$.

Define $(S_t^{(n)}, t \geq 0)$ by $S_t^{(n)} = \{s_i : X_{i,t}^{(n)} = 1\}$.

Recovery of a near-extinct population

Treat the collection of patch survival probabilities of *occupied patches* at time t as a point process on $[0, 1)$.

Define $(S_t^{(n)}, t \geq 0)$ by $S_t^{(n)} = \{s_i : X_{i,t}^{(n)} = 1\}$.

Extinction of the metapopulation by time t corresponds to the event that $S_t^{(n)}$ is the empty set.

Recovery of a near-extinct population

Treat the collection of patch survival probabilities of *occupied patches* at time t as a point process on $[0, 1)$.

Define $(S_t^{(n)}, t \geq 0)$ by $S_t^{(n)} = \{s_i : X_{i,t}^{(n)} = 1\}$.

Extinction of the metapopulation by time t corresponds to the event that $S_t^{(n)}$ is the empty set.

The aim is to show that there is a point process S_t such that $S_t^{(n)} \Rightarrow S_t$ as $n \rightarrow \infty$ and to evaluate $\lim_{t \rightarrow \infty} \Pr(S_t = \emptyset)$.

Define the *probability generating functional* (p.g.fl) of $S_t^{(n)}$ by

$$G_{S_t^{(n)}}(\xi) = \mathbb{E} \left(\prod_{s \in S_t^{(n)}} \xi(s) \right),$$

where $\xi : [0, 1) \rightarrow [0, 1]$ is some Borel function [DVJ, Definition 9.4.IV]. It determines the point process uniquely [DVJ, Theorem 9.4.V]. This, together with [DVJ, Theorem 11.1.VIII], establishes that $S_t^{(n)} \Rightarrow S_t$. Furthermore,

$$\Pr(S_t = \emptyset) = \lim_{b \downarrow 0} G_{S_t}(1_b(x)).$$

[DVJ] Daley, D. J. and Vere-Jones, D. (2008) An Introduction to the Theory of Point Processes. Volume II: General Theory and Structure, 2nd Edn., Springer, New York.

Convergence

Theorem Suppose there is a probability measure σ on $[0, 1)$ such that, for all $k \geq 1$,

$$\frac{1}{n} \sum_{i=1}^n s_i^k \xrightarrow{p} \bar{\sigma}_k := \int_0^1 x^k \sigma(dx),$$

as $n \rightarrow \infty$. Then, $S_t^{(n)}$ converges weakly to a point process S_t whose p.g.fl satisfies the recursion $G_{S_{t+1}}(\xi) = G_{S_t}(h_\xi)$ ($t \geq 0$), where h_ξ is given by

$$h_\xi(x) = (1 - x + x\xi(x)) \exp \left(-c'(0) \int_0^1 y(1 - \xi(y)) \sigma(dy) \right).$$

Probability of total extinction

Theorem S_t eventually becomes empty with probability 1 ($S_t = \emptyset$ for some $t > 0$) if

$$c'(0) \int_0^1 \frac{x}{1-x} \sigma(dx) \leq 1.$$

Otherwise, it eventually becomes empty with probability $G_{S_0}(g)$, where

$$g(x) = \frac{\psi(1-x)}{1-\psi x},$$

with $\psi (< 1)$ being the unique solution to

$$\psi = \exp \left(-c'(0) \int_0^1 \frac{(1-\psi)x}{(1-\psi x)} \sigma(dx) \right).$$