

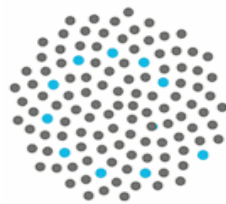
Limits of large metapopulations with patch dependent extinction probabilities

Phil Pollett

Department of Mathematics

The University of Queensland

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



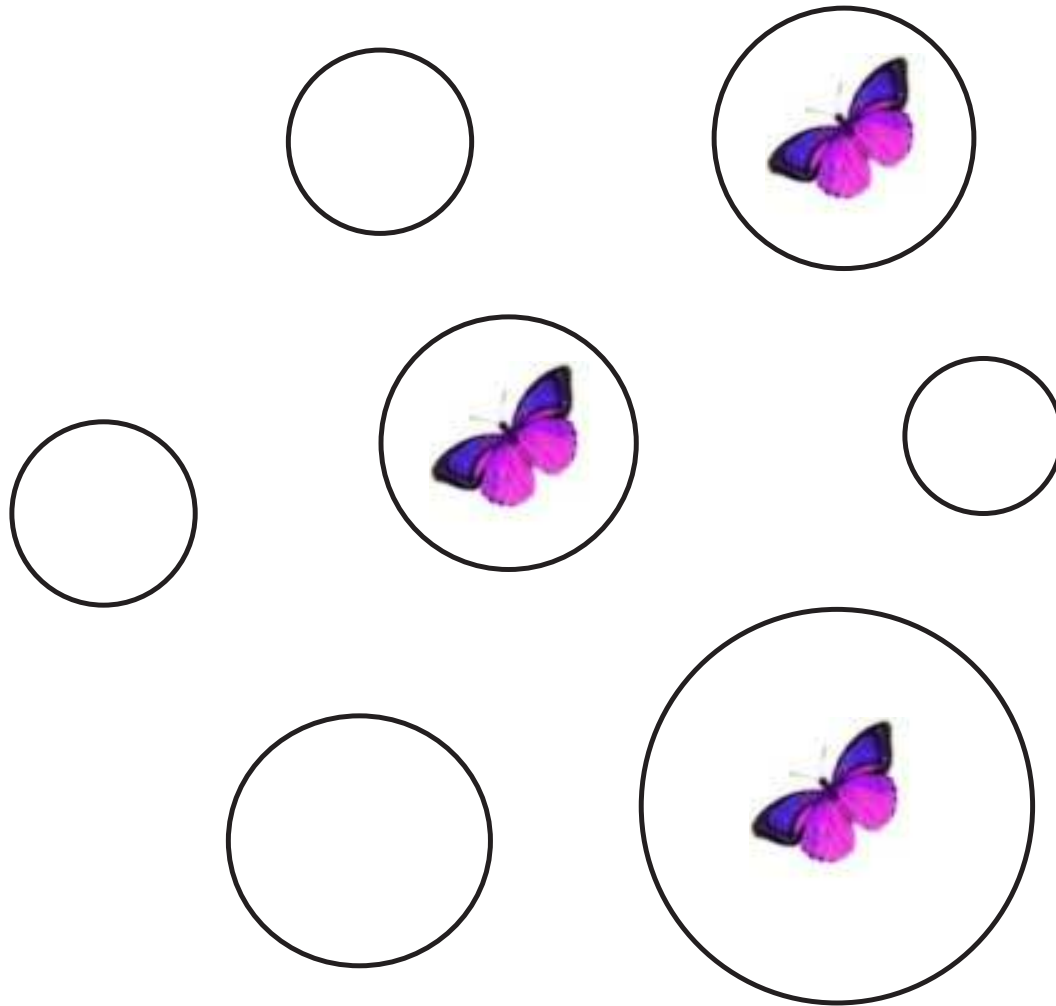
AUSTRALIAN RESEARCH COUNCIL
Centre of Excellence for Mathematics
and Statistics of Complex Systems

Ross McVinish
MASCOS
University of Queensland

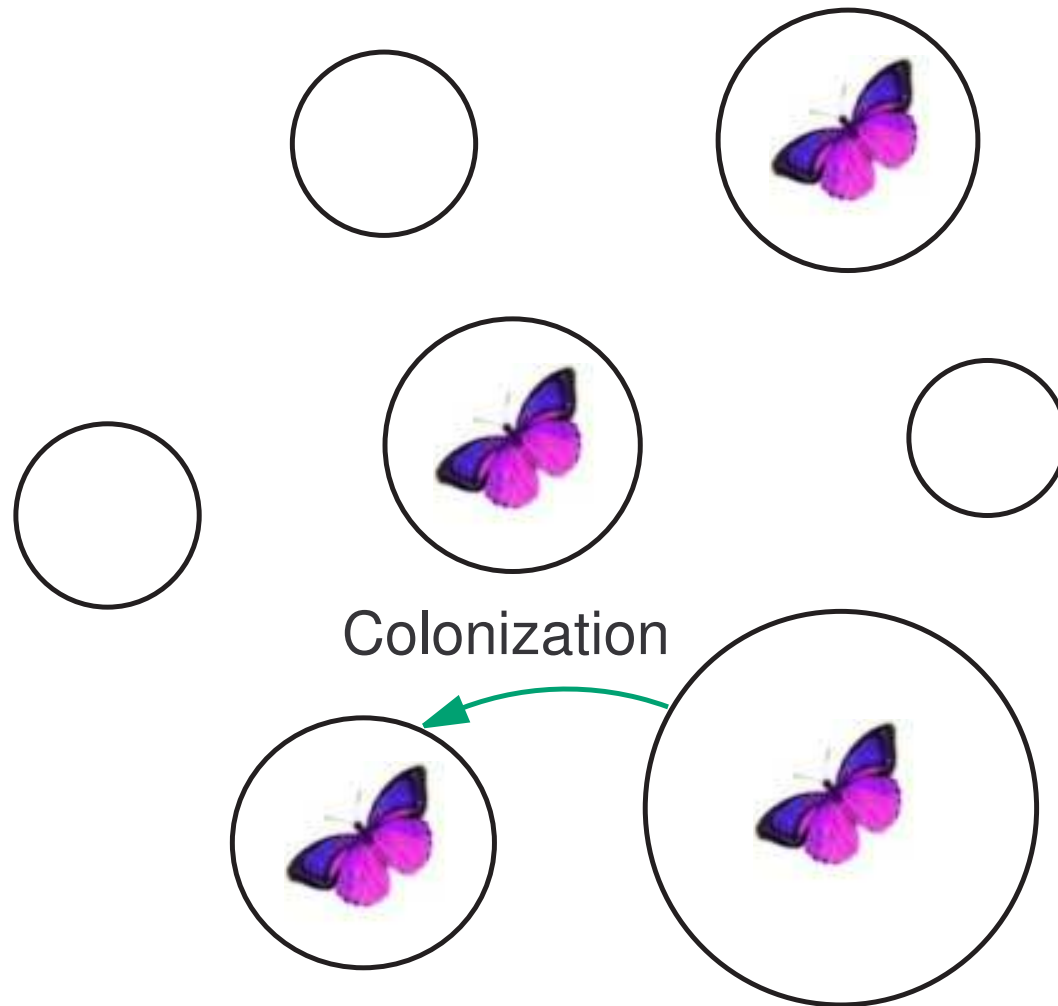


*McVinish, R. and Pollett, P.K. (2010) Limits of large metapopulations with patch dependent extinction probabilities. *Advances in Applied Probability* 42 (in press, accepted 02/09/10).

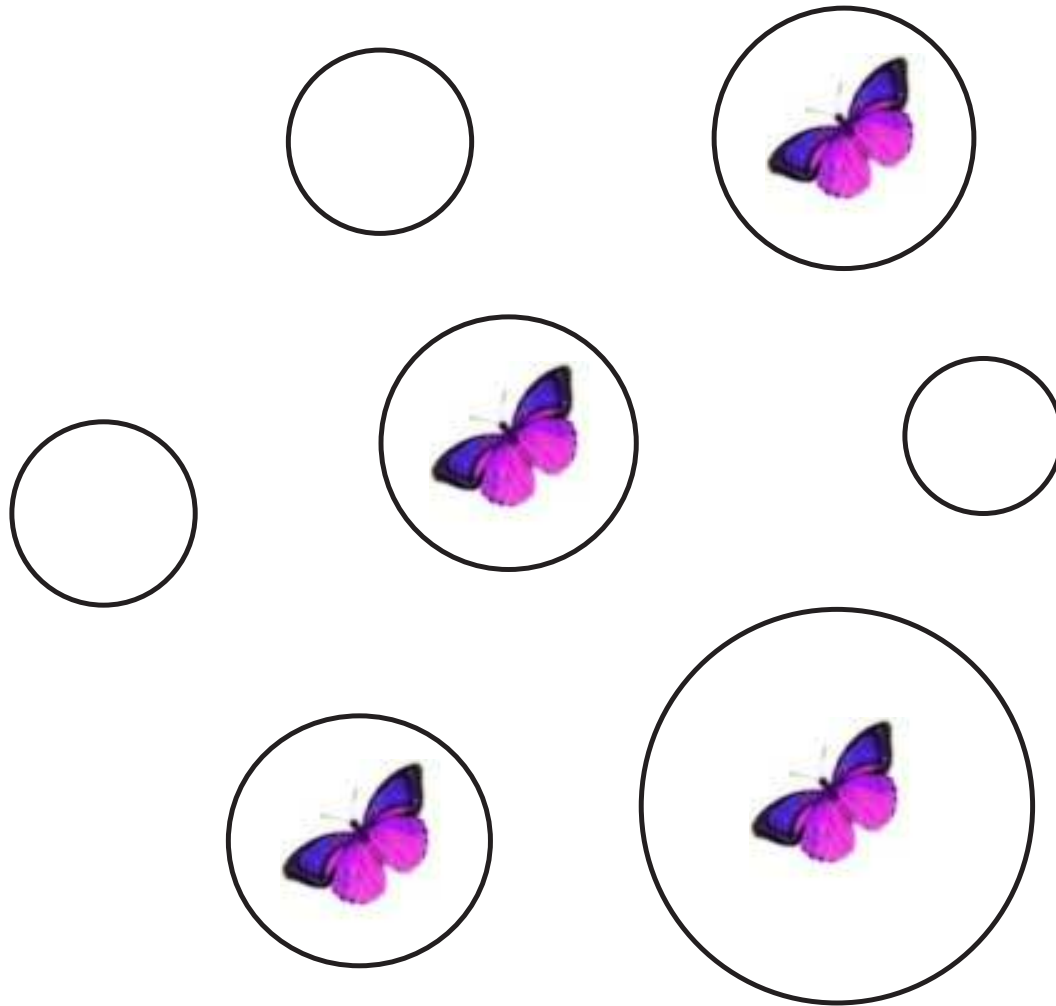
Metapopulations



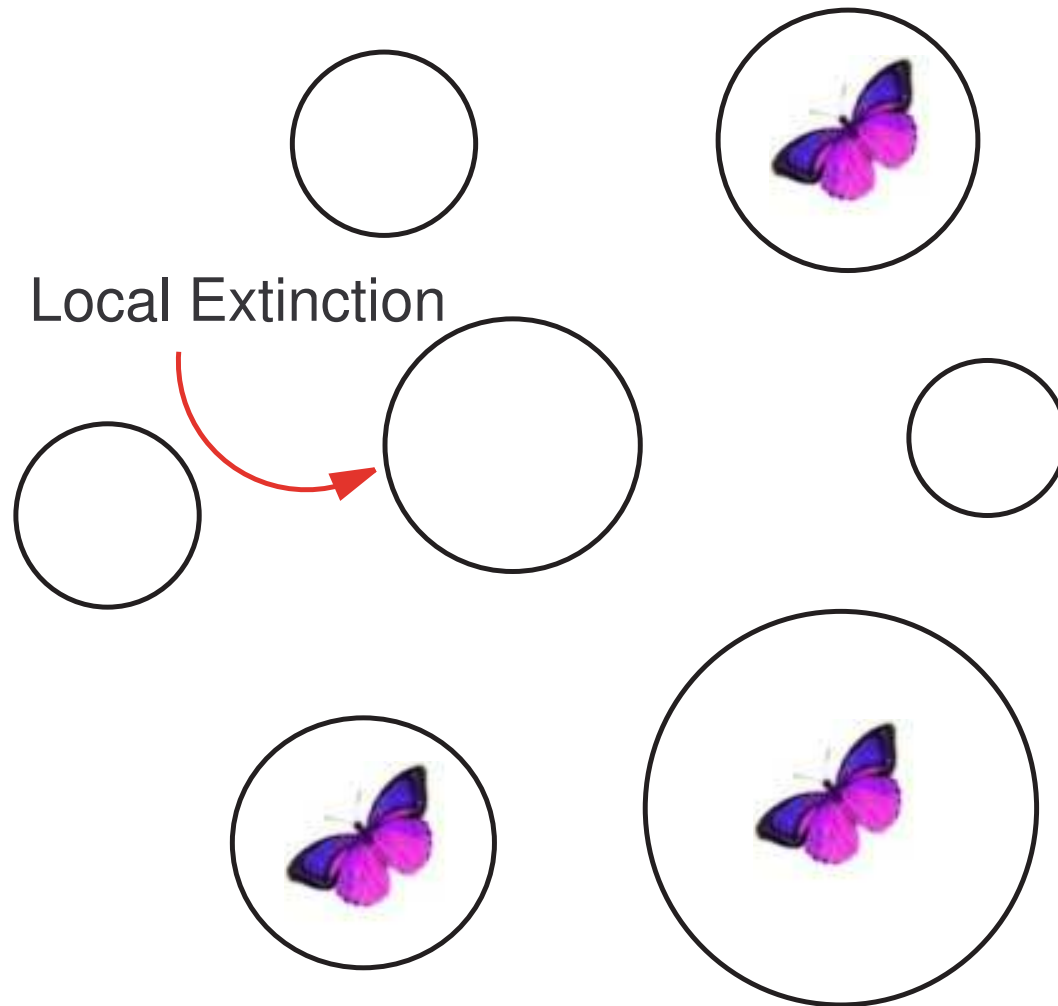
Metapopulations



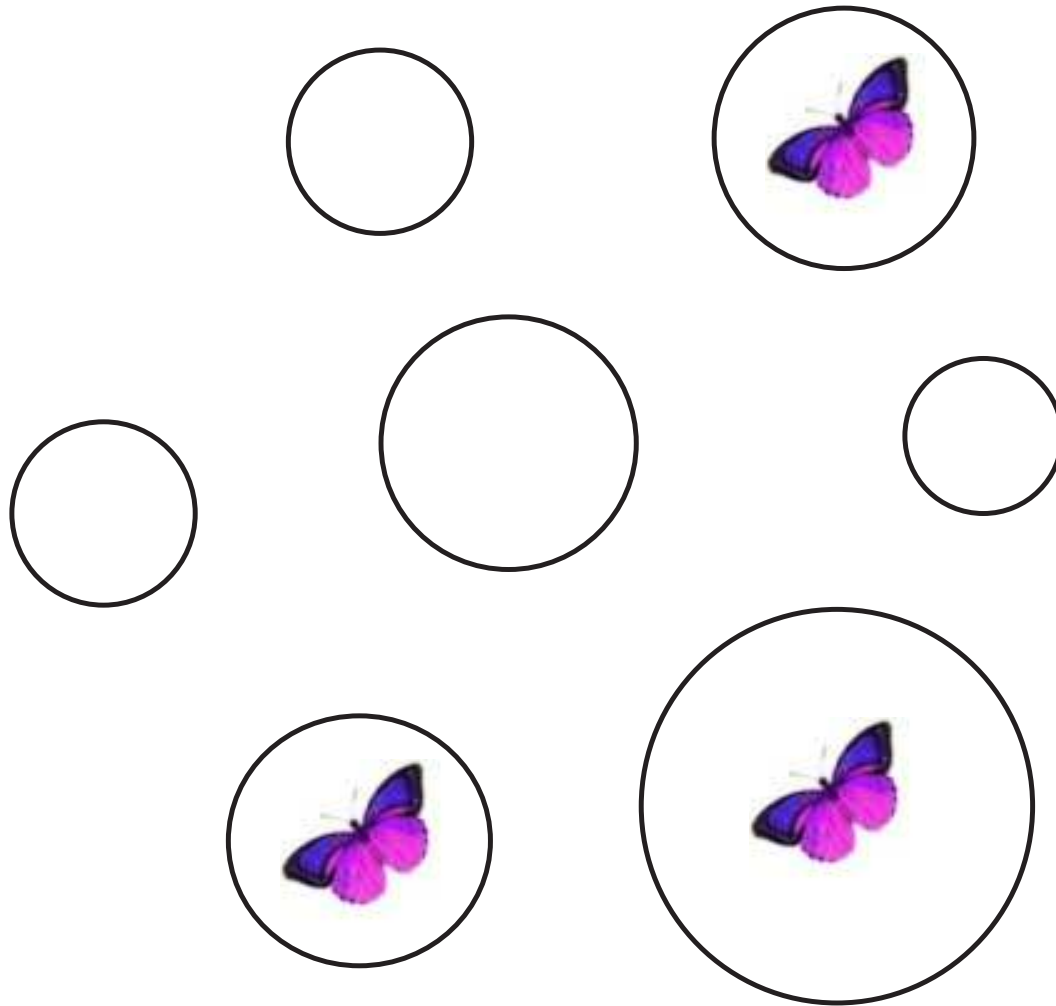
Metapopulations



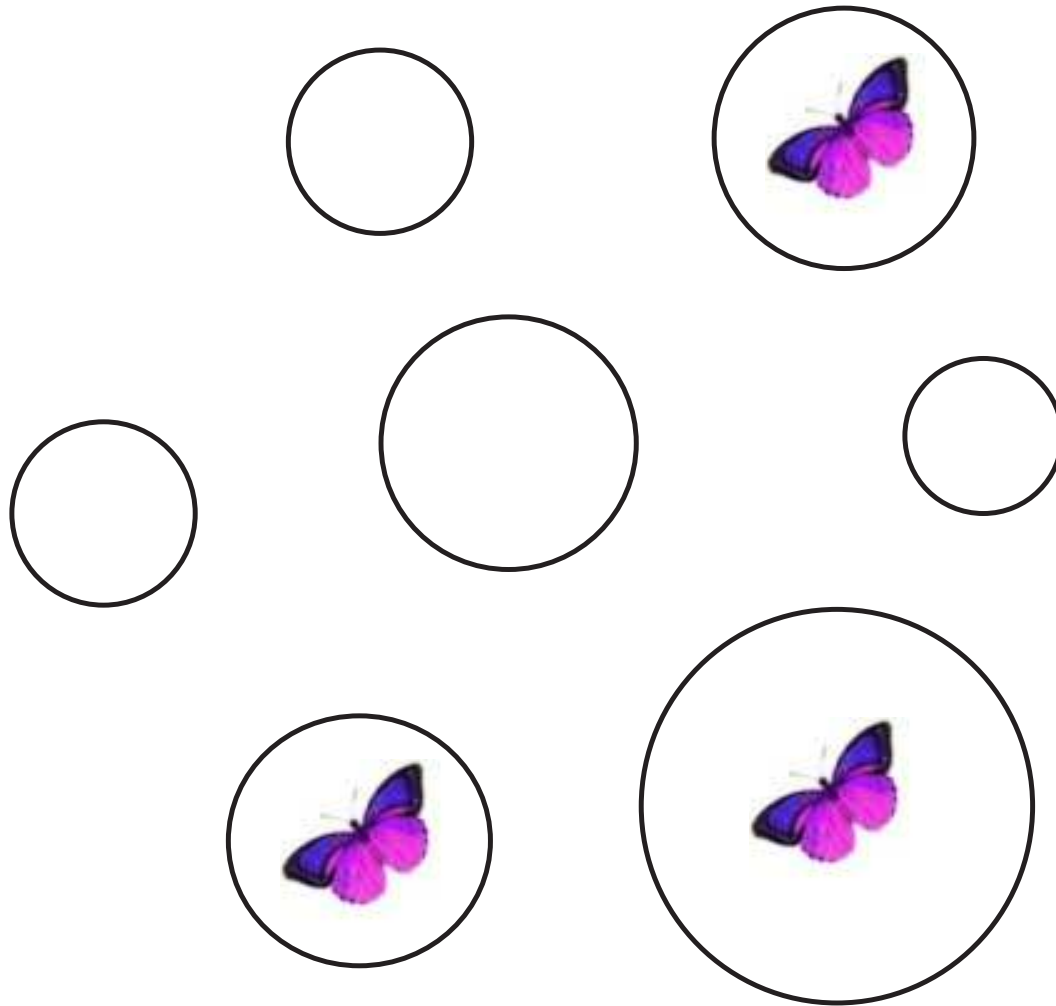
Metapopulations



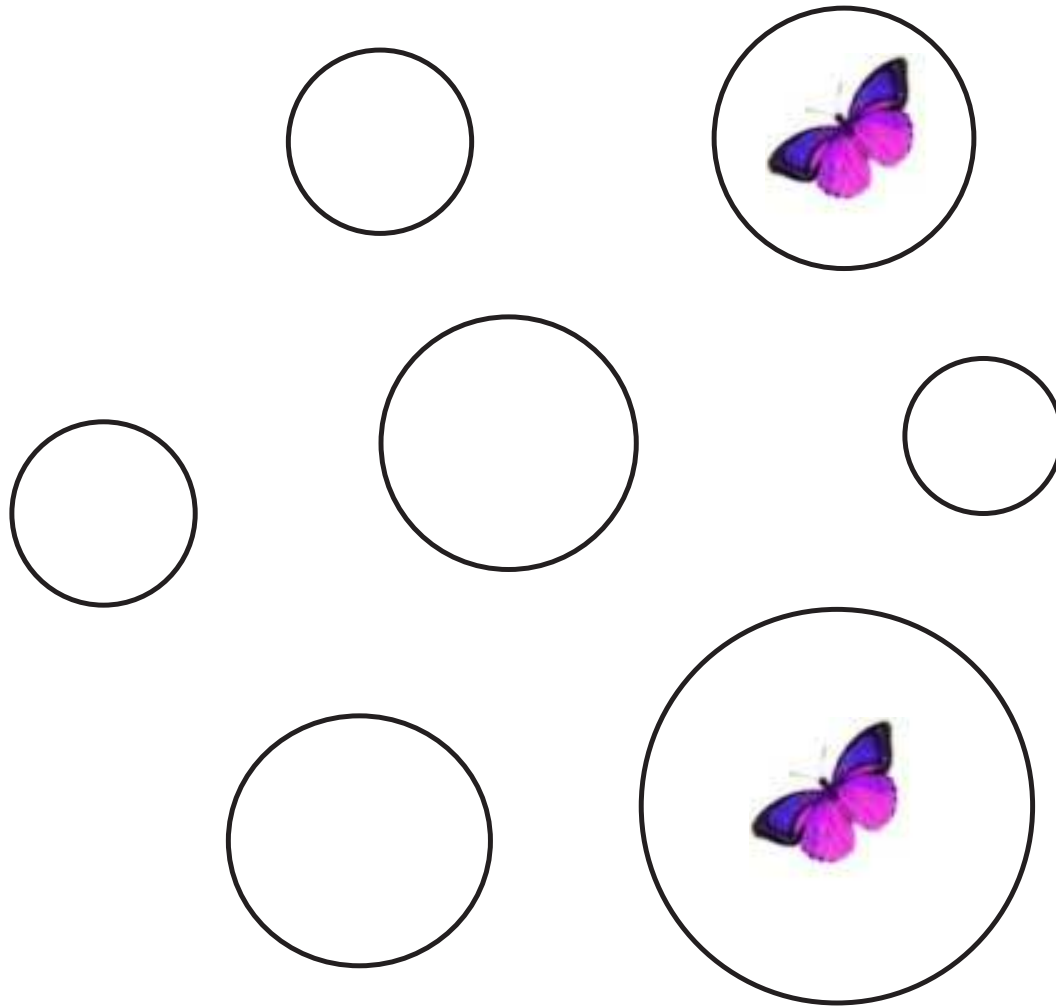
Metapopulations



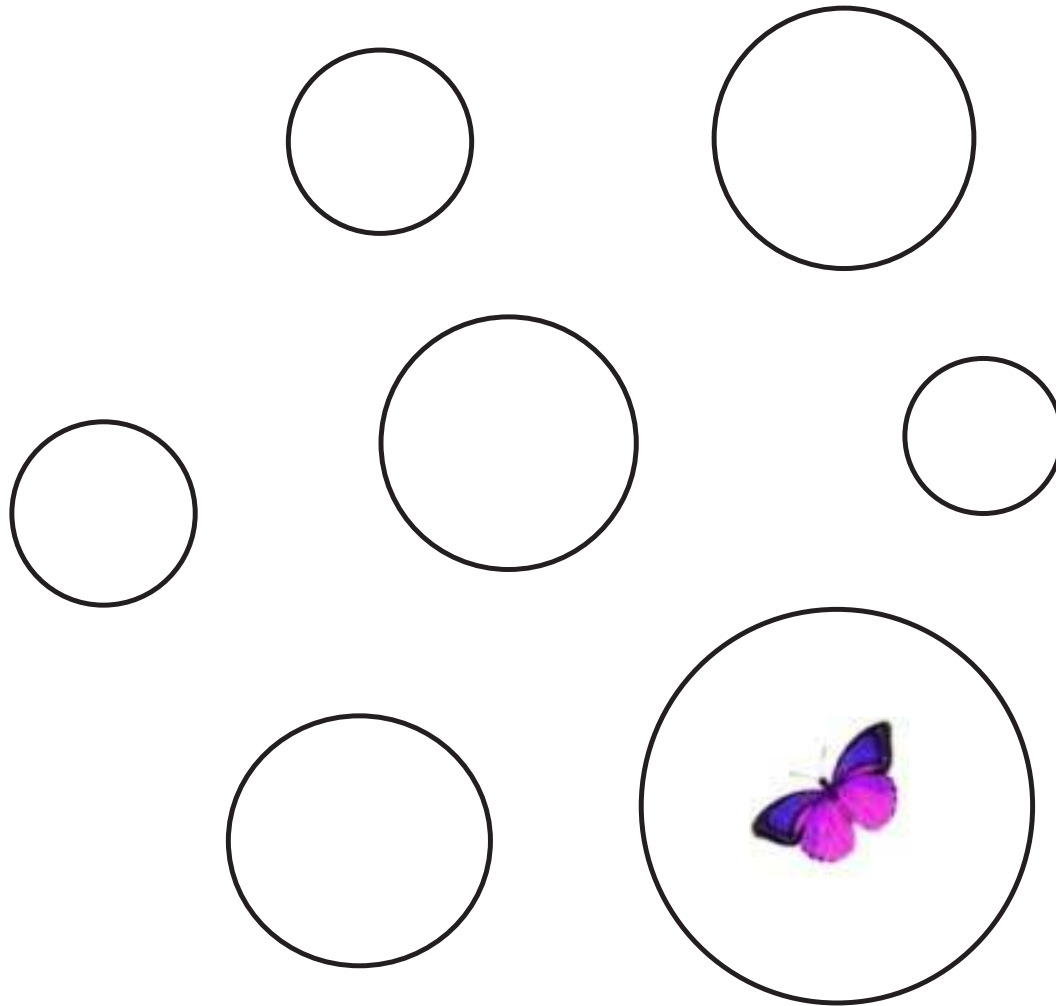
Metapopulations



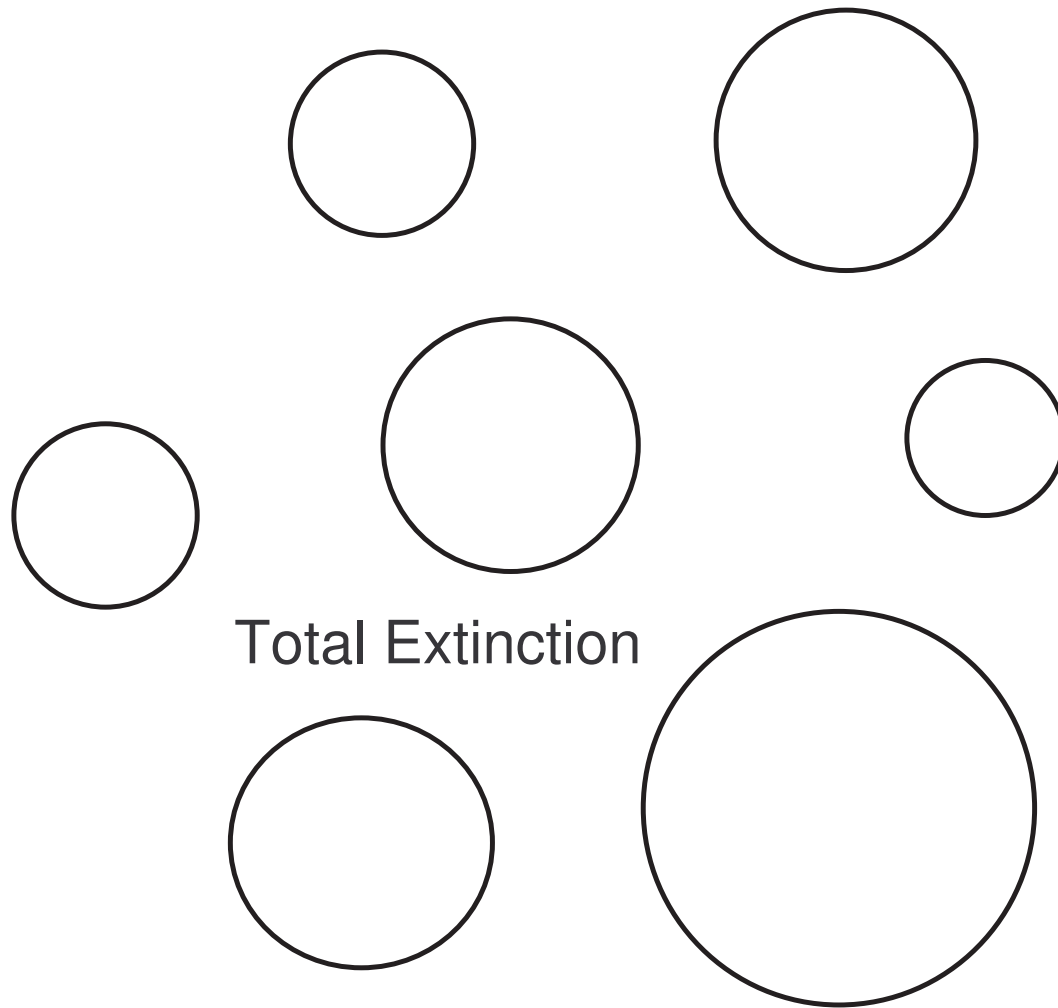
Metapopulations



Metapopulations

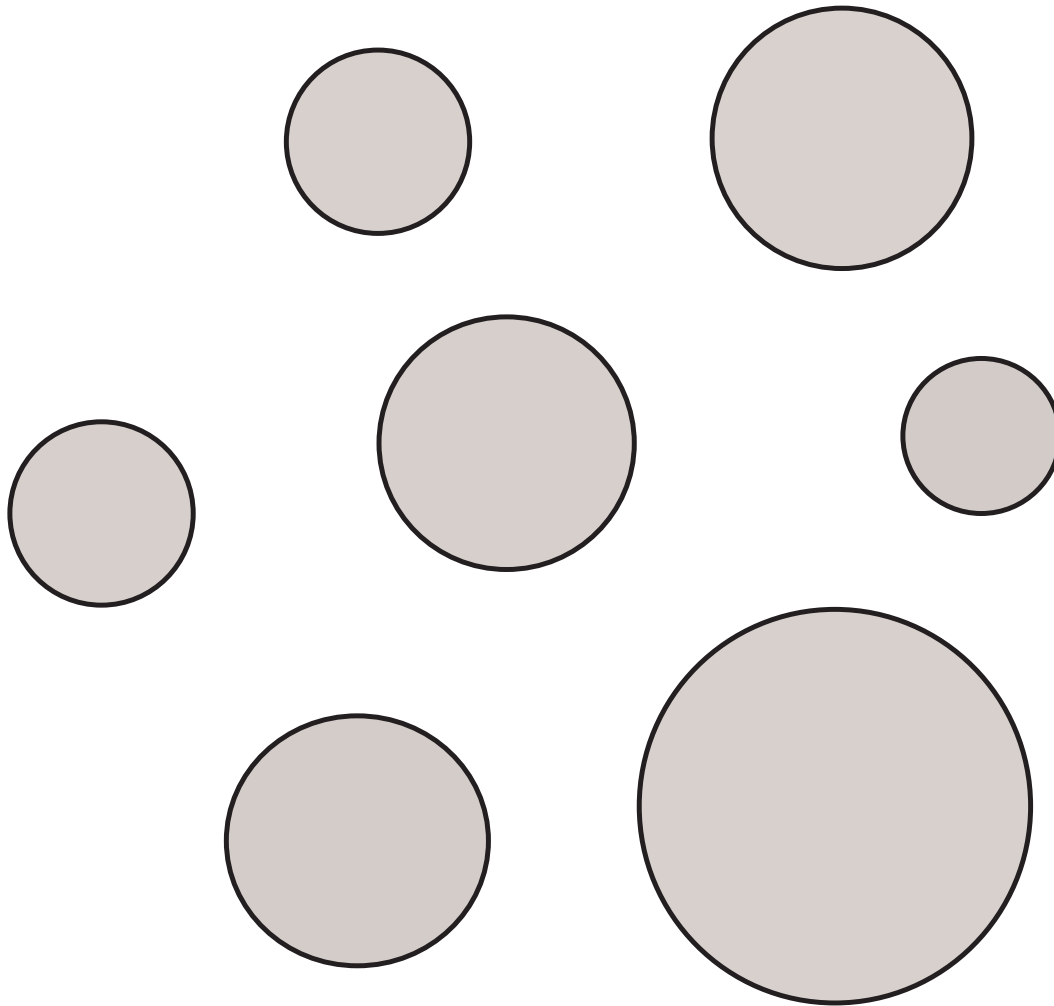


Metapopulations



Total Extinction

Metapopulations



A Stochastic Patch Occupancy Model (SPOM)

A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are n patches.

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

A Stochastic Patch Occupancy Model (SPOM)

Suppose that there are n patches.

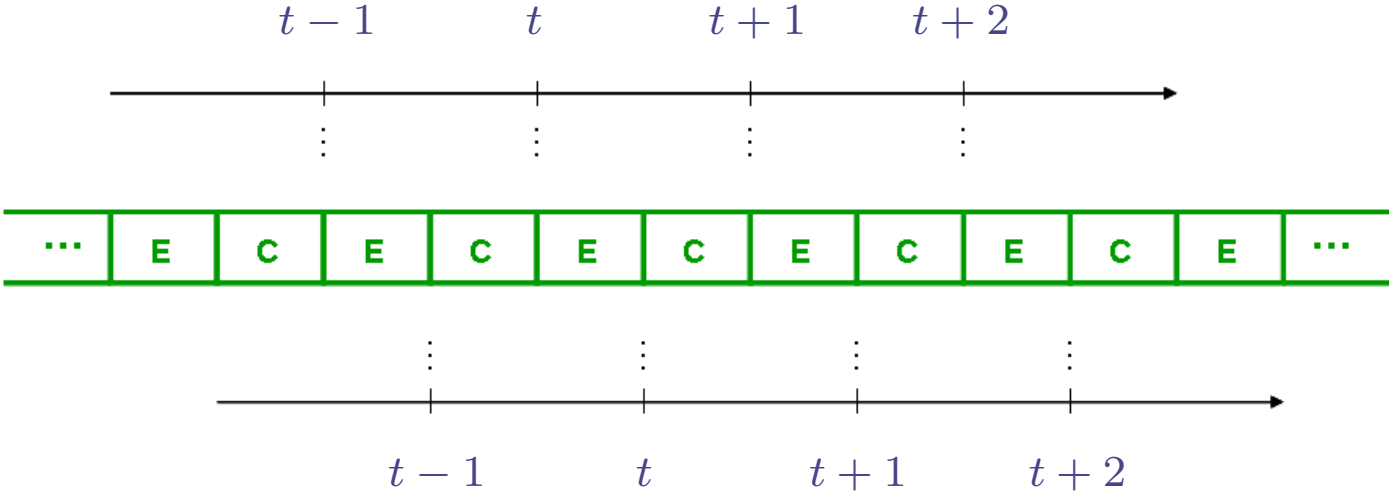
Let $X_t^{(n)} = (X_{1,t}^{(n)}, \dots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch i is occupied.

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

Colonization and extinction happen in distinct, successive phases.

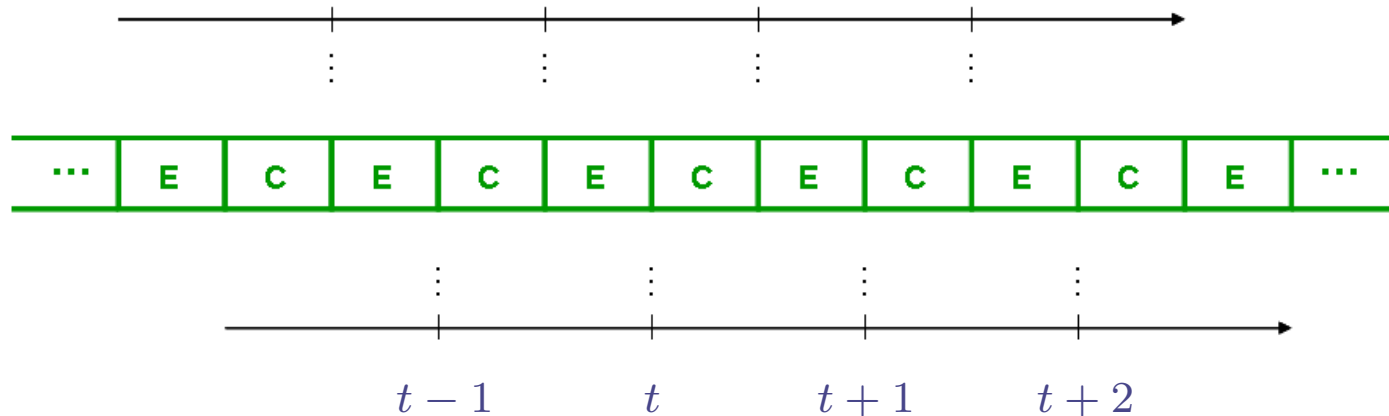
SPOM - Phase structure

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).

Colonization and extinction happen in distinct, successive phases.

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, and $c'(0) > 0$.

Colonization and extinction happen in distinct, successive phases.

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, and $c'(0) > 0$.

Extinction: occupied patch i remains occupied independently with probability S_i (random).

Thus, we have a *Chain Bernoulli* structure:

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

Thus, we have a *Chain Bernoulli* structure:

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

Notation: $\mathit{Bin}(m, p)$ is a binomial random variable with m trials and success probability p .

Thus, we have a *Chain Bernoulli* structure:

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

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:

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

Compare this with the *homogenous case*, where $S_i = s$ (non-random) is the same for each i , and we merely count the *number* $N_t^{(n)}$ of occupied patches at time t .

We have the following *Chain Binomial* structure:

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

Compare this with the *homogenous case*, where $S_i = s$ (non-random) is the same for each i , and we merely count the *number* $N_t^{(n)}$ of occupied patches at time t .

We have the following *Chain Binomial* structure:

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

Compare this with the *homogenous case*, where $S_i = s$ (non-random) is the same for each i , and we merely count the *number* $N_t^{(n)}$ of occupied patches at time t .

We have the following *Chain Binomial* structure:

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

Compare this with the *homogenous case*, where $S_i = s$ (non-random) is the same for each i , and we merely count the *number* $N_t^{(n)}$ of occupied patches at time t .

We have the following *Chain Binomial* structure:

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

Compare this with the *homogenous case*, where $S_i = s$ (non-random) is the same for each i , and we merely count the *number* $N_t^{(n)}$ of occupied patches at time t .

We have the following *Chain Binomial* structure:

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

Compare this with the *homogenous case*, where $S_i = s$ (non-random) is the same for each i , and we merely count the *number* $N_t^{(n)}$ of occupied patches at time t .

We have the following *Chain Binomial* structure:

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

Compare this with the *homogenous case*, where $S_i = s$ (non-random) is the same for each i , and we merely count the *number* $N_t^{(n)}$ of occupied patches at time t .

We have the following *Chain Binomial* structure:

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

A deterministic limit

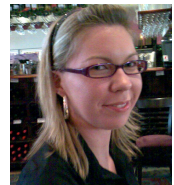
Theorem* If $N_0^{(n)}/n \xrightarrow{p} x_0$ (a constant), then

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

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

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

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

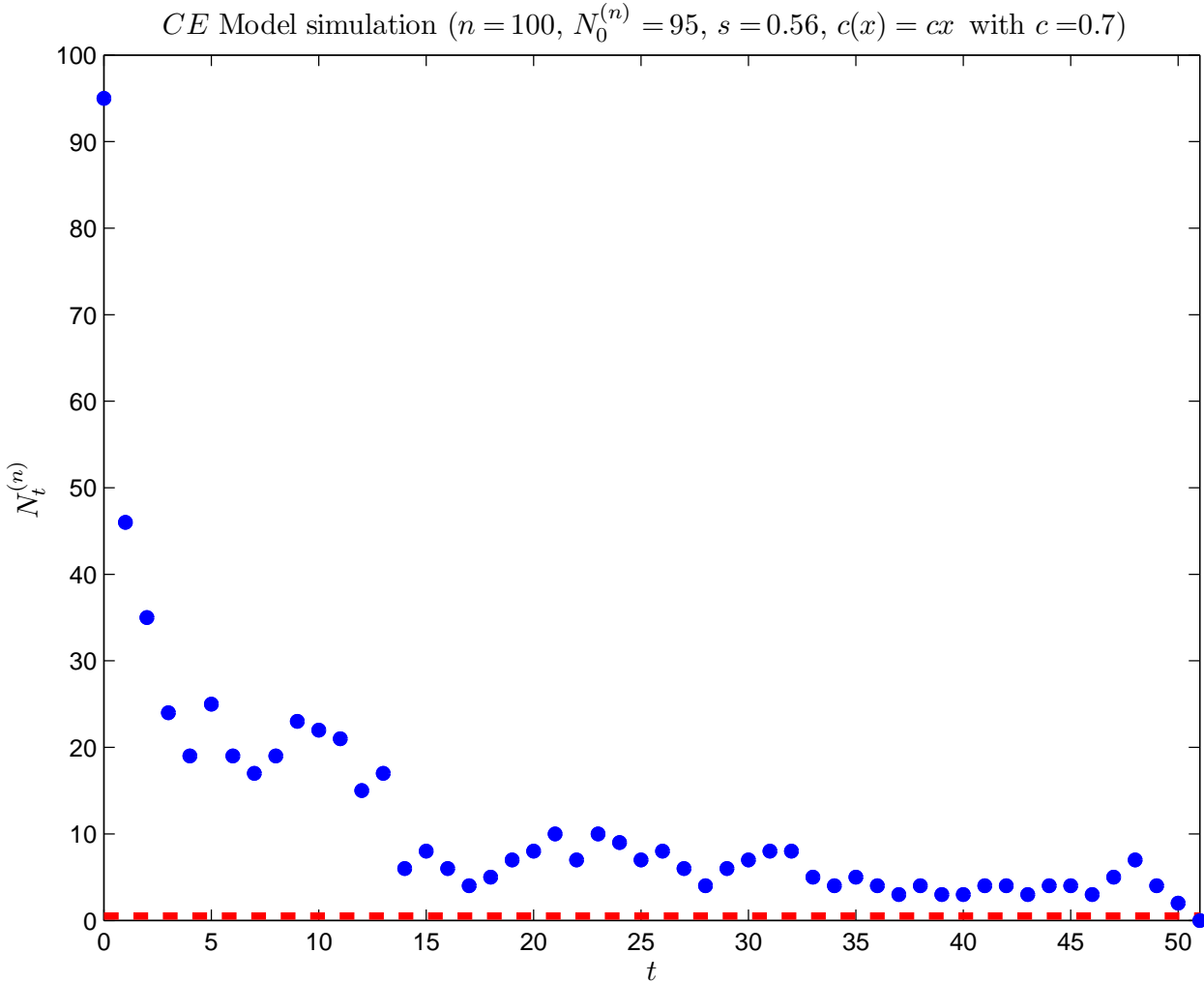


Stability

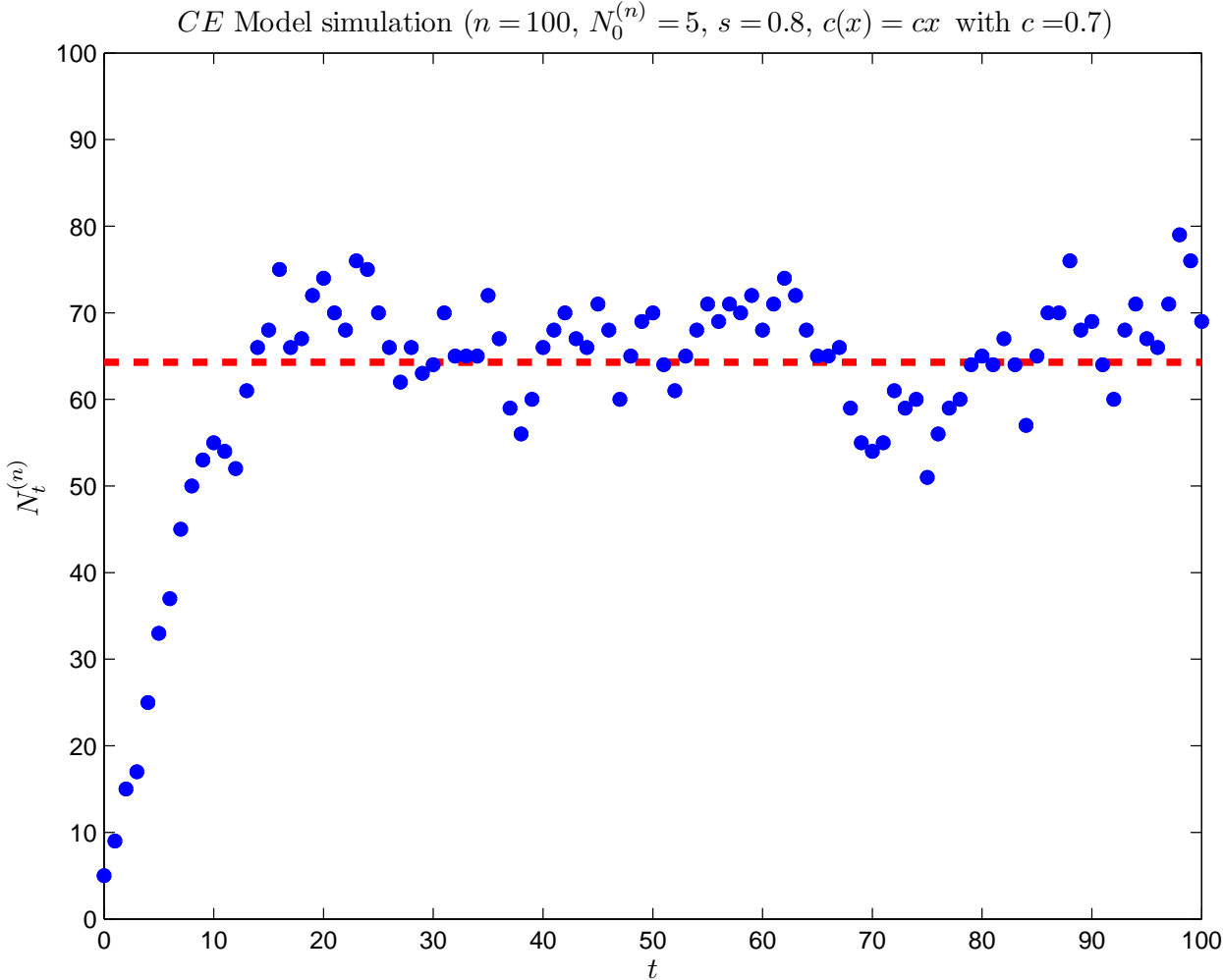
$x_{t+1} = f(x_t)$, where $f(x) = s(x + (1 - x)c(x))$.

- **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).

CE Model - Evanescence



CE Model - Quasi stationarity



A deterministic limit

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

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

A deterministic limit

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

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

First, ...

Notation: If σ is a probability measure on $[0, 1)$ and let \bar{s}_k denote its k -th moment, that is,

$$\bar{s}_k = \int_0^1 \lambda^k \sigma(d\lambda).$$

A deterministic limit

Theorem Suppose there is a probability measure σ and deterministic sequence $\{d(0, k)\}$ such that

$$\frac{1}{n} \sum_{i=1}^n S_i^k \xrightarrow{p} \bar{s}_k \quad \text{and} \quad \frac{1}{n} \sum_{i=1}^n S_i^k X_{i,0}^{(n)} \xrightarrow{p} d(0, k)$$

for all $k = 0, 1, \dots, T$. Then, there is a (deterministic) triangular array $\{d(t, k)\}$ such that, for all $t = 0, 1, \dots, T$ and $k = 0, 1, \dots, T - t$,

$$\frac{1}{n} \sum_{i=1}^n S_i^k X_{i,t}^{(n)} \xrightarrow{p} d(t, k),$$

where

$$d(t + 1, k) = d(t, k + 1) + c(d(t, 0)) (\bar{s}_{k+1} - d(t, k + 1)).$$

Remarks

- Typically, we are only interested in $d(t, 0)$, being the asymptotic proportion of occupied patches.
- However, we may still interpret the ratio $d(t, k)/d(t, 0)$ ($k \geq 1$) as the k -th moment of the conditional distribution of the patch survival probability given that the patch is occupied. (From these moments, the conditional distribution could then be reconstructed.)

Remarks

- When $\bar{s}_k = \bar{s}_1^k$ for all k , that is the patch survival probabilities are the same, then it is possible to simplify

$$d(t + 1, k) = d(t, k + 1) + c(d(t, 0)) (\bar{s}_{k+1} - d(t, k + 1)).$$

We can show by induction that $d(t, k) = \bar{s}_1^k x_t$, where

$$x_{t+1} = \bar{s}_1 (x_t + (1 - x_t) c(x_t)).$$

(Compare this with the earlier result.)

Theorem The fixed points are given by

$$d(k) = \int_0^1 \frac{c(\psi)\lambda^{k+1}}{1-\lambda+c(\psi)\lambda} \sigma(d\lambda),$$

where ψ solves

$$R(\psi) = \int_0^1 \frac{c(\psi)\lambda}{1-\lambda+c(\psi)\lambda} \sigma(d\lambda) = \psi. \quad (1)$$

If $c(0) > 0$, there is a unique $\psi > 0$. If $c(0) = 0$ and

$$c'(0) \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) \leq 1,$$

then $\psi = 0$ is the unique solution to (1). Otherwise, (1) has two solutions, one of which is $\psi = 0$.

Theorem If $c(0) = 0$ and

$$c'(0) \int_0^1 \frac{\lambda}{1-\lambda} \sigma(d\lambda) \leq 1,$$

then $d(k) \equiv 0$ is a stable fixed point. Otherwise, the non-zero solution to

$$R(\psi) = \int_0^1 \frac{c(\psi)\lambda}{1-\lambda+c(\psi)\lambda} \sigma(d\lambda) = \psi$$

provides the stable fixed point through

$$d(k) = \int_0^1 \frac{c(\psi)\lambda^{k+1}}{1-\lambda+c(\psi)\lambda} \sigma(d\lambda).$$