# Metapopulations in dynamic landscapes

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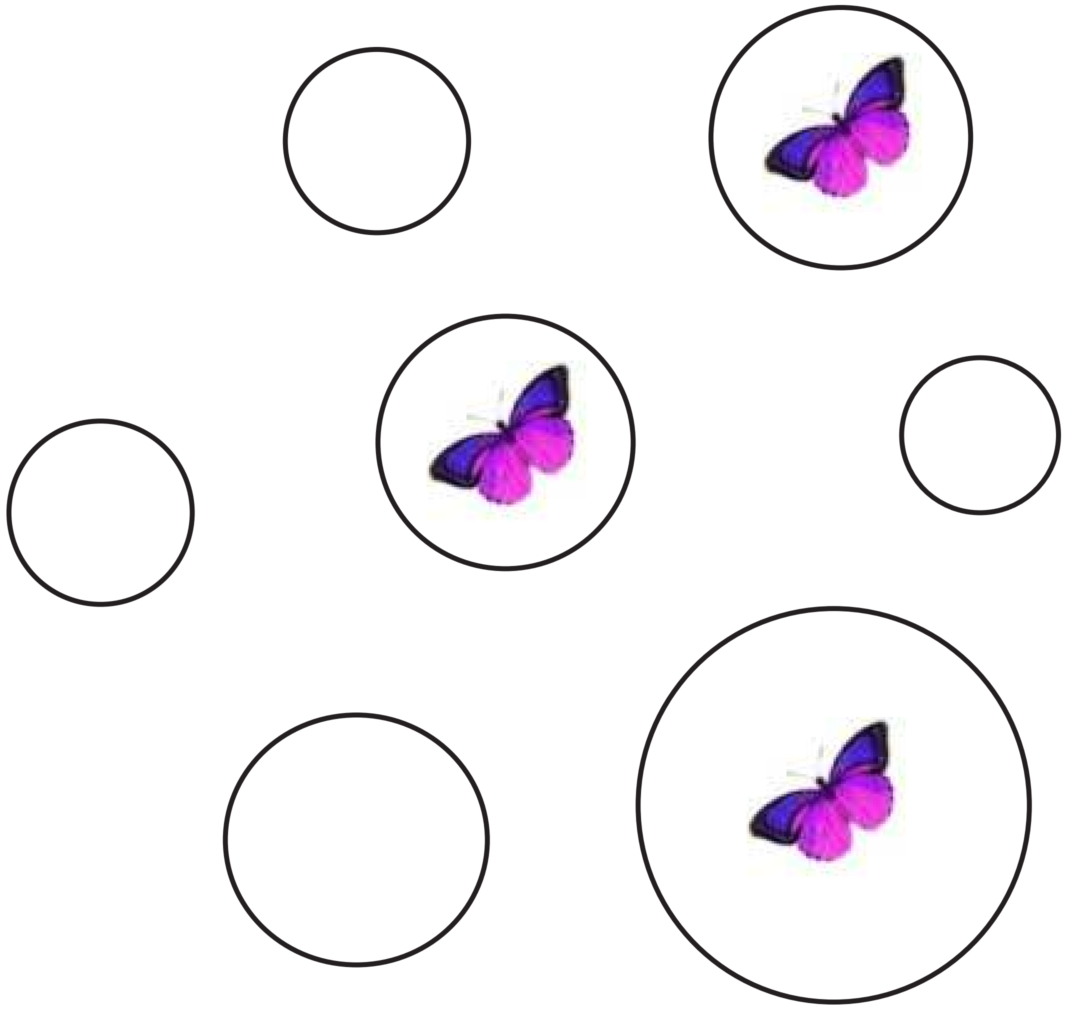
AUSTRALIAN RESEARCH COUNCIL CENTRE OF EXCELLENCE FOR MATHEMATICAL AND STATISTICAL FRONTIERS

# Metapopulations



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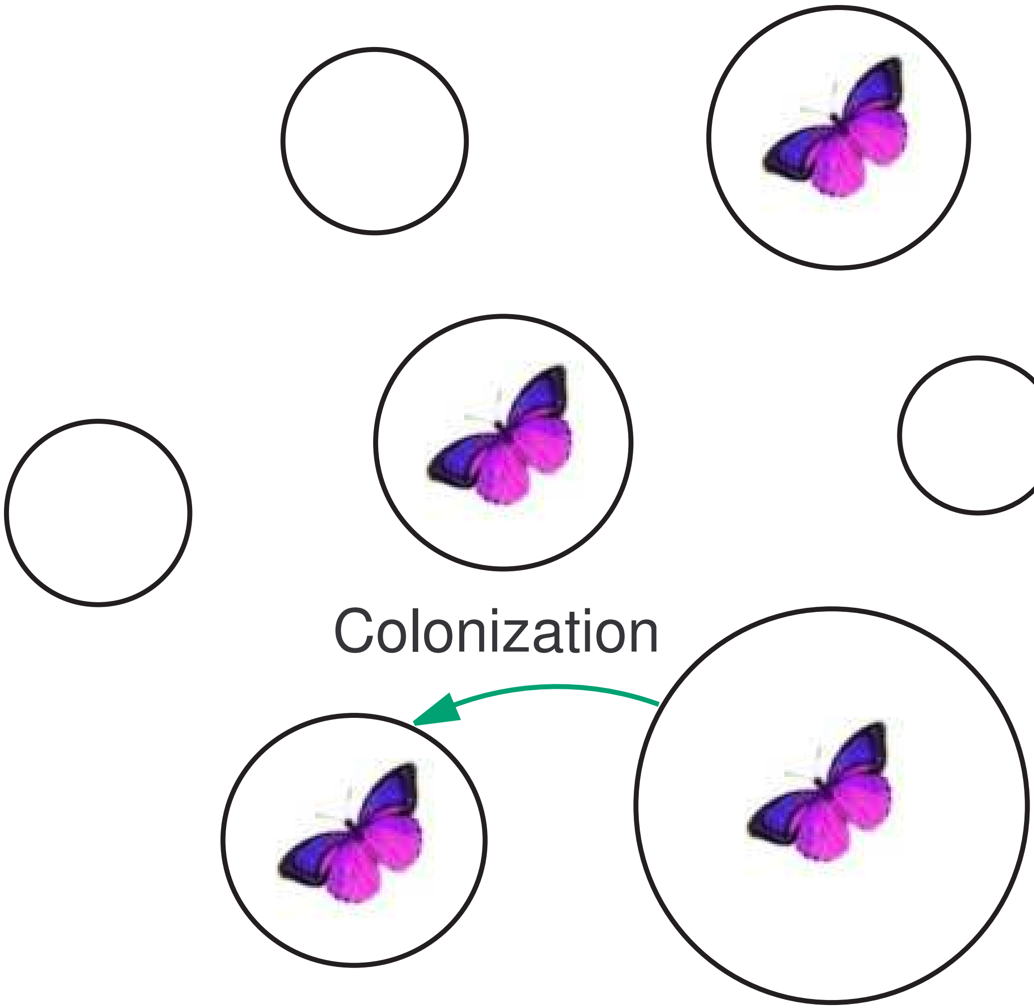

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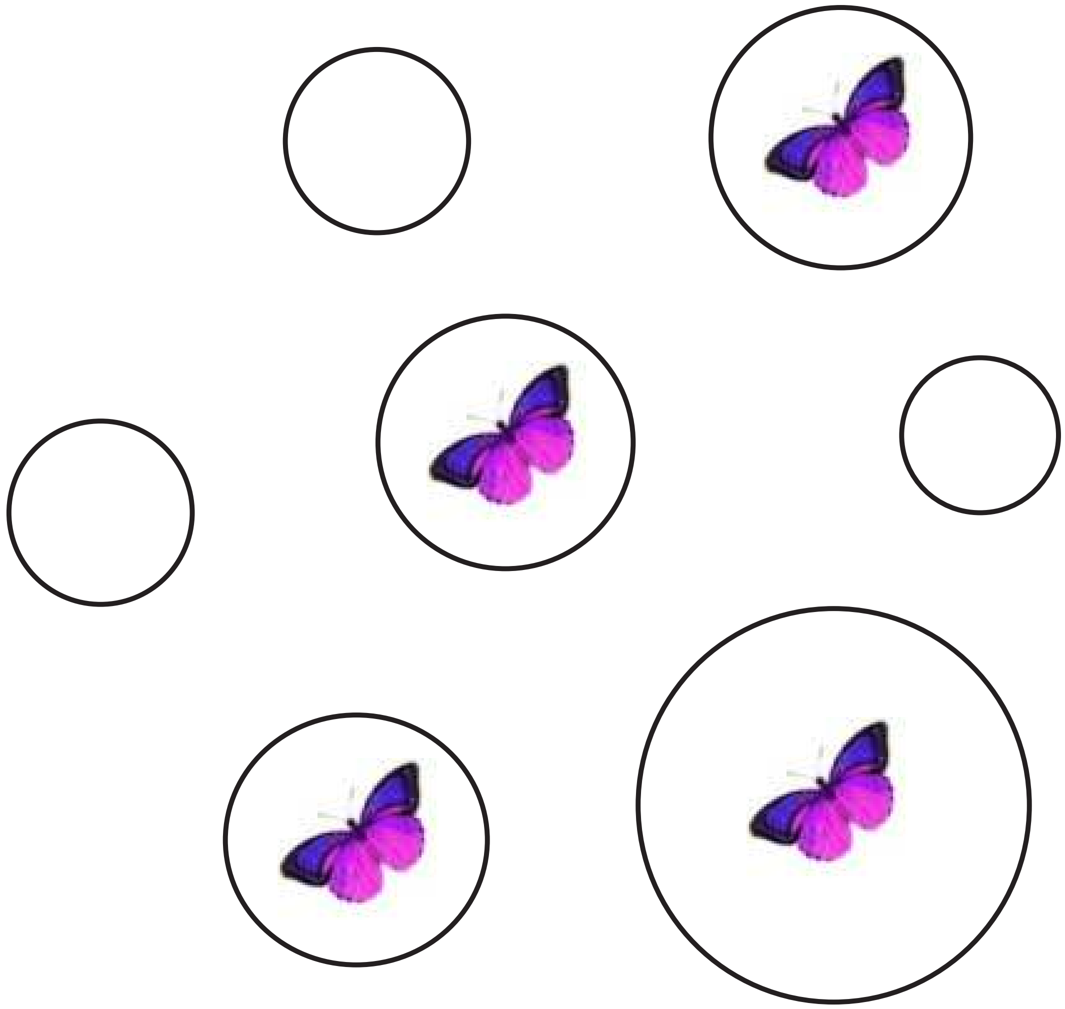

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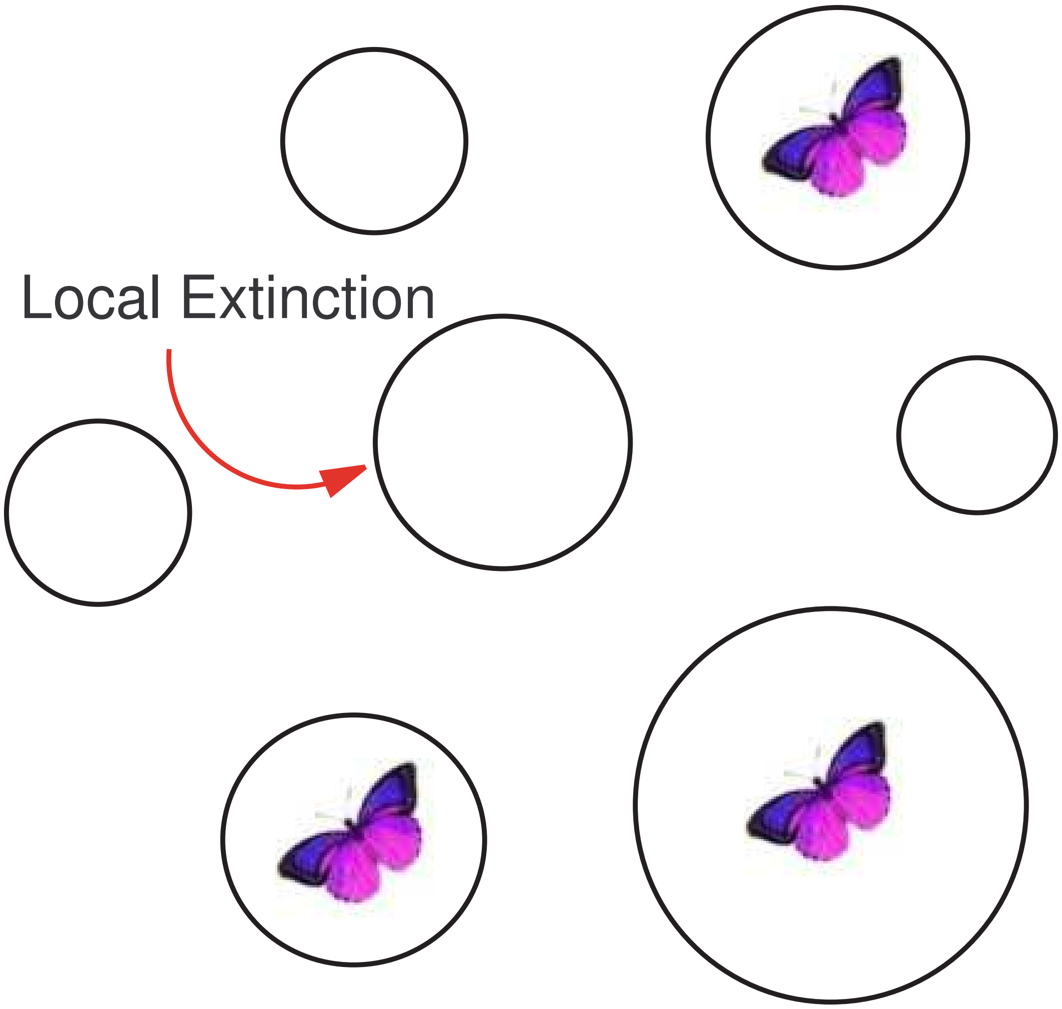

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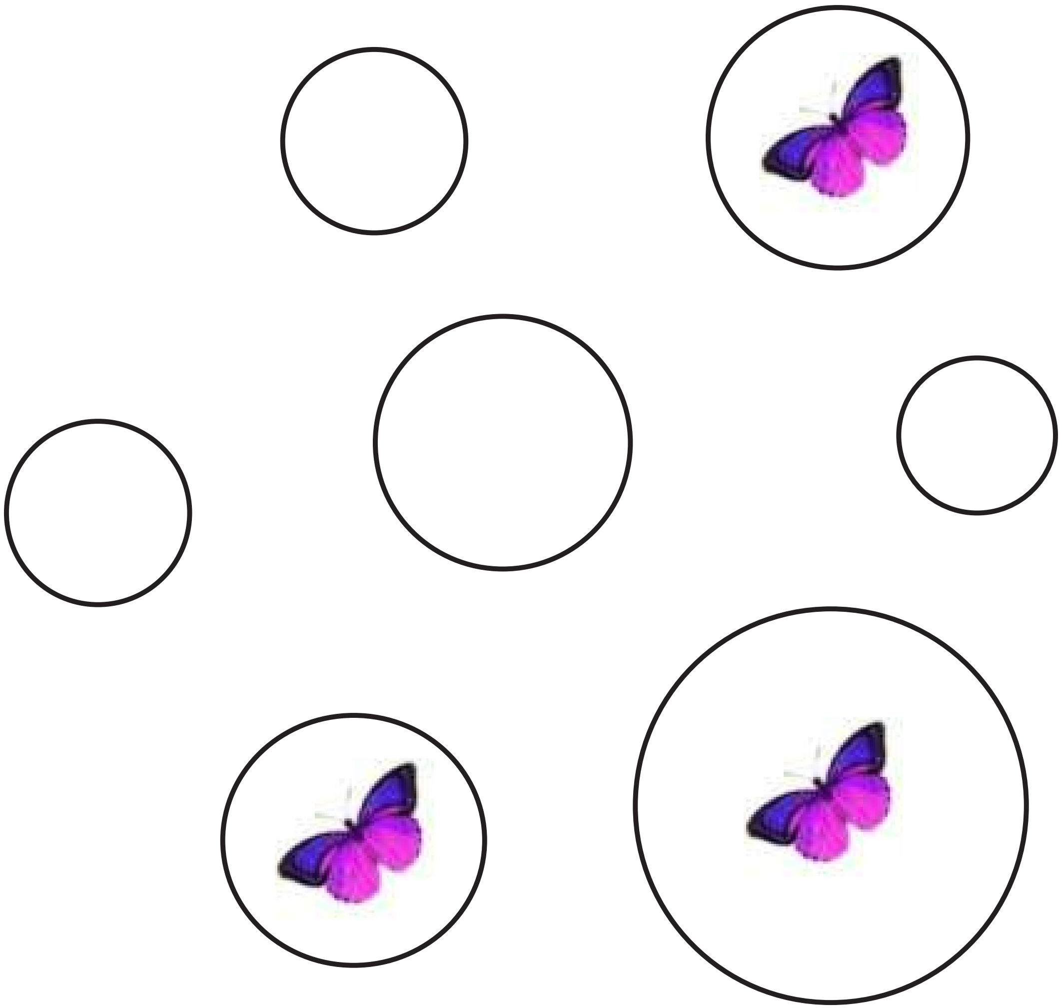

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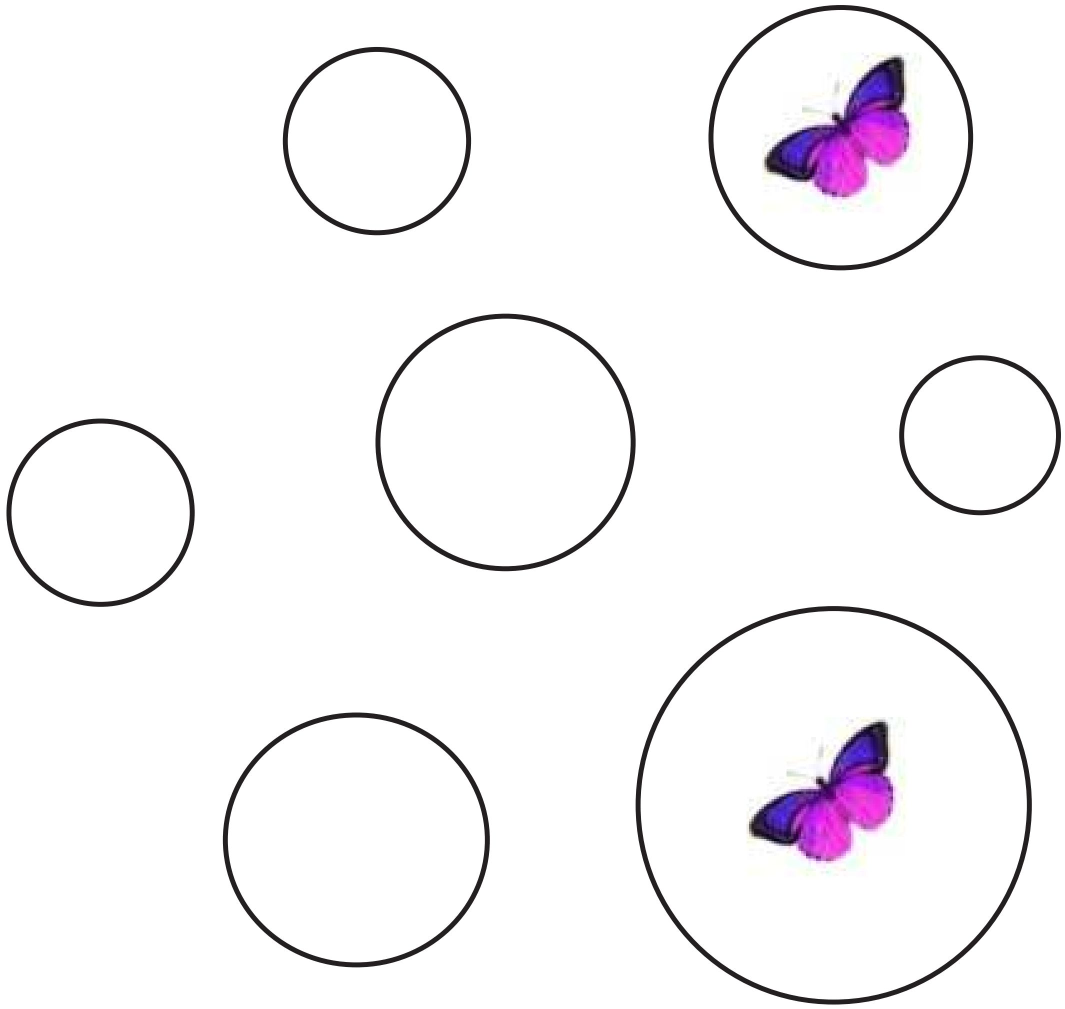

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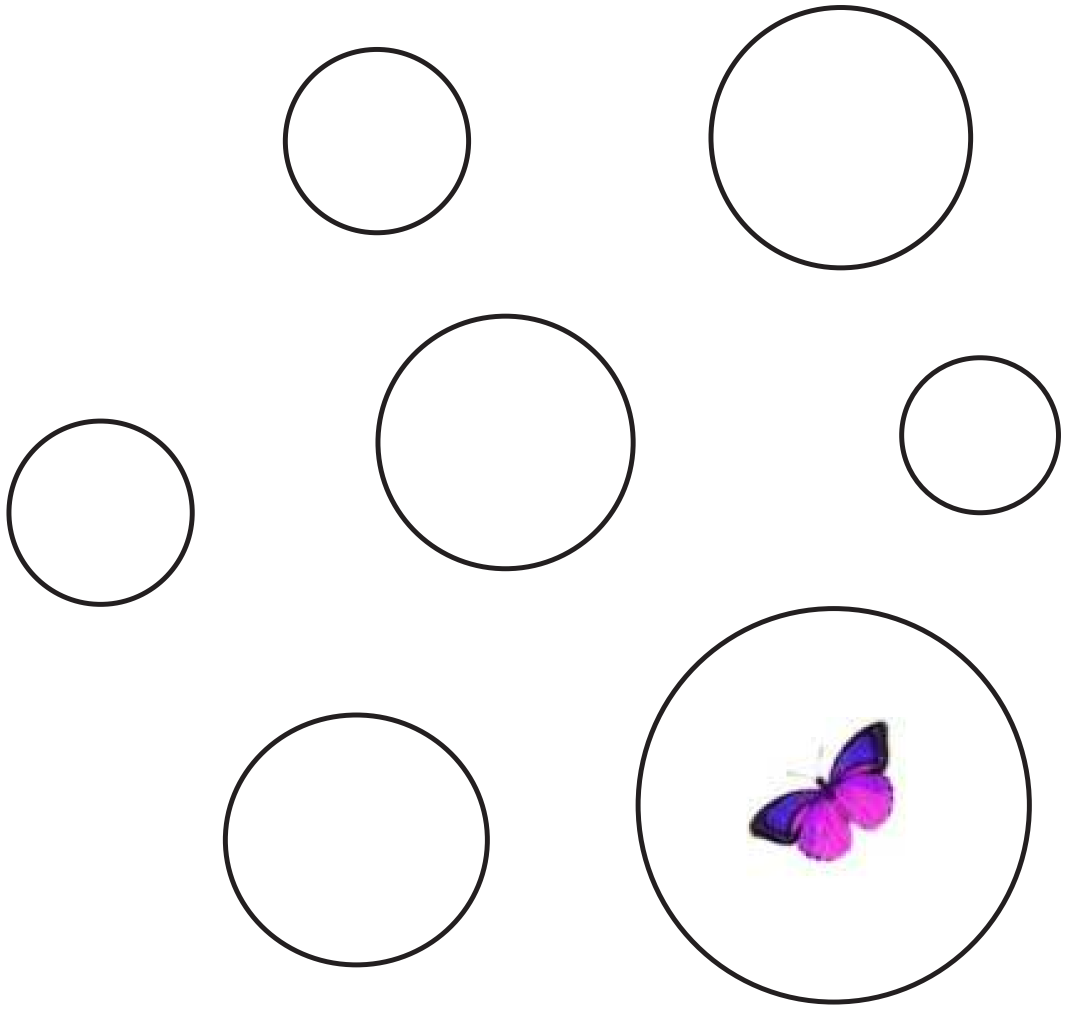

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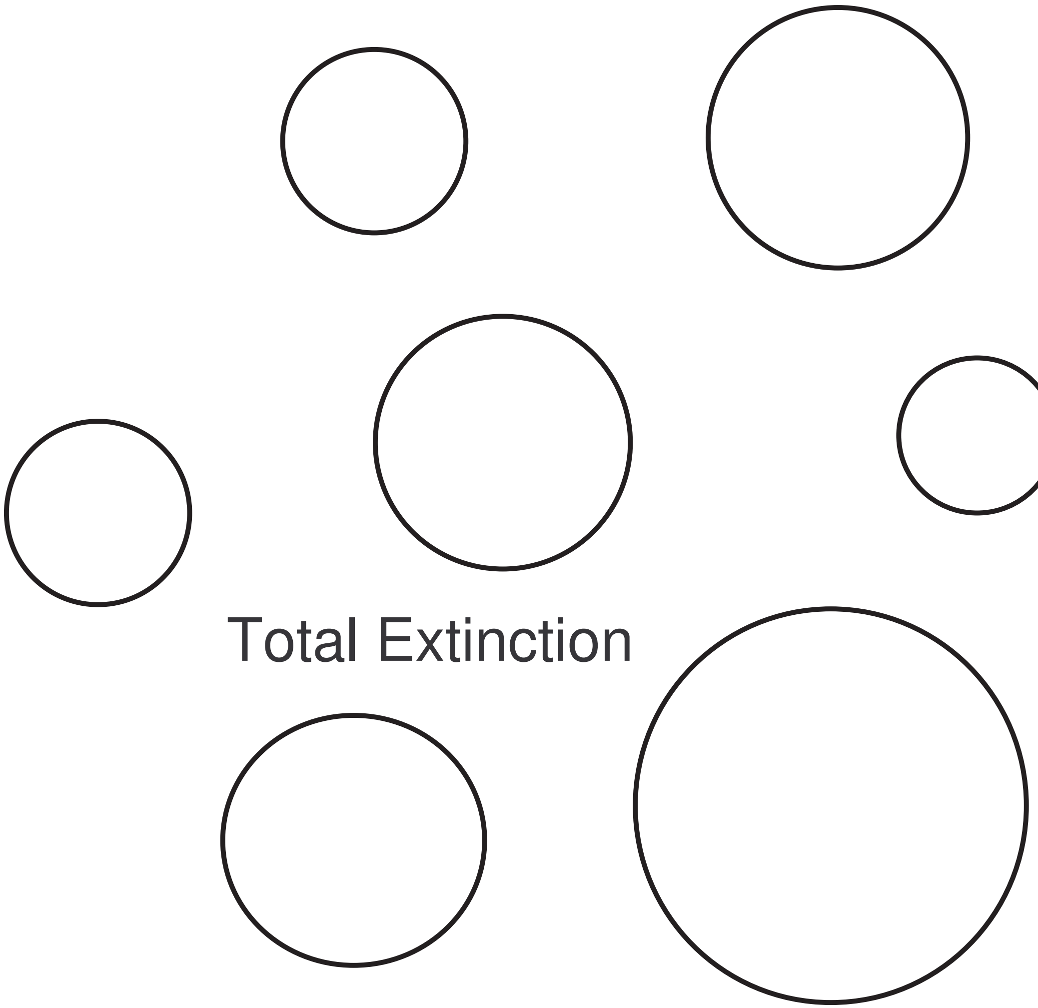

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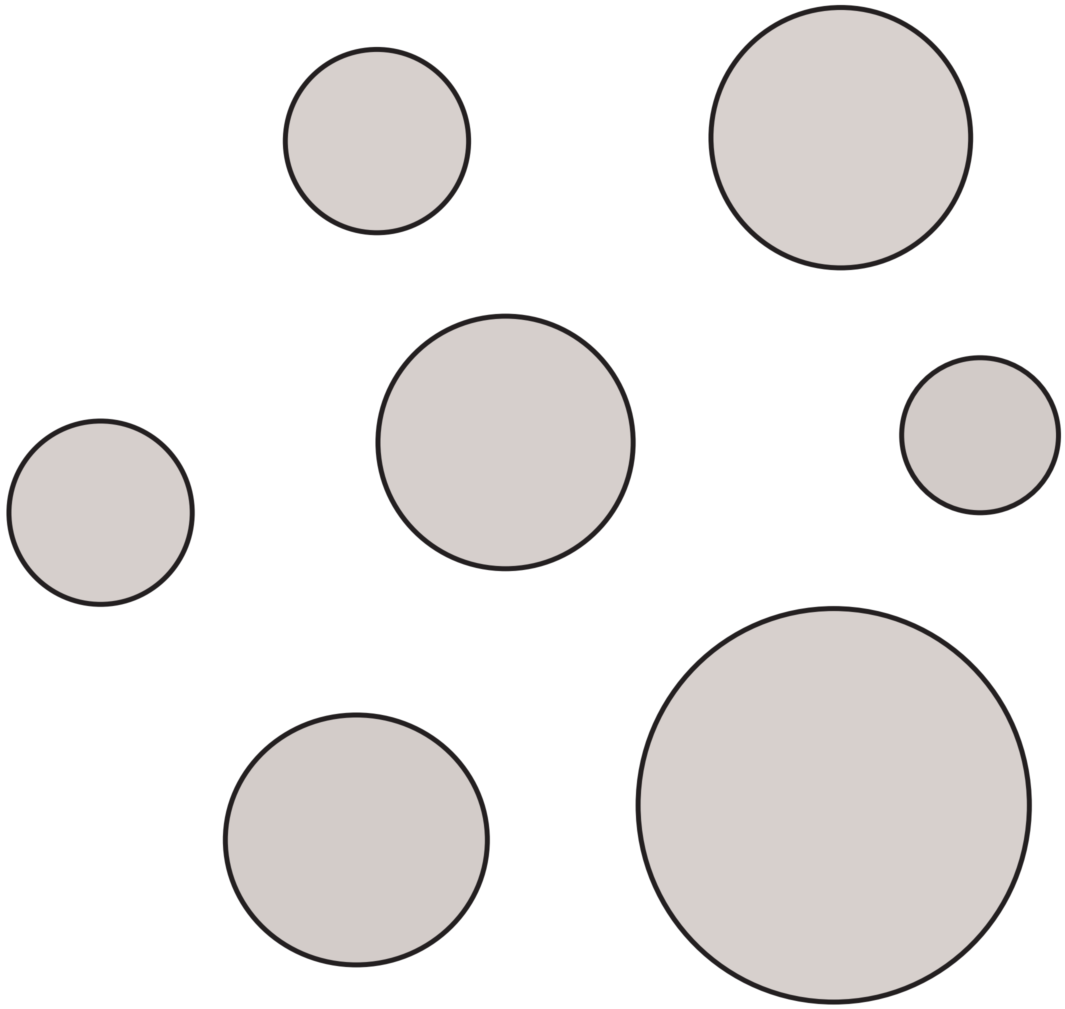

# SPOM

A *stochastic patch occupancy model* (SPOM)

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Suppose that there are $n$ patches.

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Colonization and extinction happen in distinct, successive phases.

# SPOM - Phase structure

For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle. Examples:

The Vernal pool fairy shrimp (Branchinecta lynchi) and the California linderiella (Linderiella occidentalis), both listed under the Endangered Species Act (USA)

The Jasper Ridge population of Bay checkerspot butterfly (Euphydryas editha bayensis), now extinct

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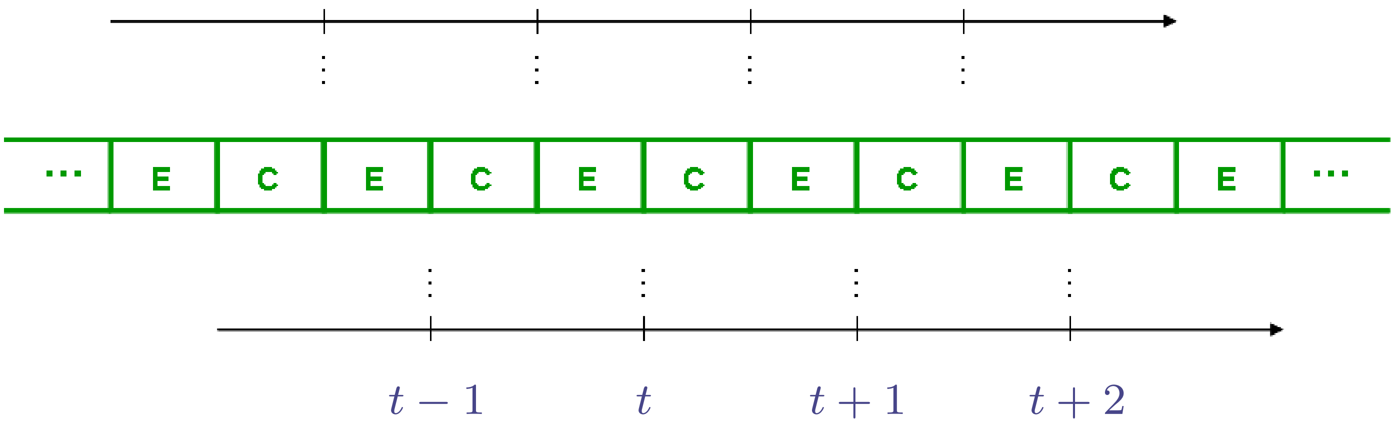


We will we assume that the population is *observed after successive extinction phases* (CE Model).

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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 $c:[0,1]\to[0,1]$ is continuous, non-decreasing and concave.

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Proportion of patches occupied

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$[$More generally, we can allow $c(\,\cdot\,)$ to depend on the *relative positions* of all patches and their *areas*, and allow the survival probabilities to *evolve in time*.$]$

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# SPOM - example

$n = 30$ patches

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

($11$ patches occupied)

# SPOM - example

$n = 30$, $c(x) = 0.7x$

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

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

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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

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# SPOM - example

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

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

0.60 0.56 0.63 0.62 0.52 0.61 0.68 0.49 0.49 0.49 0.50

0.41 0.59 0.63 0.60 0.61

[Survival probabilities listed for occupied patches only]

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| | |
|---|---|
| | 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 |
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| 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 |

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

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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

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.
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C 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
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```

# SPOM

The evolution of the process can be summarized by

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

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a "*Chain Bernoulli*" structure.

In the *homogeneous case*, where $s_i = s$ 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:

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

# A deterministic limit

Letting the initial number $N_0^{(n)}$ of occupied patches grow at the same rate as $n$ . . .

**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

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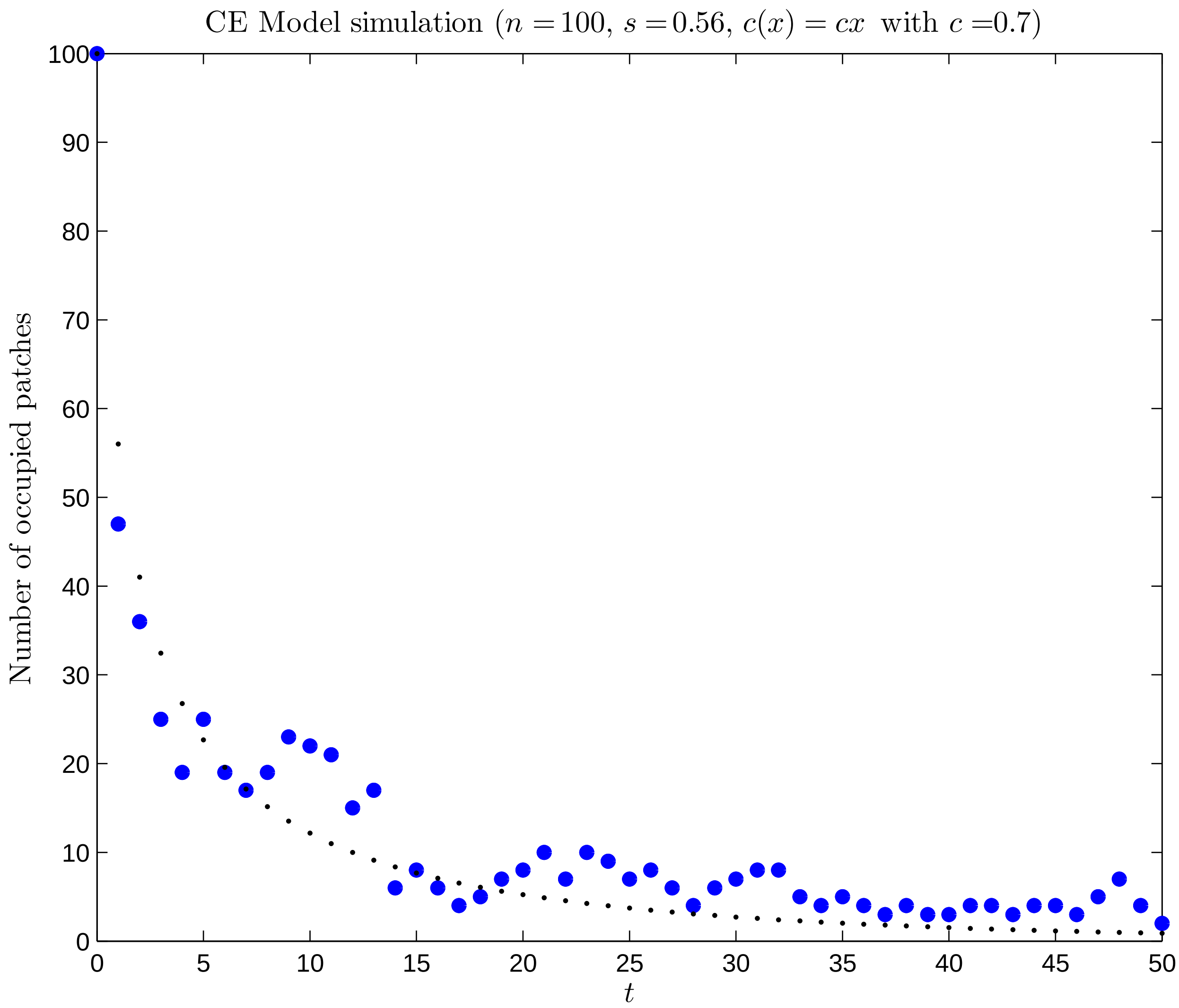
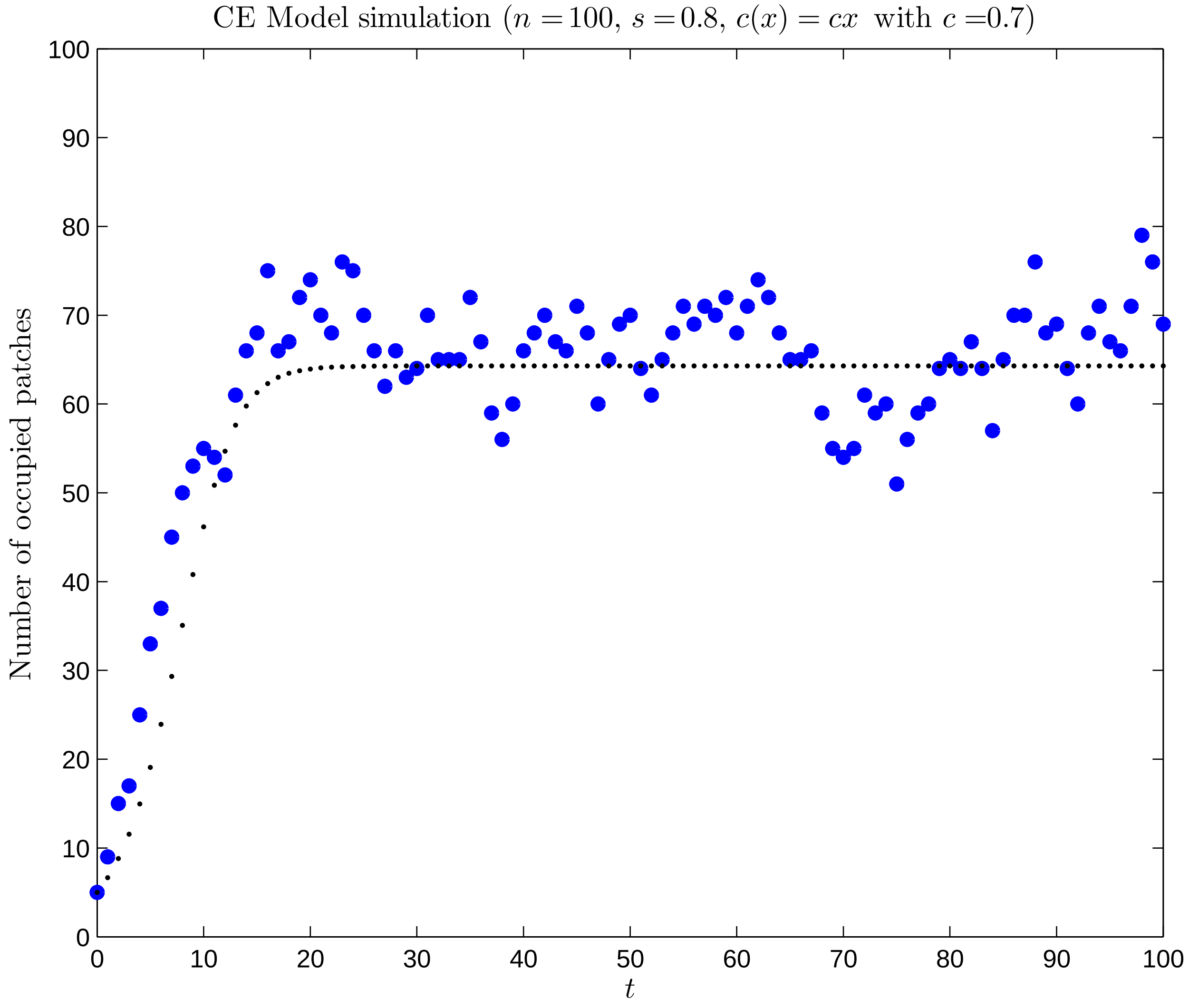
Survival probability

Colonization probability

# CE Model - Evanescence



# CE Model - Quasi stationarity



# 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 $1 + c'(0) \le 1/s$. 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).

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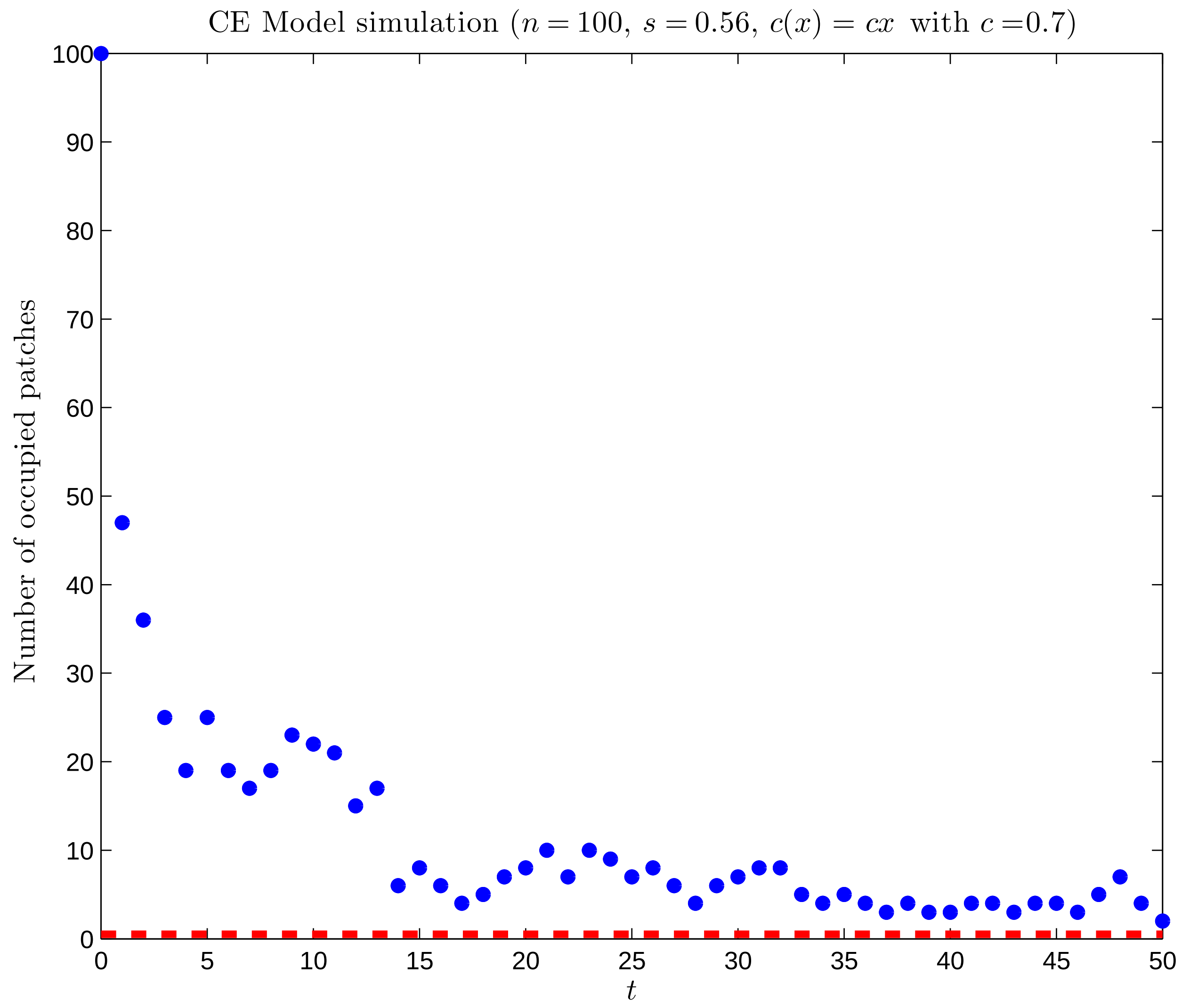

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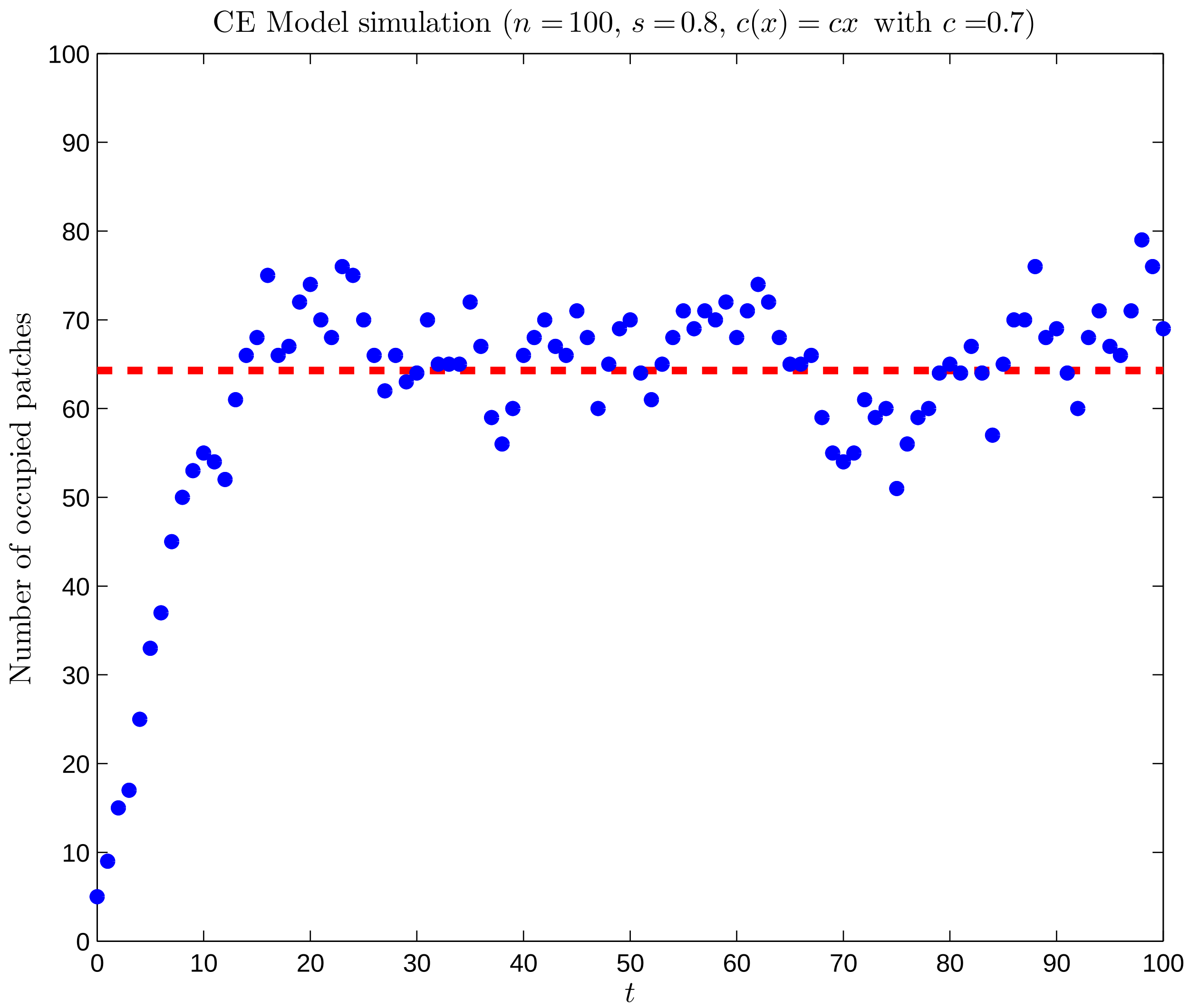

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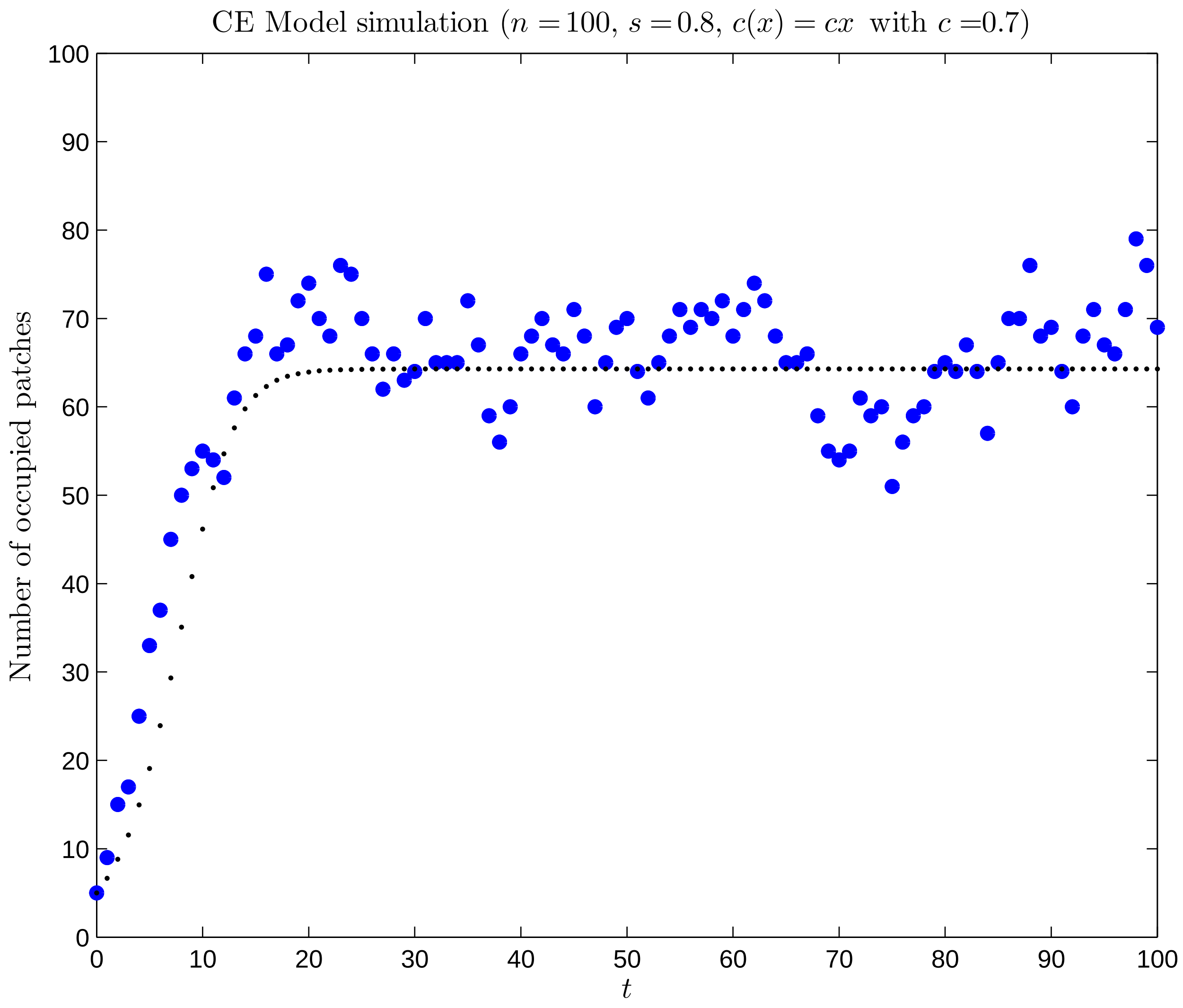


# A Gaussian limit

**Theorem** Further suppose that $c(x)$ is twice continuously differentiable, and let

$$Z_t^{(n)} = \sqrt{n}(N_t^{(n)}/n - x_t).$$

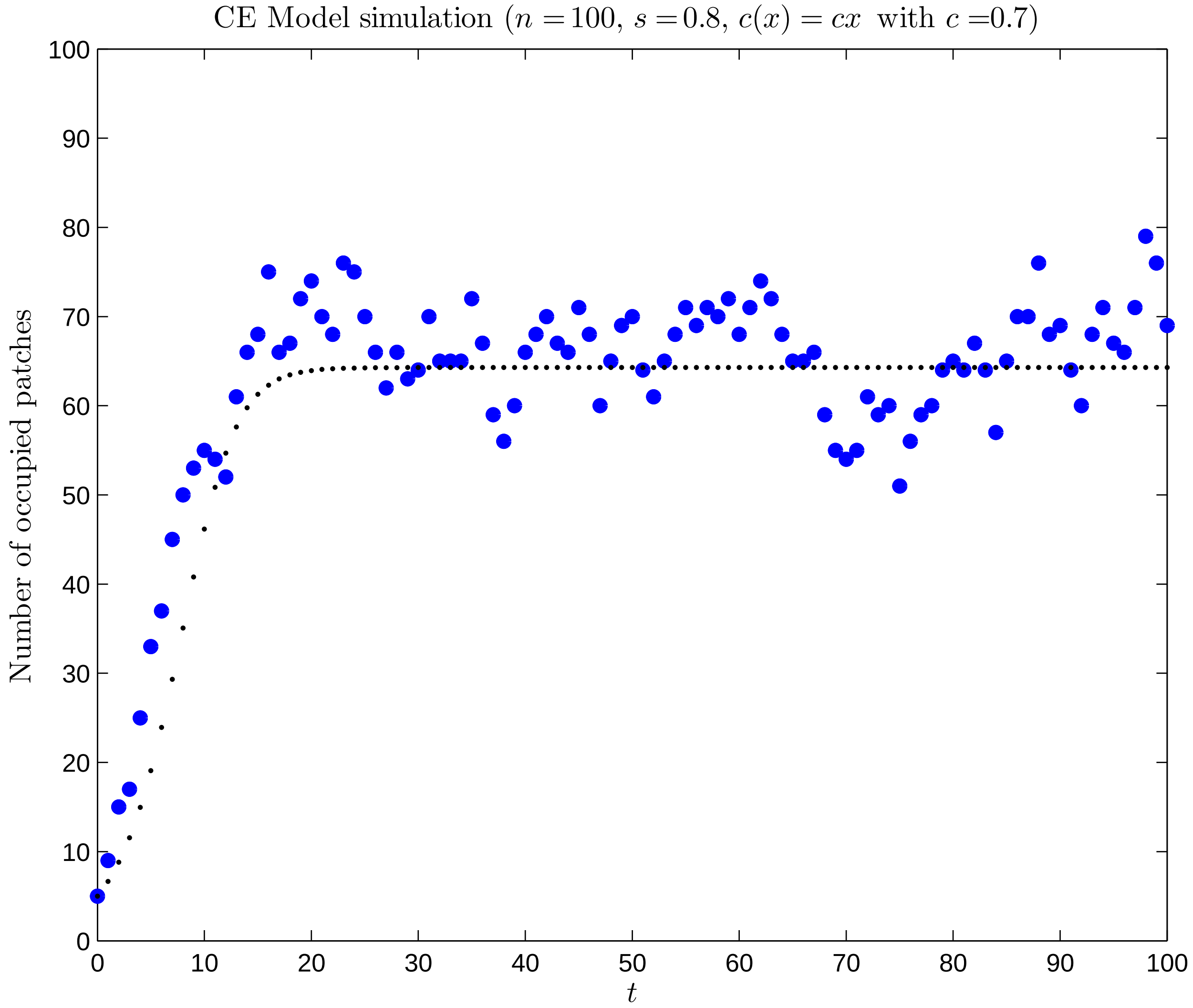
If $Z_0^{(n)} \xrightarrow{d} z_0$, then $Z_\bullet^{(n)}$ converges weakly to the Gaussian Markov chain $Z_\bullet$ defined by

$$Z_{t+1} = f'(x_t)Z_t + E_t \qquad (Z_0 = z_0),$$

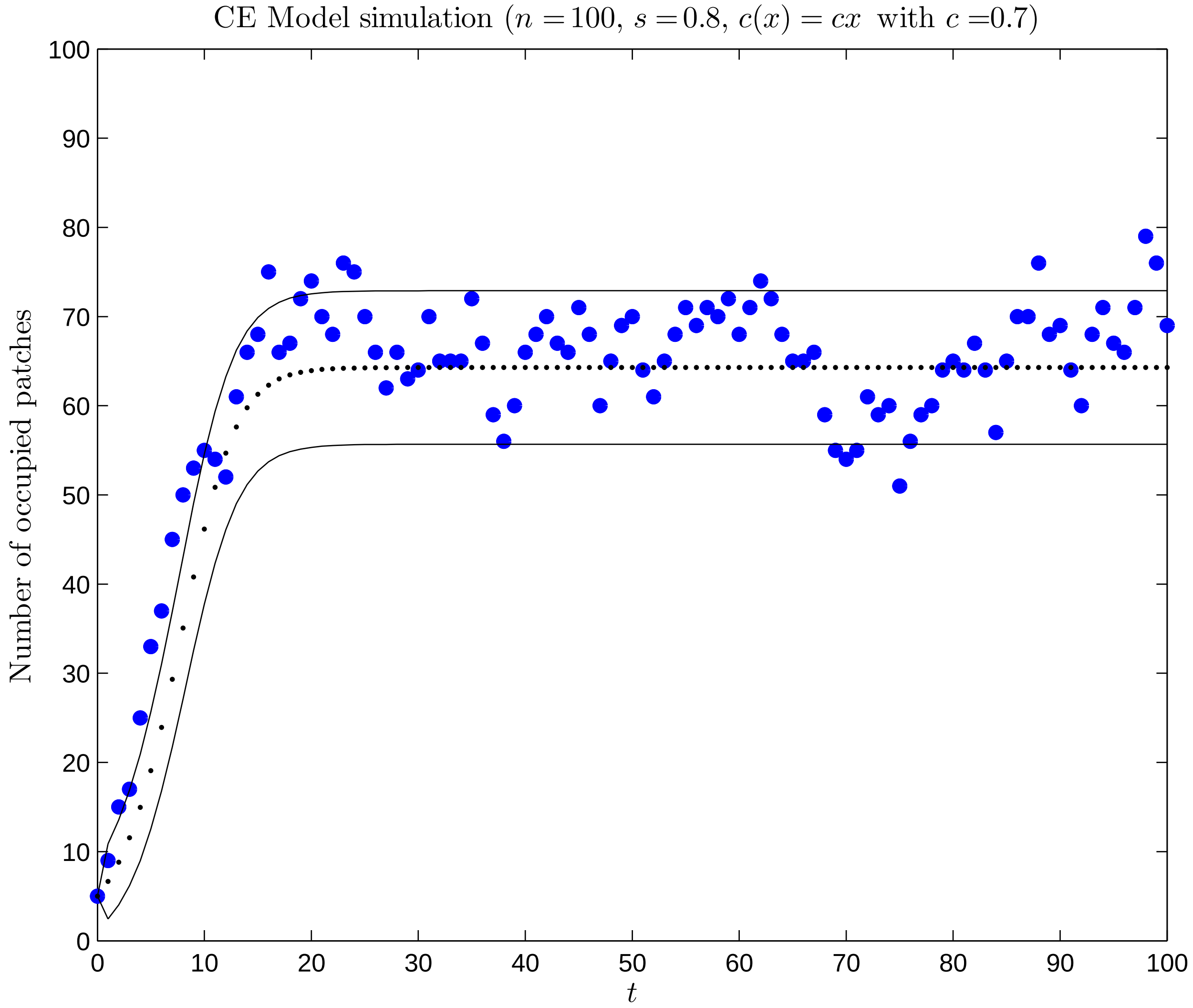
with $(E_t)$ independent and $E_t \sim \mathsf{N}(0, v(x_t))$, where

$$v(x) = s\Big[(1-s)x + (1-x)c(x)\big(1 - sc(x)\big)\Big].$$

# CE Model - Quasi stationarity



# CE Model - Gaussian approximation



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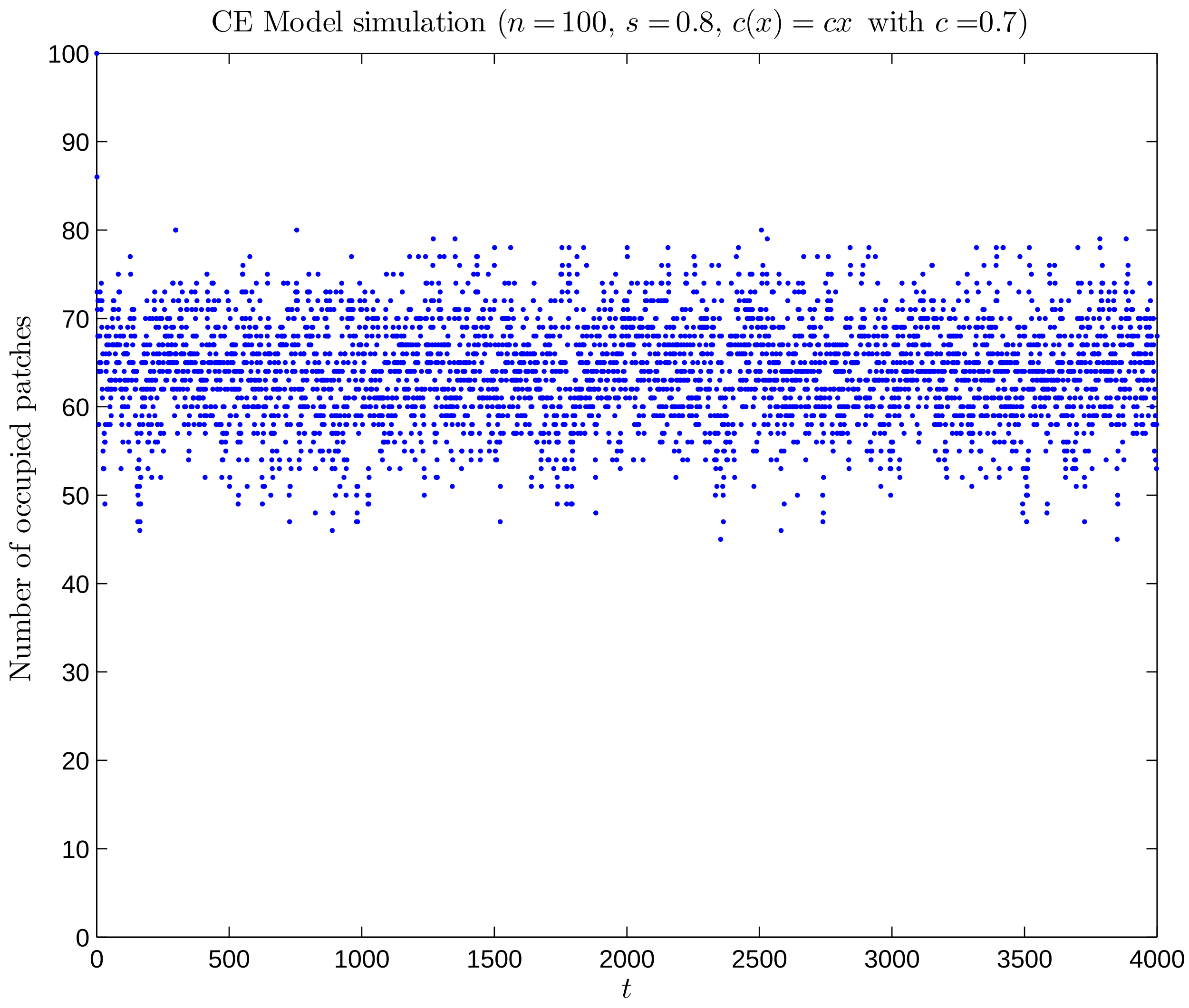

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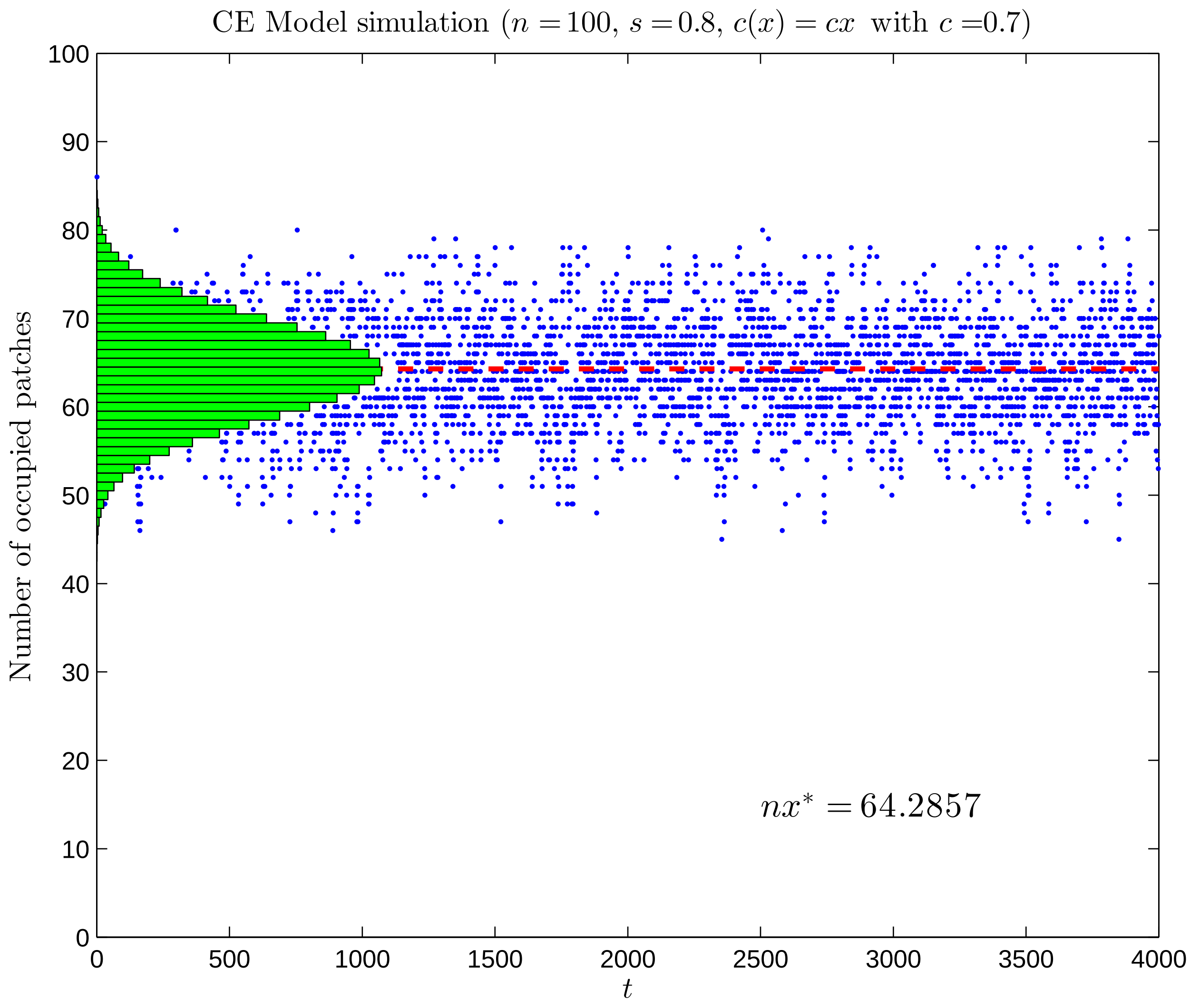

# SPOM - general case

Return now to the general case, where patch survival probabilities $(s_i)$ are *random* and *patch dependent*, and we keep track of which patches are occupied ...

$$X_{i,t+1}^{(n)} \stackrel{d}{=} \textit{Bin}\Big(X_{i,t}^{(n)} + \textit{Bin}\Big(1 - X_{i,t}^{(n)}, c\big(\tfrac{1}{n}\textstyle\sum_{j=1}^{n} X_{j,t}^{(n)}\big)\Big), s_i\Big).$$

# Our approach - Point Processes

Treat the collection of patch survival probabilities and those of *occupied patches* at time $t$ as point processes on $[0, 1]$.

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Define sequences $(\sigma_n)$ and $(\mu_{n,t})$ of random measures by

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Equivalently, we may define $(\sigma_n)$ and $(\mu_{n,t})$ by

$$\int h(s)\sigma_n(ds) = \frac{1}{n}\sum_{i=1}^{n} h(s_i)$$

$$\int h(s)\mu_{n,t}(ds) = \frac{1}{n}\sum_{i=1}^{n} X_{i,t}^{(n)}\, h(s_i),$$

for $h$ in $C^+([0,1])$, the class of continuous functions that map $[0,1]$ to $[0,\infty)$.

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for $h$ in $C^+([0,1])$, the class of continuous functions that map $[0,1]$ to $[0,\infty)$. For example $(h \equiv 1)$,

$$\int \mu_{n,t}(ds) = \frac{1}{n}\sum_{i=1}^{n} X_{i,t}^{(n)} \quad \text{(proportion occupied).}$$

# A measure-valued difference equation

**Theorem** Suppose that $\sigma_n \xrightarrow{d} \sigma$ and $\mu_{n,0} \xrightarrow{d} \mu_0$ for some non-random measures $\sigma$ and $\mu_0$. Then, $\mu_{n,t} \xrightarrow{d} \mu_t$ for all $t = 1, 2, \ldots$, where $\mu_t$ is defined by the following recursion: for $h \in C^+([0,1])$,

$$\int h(s)\mu_{t+1}(ds) = (1 - c_t)\int sh(s)\mu_t(ds) + c_t \int sh(s)\sigma(ds),$$

where $c_t = c\,(\mu_t([0,1])) = c\left(\int \mu_t(ds)\right)$.

# Homogeneous case

When $\bar{\sigma}^{(k)} = (\bar{\sigma}^{(1)})^k$ for all $k$, that is the patch survival probabilities are the same, then it is possible to simplify

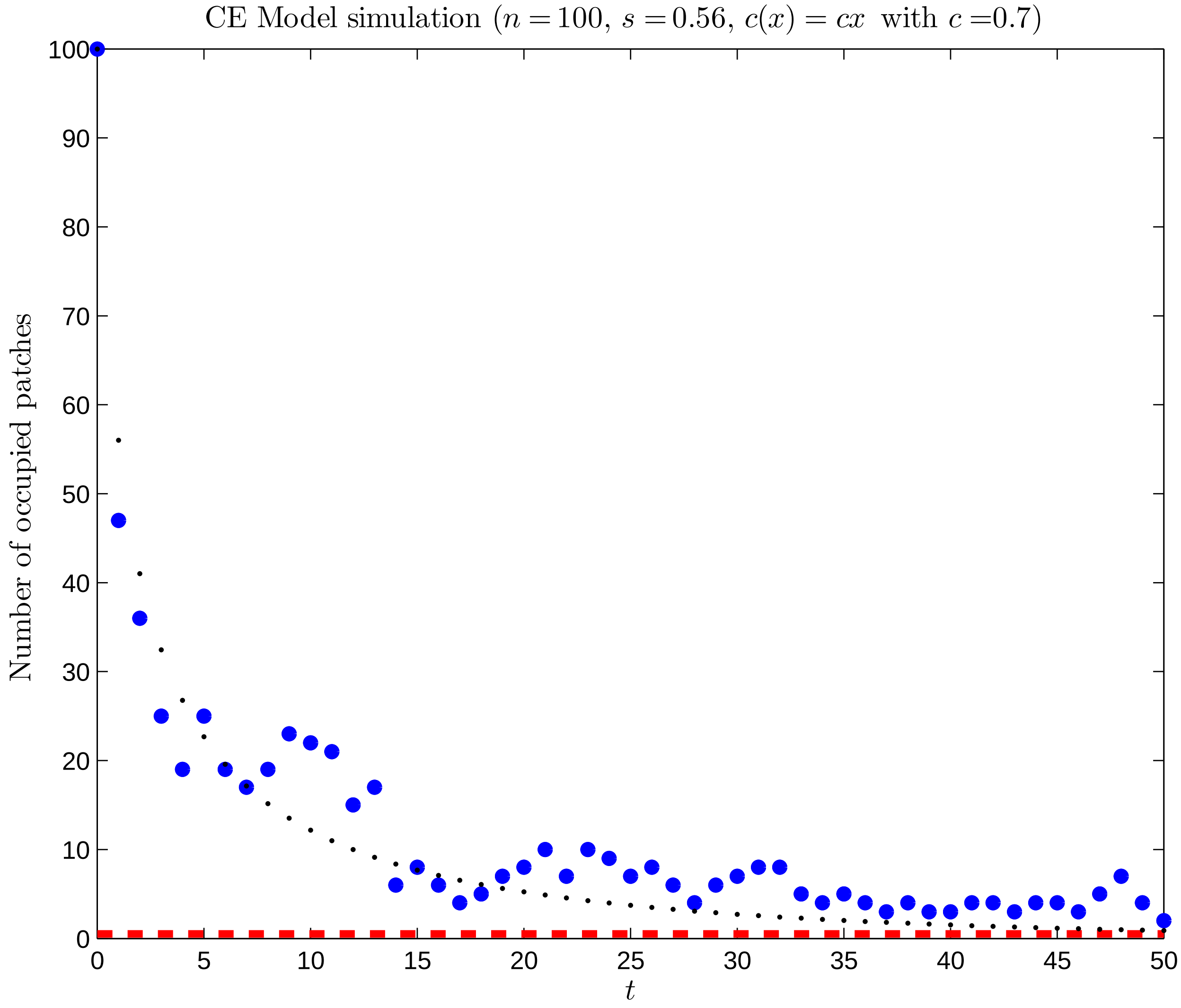
$$\bar{\mu}_{t+1}^{(k)} = (1 - \bar{\mu}_t^{(0)})\bar{\mu}_t^{(k+1)} + \bar{\mu}_t^{(0)}\bar{\sigma}^{(k+1)},$$

We can show by induction that $\mu_t^{(k)} = (\bar{\sigma}^{(1)})^k x_t$, where

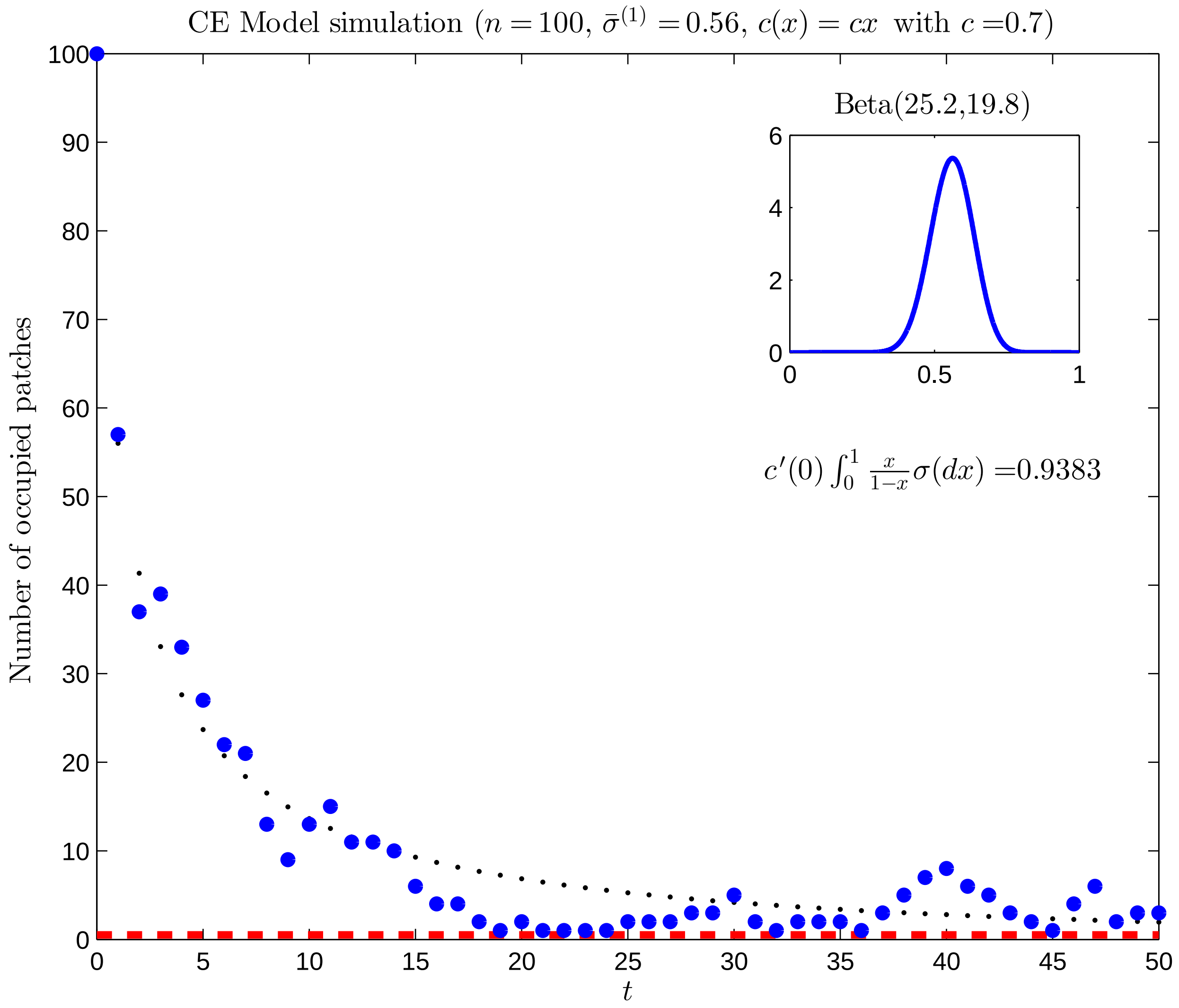
$$x_{t+1} = \bar{\sigma}^{(1)}\left(x_t + (1 - x_t)\, c(x_t)\right).$$

Compare this with the earlier result.

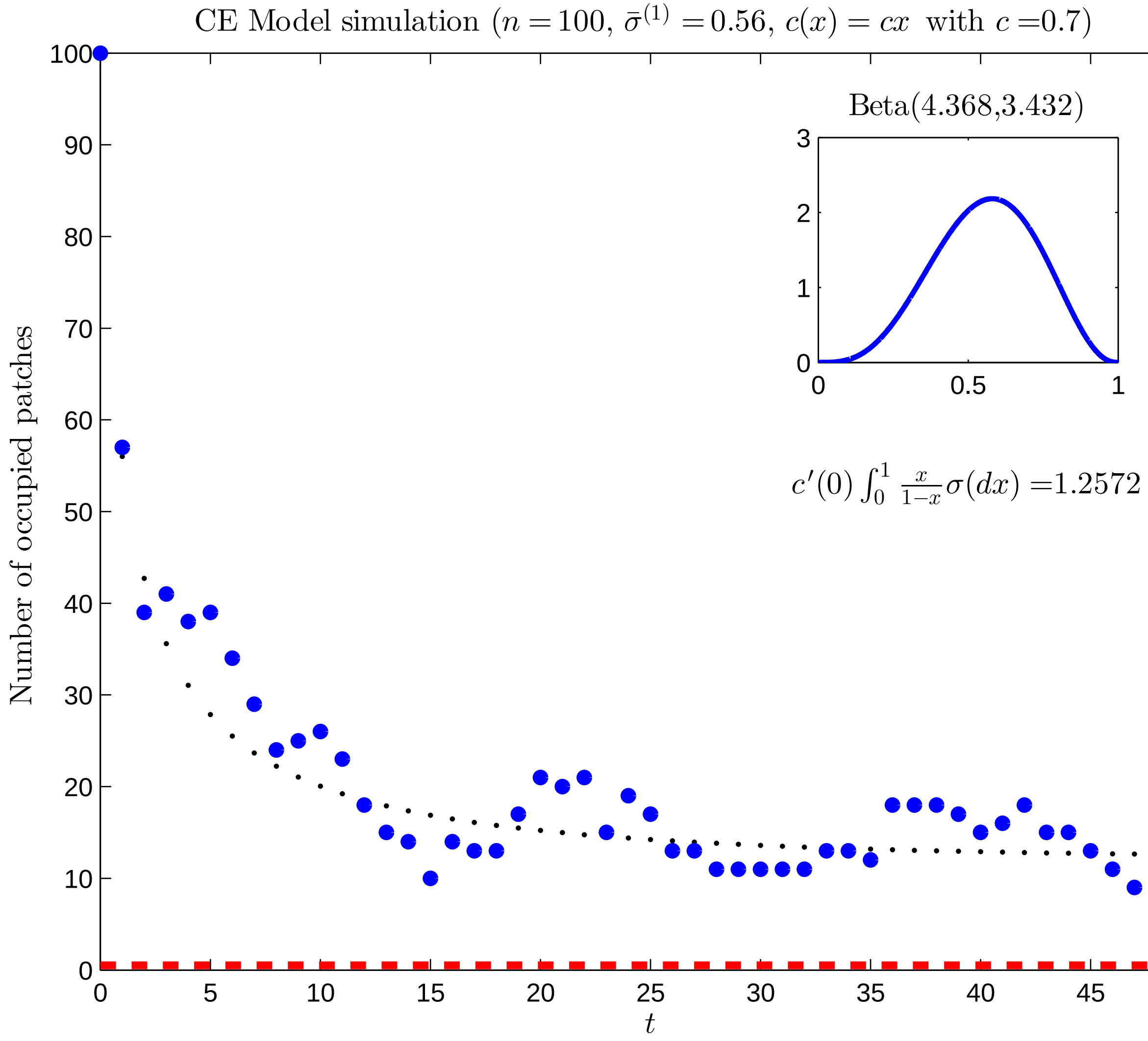
# CE Model (homogeneous) - Evanescence



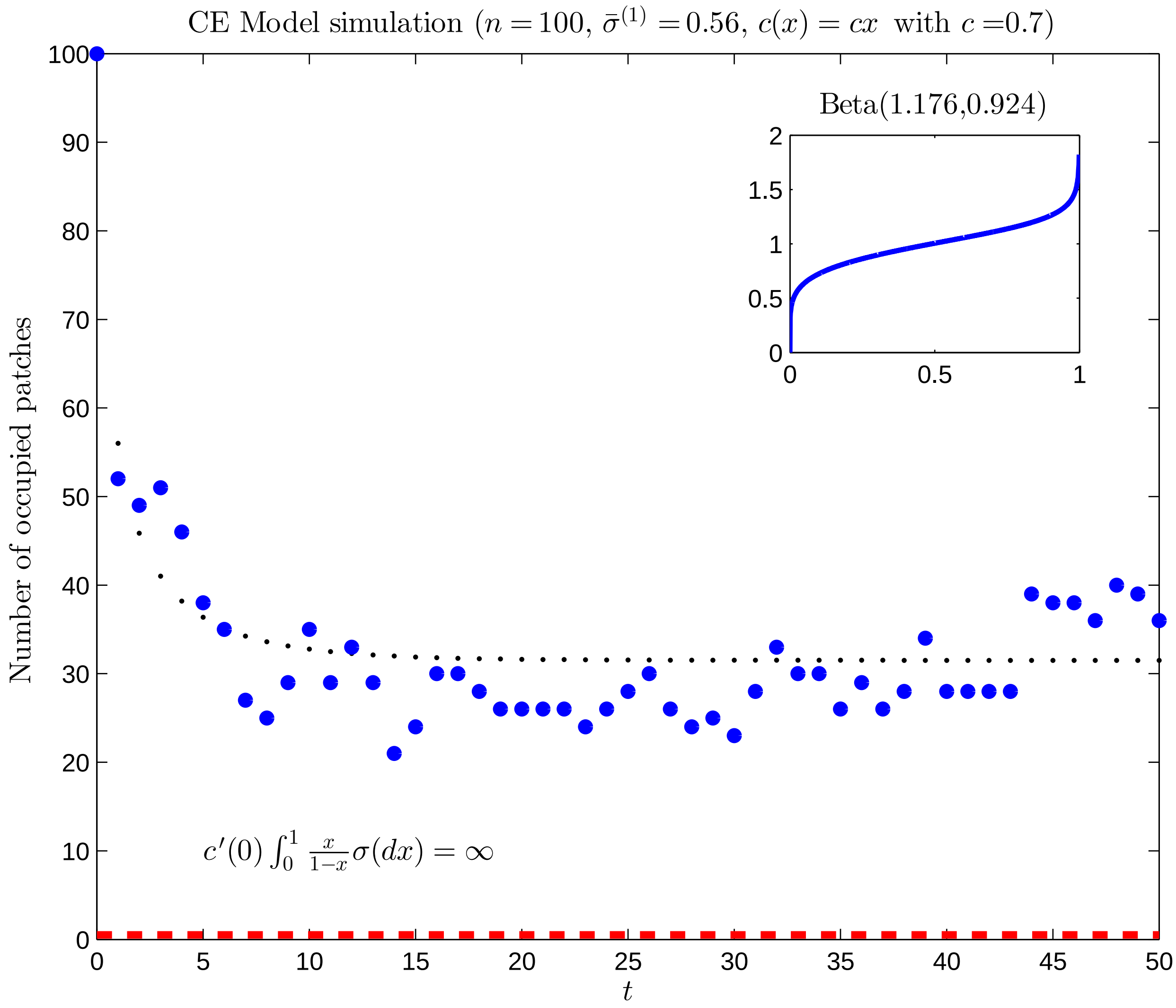
# CE Model - Evanescence



# CE Model - Quasi stationarity



# CE Model - Quasi stationarity



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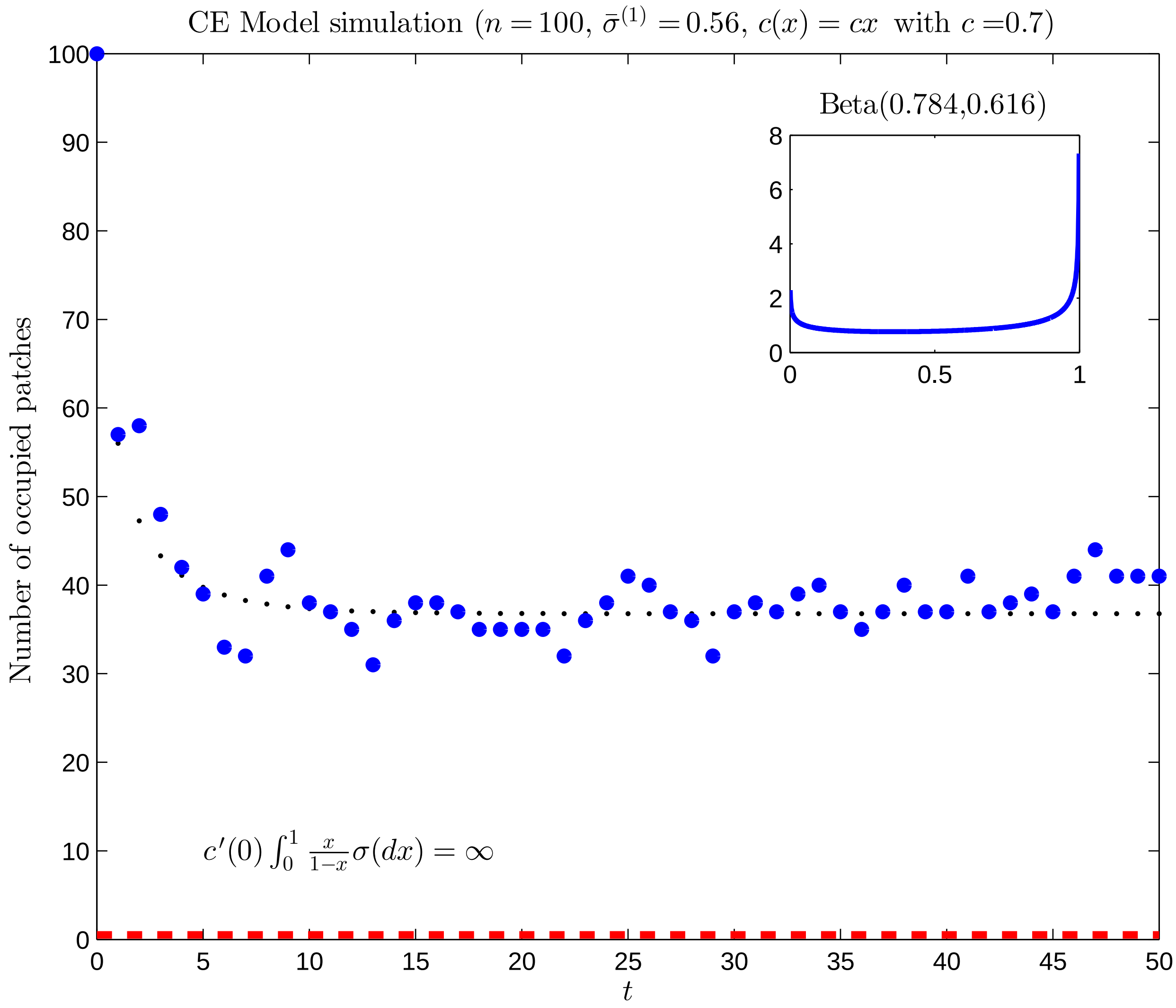

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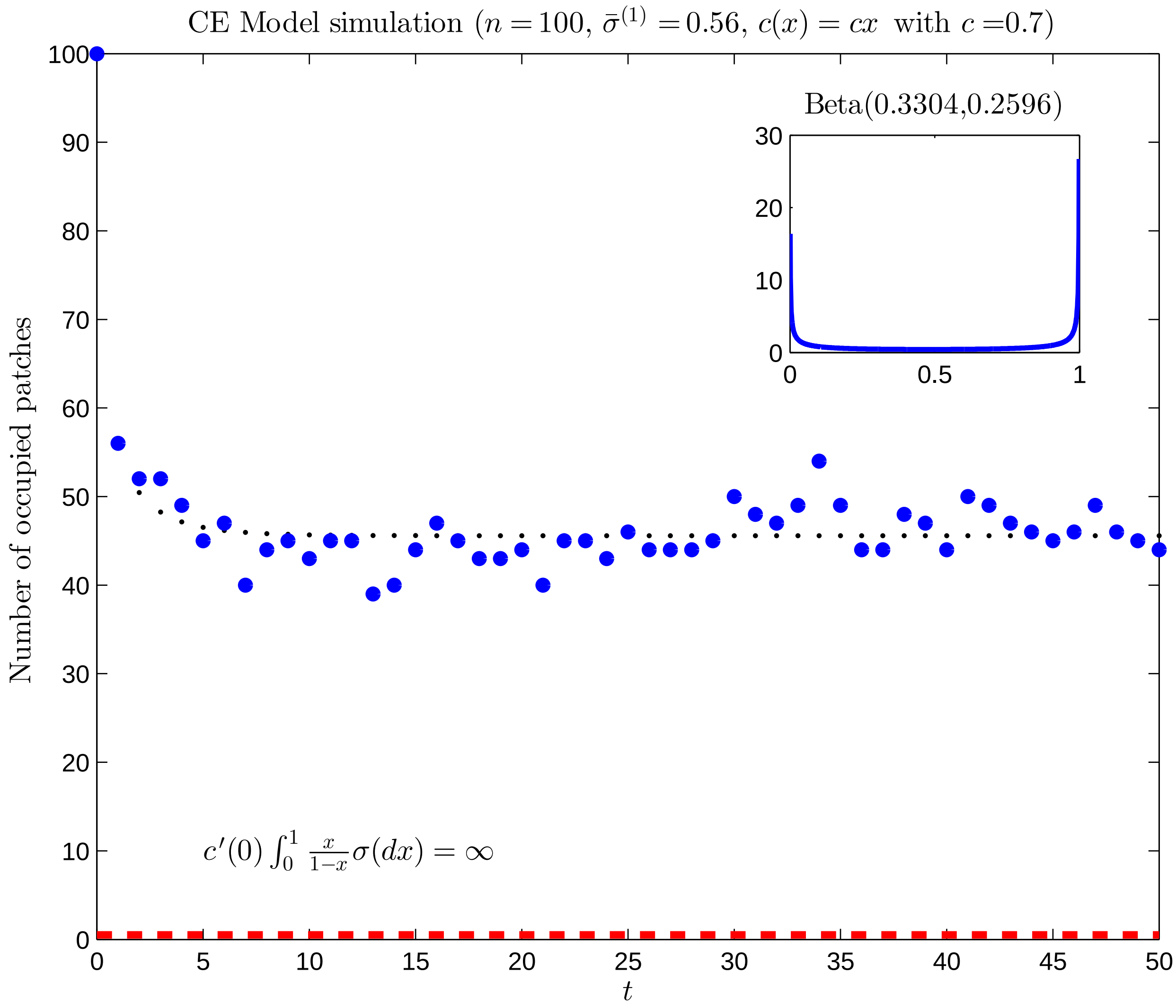

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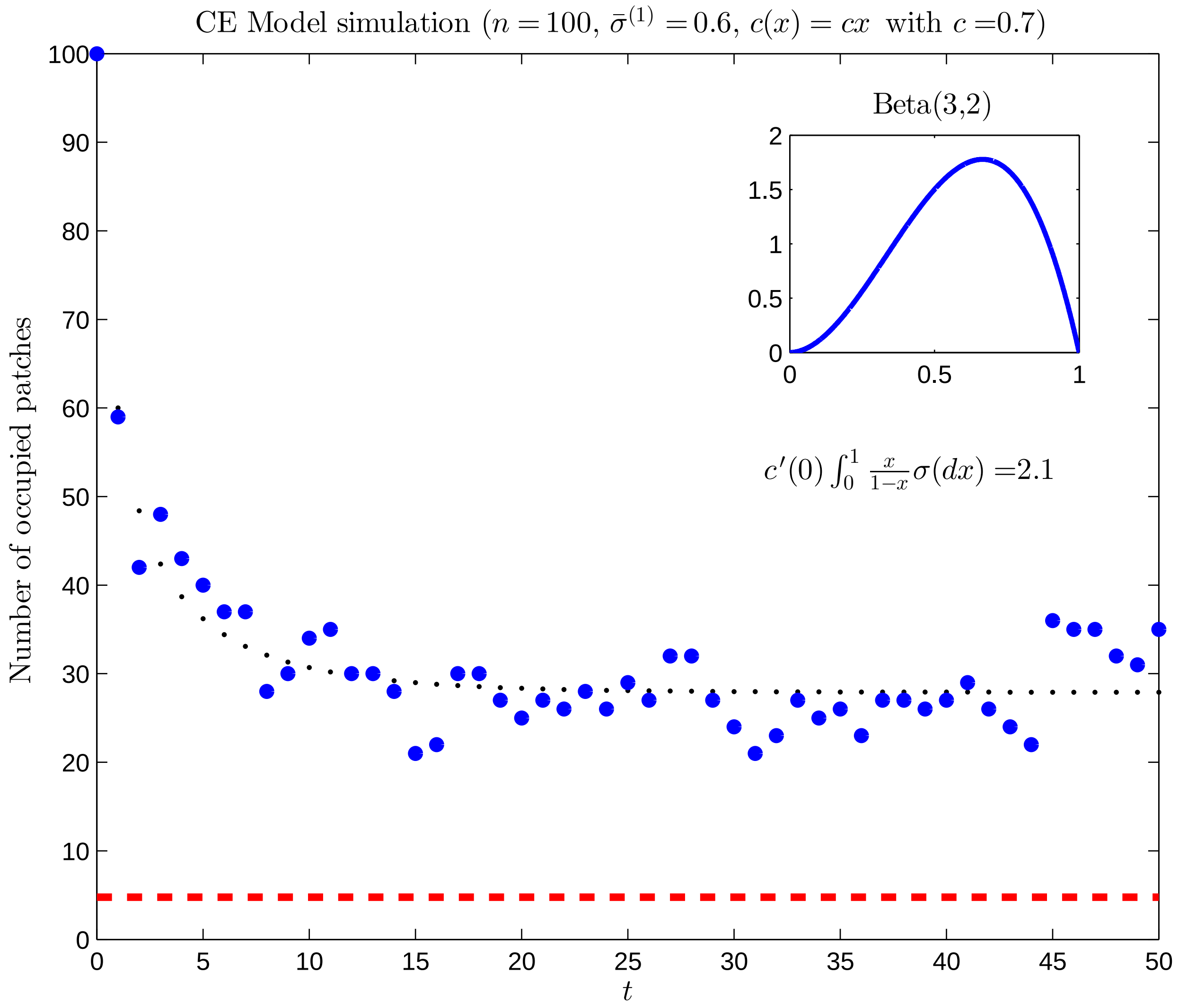

# Extra - equilibria

Our recursion is

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Let $\mathcal{M}$ be the set of measures that are absolutely continuous with respect to $\sigma$ and whose Radon-Nikodym derivative is bounded by $1$, $\sigma -$ a.e.

We shall be interested in the behaviour of solutions to our recursion starting with $\mu_0 \in \mathcal{M}$.

# Extra - equilibria

"Differentiating" with respect to $\sigma$, we see that our recursion can be written

$$\frac{\partial \mu_{t+1}}{\partial \sigma} = s\frac{\partial \mu_t}{\partial \sigma} + sc_t\left(1 - \frac{\partial \mu_t}{\partial \sigma}\right).$$

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It will be clear that $\mu_0 \in \mathcal{M}$ implies that $\mu_t \in \mathcal{M}$ for all $t$.

Furthermore, a measure $\mu_\infty \in \mathcal{M}$ will be an equilibrium point of our recursion if it satisfies

$$\frac{\partial \mu_\infty}{\partial \sigma} = s\frac{\partial \mu_\infty}{\partial \sigma} + sc_\infty\left(1 - \frac{\partial \mu_\infty}{\partial \sigma}\right),$$

where $c_\infty = c\left(\mu_\infty([0,1])\right)$.

# Extra - equilibria

**Theorem** Suppose that $c(0) = 0$ and $c'(0) < \infty$. Let $\psi^*$ be a solution to the equation

$$\psi = R_\sigma(\psi) := \int \frac{sc(\psi)}{1-s+sc(\psi)} \sigma(ds). \qquad (1)$$

The fixed points of our recursion are given by

$$\mu_\infty(ds) = \frac{sc(\psi^*)}{1-s+sc(\psi^*)} \sigma(ds).$$

Equation (1) has the unique solution $\psi^* = 0$ if and only if

$$c'(0) \int \frac{s}{1-s} \sigma(ds) \leq 1.$$

Otherwise, there are two solutions, one of which is $\psi^* = 0$.

# Extra - stability

**Theorem** If $\psi^* = 0$ is the only solution to Equation (1), then, for all $\mu_0 \in \mathcal{M}$, $\mu_t \to 0$. If Equation (1) has a non-zero solution, then, for all $\mu_0 \in \mathcal{M}$ such that $\int \mu_{0,j}(ds) > 0$ for some $j$, $\mu_t \to \mu_\infty$.