Large Population Networks with Patch Dependent Extinction Probabilities

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ACEMS
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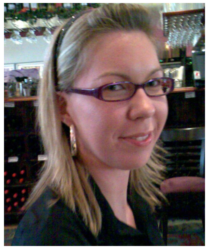

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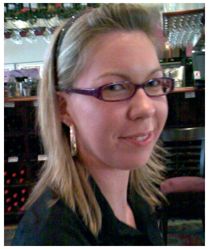

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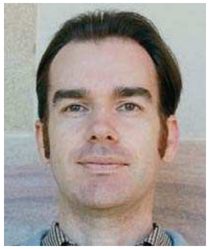

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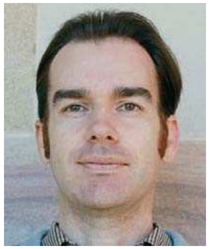

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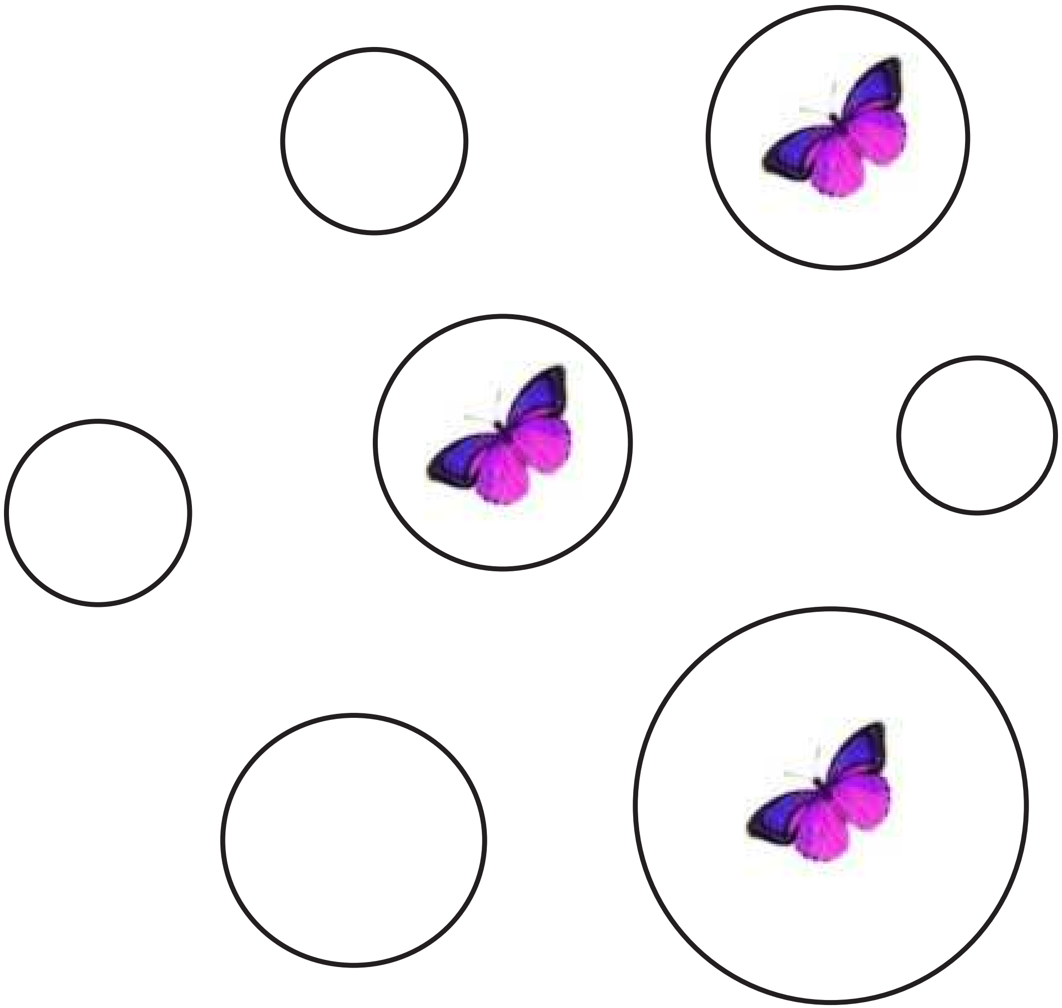
Metapopulations



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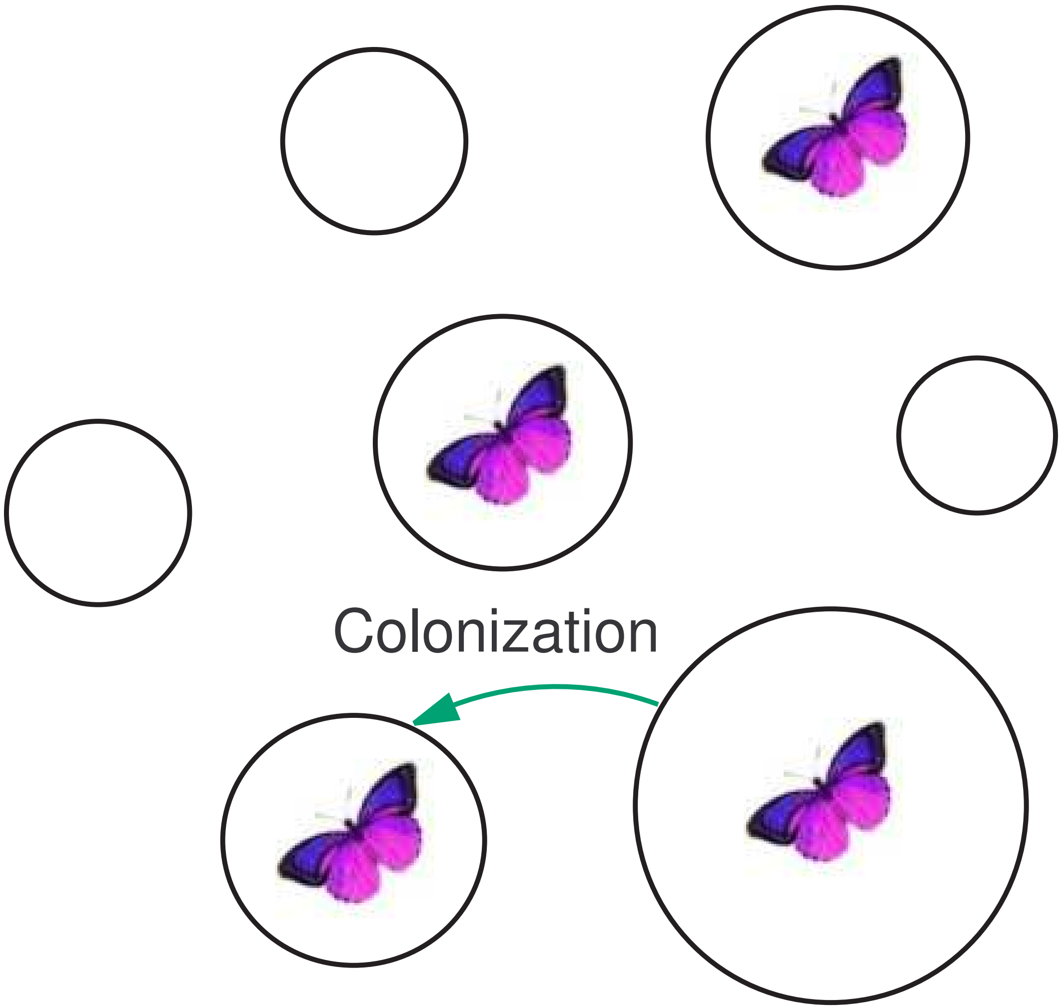

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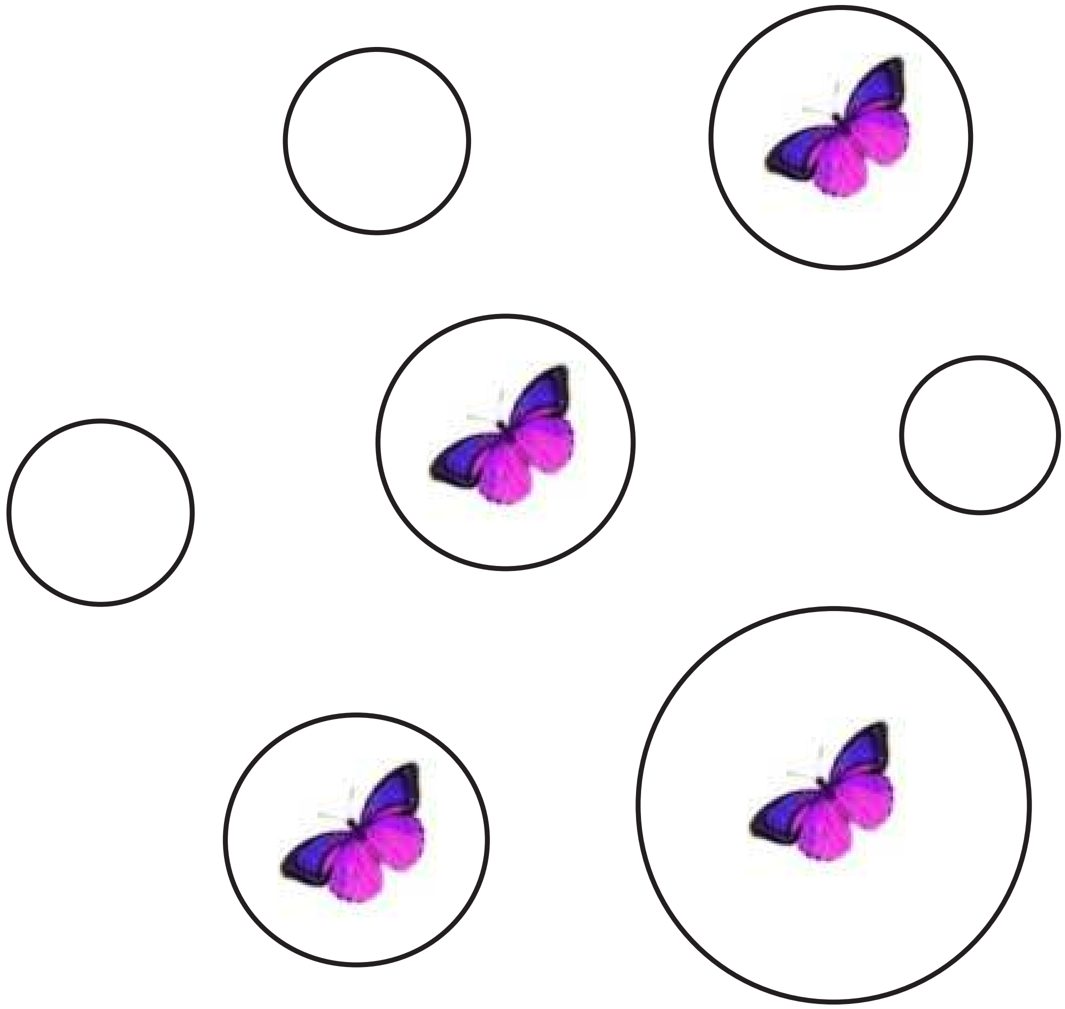

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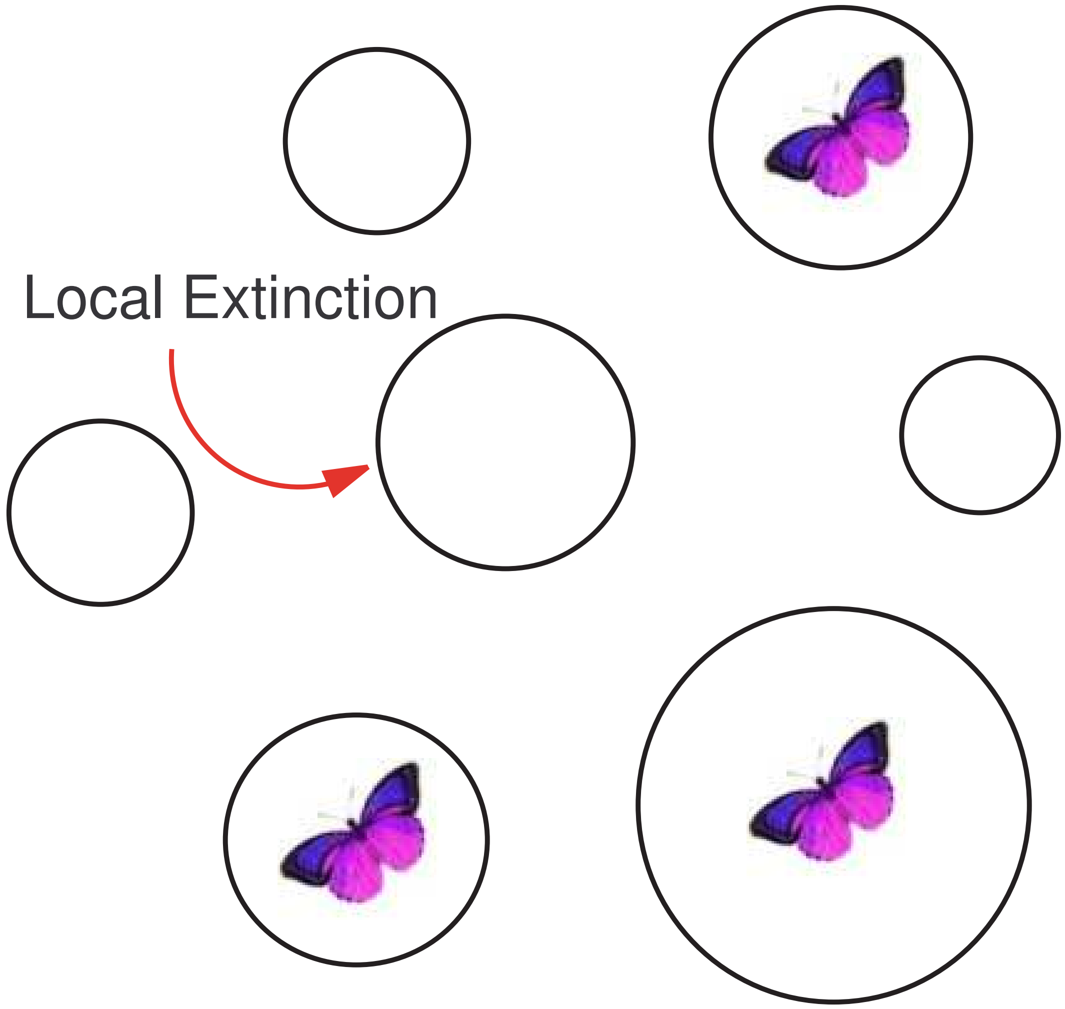

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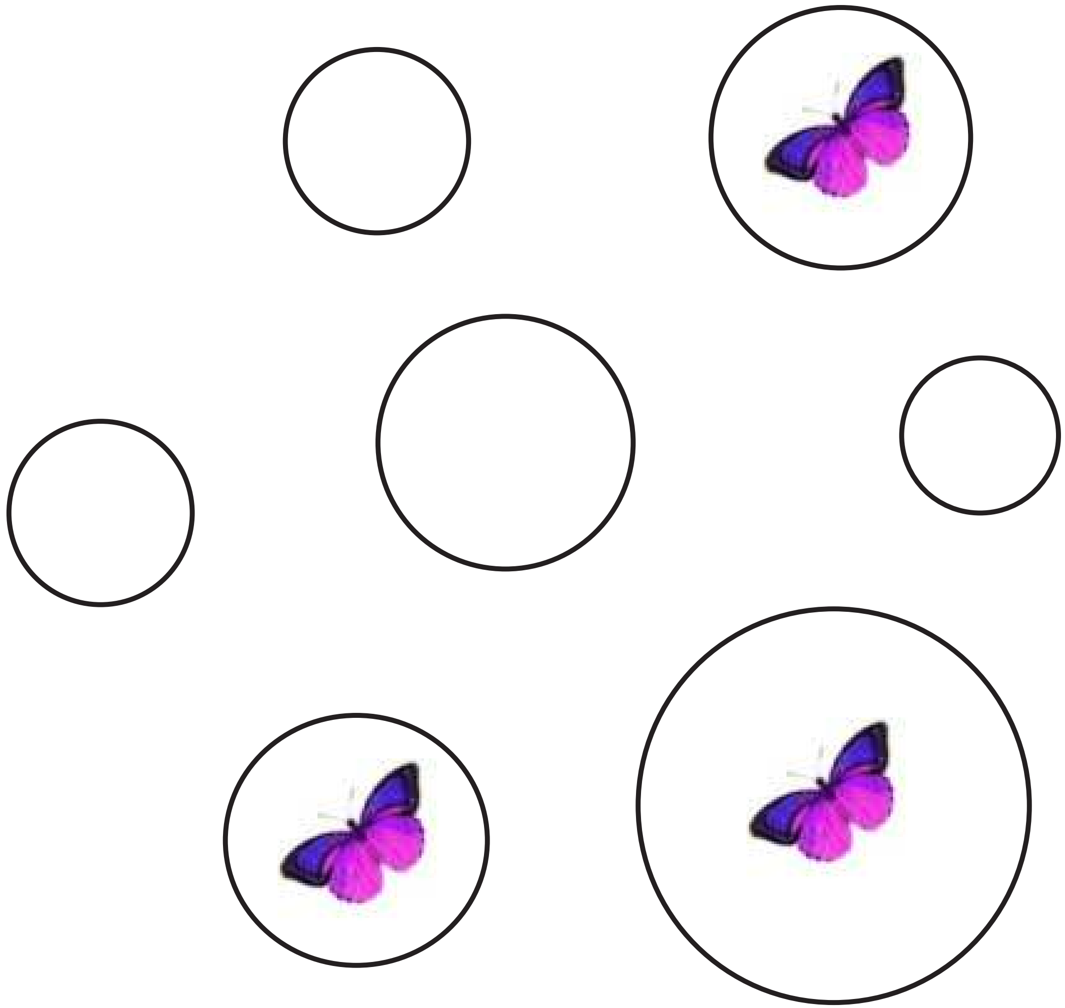

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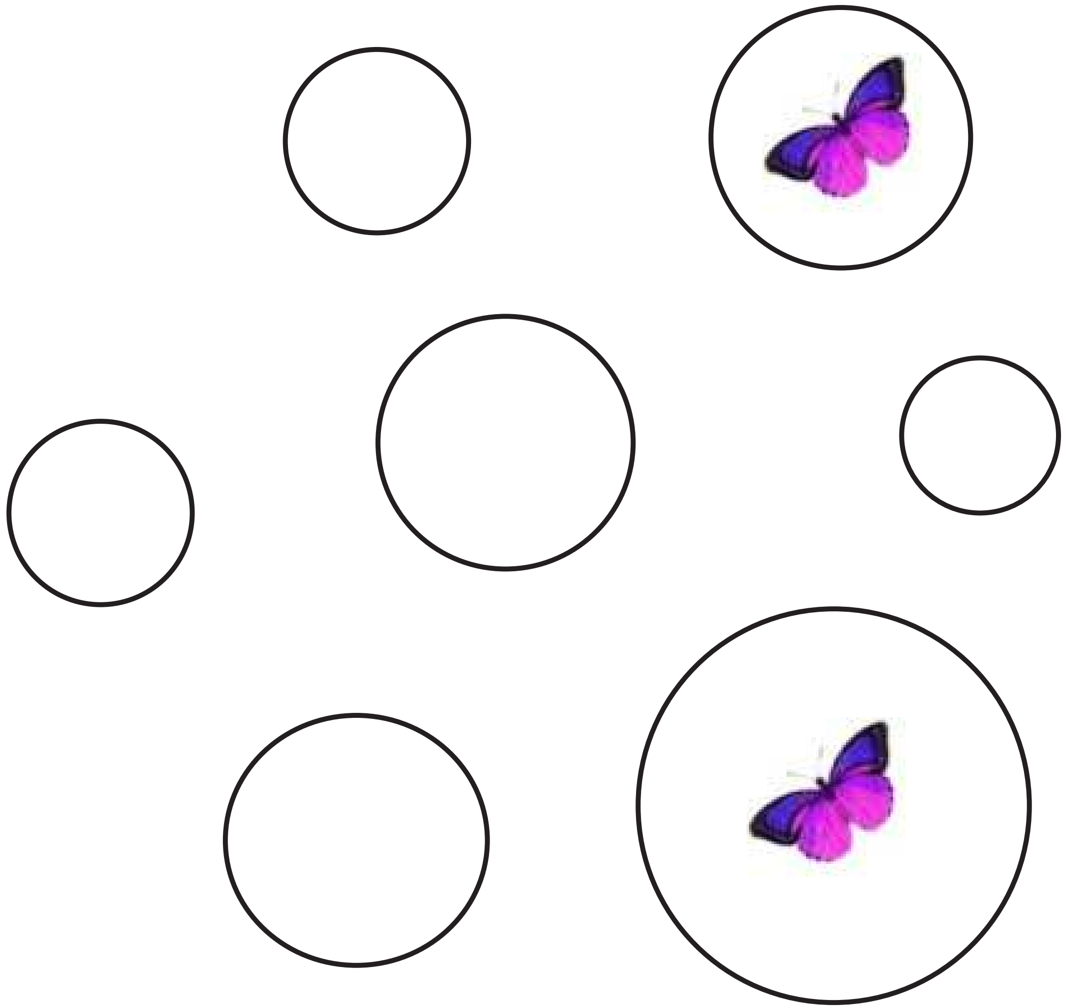

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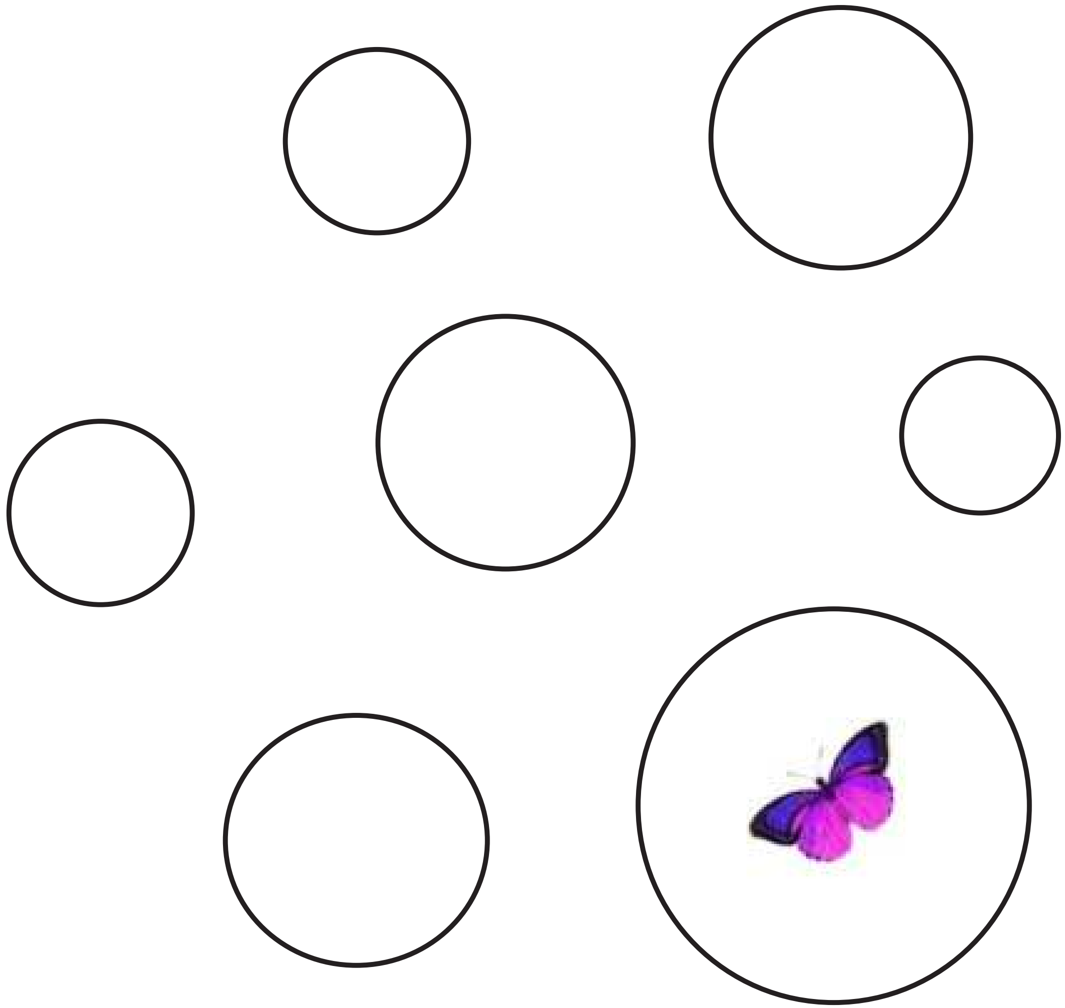

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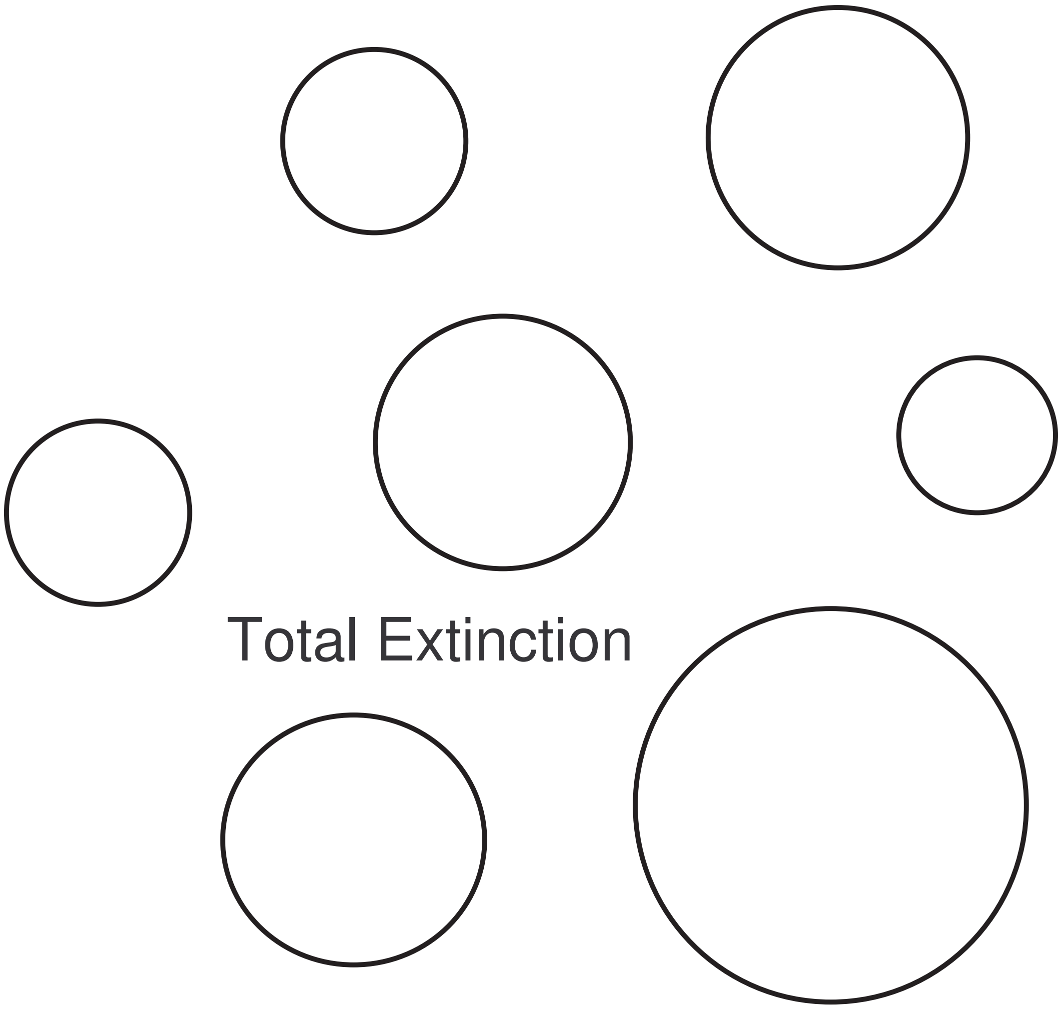

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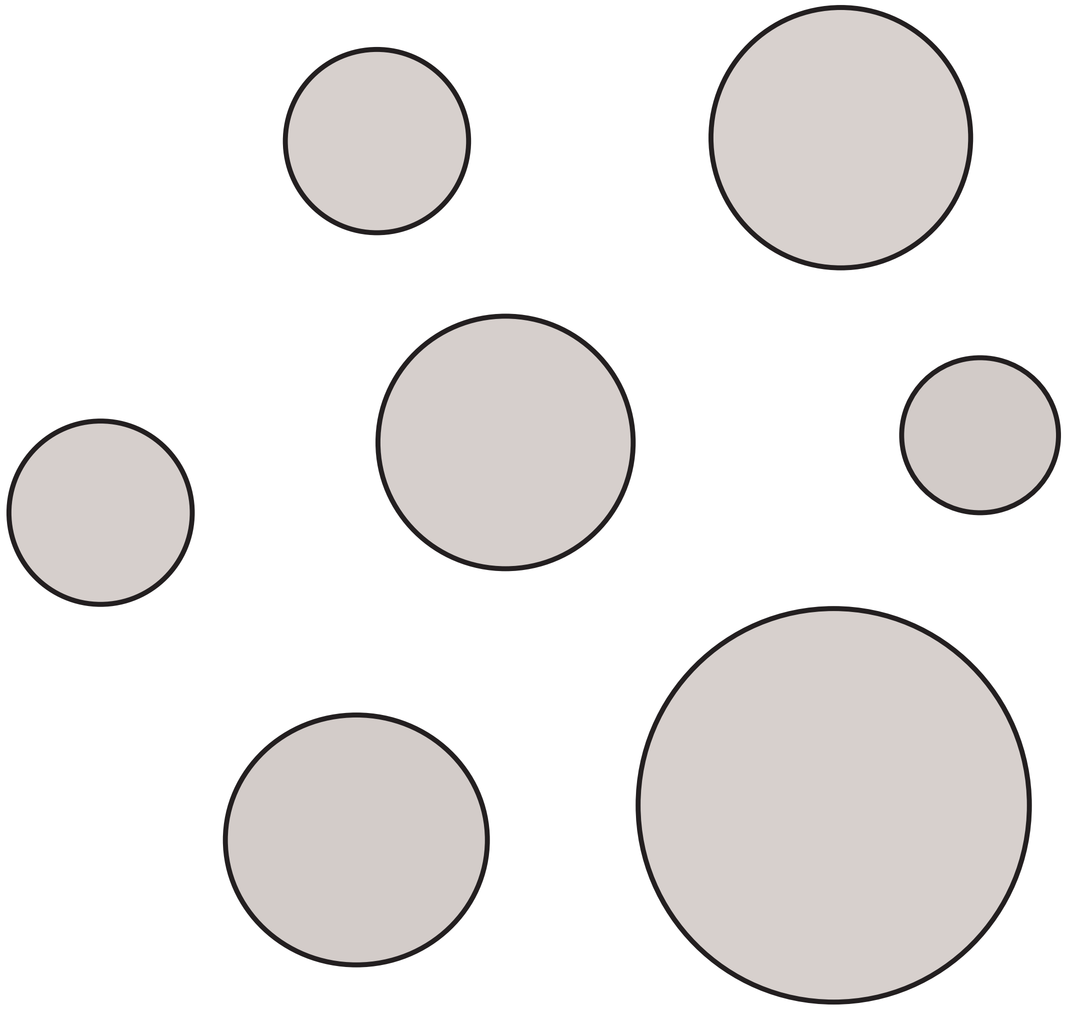

SPOM

A *stochastic patch occupancy model* (SPOM)

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Suppose that there are n patches.

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

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Colonization and extinction happen in distinct, successive phases.

SPOM - Phase structure

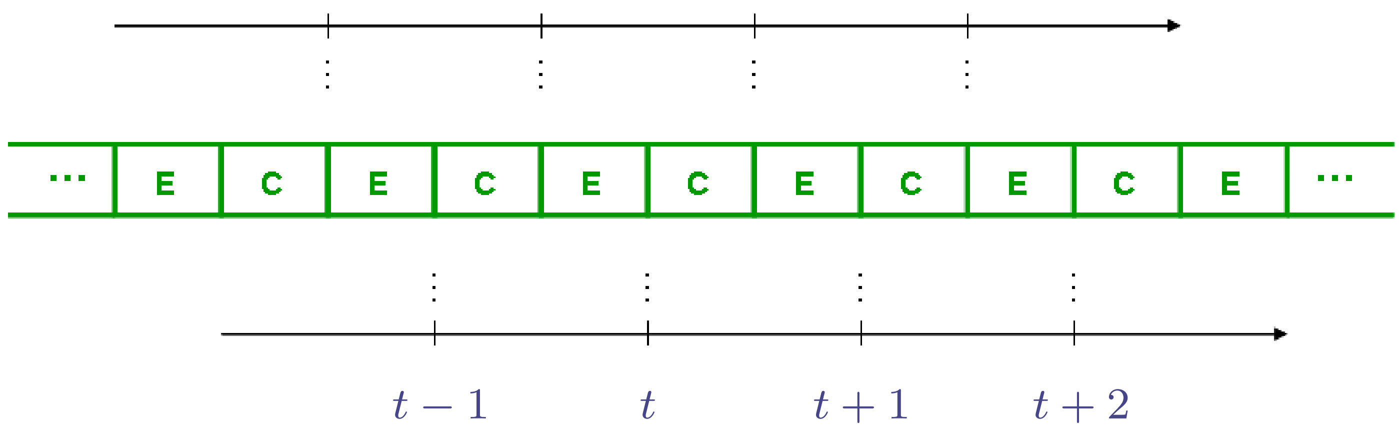
For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle. Examples:

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

SPOM - Phase structure

Colonization and extinction happen in distinct, successive phases.



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

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[In our most recent work, we allow the patch colonization probability $c(\,\cdot\,)$ to depend on the *relative positions* of all patches and their *areas*.]

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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

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

SPOM - example

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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 $s_i \sim$ 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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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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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

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

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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

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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
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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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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

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

a “*Chain Bernoulli*” structure.

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

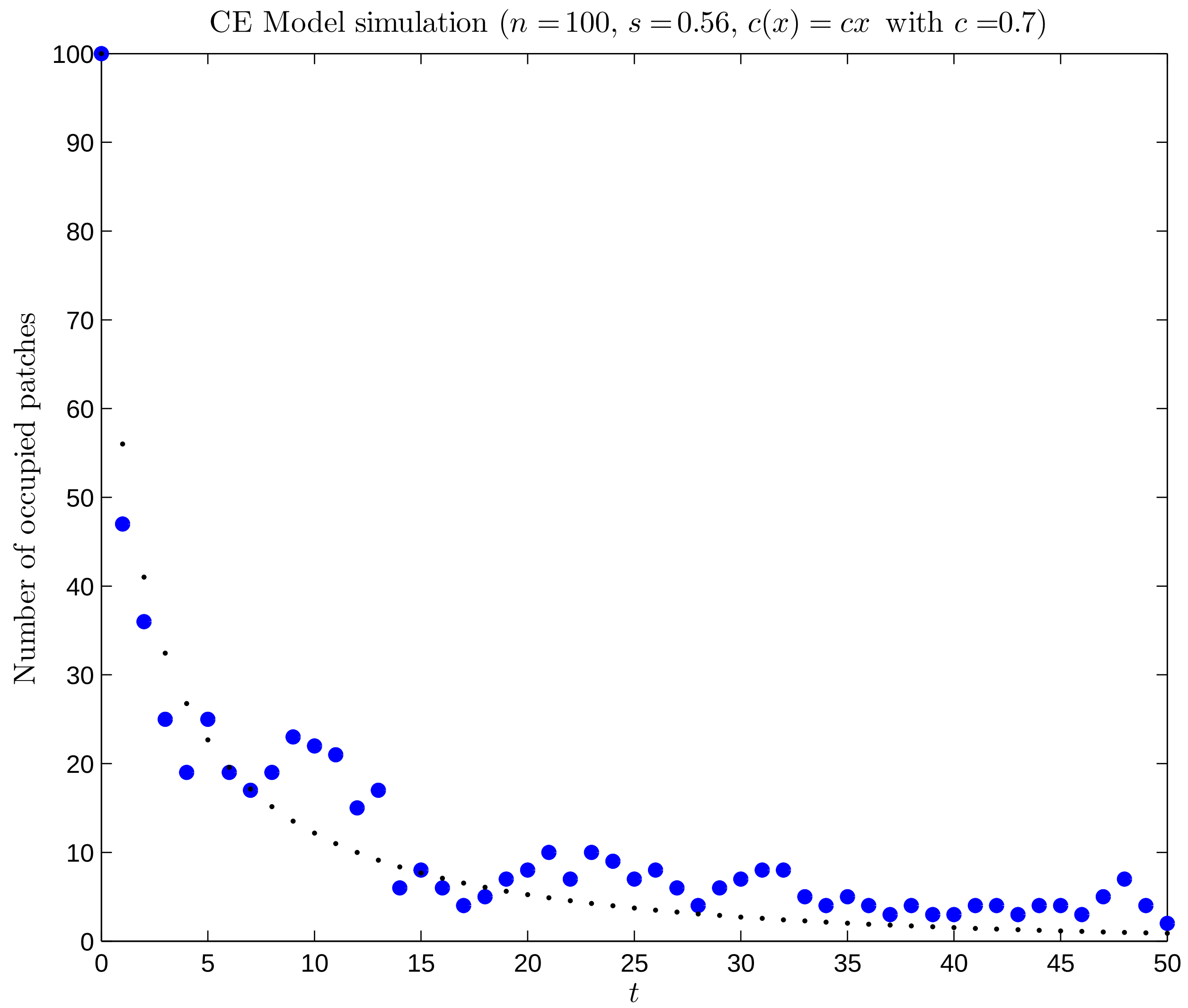
$$N_t^{(n)}/n \xrightarrow{p} x_t, \quad \text{for all } t \geq 1,$$

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

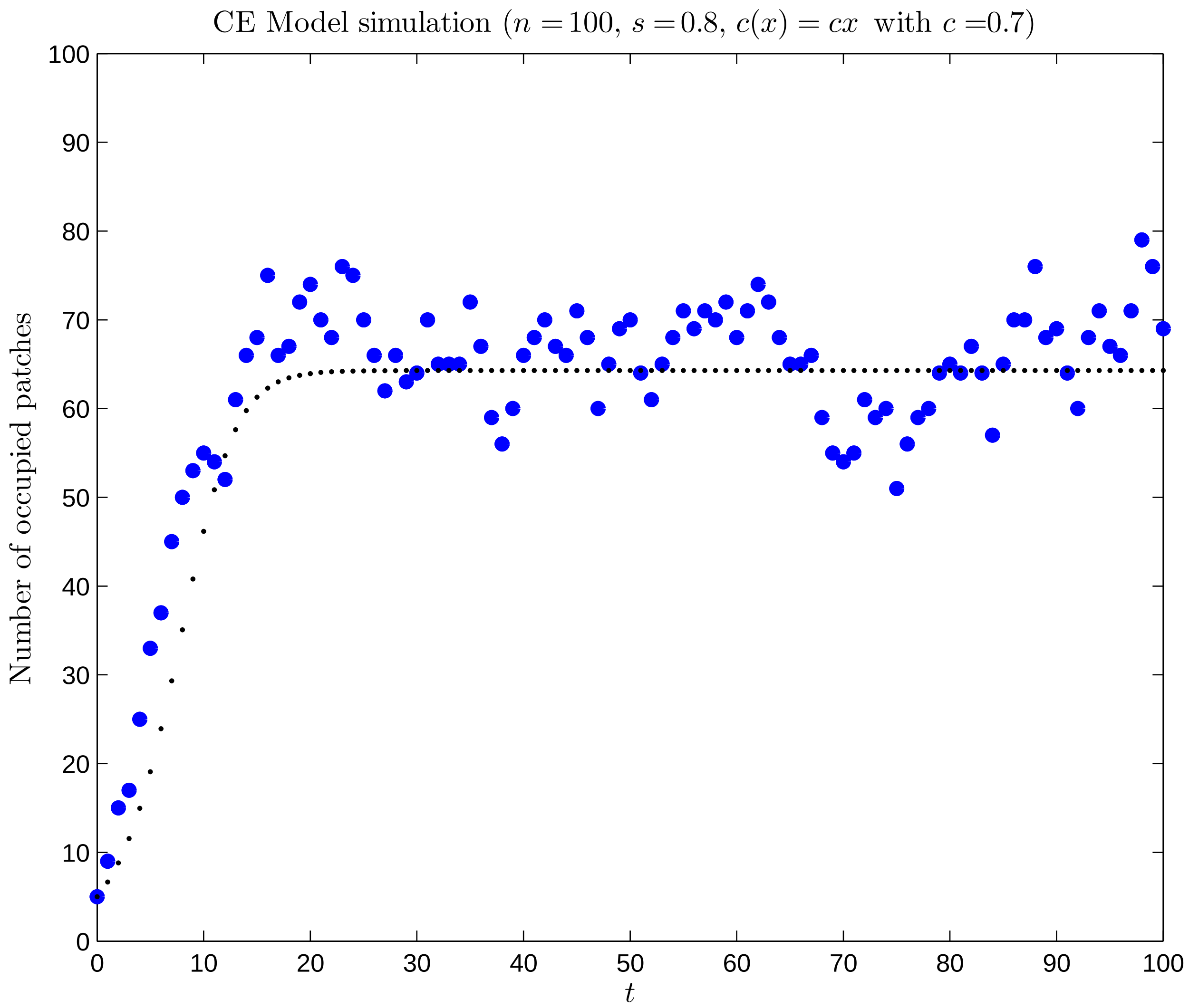
$$f(x) = s(x + (1 - x)c(x)).$$

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

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 $1 + c'(0) \leq 1/s$. 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 $c'(0) > 0$.]

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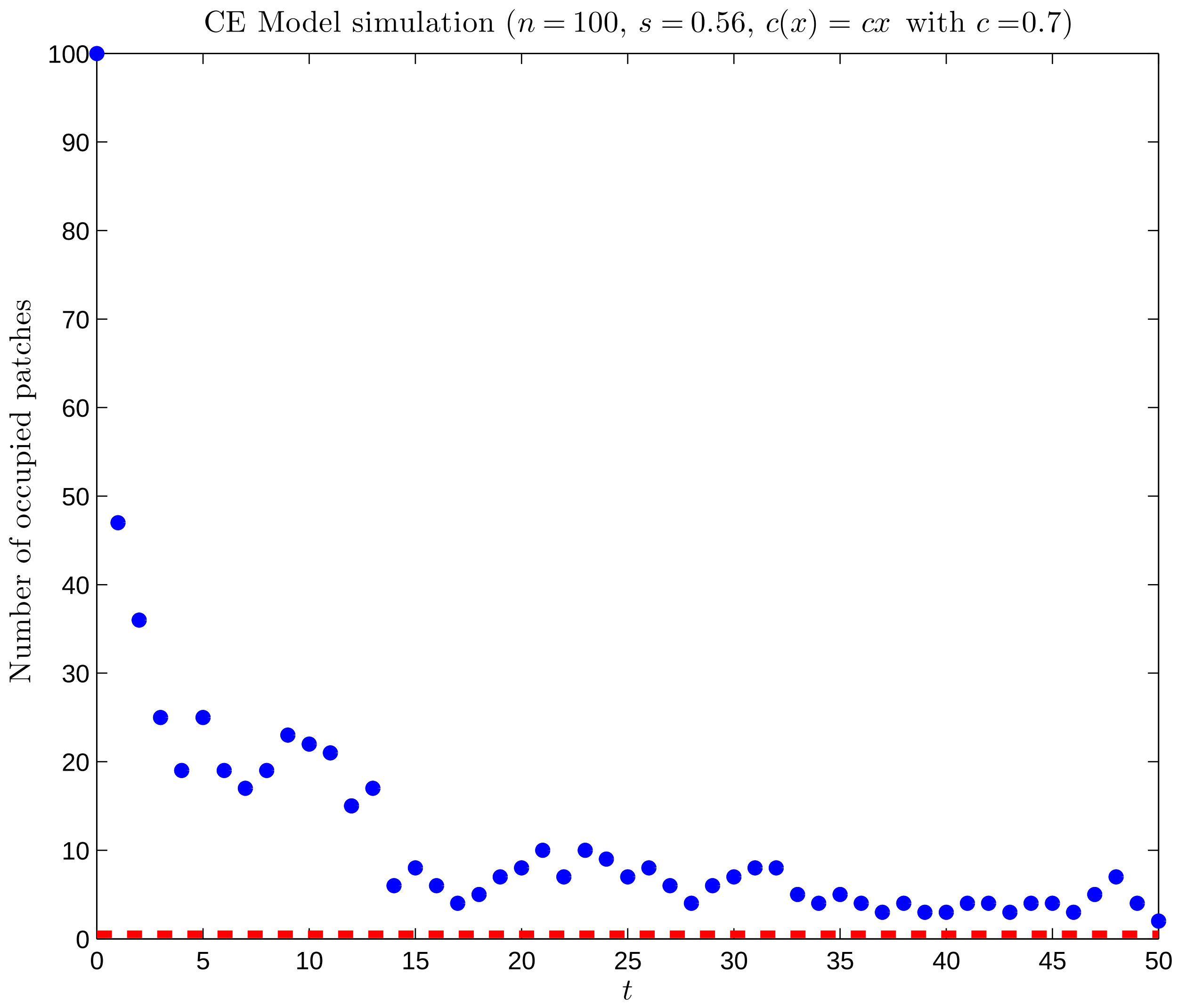

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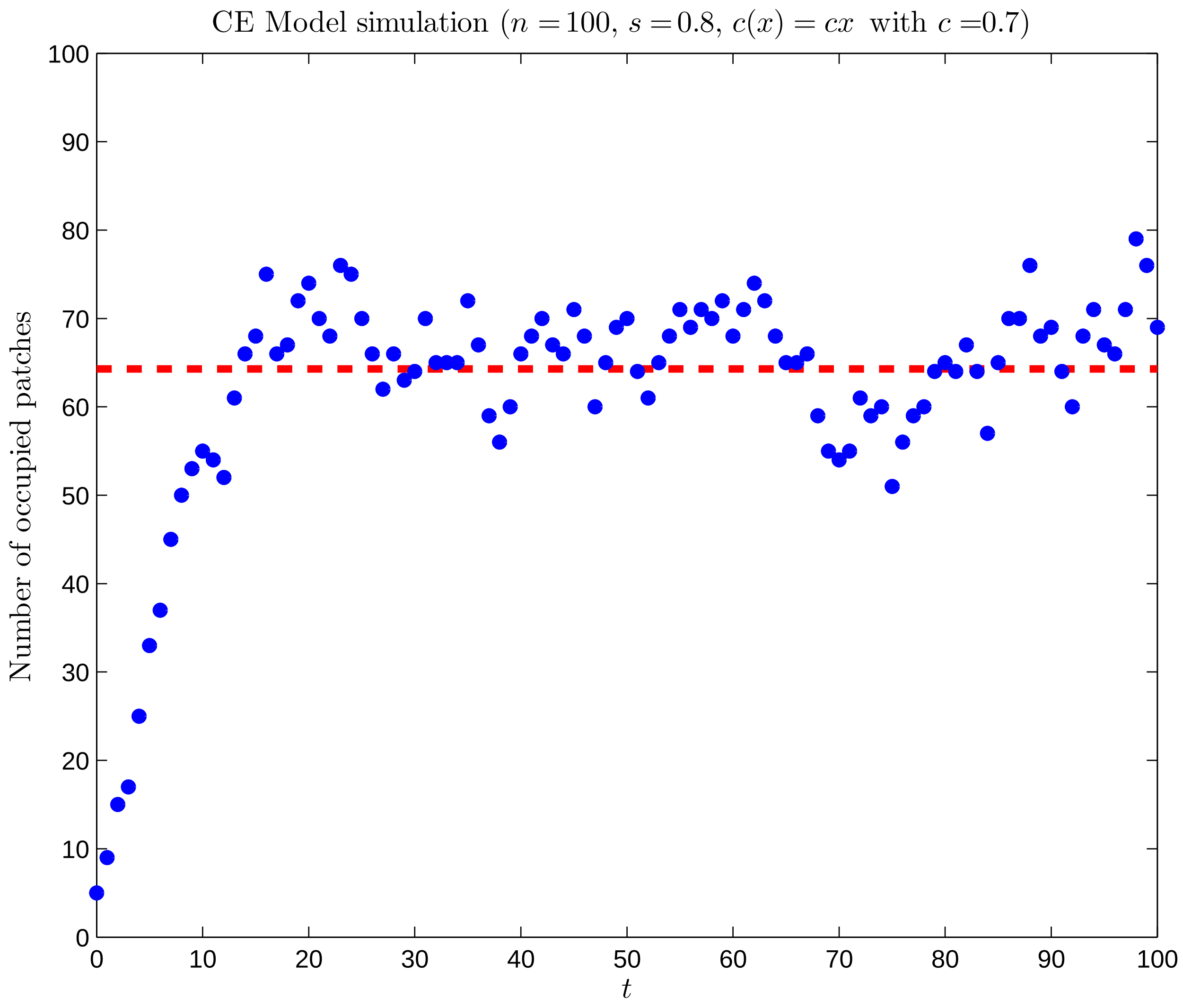

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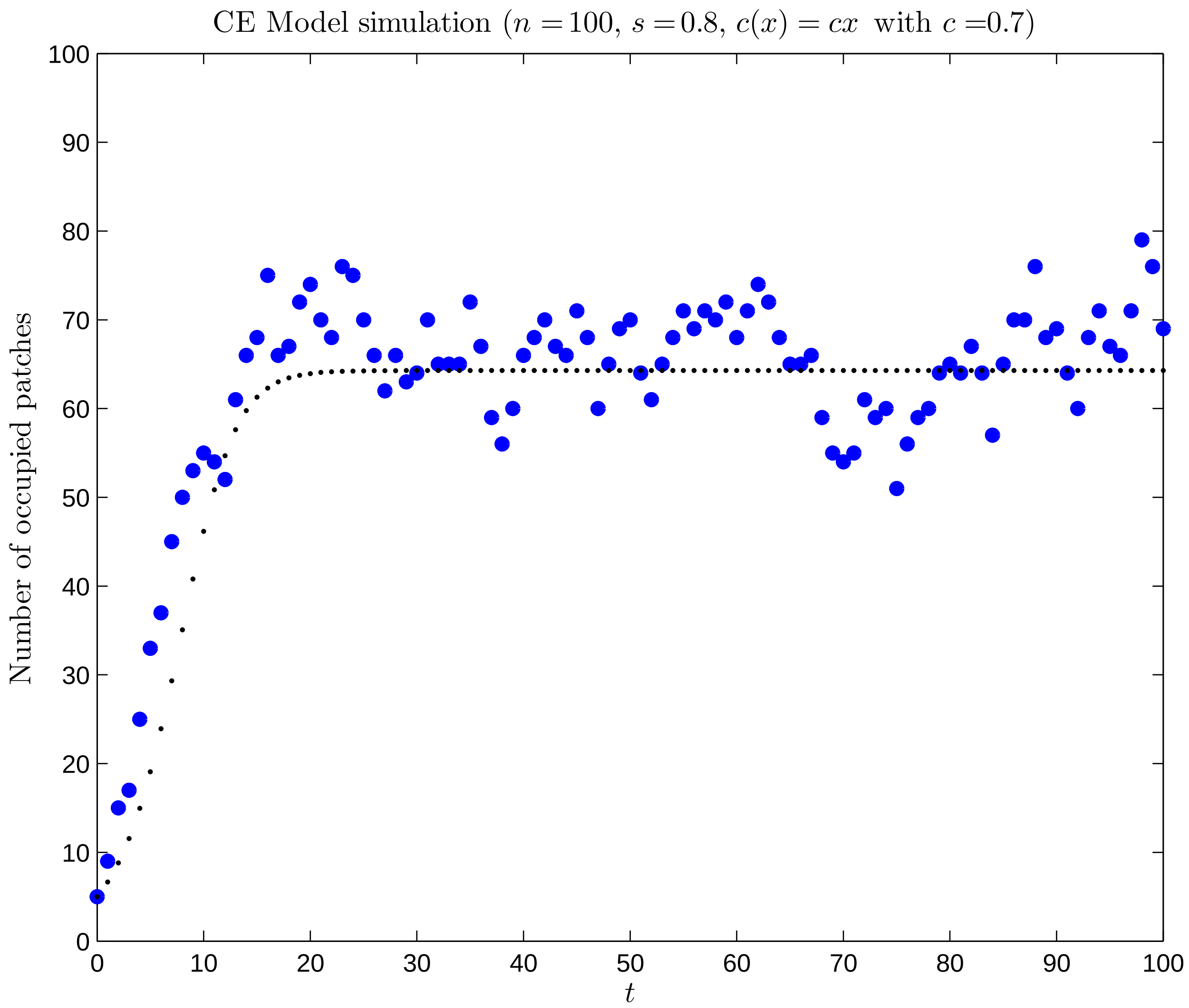


A Gaussian limit

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

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

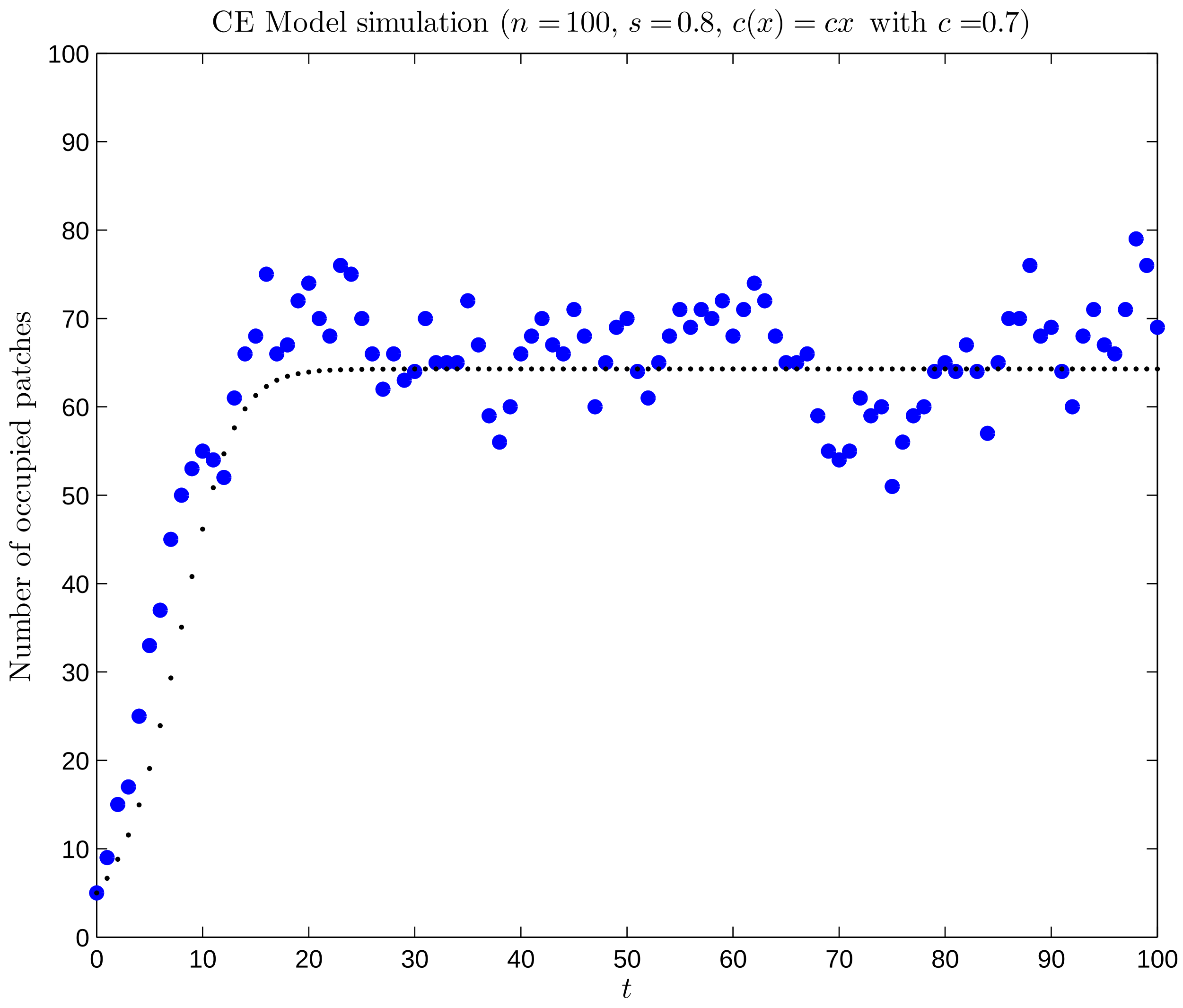
If $Z_0^{(n)} \xrightarrow{d} z_0$, then $Z_\bullet^{(n)}$ converges weakly to the Gaussian Markov chain $Z_\bullet$ defined by

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

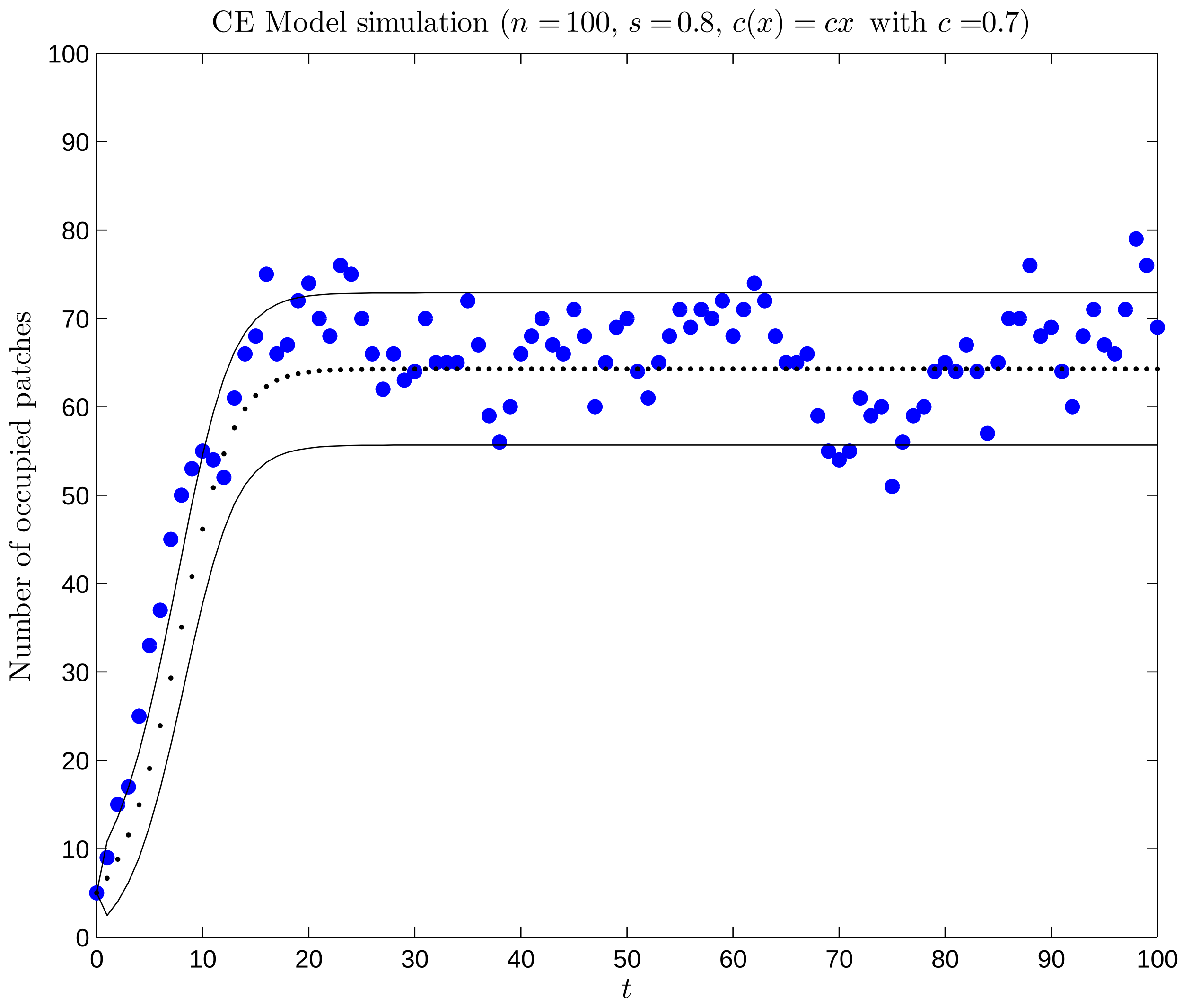
with (E_t) independent and $E_t \sim \mathsf{N}(0, v(x_t))$, where

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

CE Model - Quasi stationarity



CE Model - Gaussian approximation



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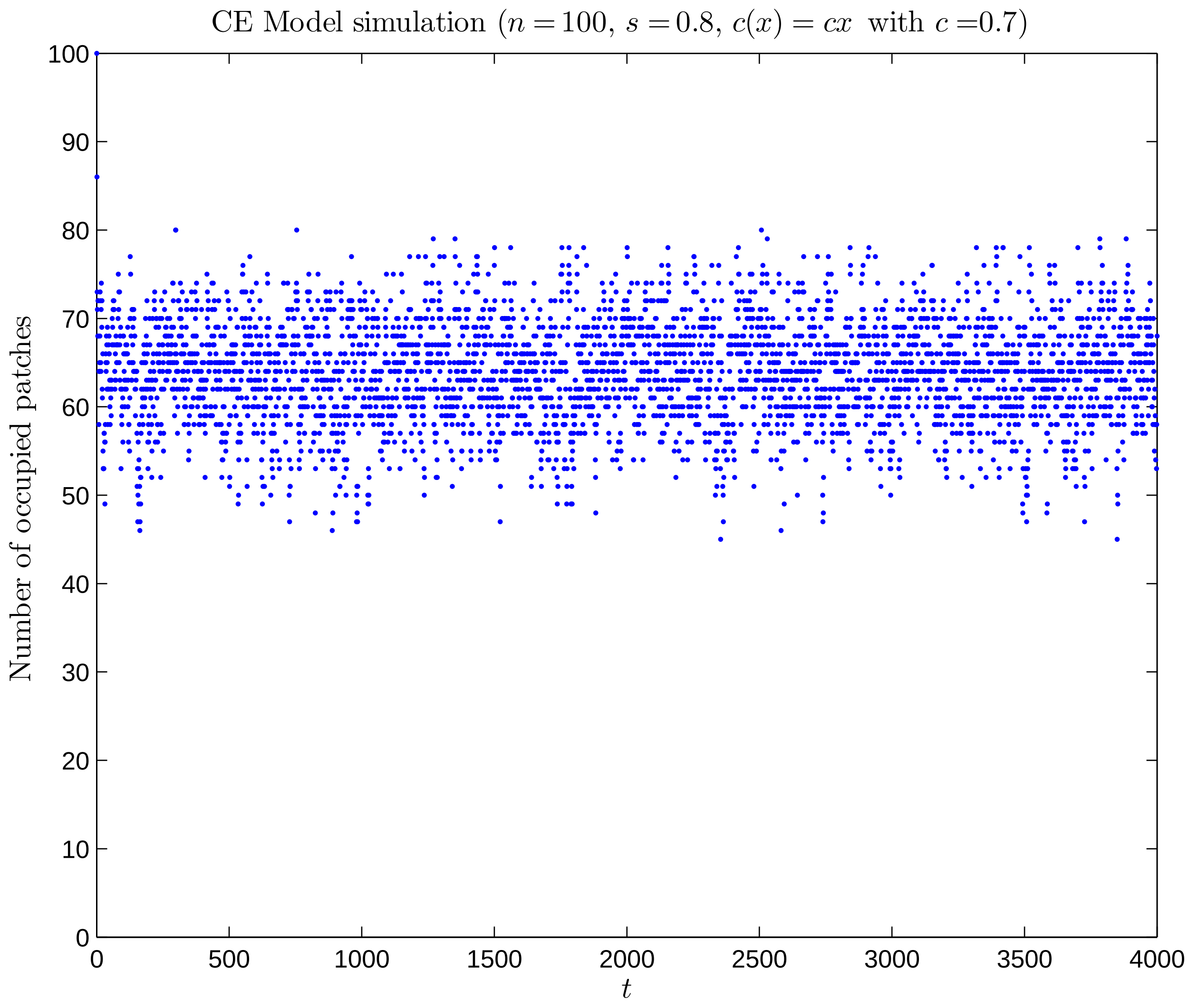

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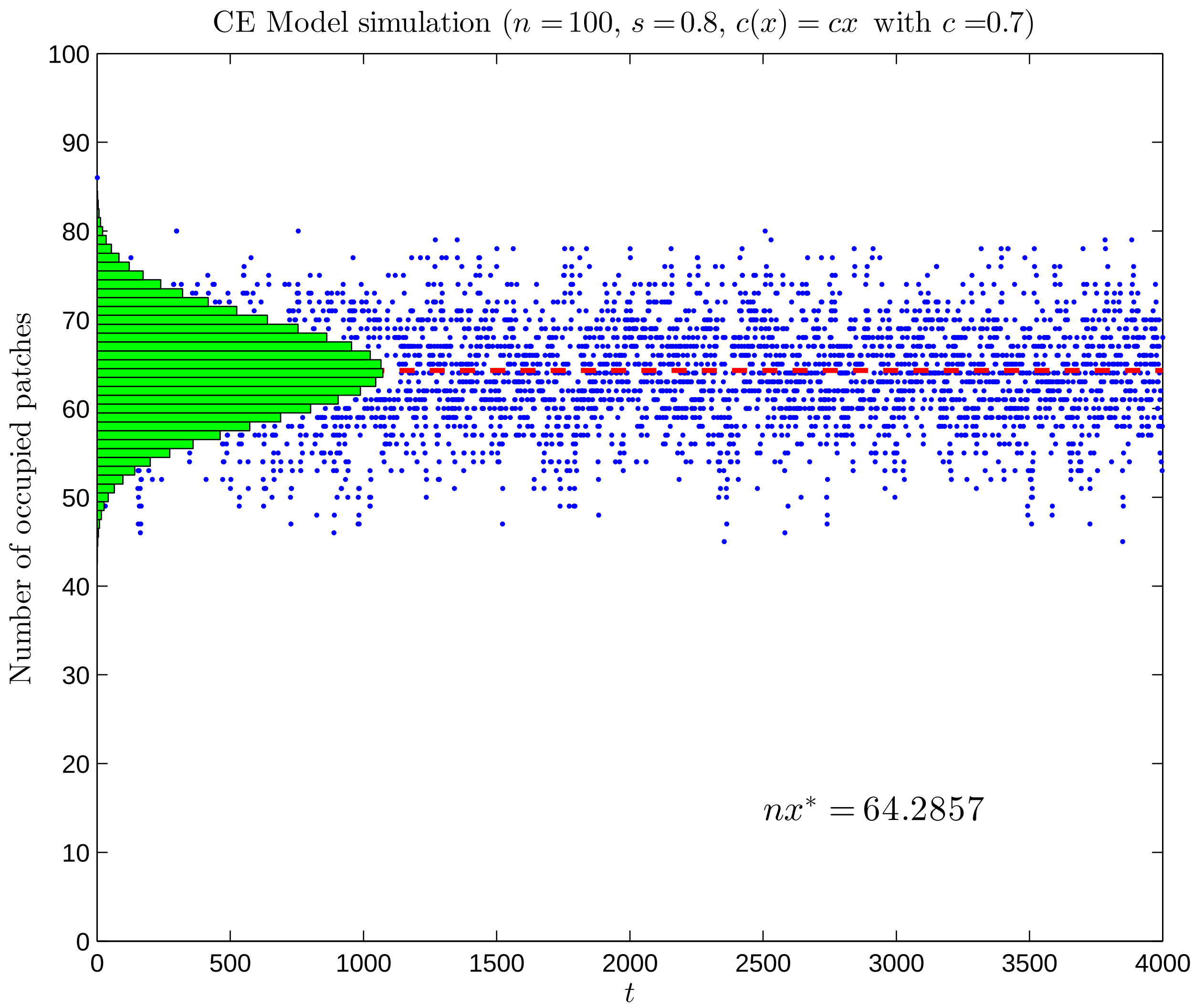

SPOM - general case

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

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

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 (σ_n) and $(\mu_{n,t})$ of random measures by

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

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

A measure-valued difference equation

Theorem [MP] Suppose that $\sigma_n \xrightarrow{d} \sigma$ and $\mu_{n,0} \xrightarrow{d} \mu_0$ for some non-random measures σ and μ_0. Then, $\mu_{n,t} \xrightarrow{d} \mu_t$ for all $t = 1, 2, \ldots$, where μ_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 $c_t = c\left(\mu_t([0,1])\right) = c\left(\int \mu_t(ds)\right)$.

[MP] McVinish, R. and Pollett, P.K. (2011) The limiting behaviour of a mainland-island metapopulation. J. Math. Biol. 67, 693-716.

Moments

Set $h(s) = s^k$. Then, our recursion is

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

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where $c_t = c\left(\mu_t([0,1])\right) = c\left(\int \mu_t(ds)\right)$. So, with moments defined by $\bar{\sigma}^{(k)} := \int s^k \sigma(ds)$ and $\bar{\mu}_t^{(k)} := \int s^k \mu_t(ds)$,

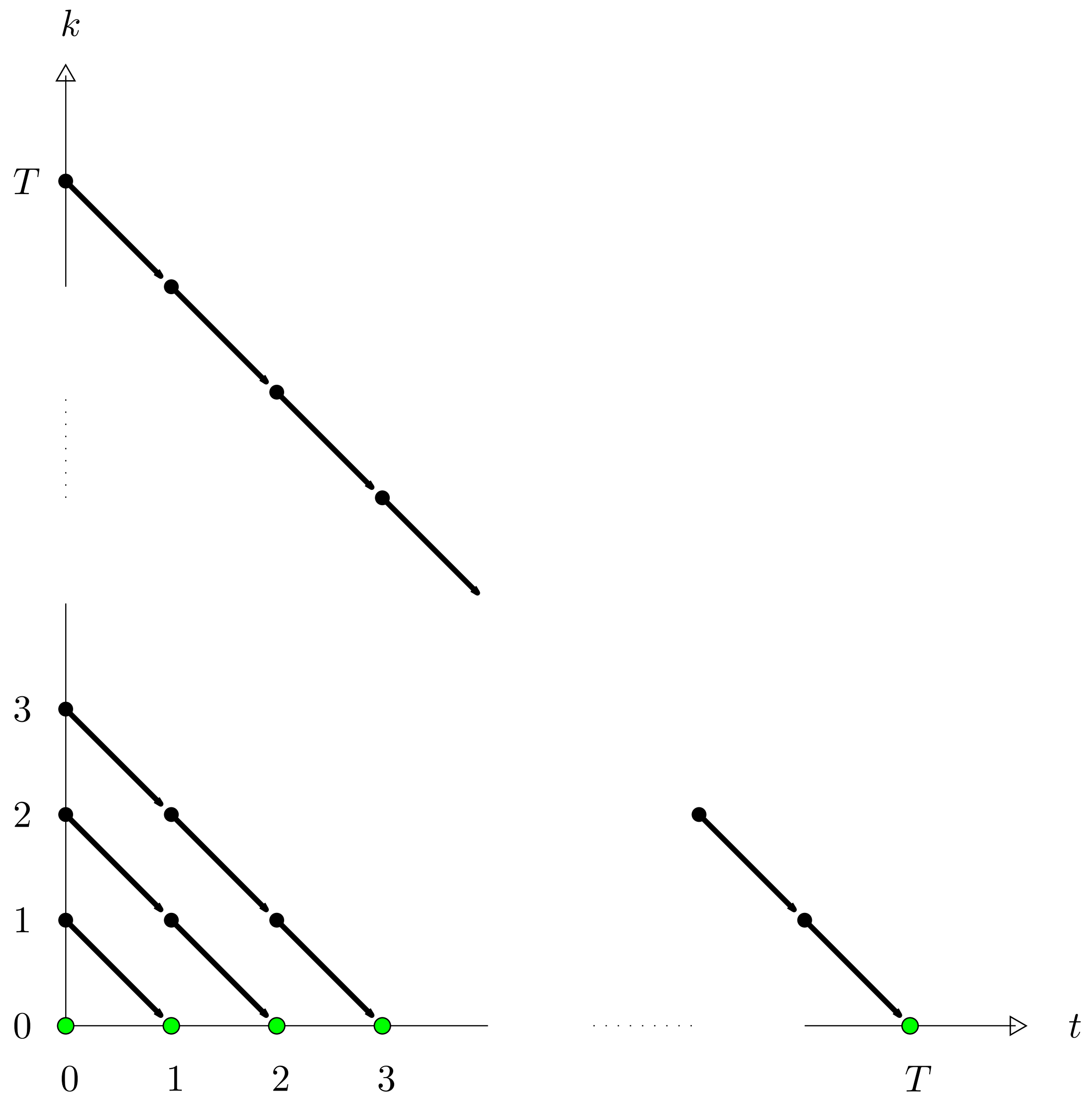
$$\bar{\mu}_{t+1}^{(k)} = (1 - \bar{\mu}_t^{(0)})\bar{\mu}_t^{(k+1)} + \bar{\mu}_t^{(0)}\,\bar{\sigma}^{(k+1)},$$

and the theorem allows to conclude that

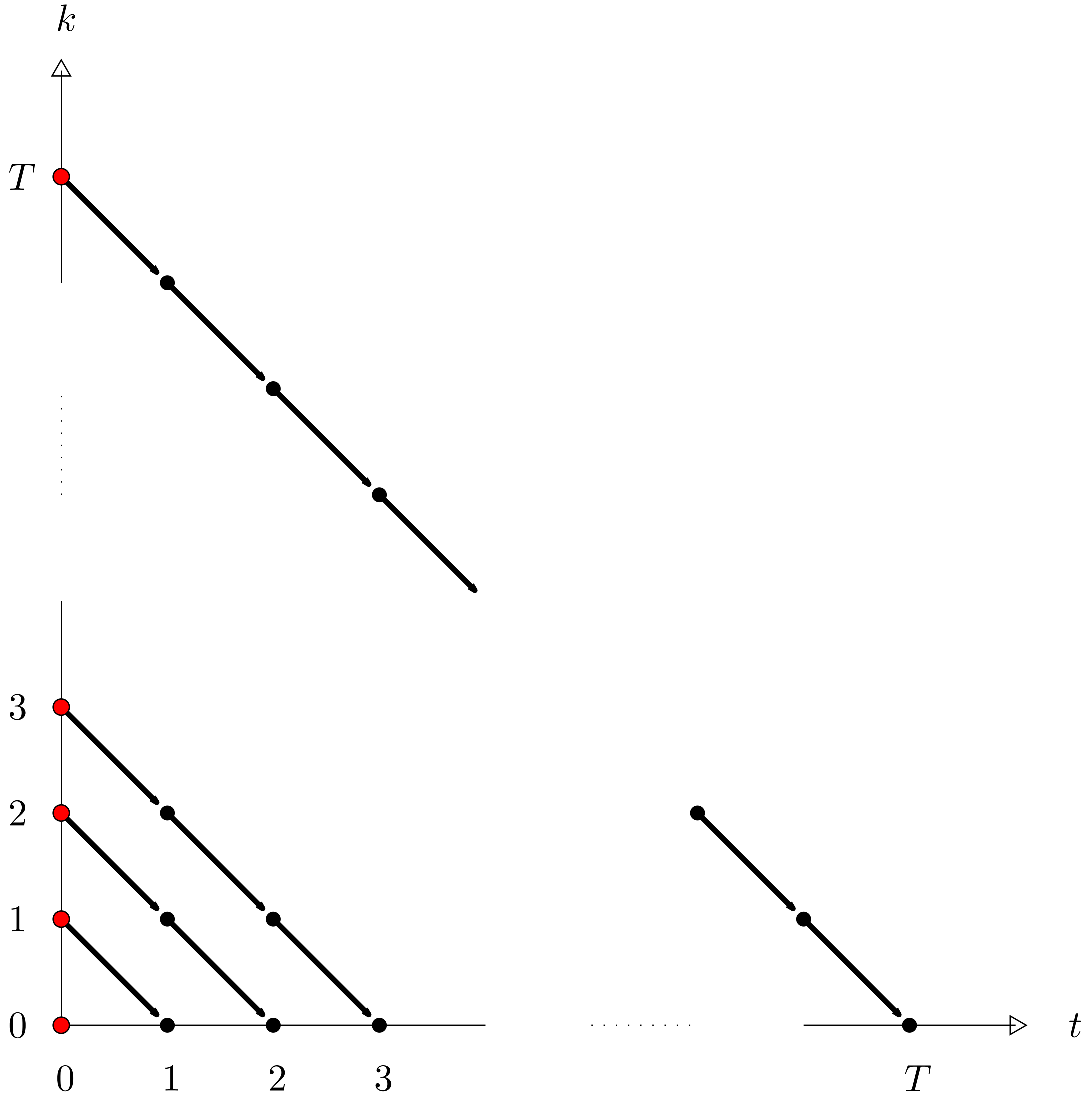
$$\frac{1}{n} \sum_{i=1}^n s_i^k X_{i,t}^{(n)} \left(= \int s^k \mu_{n,t}(ds)\right) \to \bar{\mu}_t^{(k)},$$

for example, $\frac{1}{n} \sum_{i=1}^n X_{i,t}^{(n)} \to \bar{\mu}_t^{(0)}$.

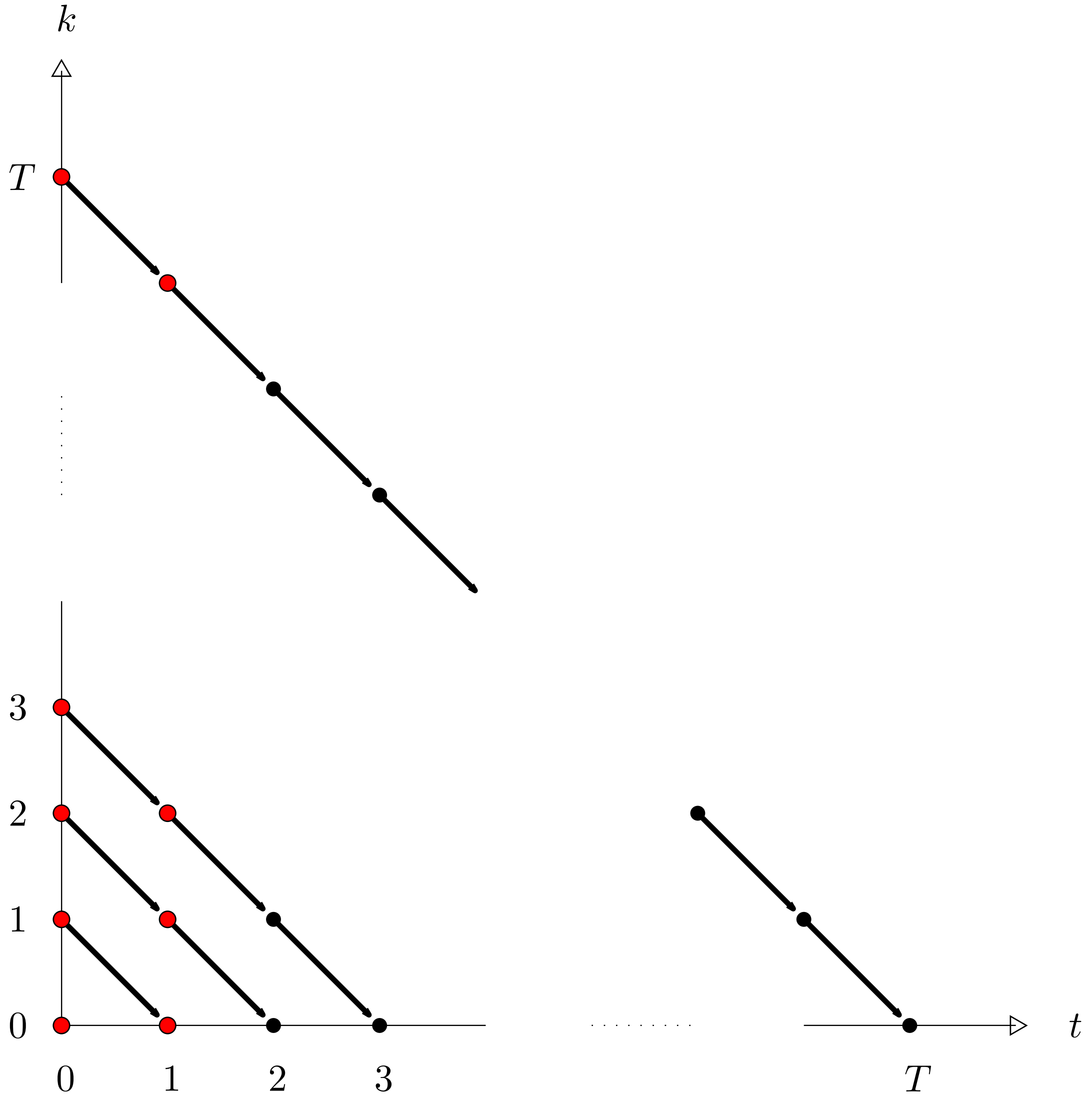
A deterministic limit $\bar{\mu}_t^{(0)}$



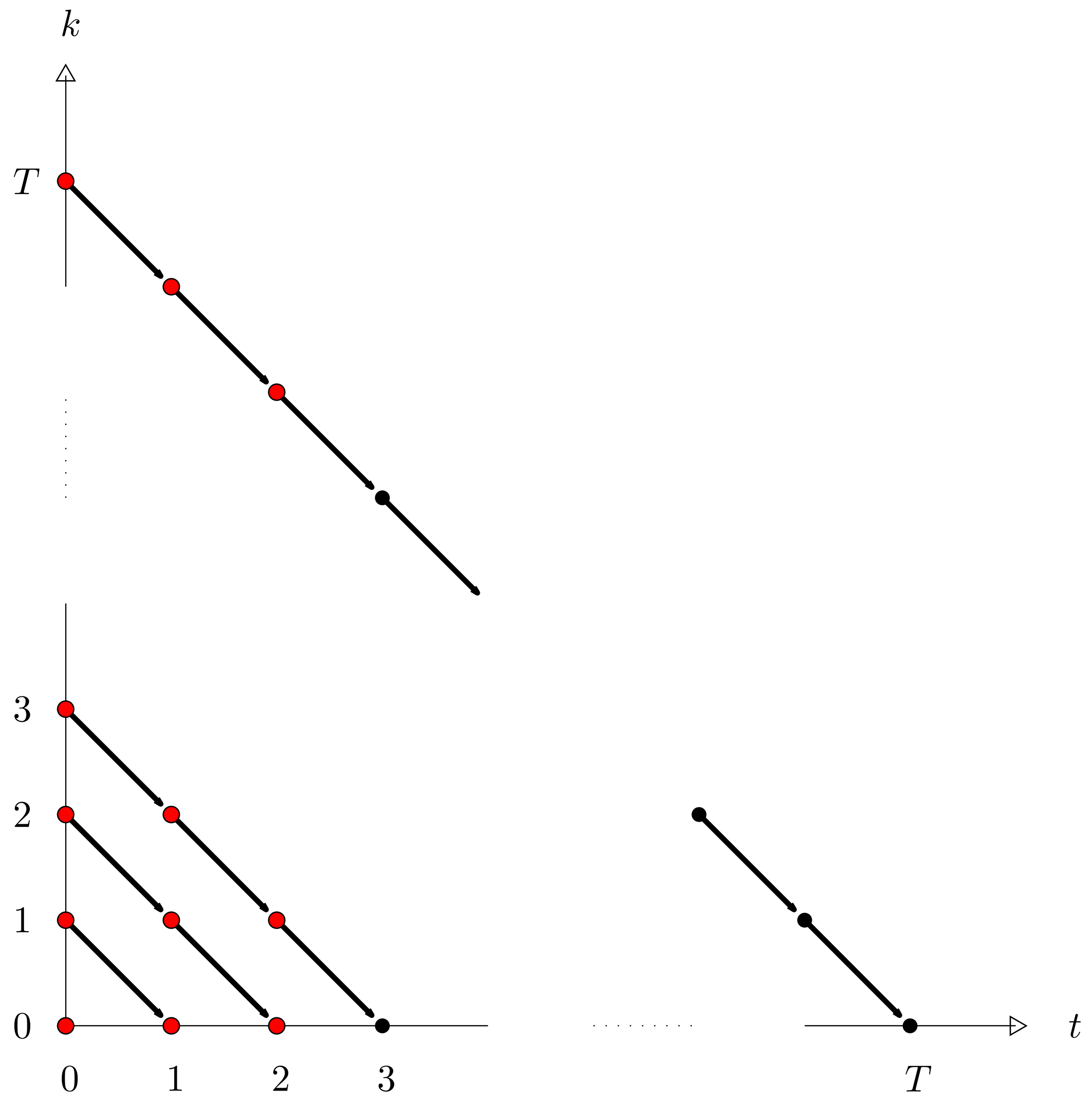
A deterministic limit $\bar{\mu}_0^{(k)}$



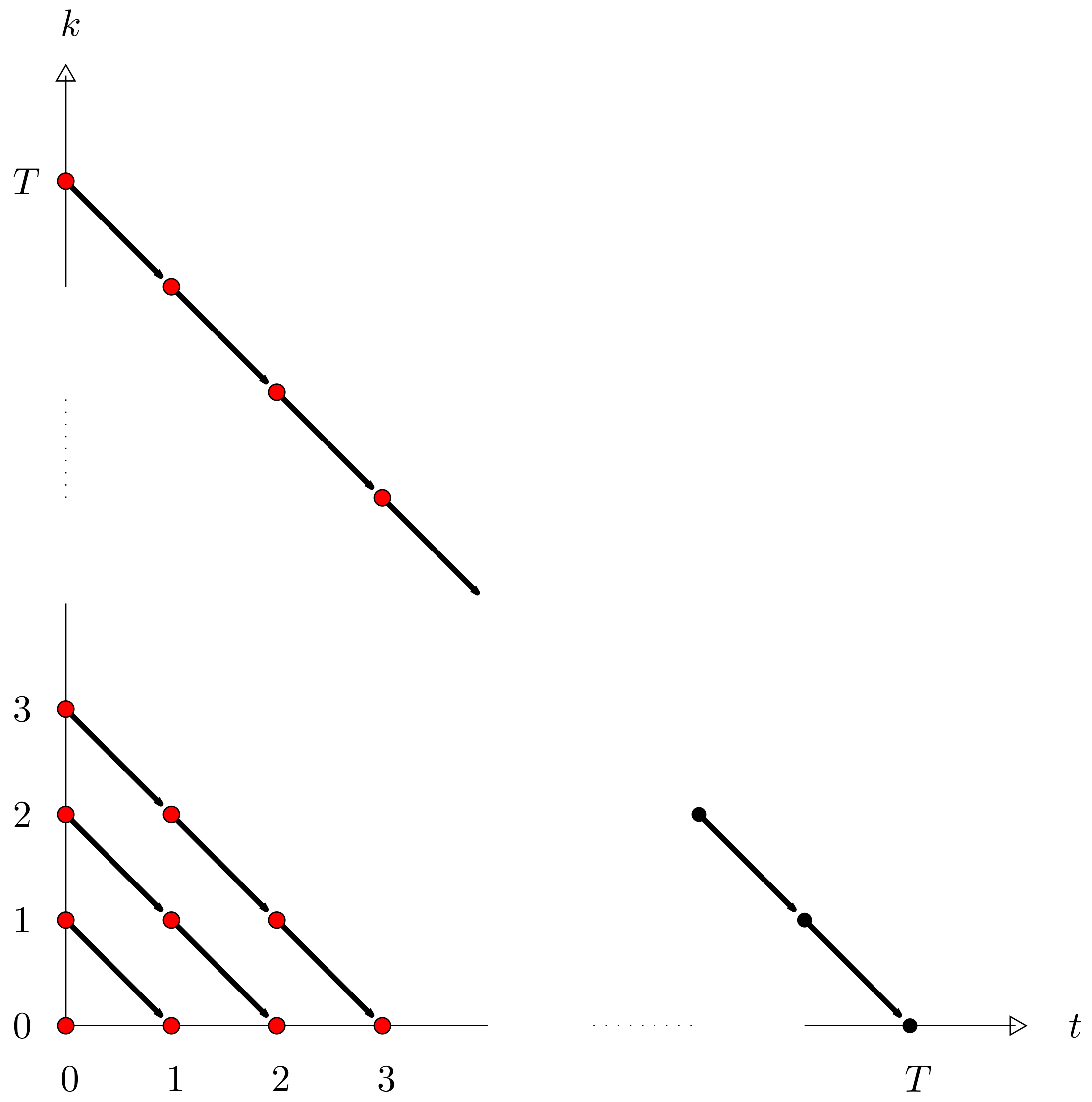
A deterministic limit $\bar{\mu}_1^{(k)}$



A deterministic limit $\bar{\mu}_2^{(k)}$



A deterministic limit $\bar{\mu}_3^{(k)}$



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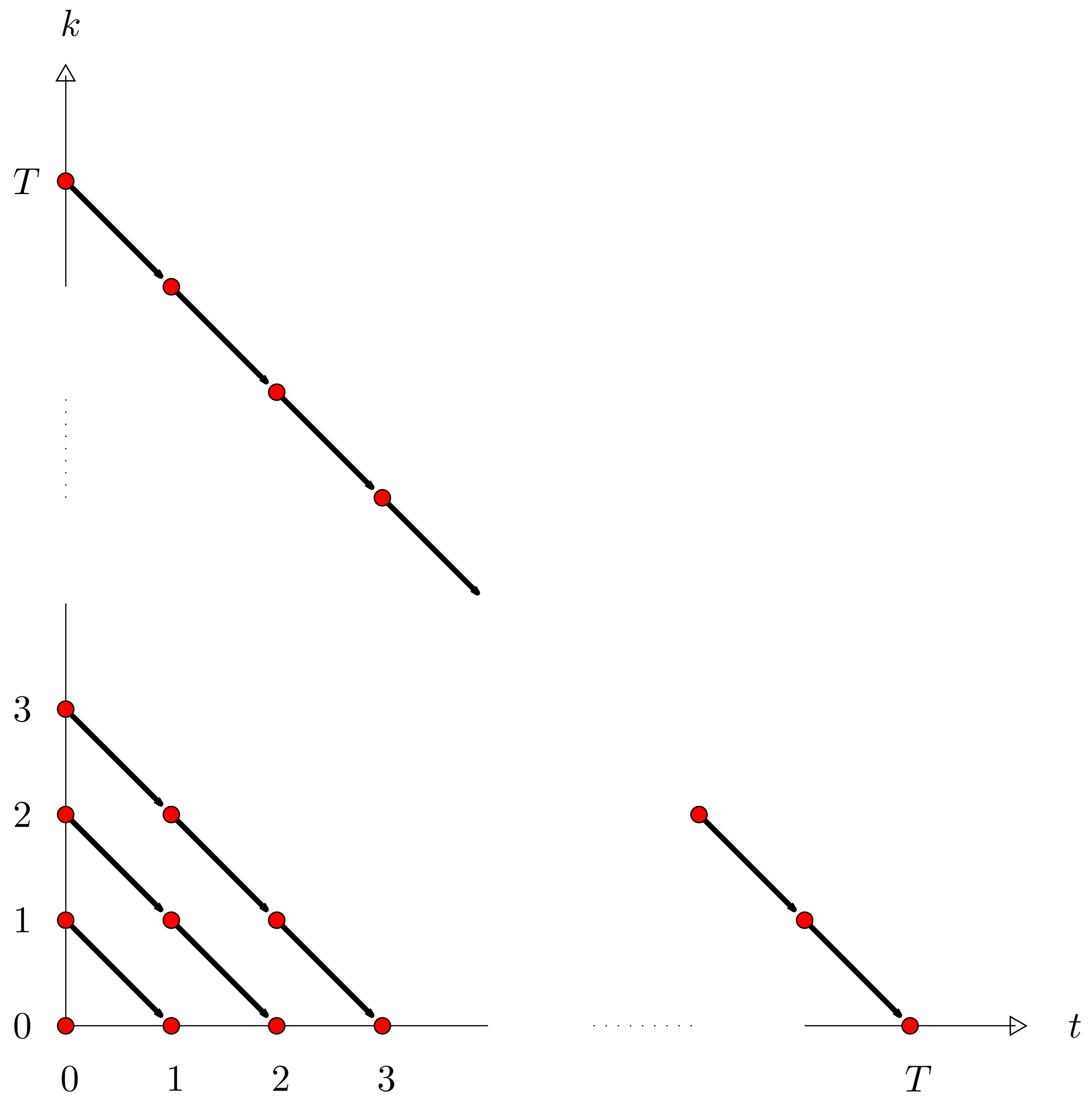

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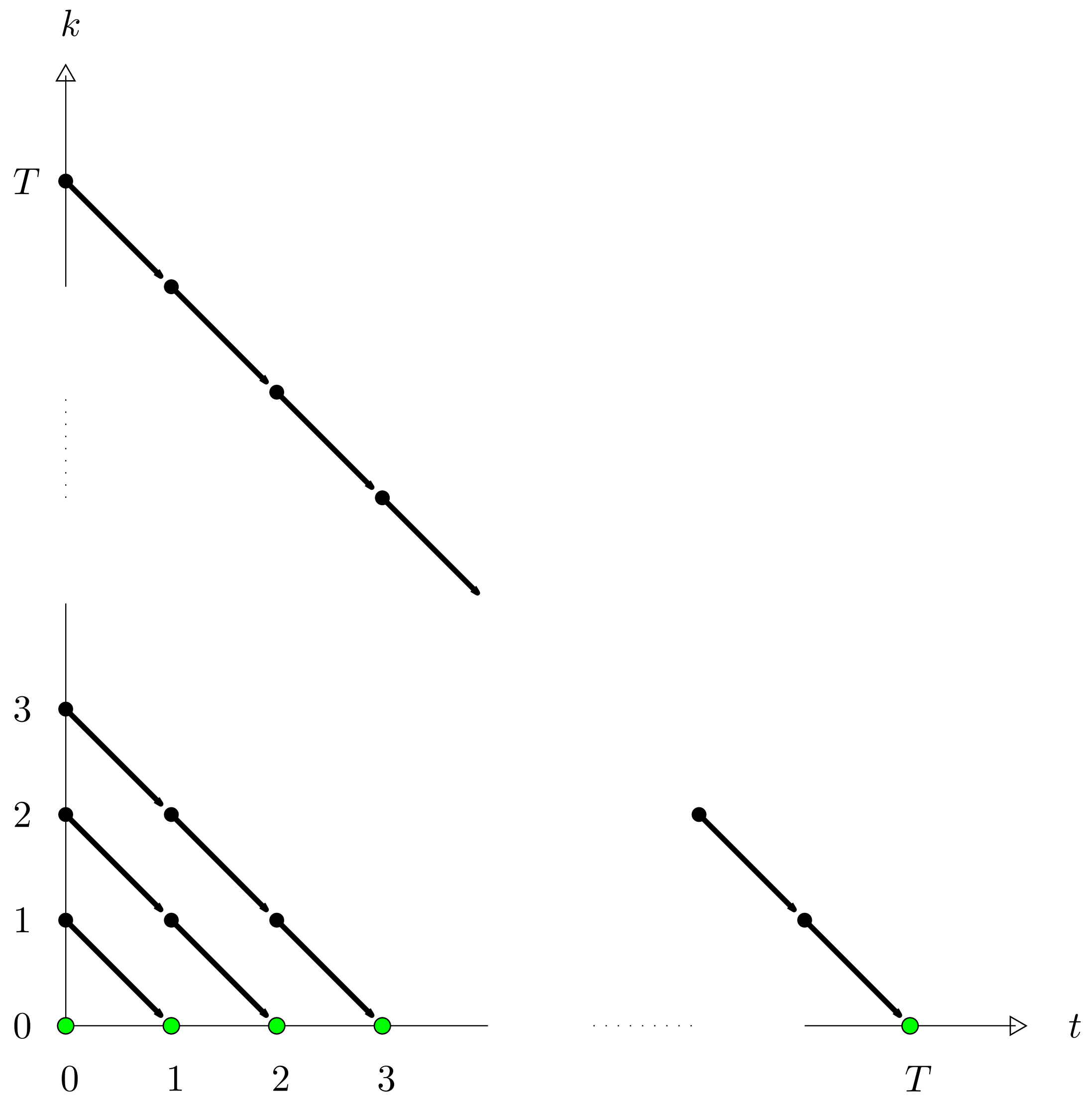
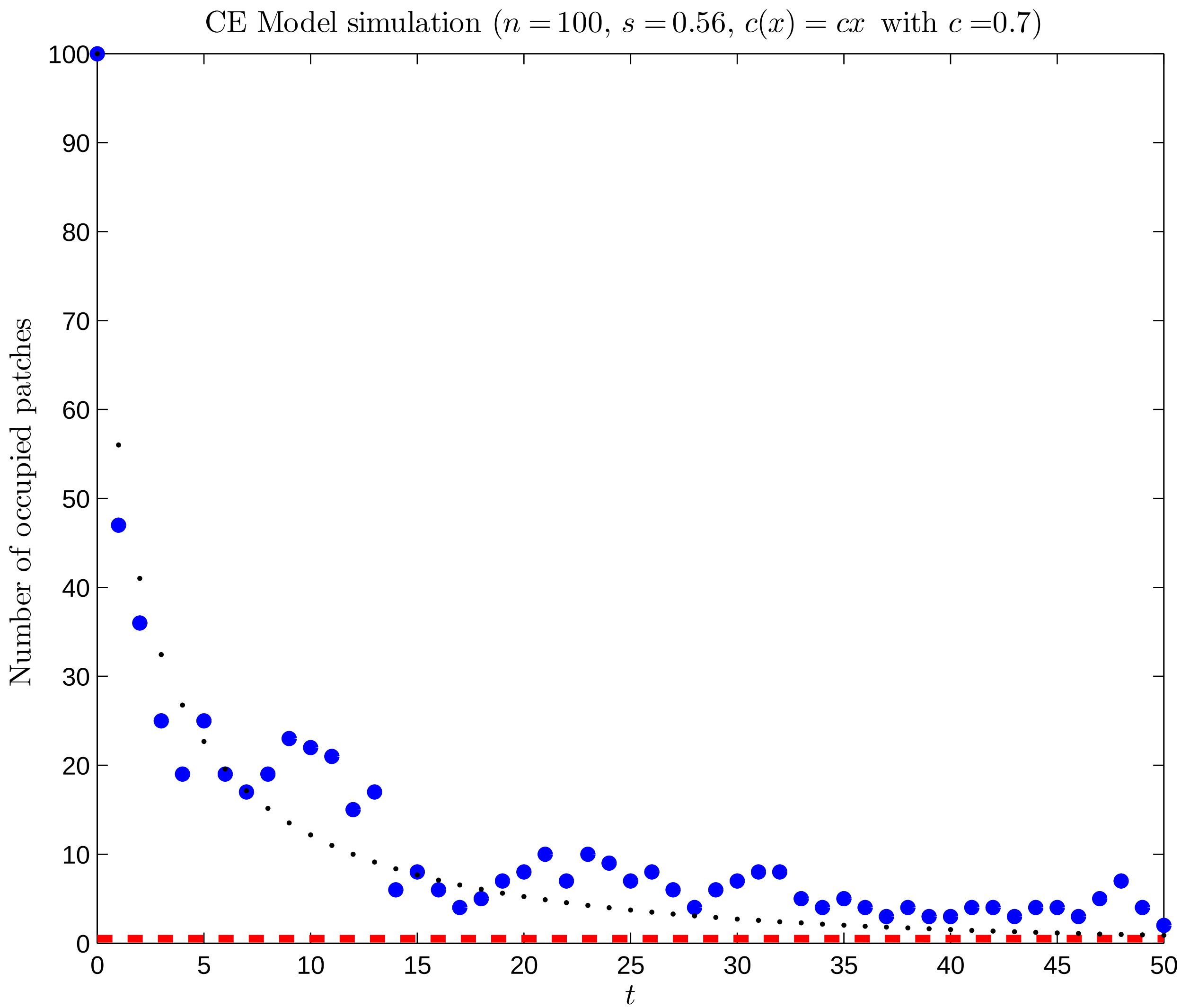


CE Model (homogeneous) - Evanescence



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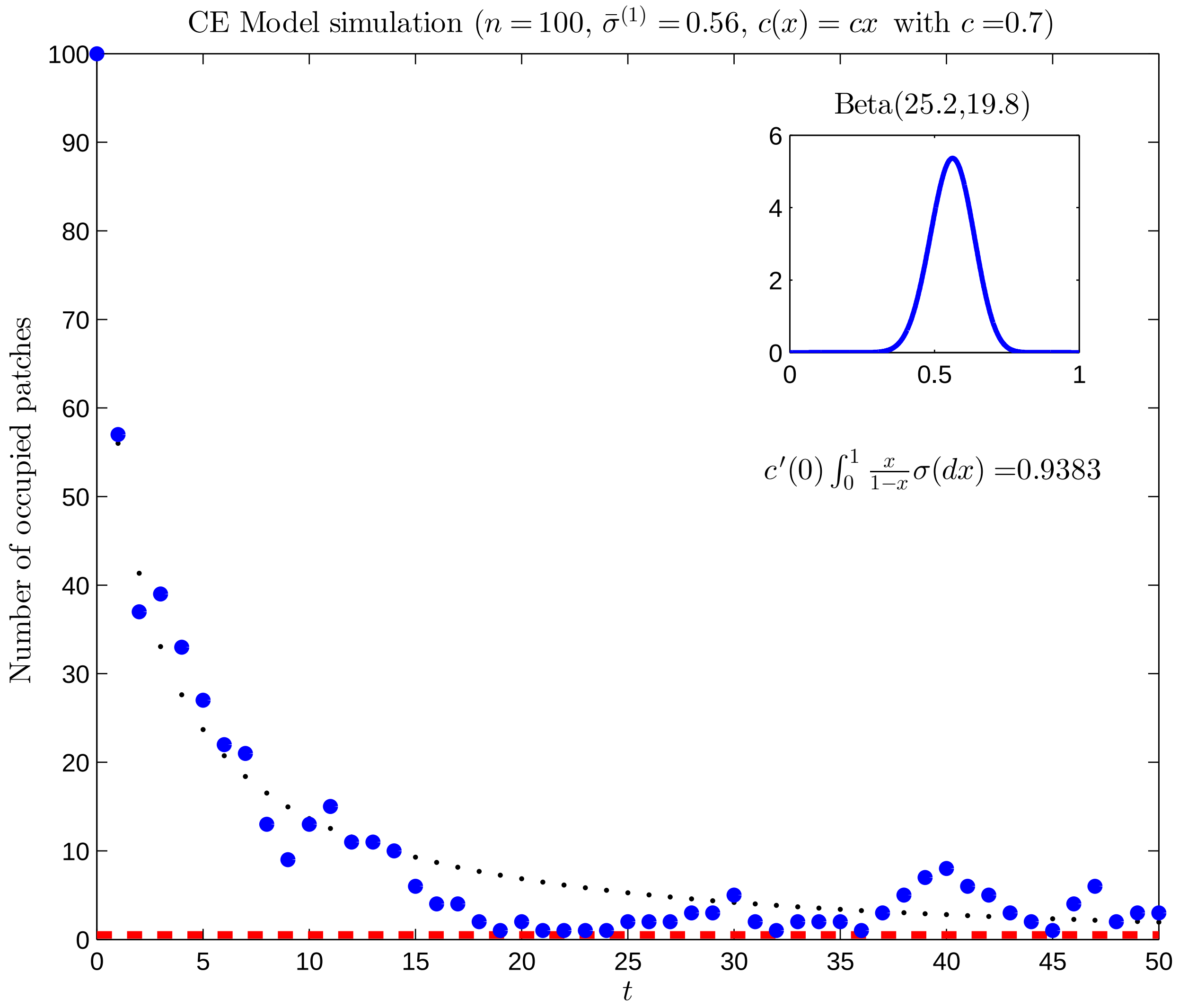
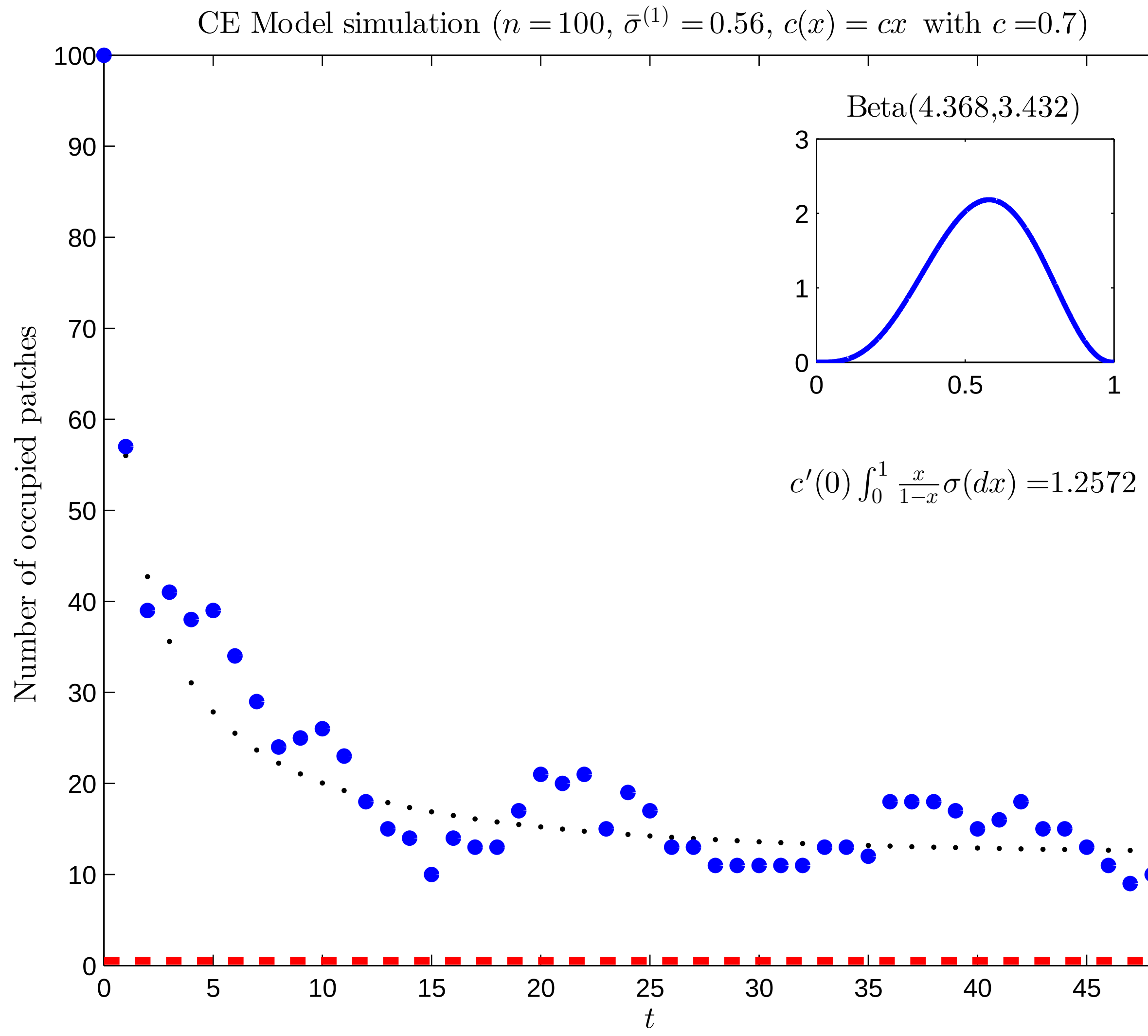


CE Model - Quasi stationarity



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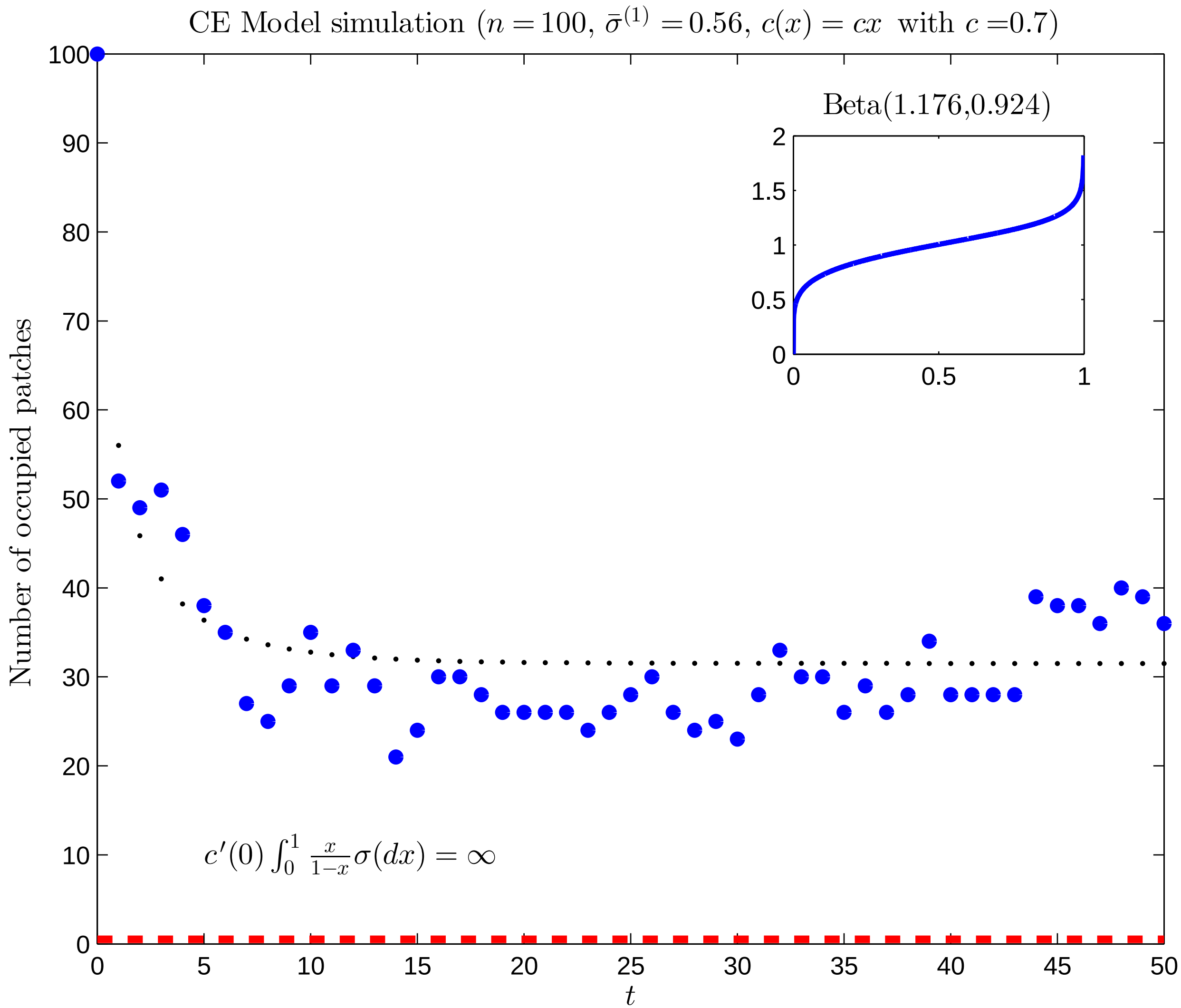

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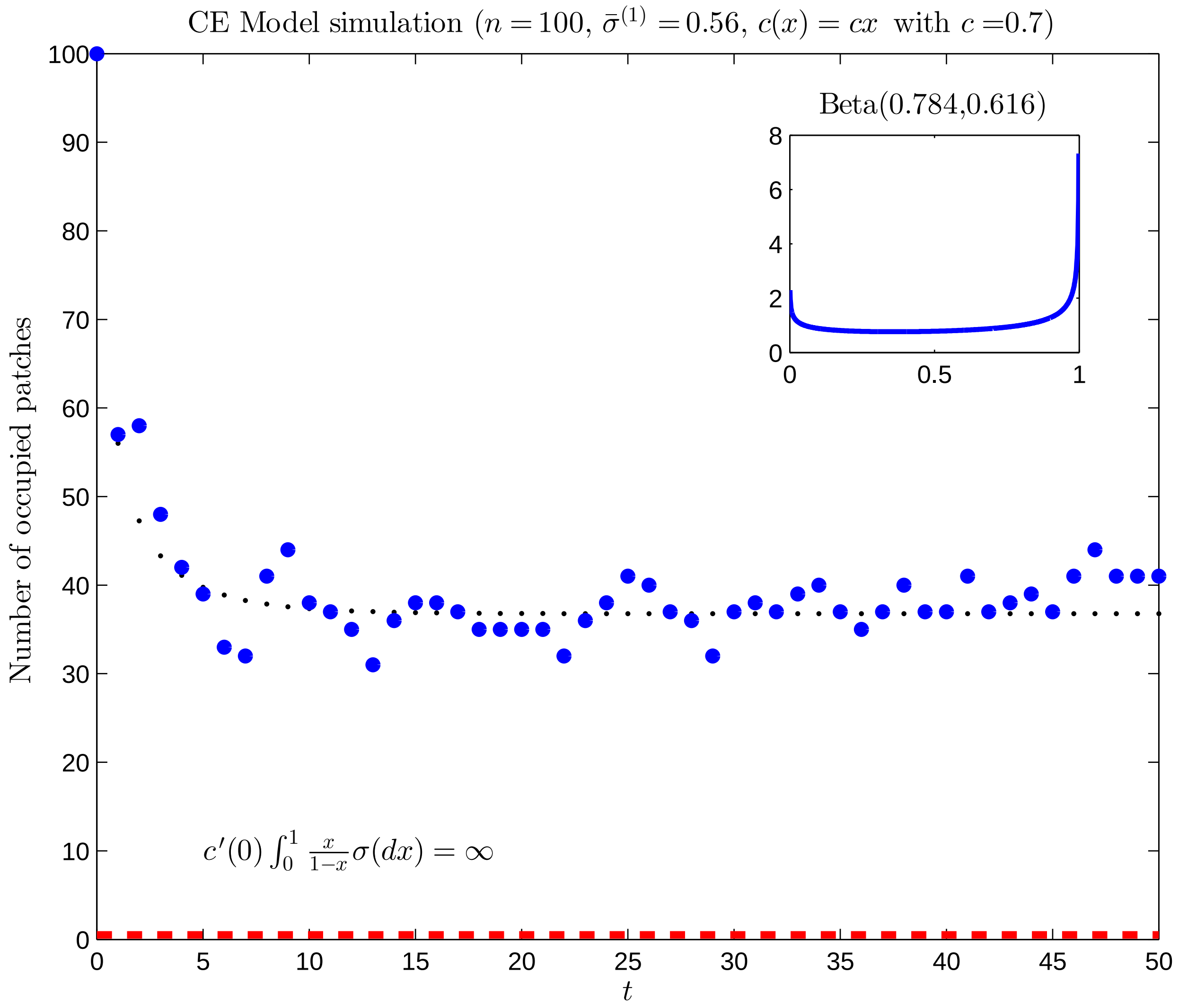

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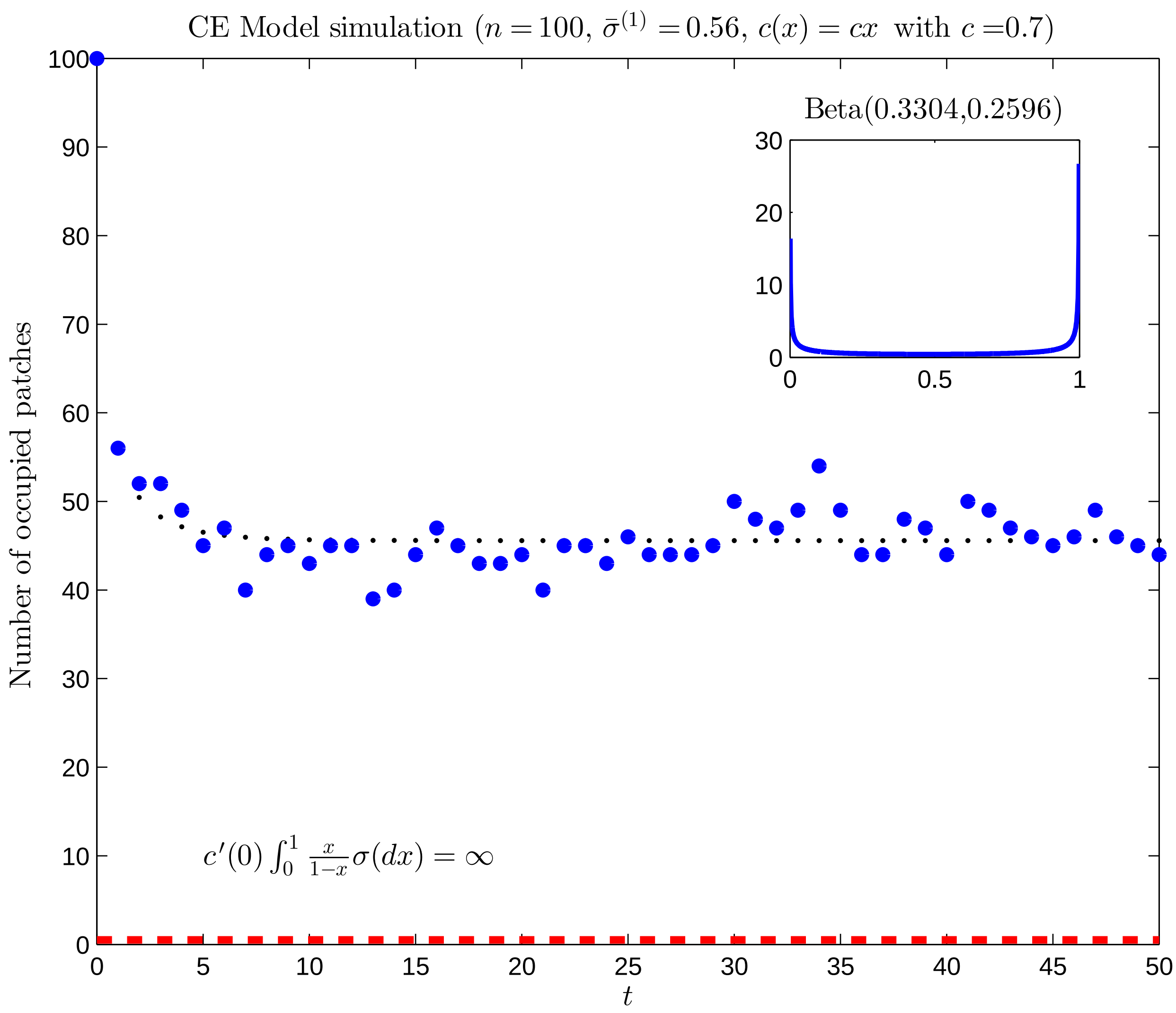

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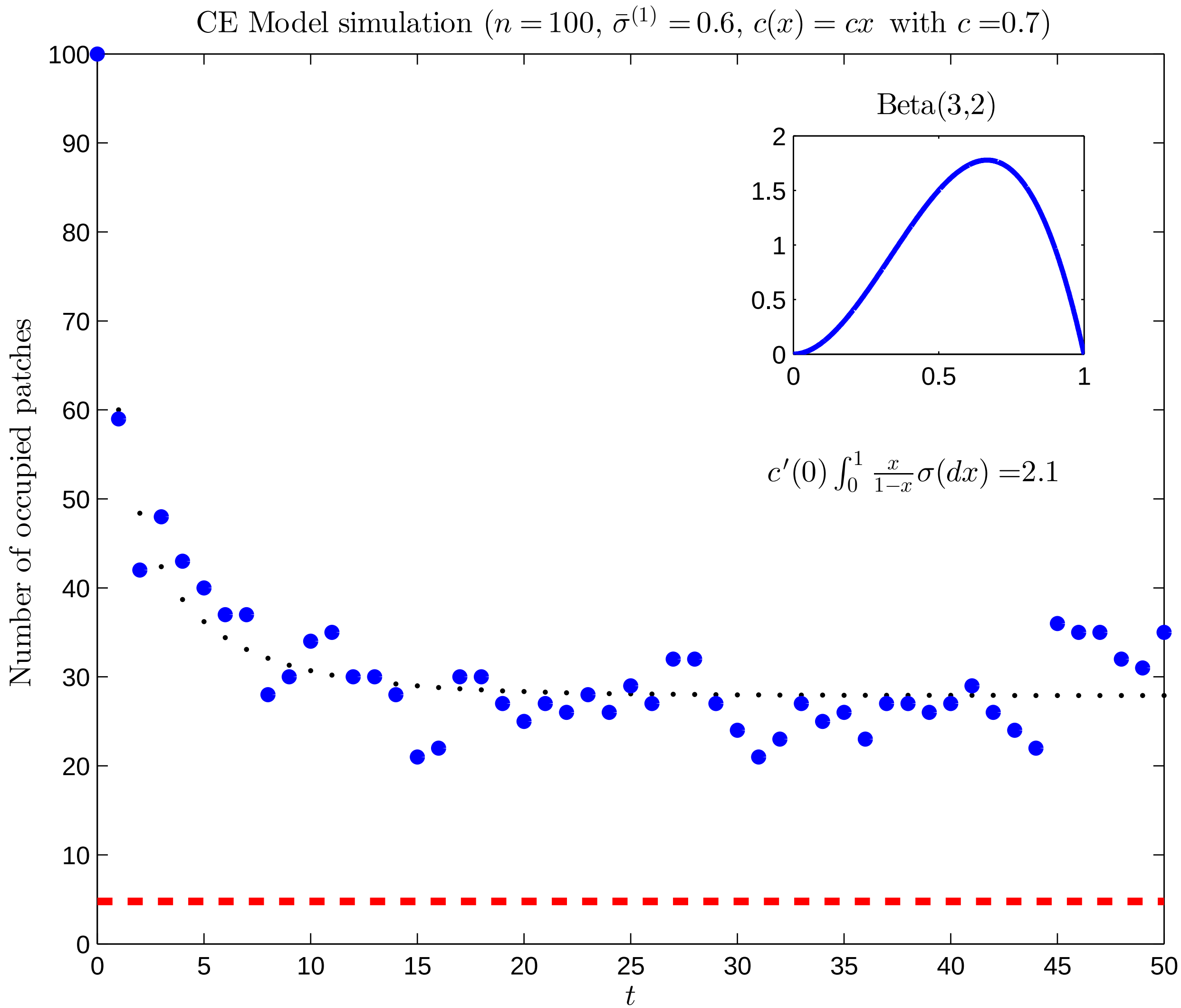

Extra - equilibria

Our recursion is

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Let $\mathcal{M}$ be the set of measures that are absolutely continuous with respect to σ 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 σ, 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 [MP] Suppose that $c(0) = 0$ and $c'(0) < \infty$. Let ψ^* be a solution to the equation

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

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

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

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

Extra - stability

Theorem [MP] 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, $\mu_t \to \mu_\infty$.