Metapopulations with dynamic extinction probabilities

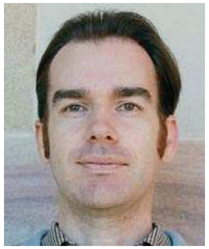
Phil Pollett

The University of Queensland
http://www.maths.uq.edu.au/~pkp

AUSTRALIAN RESEARCH COUNCIL CENTRE OF EXCELLENCE FOR
MATHEMATICAL AND STATISTICAL FRONTIERS

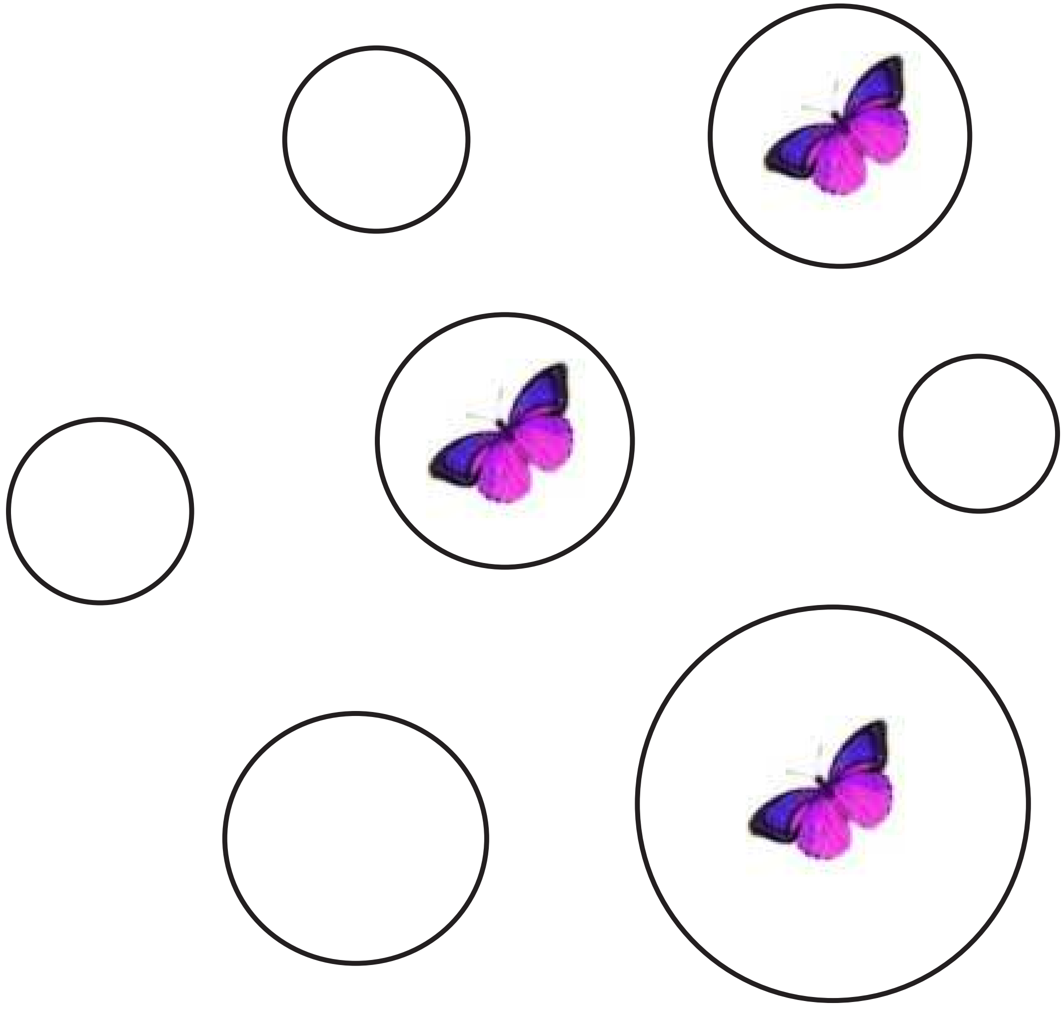
Collaborators

Ross McVinish
Department of Mathematics
University of Queensland

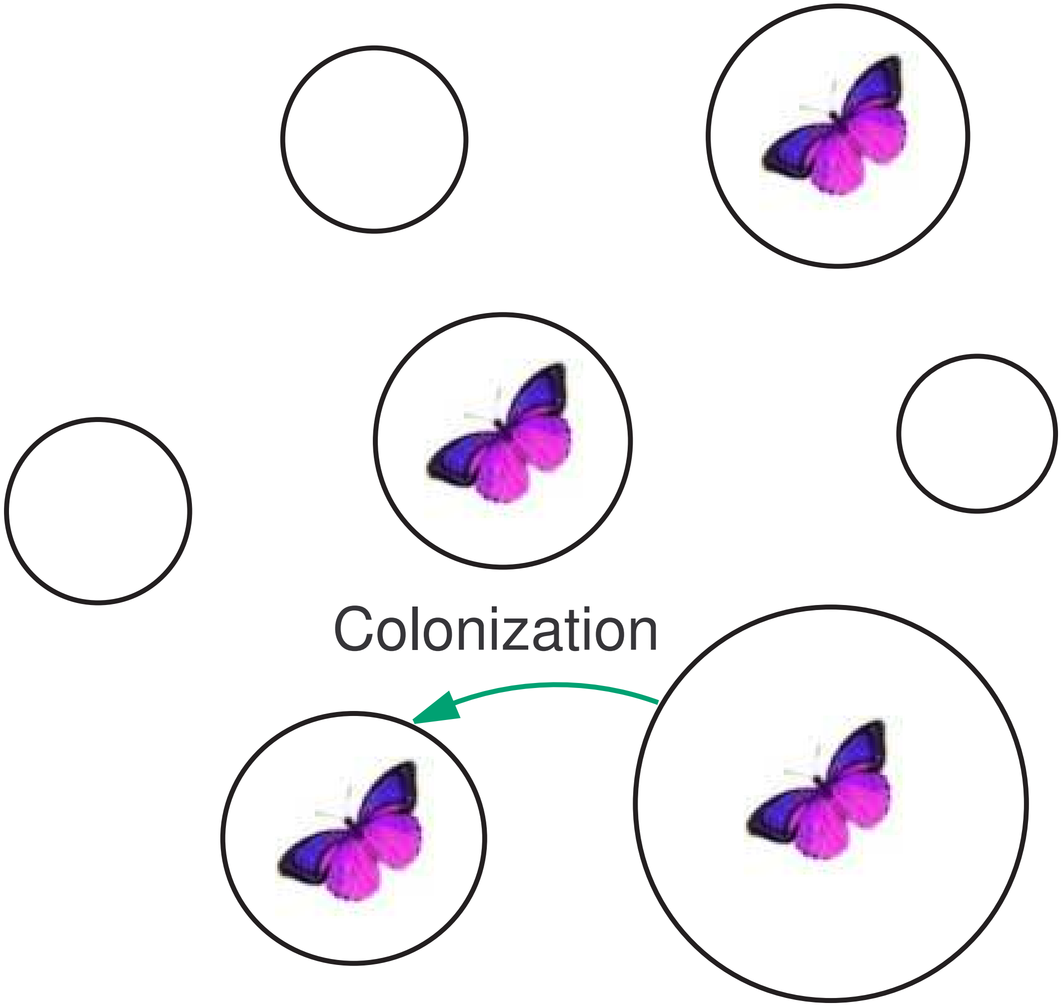


Yui Sze (Jessica) Chan
Department of Mathematics
University of Queensland

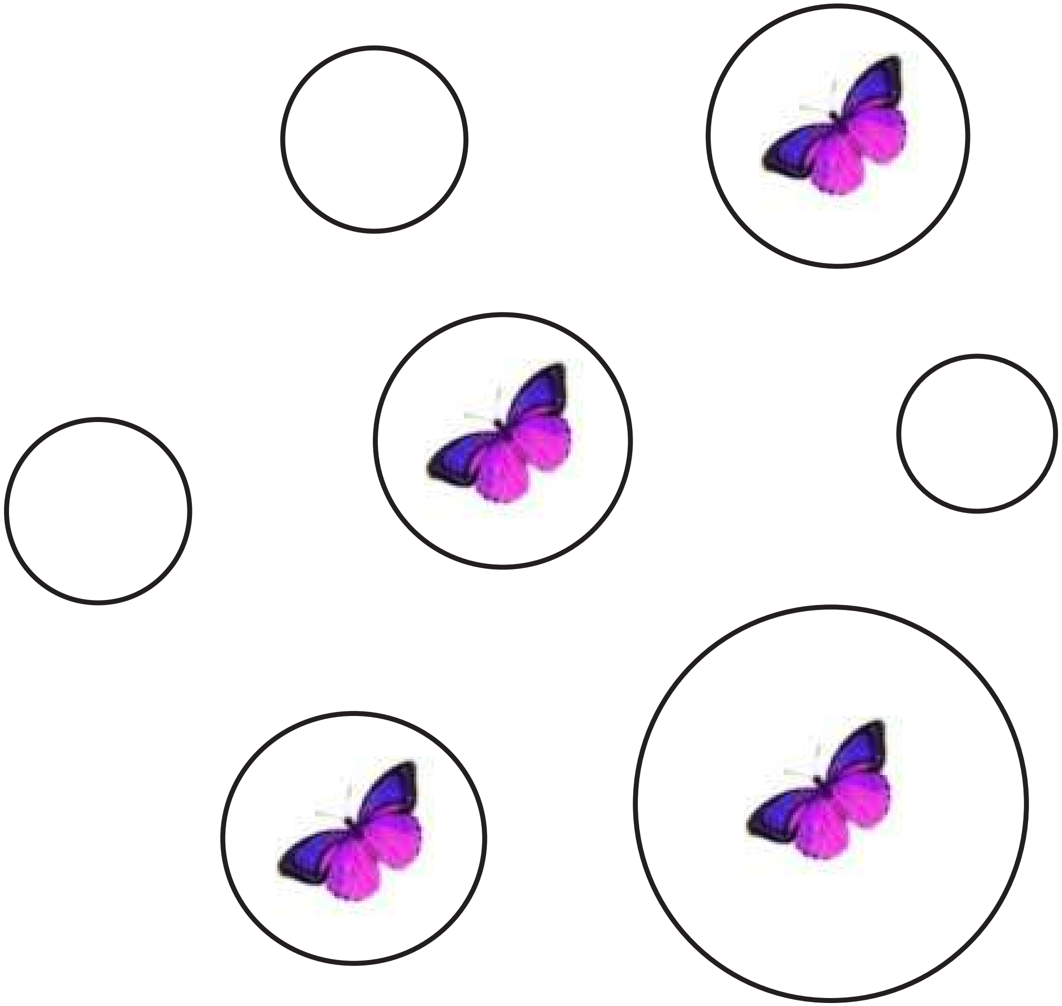
Metapopulations



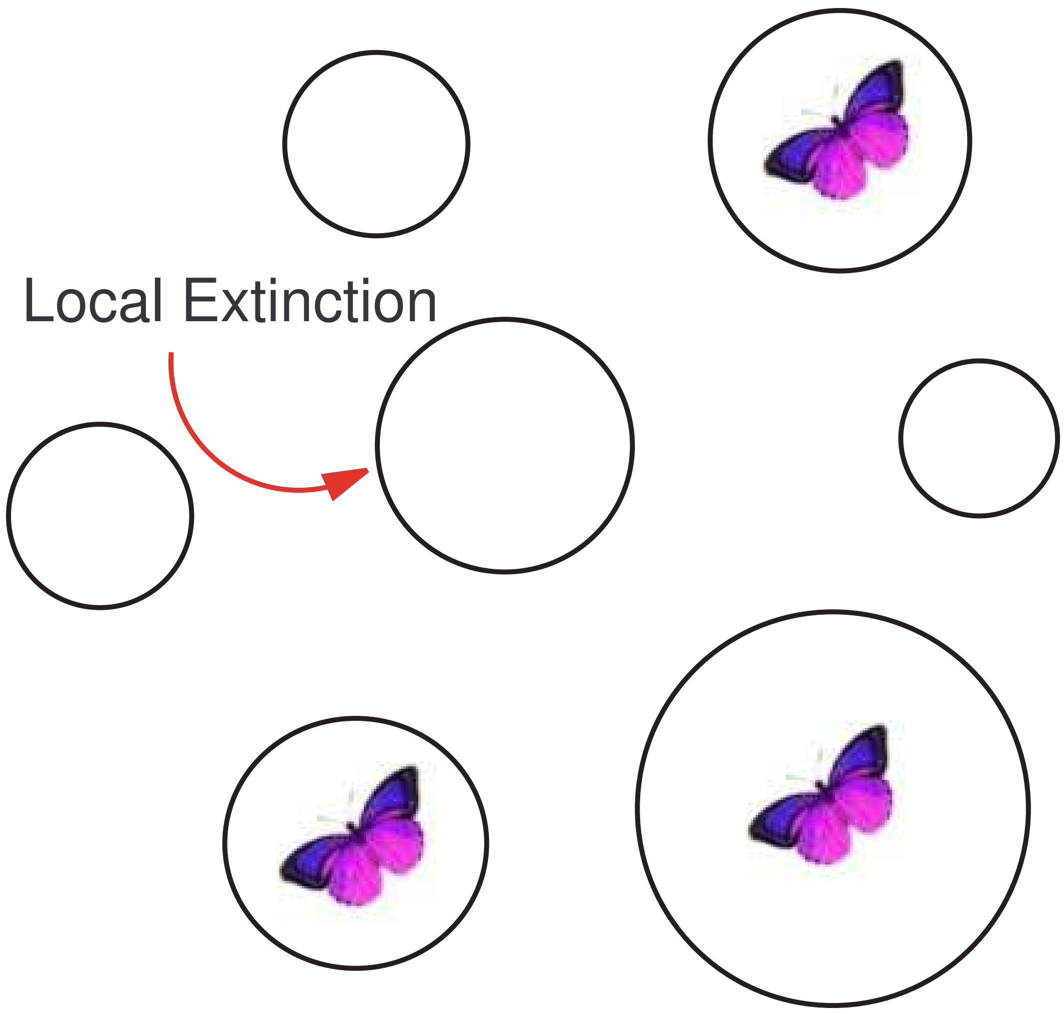
Metapopulations



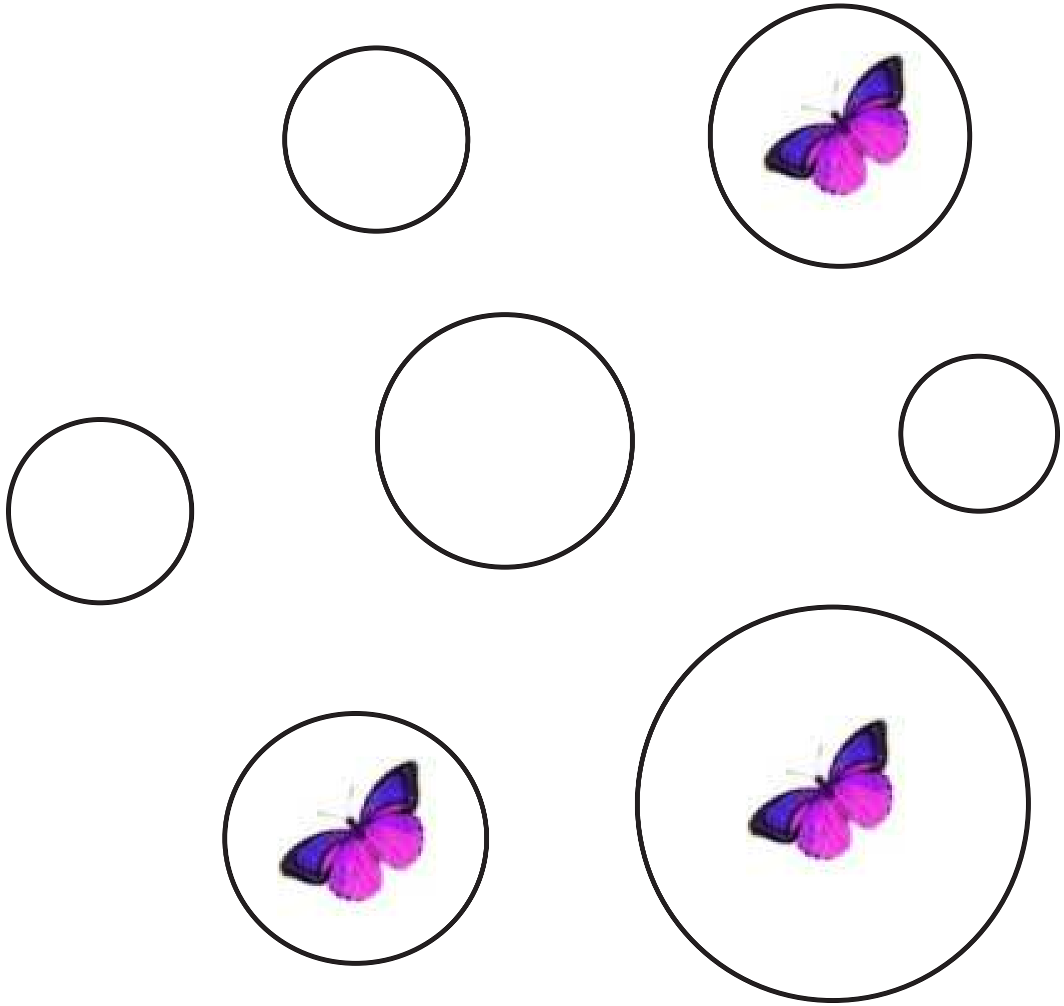
Metapopulations



Metapopulations



Metapopulations



SPOM

A *stochastic patch occupancy model* (SPOM)

SPOM

A *stochastic patch occupancy model* (SPOM)

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.

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 at time t.

Colonization and extinction happen in distinct, successive phases.

SPOM - Phase structure

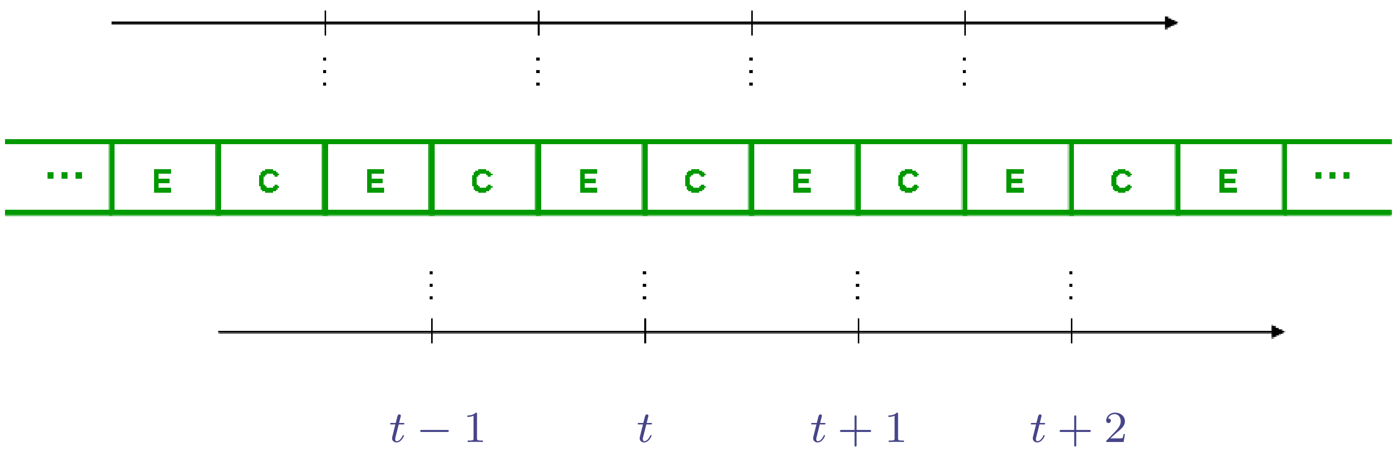
For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle. Examples:

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: unoccupied patch i becomes occupied with probability

$$c\left(\frac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)} d(z_i, z_j) a_j\right),$$

where $d(z, \tilde{z}) \geq 0$ measures the ease of movement between patches located at z and $\tilde{z}$, a_j is a weight related to the size of the patch j and $c : [0, \infty) \to [0, 1]$ $($called the *colonisation function*$)$ is increasing and Lipschitz continuous, with $c(0) = 0$ and $c'(0) > 0$.

SPOM - Phase structure

For simplicity, take $d \equiv 1$ and $a \equiv 1$. So, $\ldots$

Colonization: unoccupied patch i becomes occupied with probability $c(n^{-1}\sum_{j=1}^{n} X_{j,t}^{(n)})$, where $c : [0,1] \to [0,1]$ (called the *colonisation function*) is increasing and Lipschitz continuous, with $c(0) = 0$ and $c'(0) > 0$.

SPOM - Phase structure

For simplicity, take $d \equiv 1$ and $a \equiv 1$. So, $\ldots$

Colonization: unoccupied patch i becomes occupied with probability $c(n^{-1}\sum_{j=1}^{n} X_{j,t}^{(n)})$, where $c : [0,1] \to [0,1]$ (called the *colonisation function*) is increasing and Lipschitz continuous, with $c(0) = 0$ and $c'(0) > 0$.

Proportion of patches occupied

SPOM - Phase structure

For simplicity, take $d \equiv 1$ and $a \equiv 1$. So, $\ldots$

Colonization: unoccupied patch i becomes occupied with probability $c(n^{-1}\sum_{j=1}^{n} X_{j,t}^{(n)})$, where $c : [0,1] \to [0,1]$ (called the *colonisation function*) is increasing and Lipschitz continuous, with $c(0) = 0$ and $c'(0) > 0$.

SPOM - Phase structure

Colonization: unoccupied patch i becomes occupied with probability $c(n^{-1}\sum_{j=1}^{n} X_{j,t}^{(n)})$, where $c : [0,1] \to [0,1]$ (called the *colonisation function*) is increasing and Lipschitz continuous, with $c(0) = 0$ and $c'(0) > 0$.

Extinction: occupied patch i remains occupied with probability $s_{i,t}$.

SPOM - Phase structure

Colonization: unoccupied patch i becomes occupied with probability $c(n^{-1}\sum_{j=1}^{n} X_{j,t}^{(n)})$, where $c:[0,1]\to[0,1]$ (called the *colonisation function*) is increasing and Lipschitz continuous, with $c(0)=0$ and $c'(0)>0$.

Extinction: occupied patch i remains occupied with probability $s_{i,t}$.

Then, given the current state $X_t^{(n)}$ and survival probabilities s_t, the $X_{i,t+1}^{(n)}$ $(i=1,\ldots,n)$ are independent with transitions

$$\Pr\left(X_{i,t+1}^{(n)}=1 \,|\, X_t^{(n)}, s_t\right) = s_{i,t}X_{i,t}^{(n)} + s_{i,t}\, c\left(n^{-1}\sum_{j=1}^{n} X_{j,t}^{(n)}\right)\left(1 - X_{i,t}^{(n)}\right).$$

SPOM - Phase structure

Extinction: occupied patch i remains occupied with probability $s_{i,t}$.

We will assume that $(s_{i,t})_{t=0}^{\infty}$ $(i = 1, \ldots, n)$ are independent Markov chains taking values in $[0, 1]$ with common transition kernel $P(s, dr)$.

This covers the simple but important case where patches are classified as being suitable or unsuitable for occupancy.

SPOM - Homogeneous case

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, and, letting the initial number $N_0^{(n)}$ of occupied patches grow at the same rate as n we arrive at:

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

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

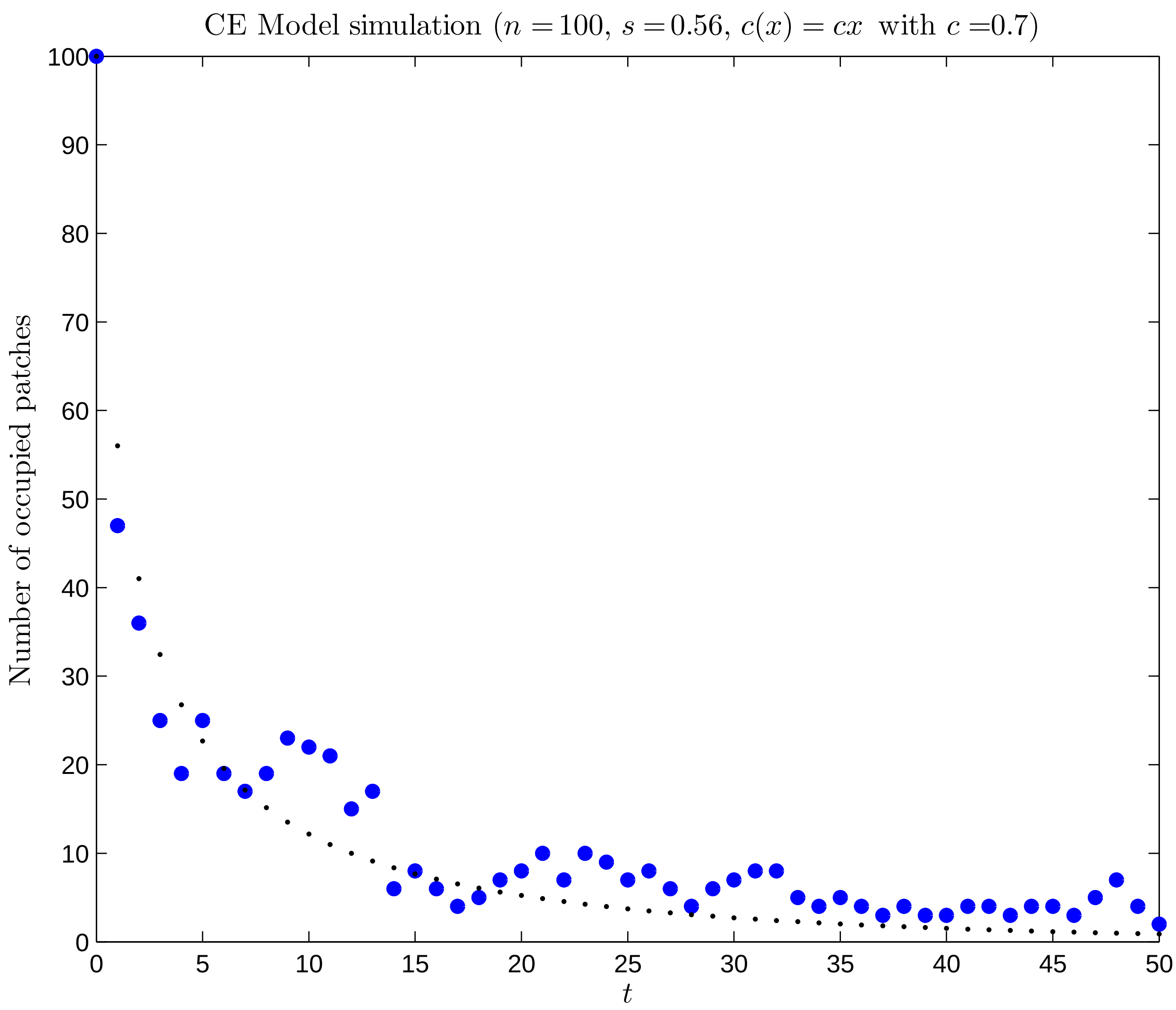
with (x_t) determined by $x_{t+1} = f(x_t)$, where

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

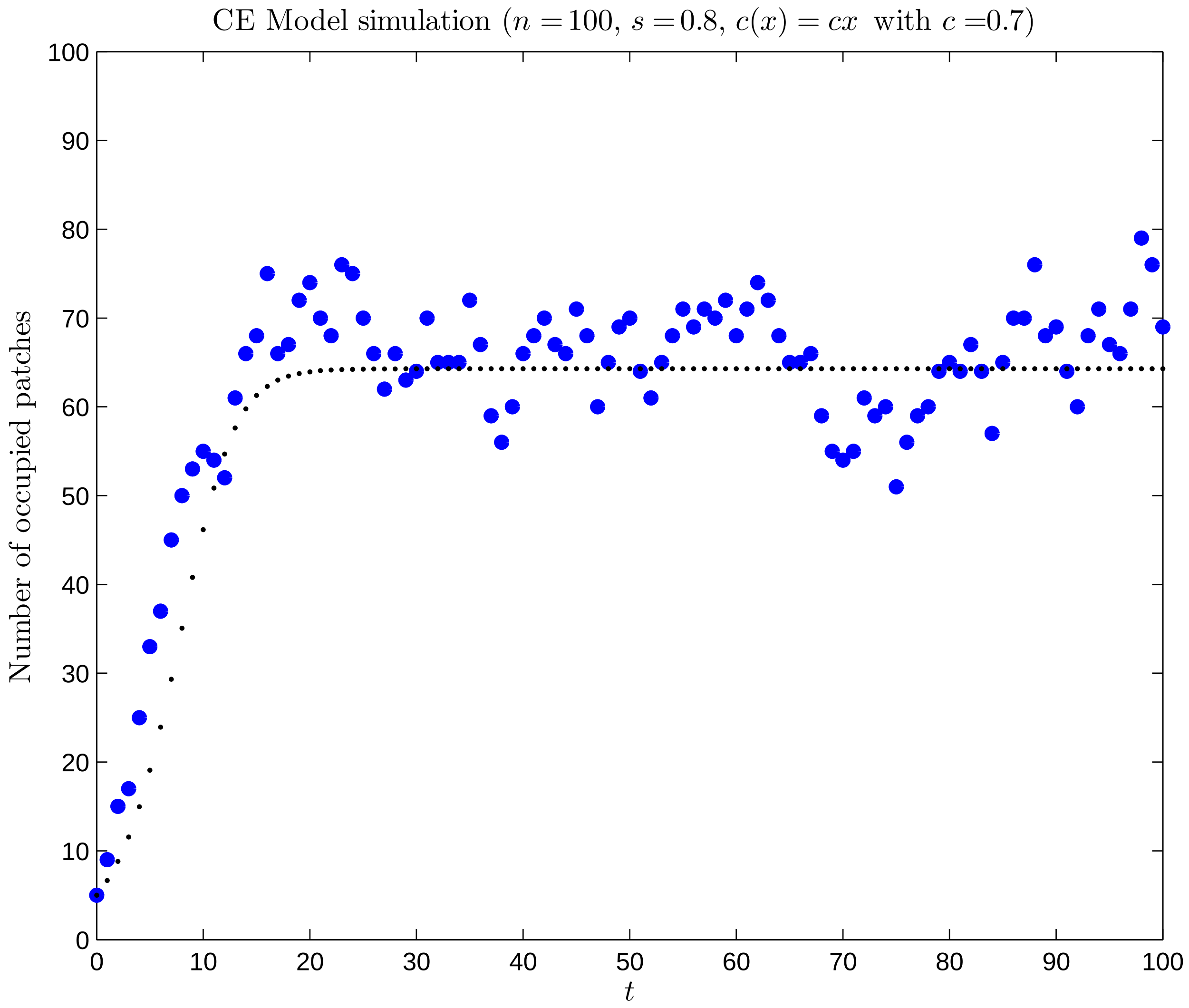
Survival probability

Colonization probability

CE Model - Evanescence



CE Model - Quasi stationarity



Stability

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

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

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

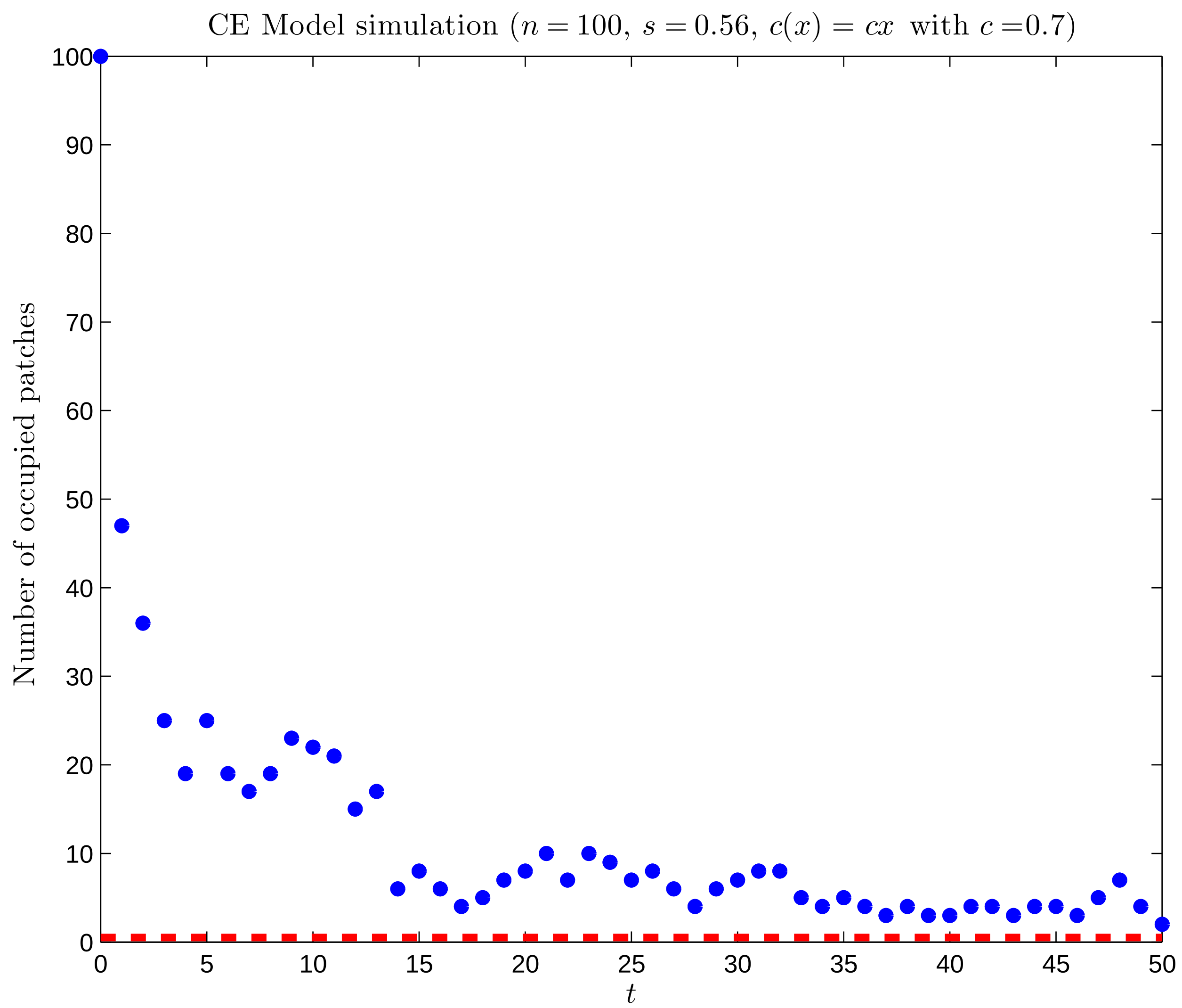
Stability

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

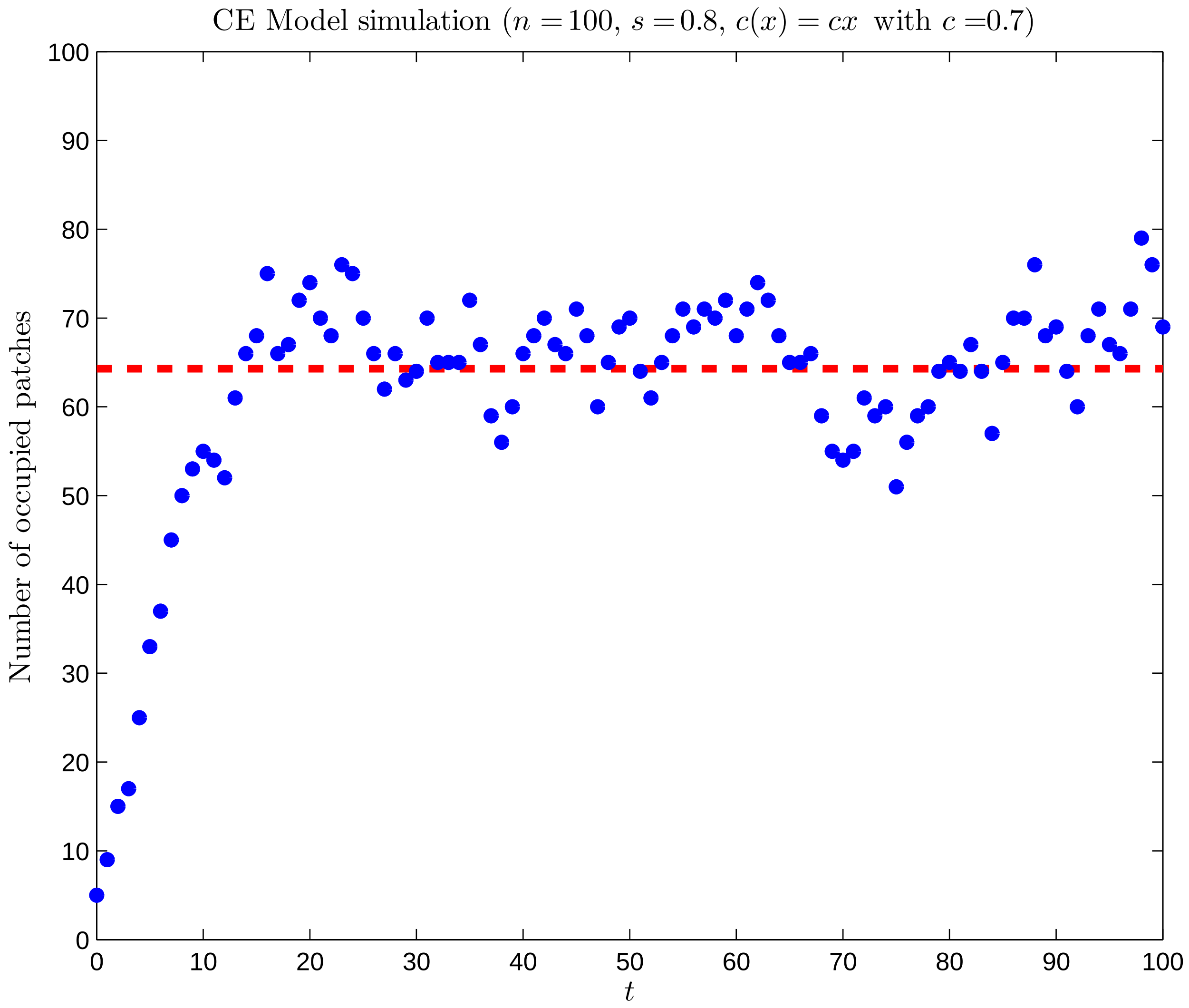
Evanescence: $1 + c'(0) \leq 1/s$. 0 is the unique fixed point in $[0,1]$. It is stable.

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

CE Model - Evanescence



CE Model - Quasi stationarity



SPOM - General case

Return now to the general case, where patch survival probabilities evolve in time, and we keep track of which patches are occupied ...

$$\Pr\Big(X_{i,t+1}^{(n)}=1 \,|\, X_t^{(n)}, s_t\Big) = s_{i,t} X_{i,t}^{(n)} + s_{i,t}\, c\bigg(n^{-1}\textstyle\sum_{j=1}^{n} X_{j,t}^{(n)}\bigg)\Big(1 - X_{i,t}^{(n)}\Big).$$

Our approach - Point processes

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

Our approach - Point processes

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

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

$$\sigma_{n,t}(B) = \#\{s_{i,t} \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

$$\mu_{n,t}(B) = \#\{s_{i,t} \in B : X_{i,t}^{(n)} = 1\}/n, \qquad B \in \mathcal{B}([0,1]).$$

Our approach - Point processes

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

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

$$\sigma_{n,t}(B) = \#\{s_{i,t} \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

$$\mu_{n,t}(B) = \#\{s_{i,t} \in B : X_{i,t}^{(n)} = 1\}/n, \qquad B \in \mathcal{B}([0,1]).$$

Our approach - Point processes

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

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

$$\sigma_{n,t}(B) = \#\{s_{i,t} \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

$$\mu_{n,t}(B) = \#\{s_{i,t} \in B : X_{i,t}^{(n)} = 1\}/n, \qquad B \in \mathcal{B}([0,1]).$$

Our approach - Point processes

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

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

$$\sigma_{n,t}(B) = \#\{s_{i,t} \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

$$\mu_{n,t}(B) = \#\{s_{i,t} \in B : X_{i,t}^{(n)} = 1\}/n, \qquad B \in \mathcal{B}([0,1]).$$

We are going to suppose that $\sigma_{n,0} \xrightarrow{d} \sigma_0$ for some non-random (probability) measure σ_0.

Our approach - Point processes

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

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

$$\sigma_{n,t}(B) = \#\{s_{i,t} \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

$$\mu_{n,t}(B) = \#\{s_{i,t} \in B : X_{i,t}^{(n)} = 1\}/n, \qquad B \in \mathcal{B}([0,1]).$$

We are going to suppose that $\sigma_{n,0} \xrightarrow{d} \sigma_0$ for some non-random (probability) measure σ_0.

Think of σ_0 as being the initial distribution of survival probabilities.

Our approach - Point processes

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

$$\int h(s)\sigma_{n,t}(ds) = \frac{1}{n}\sum_{i=1}^{n} h(s_{i,t})$$

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

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

Our approach - Point processes

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

$$\int h(s)\sigma_{n,t}(ds) = \frac{1}{n}\sum_{i=1}^{n} h(s_{i,t})$$

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

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

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

Our approach - Point processes

Suppose that $\sigma_{n,0} \xrightarrow{d} \sigma_0$ for some non-random (probability) measure σ_0. Although this assumption concerns only the initial variation in the survival probabilities, it implies a similar 'law of large numbers' for them at all times.

Lemma $\sigma_{n,t} \xrightarrow{d} \sigma_t$, where σ_t is defined by the recursion

$$\int h(s)\sigma_{t+1}(ds) = \int h(s) \int P(r, ds)\sigma_t(dr),$$

for all $h \in C^+([0,1])$.

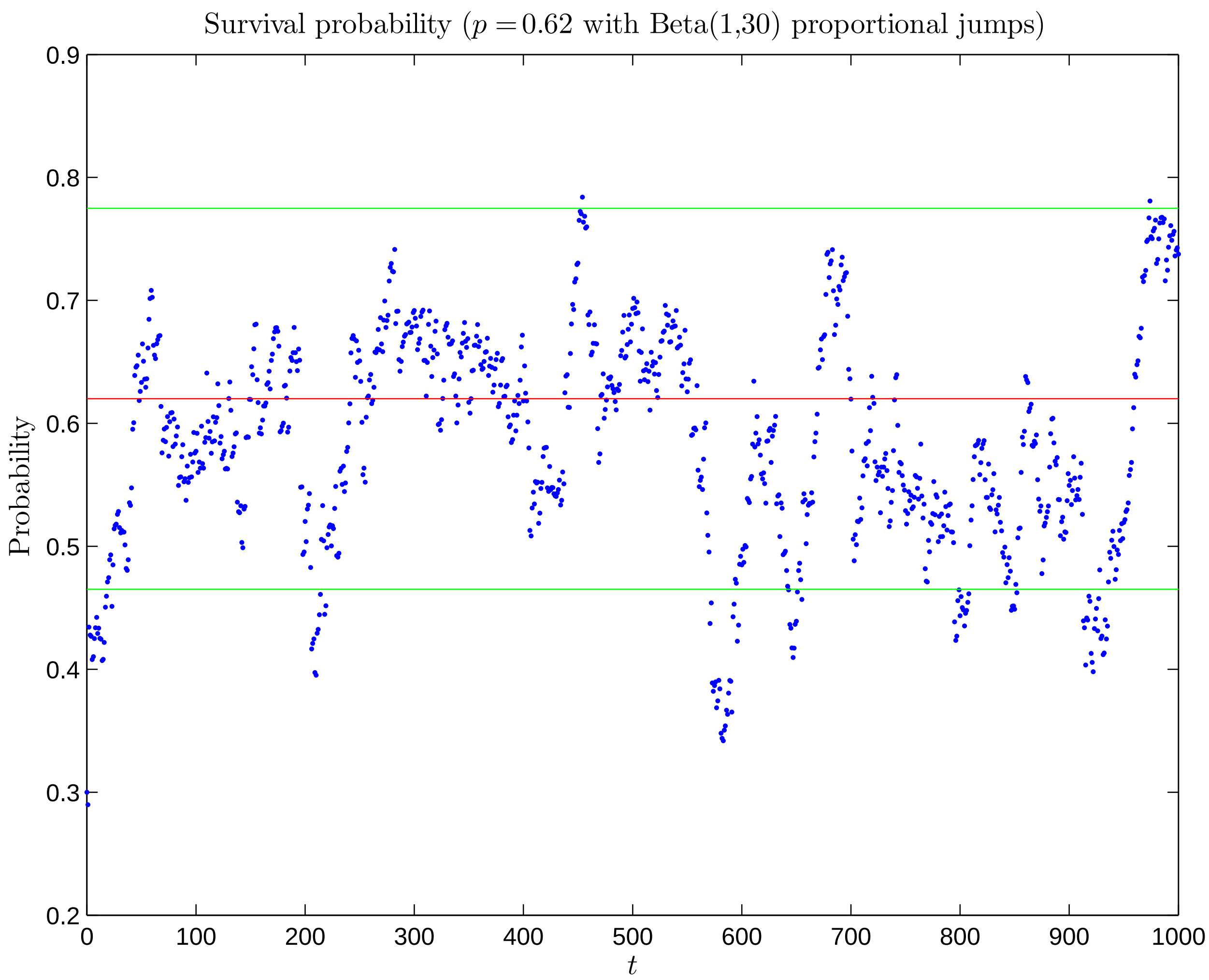
A measure-valued difference equation

Theorem Suppose that $\mu_{n,0} \xrightarrow{d} \mu_0$ for some non-random measure 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 $h \in C^+([0,1])$,

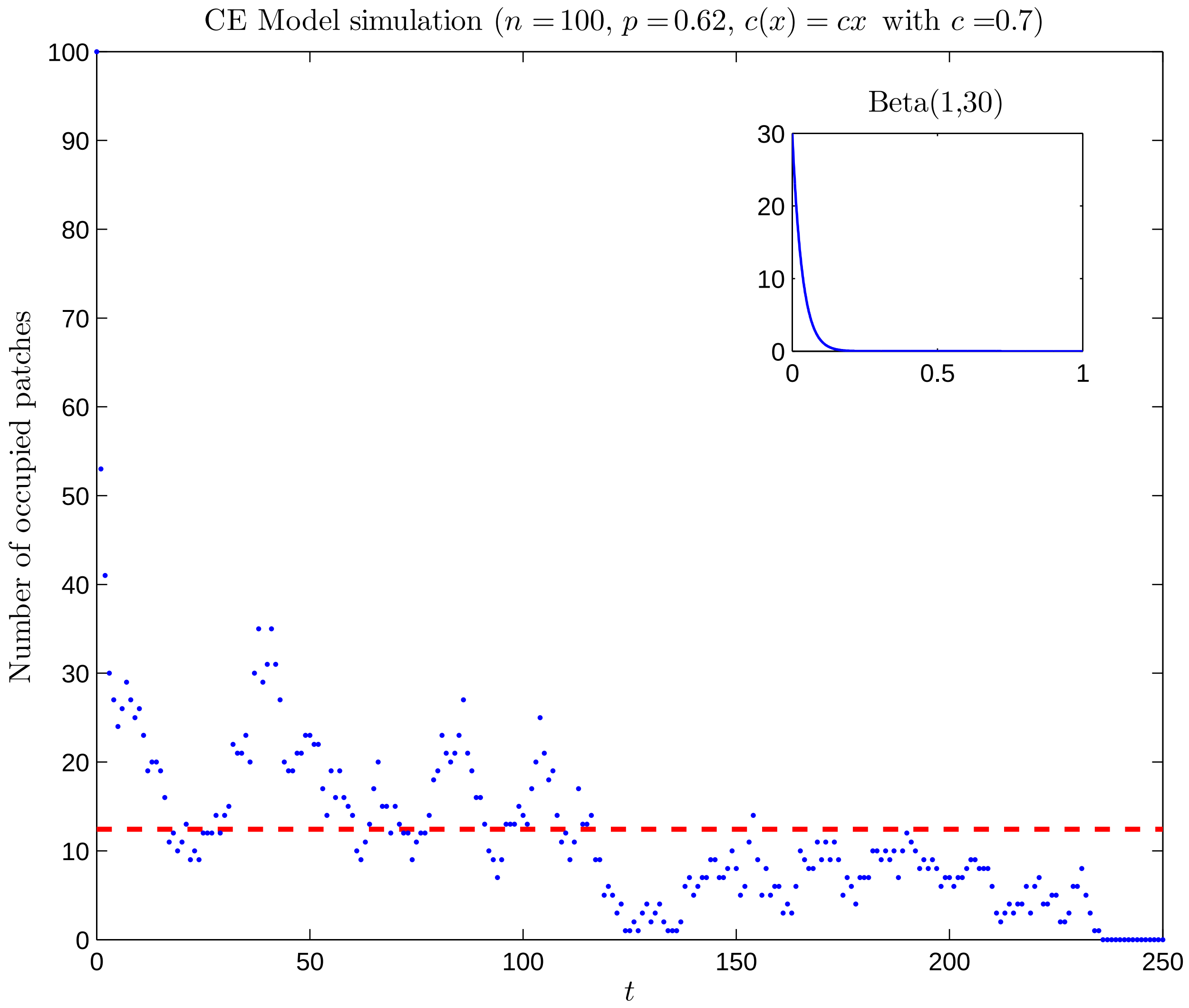
$$\int h(s)\mu_{t+1}(ds) = c_t \int s \int h(r)P(s,dr)\sigma_t(ds)$$
$$(1-c_t)\int s \int h(r)P(s,dr)\mu_t(ds),$$

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

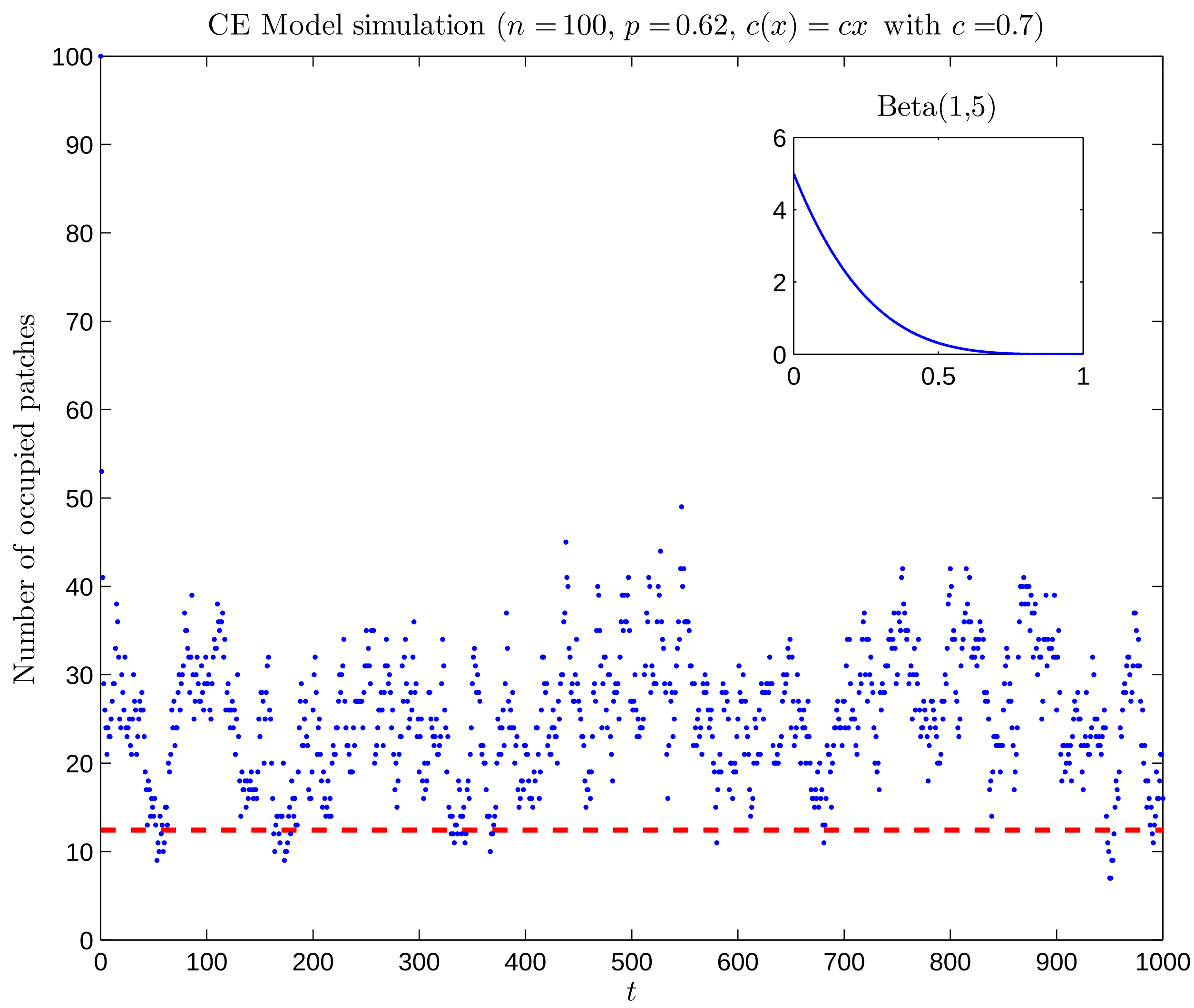
Survival probability simulation



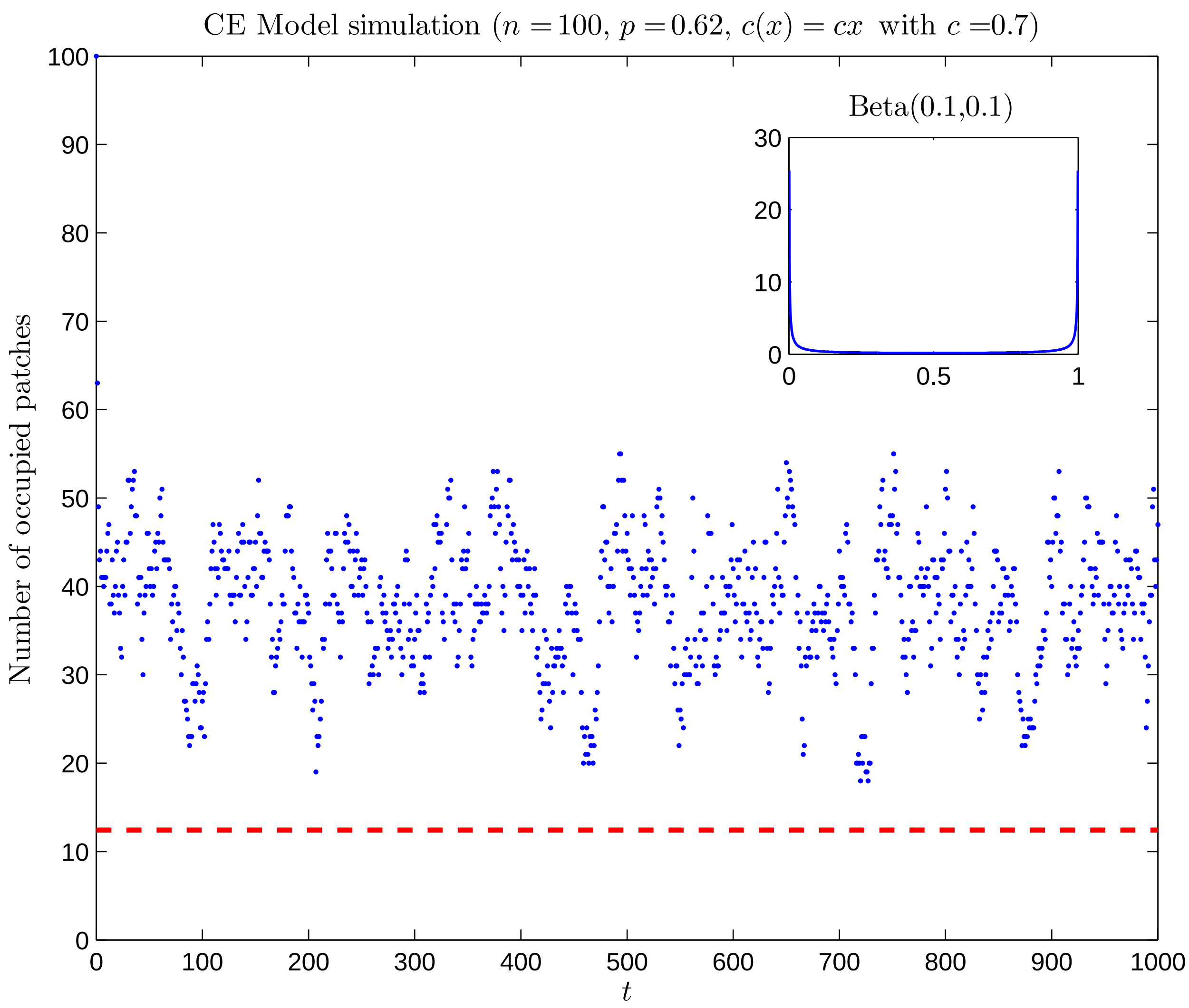
CE Model - Evanescence



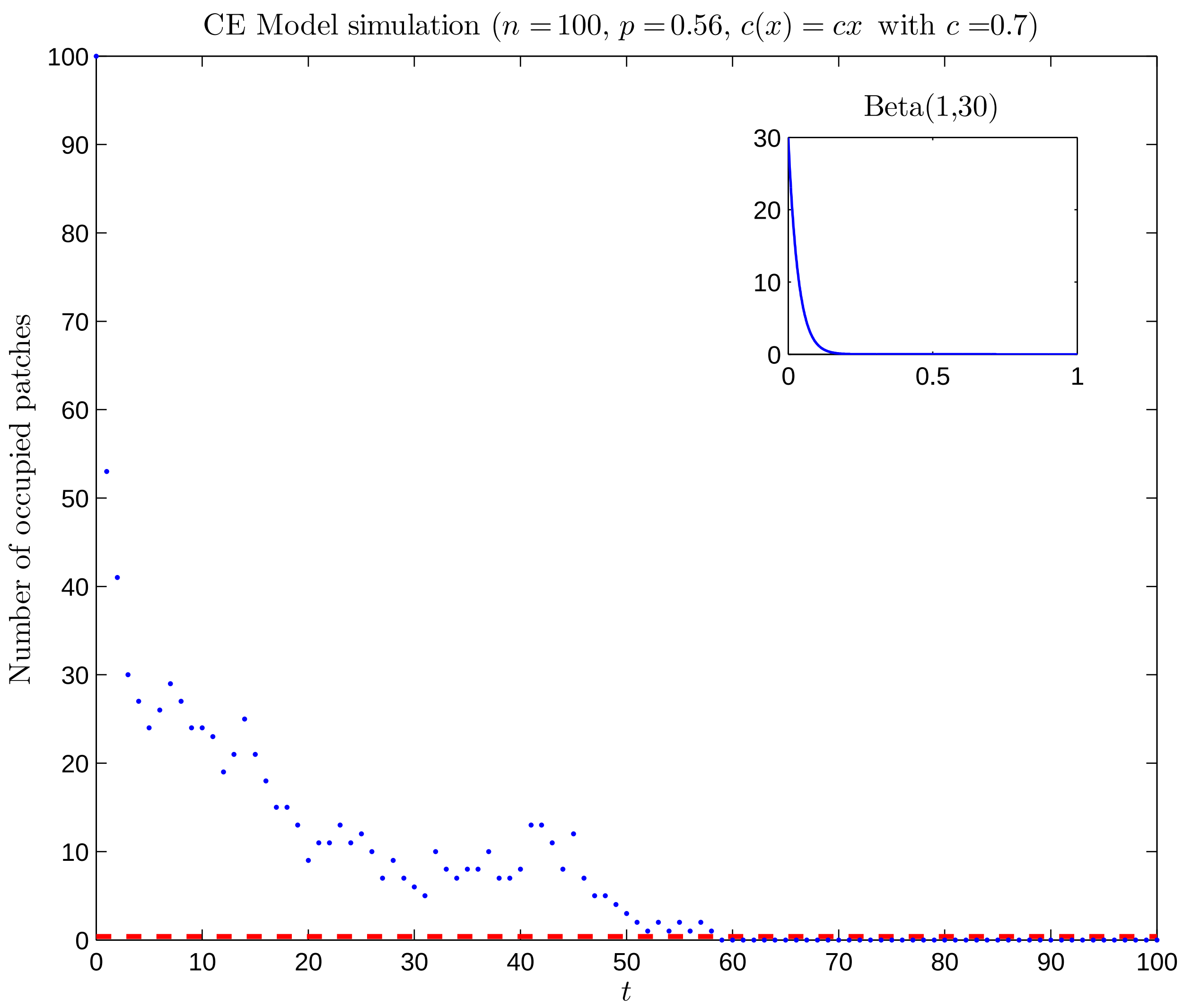
CE Model - Persistence



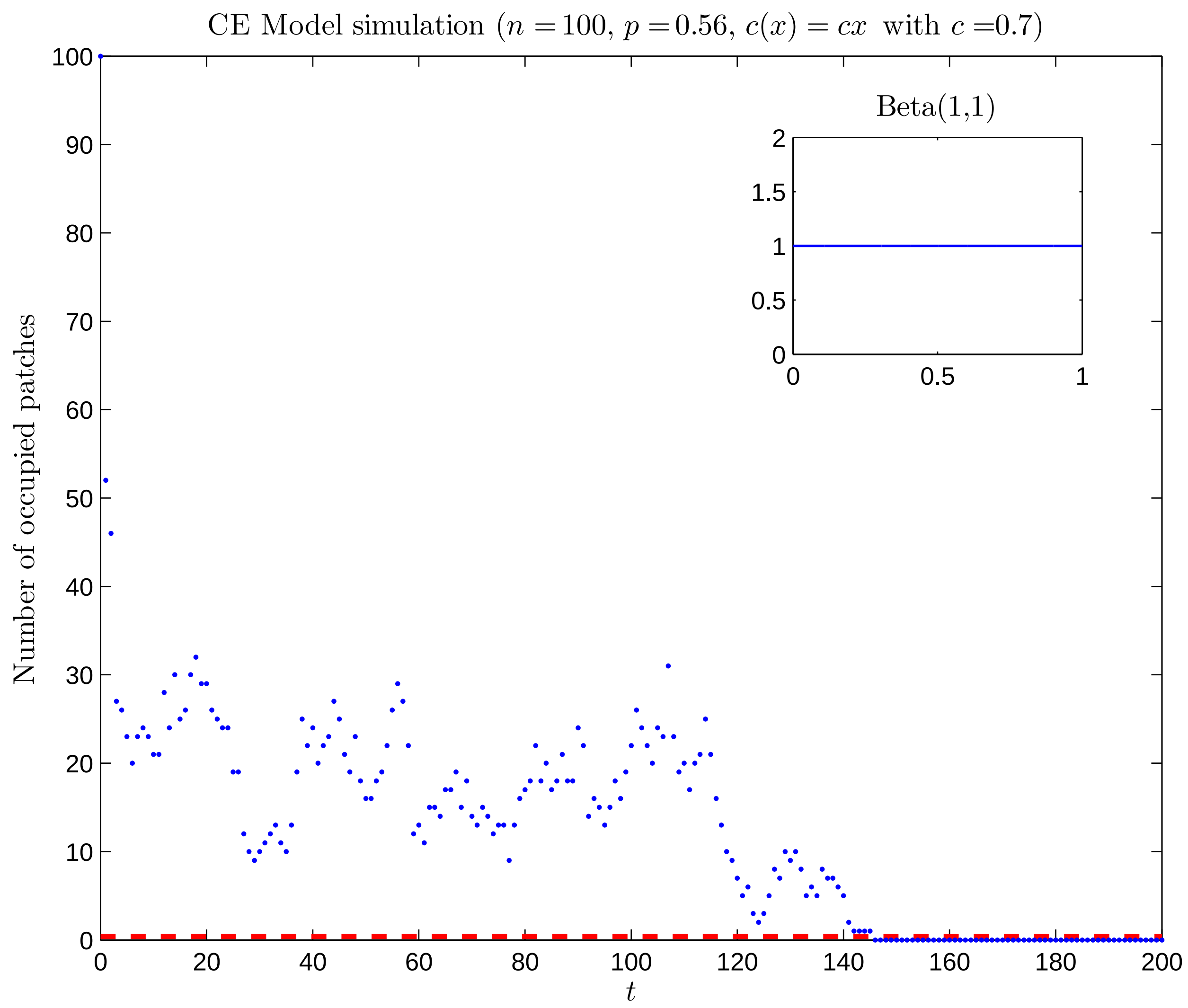
CE Model - Persistence



CE Model - Evanescence



CE Model - Evanescence



CE Model - Persistence