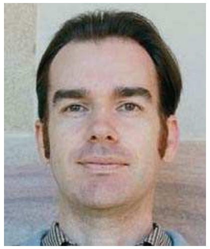
# Metapopulations in dynamic landscapes

Phil Pollett

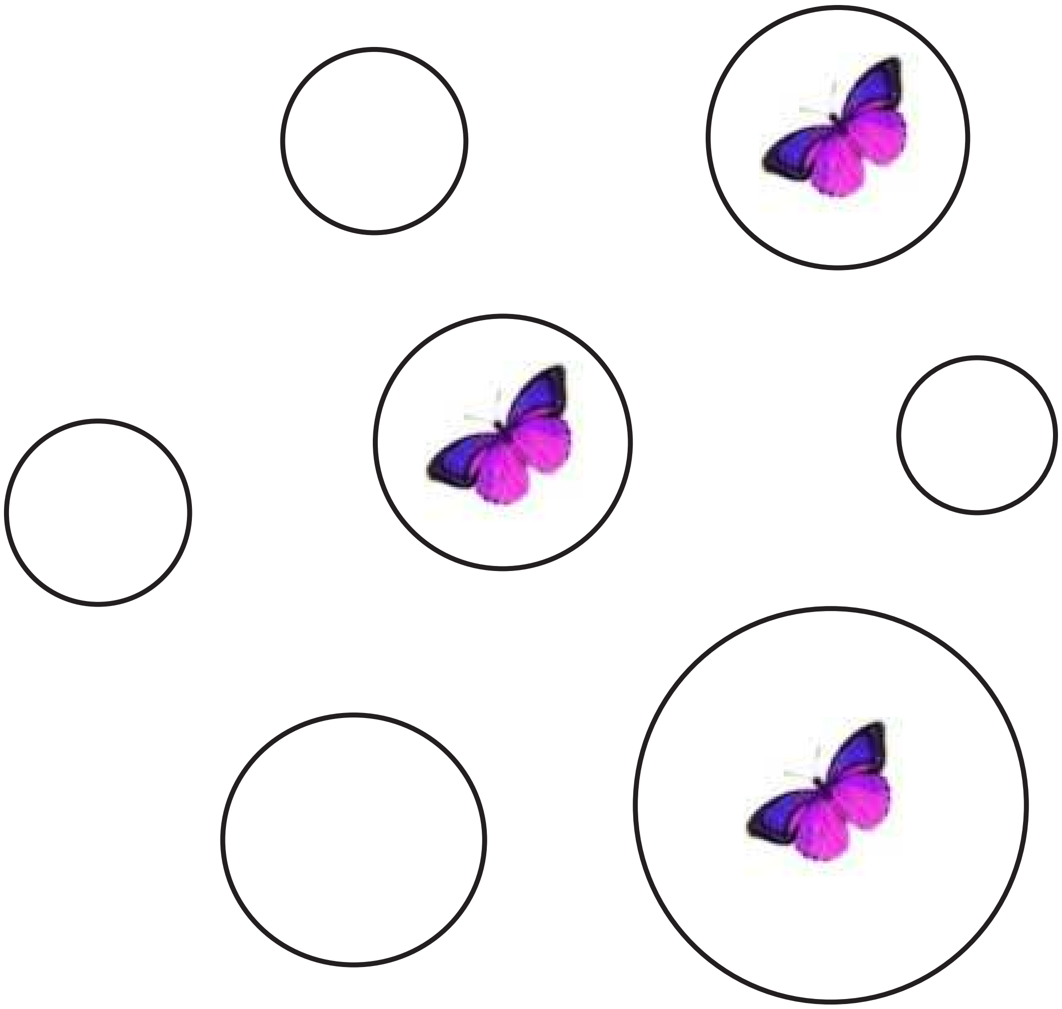
Department of Mathematics
The University of Queensland
http://www.maths.uq.edu.au/~pkp

# Collaborator

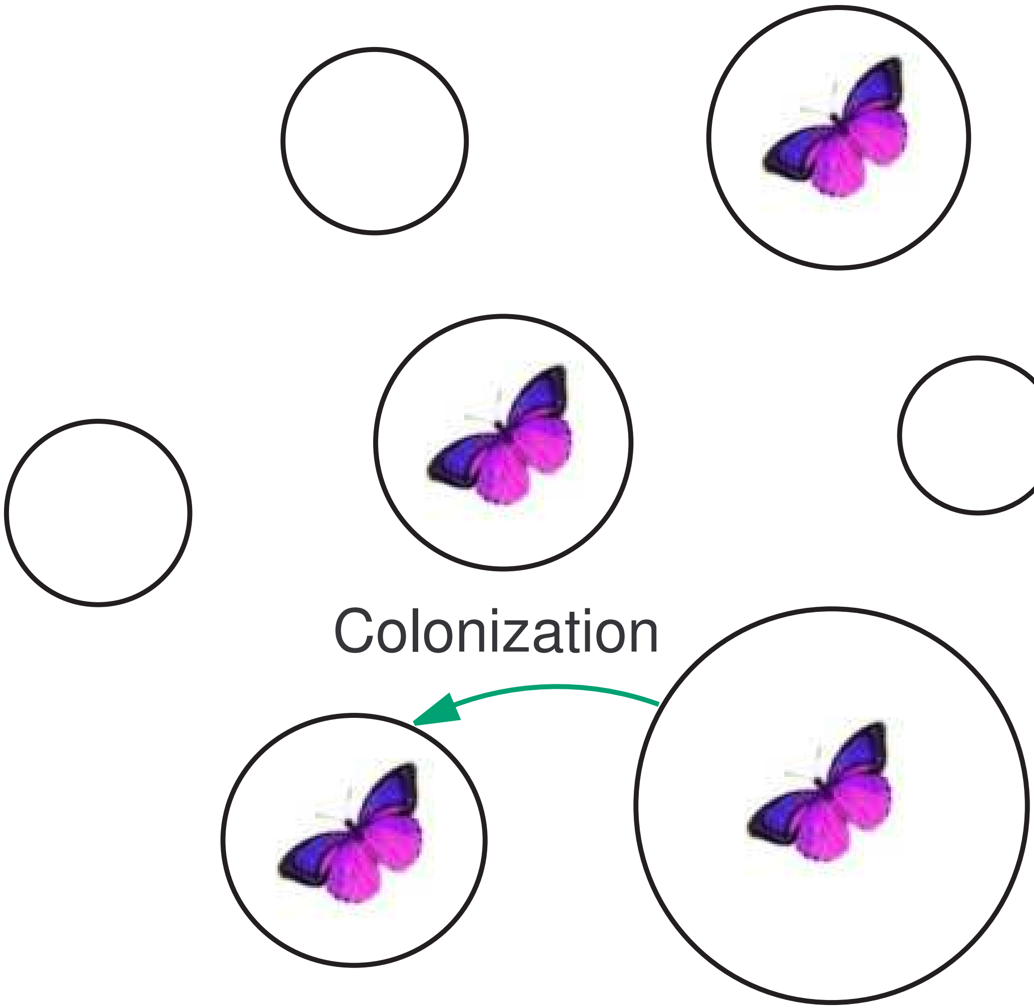
Ross McVinish
Department of Mathematics
University of Queensland



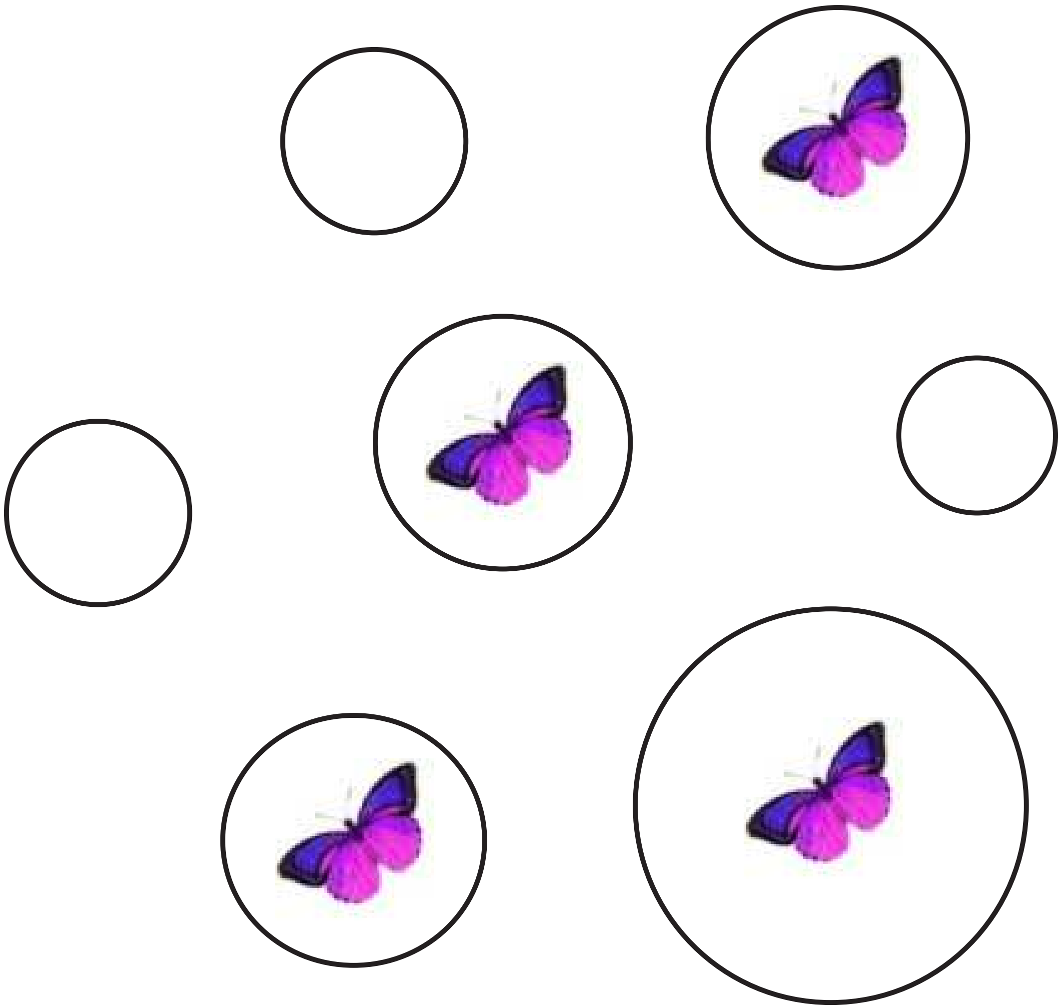
# Metapopulations



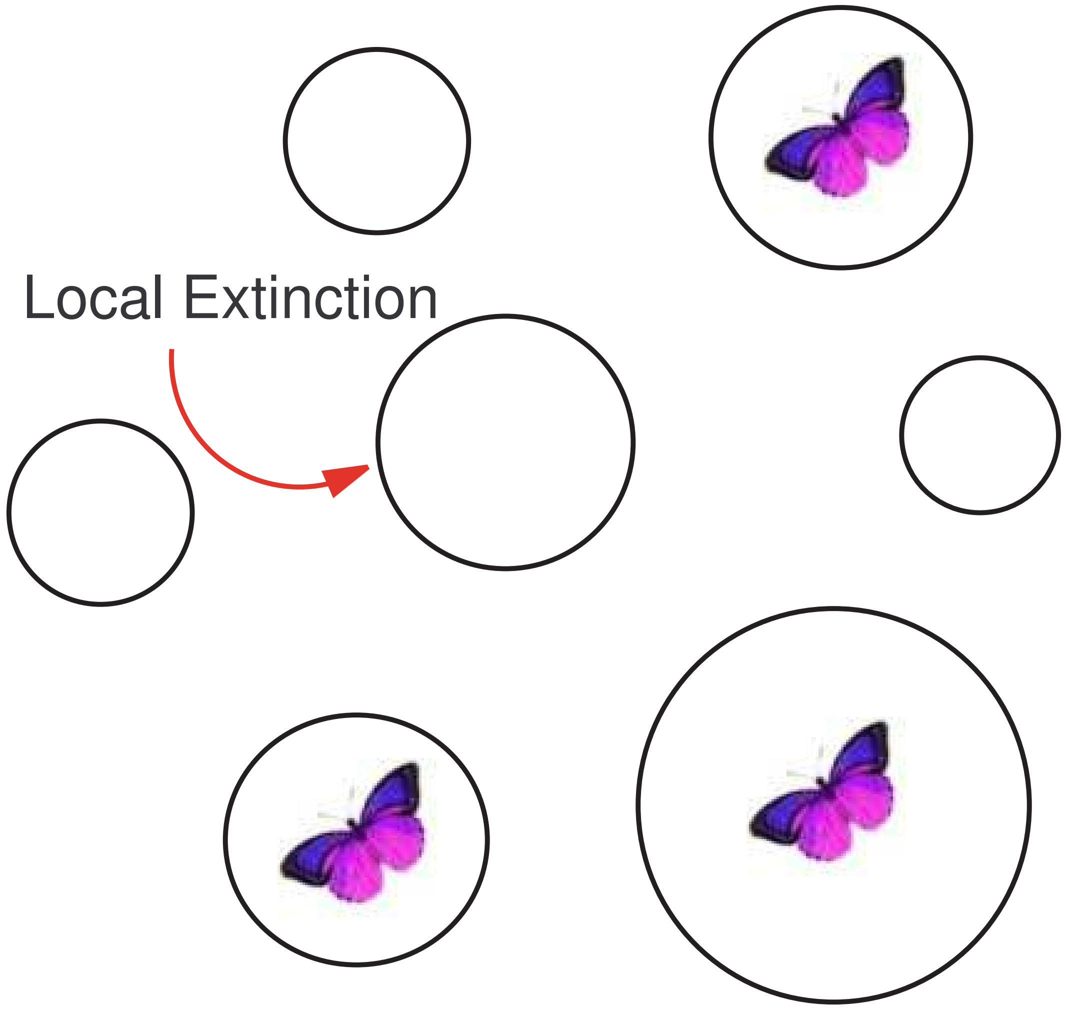
# Metapopulations



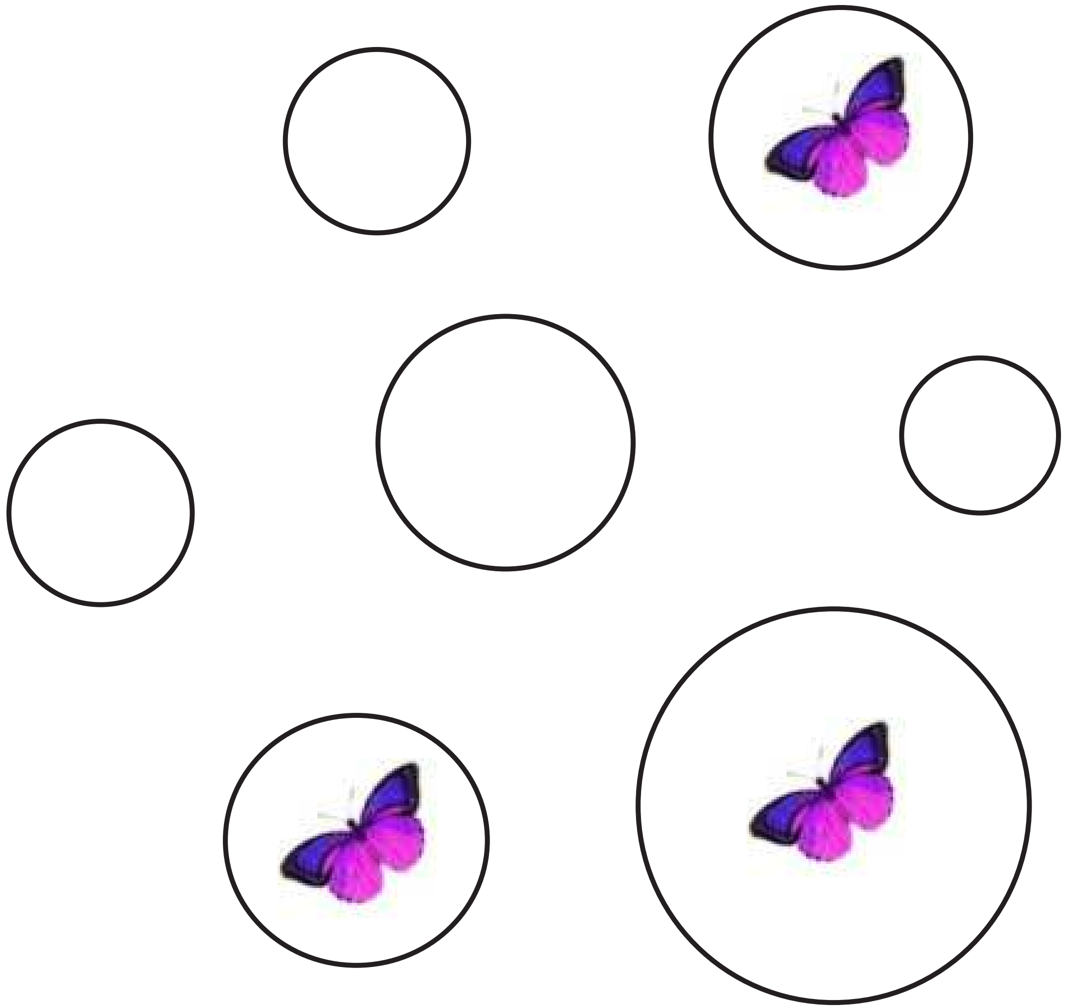
# Metapopulations



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

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

# 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 $t$.

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

Colonization and extinction happen in distinct, successive phases.

# SPOM - Phase structure

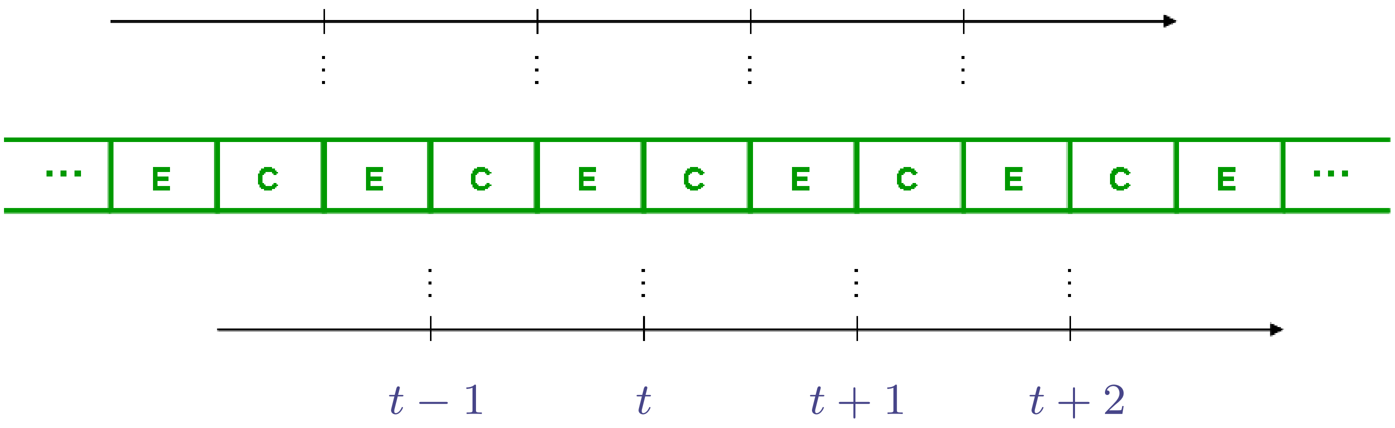
For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle. Examples:

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 independently with probability $s_i$ (fixed or random).

# 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

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

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 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 - example

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

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 - 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]

# 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 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 |

# 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 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 |

# 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 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

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

# 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 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 - 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 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 - 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 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 - 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 1 0 1 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 - 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 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
 .
 .
 .
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
E 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
```

# SPOM

The evolution of the process can be summarized by

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

a "*Chain Bernoulli*" structure.

# 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

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

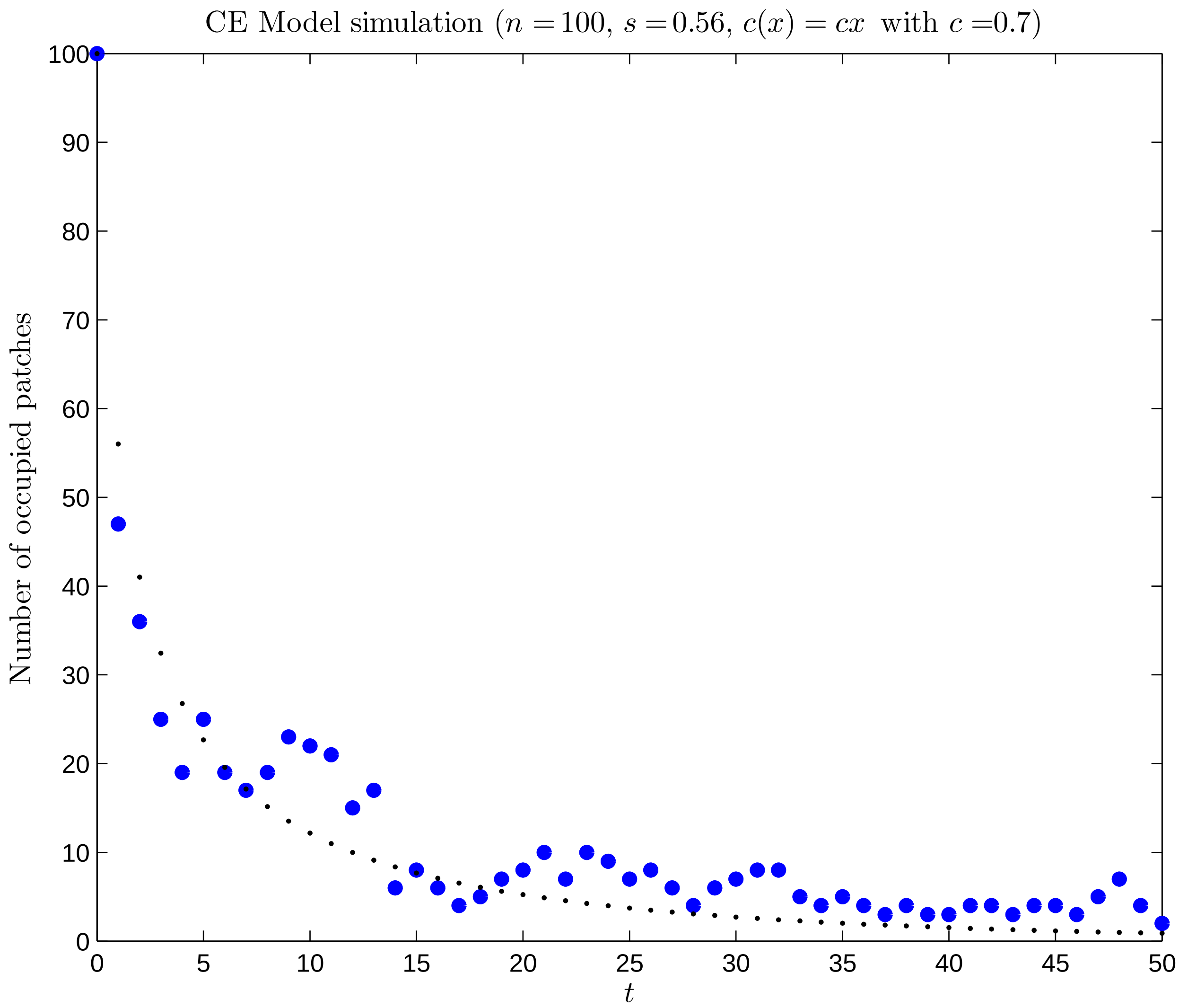
with $(x_t)$ determined by $x_{t+1} = f(x_t)$, where

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

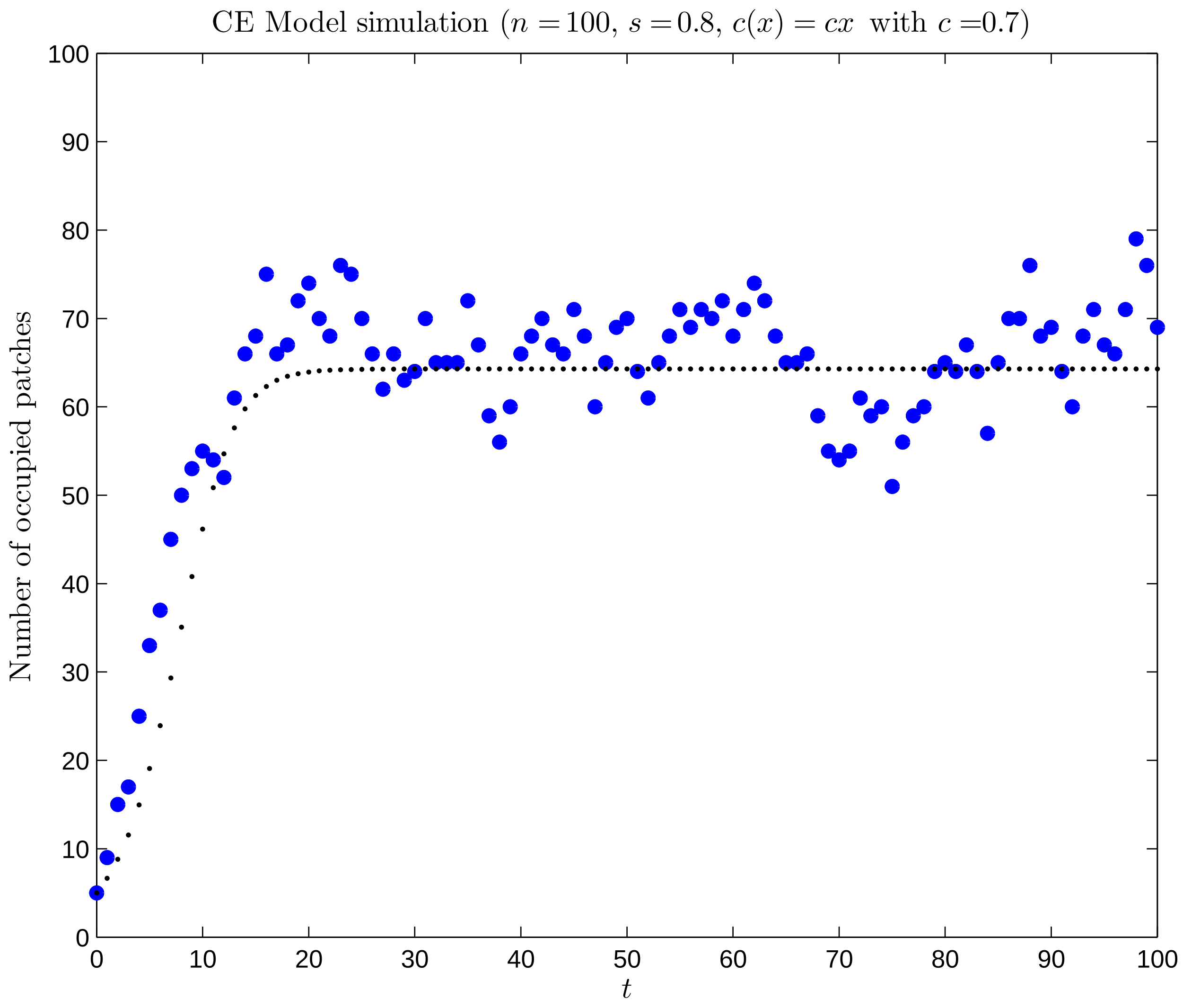
Survival probability

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).

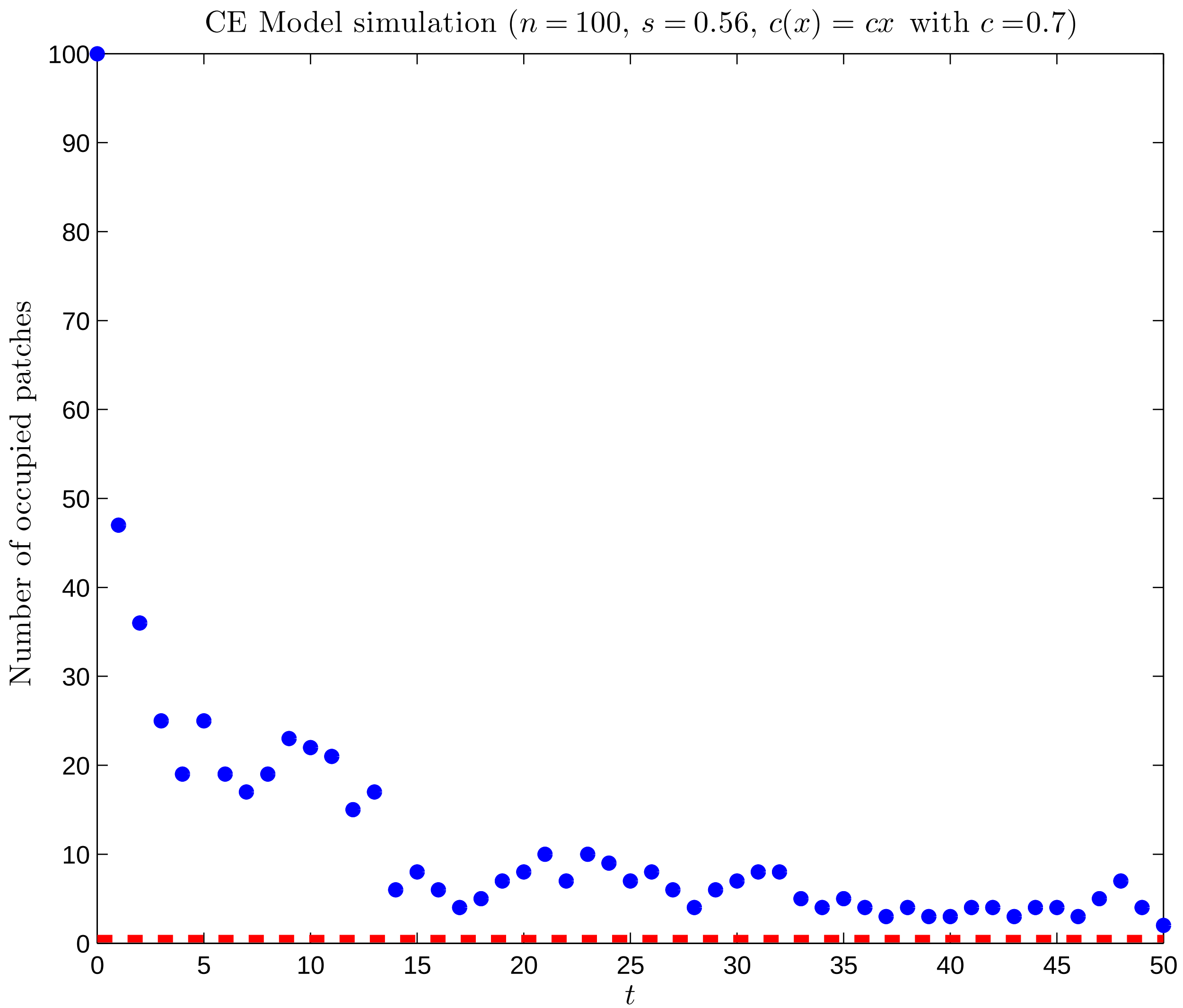
# Stability

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

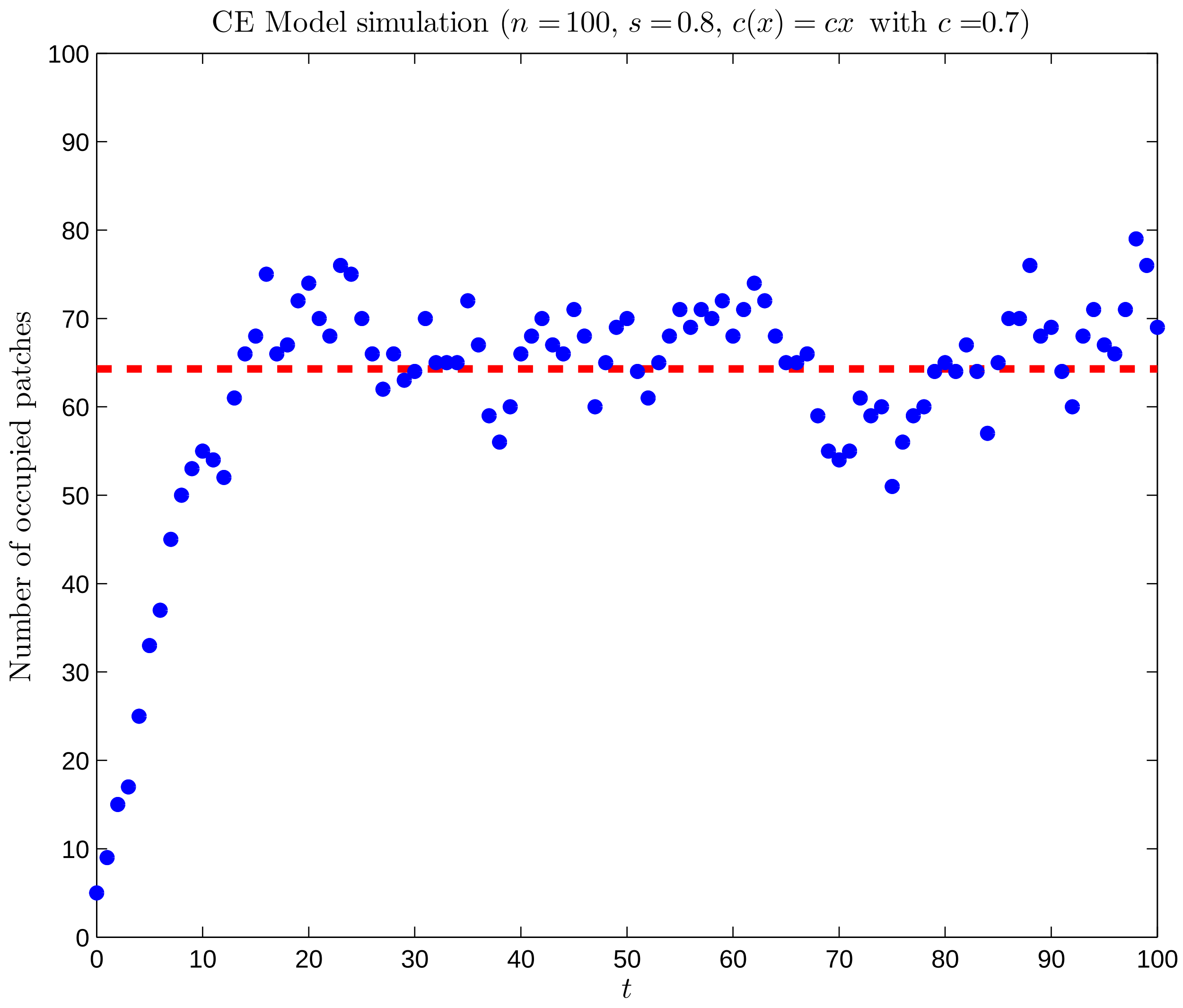
*Evanescence*: $1 + c'(0) \leq 1/s$. $0$ is the unique fixed point in $[0,1]$. It is stable.

*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

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 ...

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

# Our approach - Point Processes

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

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

$$\sigma_n(B) = \#\{s_i \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

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

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

$$\sigma_n(B) = \#\{s_i \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

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

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

$$\sigma_n(B) = \#\{s_i \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

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

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

$$\sigma_n(B) = \#\{s_i \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

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

We are going to suppose that $\sigma_n \xrightarrow{d} \sigma$ for some non-random (probability) measure $\sigma$.

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

$$\sigma_n(B) = \#\{s_i \in B\}/n, \qquad B \in \mathcal{B}([0,1]),$$

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

We are going to suppose that $\sigma_n \stackrel{d}{\to} \sigma$ for some non-random (probability) measure $\sigma$.

Think of $\sigma$ as being the distribution of survival probabilities. In the earlier simulation $\sigma$ was a Beta$(25.2,\ 19.8)$ distribution.

# Our approach - Point Processes

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 $[0,\infty)$.

# Our approach - Point Processes

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 $[0,\infty)$. For example $(h \equiv 1)$,

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

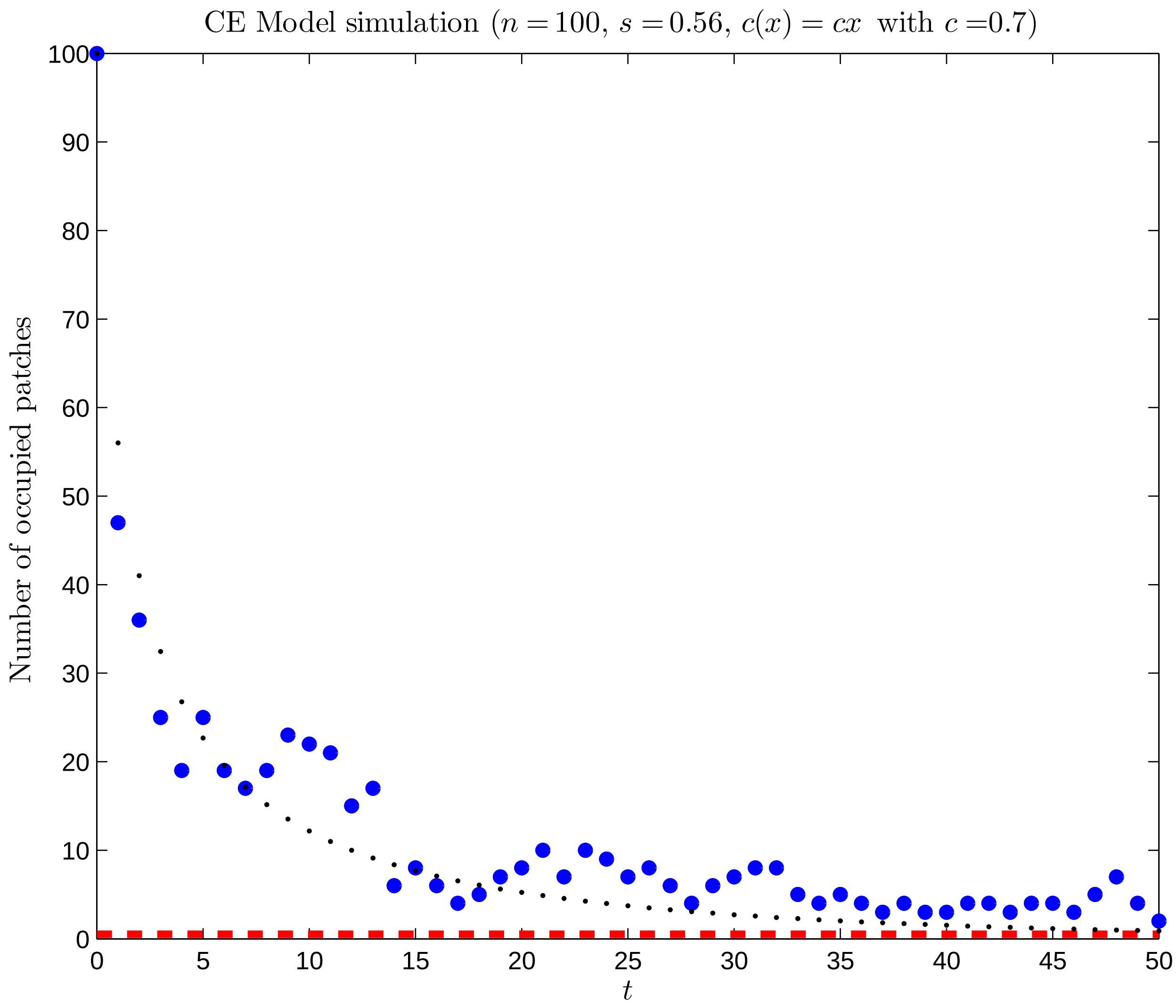
# A measure-valued difference equation

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

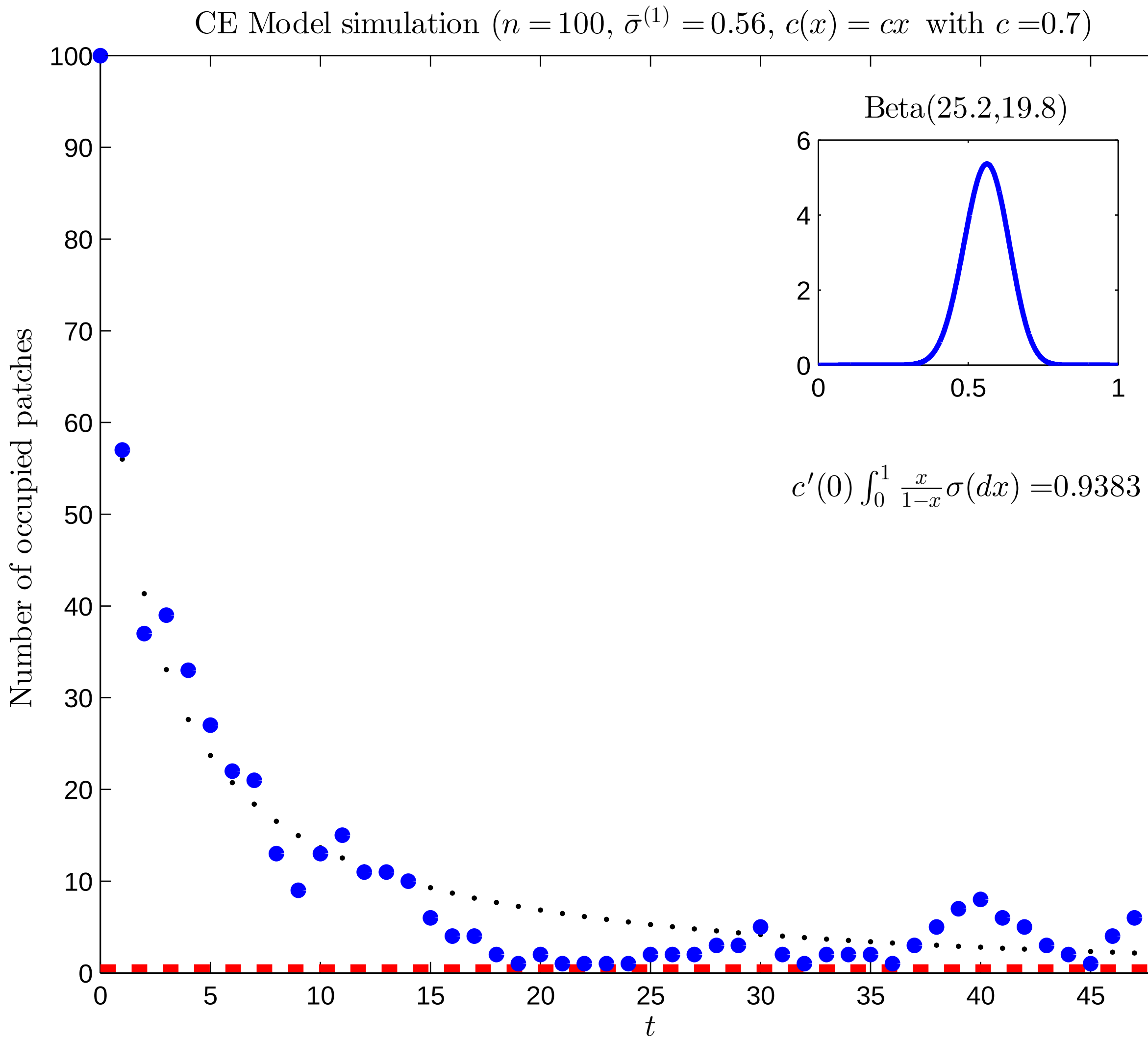
$$\int h(s)\mu_{t+1}(ds) = (1 - c_t) \int sh(s)\mu_t(ds) + c_t \int sh(s)\sigma(ds),$$

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

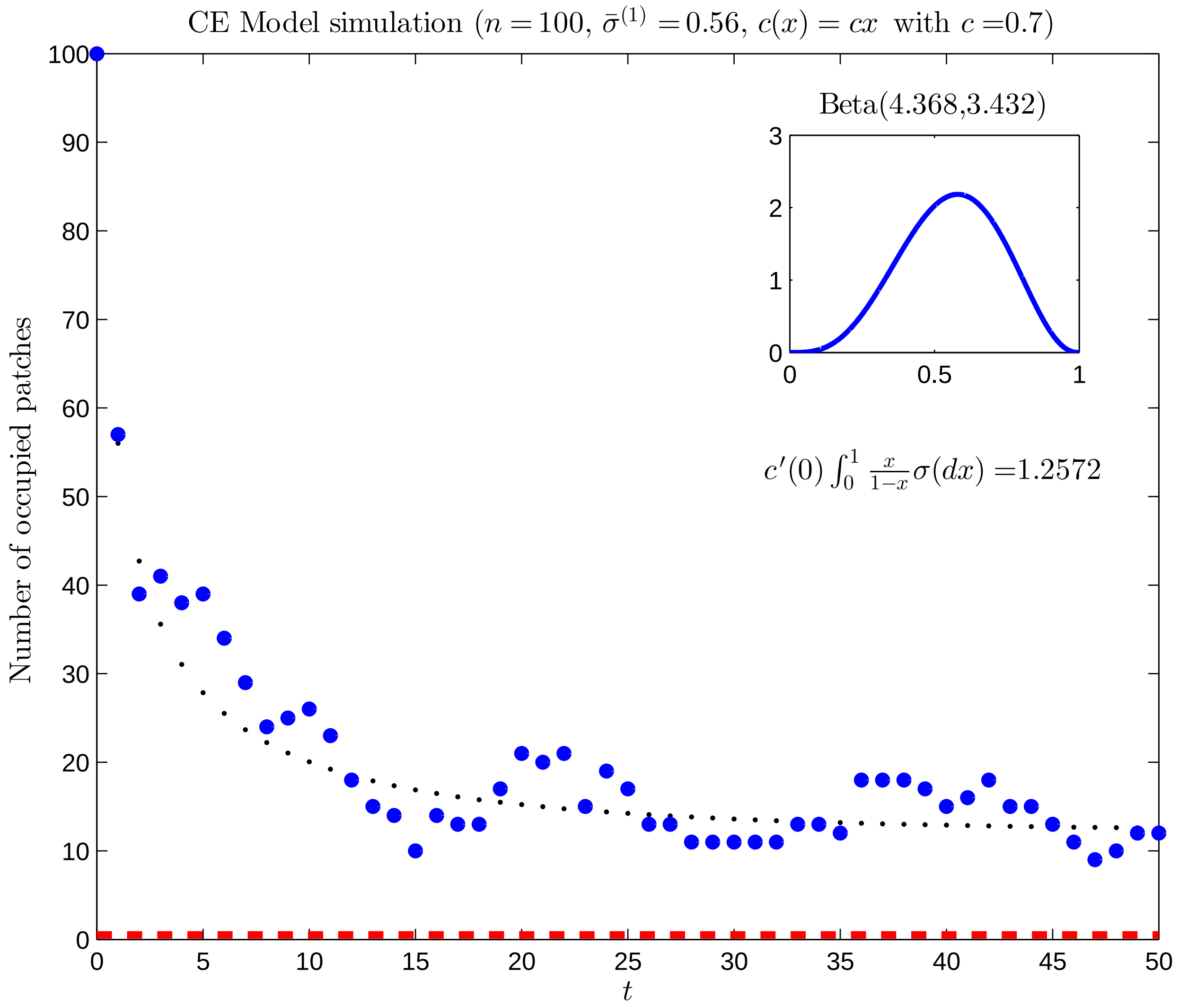
# CE Model (homogeneous) - Evanescence



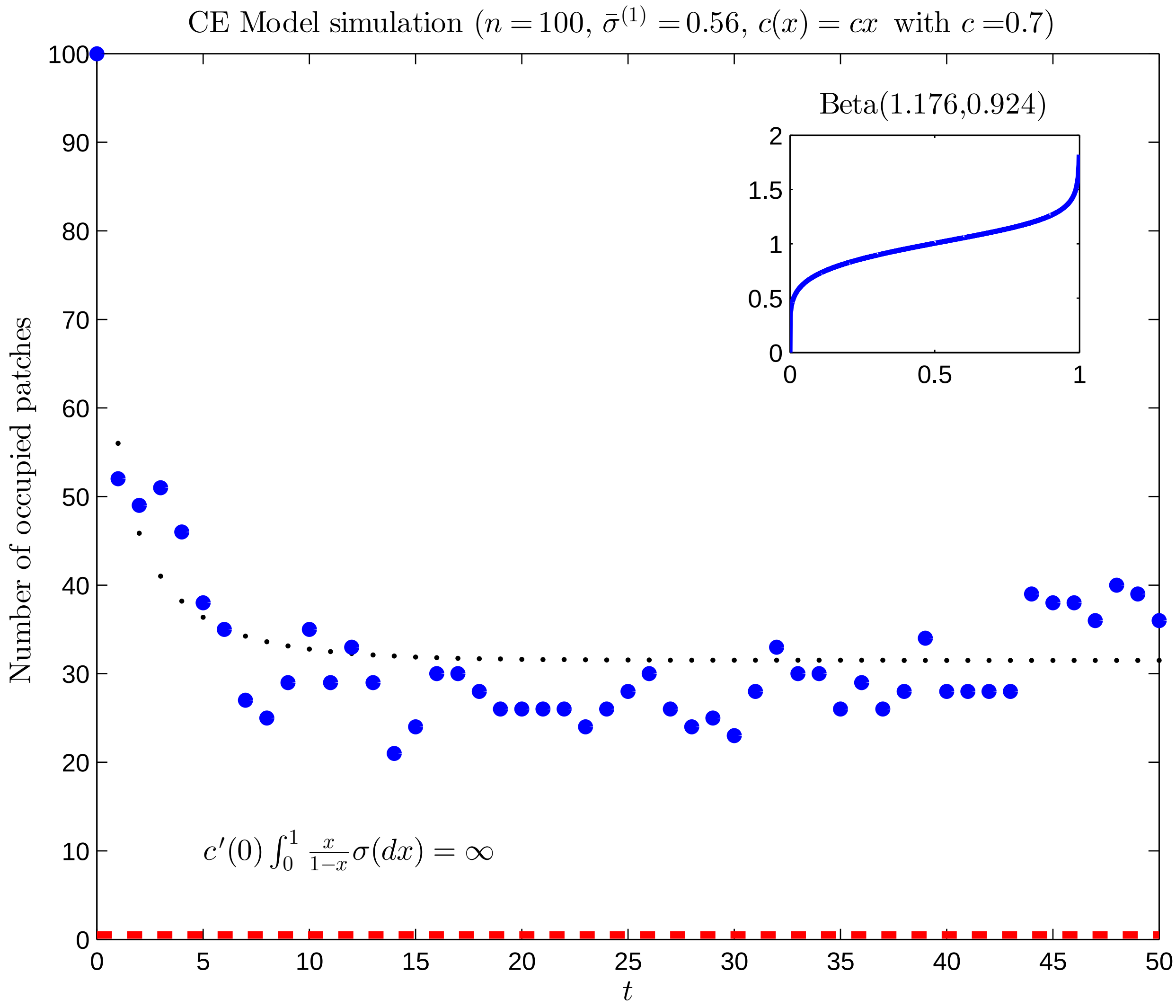
# CE Model - Evanescence



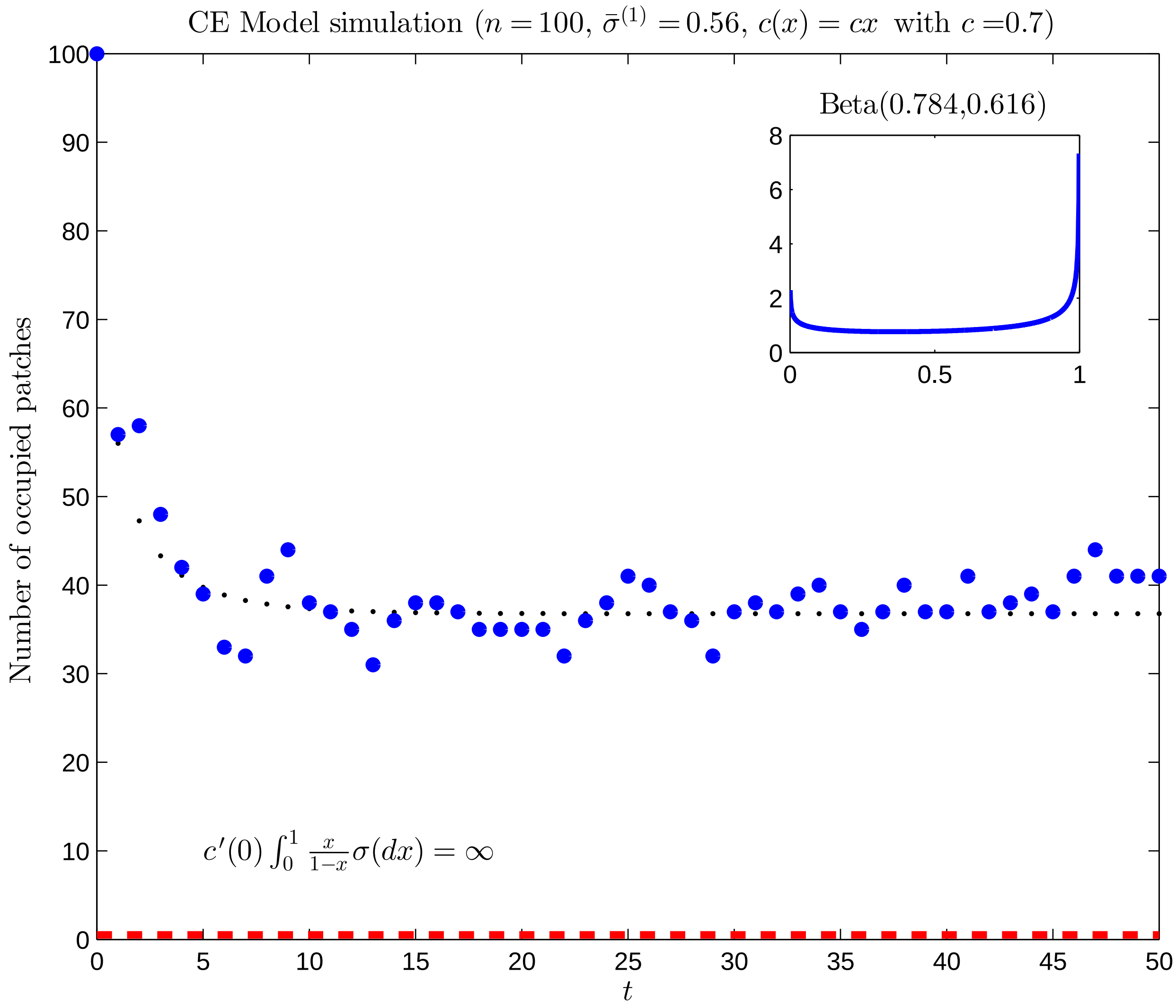
# CE Model - Quasi stationarity



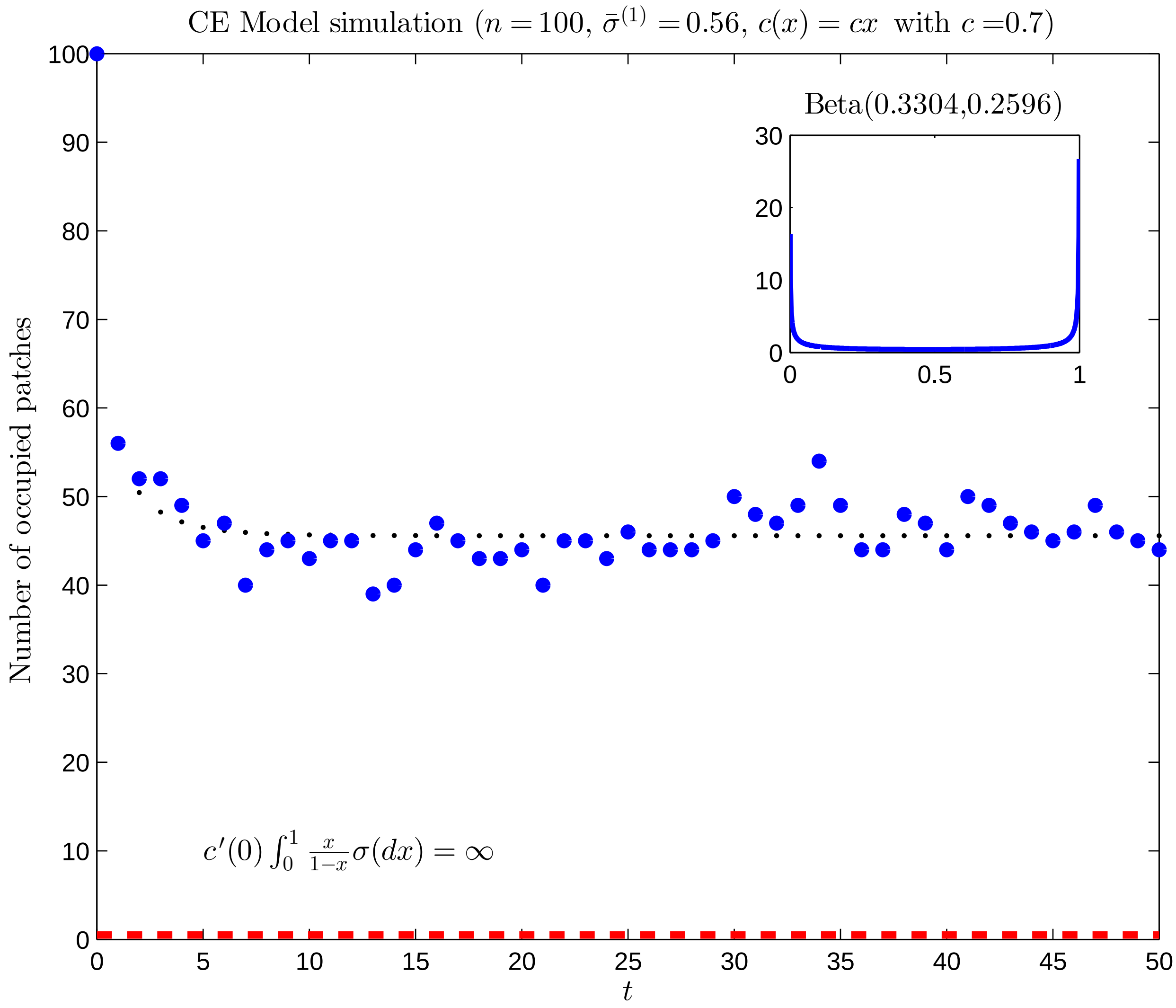
# CE Model - Quasi stationarity



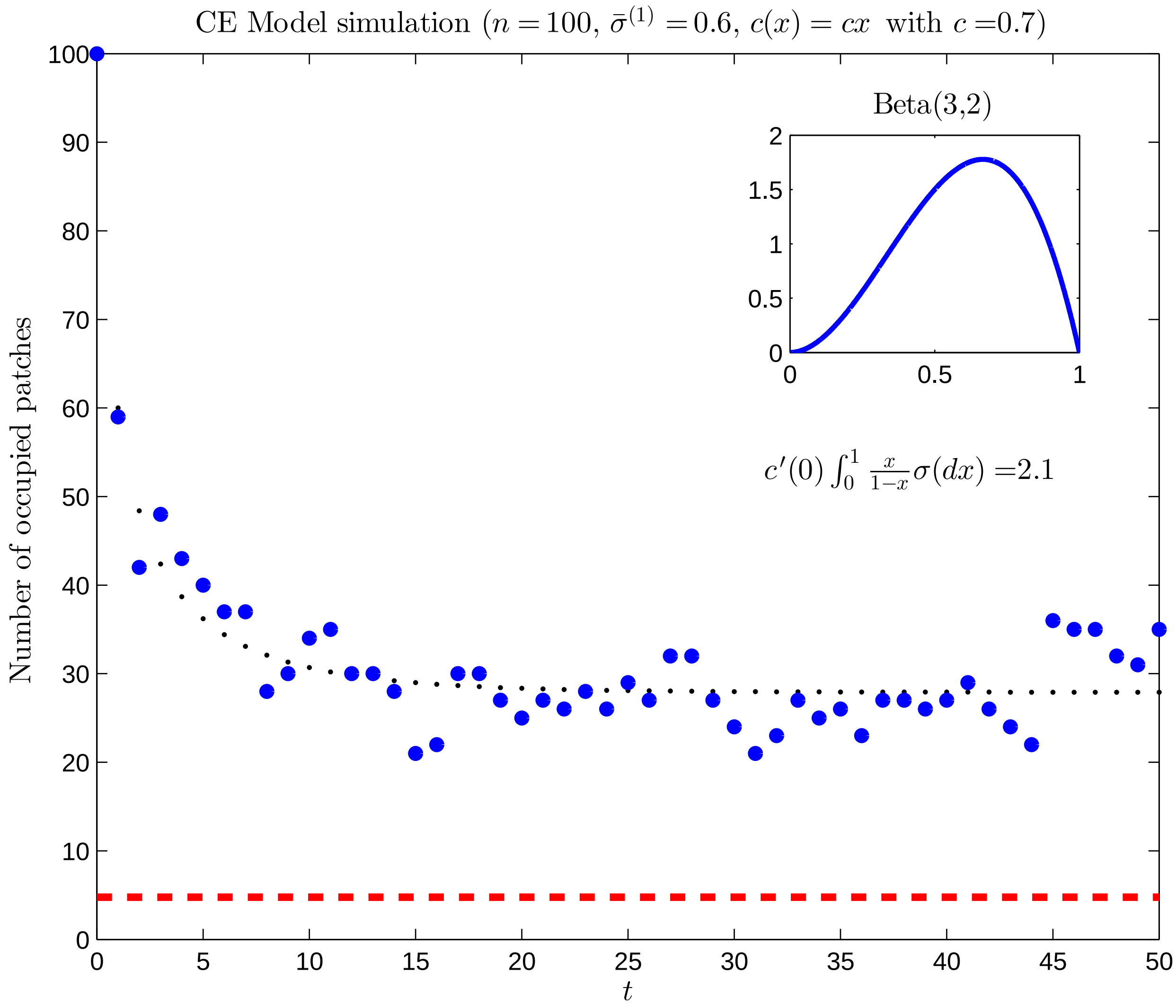
# CE Model - Quasi stationarity



# CE Model - Quasi stationarity



# CE Model - Quasi stationarity



# Extra - equilibria

Our recursion is

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

# Extra - equilibria

Our recursion is

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

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

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

# Extra - equilibria

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

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

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

# Extra - equilibria

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

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

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

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

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 $j$, $\mu_t \to \mu_\infty$.