Limit theorems for chain-binomial population models

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AUSTRALIAN RESEARCH COUNCIL
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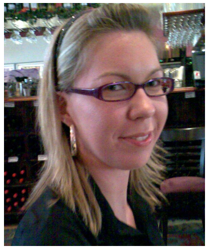

*Buckley, F.M. and Pollett, P.K. (2010) Limit theorems for discrete-time metapopulation models. Probability Surveys 7, 53-83.

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Ross McVinish
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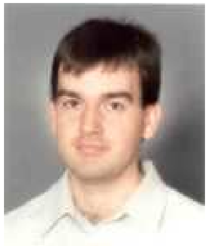
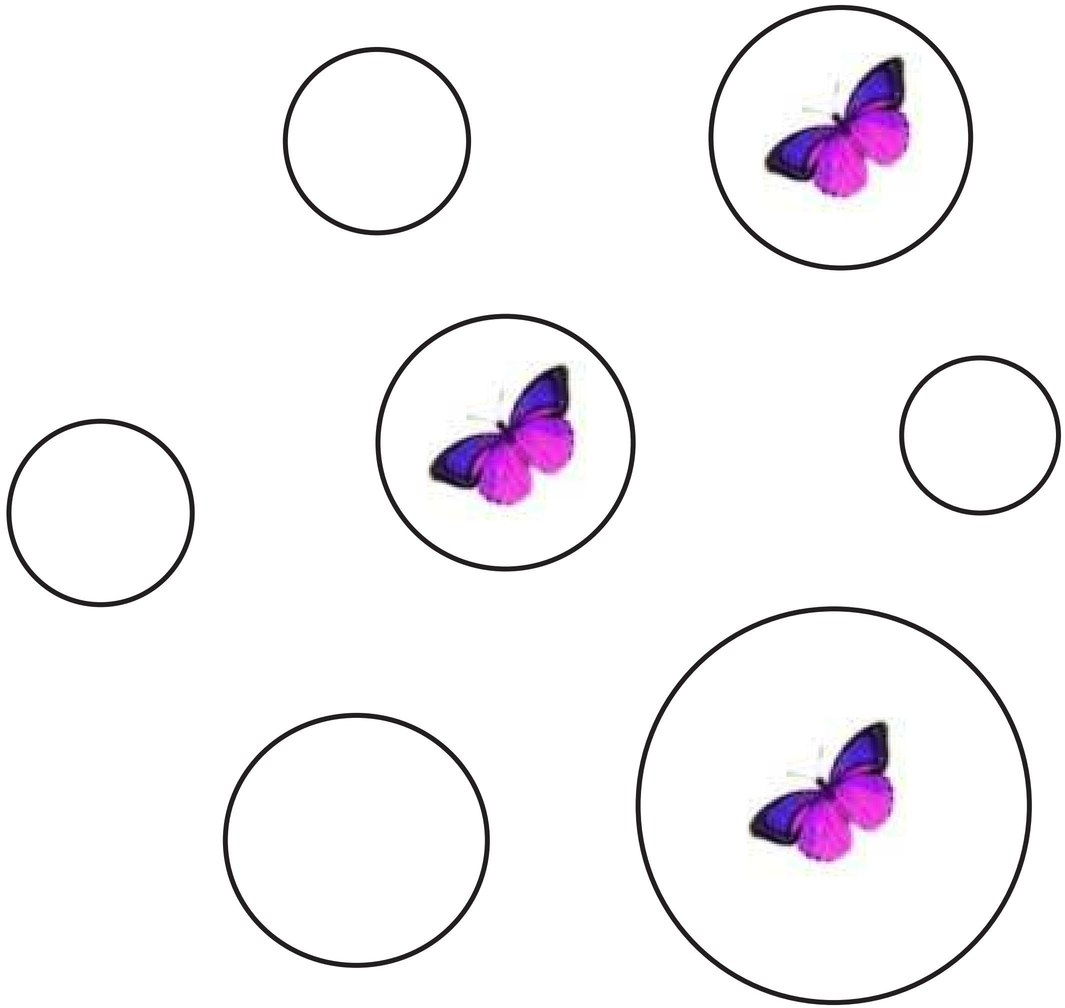


*McVinish, R. and Pollett, P.K. (2010) Limits of large metapopulations with patch dependent extinction probabilities. Advances in Applied Probability 42, 1172-1186.

Metapopulations



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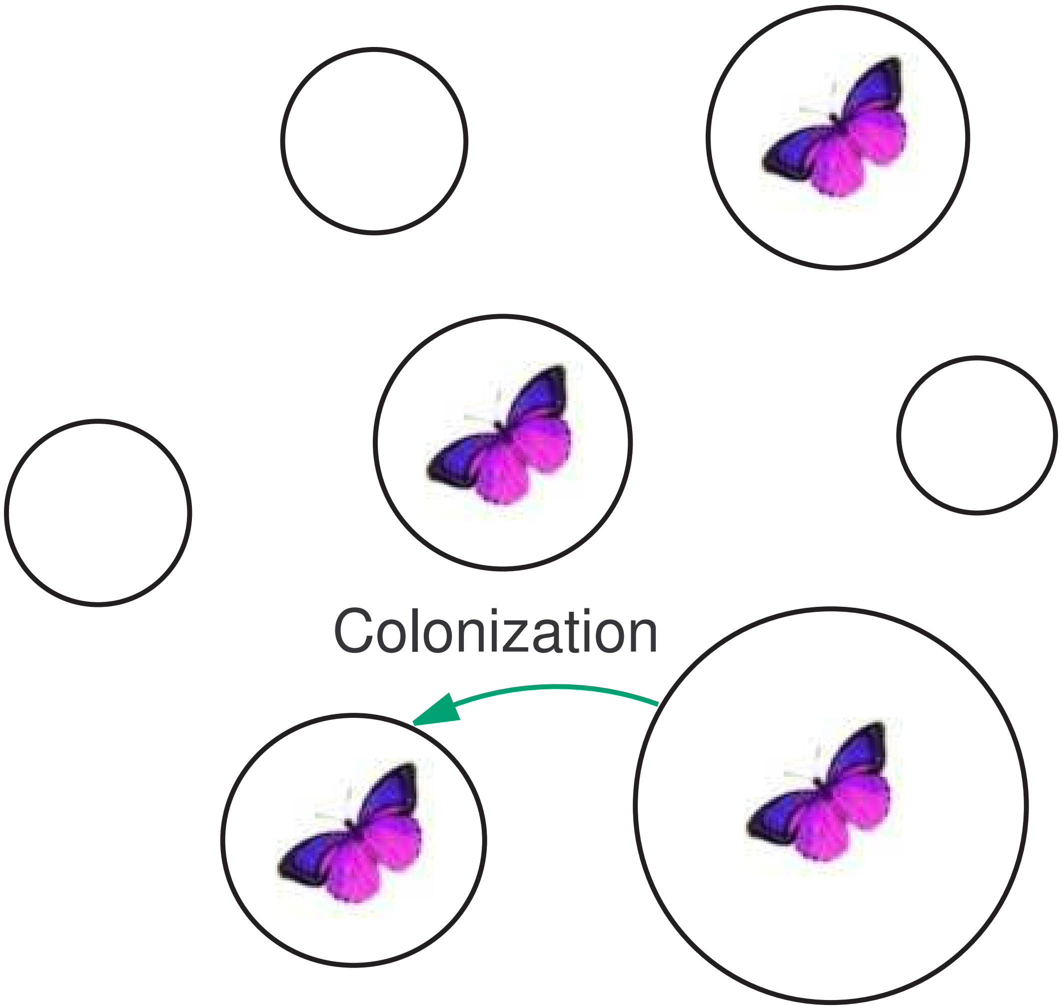

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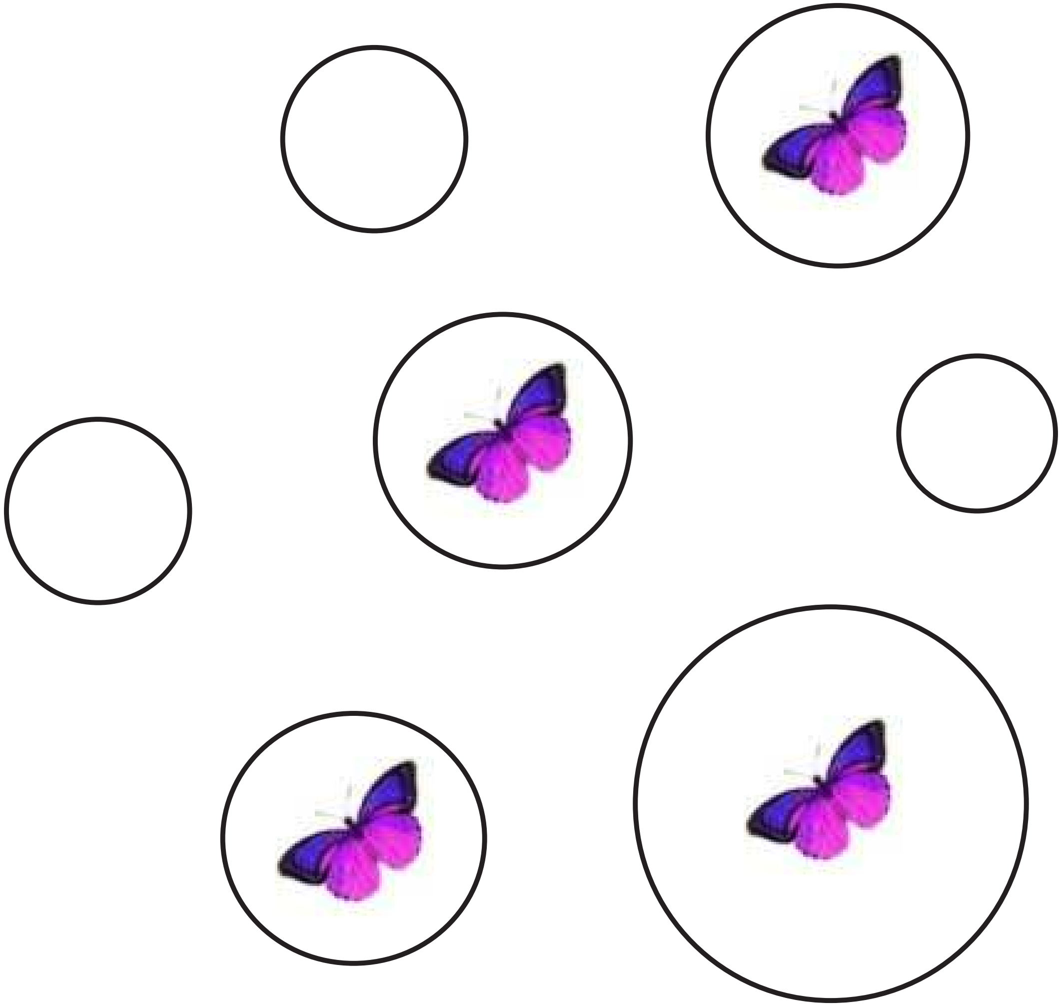

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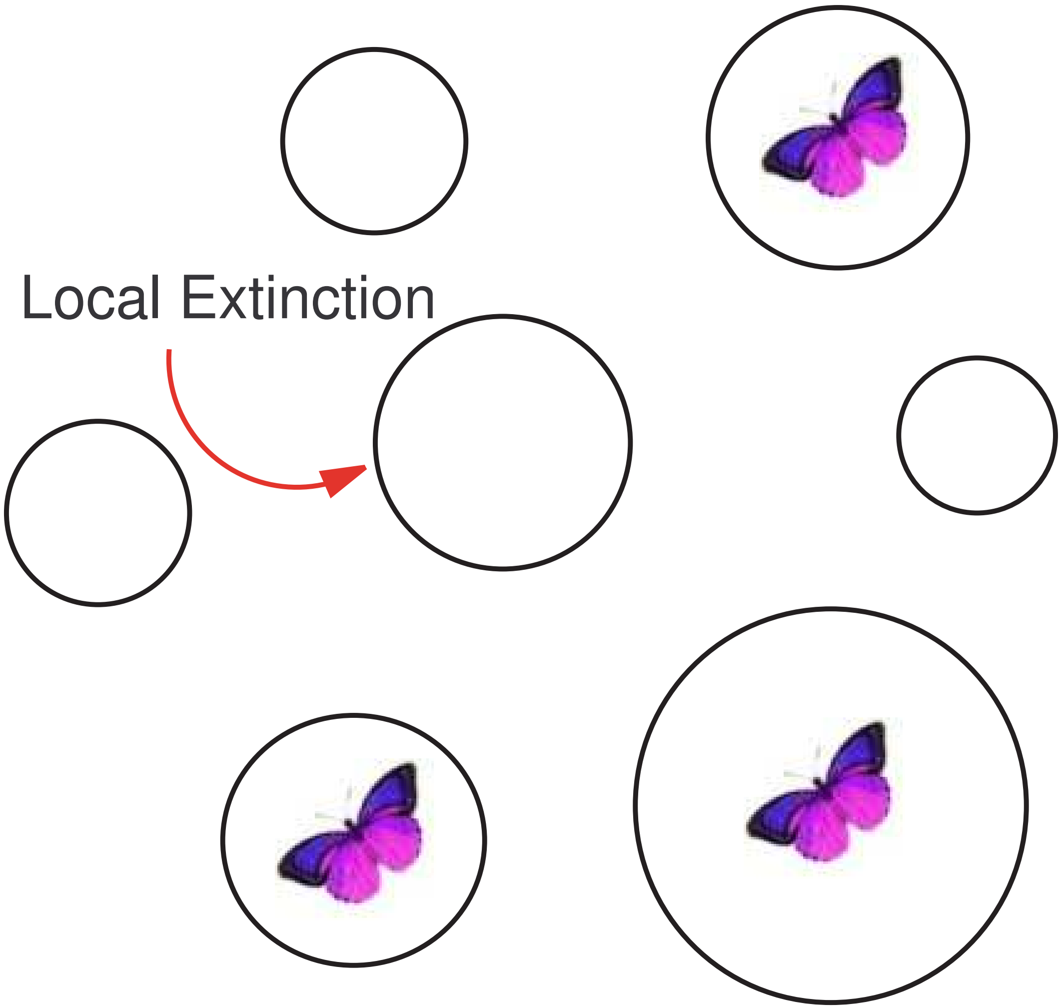

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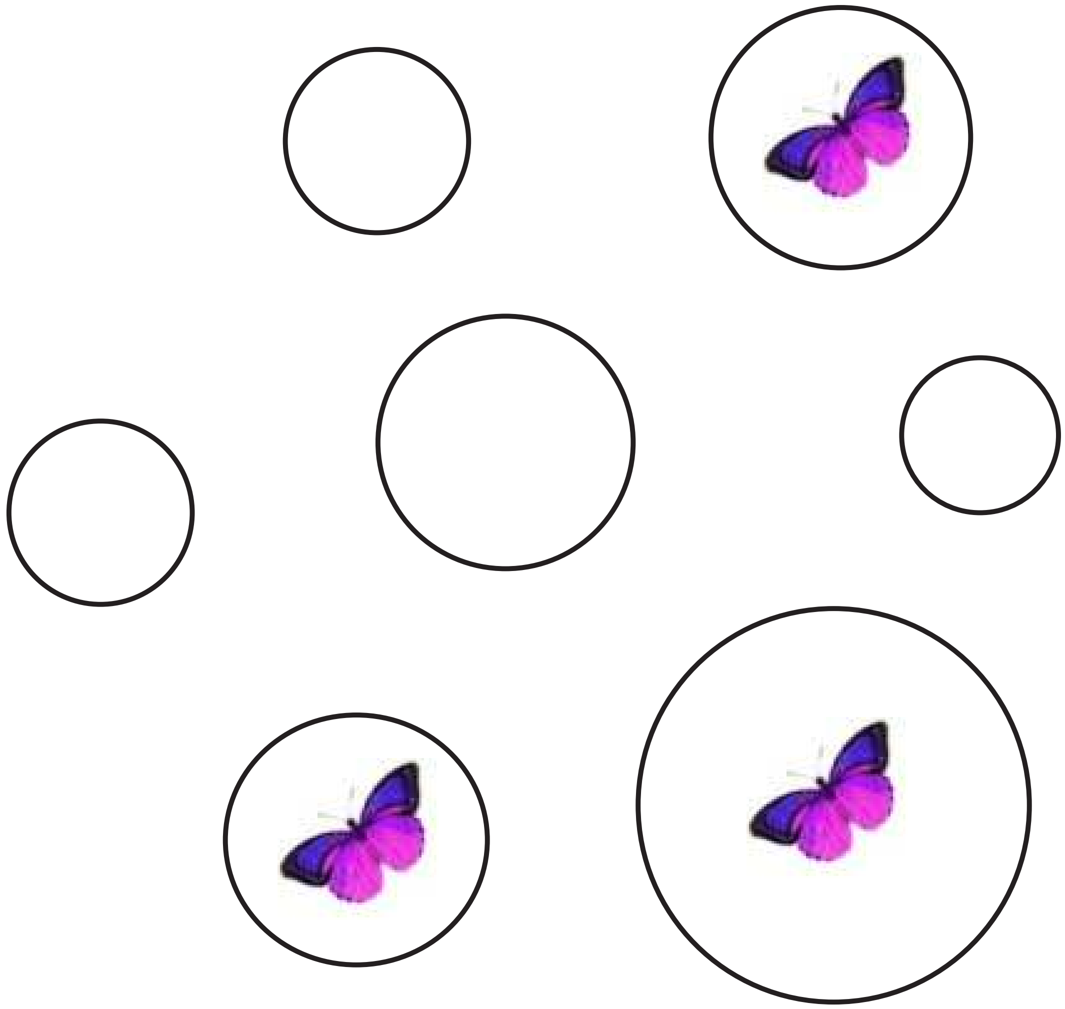

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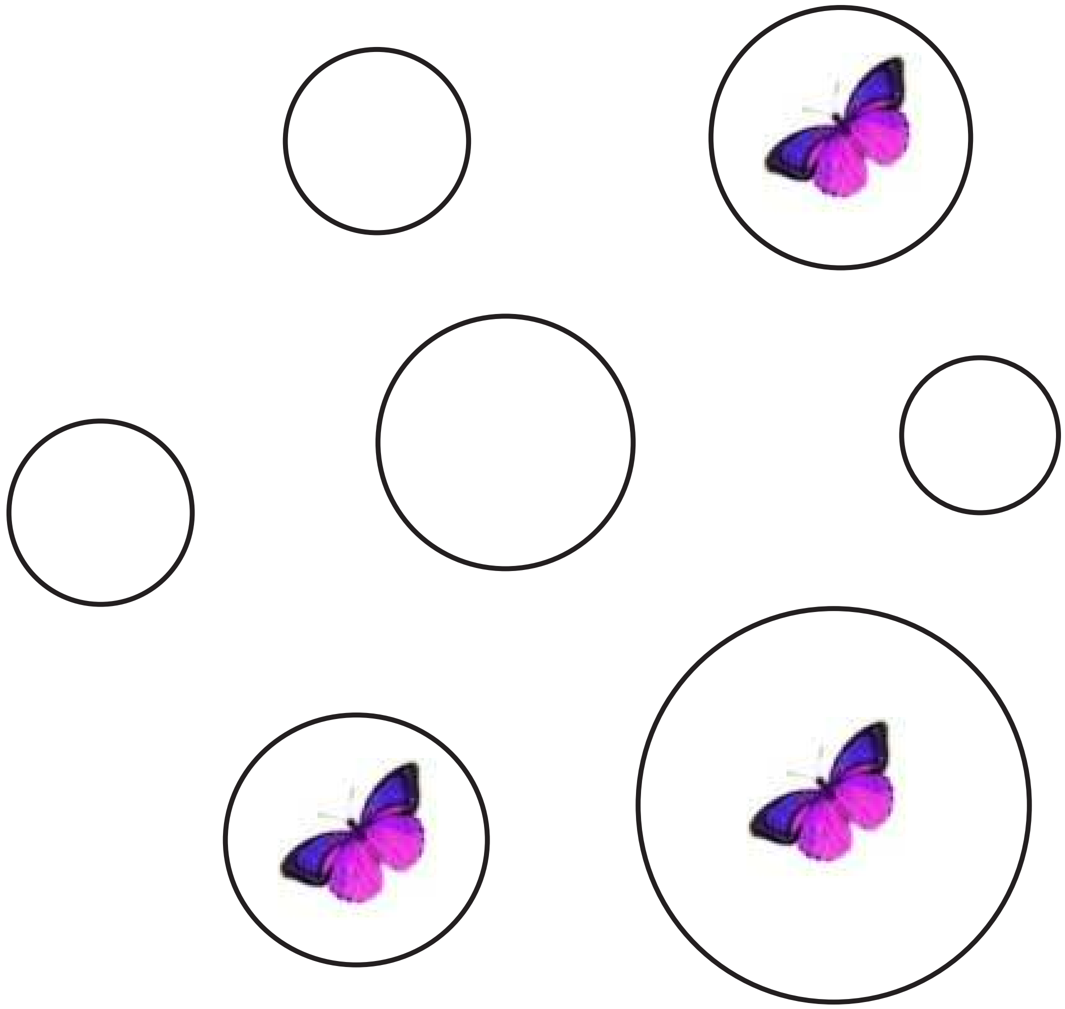

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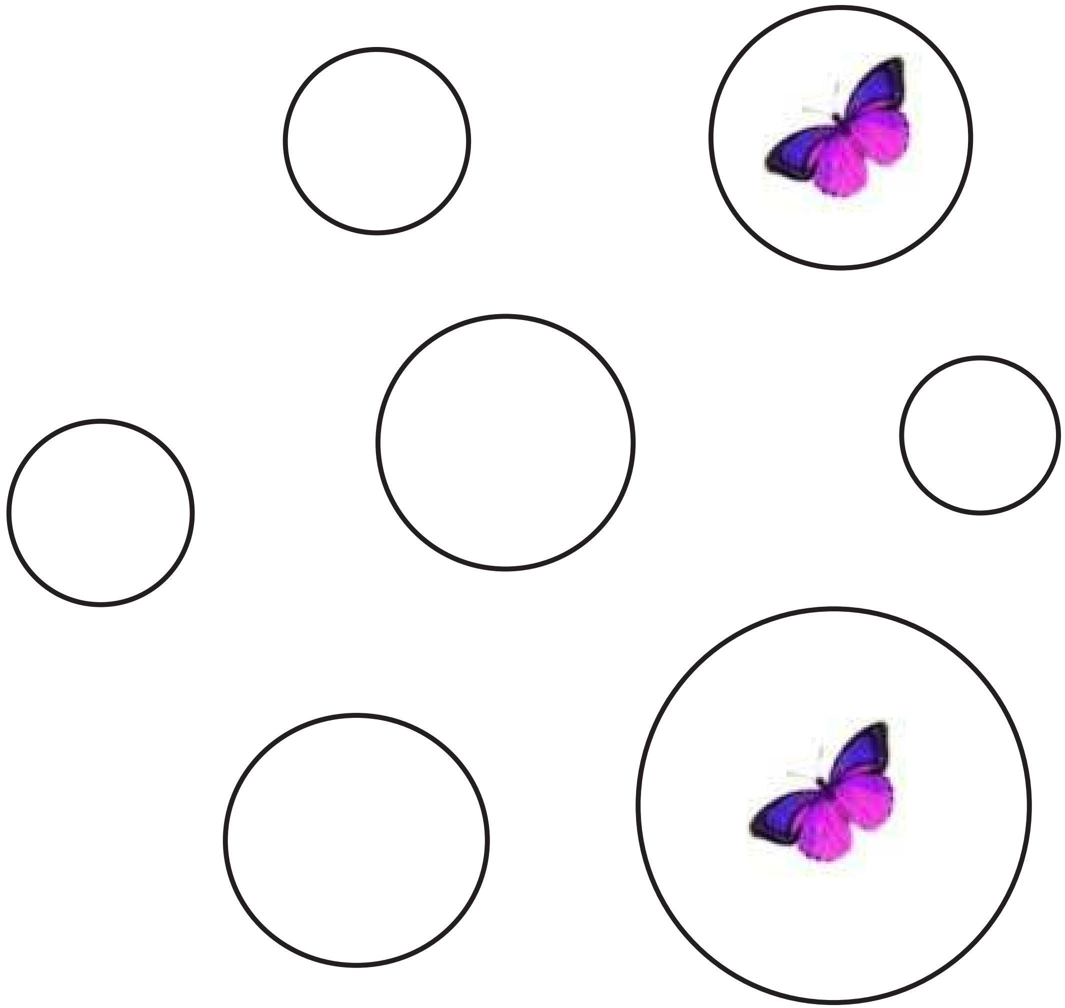

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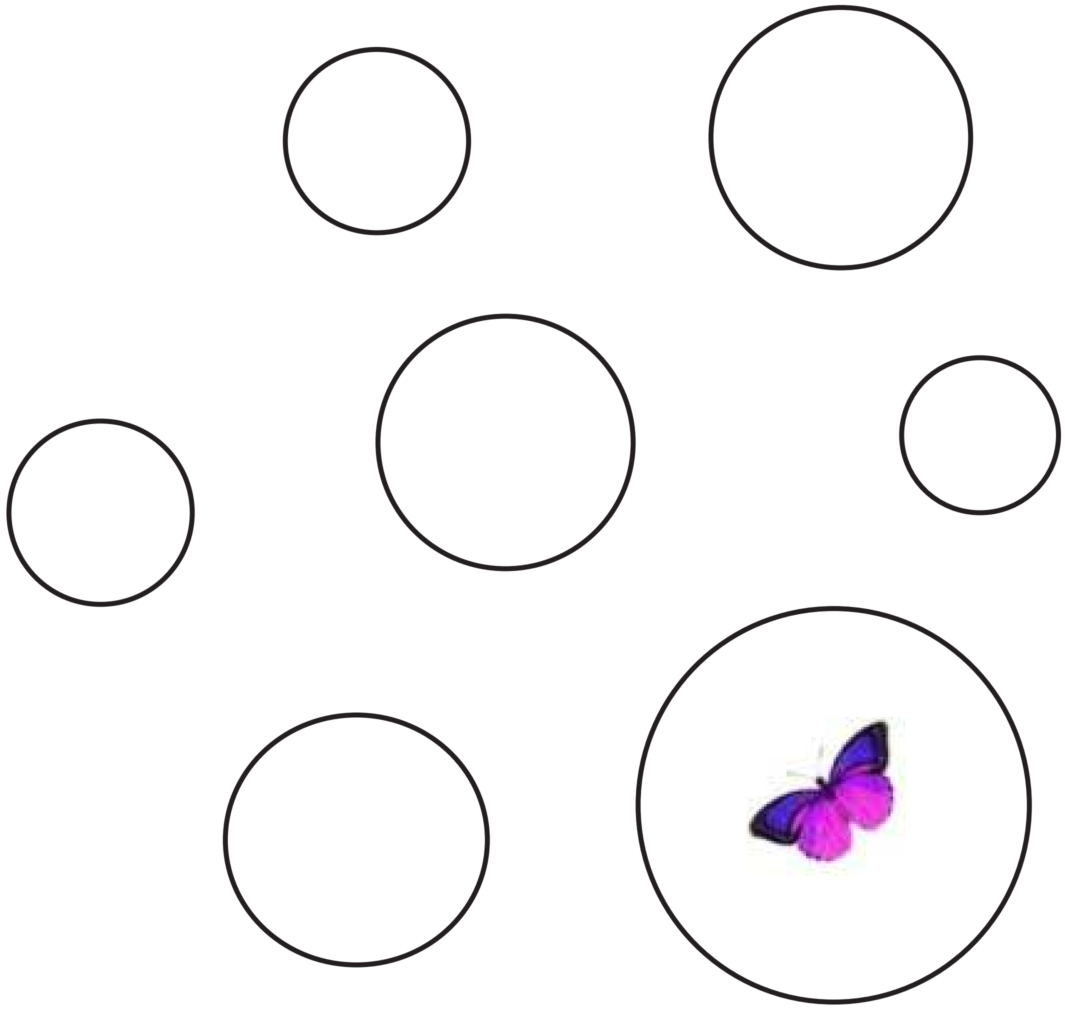

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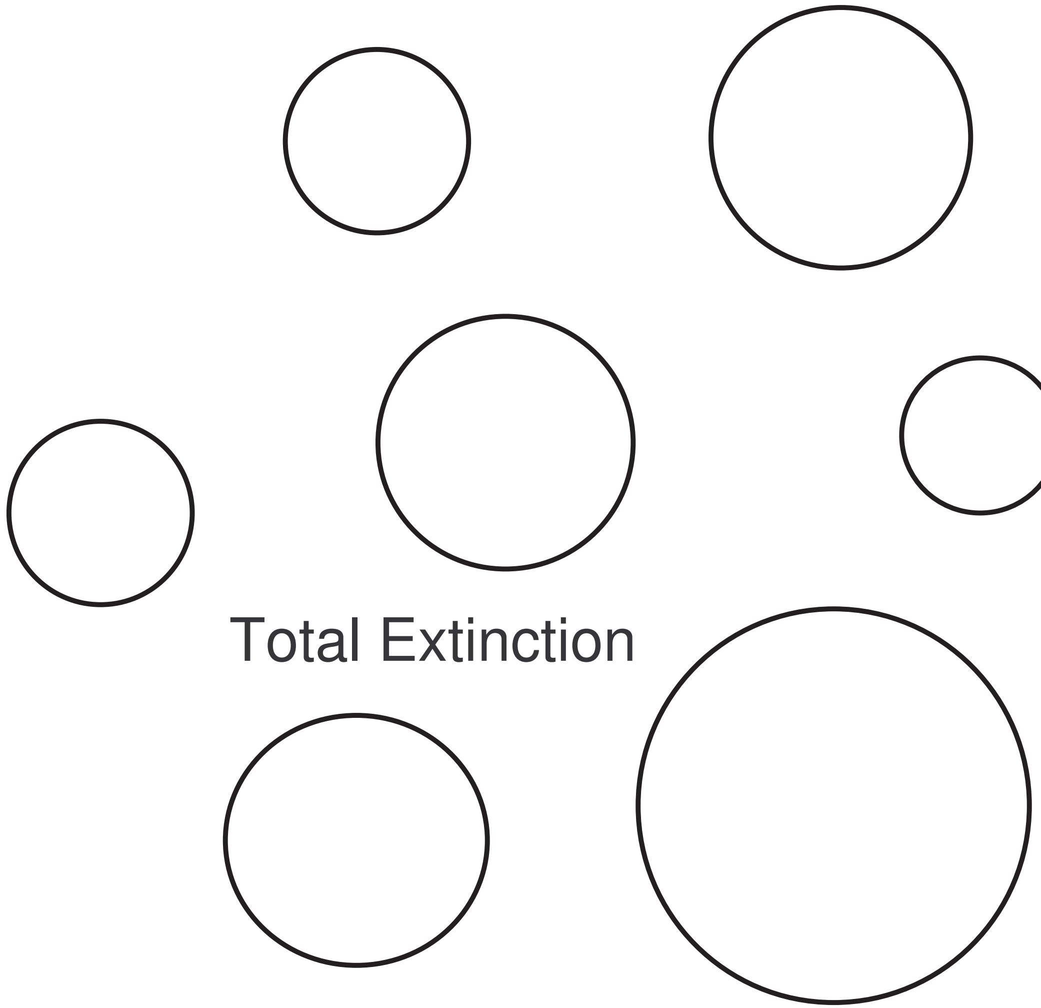

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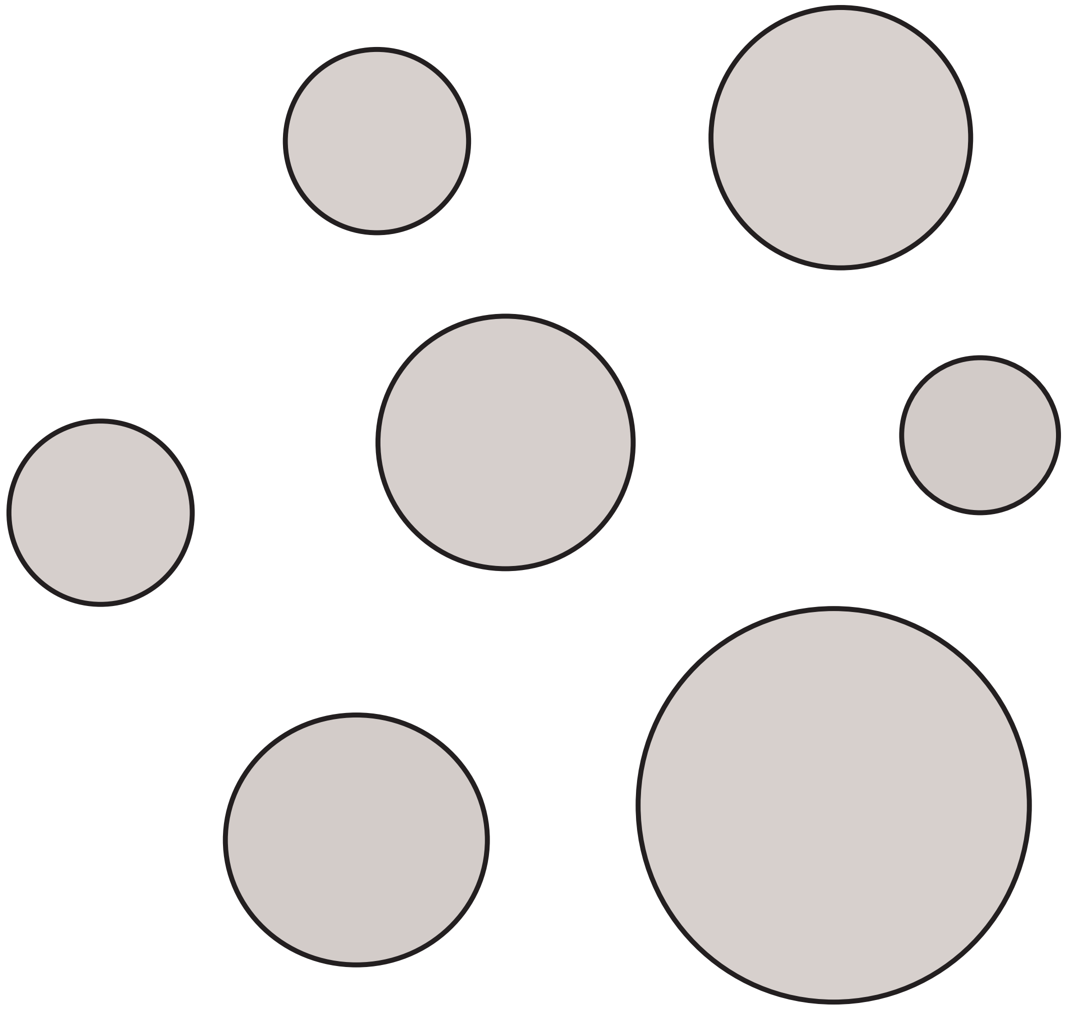

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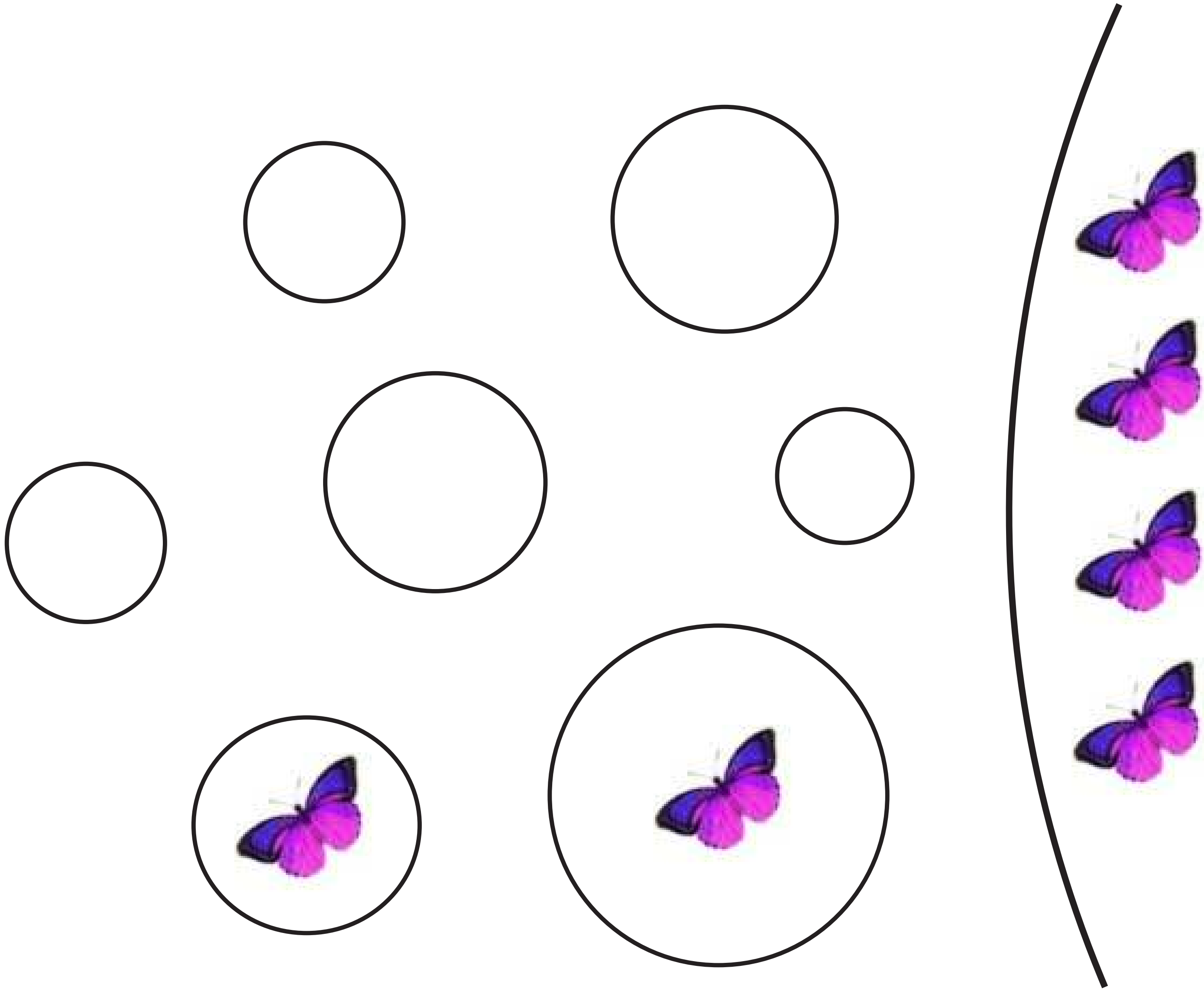

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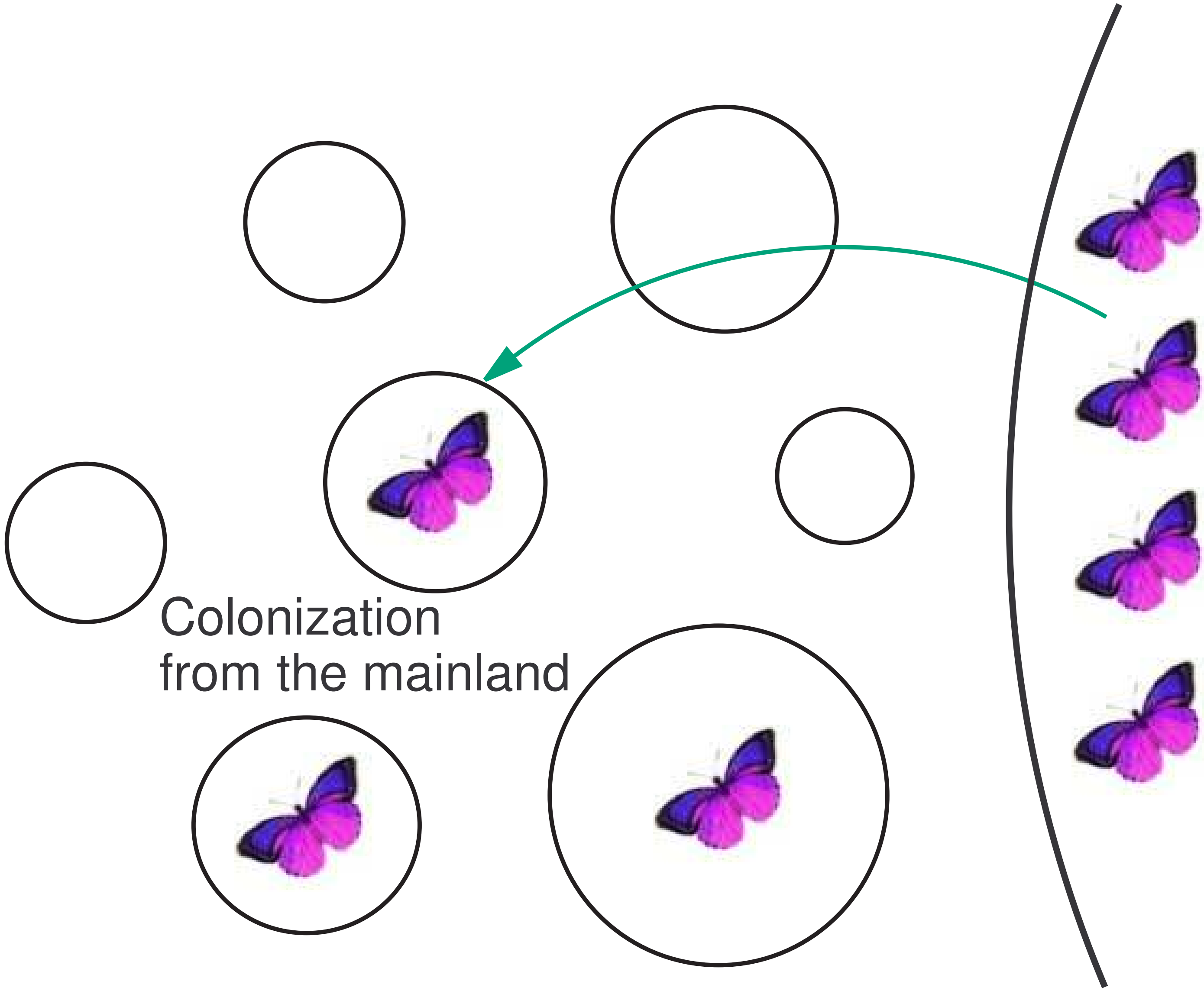

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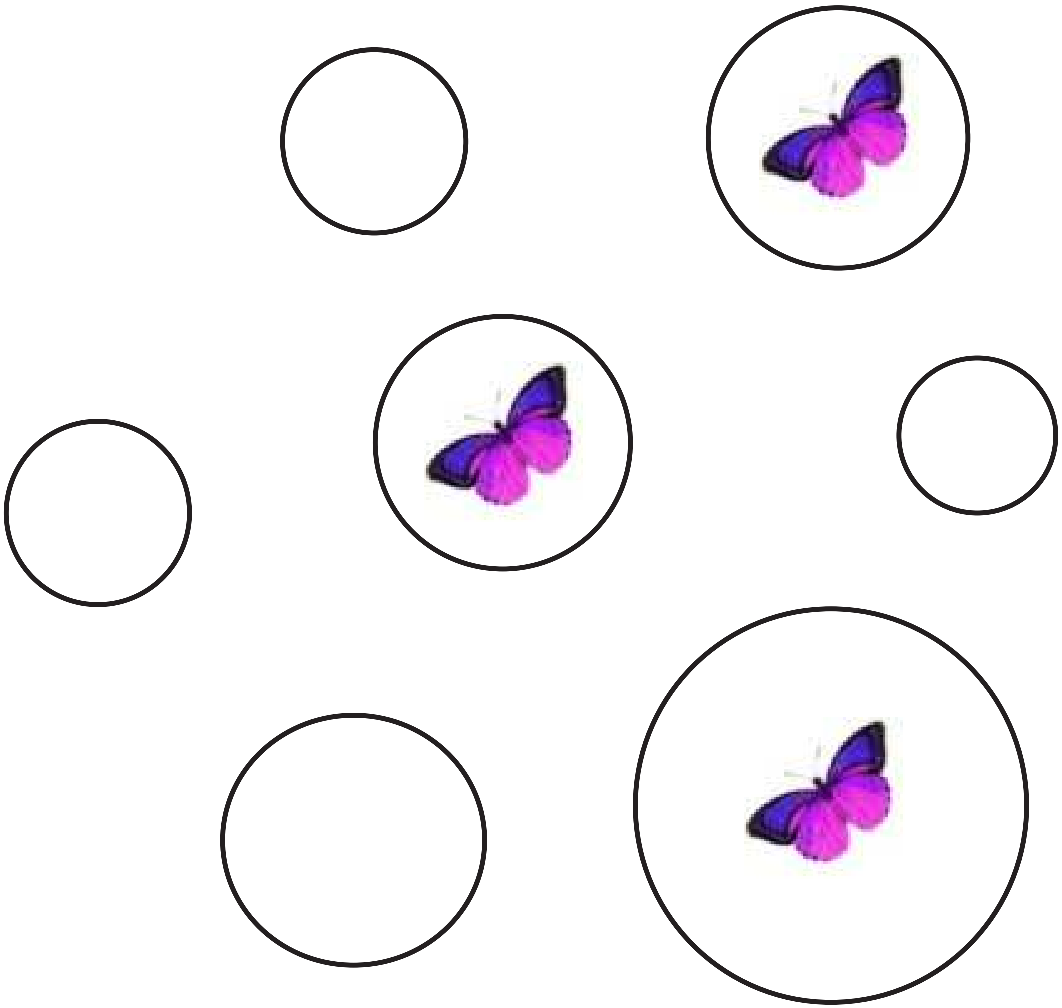

A Stochastic Patch Occupancy Model (SPOM)

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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.

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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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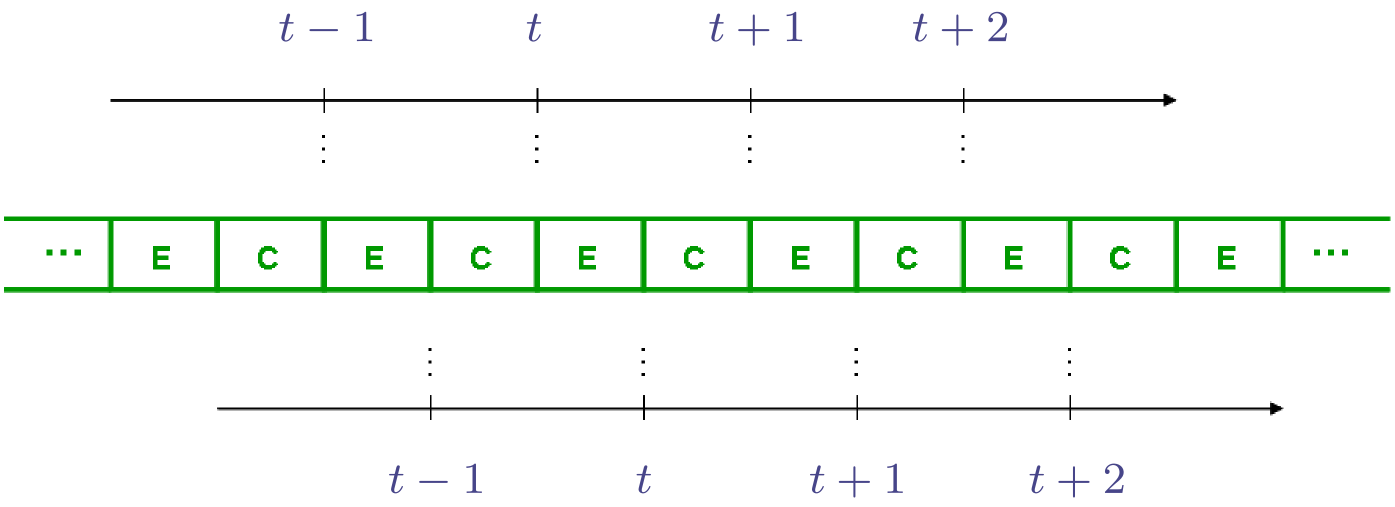

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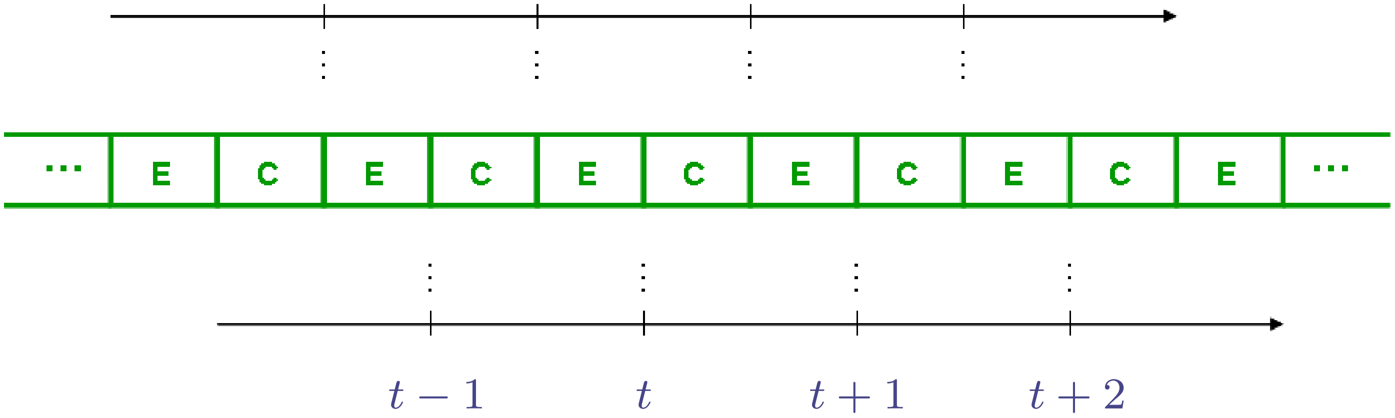

We will we assume that the population is *observed after successive extinction phases* (CE Model).

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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, increasing and concave.

Examples of $c(x)$

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- $c(x) = 1 - \exp(-x\beta) \quad (\beta > 0)$.

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

SPOM

Thus, we have a *Chain Bernoulli* structure:

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

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SPOM

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

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

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

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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 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

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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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	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	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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```

SPOM - Homogeneous case

Compare this with the *homogeneous 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:

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

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A deterministic limit

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.

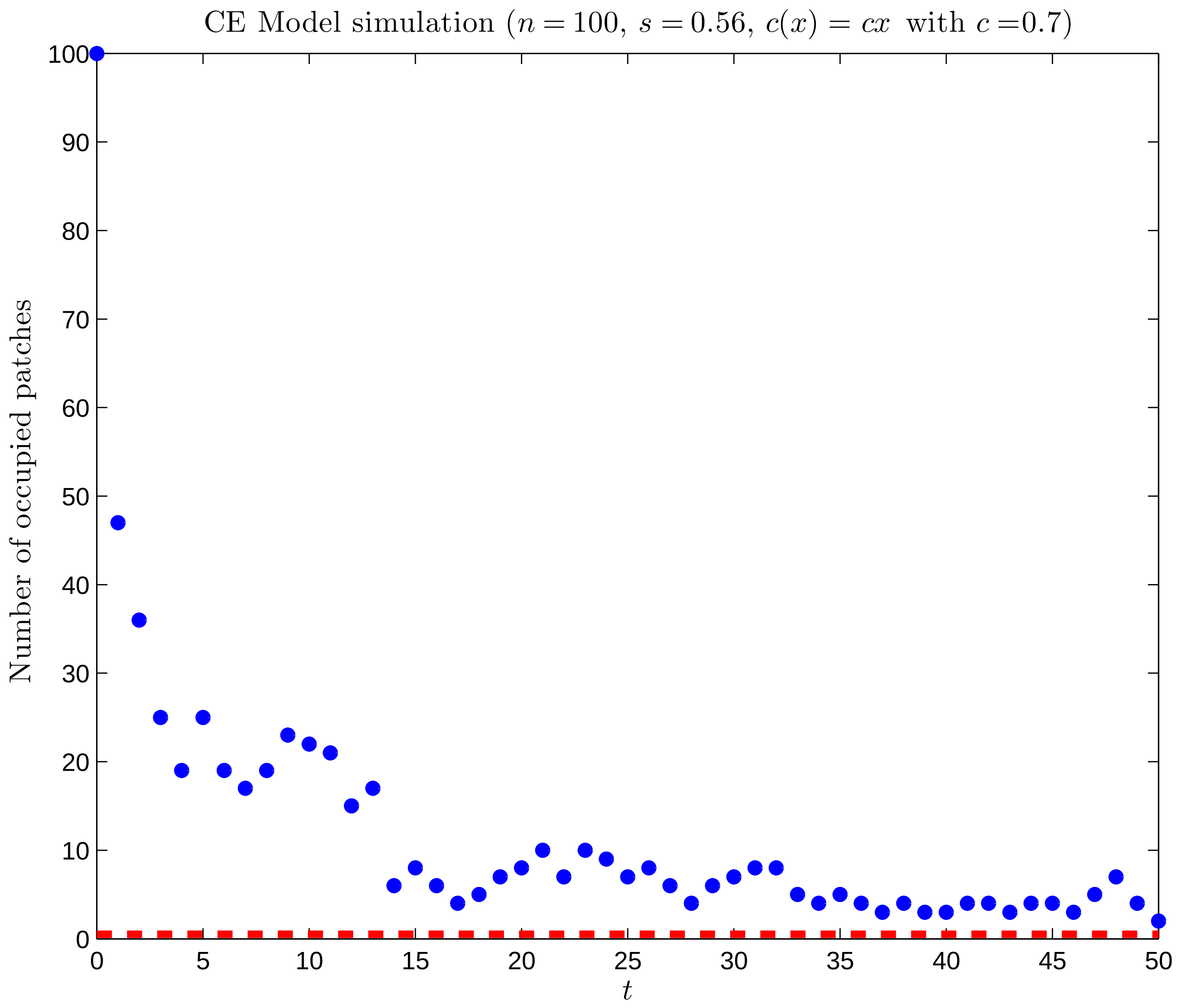
Stability

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

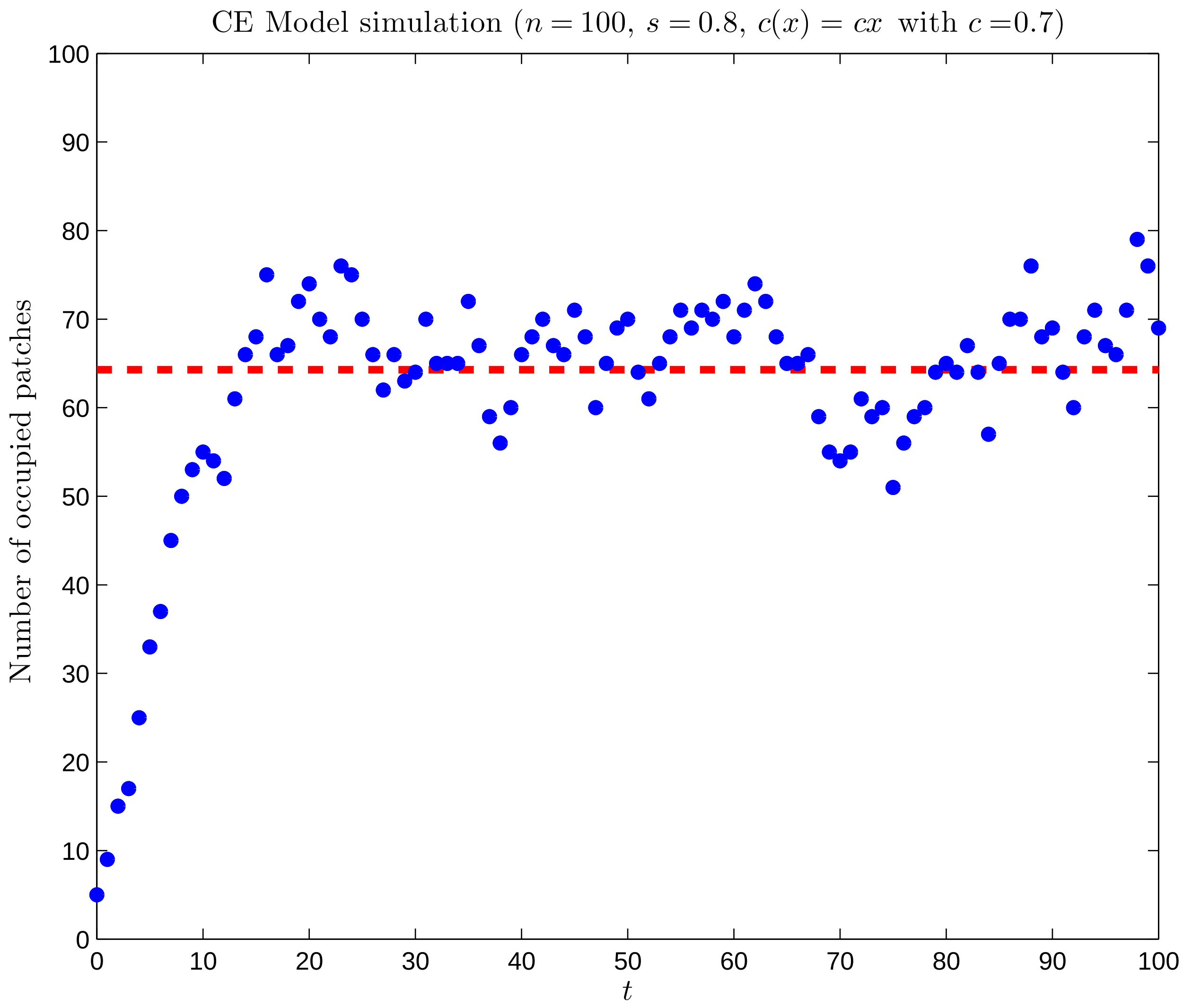
- *Stationarity*: $c(0) > 0$. There is a unique fixed point $x^* \in [0,1]$. It satisfies $x^* \in (0,1)$ and is stable.
- *Evanescence*: $c(0) = 0$ and $1 + c'(0) \le 1/s$. Now 0 is the unique fixed point in $[0,1]$. It is stable.
- *Quasi stationarity*: $c(0) = 0$ and $1 + c'(0) > 1/s$. There are two fixed points in $[0,1]$: 0 (unstable) and $x^* \in (0,1)$ (stable).

[Notice that if $c(0) = 0$, we require $c'(0) > 0$ for quasi stationarity.]

CE Model - Evanescence



CE Model - Quasi stationarity



A Gaussian limit

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

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

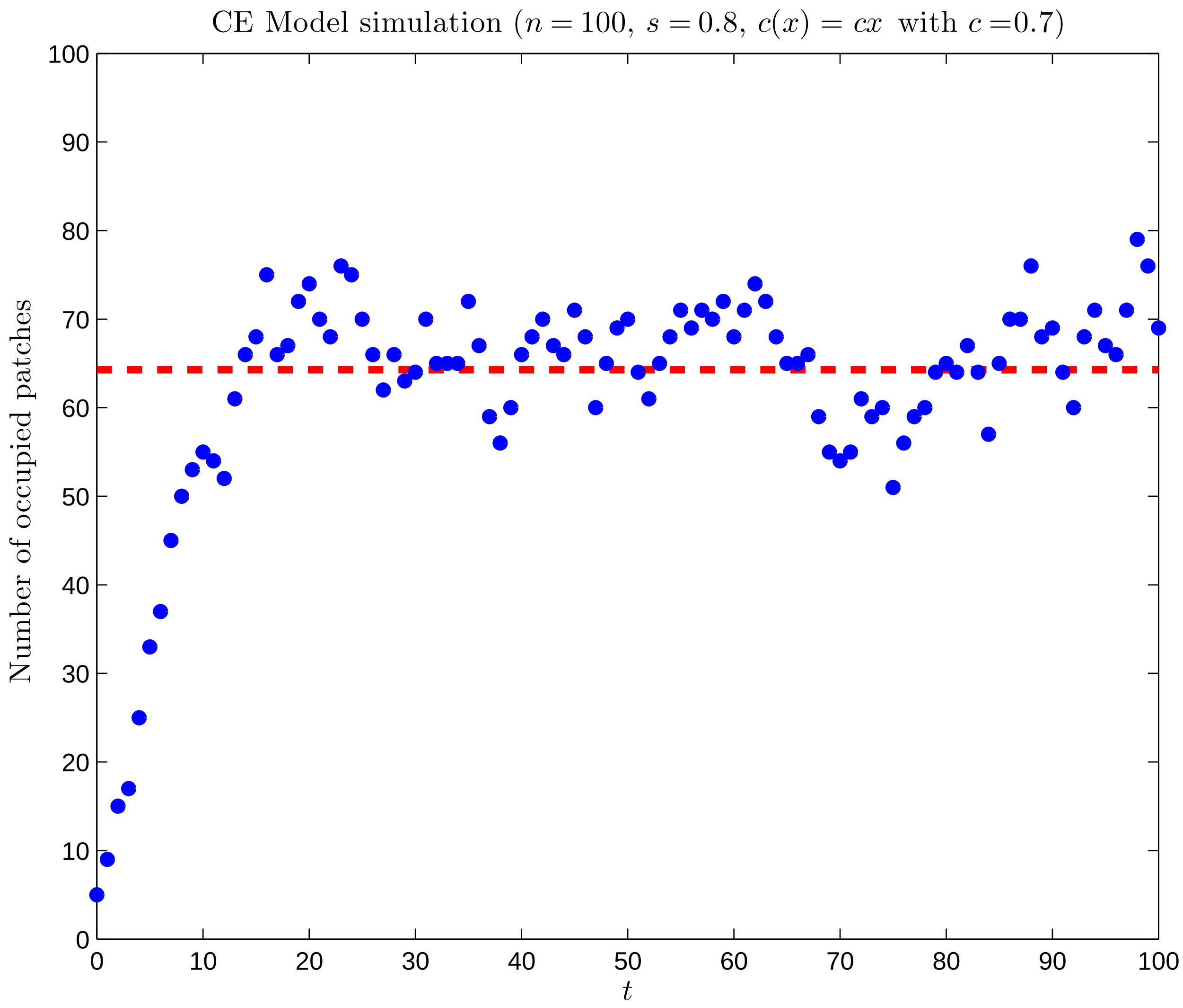
If $Z_0^{(n)} \xrightarrow{d} z_0$, then $Z_\bullet^{(n)}$ converges weakly to the Gaussian Markov chain $Z_\bullet$ defined by

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

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



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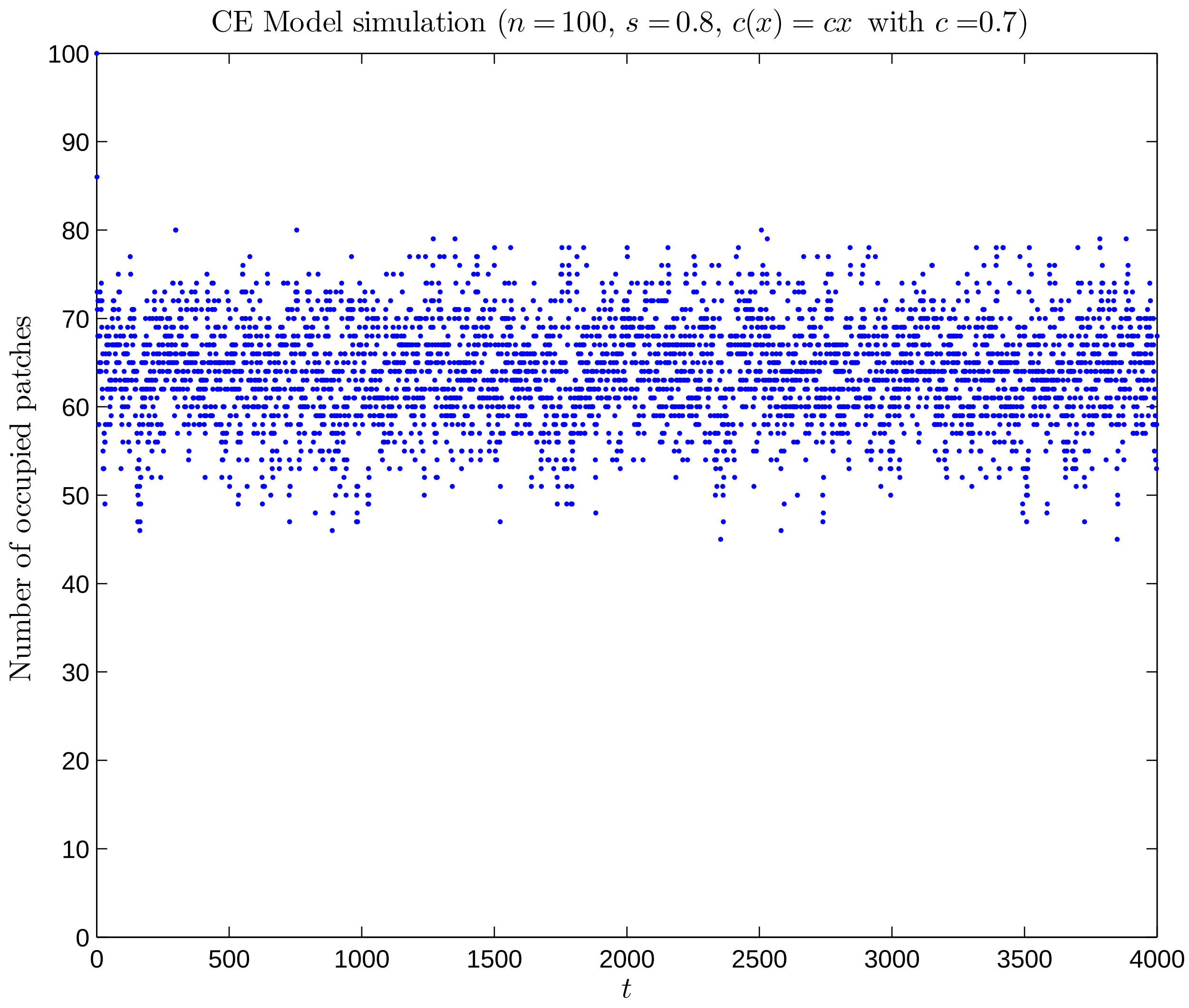
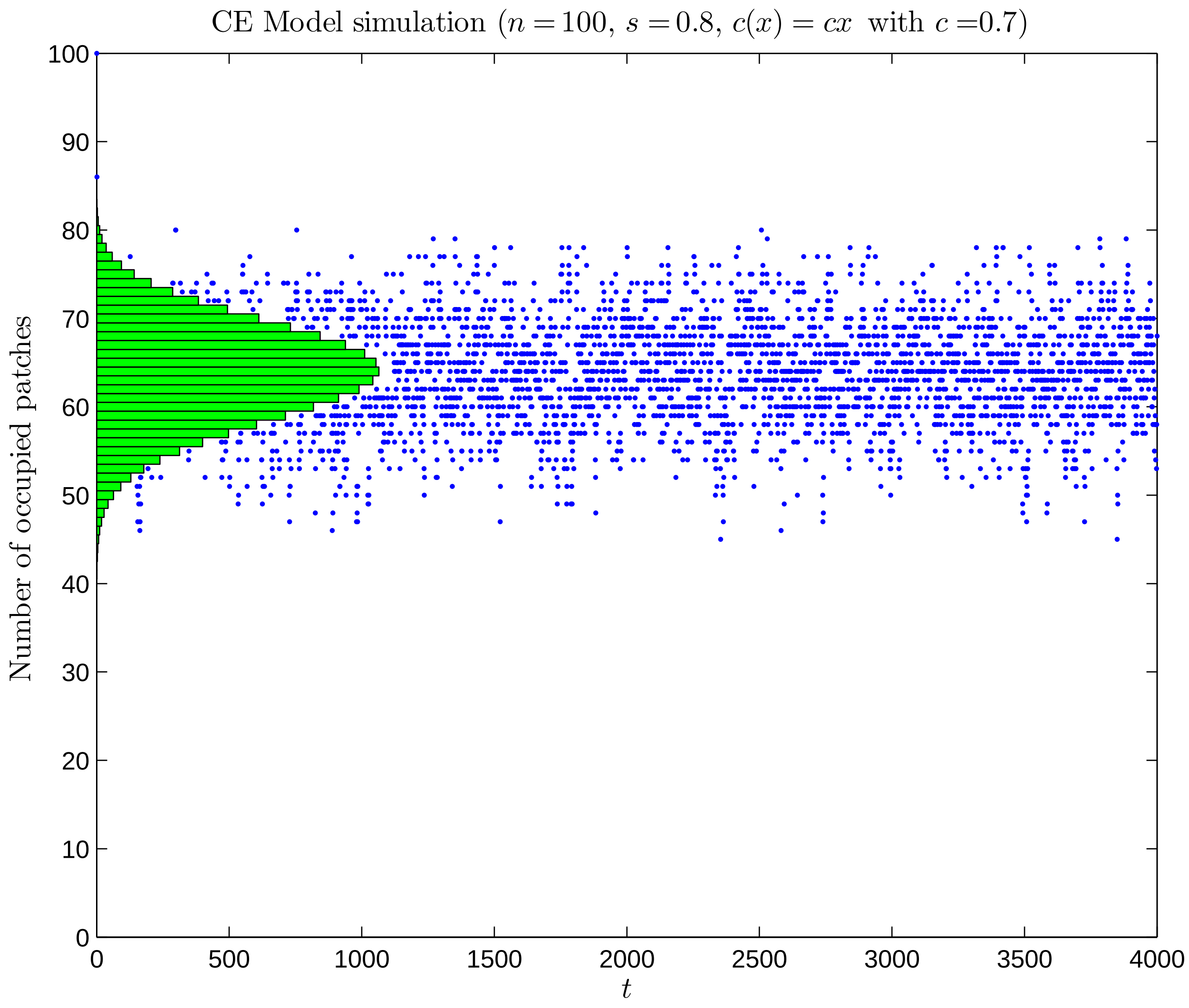
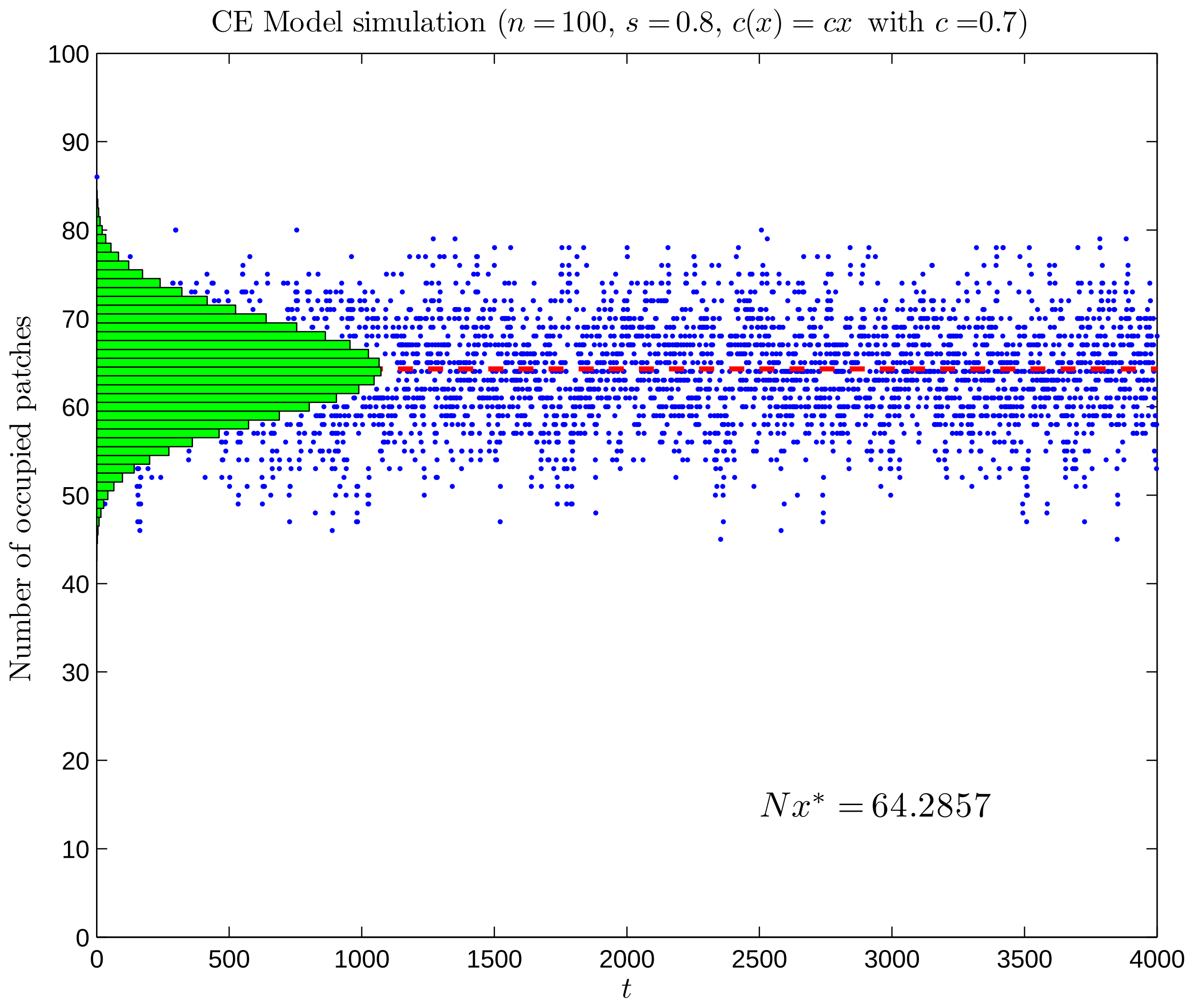


CE Model - Quasi-stationary distribution



CE Model - Gaussian approximation



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 ...

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

A deterministic limit

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First, . . .

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

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

A deterministic limit

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

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

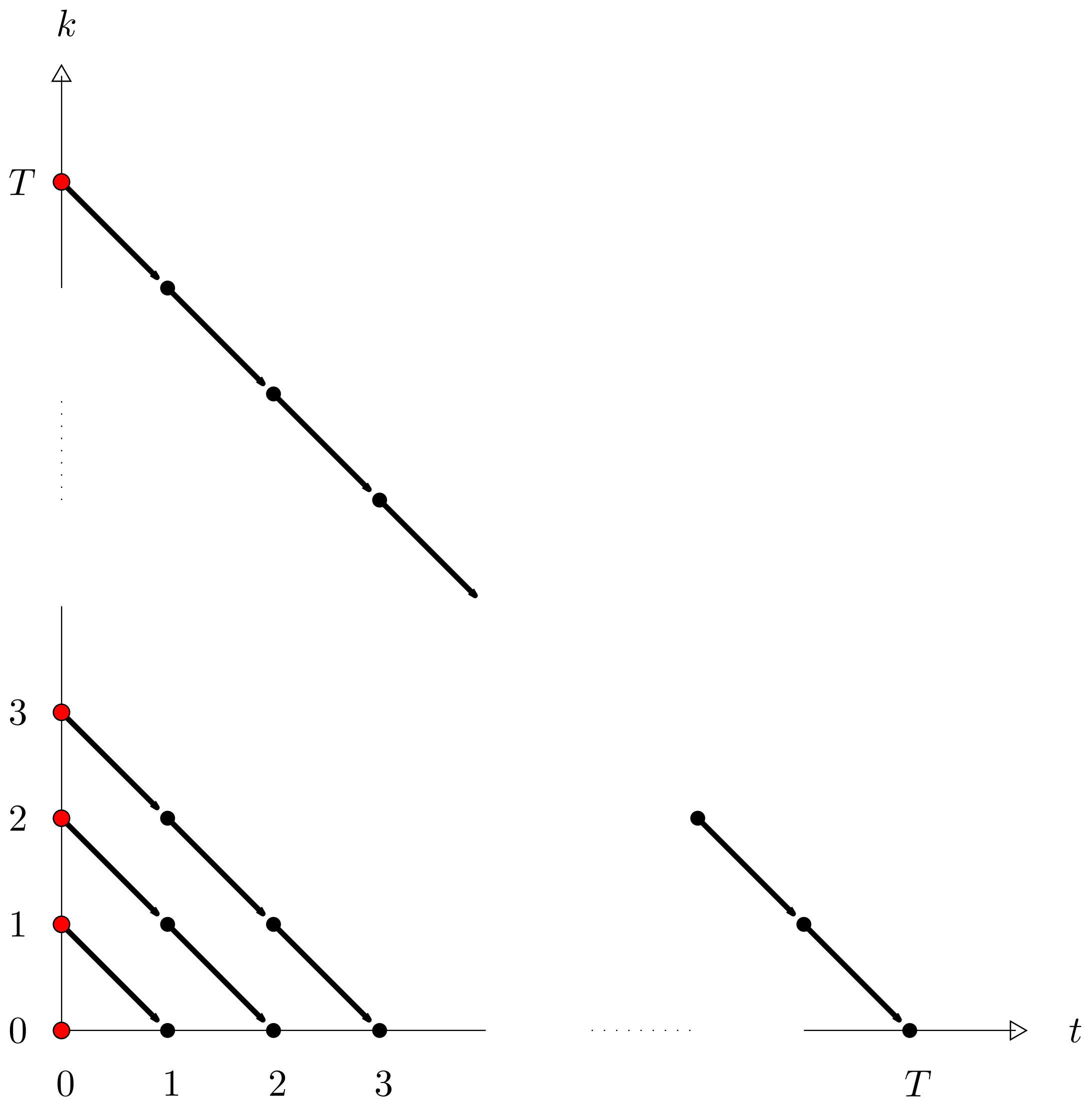
for all $k = 0, 1, \ldots, T$. Then, there is a (deterministic) triangular array $\{d(t,k)\}$ such that, for all $t = 0, 1, \ldots, T$ and $k = 0, 1, \ldots, T - t$,

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

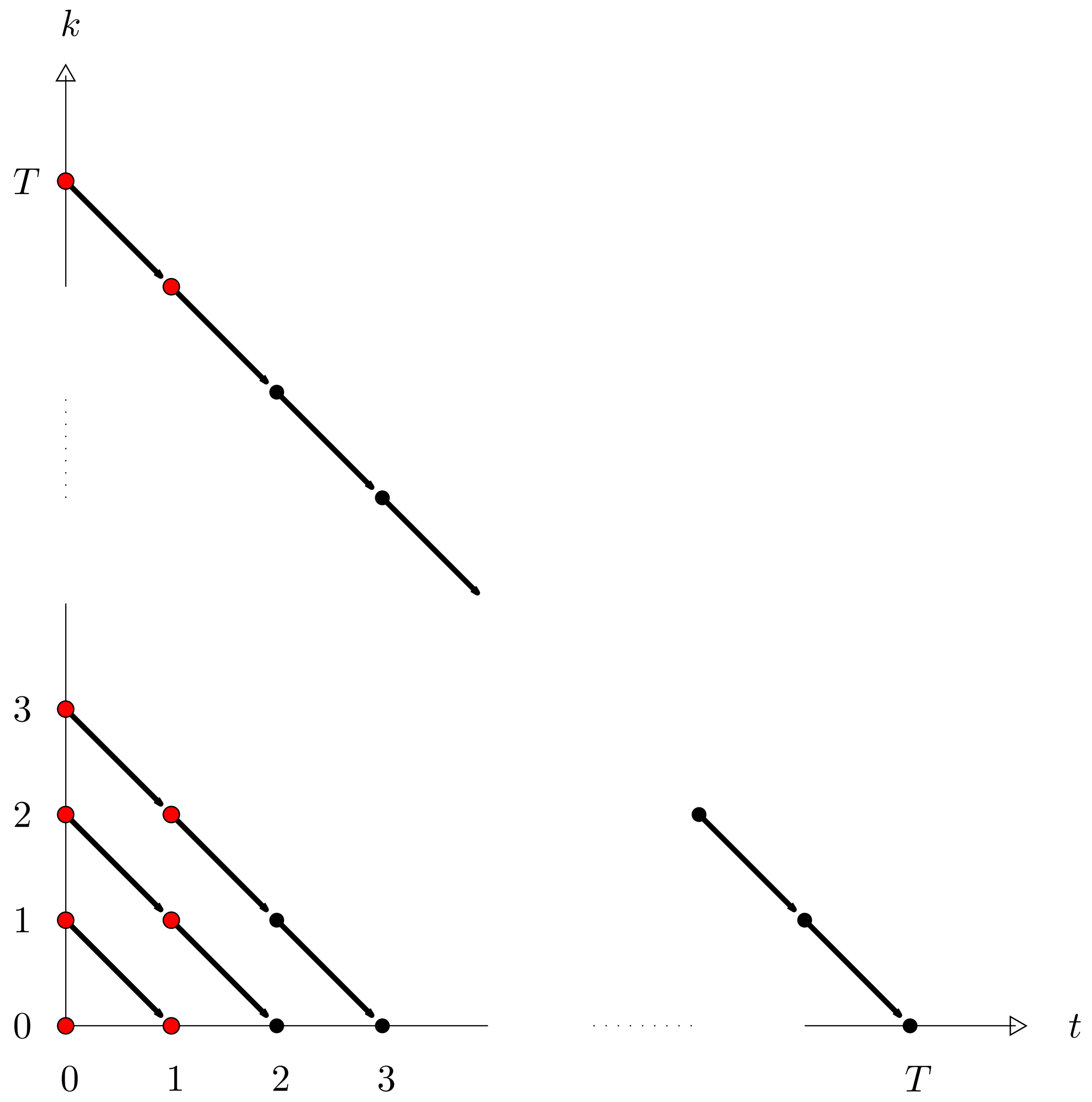
where

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

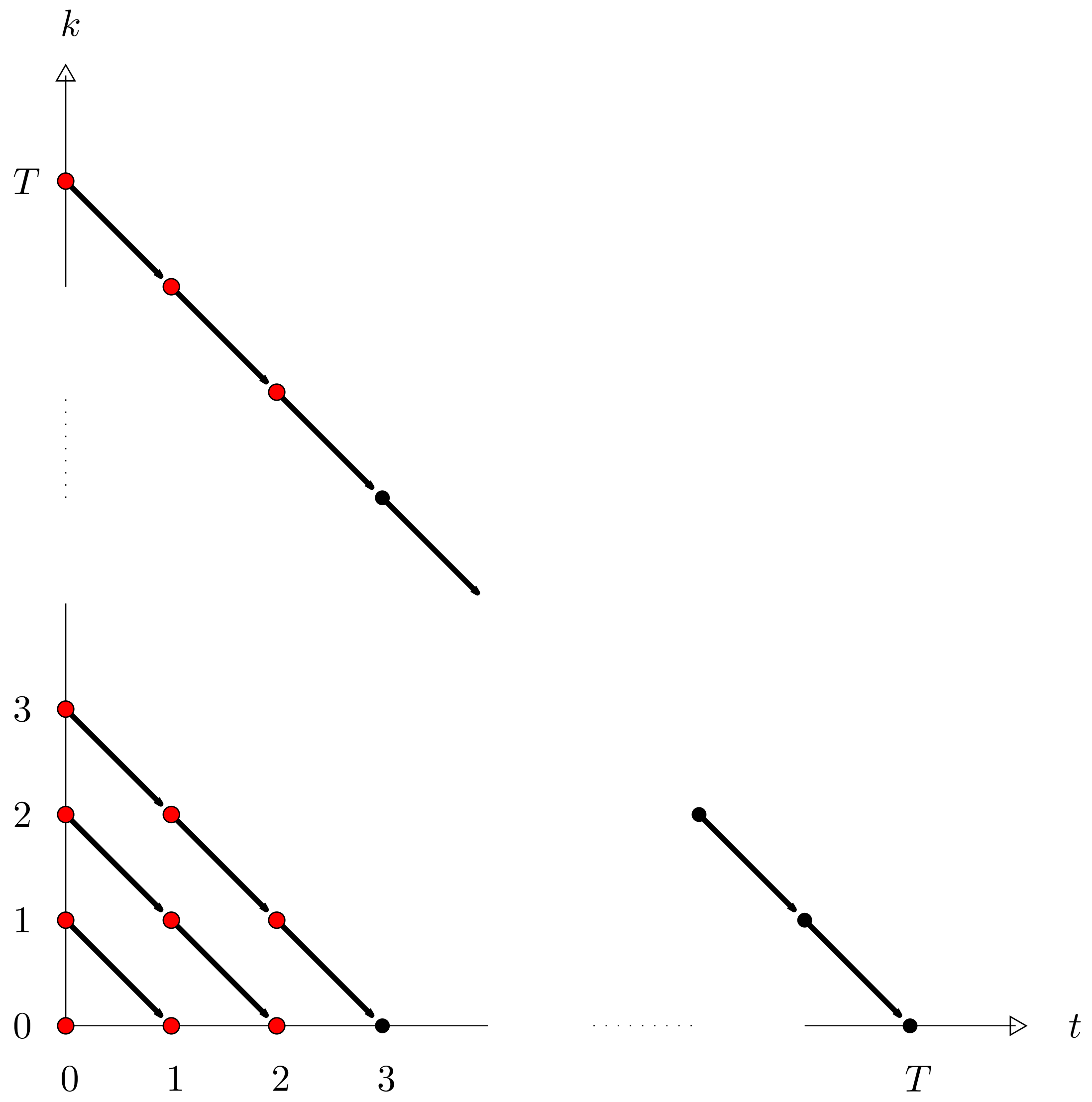
A deterministic limit $d(0,k)$



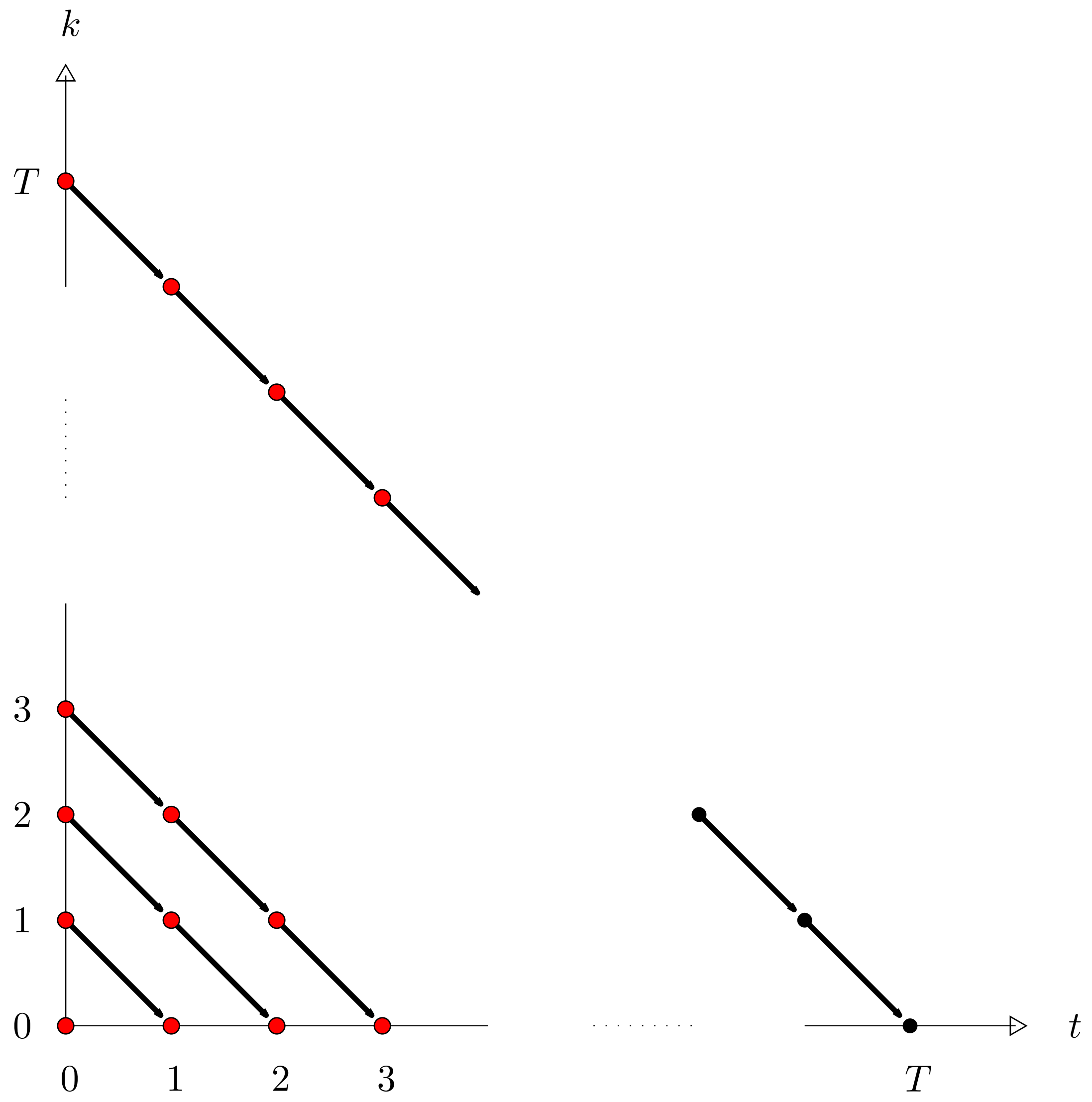
A deterministic limit $d(1,k)$



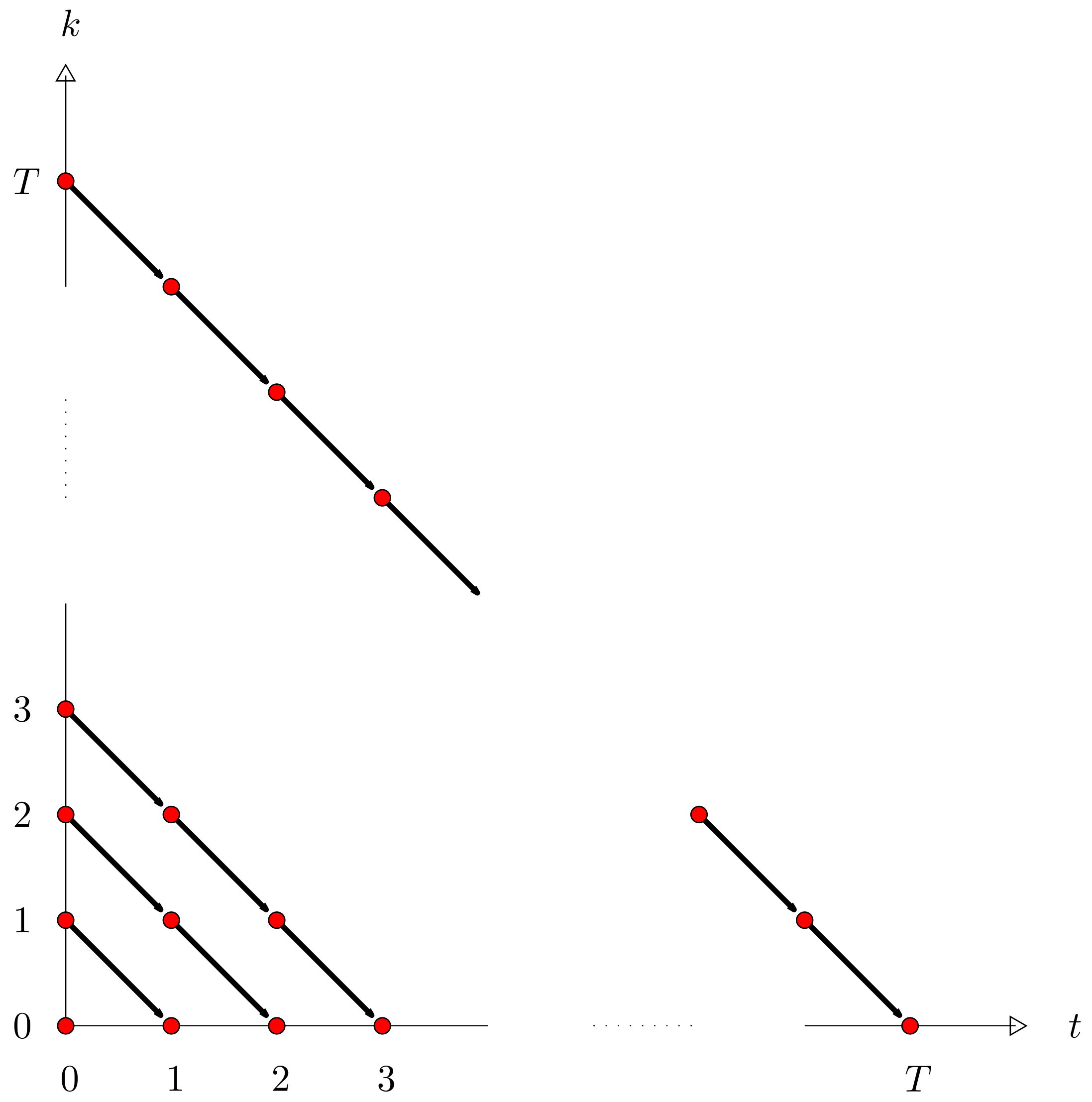
A deterministic limit $d(2,k)$



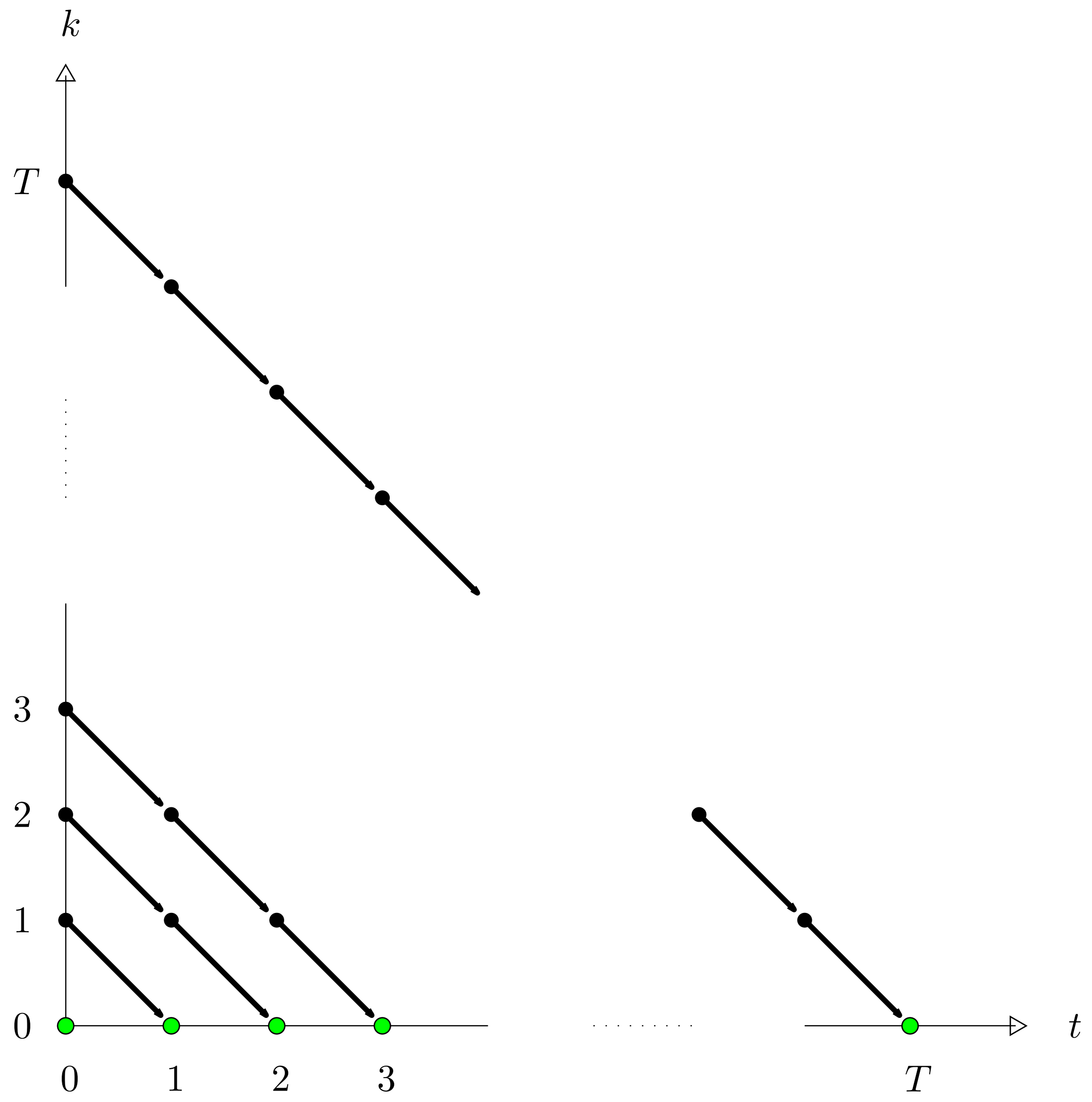
A deterministic limit $d(3,k)$



A deterministic limit $d(t,k)$



A deterministic limit $d(t,0)$

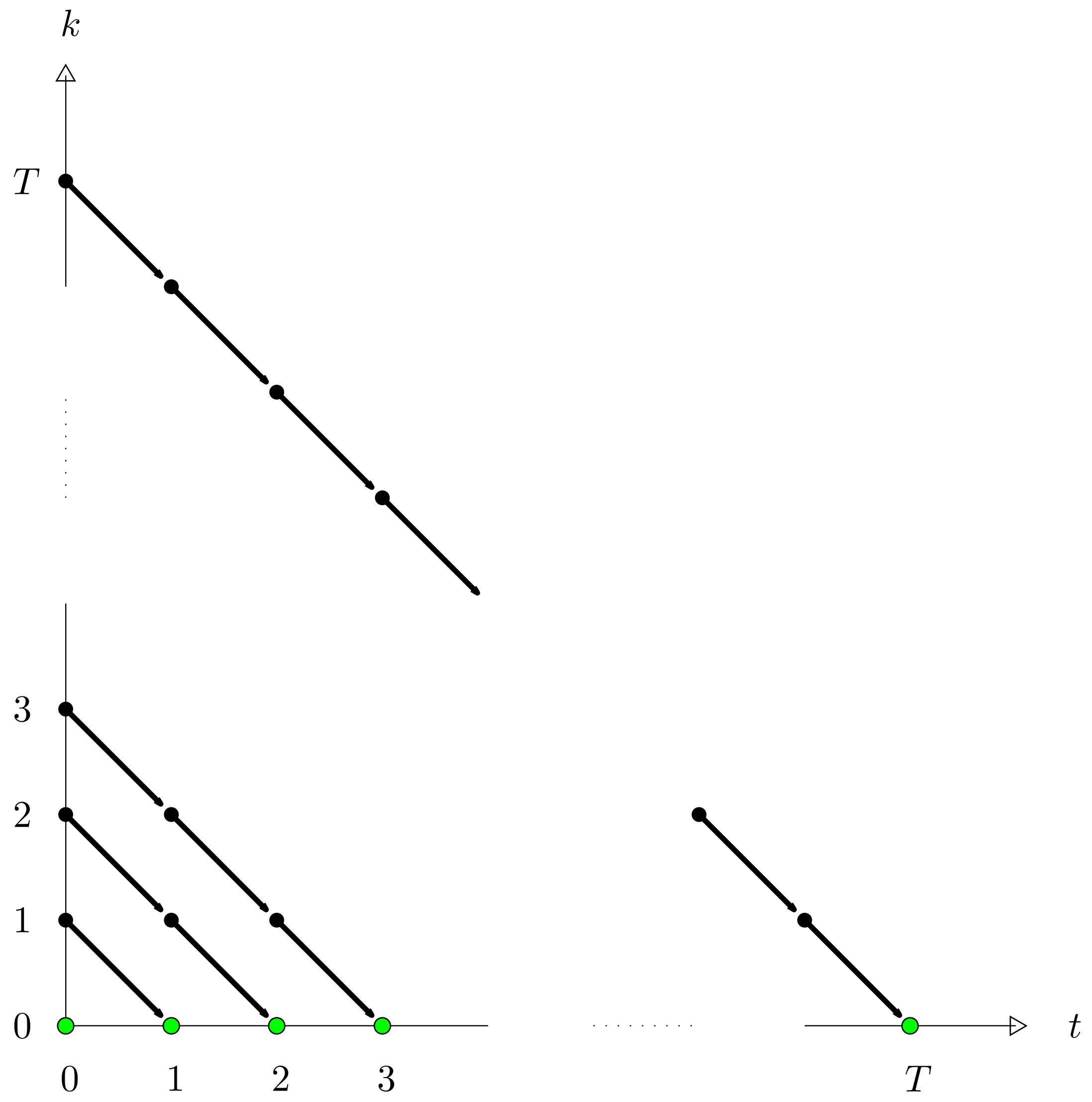


Remarks

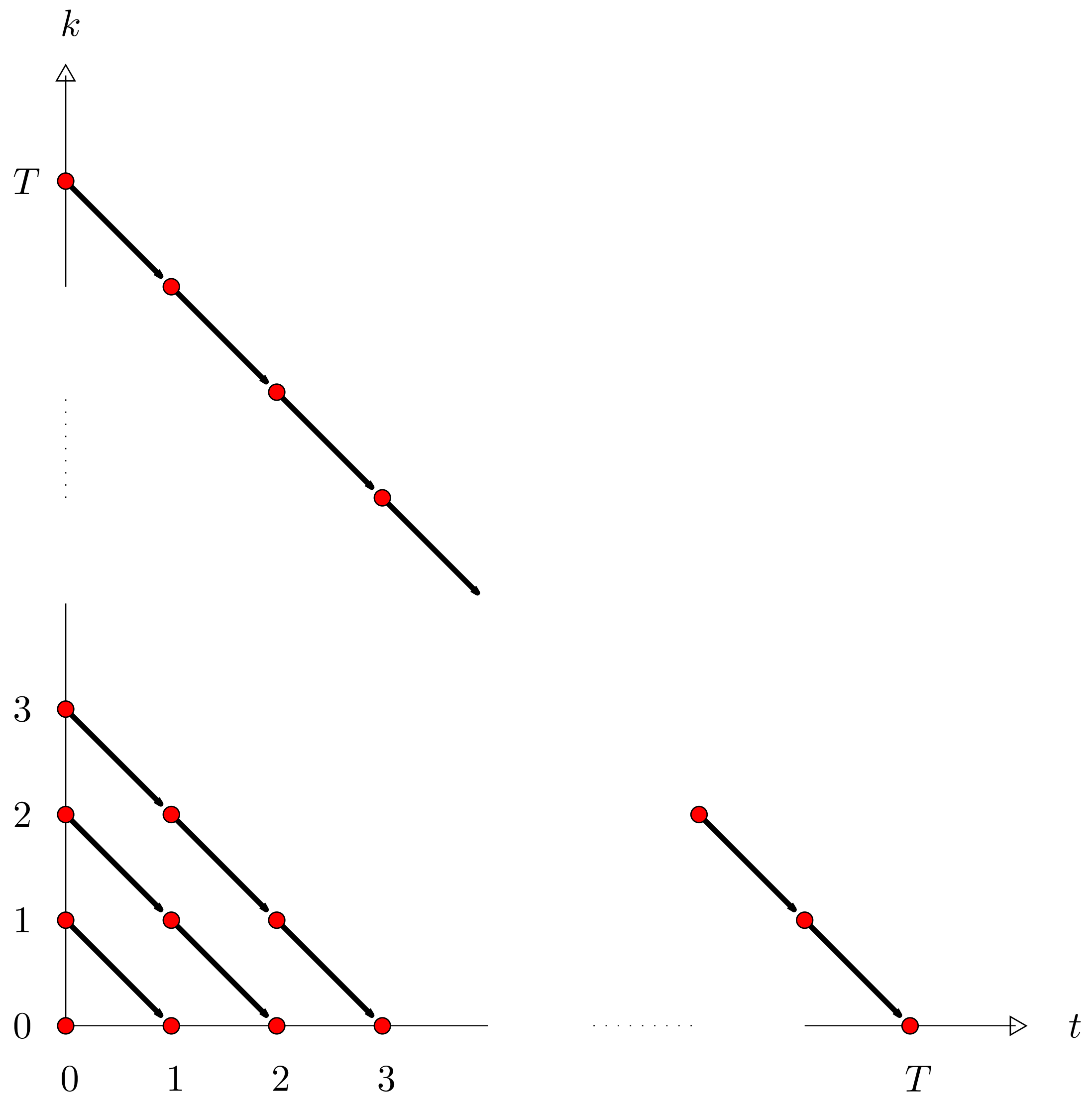
- Typically, we are only interested in $d(t,0)$, being the asymptotic proportion of occupied patches at time t:

$$\frac{1}{n}\sum_{i=1}^{n} X_{i,t}^{(n)} \xrightarrow{p} d(t,0).$$

Remarks: $d(t,0)$



Remarks: $d(t,k)$



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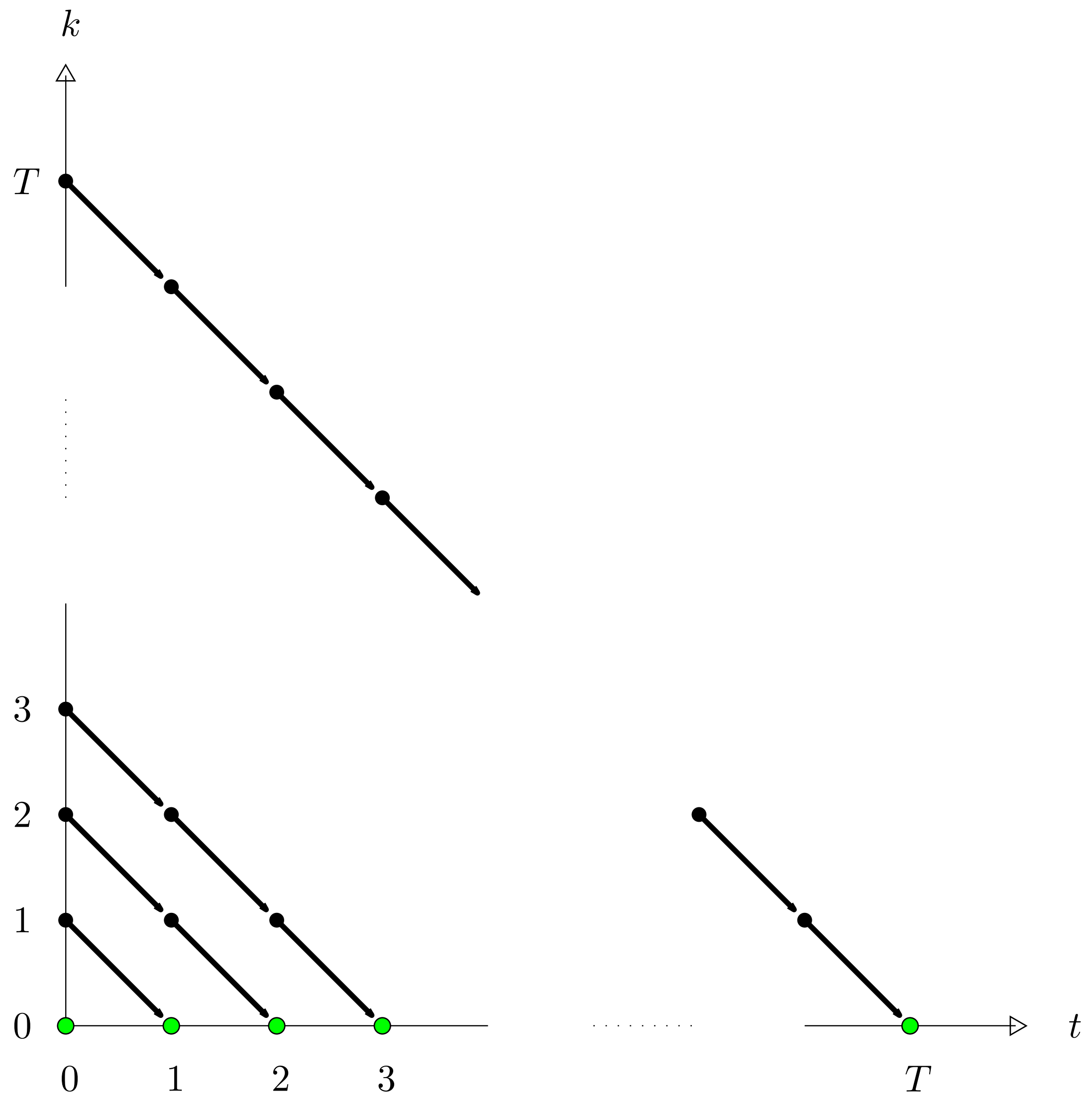

Remarks

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Remarks

- Typically, we are only interested in $d(t,0)$, being the asymptotic proportion of occupied patches at time t:

$$\frac{1}{n}\sum_{i=1}^{n} X_{i,t}^{(n)} \xrightarrow{p} d(t,0).$$

- 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.)

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

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

where

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

Homogeneous case

- 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 [BP] result....

A deterministic limit

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.

Stability

Theorem Any fixed point $d = (d(0), d(1), \dots)$ is given by

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

where ψ $(= d(0))$ solves

$$R(\psi) = \int_0^1 \frac{c(\psi)x}{1-x+c(\psi)x}\sigma(dx) = \psi. \tag{1}$$

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

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

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

Stability

Theorem If $c(0) = 0$ and

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

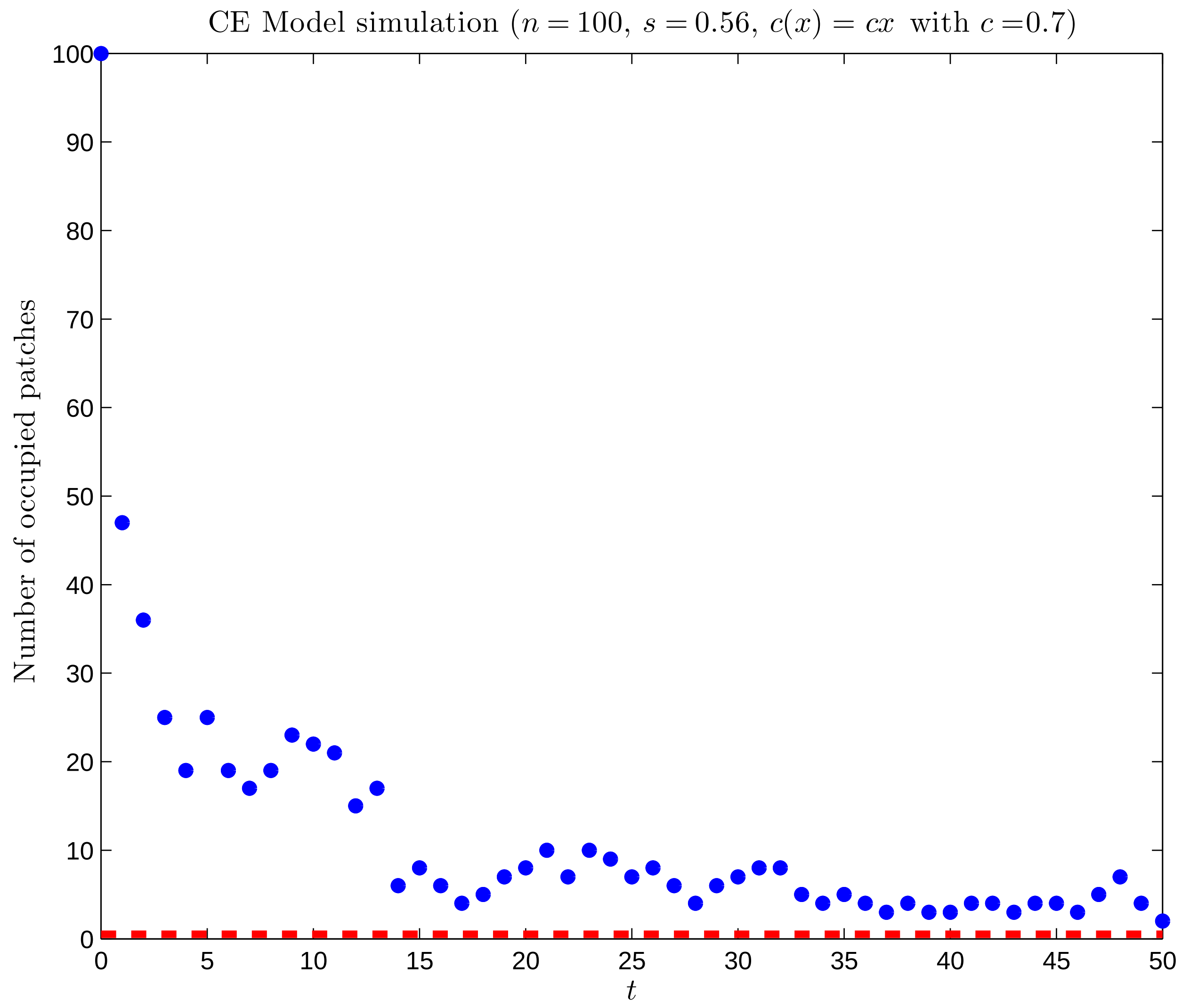
then $d(k) \equiv 0$ is a stable fixed point. Otherwise, the non-zero solution to

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

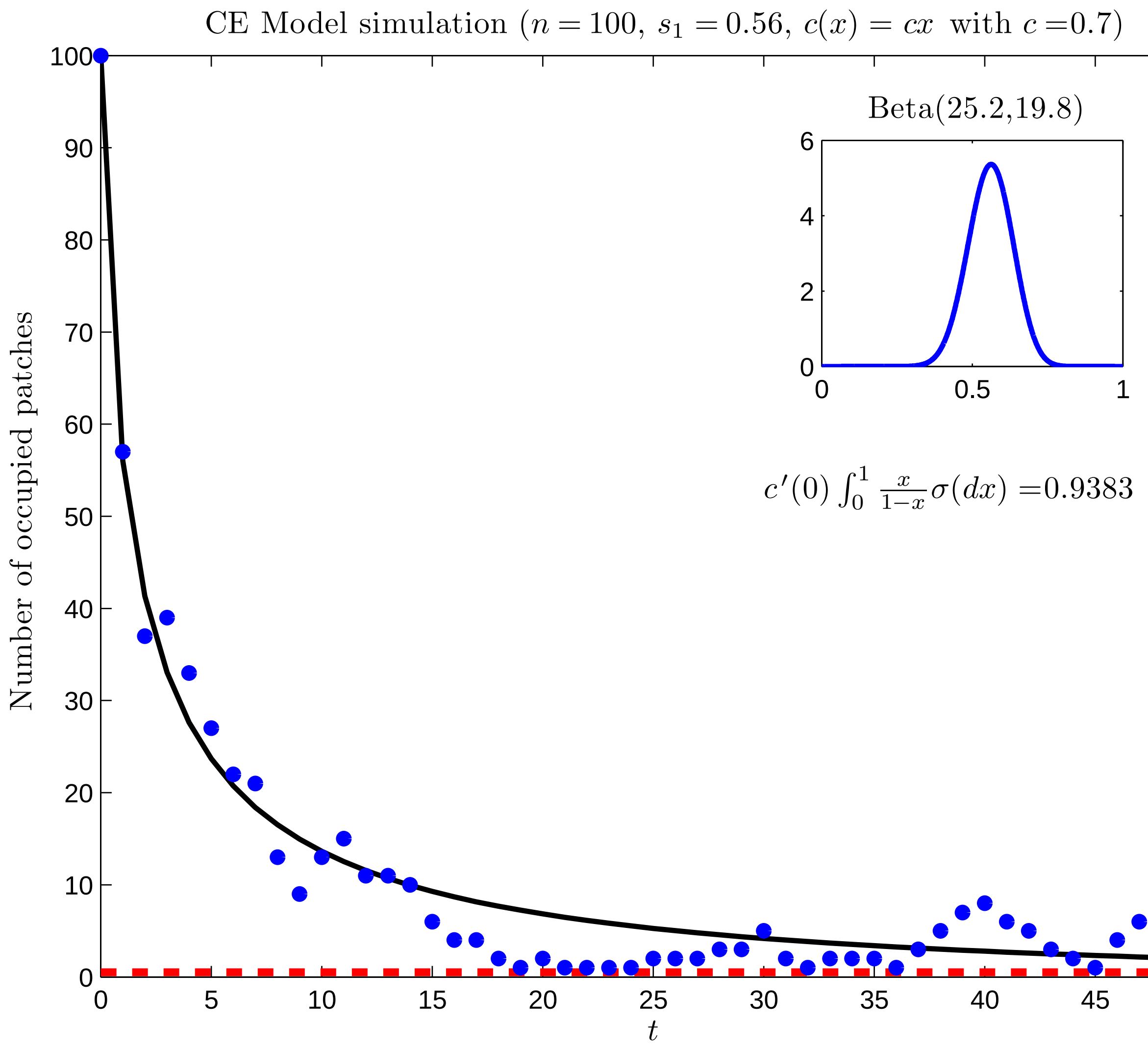
provides the stable fixed point through

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

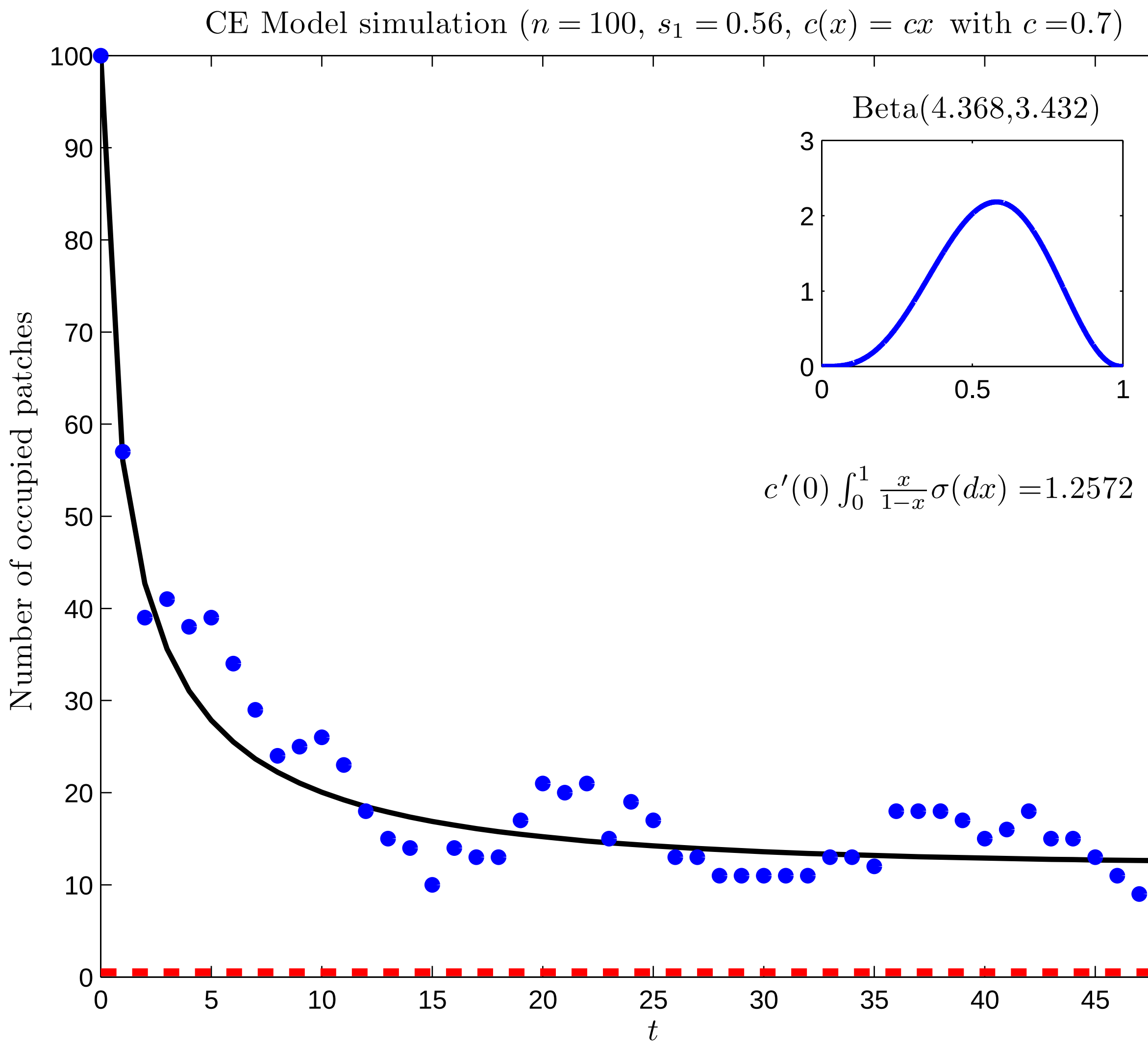
CE Model (homogeneous) - Evanescence



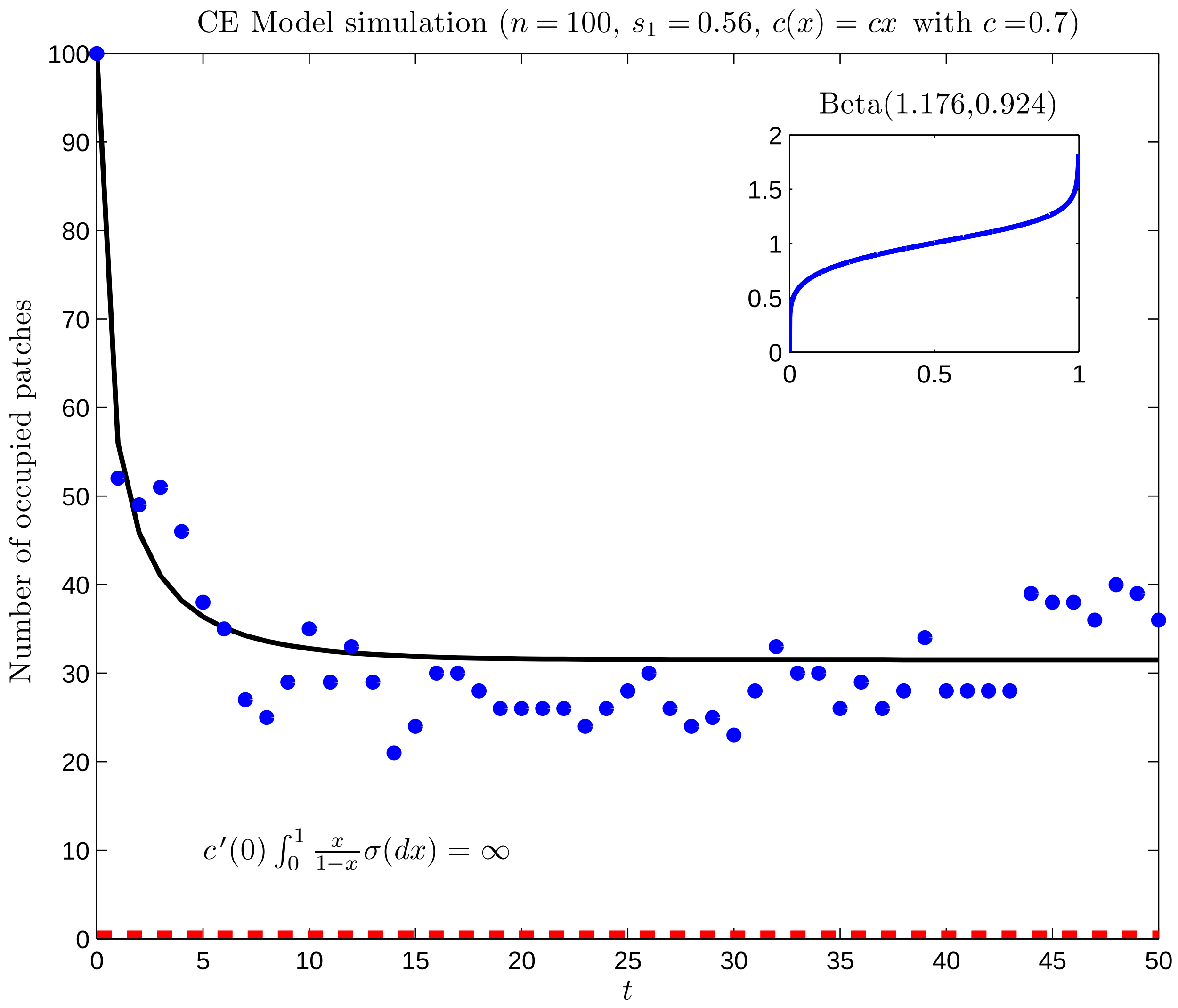
CE Model - Evanescence



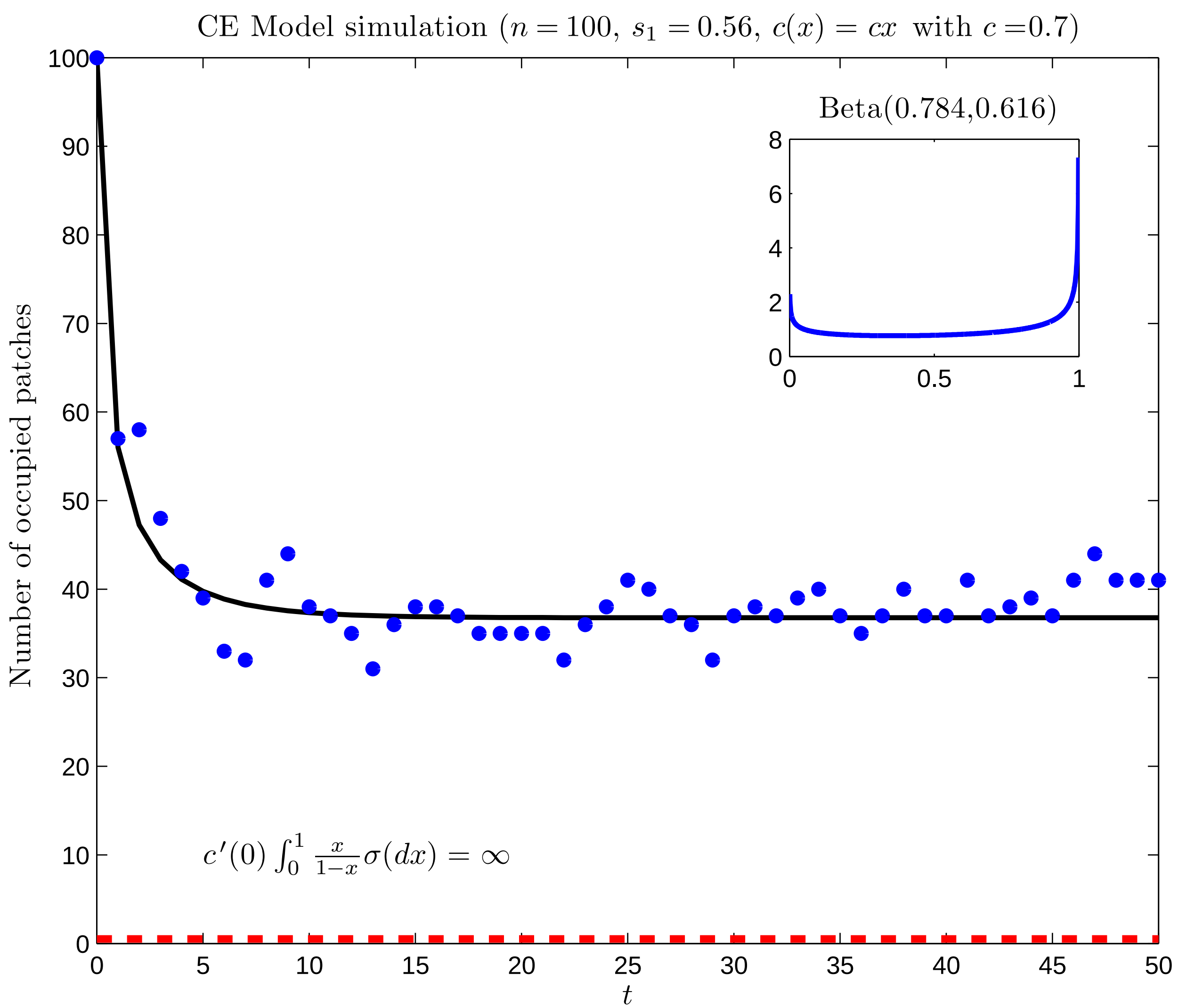
CE Model - Quasi stationarity



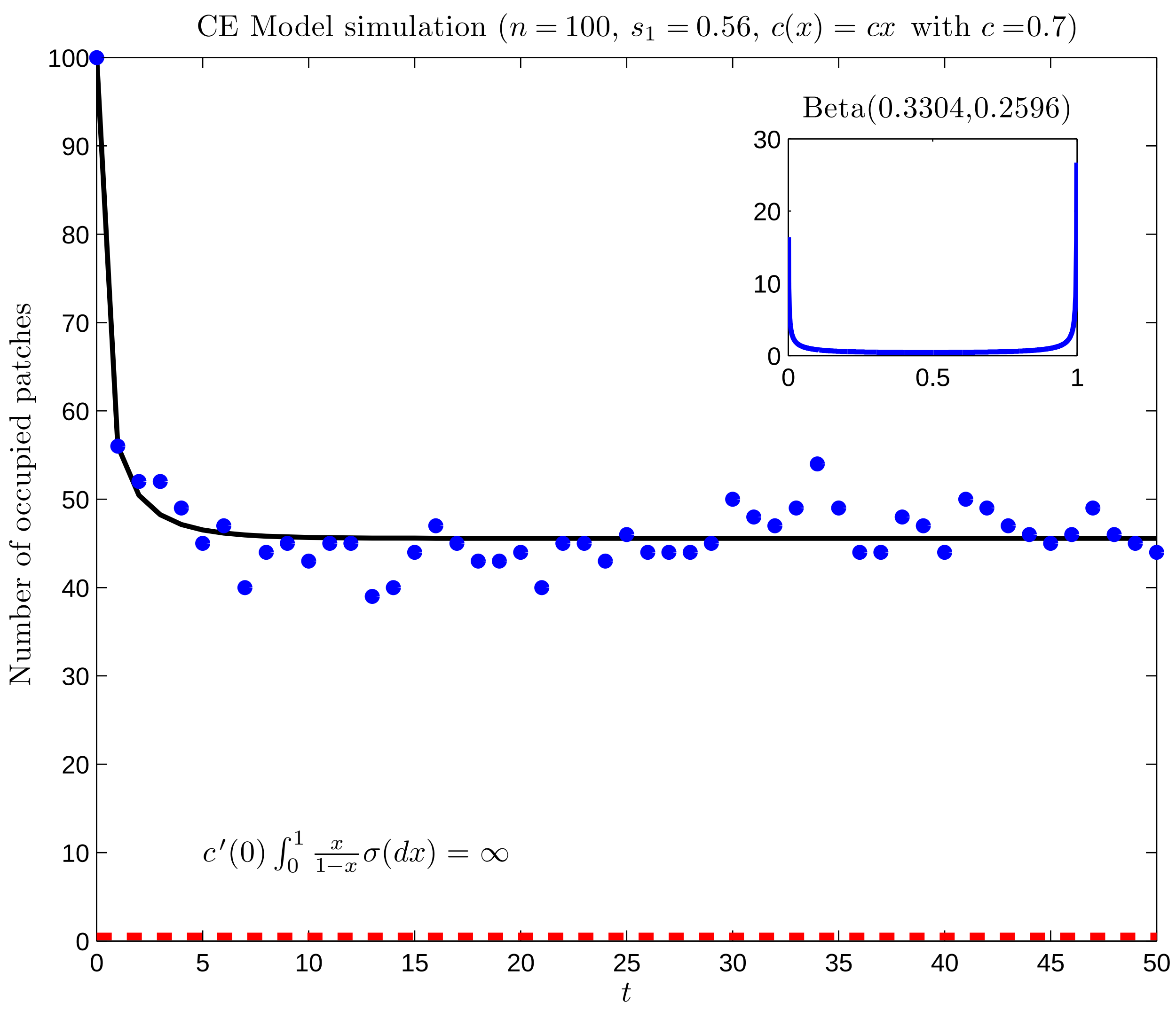
CE Model - Quasi stationarity



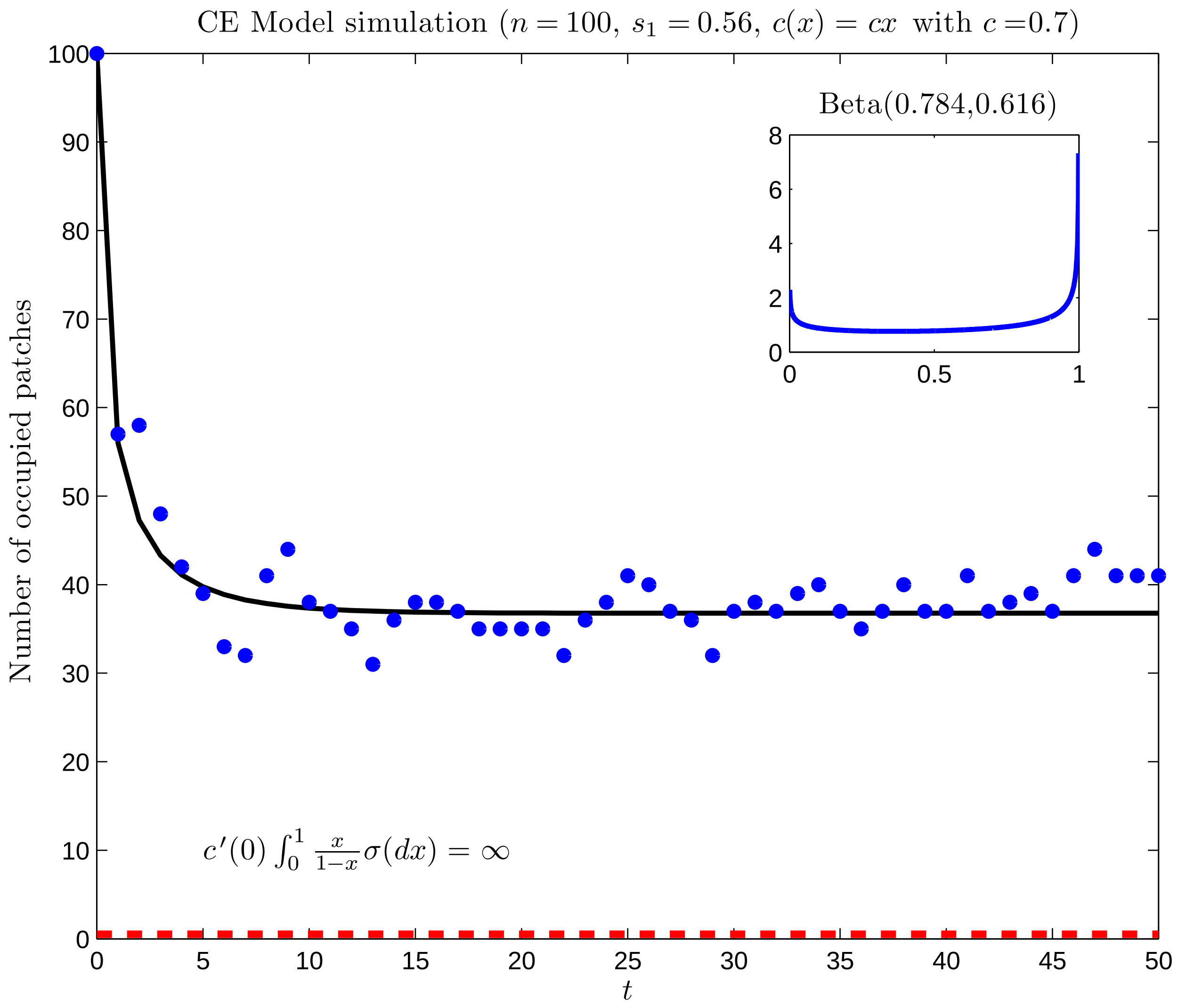
CE Model - Quasi stationarity



CE Model - Quasi stationarity



CE Model - Quasi stationarity



CE Model - Quasi stationarity