

Population networks with local extinction probabilities that evolve over time

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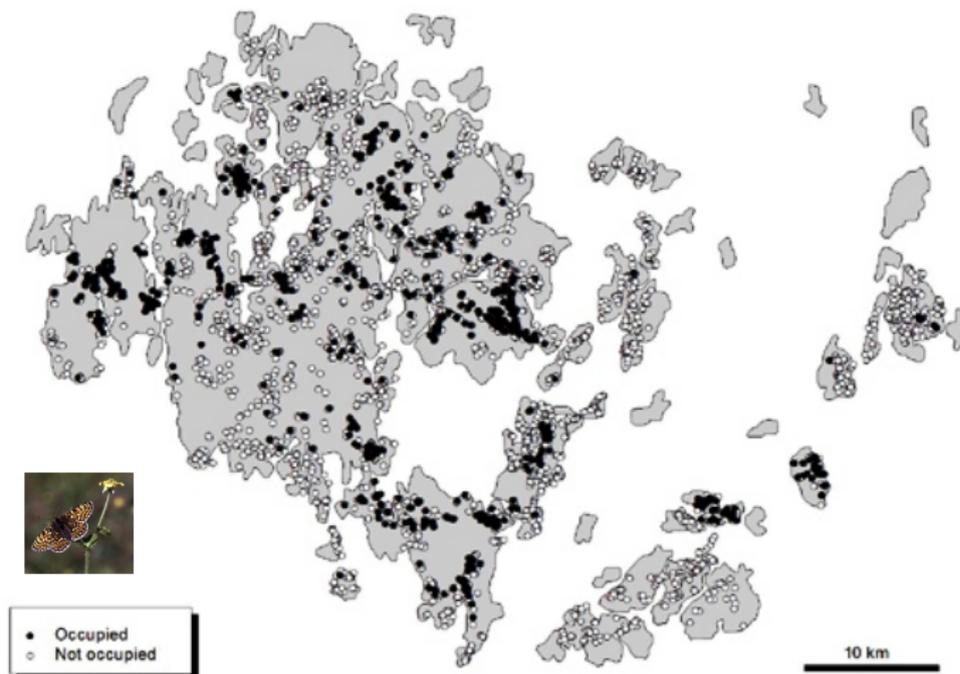
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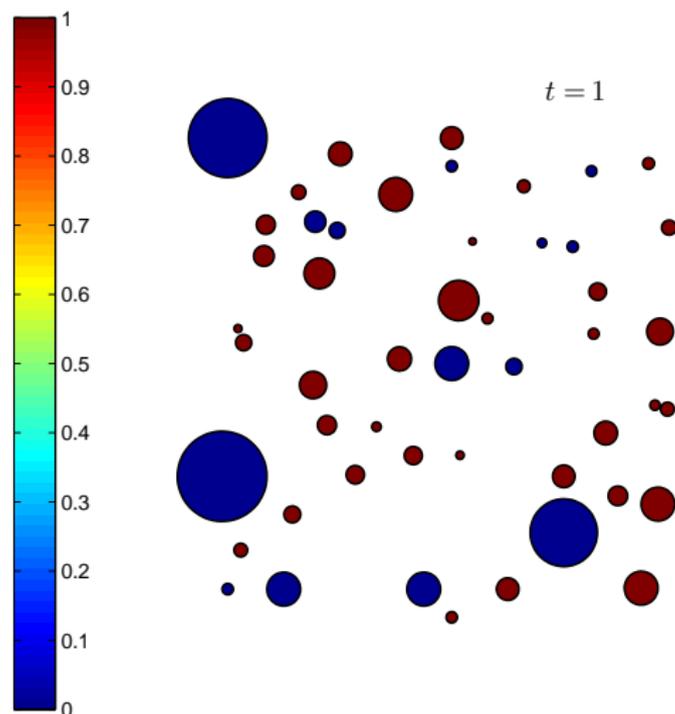


Metapopulations



Glanville fritillary butterfly (*Melitaea cinxia*) in the Åland Islands in Autumn 2005.

Occupancy simulation - proportion of time occupied



Positions: $z_i \in [-3, 3]^2$.

Tweaked spatial Poisson process.

Ease of movement:

$$D(z, \tilde{z}) = 5 \exp(-\|z - \tilde{z}\|).$$

Areas:

$$a_i = 6\pi R_i^2, \text{ where } R_i^2 \sim \exp(5000).$$

$$\mathbb{E}a_i \simeq 0.00377.$$

Colonization function:

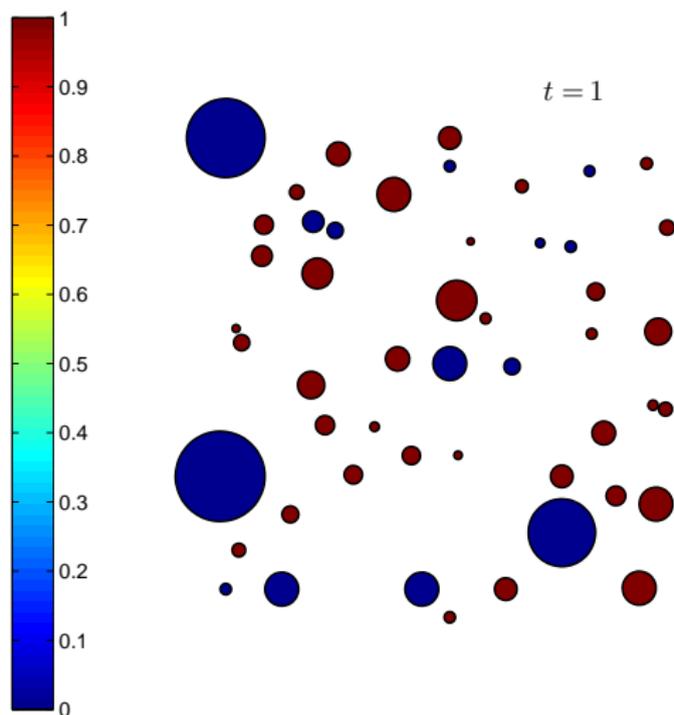
$$c(x) = 1 - \exp(-5x).$$

Survival probabilities:

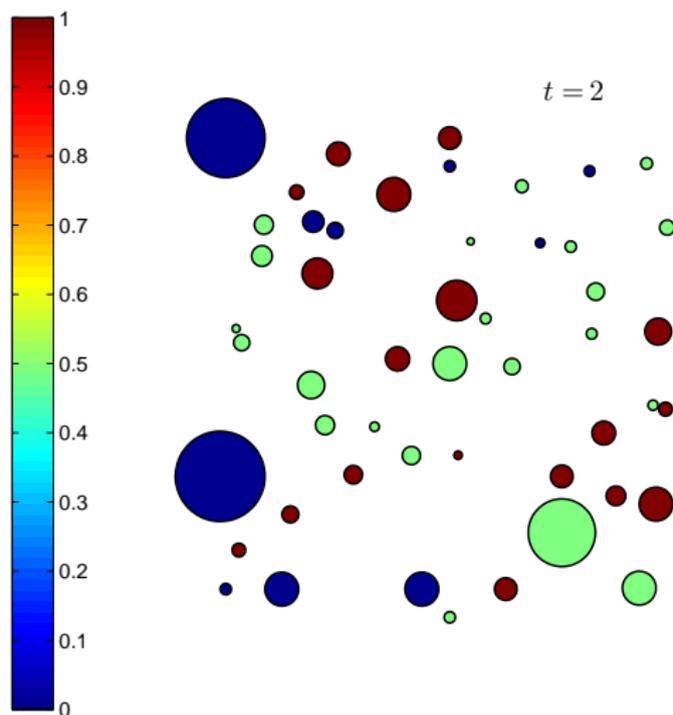
McKinlay-Borovkov model with $L_t \sim \text{Beta}(1, 1)$, $R_t \sim \text{Beta}(1, 20)$, and $\rho(s) = 9(s - 0.9) \mathbb{I}(s > 0.9)$.

Initial occupancy: 70%

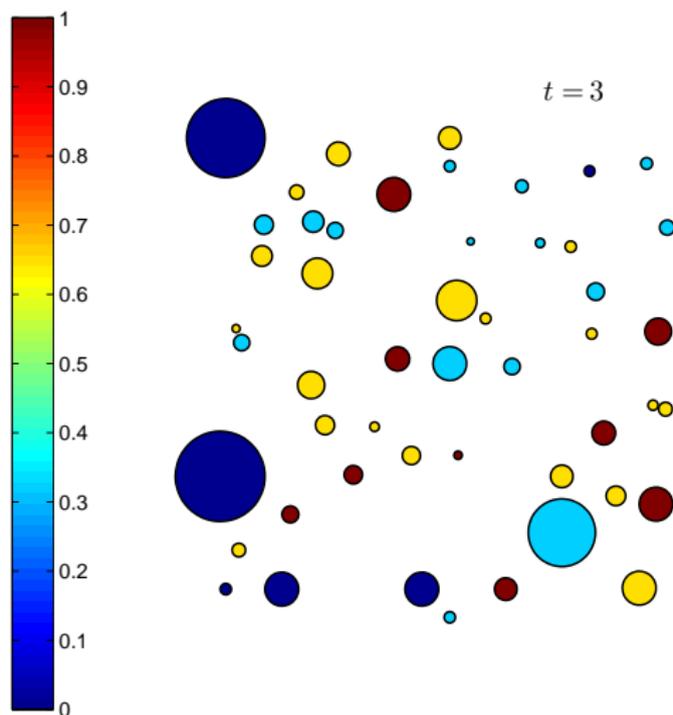
Occupancy simulation - proportion of time occupied



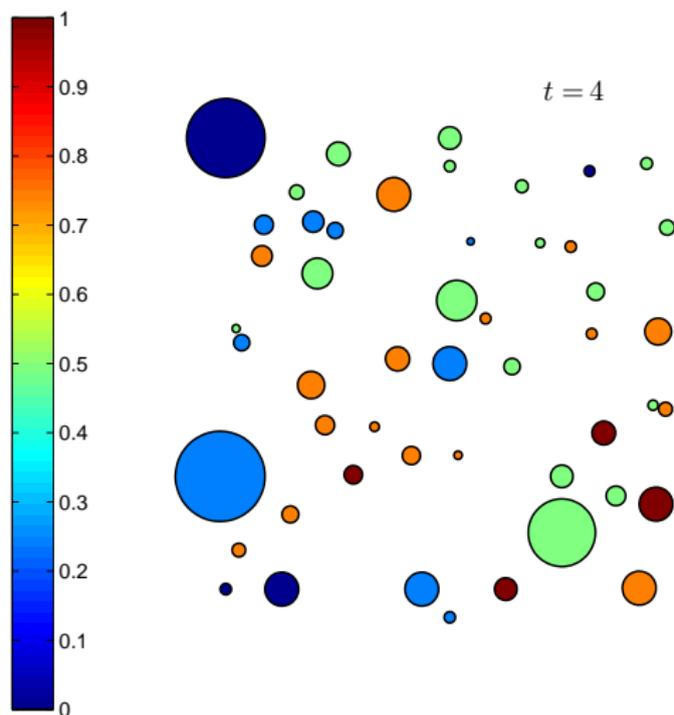
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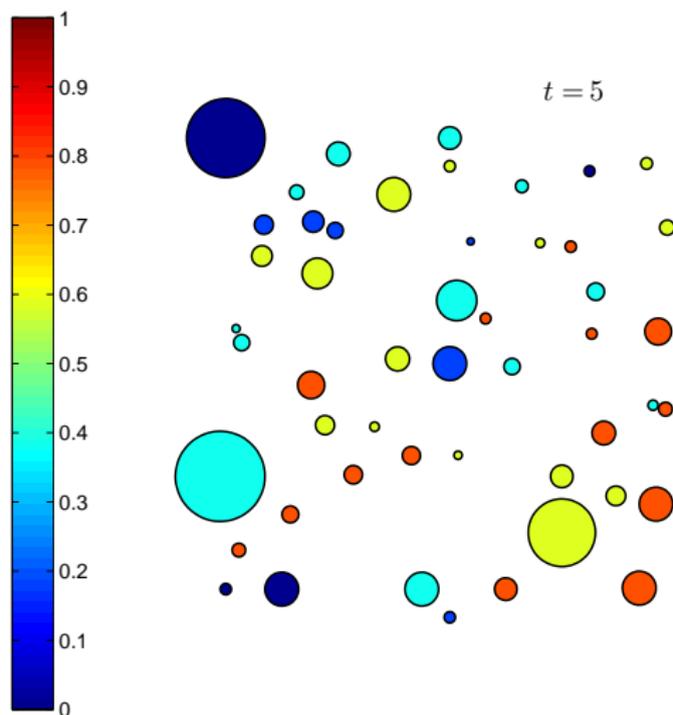
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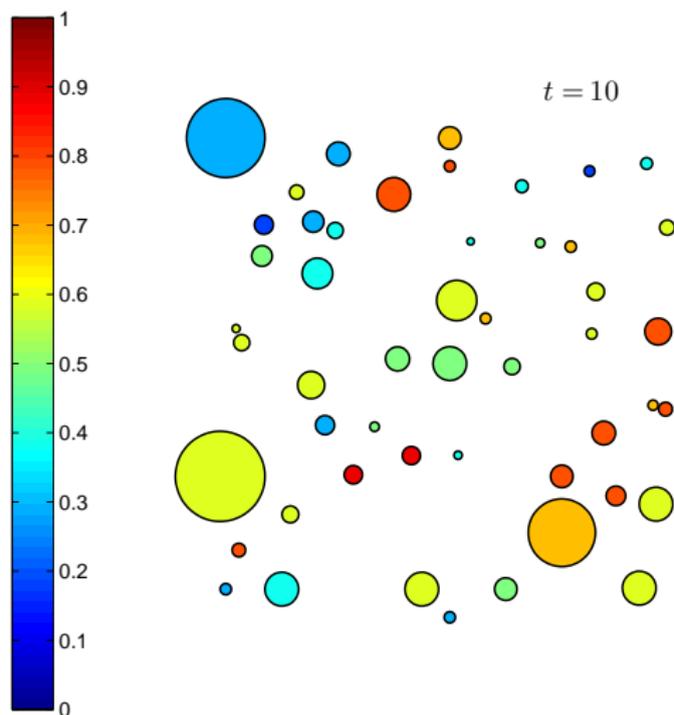
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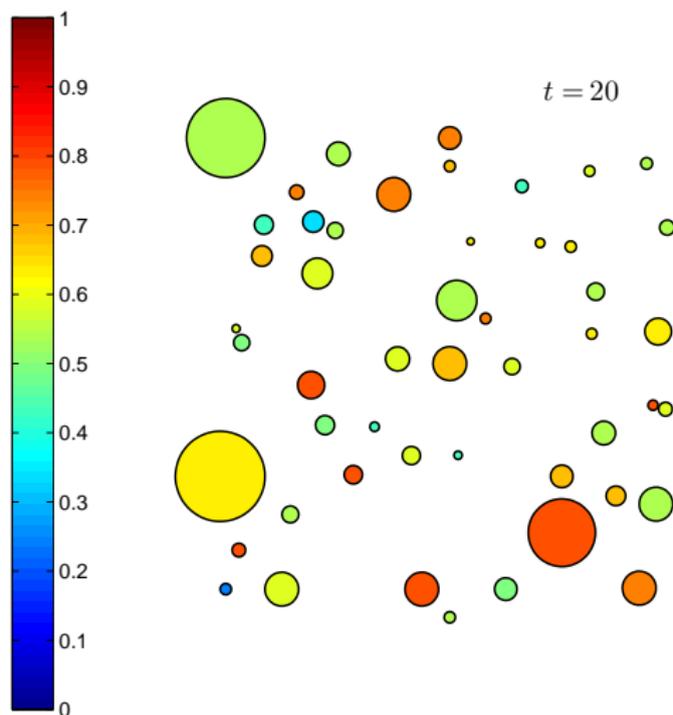
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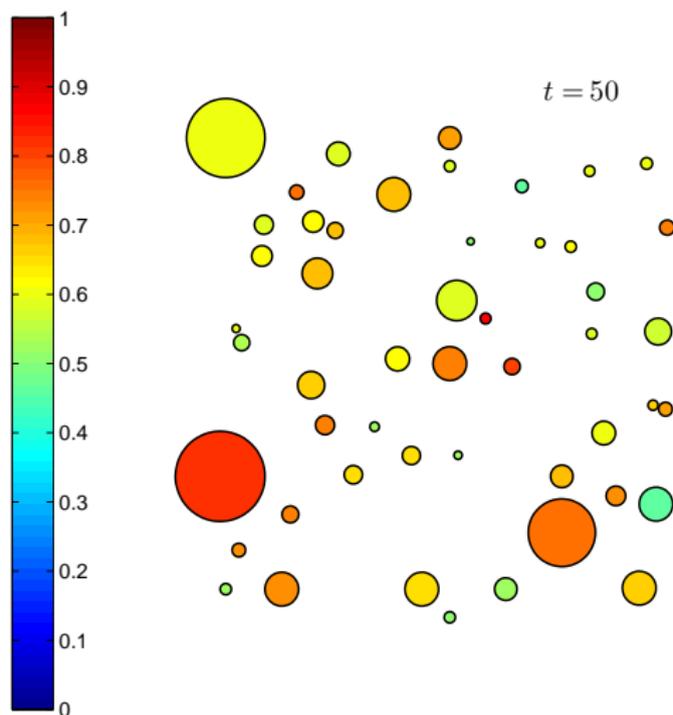
Occupancy simulation - proportion of time occupied



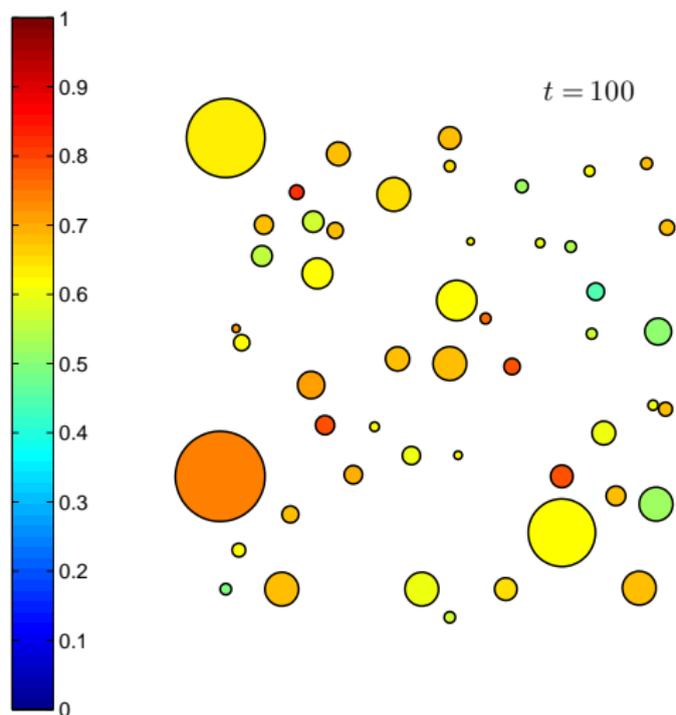
Occupancy simulation - proportion of time occupied



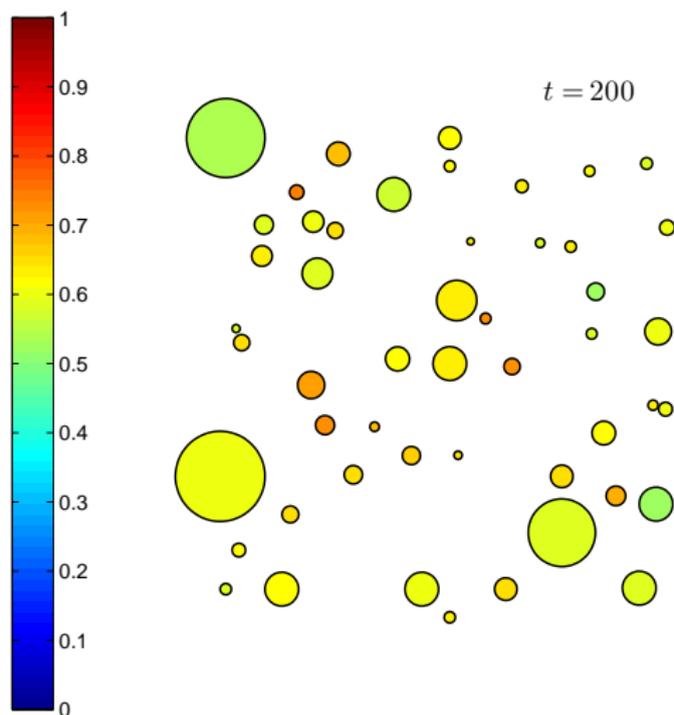
Occupancy simulation - proportion of time occupied



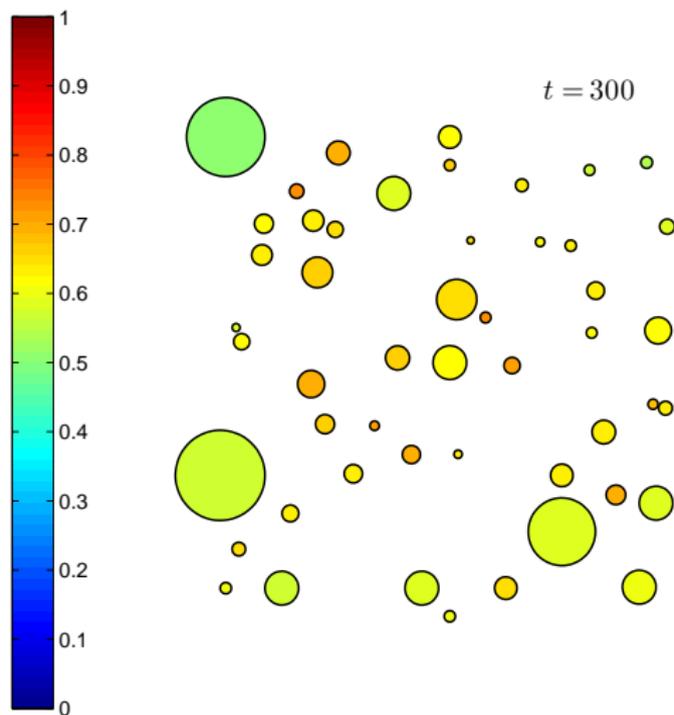
Occupancy simulation - proportion of time occupied



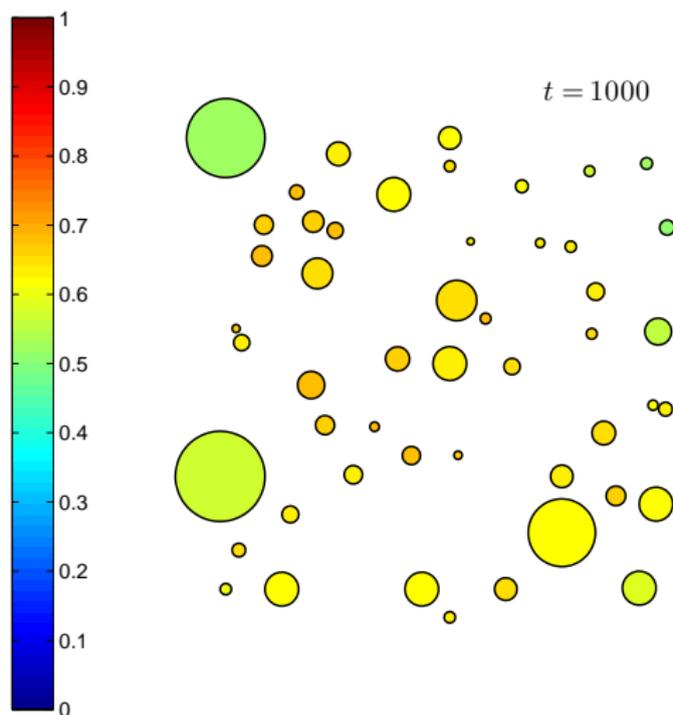
Occupancy simulation - proportion of time occupied



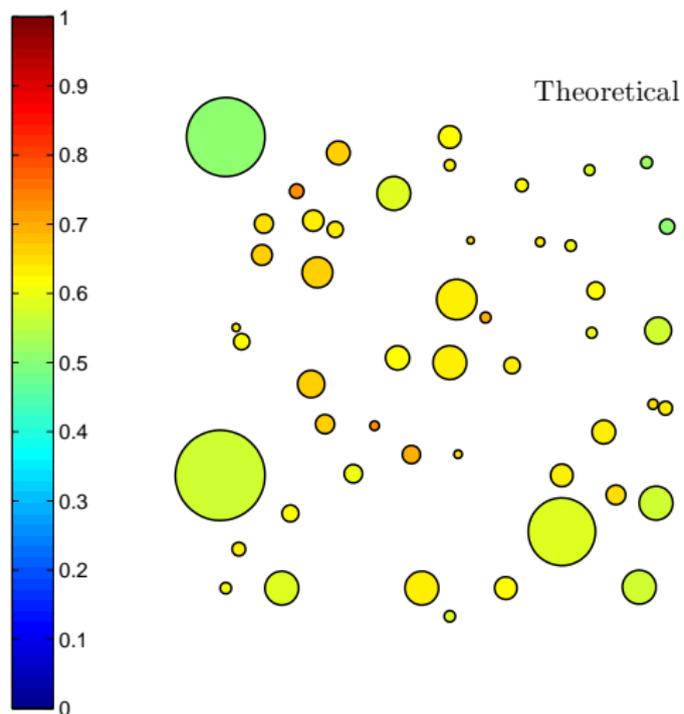
Occupancy simulation - proportion of time occupied



Occupancy simulation - proportion of time occupied



Theoretical - proportion of time occupied



A *stochastic patch occupancy model* (SPOM)

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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 .

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

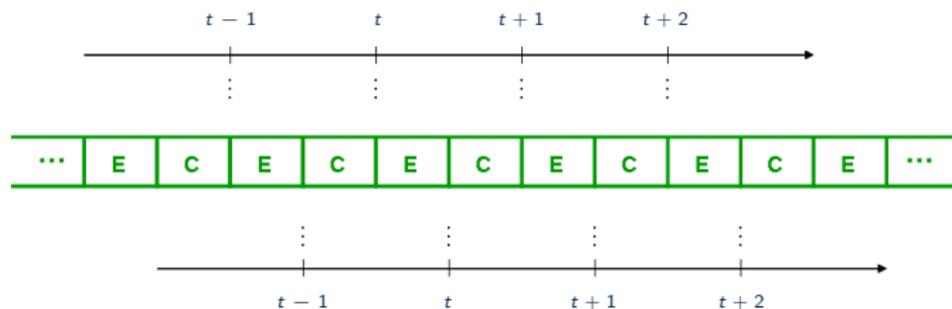
The Vernal pool fairy shrimp (*Branchinecta lynchi*) and the California linderiella (*Linderiella occidentalis*), both listed under the Endangered Species Act (USA)



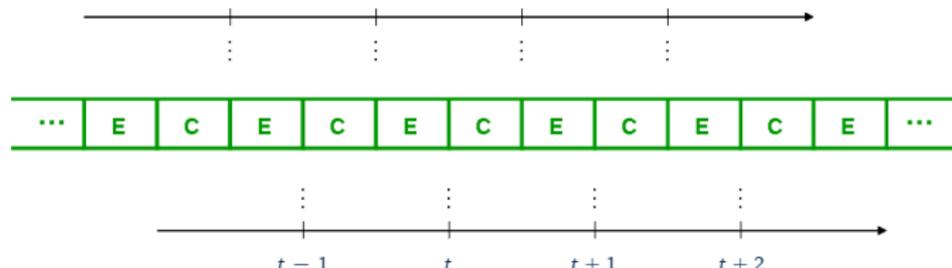
The Jasper Ridge population of Bay checkerspot butterfly (*Euphydryas editha bayensis*), now extinct



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

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 at z and \tilde{z} , a_j is a weight related to the size of the patch j and $c : [0, \infty) \rightarrow [0, 1]$ (*colonisation function*).

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Assumptions:

- (A) $a_i \in (0, A]$ for some $A < \infty$.
- (B) $z_i \in \Omega$ where Ω is a compact subset of \mathbb{R}^d .
- (C) $D(z, \tilde{z})$ is positive, uniformly bounded, and equicontinuous: for every $\epsilon > 0$ there exists a $\delta > 0$ such that if $\|z_1 - z_2\| < \delta$, then $\sup_{z \in \Omega} |D(z_1, z) - D(z_2, z)| < \epsilon$.
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Examples: $D(z, \tilde{z}) = \exp(-\beta \|z - \tilde{z}\|)$ and $c(x) = 1 - \exp(-\alpha x)$, where $\alpha, \beta > 0$.

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

$$\Pr \left(X_{i,t+1}^{(n)} = 1 \mid X_t^{(n)}, S_t^{(n)} \right) = s_{i,t} X_{i,t}^{(n)} + s_{i,t} c \left(\frac{1}{n} \sum_{j=1}^n X_{j,t}^{(n)} D(z_i, z_j) a_j \right) (1 - X_{i,t}^{(n)}).$$

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- (E) We will assume that $(s_{i,t})_{t=0}^{\infty}$, $i = 1, \dots, n$, are independent Markov chains taking values in $[0, 1]$ with common transition kernel $P(s, dr)$ that is assumed to satisfy the weak Feller property: for every continuous function h on $[0, 1]$, the function defined by $Ph(s) := \int h(r)P(s, dr)$, $s \in [0, 1]$, is also continuous.

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

$$P(s, dr) = q(s)\delta_{s^*}(dr) + (1 - q(s))\delta_0(dr).$$

Example of the survival probability model

Henceforth the Markov chain $(s_t)_{t=0}^{\infty}$ will be the survival probability model for any particular patch (recall that they are independent from patch to patch).

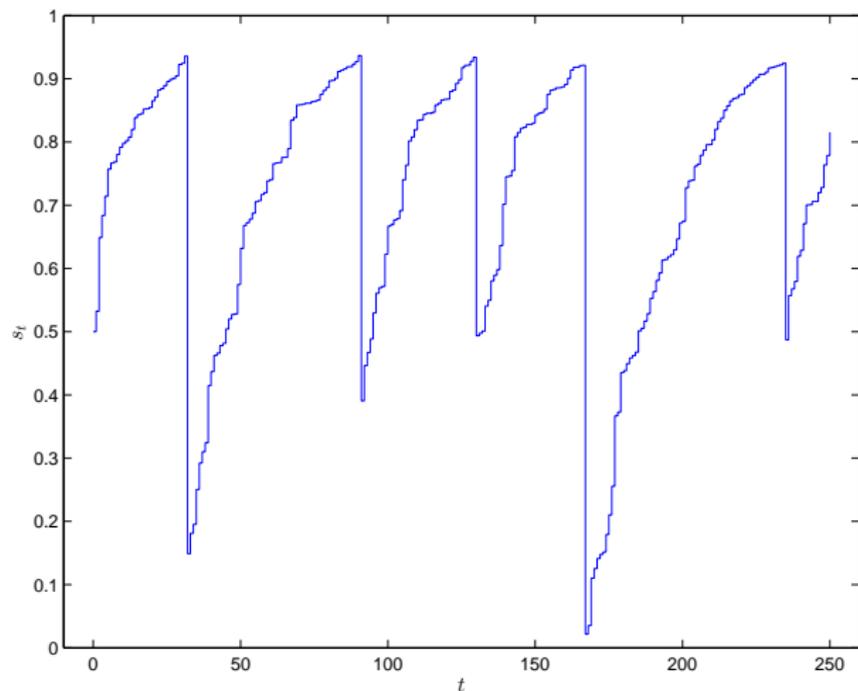
Example Following McKinlay and Borovkov*, suppose that

$$s_{t+1} = \begin{cases} s_t(1 - L_{t+1}) & \text{with probability } p(s_t) \\ s_t + (1 - s_t)R_{t+1} & \text{with probability } 1 - p(s_t), \end{cases}$$

where $p : [0, 1] \mapsto [0, 1]$, and (L_t) and (R_t) are sequences of independent and identically distributed random variables on $[0, 1]$ with distributions F_L and F_R , respectively. If p is continuous, then the transition kernel $P(s, dr)$ satisfies the weak Feller property.

*McKinlay, S. and Borovkov, K. (2015) On explicit form of the stationary distributions for a class of bounded Markov chains. *J. Appl. Probab.* (to appear) [arXiv:1412.1278 (math.PR)].

Climax community species



$L_t \sim \text{Beta}(1, 1)$, $R_t \sim \text{Beta}(1, 20)$, and $p(s) = 9(s - 0.9) \mathbb{I}(s > 0.9)$.

In the *homogeneous case*, where $D \equiv 1$, $a \equiv 1$, and $s_i = s$ 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:

Proposition 1 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

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

SPOM - Homogeneous case - Law of Large Numbers

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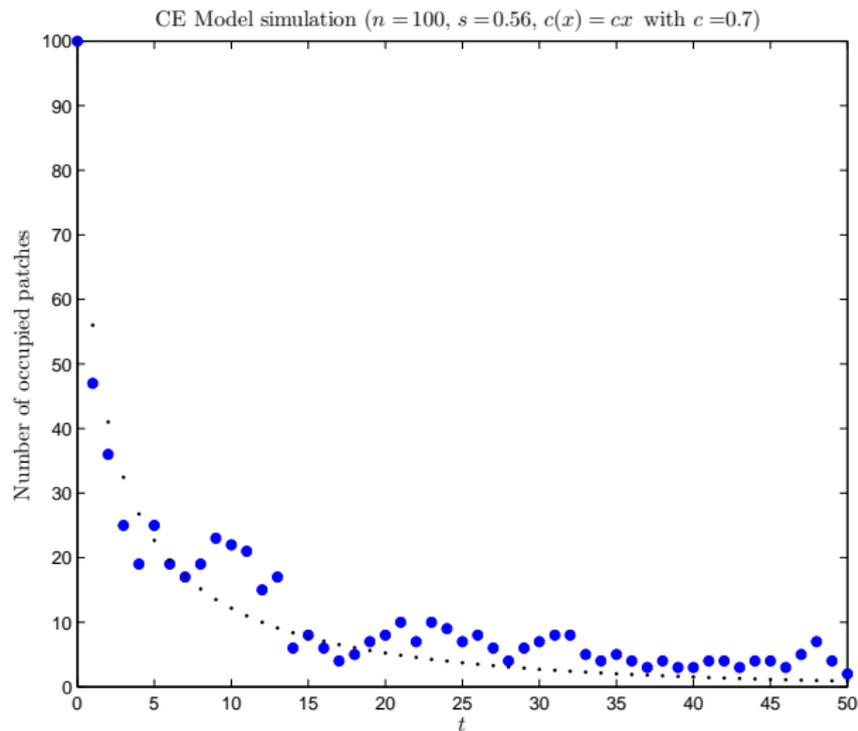
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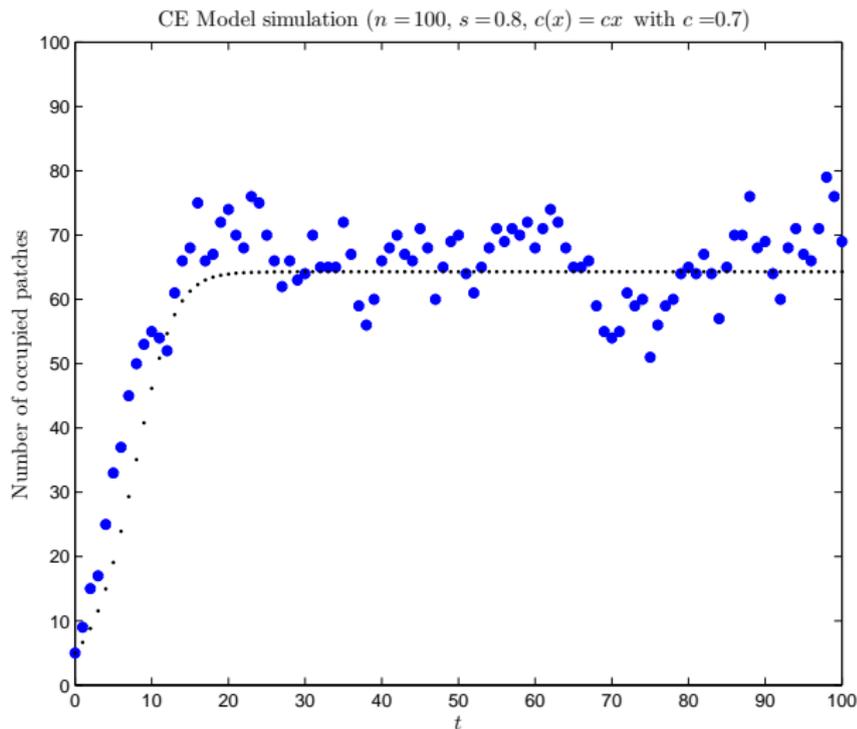
Survival probability

Colonization probability

CE Model - Evanescence



CE Model - Quasi stationarity



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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).

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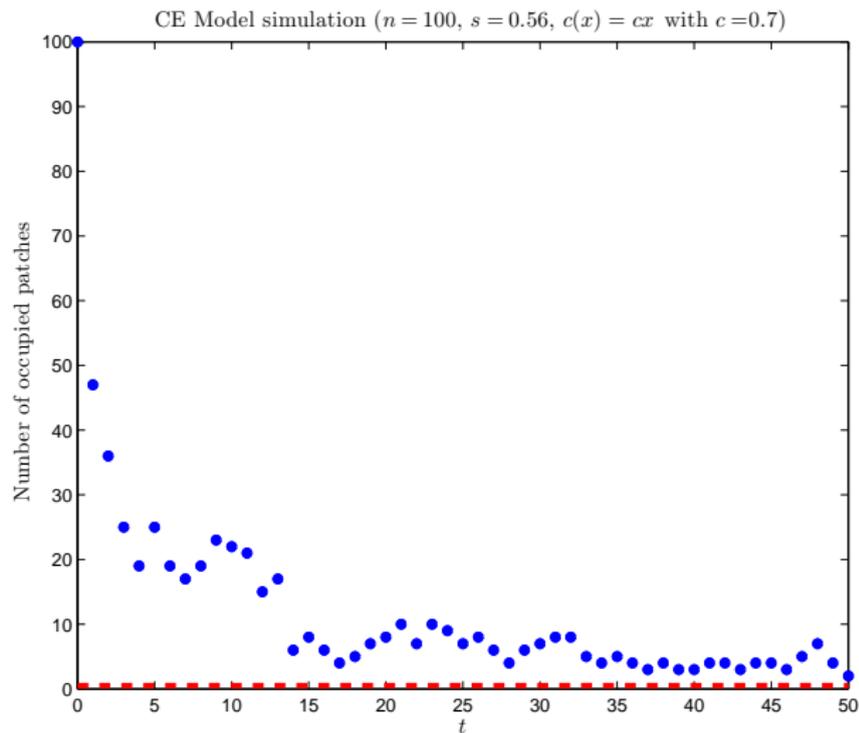
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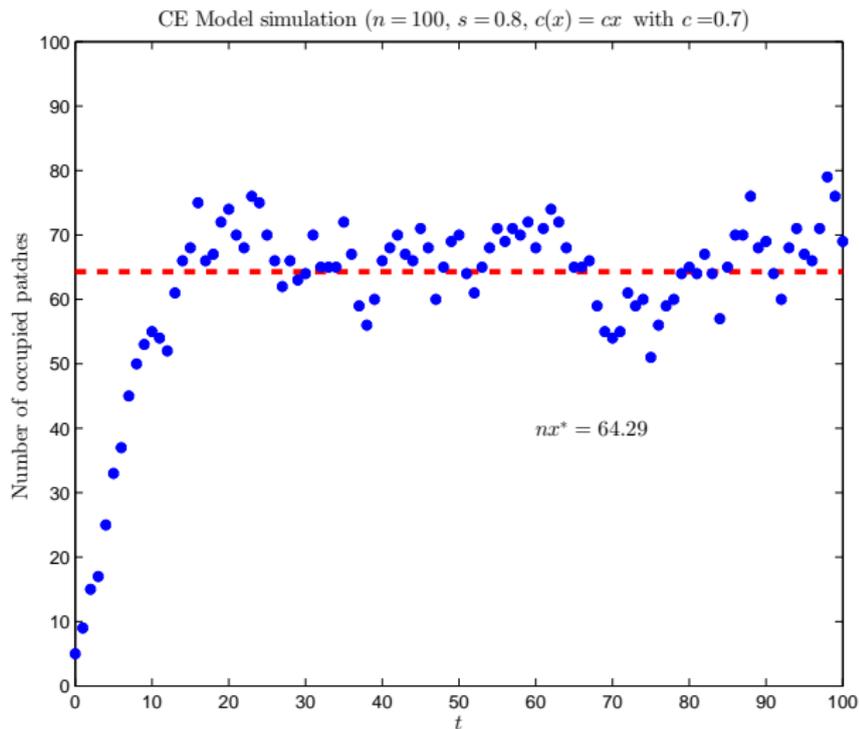
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CE Model - Evanescence



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

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

$$\int h(s, z) \sigma_{n,t}(ds, dz) = \frac{1}{n} \sum_{i=1}^n a_i h(s_{i,t}, z_i), \quad h \in C^+([0, 1] \times \Omega),$$

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where $C^+([0, 1] \times \Omega)$ is the space of continuous functions $h : [0, 1] \times \Omega \mapsto [0, \infty)$.

For example ($h \equiv 1$), $\int \mu_{n,t}(ds, dz) = \frac{1}{n} \sum_{i=1}^n a_i X_{i,t}^{(n)}$, the proportion of occupied patches at time t weighted according to patch size.

(F) Assume that $\sigma_{n,0} \xrightarrow{d} \sigma_0$ for some non-random measure σ_0 .

Limiting behaviour of the landscape

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For example, if the random vectors $(a_i, s_{i,0}, z_i)$, $i = 1, 2, \dots$, are iid with distribution F , then $\sigma_{n,0} \xrightarrow{d} \sigma_0$, where $\sigma_0(B) = \int aF(da, B)$, for any (measurable) $B \subset [0, 1] \times \Omega$.

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Lemma 1 $\sigma_{n,t} \xrightarrow{d} \sigma_t$ for all $t = 1, 2, \dots$, where σ_t is defined by the recursion

$$\int h(s, z) \sigma_{t+1}(ds, dz) = \int h(s, z) \int P(r, ds) \sigma_t(dr, dz), \quad h \in C^+([0, 1] \times \Omega).$$

[Recall that $P(s, dr)$ is the common transition kernel of the $(s_{i,t})_{t=0}^\infty$, $i = 1, \dots, n$.]

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[Recall that $P(s, dr)$ is the common transition kernel of the $(s_{i,t})_{t=0}^\infty$, $i = 1, \dots, n$.]

For a large population (n large), $\sigma_t(ds, dz)$ describes the landscape at time t .

Limiting behaviour of the metapopulation

Theorem 1 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 $t = 1, 2, \dots$, where μ_t is defined by the following recursion: for $h \in C^+([0, 1] \times \Omega)$,

$$\int h(s, z) \mu_{t+1}(ds, dz) = \int s Ph(s, z) (1 - c_t(z)) \mu_t(ds, dz) + \int s Ph(s, z) c_t(z) \sigma_t(ds, dz),$$

where

$$Ph(s, z) = \int h(r, z) P(s, dr) \quad \text{and} \quad c_t(z) = c \left(\int D(z, \tilde{z}) \mu_t(d\tilde{s}, d\tilde{z}) \right).$$

[Recall that $c(\cdot)$ is the colonization function.]

Limiting behaviour of the metapopulation

Theorem 1 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 $t = 1, 2, \dots$, where μ_t is defined by the following recursion: for $h \in C^+([0, 1] \times \Omega)$,

$$\int h(s, z) \mu_{t+1}(ds, dz) = \int s Ph(s, z) (1 - c_t(z)) \mu_t(ds, dz) + \int s Ph(s, z) c_t(z) \sigma_t(ds, dz),$$

where

$$Ph(s, z) = \int h(r, z) P(s, dr) \quad \text{and} \quad c_t(z) = c \left(\int D(z, \tilde{z}) \mu_t(d\tilde{s}, d\tilde{z}) \right).$$

[Recall that $c(\cdot)$ is the colonization function.]

Think of $c_t(z)$ as being the limiting ($n \rightarrow \infty$) potential of the metapopulation at time t to colonize a patch located at z .

Limiting behaviour of the metapopulation

A consequence of the theorem is that the limiting occupancy of a single patch follows a Markov chain $(X_{i,t}, s_{i,t})_{t=0}^{\infty}$ with time dependent transition probabilities:

Corollary 1 Fix i . Then, $X_{i,0}^{(n)} \xrightarrow{P} X_{i,0}$ implies that $X_{i,t}^{(n)} \xrightarrow{P} X_{i,t}$ for all $t = 1, 2, \dots$, where

$$\Pr(X_{i,t+1} = 1 \mid X_{i,t}, s_{i,t}) = s_{i,t}X_{i,t} + s_{i,t}c_t(z_i)(1 - X_{i,t}).$$

[Recall that $c_t(z) = c(\int D(z, \tilde{z})\mu_t(d\tilde{s}, d\tilde{z}))$.]

When the landscape is in equilibrium

- (G) Assume that the survival probability model is stationary, aperiodic, and Harris positive recurrent with invariant measure ν : $\nu(dr) = \int_0^1 \nu(ds)P(s, dr)$.

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Let P^* be the *dual* (or *time-reverse*) transition kernel:

$$\int_A \nu(dx)P(x, B) = \int_B \nu(dx)P^*(x, A), \quad \text{measurable } A, B \subset [0, 1].$$

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Theorem 2 The limiting measure μ_t is absolutely continuous with respect to σ and the corresponding Radon-Nikodym derivative satisfies the recursion

$$\frac{\partial \mu_{t+1}}{\partial \sigma}(s, z) = \int_0^1 r \frac{\partial \mu_t}{\partial \sigma}(r, z) P^*(s, dr) + c_t(z) \int_0^1 r \left(1 - \frac{\partial \mu_t}{\partial \sigma}(r, z)\right) P^*(s, dr).$$

When the landscape is in equilibrium

In addition to enabling a simplified recursion

$$\frac{\partial \mu_{t+1}}{\partial \sigma}(s, z) = \int_0^1 r \frac{\partial \mu_t}{\partial \sigma}(r, z) P^*(s, dr) + c_t(z) \int_0^1 r \left(1 - \frac{\partial \mu_t}{\partial \sigma}(r, z) \right) P^*(s, dr)$$

for the limiting measure μ_t , the Radon-Nikodym derivative has a nice interpretation as the probability that a given patch is occupied when the number of patches is large:

Corollary 2 Fix i and let $(X_{i,t}, s_{i,t})_{t=0}^{\infty}$ be the Markov chain in the last corollary. If

$$\Pr(X_{i,0} = 1 \mid s_{i,0} = s, z_i = z) = \frac{\partial \mu_0}{\partial \sigma}(s, z),$$

then

$$\Pr(X_{i,t} = 1 \mid s_{i,t} = s, z_i = z) = \frac{\partial \mu_t}{\partial \sigma}(s, z),$$

for all $t = 1, 2, \dots$

The limiting metapopulation in equilibrium

We seek fixed points $\frac{\partial \mu_\infty}{\partial \sigma}$ of the simplified recursion

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$$\frac{\partial \mu_\infty}{\partial \sigma}(s, z) = c(\psi(z)) \int r P^*(s, dr) + (1 - c(\psi(z))) \int r \frac{\partial \mu_\infty}{\partial \sigma}(r, z) P^*(s, dr),$$

where $\psi(z) = \int D(z, \tilde{z}) \mu_\infty(d\tilde{s}, d\tilde{z})$.

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where $\psi(z) = \int D(z, \tilde{z}) \mu_\infty(d\tilde{s}, d\tilde{z})$.

Think of $\psi(z)$ as being the equilibrium large-metapopulation connectivity for a patch located at z , and $c(\psi(z))$ as being the corresponding equilibrium potential of the population to colonize that patch.

The limiting metapopulation in equilibrium

Treating ψ as fixed,

$$\frac{\partial \mu_\infty}{\partial \sigma}(s, z) = c(\psi(z)) \int r P^*(s, dr) + (1 - c(\psi(z))) \int r \frac{\partial \mu_\infty}{\partial \sigma}(r, z) P^*(s, dr)$$

is a Fredholm integral equation of the second kind: $g(s, z) = \phi(s, z) + (\mathcal{A}g)(s, z)$.

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It has a unique solution given by the Neumann series

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where (s_t^*) is the Markov chain with transition kernel P^* .

The limiting metapopulation in equilibrium

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Then, using the duality relationship (time reversal),

$$\frac{\partial \mu_\infty}{\partial \sigma}(s, z) = \sum_{n=0}^{\infty} c(\psi(z)) (1 - c(\psi(z)))^n \mathbb{E}(s_0 \cdots s_n | s_{n+1} = s).$$

The limiting metapopulation in equilibrium

Now

$$\psi(z) = \int D(z, \tilde{z}) \mu_\infty(d\tilde{s}, d\tilde{z}) = \int D(z, \tilde{z}) \frac{\partial \mu_\infty}{\partial \sigma}(\tilde{s}, \tilde{z}) \sigma(d\tilde{s}, d\tilde{z}).$$

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we get a fixed point equation for $\psi(z)$:

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The limiting metapopulation in equilibrium

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Note that the equilibrium proportion of time a patch at location z is occupied is

$$\int \frac{\partial \mu_\infty}{\partial \sigma}(s, z) \nu(ds) = \sum_{n=0}^{\infty} c(\psi(z)) (1 - c(\psi(z)))^n \mathbb{E}(s_0 \cdots s_n).$$

The limiting metapopulation in equilibrium

To justify these steps and to elucidate stability conditions, we need the following assumptions.

- (H) The colonisation function c is strictly concave.
- (I) For every $z \in \Omega$ and every open neighbourhood N_z of z , $\sigma([0, 1] \times N_z) > 0$.
- (J) The survival probability model satisfies $\inf_s \mathbb{E}(s_0 \mid s_1 = s) = \inf_s \int u P^*(s, du) > 0$.

The limiting metapopulation in equilibrium

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Theorem 3 Let $\mathcal{G} : C(\Omega) \mapsto C(\Omega)$ be the bounded linear operator defined by

$$\mathcal{G}\phi(z) := c'(0) \sum_{m=0}^{\infty} \mathbb{E}(s_0 \cdots s_m) \int D(z, \tilde{z}) \phi(\tilde{z}) \bar{\sigma}_0(d\tilde{z}), \quad \phi \in C(\Omega),$$

and let $r(\mathcal{G})$ be the spectral radius of \mathcal{G} . If $r(\mathcal{G}) \leq 1$, then the simplified recursion has only the trivial fixed point $\frac{\partial \mu}{\partial \sigma}(s, z) = 0$, and this fixed point is globally stable (*evanescence*). If $r(\mathcal{G}) > 1$, then it has a unique non-zero fixed point and all non-zero trajectories converge to this fixed point (*persistence*).

The limiting metapopulation in equilibrium

In order to obtain information about the fixed points of the simplified recursion, we make the following assumptions.

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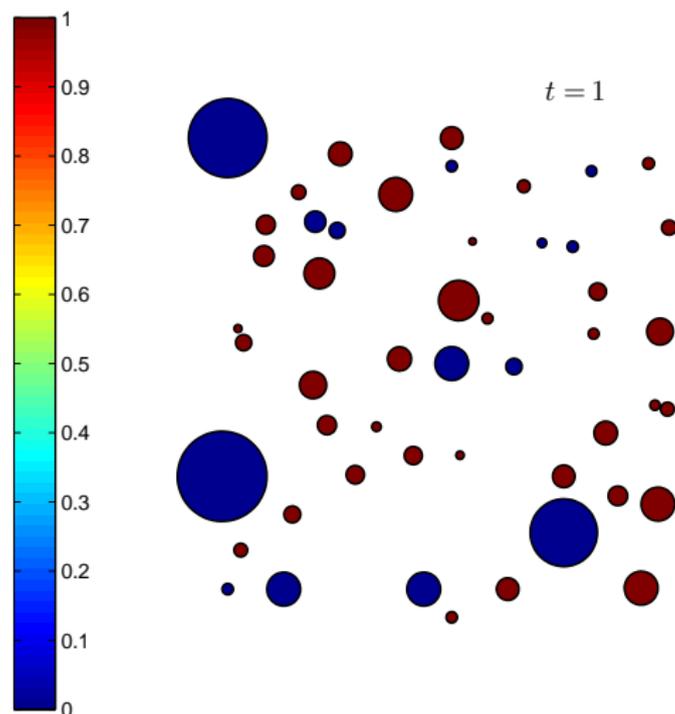
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Occupancy simulation - proportion of time occupied



Positions: $z_i \in [-3, 3]^2$.

Tweaked spatial Poisson process.

Ease of movement:

$$D(z, \tilde{z}) = 5 \exp(-\|z - \tilde{z}\|).$$

Areas:

$$a_i = 6\pi R_i^2, \text{ where } R_i^2 \sim \exp(5000).$$

$$\mathbb{E}a_i \simeq 0.00377.$$

Colonization function:

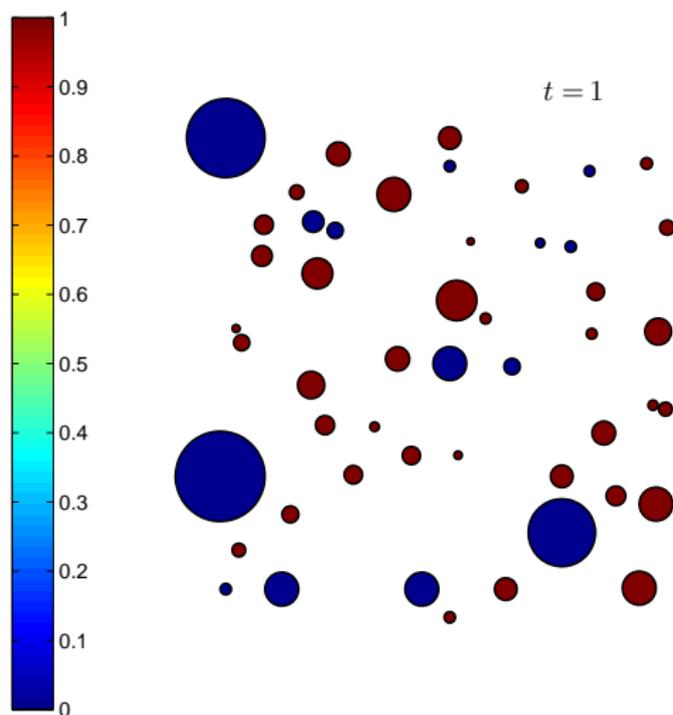
$$c(x) = 1 - \exp(-5x).$$

Survival probabilities:

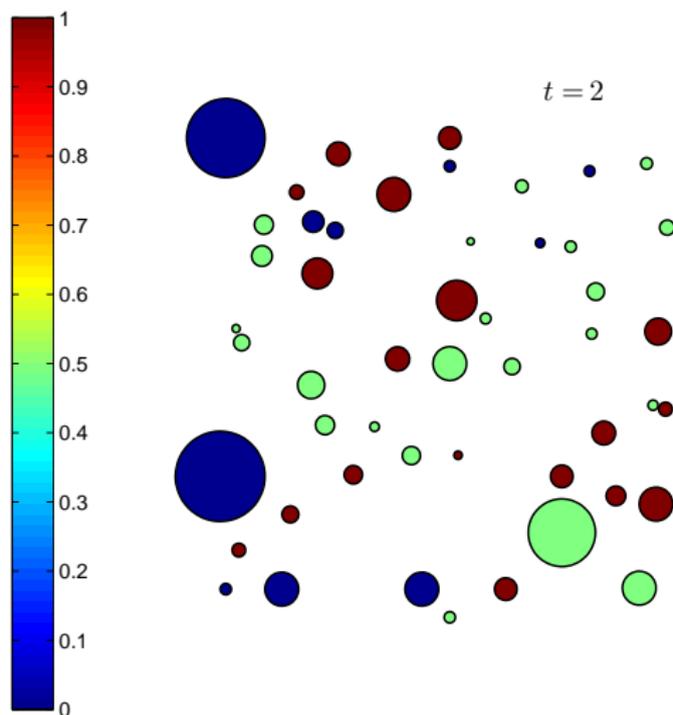
McKinlay-Borovkov model with $L_t \sim \text{Beta}(1, 1)$, $R_t \sim \text{Beta}(1, 20)$, and $\rho(s) = 9(s - 0.9) \mathbb{I}(s > 0.9)$.

Initial occupancy: 70%

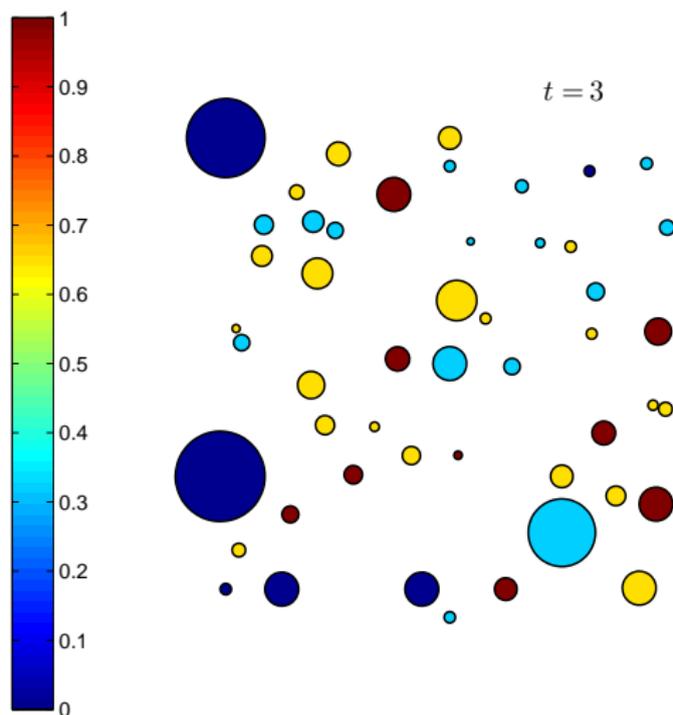
Occupancy simulation - proportion of time occupied



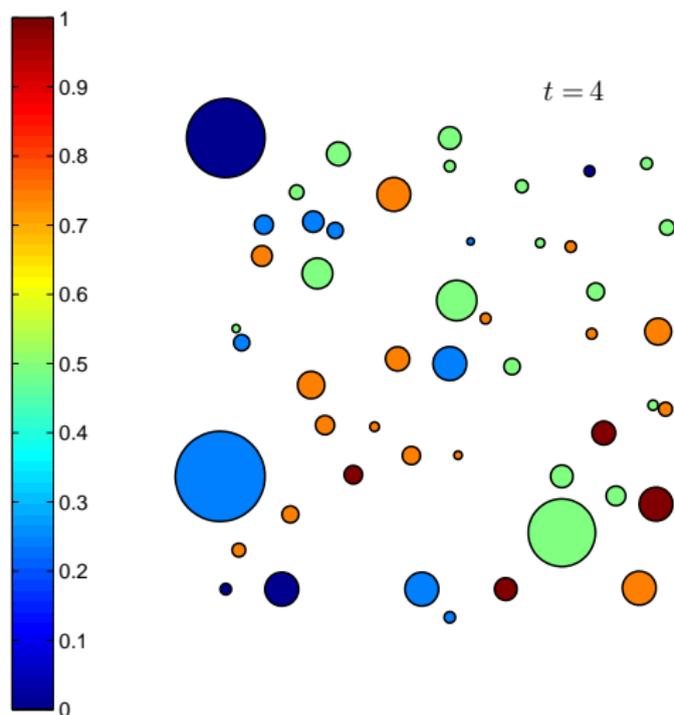
Occupancy simulation - proportion of time occupied



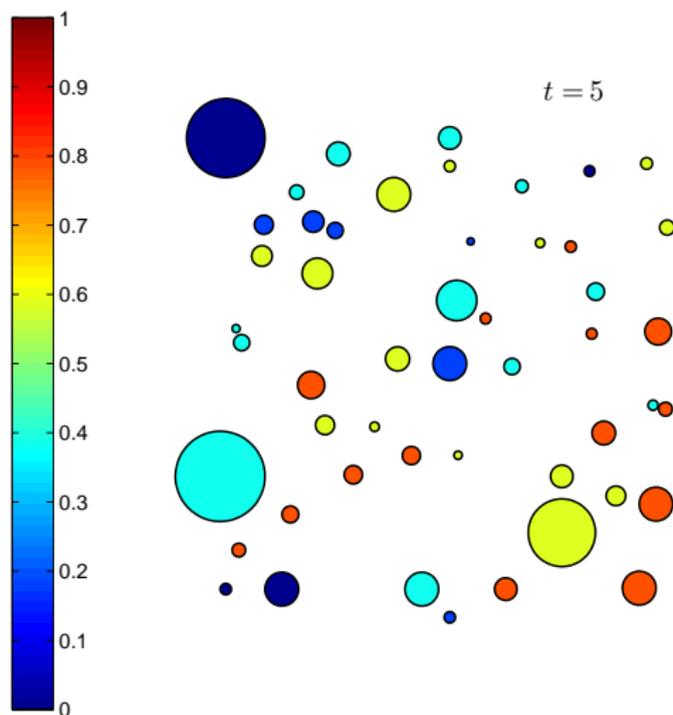
Occupancy simulation - proportion of time occupied



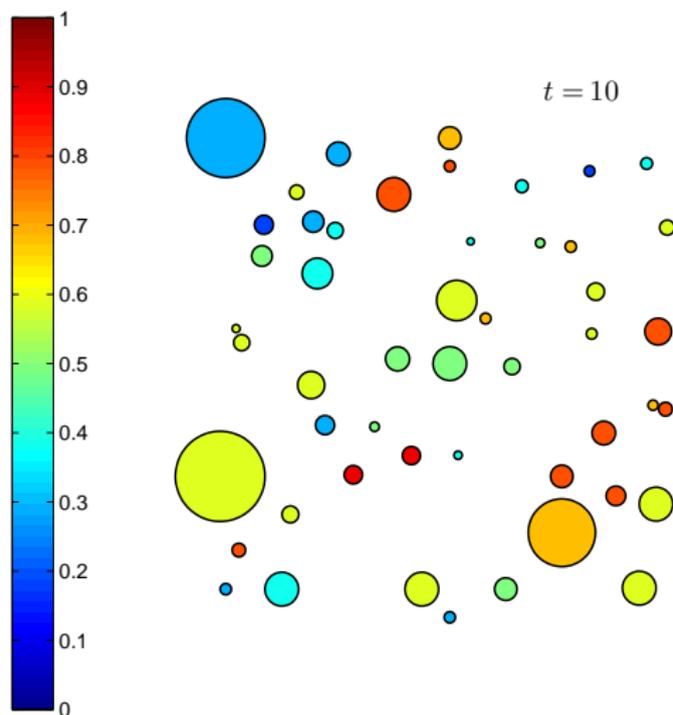
Occupancy simulation - proportion of time occupied



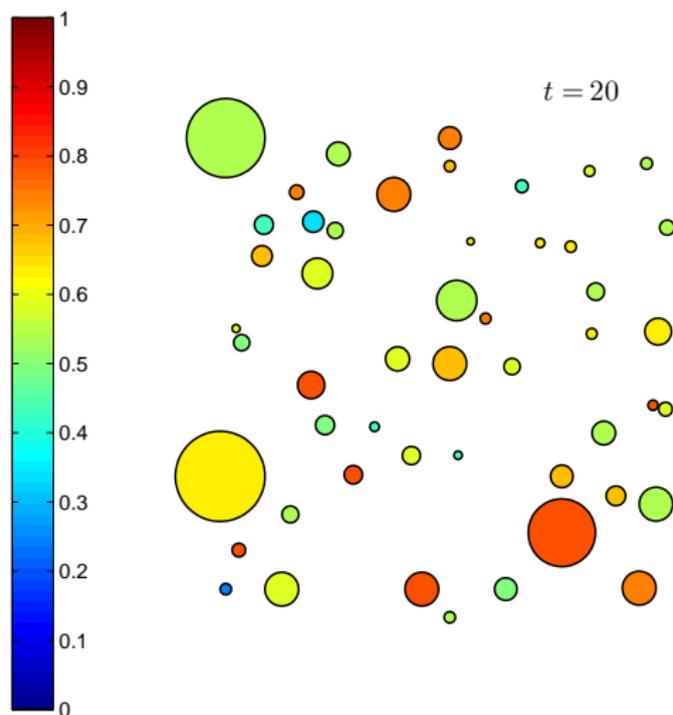
Occupancy simulation - proportion of time occupied



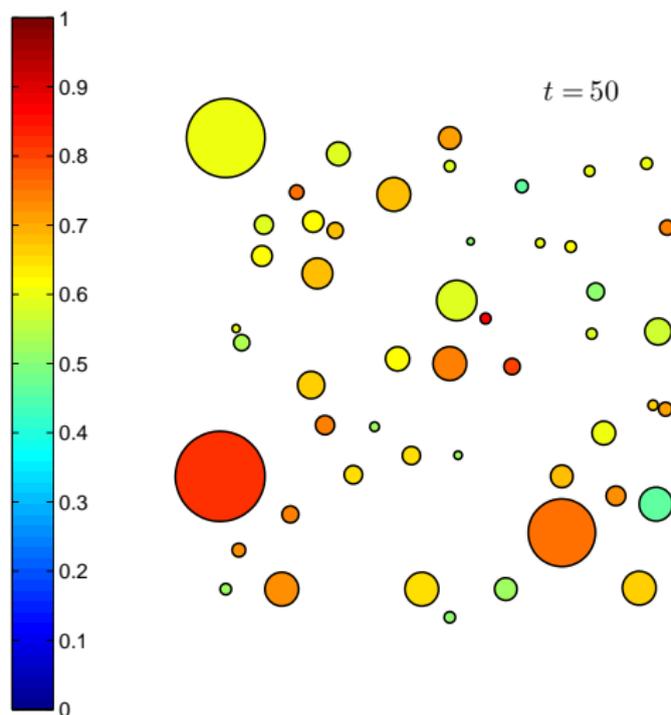
Occupancy simulation - proportion of time occupied



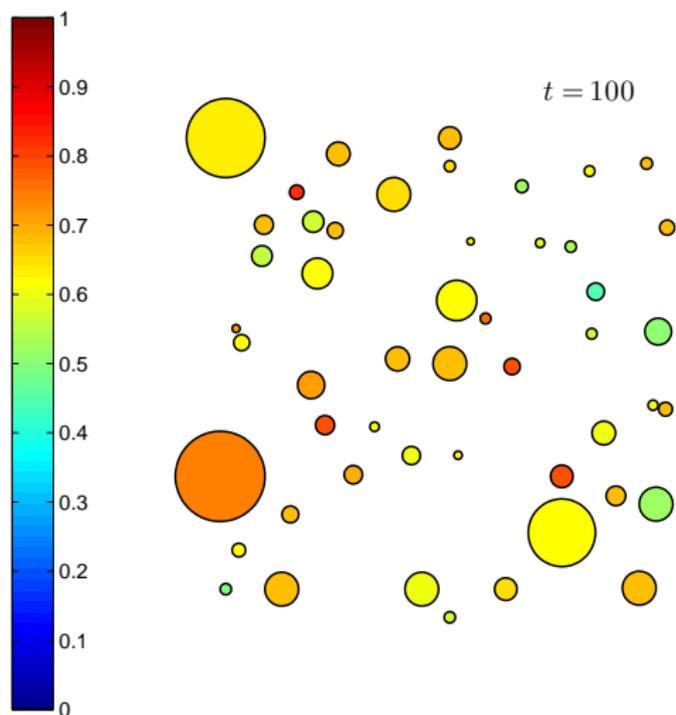
Occupancy simulation - proportion of time occupied



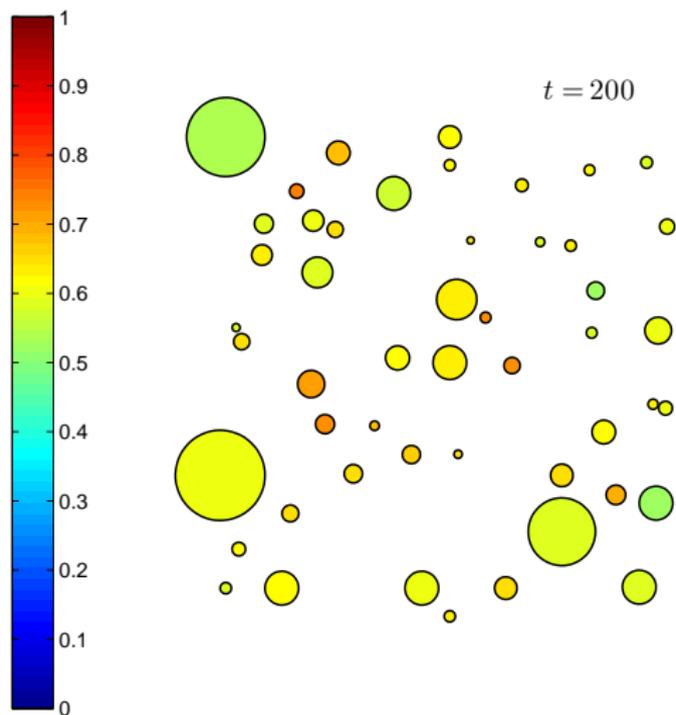
Occupancy simulation - proportion of time occupied



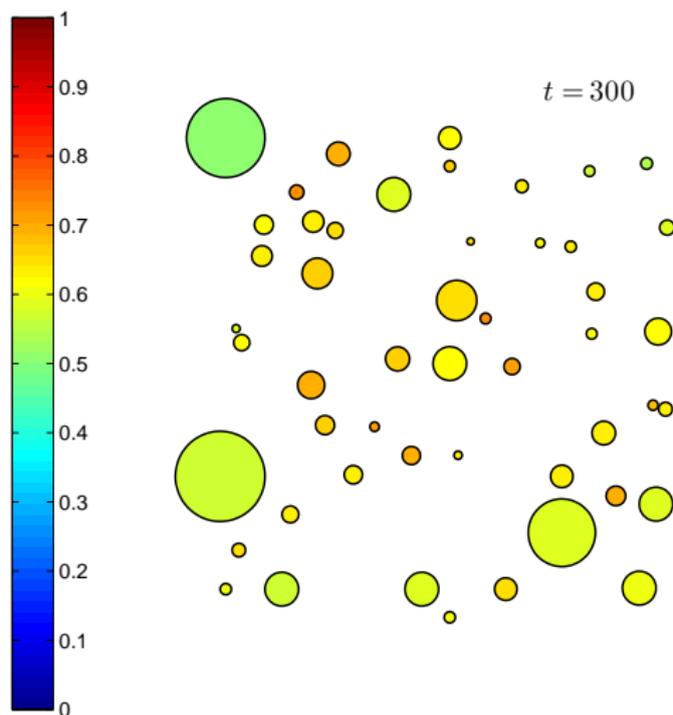
Occupancy simulation - proportion of time occupied



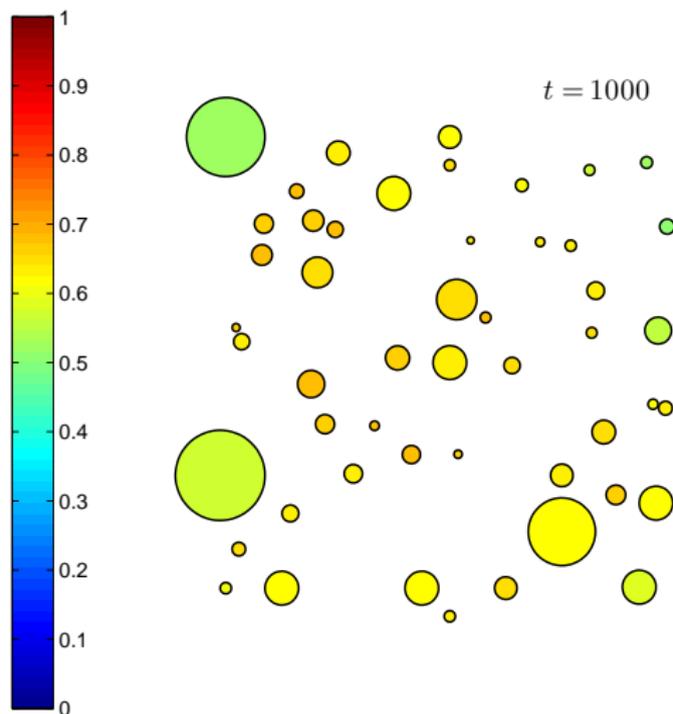
Occupancy simulation - proportion of time occupied



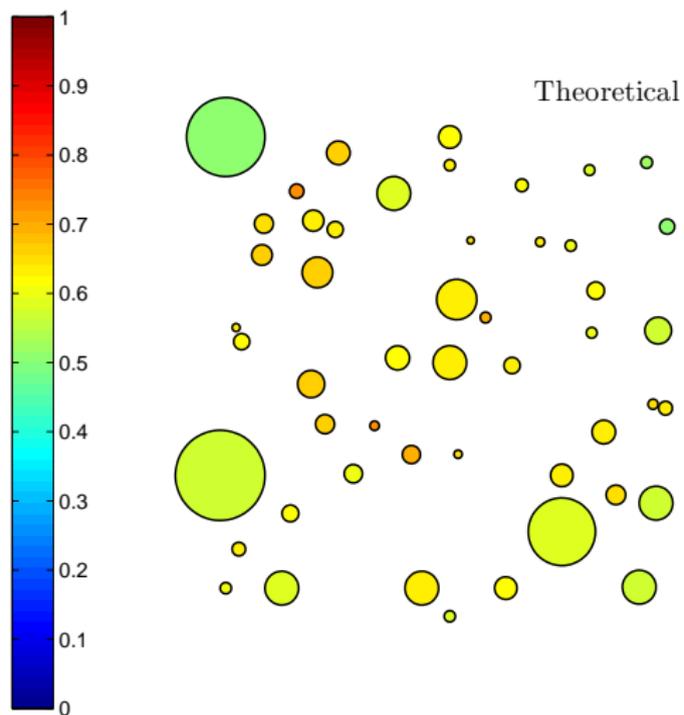
Occupancy simulation - proportion of time occupied



Occupancy simulation - proportion of time occupied



Theoretical - proportion of time occupied



EXTRAS: Interpretation of the operator \mathcal{G}

Once a patch has been colonised, it remains occupied until the local population dies out during an extinction phase. The probability of the local population surviving at least m extinction phases is $\mathbb{E}(s_0 \cdots s_{m-1})$. Thus, the factor $\sum_{m=0}^{\infty} \mathbb{E}(s_0 \cdots s_m)$ is the expected number of extinction phases a local population survives before going extinct.

If patch j is the only patch occupied, then the probability that patch i is colonised during the next colonisation phase is approximately $c'(0)n^{-1}D(z_i, z_j)a_j$. Therefore, when n is large, the probability that patch j is colonised by patch i prior to the local extinction at patch i is approximately

$$G_{ij} = f'(0) \frac{1}{n} D(z_i, z_j) a_j \sum_{m=0}^{\infty} \mathbb{E}(s_0 \cdots s_m).$$

Under Assumptions (A)-(C) and (F), the matrix G converges to the operator \mathcal{G} in the sense that, for any $\phi \in C(\Omega)$,

$$\sum_{j=1}^n G_{ij} \phi(z_j) \xrightarrow{d} c'(0) \sum_{m=0}^{\infty} \mathbb{E}(s_0 \cdots s_m) \int D(z_i, \tilde{z}) \phi(\tilde{z}) \bar{\sigma}_0(d\tilde{z}), \quad \text{as } n \rightarrow \infty.$$



EXTRAS: Interpretation of the operator \mathcal{G}

Theorem 3 tells us that the landscape dynamics affects the persistence of the metapopulation through the quantity $\sum_{m=0}^{\infty} \mathbb{E}(s_0 \cdots s_m)$.

Hölder's inequality allows us deduce that this is maximised for the static landscape:

Corollary 3 If the survival probability model (s_t) is stationary, then

$$\mathbb{E}(s_0 \cdots s_m) \leq \mathbb{E}(s_0^{m+1}),$$

the upper bound achieved when $s_t = s_0$ for all t , corresponding to a static landscape.

The persistence of the metapopulation with static landscape is determined by the spectral radius of the operator $\tilde{\mathcal{G}} : C(\Omega) \mapsto C(\Omega)$ given by

$$\tilde{\mathcal{G}}\phi(z) = f'(0) \int D(z, \tilde{z}) \frac{\tilde{s}}{1 - \tilde{s}} \phi(\tilde{z}) \sigma(d\tilde{s}, d\tilde{z}), \quad \phi \in C(\Omega).$$

The operators $\tilde{\mathcal{G}}$ and \mathcal{G} coincide for the static landscape when σ is a product measure.

In the case of persistence, our fixed point is bounded above by the fixed point for a corresponding static landscape.



EXTRAS: The case $D \equiv 1, a \equiv 1$

The random measures: for $h \in C^+([0, 1])$,

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

The recursion for the limiting measure, with $c_t = c(\int \mu_t(ds))$, $Ph(s) = \int h(r)P(s, dr)$:

$$\int h(s) \mu_{t+1}(ds) = (1 - c_t) \int s Ph(s) \mu_t(ds) + c_t \int s Ph(s) \sigma_t(ds), \quad h \in C^+([0, 1]).$$

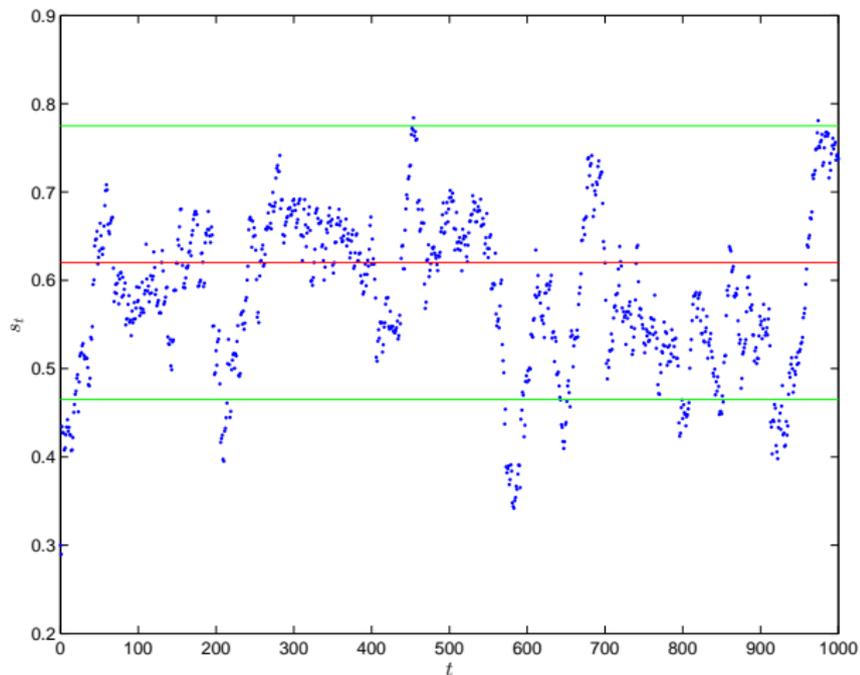
The recursion for the Radon-Nikodym derivative of μ_t with respect to σ :

$$\frac{\partial \mu_{t+1}}{\partial \sigma}(s) = \int_0^1 r \frac{\partial \mu_t}{\partial \sigma}(r) P^*(s, dr) + c_t \int_0^1 r \left(1 - \frac{\partial \mu_t}{\partial \sigma}(r)\right) P^*(s, dr).$$

We get *evanescence* if $r := c'(0) \sum_{m=0}^{\infty} \mathbb{E}(s_0 \cdots s_m) \leq 1$, and *persistence* if $r > 1$.

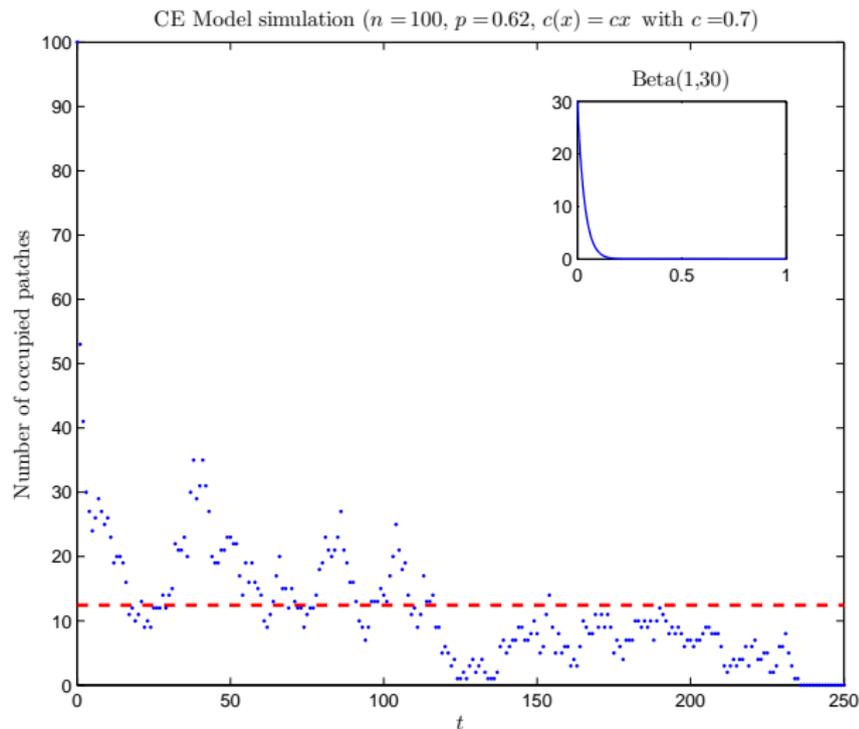


EXTRAS: Survival probability simulation

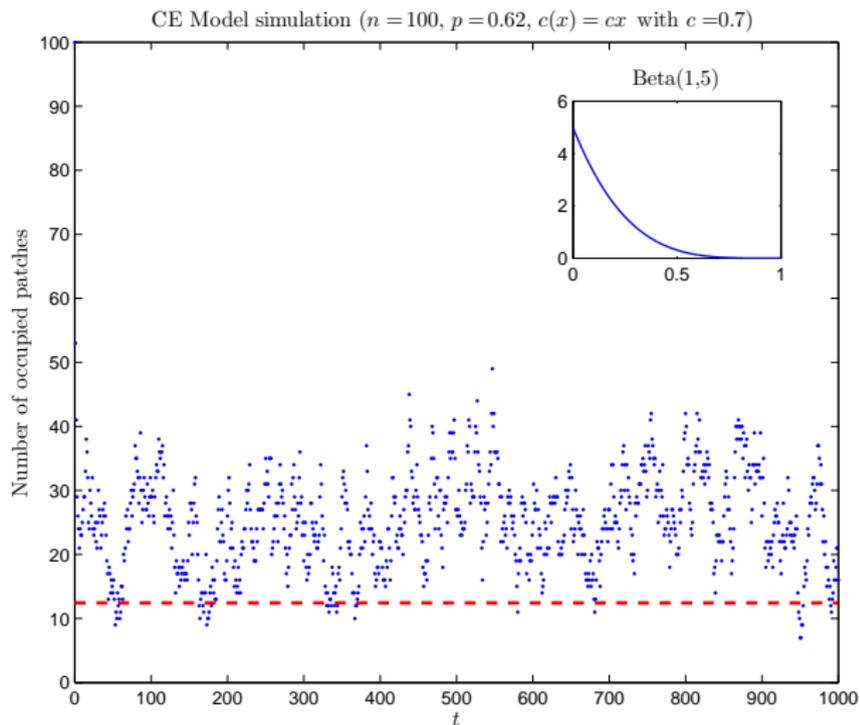


$L_t \sim \text{Beta}(1, 20)$, $R_t \sim \text{Beta}(1, 20)$, and $\rho(s) = 0.62$.

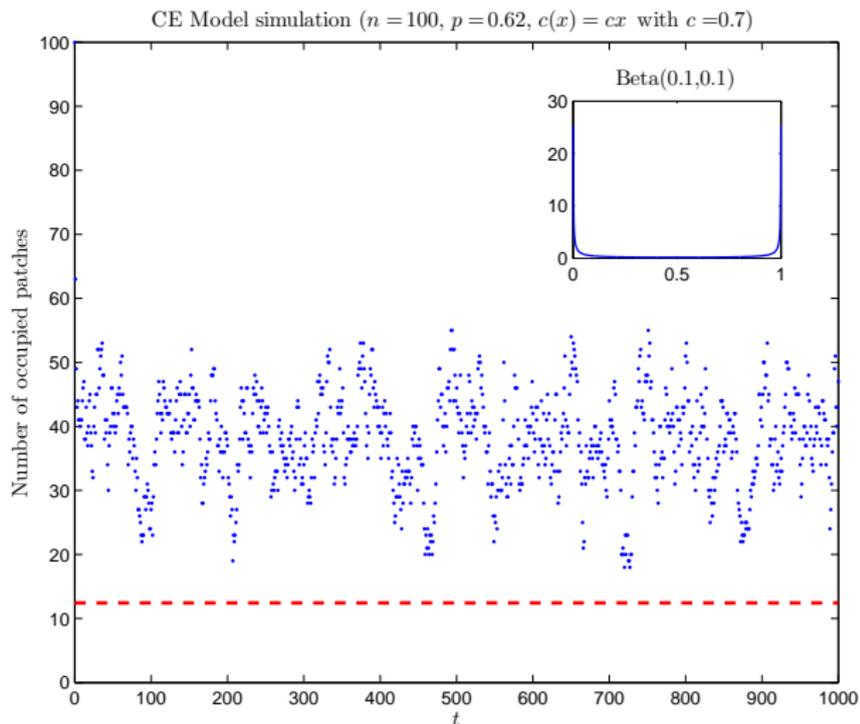
EXTRAS: CE Model - Evanescence



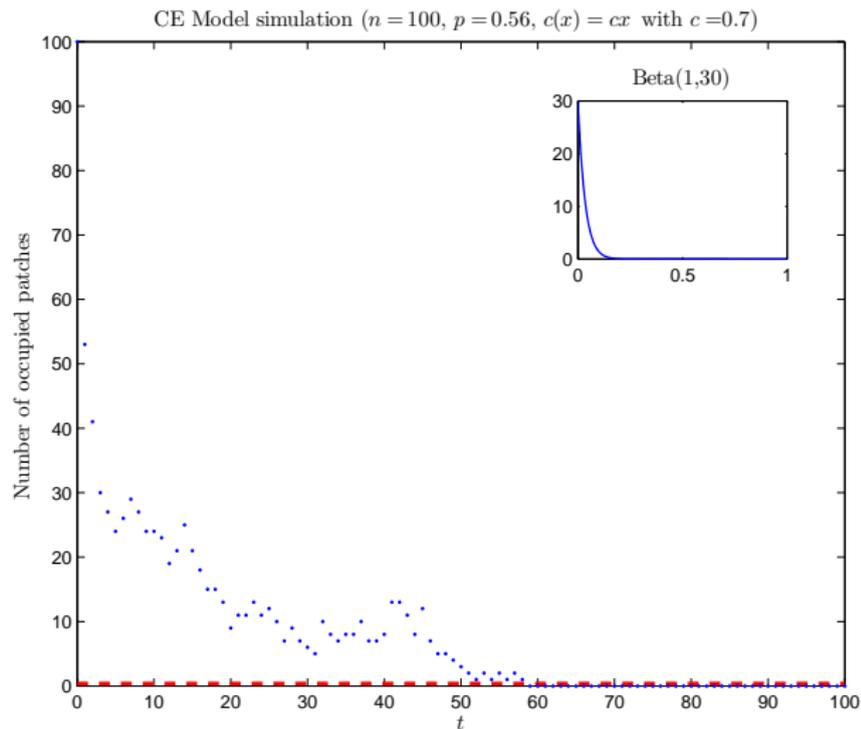
EXTRAS: CE Model - Persistence



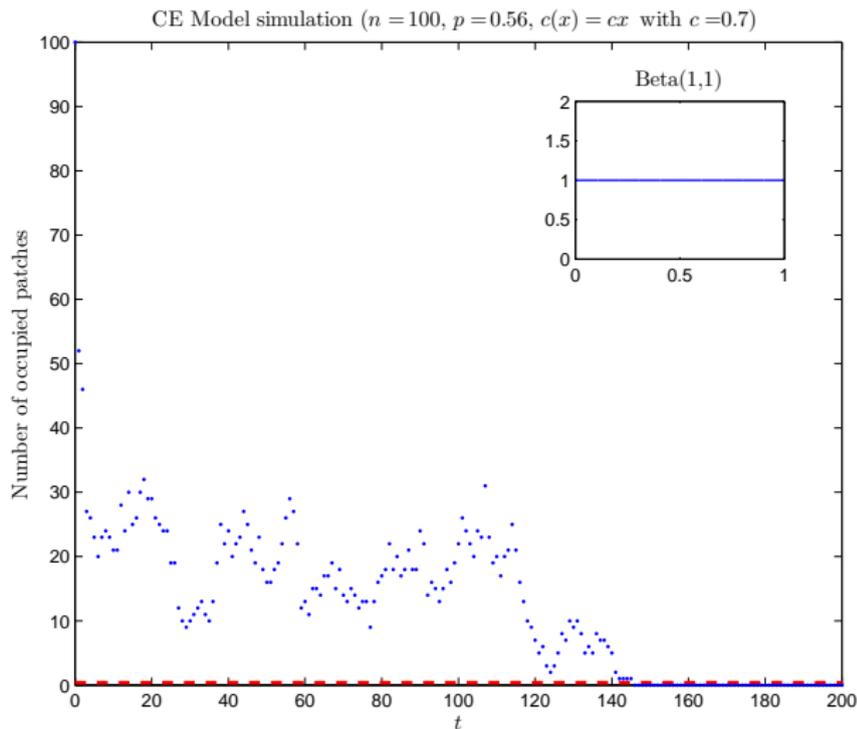
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EXTRAS: CE Model - Evanescence



EXTRAS: CE Model - Evanescence



EXTRAS: CE Model - Persistence

