High-density limits for metapopulations with no occupancy ceiling

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Workshop in celebration of Ron Doney's 80th birthday

University of Manchester, 26-28 July 2022

This is joint work with . . .

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The basic model

An *infinite occupancy process* $\boldsymbol{X}_t = (X_{i,t})_{i=1}^{\infty}$ is a (time-homogeneous) Markov chain on $\{0,1\}^{\mathbb{Z}_+}$ with the property that, conditional on $\boldsymbol{X}_t$, the occupancies $X_{1,t+1}, X_{2,t+1}, \ldots$, at time $t+1$, are mutually independent. In particular, the dynamics are determined by the collection of functions

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Voter Model: $S_i(\boldsymbol{x}) = 1 - \sum_{j=1}^{\infty} p_{ij}(1 - x_j)$, $C_i(\boldsymbol{x}) = \sum_{j=1}^{\infty} p_{ij} x_j$ $(p_{ii} = 0)$.

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Domany-Kinzel PCA: $S_i(\boldsymbol{x}) = (q_2 - q_1) x_{i+1}$, $C_i(\boldsymbol{x}) = q_1 x_{i+1}$, $q_1, q_2 \in [0,1]$.

A metapopulation model

The sites $i = 1, 2, \ldots$ are habitat patches, and $X_{i,t}$ is 1 or 0 according to whether patch i is occupied or unoccupied at time t. $S_i(\boldsymbol{x}) = s_i$ (patch i *survival probability*) is the same for all $\boldsymbol{x}$, and

$$C_i(\boldsymbol{x}) = f\left(a_i \sum_{j=1}^{\infty} d_{ij} x_j\right),$$

where $f : [0, \infty) \to [0, 1]$ (called the *colonisation function*) satisfies $f(0) = 0$ (so there is total extinction at $\boldsymbol{x} \equiv 0$), and is typically an increasing function, a_i is a weight that may be interpreted as the capacity, or area, of patch i, and d_{ij} is the migration potential from patch j to patch i. (Further assumptions will be added later.)

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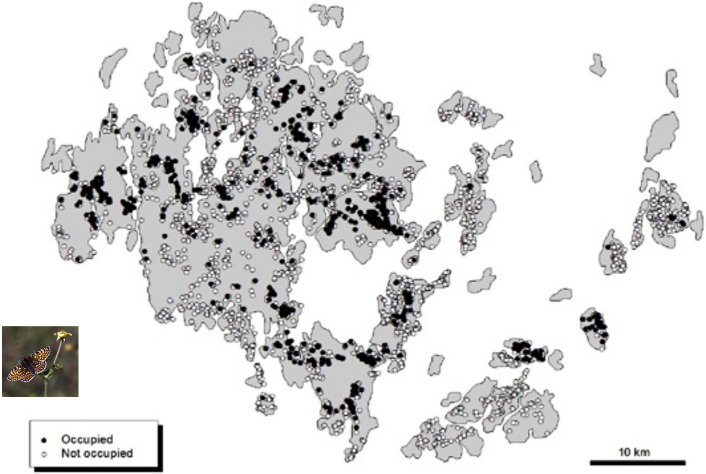
This particular form is reminiscent of the *Hanski incidence function model* [1], but now there is *no fixed upper limit* on the number of patches that can be occupied.

[1] McVinish, R. and Pollett, P.K. (2014) The limiting behaviour of Hanski's incidence function metapopulation model. *J. Appl. Probab.* 51, 297–316.

A famous example (Note: only *known* patches are shown)



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

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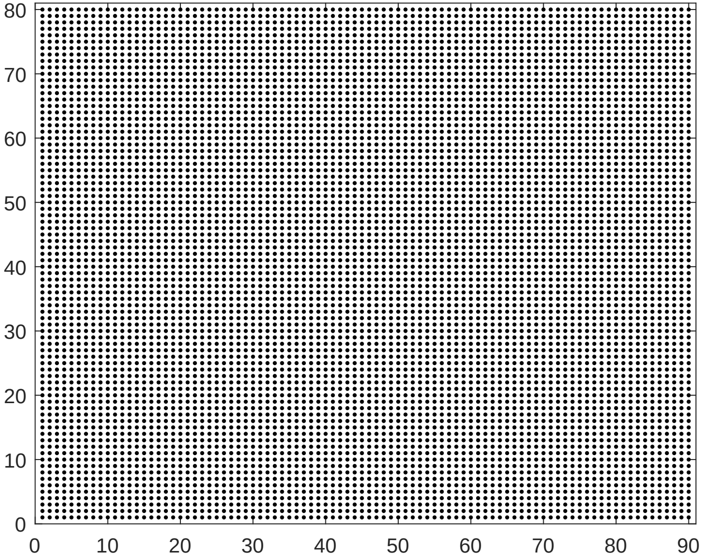
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$



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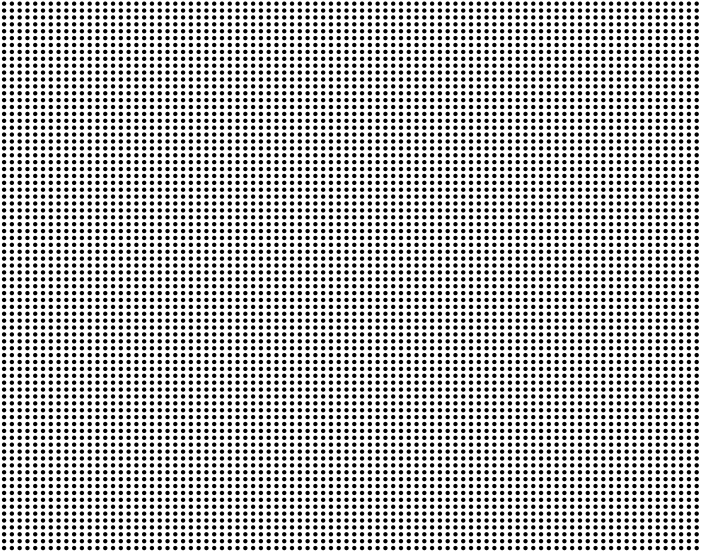
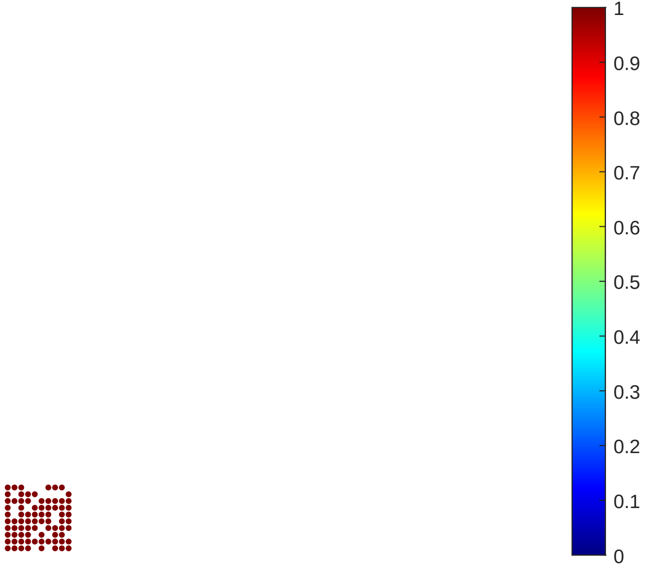
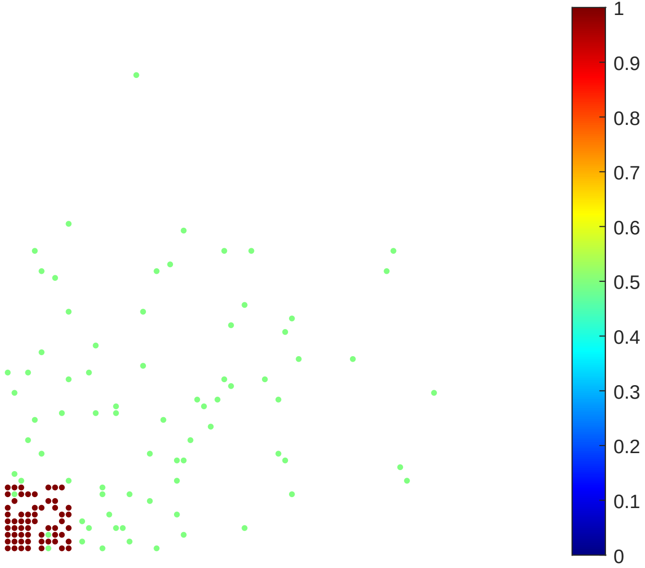


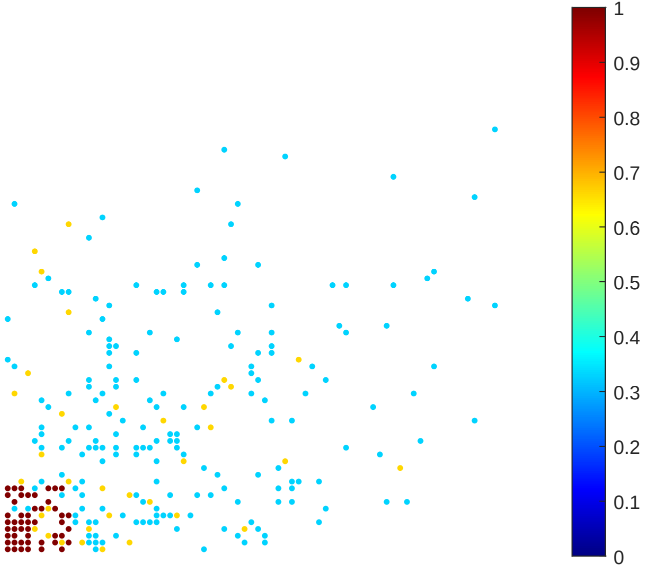
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ $(t = 0)$



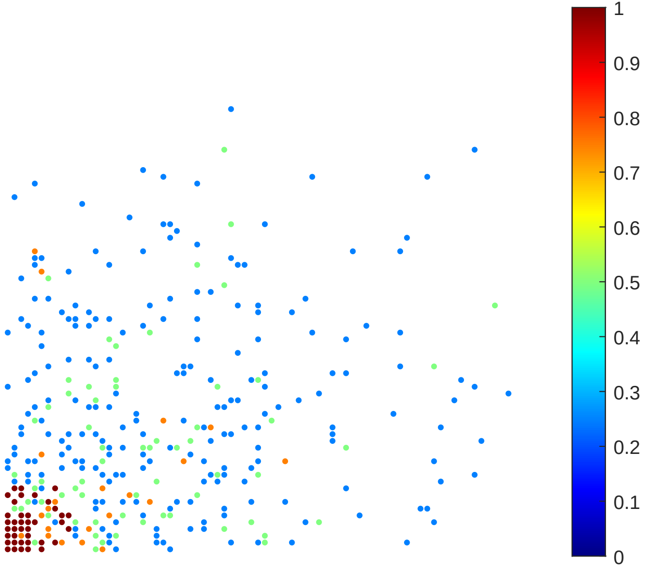
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ($t = 1$)



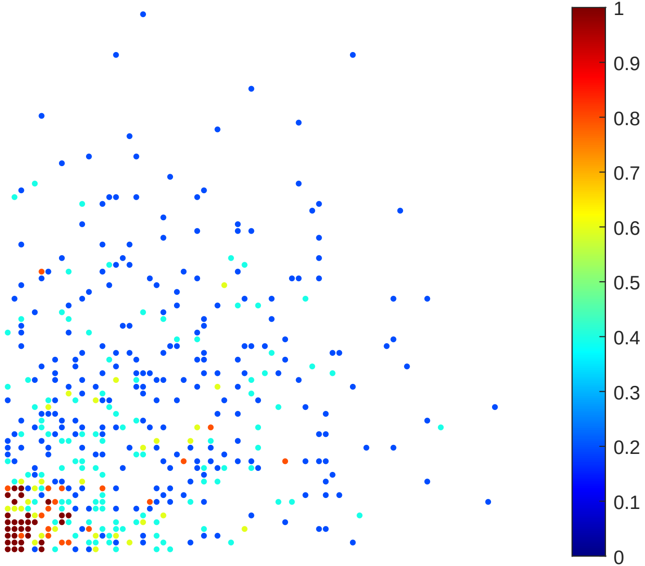
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ($t = 2$)



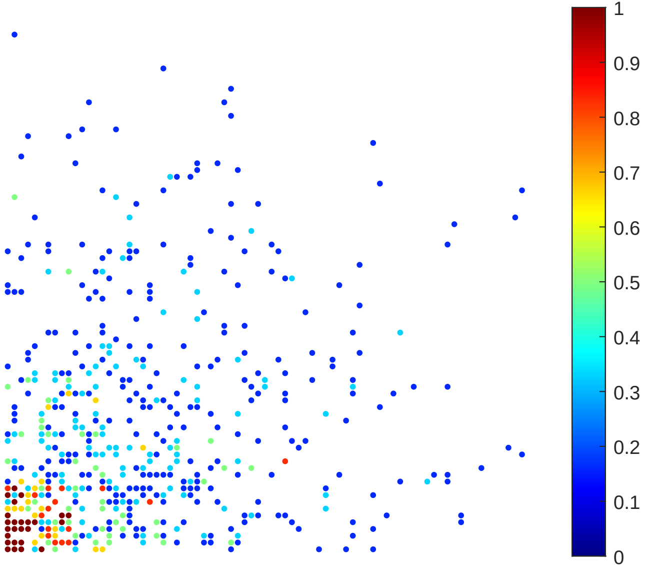
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ $(t = 3)$



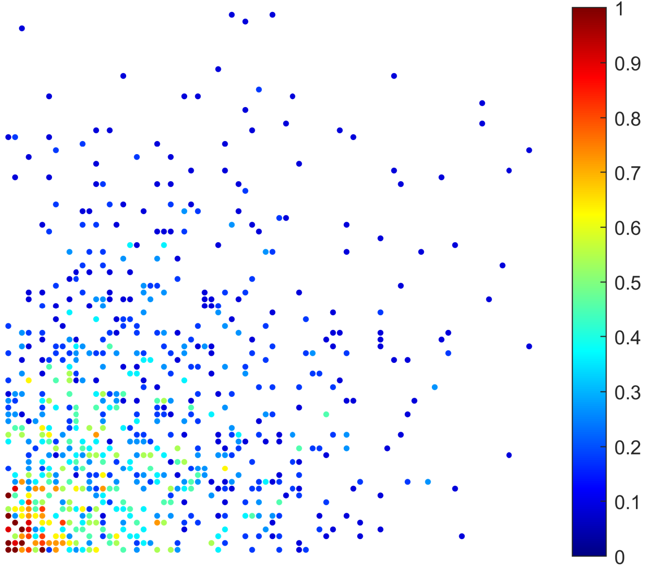
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ $(t = 4)$



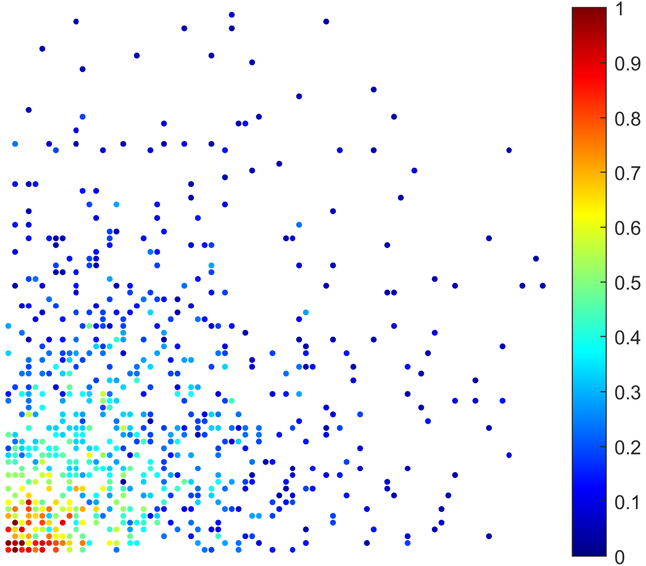
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ($t = 5$)



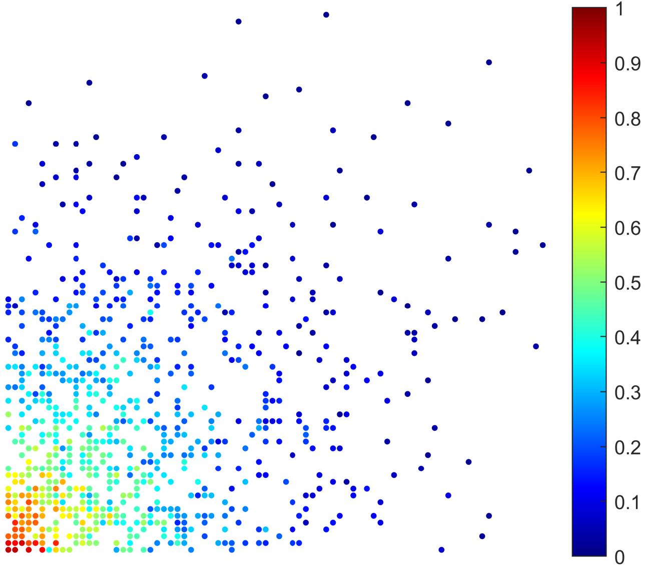
A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ($t = 10$)



A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ($t = 20$)



A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ($t = 50$)



Two approximating models

Returning to the general case

$$\mathbb{P}(X_{i,t+1} = 1 | \boldsymbol{X}_t) = S_i(\boldsymbol{X}_t) X_{i,t} + C_i(\boldsymbol{X}_t)(1 - X_{i,t}), \quad i = 1, 2, \ldots, \; t = 0, 1, \ldots,$$

we consider a *deterministic analogue*[2] $\boldsymbol{p}_t = \{p_{i,t}\}_{i=1}^{\infty}$ that evolves according to

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[2] Barbour, A.D., McVinish, R. and Pollett, P.K. (2015) Connecting deterministic and stochastic metapopulation models. *J. Math. Biol.* 71, 1481–1504.

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The closeness of $\boldsymbol{X}_t$ and $\boldsymbol{p}_t$ (in a weak sense) is established by coupling $\boldsymbol{X}_t$ with an *independent site approximation*[2] $\boldsymbol{W}_t=\{W_{i,t}\}_{i=1}^{\infty}$ satisfying

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In particular, for any t, $W_{1,t},W_{2,t},\dots$ are independent and satisfy $\mathbb{E}W_{i,t}=p_{i,t}$.

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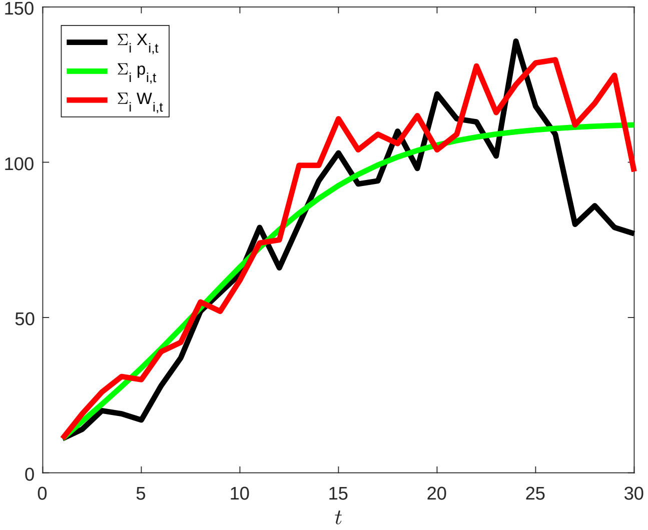

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The main result

To assess the quality of our approximation, we shall let [3]

$$\alpha = \sup_{j \in \mathbb{Z}_+} \sum_{i=1}^{\infty} \|\partial_j P_i\|_\infty \quad \beta = \sum_{i=1}^{\infty} \left(\sum_{j=1,\, j \neq i}^{\infty} \|\partial_j P_i\|_\infty^2 \right)^{1/2} \quad \gamma = \sum_{i,j=1}^{\infty} \|\partial_j^2 P_i\|_\infty$$

and assume these quantities are all finite. Here ∂_j and ∂_j^2 are the first and second partial derivative operators in the j-th coordinate.

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Theorem 1 There is a constant $C \in (0, 2\sqrt{\pi}]$ such that, for any $\boldsymbol{w} \in \ell^\infty$ and $t \geqslant 0$,

$$\mathbb{E} \left| \sum_{i=1}^{\infty} w_i (X_{i,t} - p_{i,t}) \right| \leqslant C \|\boldsymbol{w}\|_\infty (\beta + \gamma)(1 + 2\alpha)^t + \left(\sum_{i=1}^{\infty} w_i^2 p_{i,t} \right)^{1/2}.$$

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Assume that $X_{i,0}^{(m)}$, $i = 1, 2, \ldots$, are independent Bernoulli random variables with $\mathbb{P}(X_{i,0}^{(m)} = 1) = r_i^{(m)}$, for a sequence $\boldsymbol{r}^{(m)} = \{r_i^{(m)}\}_{i=1}^{\infty}$ of probabilities with $\sum_i r_i^{(m)} < \infty$.

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Write $\langle x, y \rangle = \sum_{i=1}^{\infty} x_i y_i$, and suppose that

$$m^{-1}\mathbb{E}\langle \boldsymbol{w}, \boldsymbol{X}_0^{(m)} \rangle = m^{-1}\langle \boldsymbol{w}, \boldsymbol{r}^{(m)} \rangle \to x_0, \qquad \text{as } m \to \infty,$$

where x_0 depends on $\boldsymbol{w}$. So, as m gets large, *increasingly more sites are occupied*.

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But the same is true also for $t \geqslant 0$; by way of Theorem 1 we can prove:

Theorem 2 Suppose that, for each $t \geqslant 0$, there is a function $x_t : \ell^{\infty} \to \mathbb{R}$ such that $m^{-1}\langle \boldsymbol{w}, \boldsymbol{p}_t^{(m)} \rangle \to x_t$ for all $t \geqslant 0$ and $\boldsymbol{w} \in \ell^{\infty}$. If $\{\alpha_m\}$ is bounded, and $m^{-1}(\beta_m + \gamma_m) \to 0$ as $m \to \infty$, then $m^{-1}\langle \boldsymbol{w}, \boldsymbol{X}_t^{(m)} \rangle \xrightarrow{\mathbb{P}} x_t$ for all $t \geqslant 0$.

The metapopulation model

In our metapopulation model

$$P_i(\boldsymbol{x}) := s_i x_i + f\left(a_i \sum_j d_{ij} x_j\right)(1 - x_i), \qquad \boldsymbol{x} \in [0,1]^{\mathbb{Z}_+}.$$

Recall that s_i is the patch i survival probability, a_i is the patch weight, d_{ij} is the migration potential from patch j to patch i, and $f : [0,\infty) \to [0,1]$, the colonisation function, satisfies $f(0) = 0$.

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Now assume that $\sum_i a_i < +\infty$ (the total weight of all patches is finite), and suppose that $d_{ij} = D(z_i, z_j) := \kappa(\|z_i - z_j\|)$, for patches located at points $\{z_i\}$ in $\mathbb{R}^d$, where κ is a smooth, non-negative, monotone decreasing function (typically $\kappa(x) = e^{-\psi x}$, or $\kappa(x) = e^{-\psi x^2}$, $\psi > 0$). These assumptions are enough to ensure that α, β, γ are all finite.

The metapopulation model - a high density limit

We shall suppose that the patch locations are spaced according to some measure σ. In particular, for any bounded continuous function g,

$$\frac{1}{m^d}\sum_{i=1}^{\infty} g(m^{-1}z_i) \to \int_{\mathbb{R}^d} g(z)\sigma(\mathrm{d}z), \qquad \text{as } m \to \infty.$$

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Suppose that there is a sequence of models $\{\boldsymbol{X}_t^{(m)}\}_{m=1}^{\infty}$ with parameters $s_i^{(m)}, a_i^{(m)}, d_{ij}^{(m)}$, and the same colonisation function f, such that

$$s_i^{(m)} = s\left(m^{-1}z_i\right), \quad a_i^{(m)} = a\left(m^{-1}z_i\right), \quad d_{ij}^{(m)} = m^{-d}\kappa\left(m^{-1}\|z_i - z_j\|\right),$$

for smooth functions $\kappa : \mathbb{R}_+ \to \mathbb{R}_+$, $a : \mathbb{R}^d \to \mathbb{R}_+$, and $s : \mathbb{R}^d \to [0, 1]$.

In this way, the patch locations are effectively being drawn together as $m \to \infty$.

To cut a long story short, we use the earlier result,

$$\mathbb{E}\left|\sum_{i=1}^{\infty} w_i(X_{i,t}-p_{i,t})\right| \leqslant C\|\boldsymbol{w}\|_\infty(\beta+\gamma)(1+2\alpha)^t + \left(\sum_{i=1}^{\infty} w_i^2 p_{i,t}\right)^{1/2},$$

to compare the finite measure $\pi_t^{(m)}$ defined by

$$\pi_t^{(m)}(B) = m^{-d}\sum_{i=1}^{\infty} p_{i,t}^{(m)} \mathbb{1}\{m^{-1}z_i \in B\}, \qquad B \in \mathcal{B}(\mathbb{R}^d),$$

with the *random measure* $\mu_t^{(m)}$ defined by

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To cut a long story short, we use the earlier result,

$$\mathbb{E}\left|\sum_{i=1}^{\infty} w_i(X_{i,t} - p_{i,t})\right| \leqslant C\|\boldsymbol{w}\|_{\infty}(\beta+\gamma)(1+2\alpha)^t + \left(\sum_{i=1}^{\infty} w_i^2 p_{i,t}\right)^{1/2},$$

to compare the finite measure $\pi_t^{(m)}$ defined by

$$\int g(z)\pi_t^{(m)}(\mathrm{d}z) = m^{-d}\sum_{i=1}^{\infty} p_{i,t}^{(m)} g(m^{-1}z_i),$$

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The metapopulation model - a high density limit

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$$\int g(z)\mu_t^{(m)}(\mathrm{d}z) = m^{-d}\sum_{i=1}^{\infty} X_{i,t}^{(m)} g(m^{-1}z_i).$$

We prove that, as $m\to\infty$, $\int g(z)\mu_t^{(m)}(\mathrm{d}z) \to \int g(z)p_t(z)\sigma(\mathrm{d}z)$, for some function p_t. In particular, the functions p_t, $t=0,1,\ldots,$ satisfy the recursion

$$p_{t+1}(z) = s(z)p_t(z) + (1-p_t(z))f\left(a(z)\int \kappa(\|z-x\|)p_t(x)\sigma(\mathrm{d}z)\right), \quad z\in\mathbb{R}^d.$$

Nice interpretation: if a patch is located at z, $p_t(z)$ is the chance it is occupied.

The earlier simulation - patches located on the integer lattice $\mathbb{Z}_+^2$

Details

$d = 2$

Colonisation function: $f(x) = 1 - \exp(-\alpha x)$ with $\alpha = 0.01$.

Survival function: $s(\boldsymbol{z}) = \exp(-\phi\|\boldsymbol{z}\|)$ with $\phi = 0.25$.

Patch weight function: $a(\boldsymbol{z}) = \exp(-\theta\|\boldsymbol{z}\|)$ with $\theta = 0.25$.

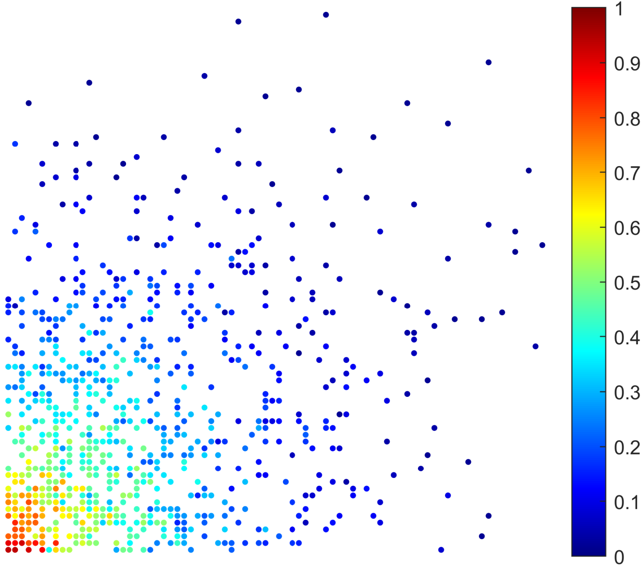
Easy of movement function: $d(\boldsymbol{x}, \boldsymbol{z}) = b\exp(-\psi\|\boldsymbol{x} - \boldsymbol{z}\|)$ with $b = 25$ and $\psi = 0.4$.

Scaling: $m = 8$

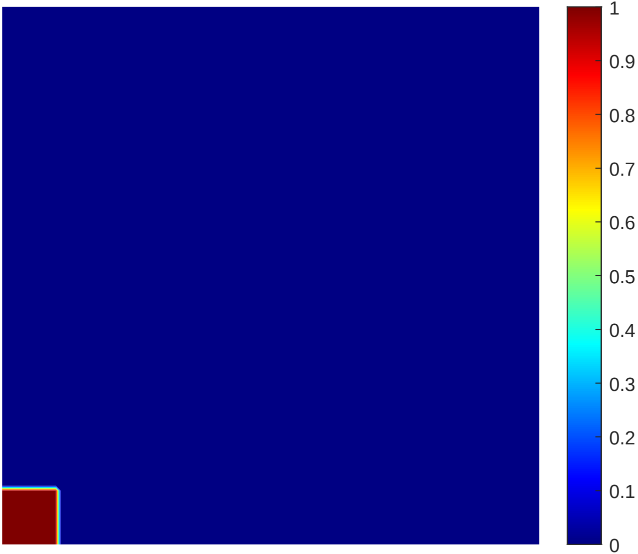
$$s_i^{(m)} = s\left(m^{-1}z_i\right), \quad a_i^{(m)} = a\left(m^{-1}z_i\right), \quad d_{ij}^{(m)} = m^{-2}\kappa\left(m^{-1}\|z_i - z_j\|\right)$$

Initially configuration: 70 percent of patches are occupied in $\{1, 2, \ldots, 10\}^2$.

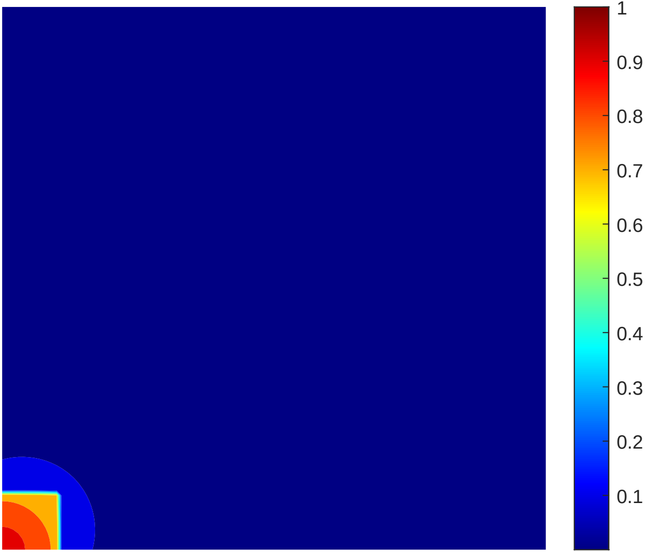
The earlier simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ($t = 50$)



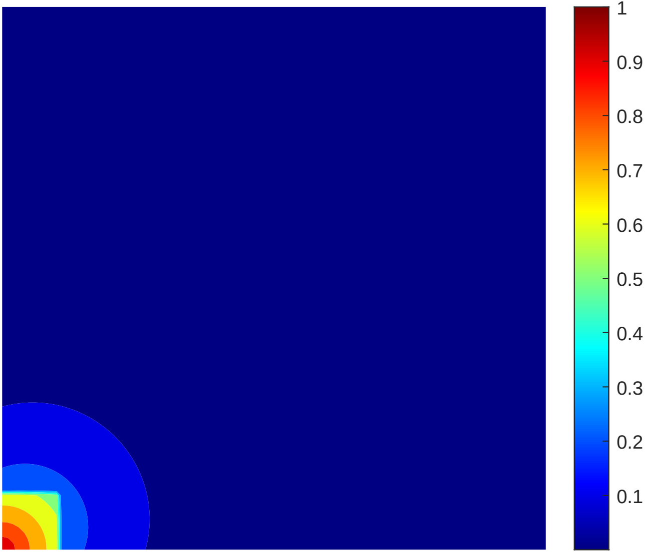
Occupancy probability heatmap $p_t(\boldsymbol{z})$ $(t = 0)$



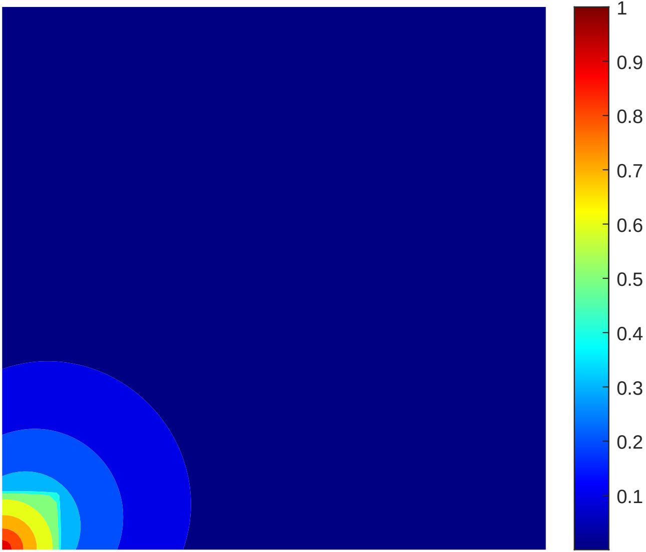
Occupancy probability heatmap $p_t(\boldsymbol{z})$ $(t = 1)$



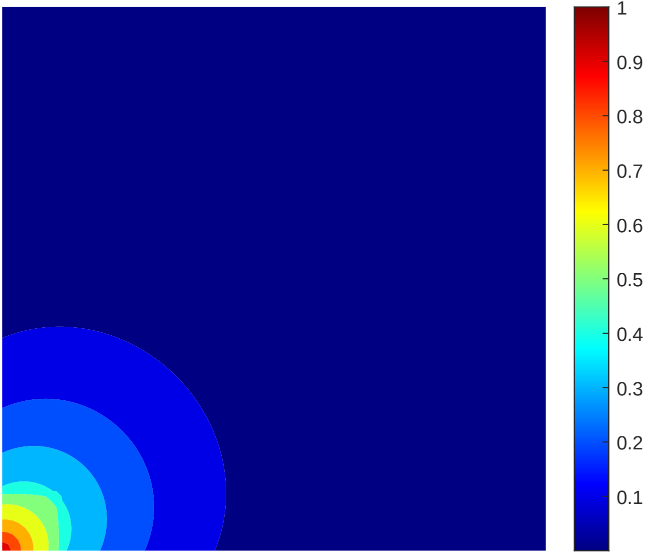
Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 2$)



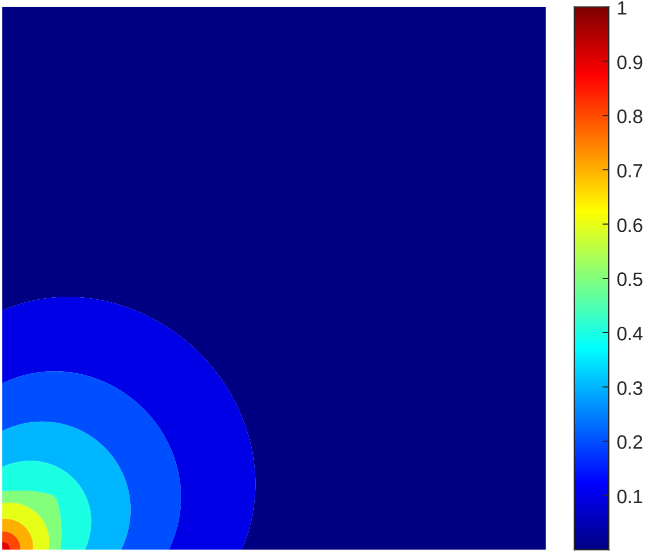
Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 3$)



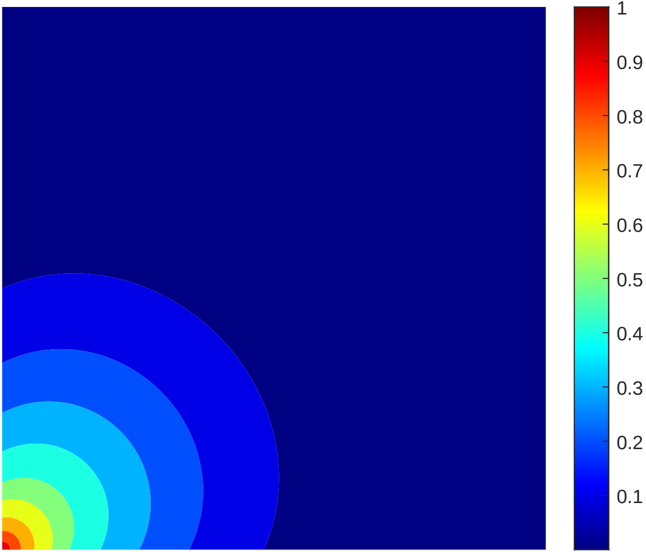
Occupancy probability heatmap $p_t(\boldsymbol{z})$ $(t = 4)$



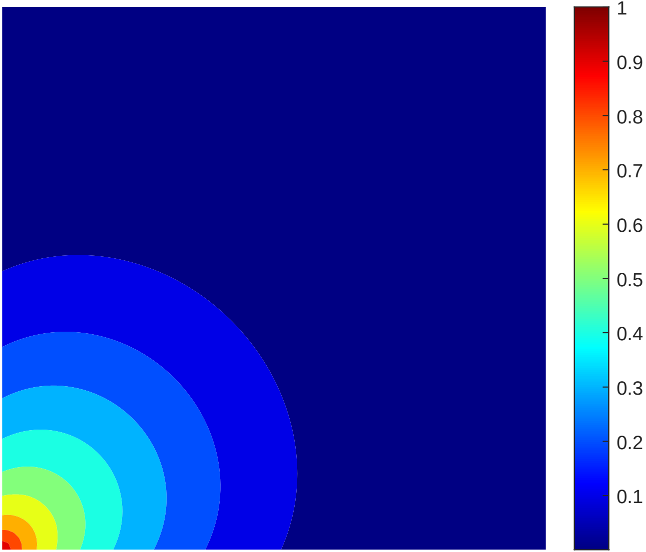
Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 5$)



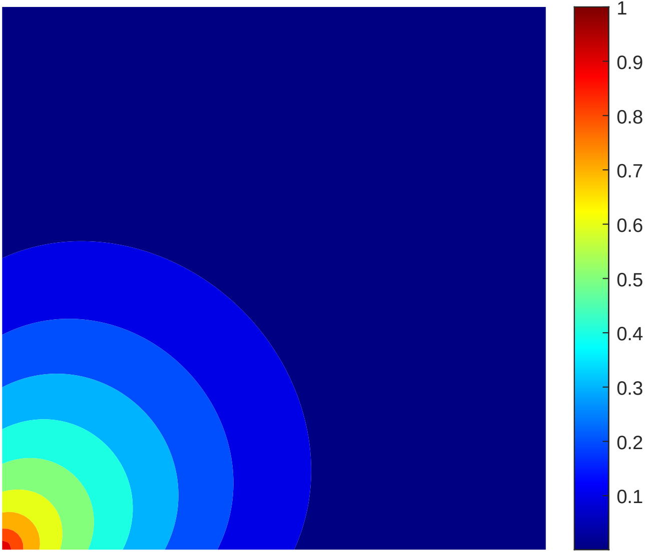
Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 6$)



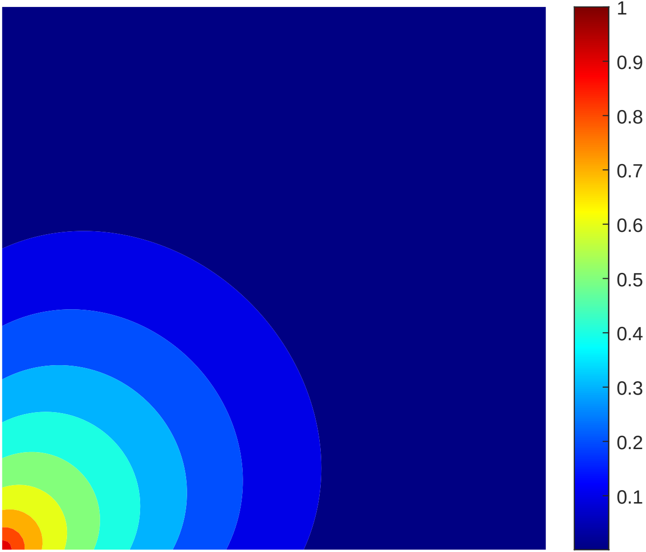
Occupancy probability heatmap $p_t(\boldsymbol{z})$ $(t = 7)$



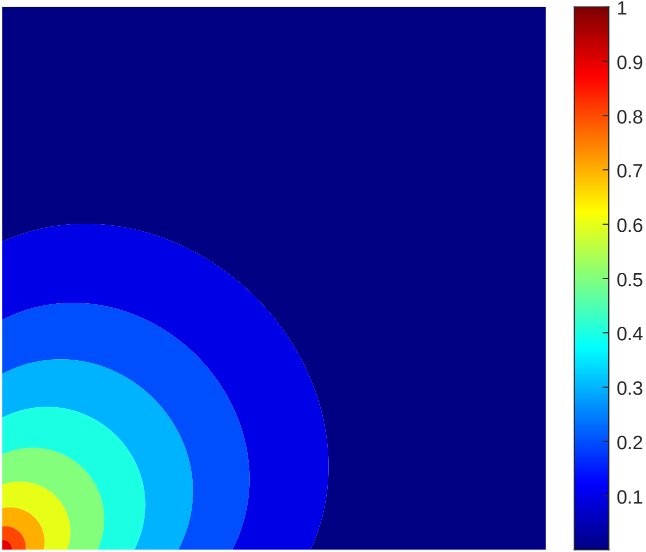
Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 8$)



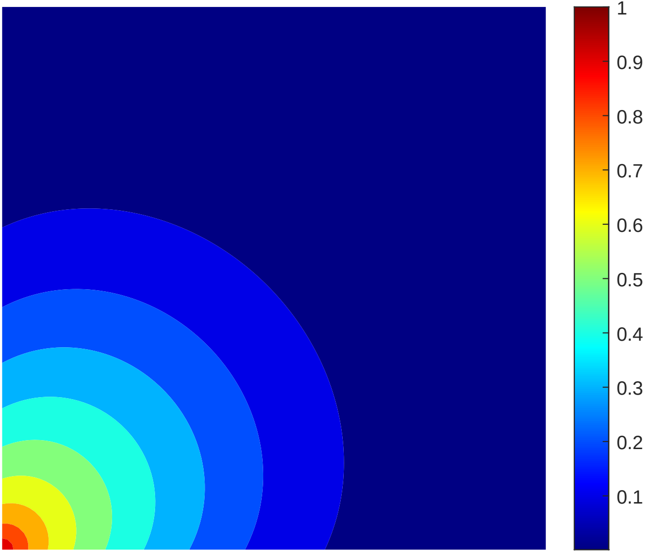
Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 9$)



Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 10$)



Occupancy probability heatmap $p_t(\boldsymbol{z})$ ($t = 50$)



A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ $(t = 50)$