

# High-density limits for infinite occupancy processes

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This is joint work with ...

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UC Berkeley



## The basic model

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

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where  $S_i, C_i : \{0, 1\}^{\mathbb{Z}^+} \rightarrow [0, 1]$ ;  $C_i(\mathbf{x})$  and  $1 - S_i(\mathbf{x})$  are the (configuration dependent) “flip” probabilities.

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*Domany-Kinzel PCA* on the discrete torus of length  $n$ :  $S_i(\mathbf{x}) = (q_2 - q_1)x_{i+1}$ ,  $C_i(\mathbf{x}) = q_1x_{i+1}$ ,  $q_1, q_2 \in [0, 1]$ .



## A metapopulation model

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

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where  $f : [0, \infty) \rightarrow [0, 1]$  (called the *colonisation function*) satisfies  $f(0) = 0$  (so there is total extinction at  $\mathbf{x} \equiv 0$ ), 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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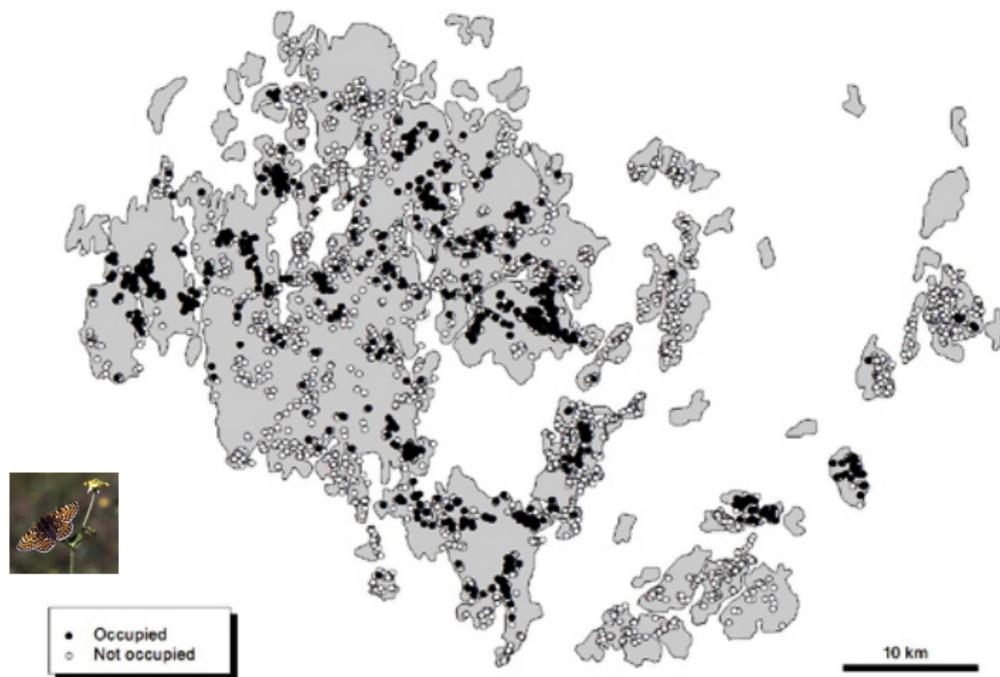
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This particular form is reminiscent of the *Hanski incidence function model*<sup>1</sup>, but now there is *no fixed upper limit* on the number of patches that can be occupied.

<sup>1</sup>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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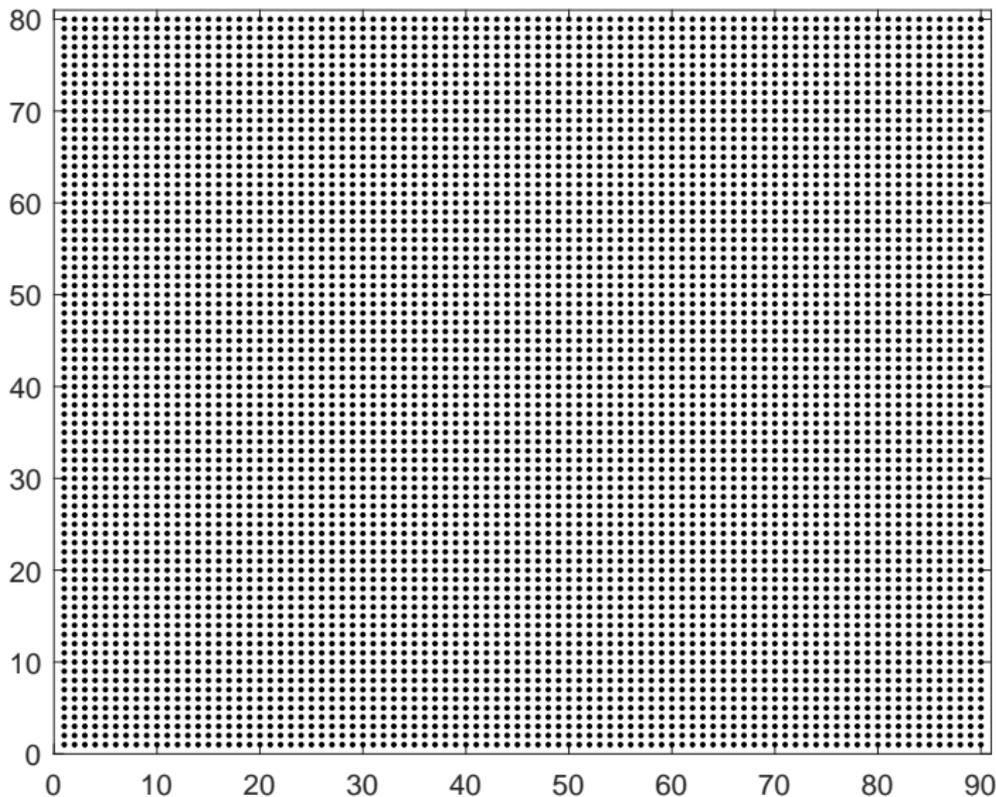
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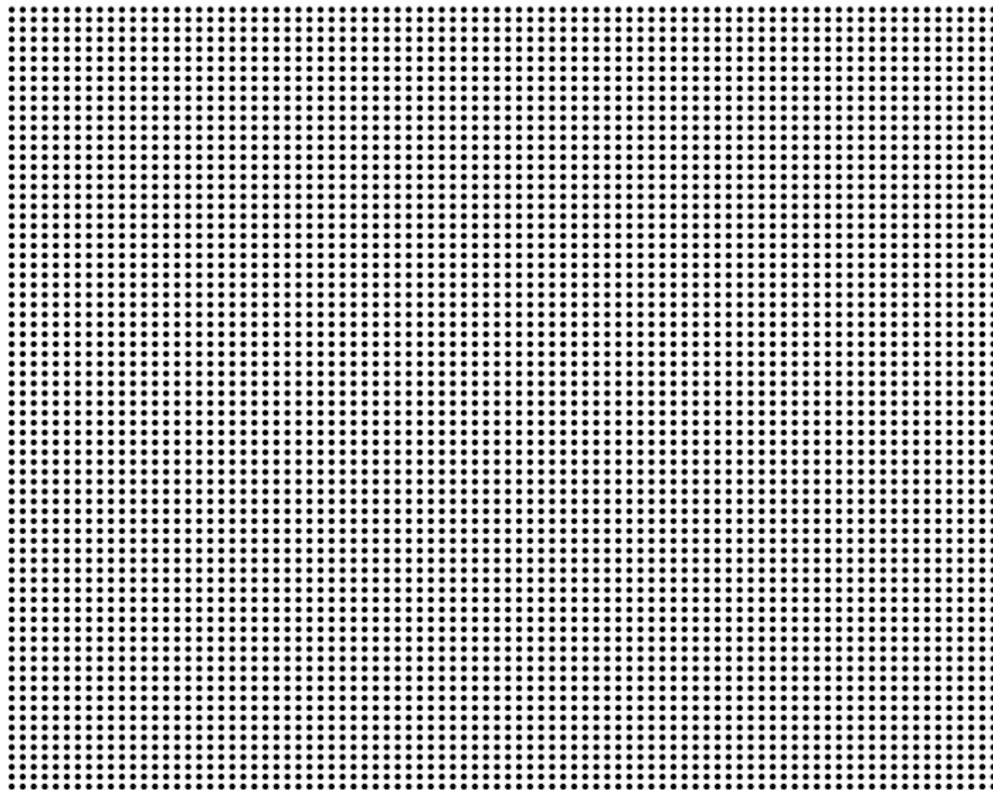
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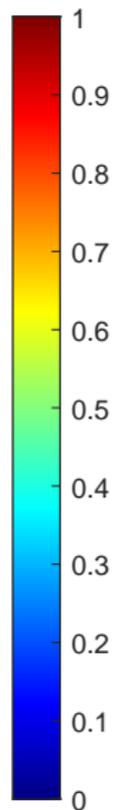
A simulation - patches located on the integer lattice  $\mathbb{Z}_+^2$



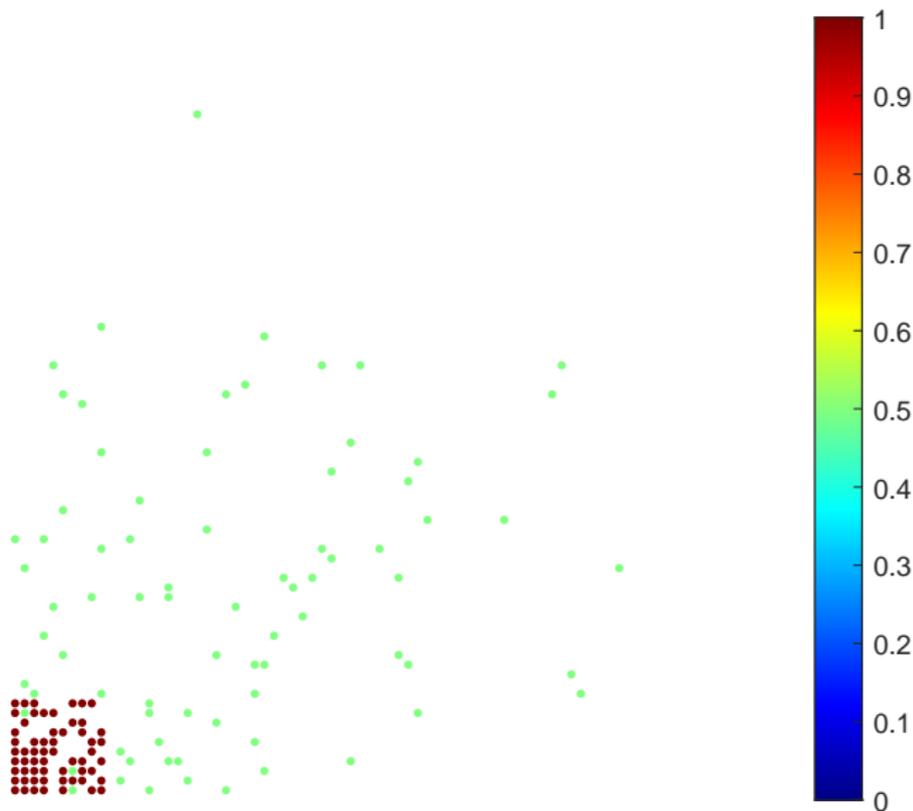
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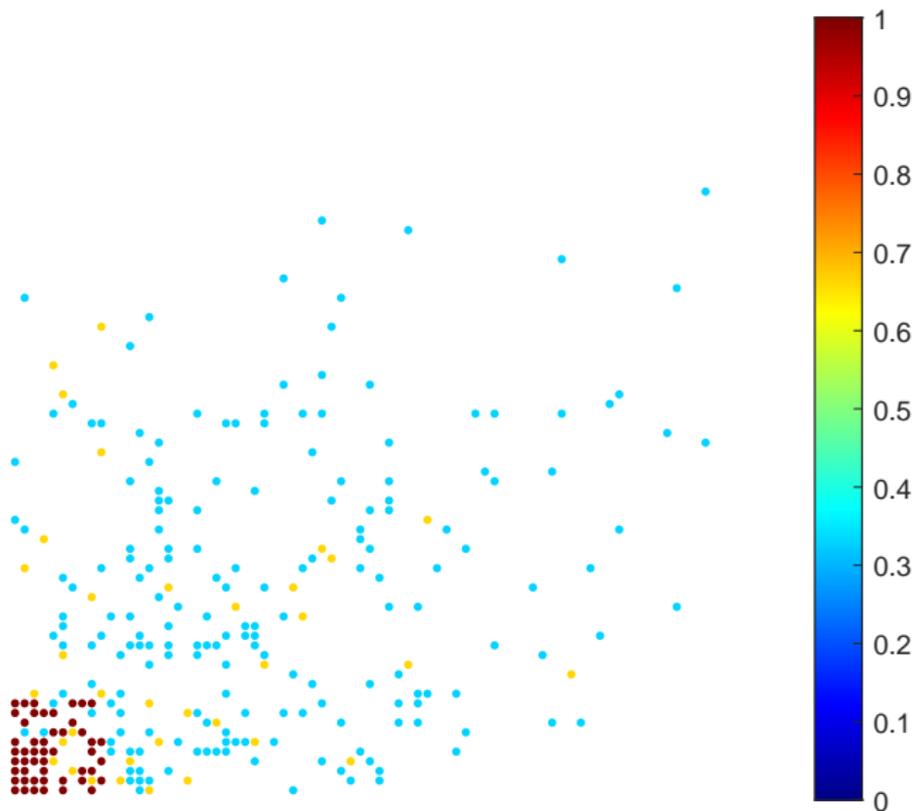
A simulation - patches located on the integer lattice  $\mathbb{Z}_+^2$  ( $t = 0$ )



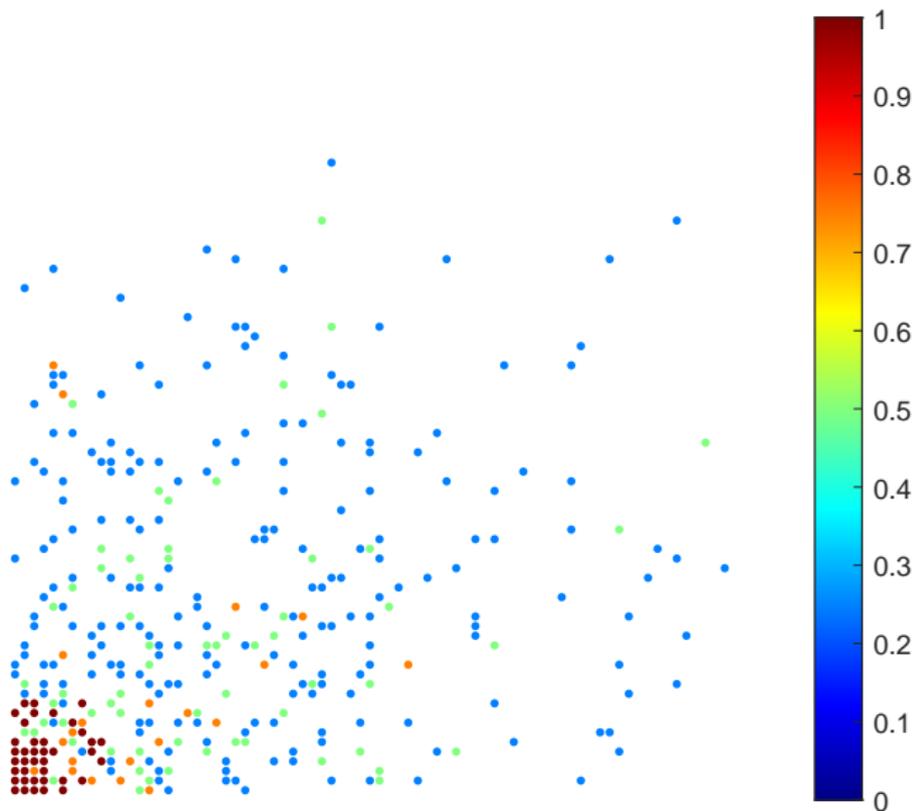
# A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ( $t = 1$ )



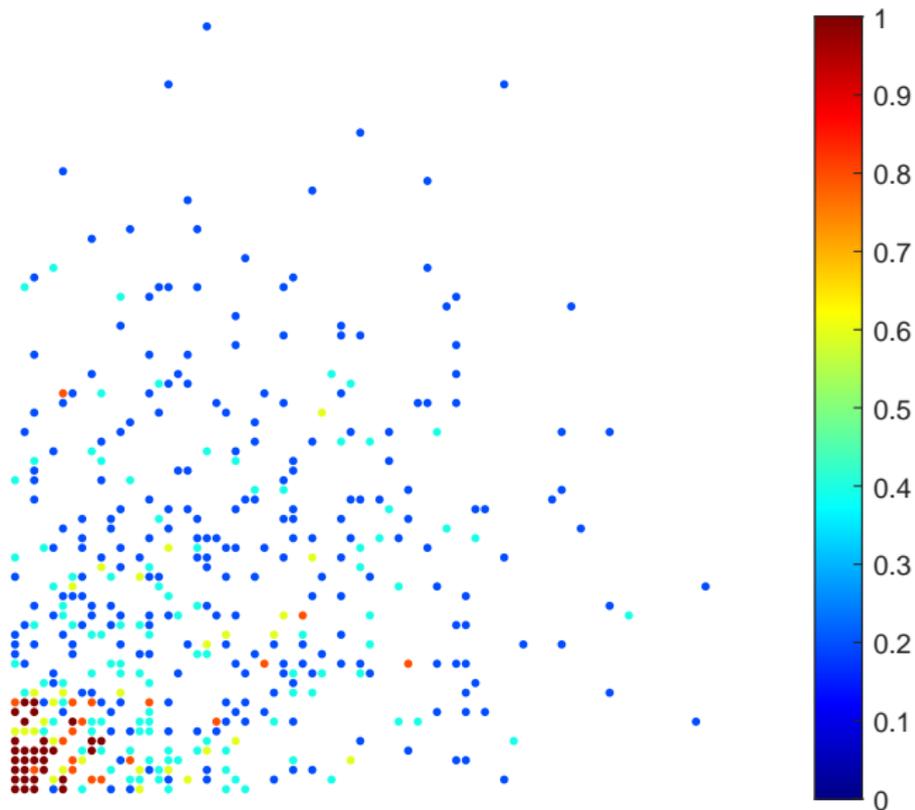
# A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ( $t = 2$ )



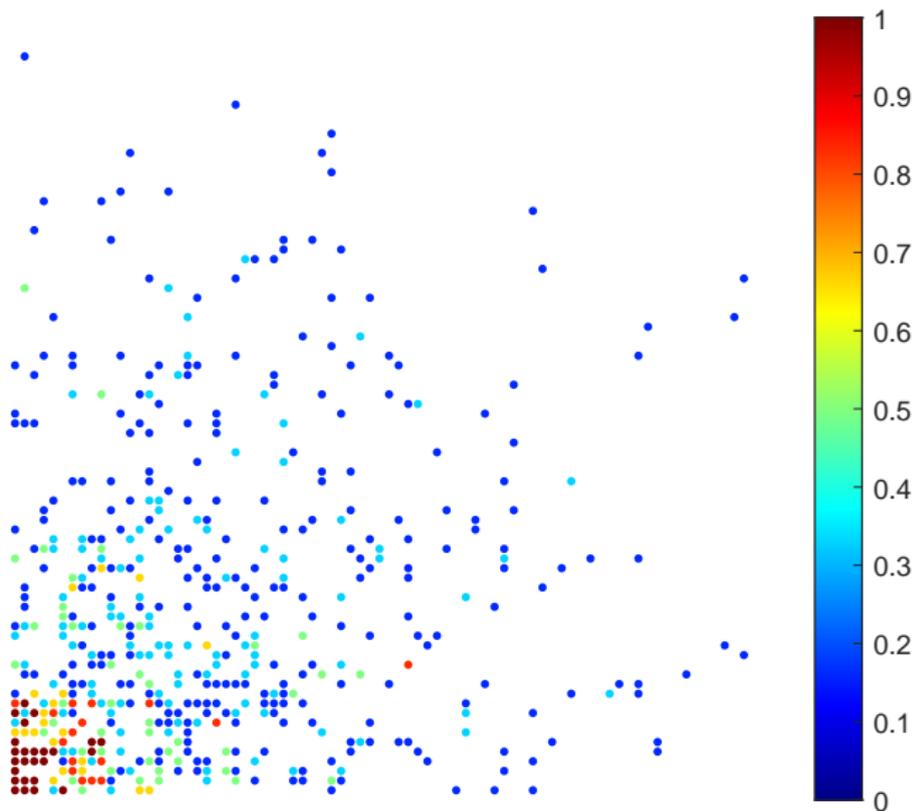
# A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ( $t = 3$ )



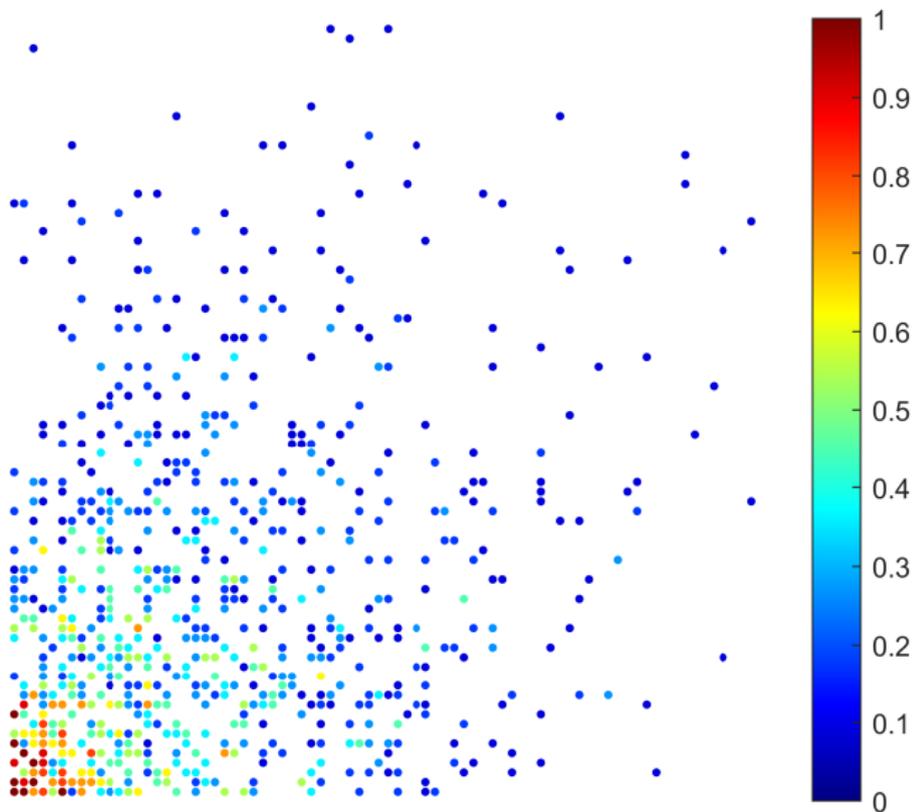
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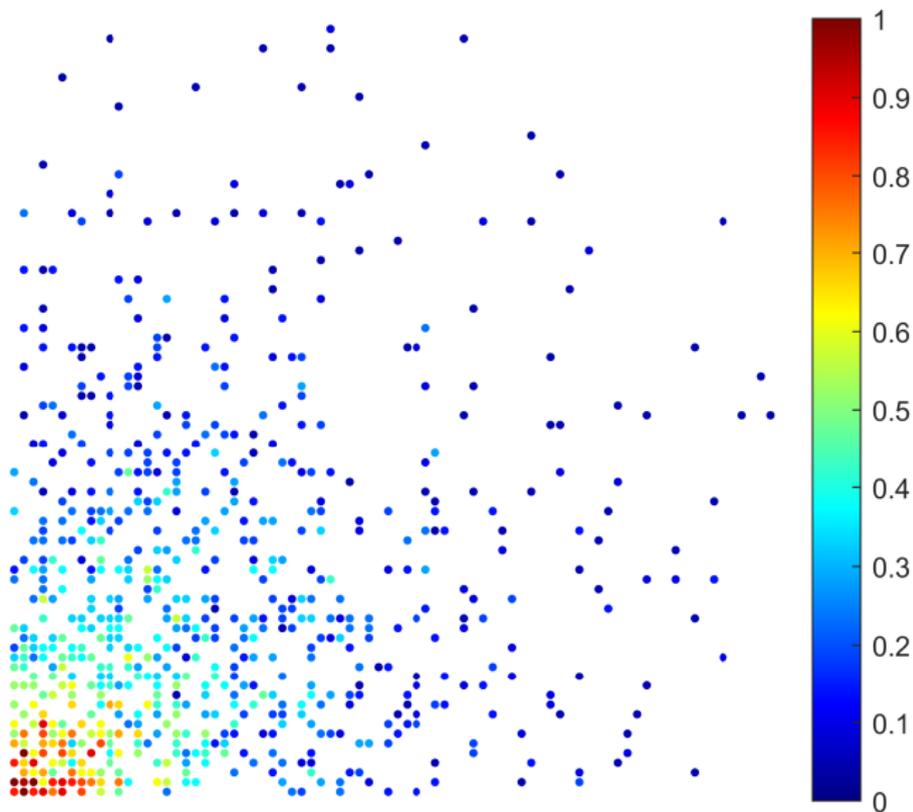
# A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ( $t = 5$ )



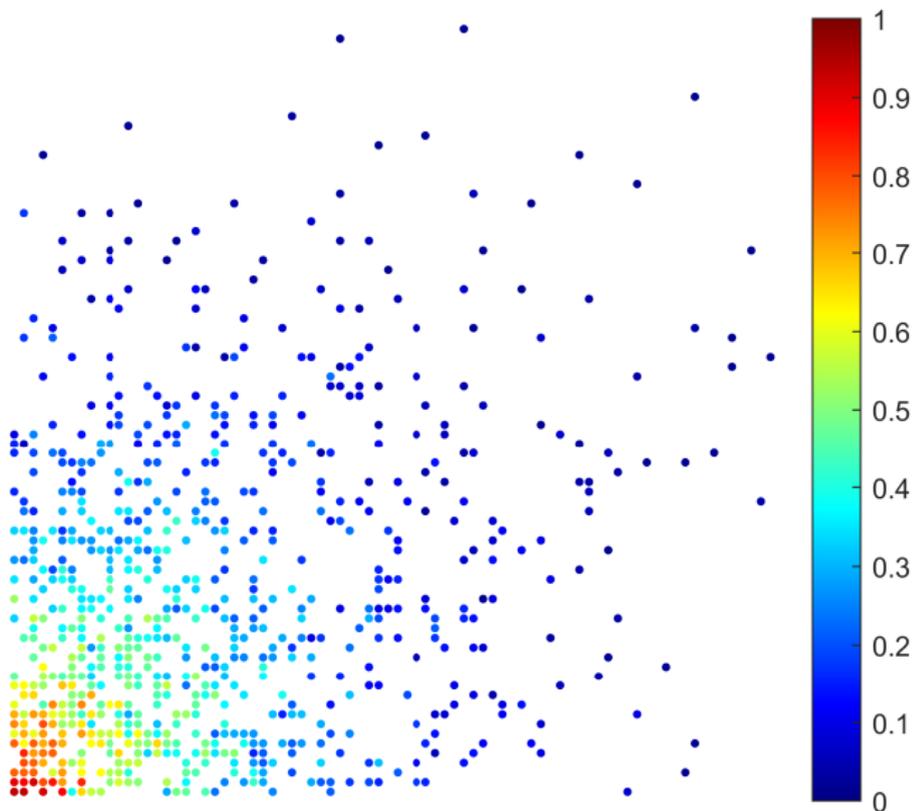
# A simulation - patches located on the integer lattice $\mathbb{Z}_+^2$ ( $t = 10$ )



# 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

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

we will assume that, for some  $M > 0$ ,  $\sum_i C_i(\mathbf{x}) \leq M \sum_i x_i$  for all  $\mathbf{x} \in E$ , where  $E$  is the subset of  $\{0, 1\}^{\mathbb{Z}_+}$  with finitely many non-zero entries (finitely many sites occupied).

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Extending the domains of  $S_i$  and  $C_i$  to  $[0, 1]^{\mathbb{Z}^+}$ , we consider a *deterministic analogue*<sup>2</sup>  $\mathbf{p}_t = \{p_{i,t}\}_{i=1}^{\infty}$  that evolves according to

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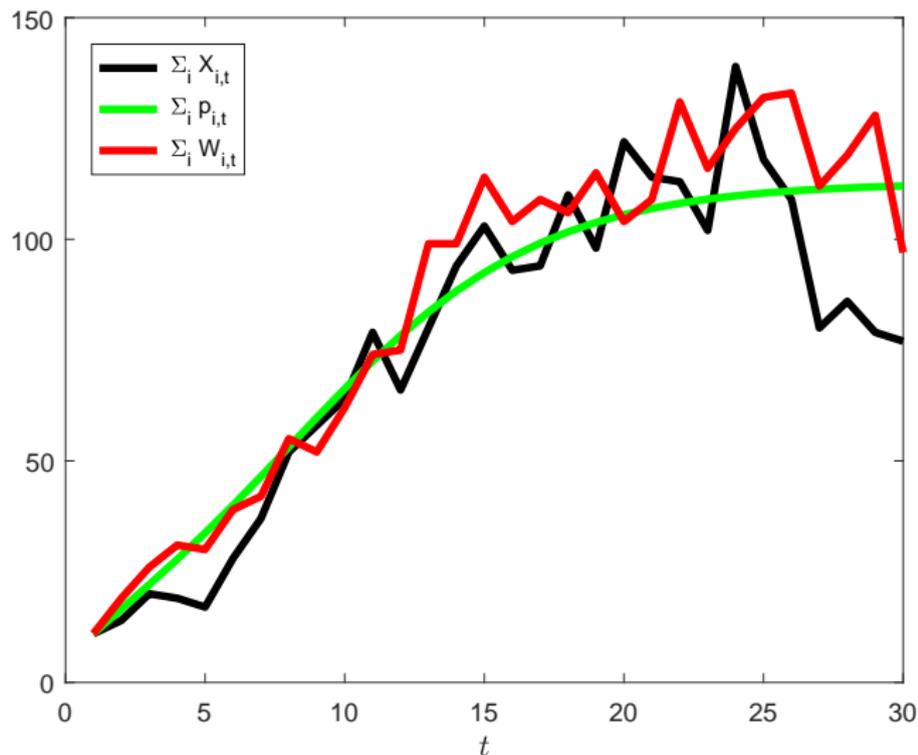
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We use common random numbers  $\{U_{i,t}\}$  (independent, uniformly distributed on  $[0, 1]$ ):

$$\begin{aligned} X_{i,t+1} &= B_{i,t}(S_i(\mathbf{X}_t))X_{i,t} + B_{i,t}(C_i(\mathbf{X}_t))(1 - X_{i,t}) \\ W_{i,t+1} &= B_{i,t}(S_i(\mathbf{p}_t))W_{i,t} + B_{i,t}(C_i(\mathbf{p}_t))(1 - W_{i,t}) \end{aligned}$$

with  $\mathbf{X}_0 = \mathbf{W}_0$ , where  $B_{i,t}(x) = \mathbb{1}\{U_{i,t} \geq 1 - x\}$ ,  $x \in [0, 1]$ , is the quantile function of the Bernoulli distribution with success probability  $x$ .



## The main result

To assess the quality of our approximations, we shall let<sup>3</sup>

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

and assume these quantities are all finite. Here  $\partial_j$  and  $\partial_j^2$  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  $\mathbf{w} \in \ell^{\infty}$  and  $t \geq 0$ ,

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

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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  $f : [0, \infty) \rightarrow [0, 1]$ , the colonisation function, satisfies  $f(0) = 0$ .

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- (i)  $\sum_i a_i < +\infty$  (the total weight of all patches is finite), and
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A typically case for which Assumption (ii) holds is  $d_{ij} = D(z_i, z_j) := \kappa(\|z_i - z_j\|)$ , for patches located at points  $\{z_i\}$  in  $\mathbb{R}^d$ , where  $\kappa$  is a smooth, non-negative, monotone decreasing function (typically  $\kappa(x) = e^{-\psi x}$ , or  $\kappa(x) = e^{-\psi x^2}$ ,  $\psi > 0$ ).

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- (i)  $\sum_i a_i < +\infty$  (the total weight of all patches is finite), and
- (ii) there exists a  $\bar{D}$  such that  $\sup_j \sum_i d_{ij} \leq \bar{D}$  and  $\sup_i \sum_j d_{ij} \leq \bar{D}$ .

A typically case for which Assumption (ii) holds is  $d_{ij} = D(z_i, z_j) := \kappa(\|z_i - z_j\|)$ , for patches located at points  $\{z_i\}$  in  $\mathbb{R}^d$ , where  $\kappa$  is a smooth, non-negative, monotone decreasing function (typically  $\kappa(x) = e^{-\psi x}$ , or  $\kappa(x) = e^{-\psi x^2}$ ,  $\psi > 0$ ).

Assumptions (i) and (ii) are enough to ensure that  $\alpha, \beta, \gamma$  are all finite.



## The metapopulation model

Let's check.

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

Since  $\{a_i\}$  is necessarily bounded by some constant  $A$ , the Mean Value Theorem together with the assumption that  $f(0) = 0$  gives

$$\alpha := \sup_j \sum_i \|\partial_j P_i\|_\infty \leq \|f'\|_\infty \sup_j \sum_i a_i d_{ij} \leq \|f'\|_\infty A \bar{D}.$$

Similarly,

$$\beta := \sum_i \left( \sum_{j \neq i} \|\partial_j P_i\|_\infty^2 \right)^{1/2} \leq \|f'\|_\infty \sum_i a_i \left( \sum_{j \neq i} d_{ij}^2 \right)^{1/2} \leq \|f'\|_\infty \bar{D} \sum_i a_i < \infty,$$

and

$$\gamma := \sum_i \sum_j \|\partial_j^2 P_i\|_\infty \leq \|f''\|_\infty \sum_i a_i^2 \sum_j d_{ij}^2 \leq \|f''\|_\infty A \bar{D}^2 \sum_i a_i < \infty.$$

## The metapopulation model - a high density limit

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

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

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

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

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

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

## The metapopulation model - a high density limit

Define, for each  $m$  and  $t$ , a finite measure  $\pi_t^{(m)}$  by

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

and assume that  $\pi_0^{(m)} \rightarrow \pi_0$  for some finite measure  $\pi_0$ . Evidently,  $\pi_0$  will be absolutely continuous with respect to  $\sigma$ , and so there exists a function  $p_0$  such that, for any bounded continuous function  $g$ ,

$$\int g(z) \pi_0^{(m)}(dz) = \frac{1}{m^d} \sum_{i=1}^{\infty} g(m^{-1}z_i) p_{i,0}^{(m)} \rightarrow \int g(z) p_0(z) \sigma(dz).$$

One can show<sup>1</sup>, furthermore, that there exists a finite measure  $\pi_t$ , which is absolutely continuous with respect to  $\sigma$ , such that  $\pi_t^{(m)} \rightarrow \pi_t$ .

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

## The metapopulation model - a high density limit

Consequently,

$$\int g(z)\pi_t^{(m)}(dz) = \frac{1}{m^d} \sum_{i=1}^{\infty} g(m^{-1}z_i)p_{i,t}^{(m)} \rightarrow \int g(z)p_t(z)\sigma(dz),$$

for some function  $p_t$ . In particular, the functions  $p_t$  satisfy the recursion

$$p_{t+1}(x) = s(x)p_t(x) + (1 - p_t(x))f\left(a(x) \int \kappa(\|x - z\|)p_t(z)\sigma(dz)\right).$$

Define, for each  $m$  and  $t$ , a random measure  $\mu_t^{(m)}$  by

$$\mu_t^{(m)}(B) = \frac{1}{m^d} \sum_{i=1}^{\infty} X_{i,t}^{(m)} \mathbb{1}_{\{m^{-1}z_i \in B\}}, \quad B \in \mathcal{B}(\mathbb{R}^d).$$

Assuming that each  $X_{i,0}^{(m)}$  is a Bernoulli random variable with success probability  $p_{i,0}^{(m)}$ , it is clear that  $\mu_0^{(m)} \xrightarrow{\mathcal{D}} \pi_0$  as  $m \rightarrow \infty$ . Our objective is to show that  $\mu_t^{(m)} \xrightarrow{\mathcal{D}} \pi_t$  for every  $t \geq 1$ .

## The metapopulation model - a high density limit

Recall the bound in the earlier Theorem 2: there is a constant  $C \in (0, 2\sqrt{\pi}]$  such that, for any  $\mathbf{w} \in \ell^\infty$  and  $t \geq 0$ ,

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

We apply this with weights  $w_i^{(m)} = g(m^{-1}z_i)$ , where  $g$  is any bounded continuous function, and all quantities are indexed by  $m$ . Since

$$\frac{1}{m^d} \sum_{i=1}^{\infty} \left( w_i^{(m)} \right)^2 p_{i,t}^{(m)} = \int g^2(z) \pi_t^{(m)}(dz) \rightarrow \int g^2(z) \pi_t(dz),$$

we conclude that if  $\{\alpha_m\}_{m=1}^\infty$  is bounded and  $m^{-d}\beta_m, m^{-d}\gamma_m \rightarrow 0$  as  $m \rightarrow \infty$ , then

$$\mathbb{E} \left| \int g(z) \mu_t^{(m)}(dz) - \int g(z) \pi_t^{(m)}(dz) \right| \rightarrow 0.$$

Then,  $\pi_t^{(m)} \xrightarrow{\mathcal{D}} \pi_t$  will imply that  $\mu_t^{(m)} \xrightarrow{\mathcal{D}} \pi_t$ .



## The metapopulation model - a high density limit

Let's check: (i)  $\{\alpha_m\}$  is bounded because

$$\alpha \leq \|f'\|_\infty \sup_j \sum_i a_i d_{ij} = \|f'\|_\infty \sup_j \frac{1}{m^d} \sum_i a\left(\frac{z_i}{m}\right) \kappa(m^{-1}\|z_i - z_j\|)$$

$$\rightarrow \|f'\|_\infty \sup_x \int a(y) \kappa(\|x - y\|) \sigma(dy).$$

(ii)  $m^{-d}\beta_m \rightarrow 0$  because

$$m^{-d/2}\beta_m \leq \|f'\|_\infty \frac{1}{m^d} \sum_i a\left(\frac{z_i}{m}\right) \left(\sum_j \frac{1}{m^d} \kappa(m^{-1}\|z_i - z_j\|)^2\right)^{1/2}$$

$$\rightarrow \|f'\|_\infty \int a(x) \left(\int \kappa(\|x - y\|)^2 d\sigma(y)\right)^{1/2} d\sigma(x).$$

(iii)  $m^{-d}\gamma_m \rightarrow 0$  because

$$\gamma_m \leq \|f''\|_\infty \sum_i a_i^2 \sum_j d_{ij}^2 = \|f''\|_\infty \frac{1}{m^d} \sum_i a^2\left(\frac{z_i}{m}\right) \sum_j \frac{1}{m^d} \kappa(m^{-1}\|z_i - z_j\|)^2$$

$$\rightarrow \|f''\|_\infty \int a^2(x) \kappa(\|x - y\|)^2 d\sigma(x) d\sigma(y).$$



## 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:  $s(\mathbf{z}) = \exp(-\phi \|\mathbf{z}\|)$  with  $\phi = 0.25$ .

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

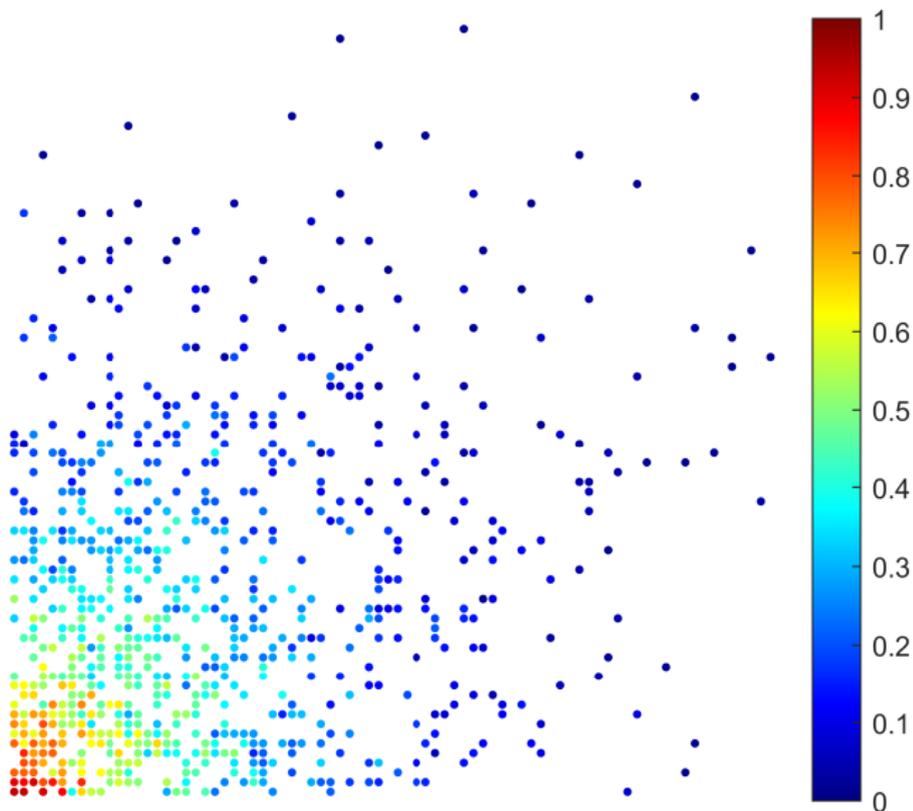
Easy of movement function:  $d(\mathbf{x}, \mathbf{z}) = b \exp(-\psi \|\mathbf{x} - \mathbf{z}\|)$  with  $b = 25$  and  $\psi = 0.4$ .

Scaling:  $m = 8$

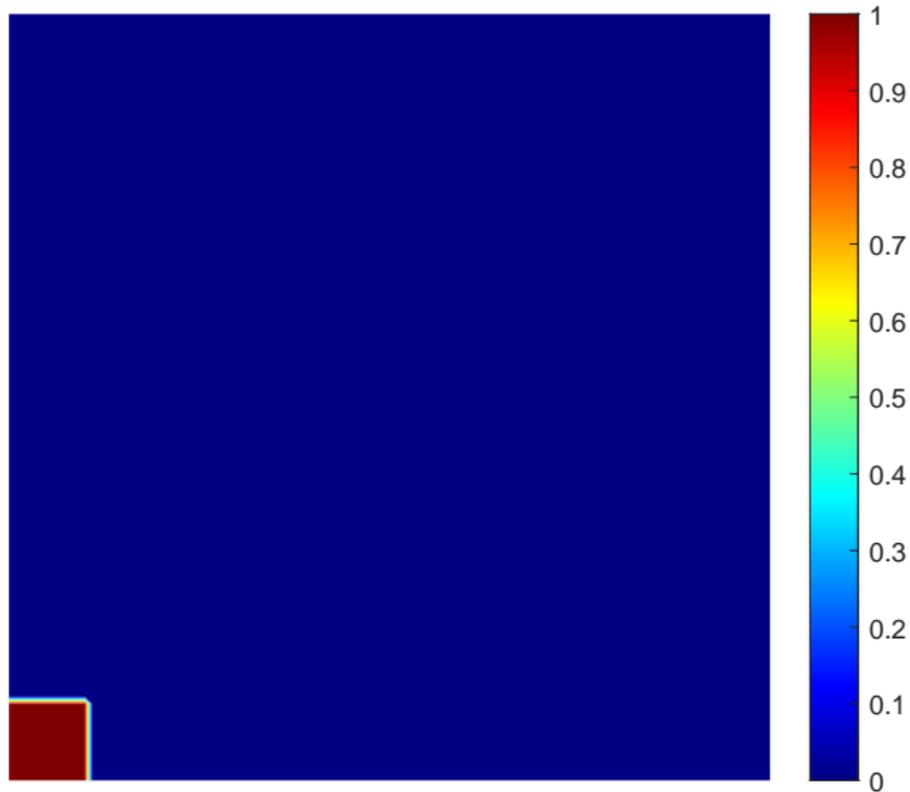
$$s_i^{(m)} = s(m^{-1}z_i), \quad a_i^{(m)} = a(m^{-1}z_i), \quad d_{ij}^{(m)} = m^{-2} \kappa(m^{-1}\|z_i - z_j\|)$$

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

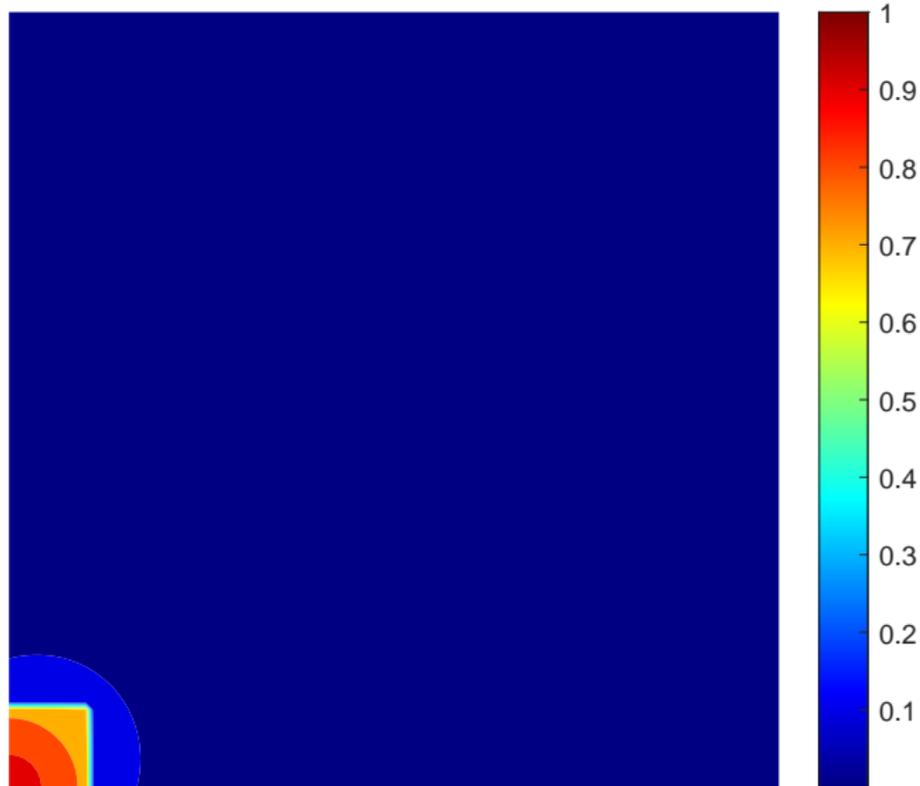
The earlier simulation - patches located on the integer lattice  $\mathbb{Z}_+^2$  ( $t = 50$ )



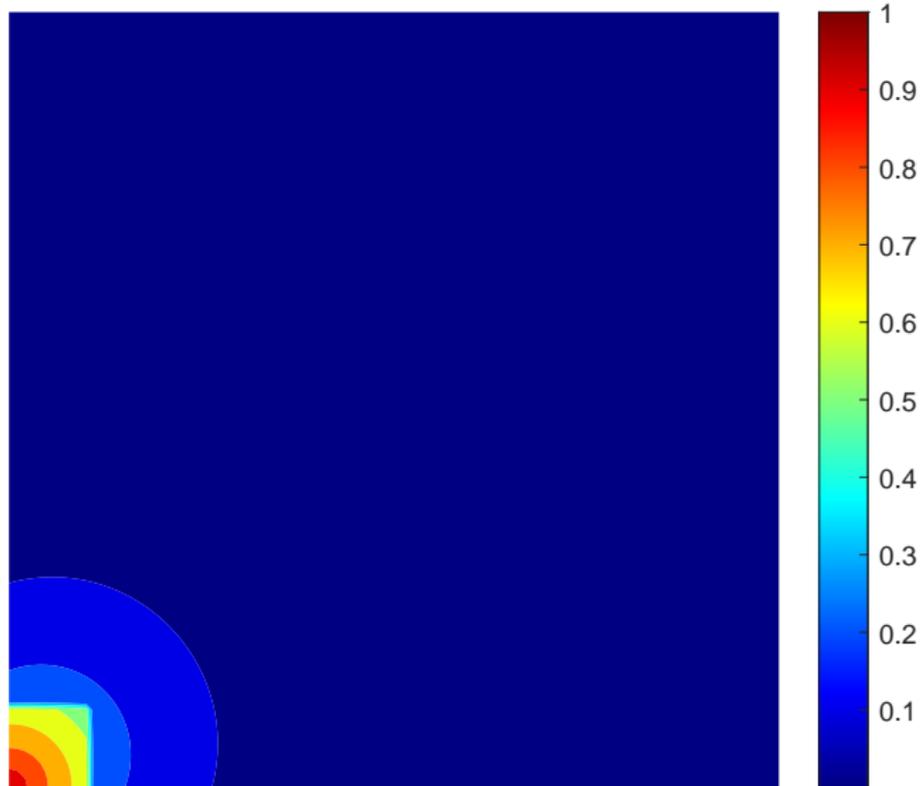
# Occupancy probability heatmap $p_t(z)$ ( $t = 0$ )



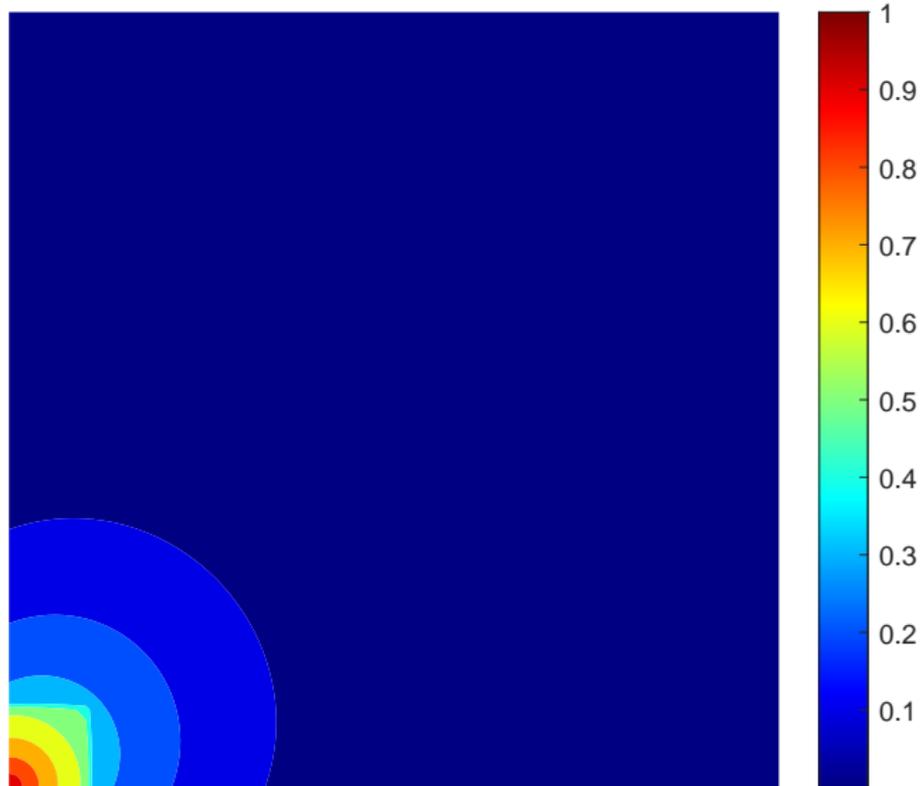
# Occupancy probability heatmap $p_t(z)$ ( $t = 1$ )



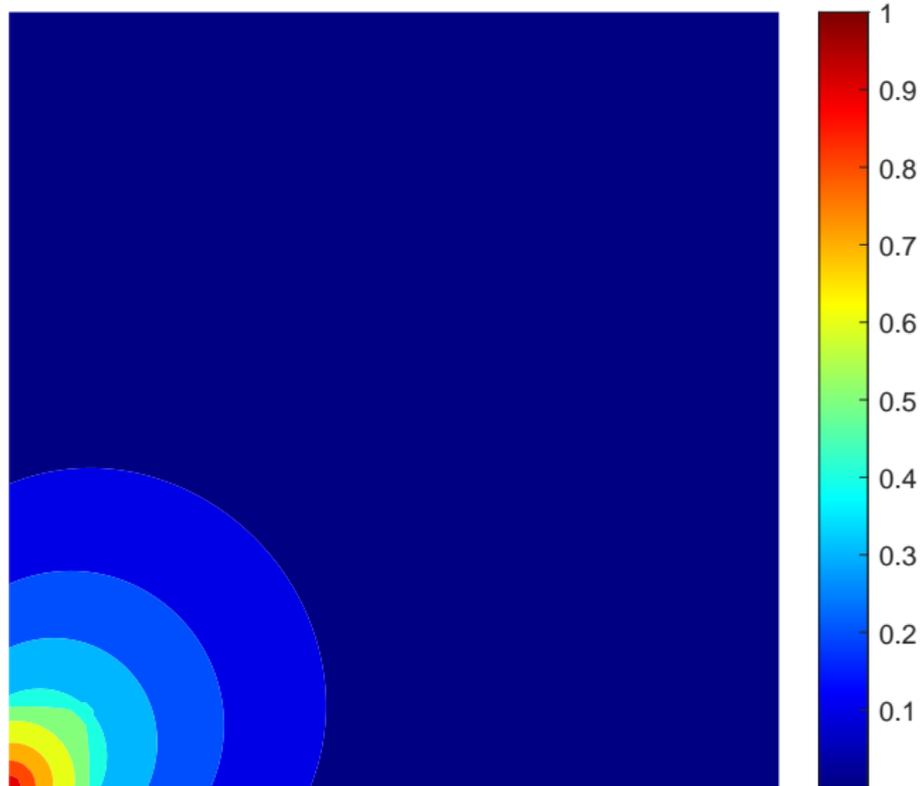
# Occupancy probability heatmap $p_t(z)$ ( $t = 2$ )



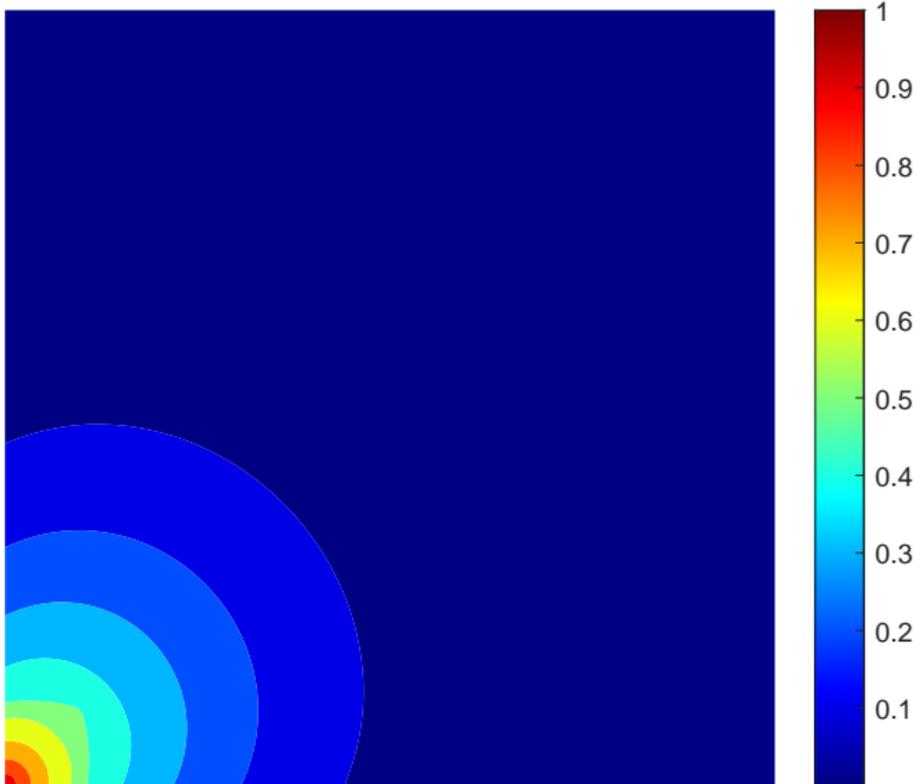
# Occupancy probability heatmap $p_t(z)$ ( $t = 3$ )



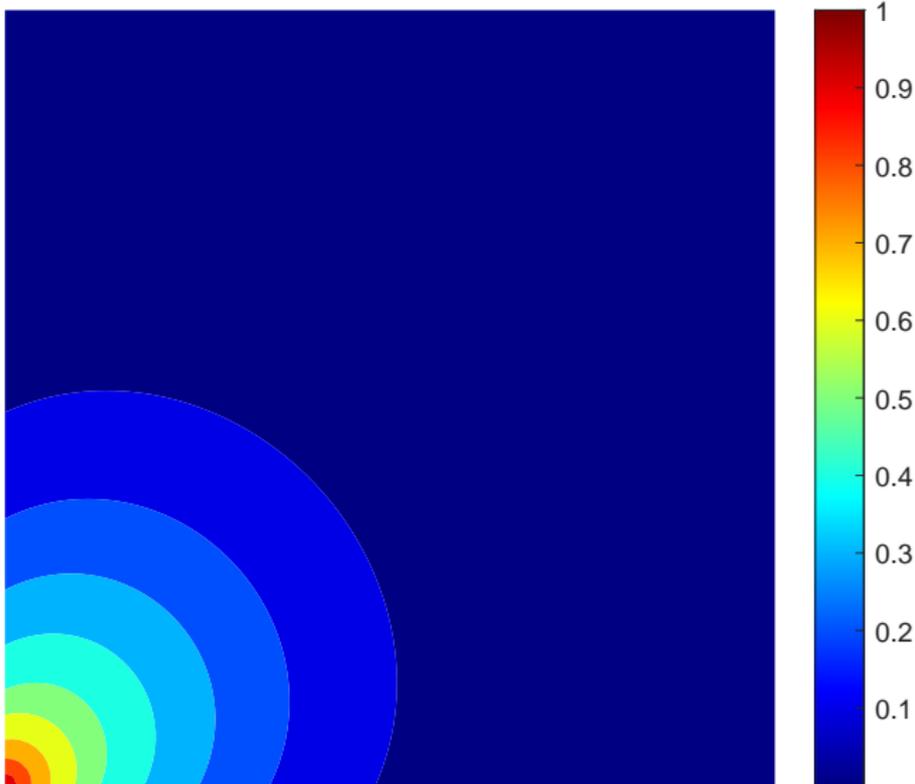
# Occupancy probability heatmap $p_t(z)$ ( $t = 4$ )



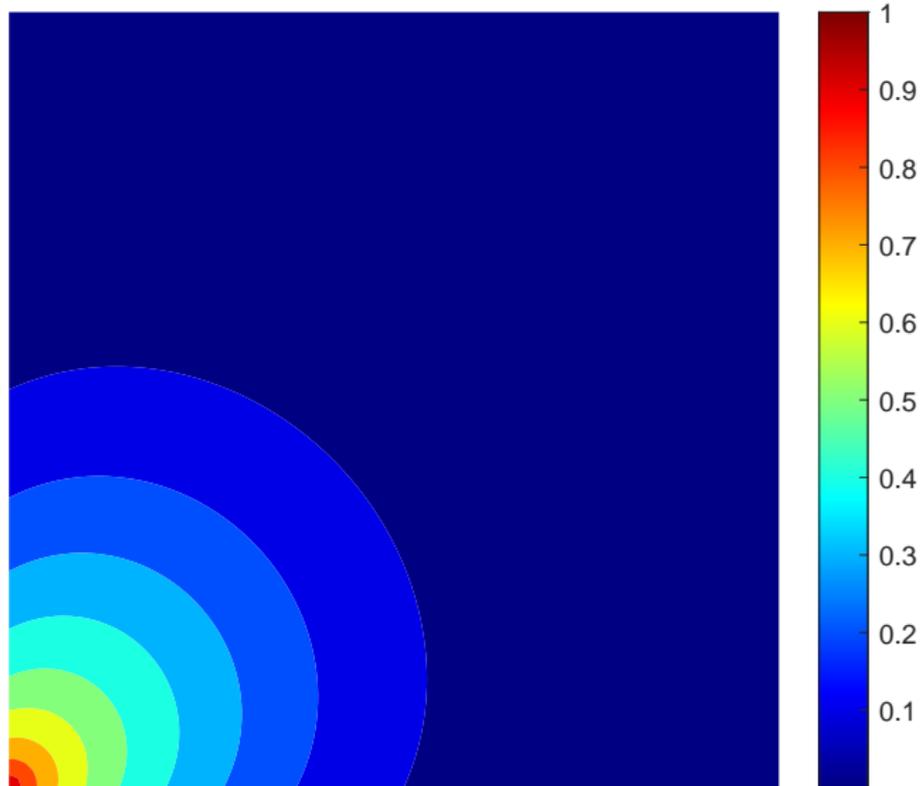
# Occupancy probability heatmap $p_t(z)$ ( $t = 5$ )



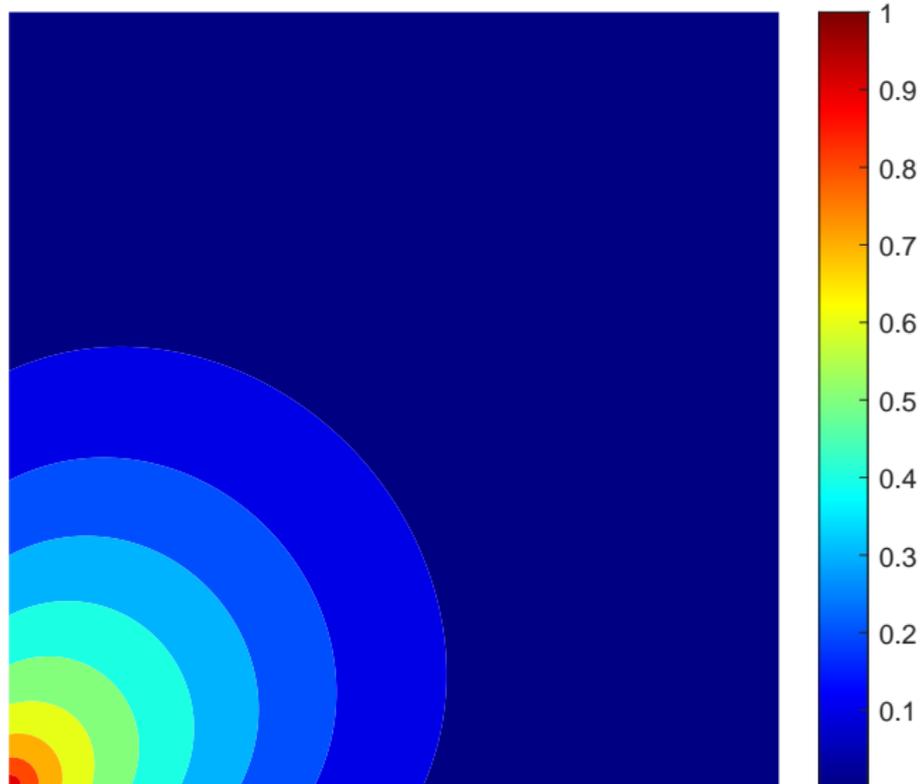
# Occupancy probability heatmap $p_t(z)$ ( $t = 6$ )



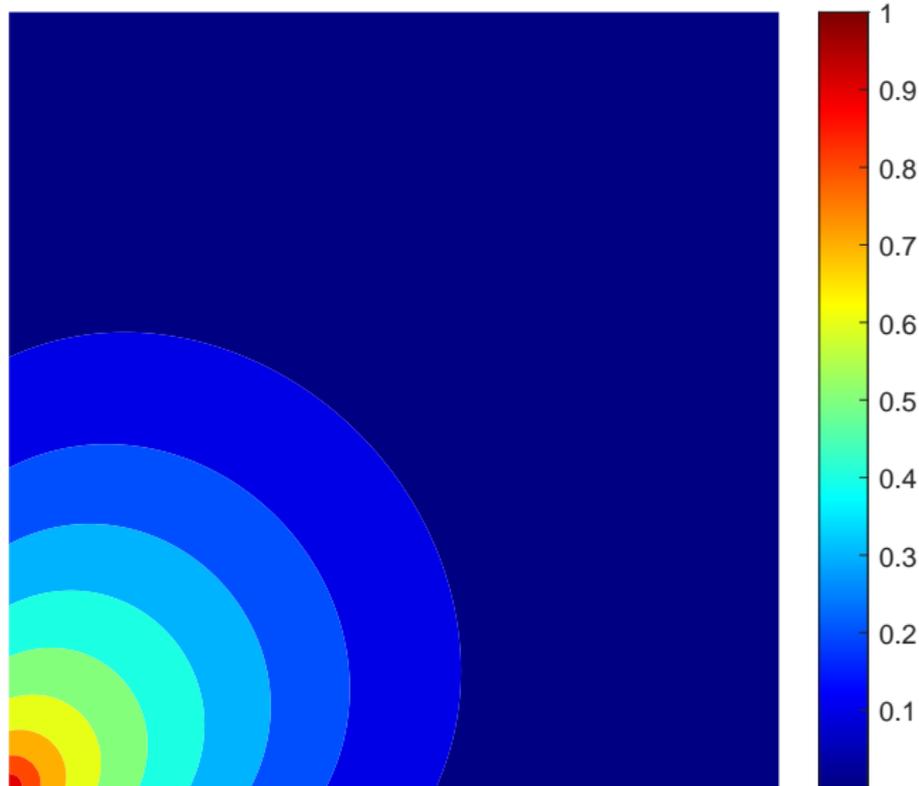
# Occupancy probability heatmap $p_t(z)$ ( $t = 7$ )



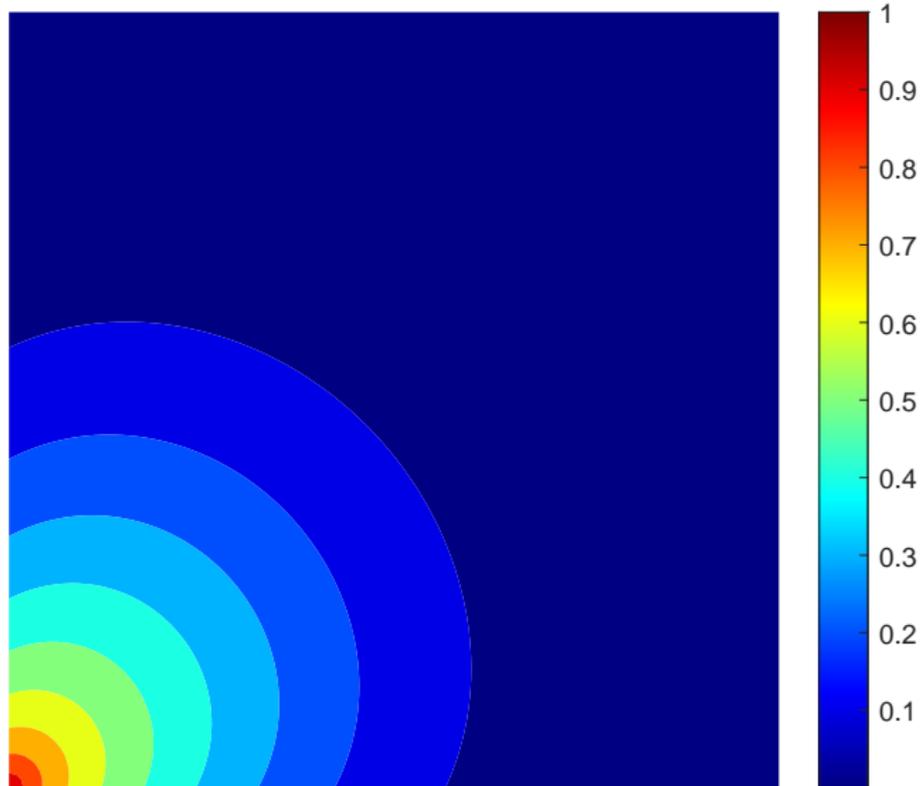
# Occupancy probability heatmap $p_t(z)$ ( $t = 8$ )



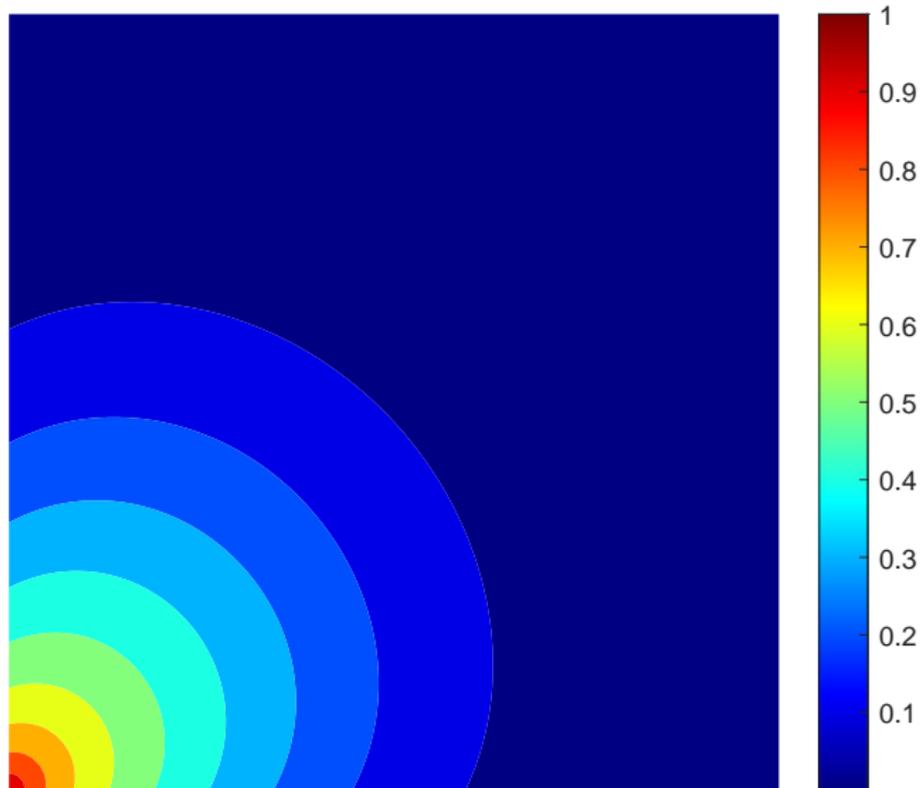
# Occupancy probability heatmap $p_t(z)$ ( $t = 9$ )



# Occupancy probability heatmap $p_t(z)$ ( $t = 10$ )



# Occupancy probability heatmap $p_t(z)$ ( $t = 50$ )



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

