# Metapopulations in evolving landscapes

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[Joint work with Ross McVinish and Jessica Chan]

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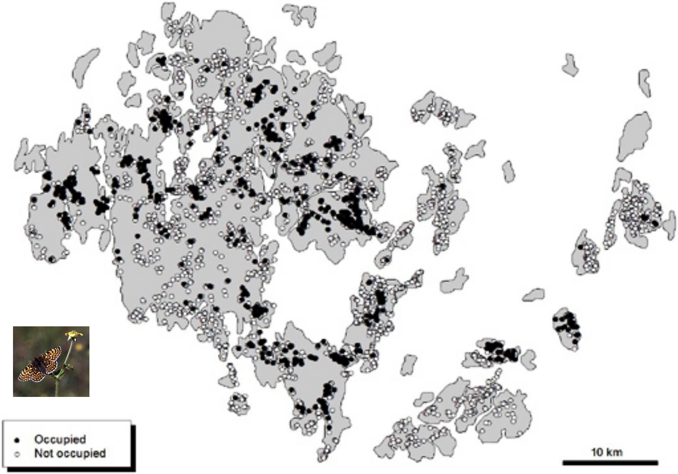
MATHEMATICAL AND STATISTICAL FRONTIERS

# Metapopulations




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

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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

## SPOM - Phase structure

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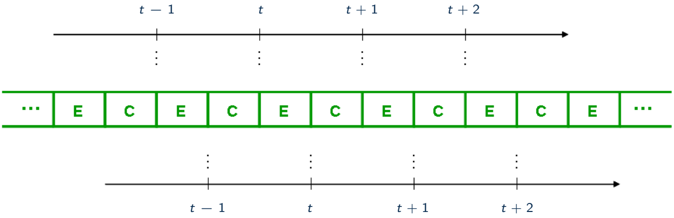

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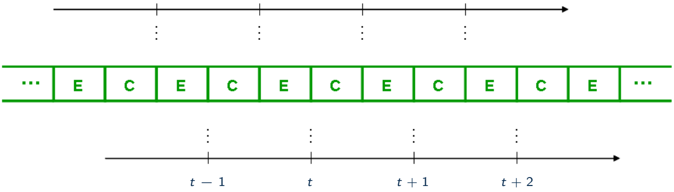


We will we assume that the population is *observed after successive extinction phases* (CE Model).

*Colonization*: unoccupied patch $i$ becomes occupied with probability $c(\bar{X}_{i,t}^{(n)})$, where

$$\bar{X}_{i,t}^{(n)} = \frac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)} D(z_i, z_j) a_j \quad (\text{“connectivity”}).$$

$D(z, \tilde{z}) \geq 0$ measures ease of movement between patches located at $z$ and at $\tilde{z}$, $a_j$ is a weight related to the size of the patch $j$ and $c : [0, \infty) \to [0, 1]$ (*colonisation function*).

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**Assumptions**:

(A) $a_i \in (0, A]$ for some $A < \infty$.

(B) $z_i \in \Omega$ where $\Omega$ 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 $\sup_{z\in\Omega} |D(z_1, z) - D(z_2, z)| < \epsilon$.

(D) $c$ is increasing and Lipschitz continuous, with $c(0) = 0$ and $c'(0) > 0$.

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$$\Pr\left(X_{i,t+1}^{(n)} = 1 \,\middle|\, \boldsymbol{X}_t^{(n)}, \boldsymbol{S}_t^{(n)}\right) = s_{i,t} X_{i,t}^{(n)} + s_{i,t}\, c(\bar{X}_{i,t}^{(n)}) \left(1 - X_{i,t}^{(n)}\right).$$

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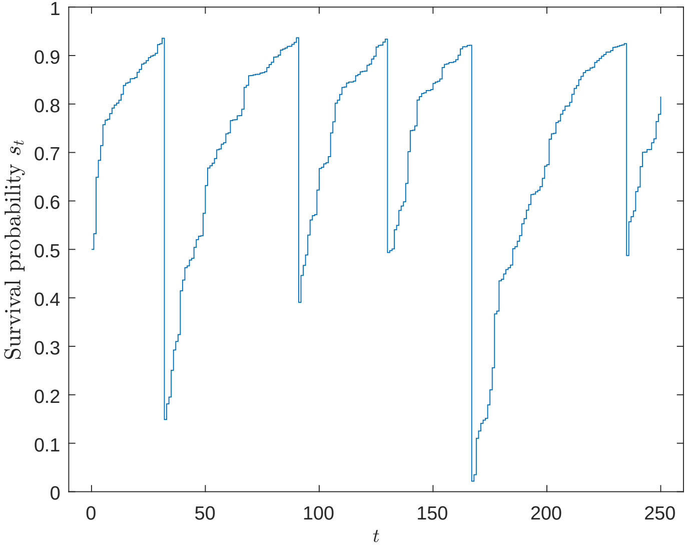
(E) We will assume that $(s_{i,t})_{t=0}^{\infty}$, $i = 1, \ldots, n$, are independent Markov chains taking values in $[0, 1]$ with common (Feller) transition kernel $P(s, dr)$.

# Example: climax community species



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

$$\sigma_{n,t}(B) = \frac{1}{n}\sum_{i=1}^{n} a_i \mathbb{1}_{\{(s_{i,t},\, z_i)\in B\}}, \qquad B \in \mathcal{B}([0,1]\times\Omega),$$

$$\mu_{n,t}(B) = \frac{1}{n}\sum_{i=1}^{n} a_i X_{i,t}^{(n)} \mathbb{1}_{\{(s_{i,t},\, z_i)\in B\}}, \qquad B \in \mathcal{B}([0,1]\times\Omega).$$

# Our approach - random measures

Equivalently, define $(\sigma_{n,t})$ and $(\mu_{n,t})$ by

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

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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.

# Executive summary

The landscape $(s_{i,t}^{(n)}, a_i, z_i)$ at time $t$ is summarized by $\sigma_{n,t}$. The metapopulation (occupancy process) is summarized by $\mu_{n,t}$.

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If (time $t = 0$) $\sigma_{n,0} \xrightarrow{d} \sigma_0$, then $\sigma_{n,t} \xrightarrow{d} \sigma_t$ *for all* $t$, and $\sigma_{t+1} = \mathcal{G}(\sigma_t)$.

Similarly if $\mu_{n,0} \xrightarrow{d} \mu_0$, then $\mu_{n,t} \xrightarrow{d} \mu_t$ *for all* $t$, and $\mu_{t+1} = \mathcal{H}(\mu_t, \sigma_t)$.

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**Landscape in equilibrium**. Next we see that if the survival probability model $(\boldsymbol{S}_t^{(n)})$ is stationary, then $\sigma_t \to \sigma$ as $t \to \infty$. We find that $\mu_t$ is absolutely continuous with respect to $\sigma$, and the corresponding Radon-Nikodym derivative $\phi_t := \partial\mu_t/\partial\sigma$ satisfies a simplified recursion $\phi_{t+1} = \mathcal{R}(\phi_t)$. We learn that if a given patch with survival probability $s$ is located at $z$, then $\phi_t(s, z)$ is the large-metapopulation probability that it is occupied.

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**Metapopulation in equilibrium**. Finally, we find the fixed points $\phi_\infty := \partial\mu_\infty/\partial\sigma$ of $\mathcal{R}$, and distinguish between the (complementary) cases (i) where there is only the trivial fixed point $\partial\mu_\infty/\partial\sigma = 0$, being globally stable (*evanescence*), and (ii) where there is a unique non-zero fixed point and all non-zero trajectories converge to it (*persistence*).

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# Limiting behaviour of the landscape ($n$ large)

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**Lemma 1** $\sigma_{n,t} \xrightarrow{d} \sigma_t$ for all $t = 1, 2, \ldots,$ where $\sigma_t$ is defined by the recursion $\mathcal{G}$:

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

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

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

## Limiting behaviour of the metapopulation ($n$ large)

**Theorem 1** Suppose that $\mu_{n,0} \xrightarrow{d} \mu_0$ for some non-random measure $\mu_0$. Then, $\mu_{n,t} \xrightarrow{d} \mu_t$ for all $t = 1, 2, \ldots$, where $\mu_t$ is defined by the recursion $\mathcal{H}$: for $h \in C^+([0,1] \times \Omega)$,

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

Think of $\psi_t(z)$ as being the large-metapopulation ($n \to \infty$) connectivity at time $t$ for a patch located at $z$, and $c(\psi_t(z))$ as being the corresponding potential of the metapopulation to colonize that patch.

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

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**Theorem 2** The limiting measure $\mu_t$ is absolutely continuous with respect to $\sigma$ and the corresponding Radon-Nikodym derivative $\phi_t := \partial\mu_t/\partial\sigma$ satisfies the recursion $\mathcal{R}$:

$$\phi_{t+1}(s, z) = \int_0^1 r\, \phi_t(r, z)P^*(s, dr) + c(\psi_t(z)) \int_0^1 r\, (1 - \phi_t(r, z))\, P^*(s, dr),$$

where (now we may write) $\psi_t(z) = \int D(z, \tilde{z}) \int \phi_t(\tilde{s}, \tilde{z})\nu(d\tilde{s})\bar{\sigma}_0(d\tilde{z})$.

## When the landscape is in equilibrium

In addition to providing a simplified recursion

$$\phi_{t+1}(s,z) = \int_0^1 r\,\phi_t(r,z)P^*(s,dr) + c(\psi_t(z))\int_0^1 r\,(1-\phi_t(r,z))\,P^*(s,dr).$$

to describe large-metapopulation behaviour, 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** 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: For fixed $i$, $X_{i,0}^{(n)} \xrightarrow{p} X_{i,0}$ implies that $X_{i,t}^{(n)} \xrightarrow{p} X_{i,t}$ for all $t = 1, 2, \ldots$, where

$$\Pr\left(X_{i,t+1} = 1 \mid X_{i,t},\, s_{i,t}\right) = s_{i,t}X_{i,t} + s_{i,t}c(\psi_t(z_i))\left(1 - X_{i,t}\right),$$

and, if

$$\Pr\left(X_{i,0} = 1 \mid s_{i,0} = s, z_i = z\right) = \phi_0(s,z),$$

then

$$\Pr\left(X_{i,t} = 1 \mid s_{i,t} = s, z_i = z\right) = \phi_t(s,z).$$

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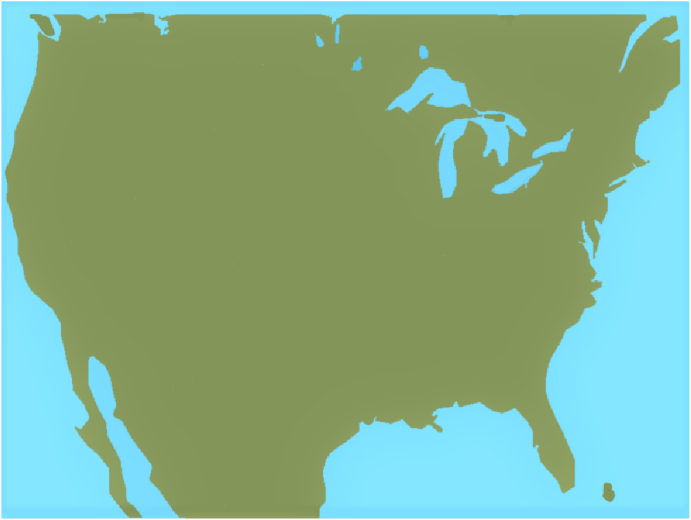
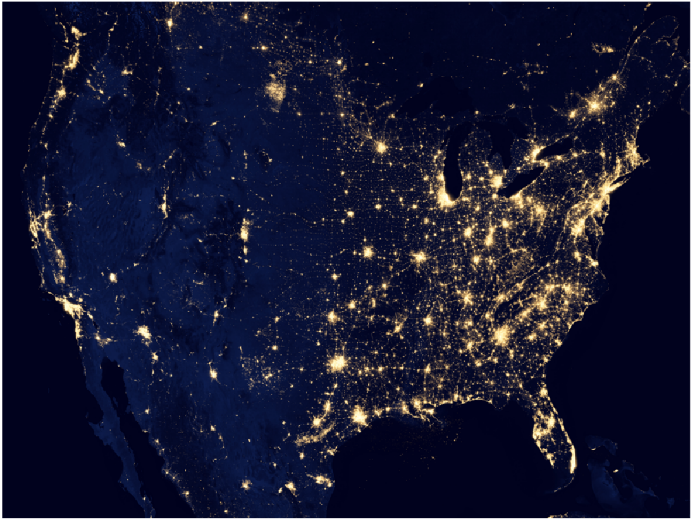
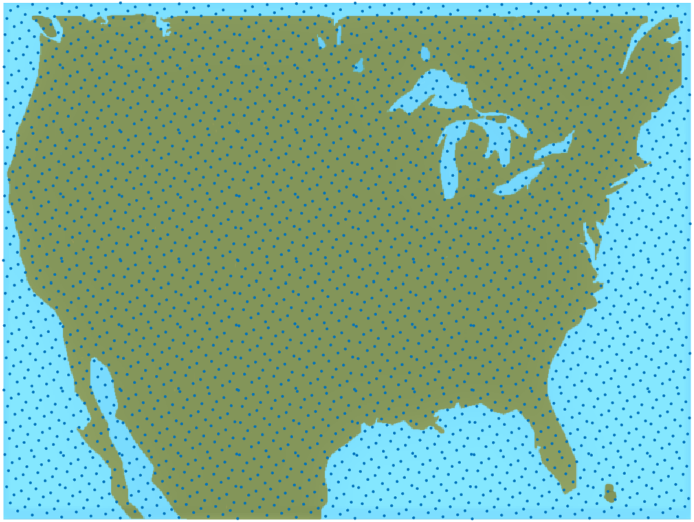


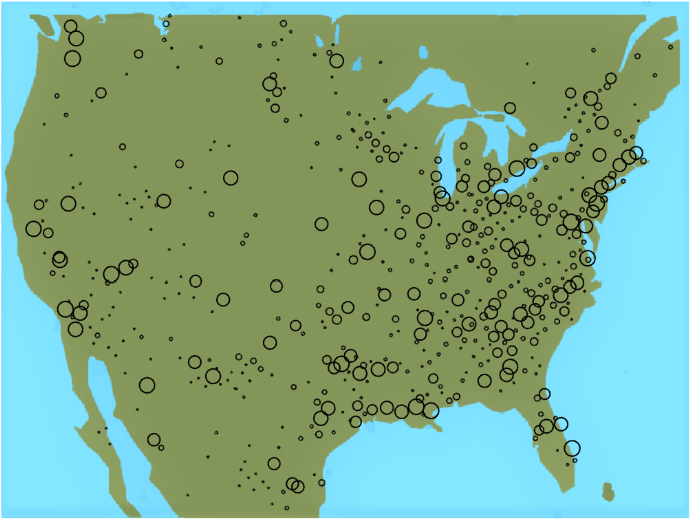
# USA light polution - proxy for patch weight



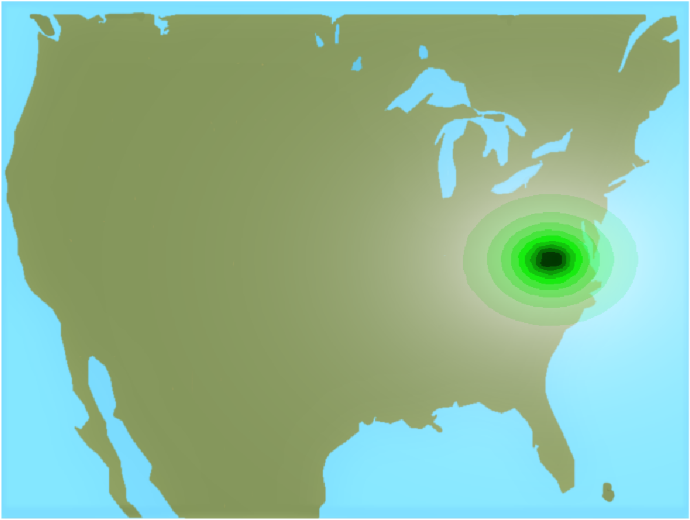
# Potential patch positions ($z_i$)



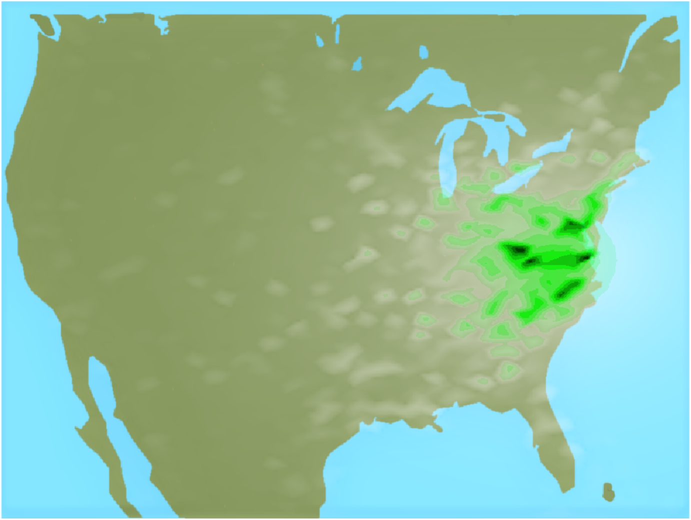
# Patch weights ($n = 540$)



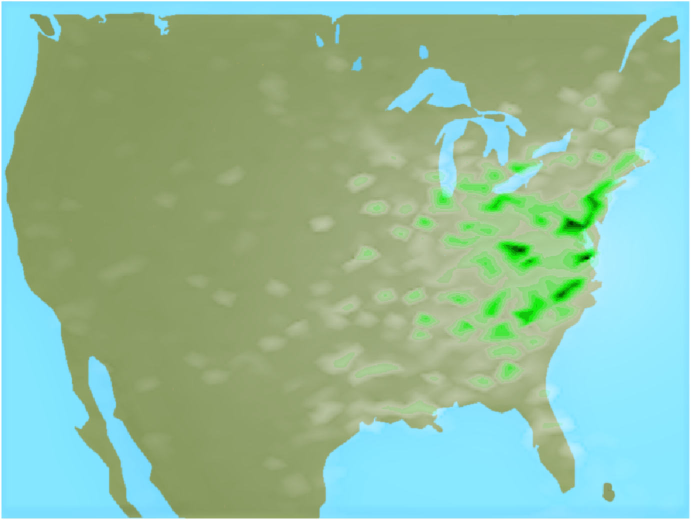
# Evolution of $\phi_t(s, z)$ $(t = 0)$



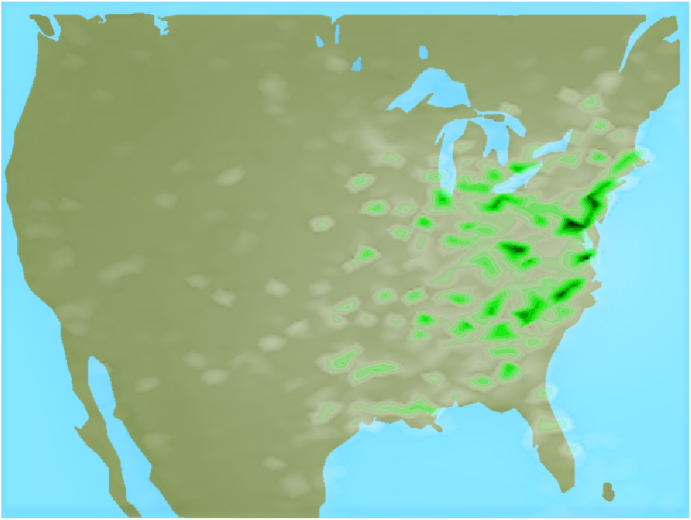
# Evolution of $\phi_t(s, z)$ $(t = 1)$



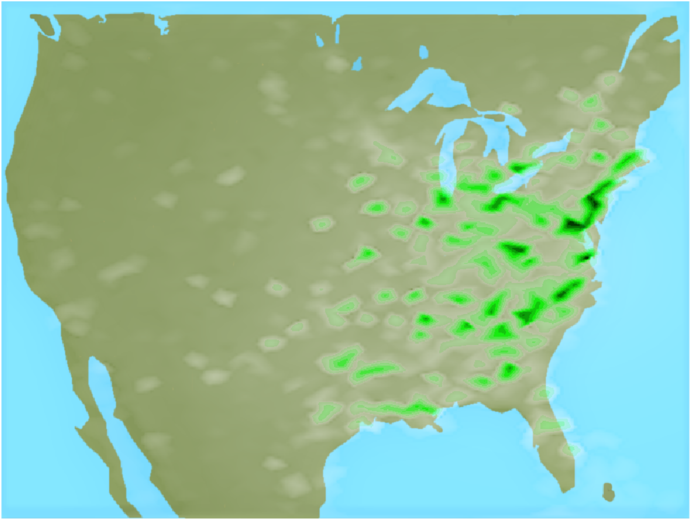
# Evolution of $\phi_t(s, z)$ $(t = 2)$



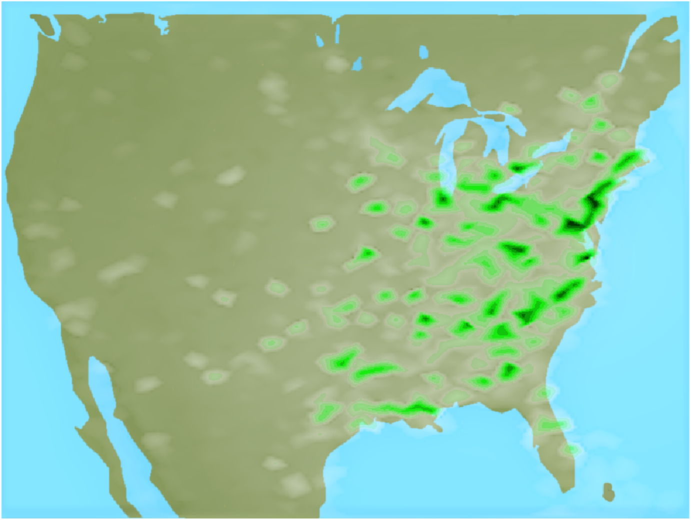
# Evolution of $\phi_t(s, z)$ $(t = 3)$



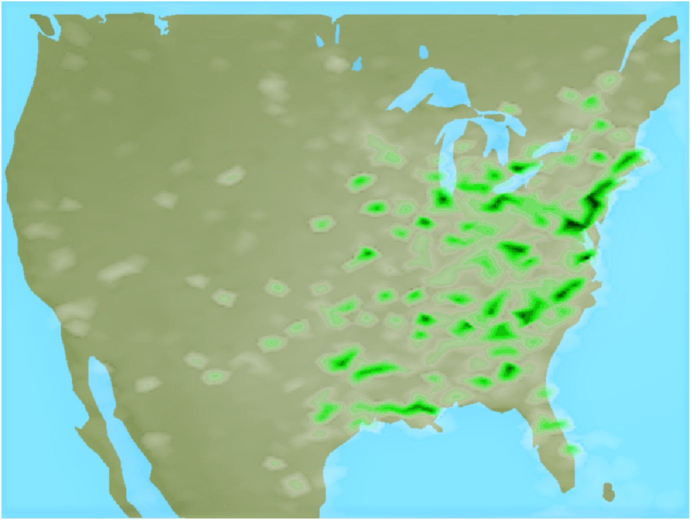
# Evolution of $\phi_t(s,z)$ $(t=4)$



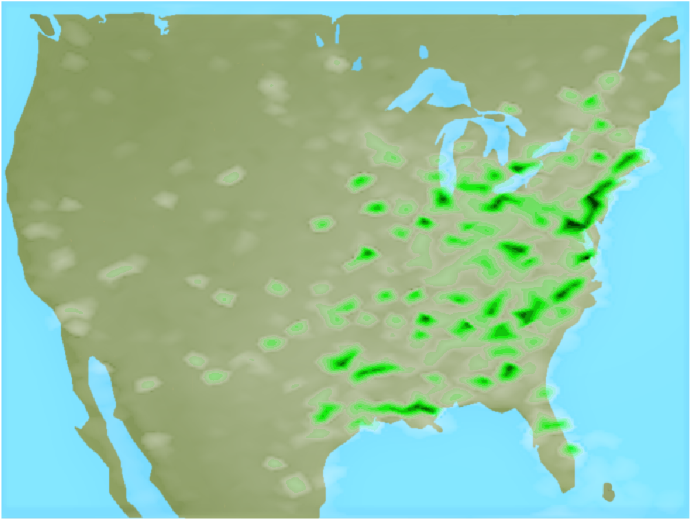
# Evolution of $\phi_t(s, z)$ $(t = 5)$



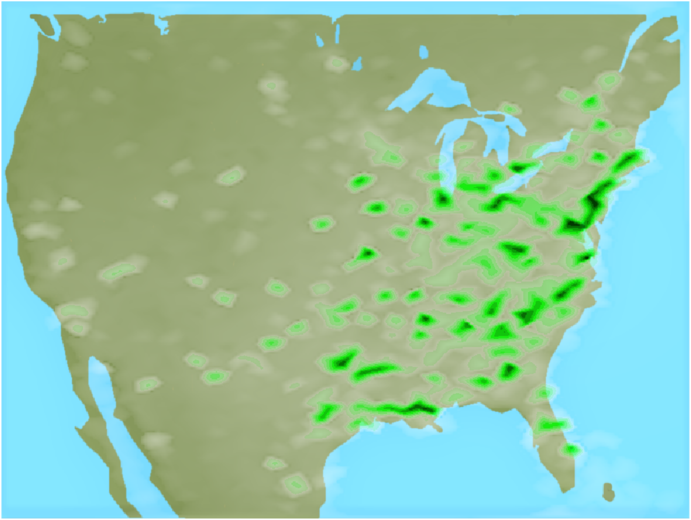
# Evolution of $\phi_t(s, z)$ $(t = 6)$



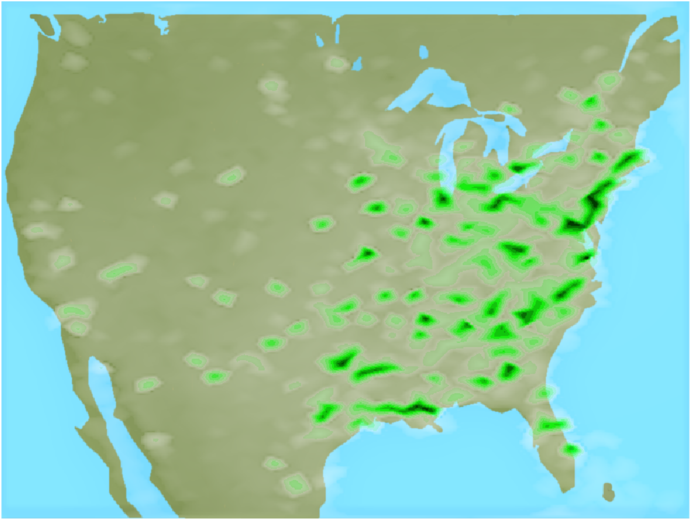
# Evolution of $\phi_t(s, z)$ $(t = 7)$



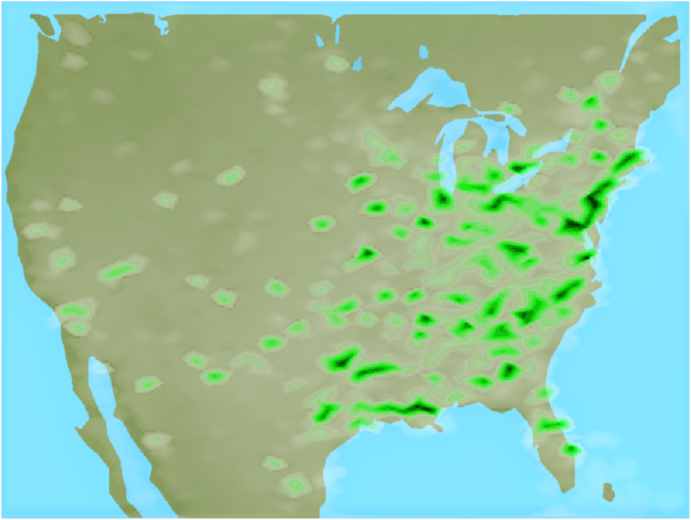
## Evolution of $\phi_t(s, z)$ $(t = 8)$



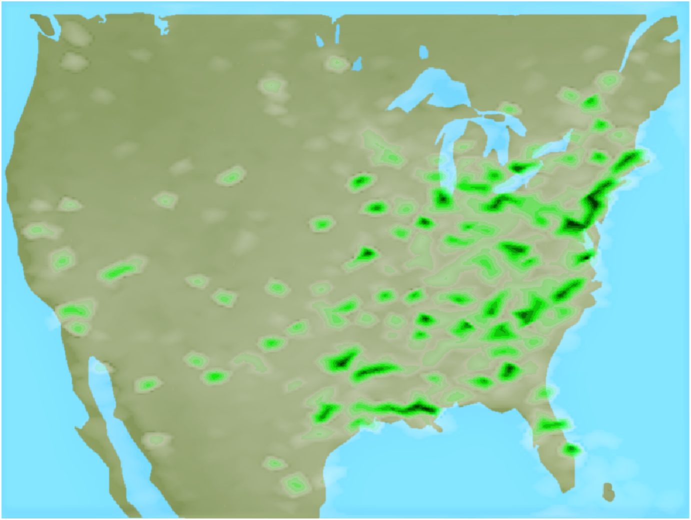
# Evolution of $\phi_t(s, z)$ $(t = 9)$



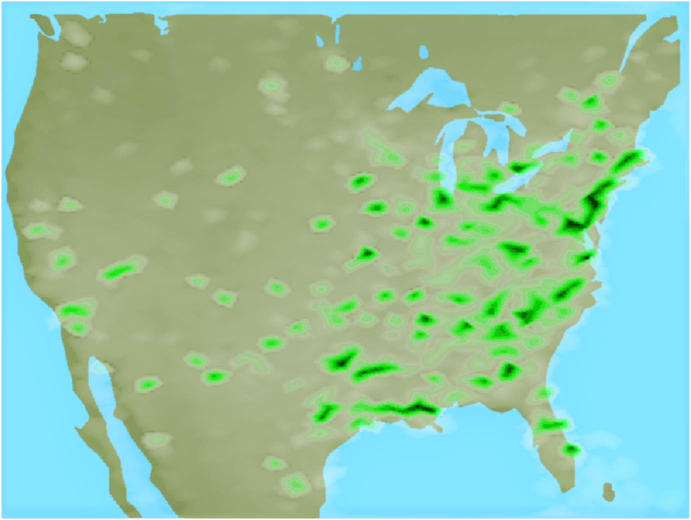
# Evolution of $\phi_t(s, z)$ $(t = 10)$



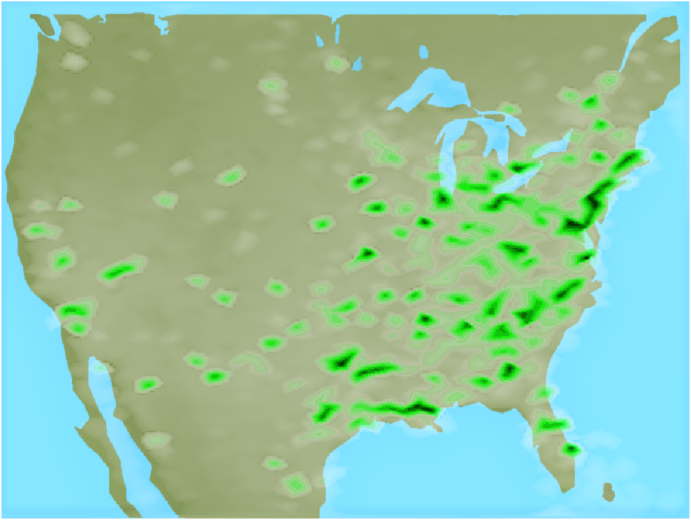
# Evolution of $\phi_t(s, z)$ $(t = 11)$



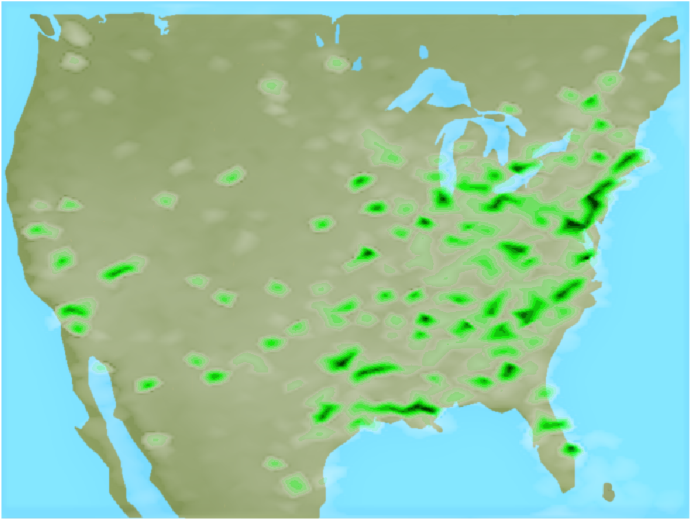
# Evolution of $\phi_t(s, z)$ $(t = 12)$



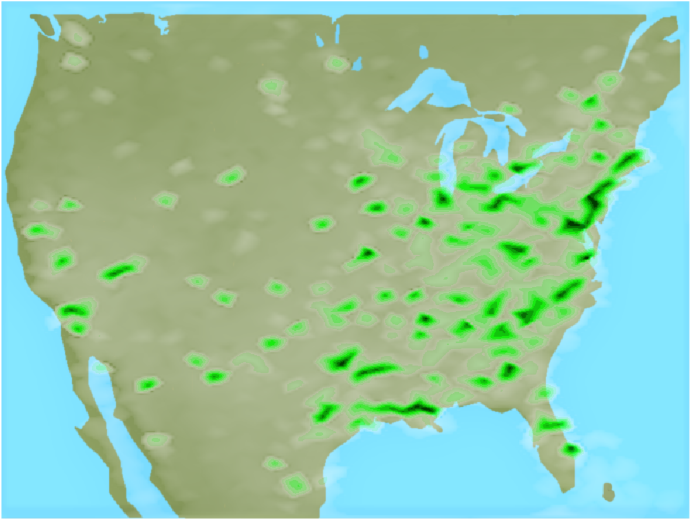
## Evolution of $\phi_t(s, z)$ $(t = 13)$



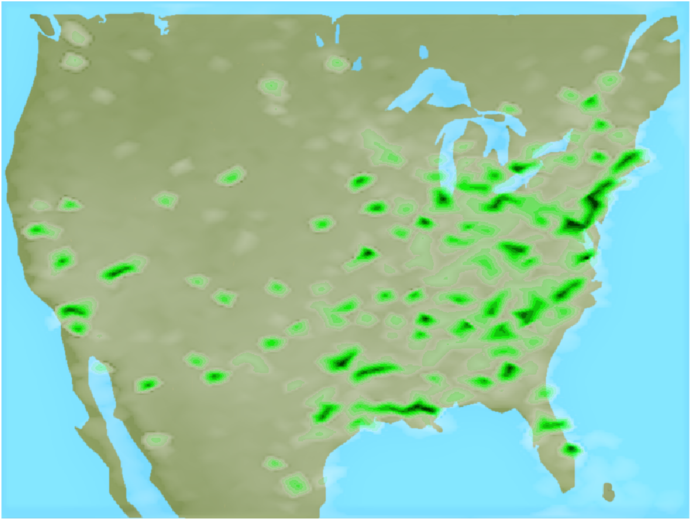
# Evolution of $\phi_t(s, z)$ $(t = 14)$



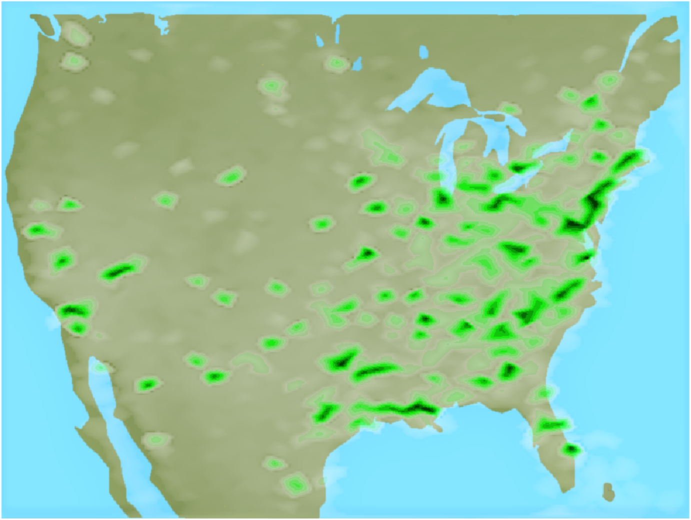
# Evolution of $\phi_t(s, z)$ ($t = 15$)



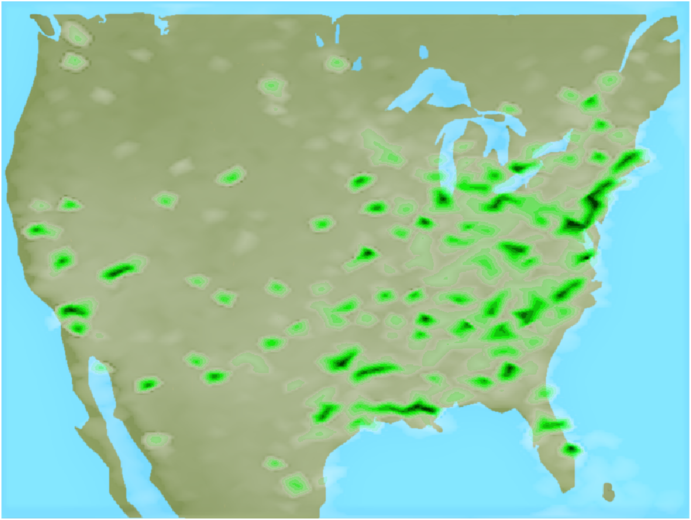
# Evolution of $\phi_t(s, z)$ $(t = 16)$



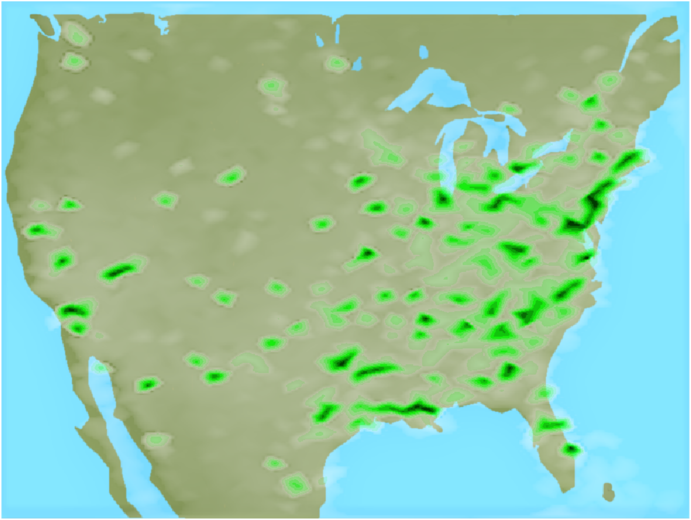
# Evolution of $\phi_t(s, z)$ ($t = 17$)



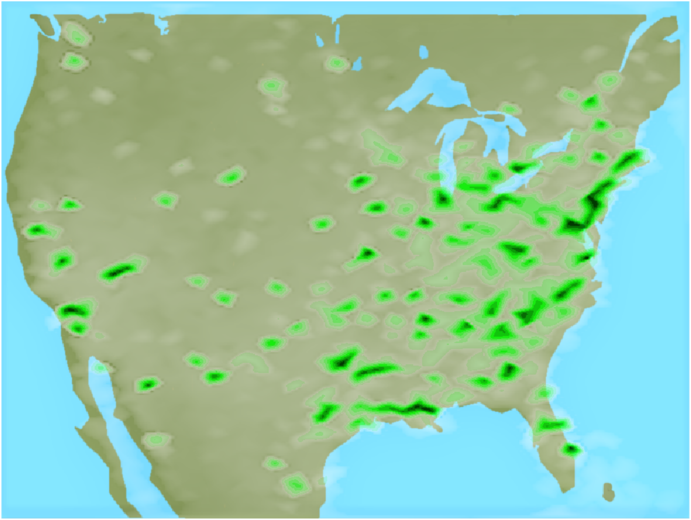
# Evolution of $\phi_t(s, z)$ $(t = 18)$

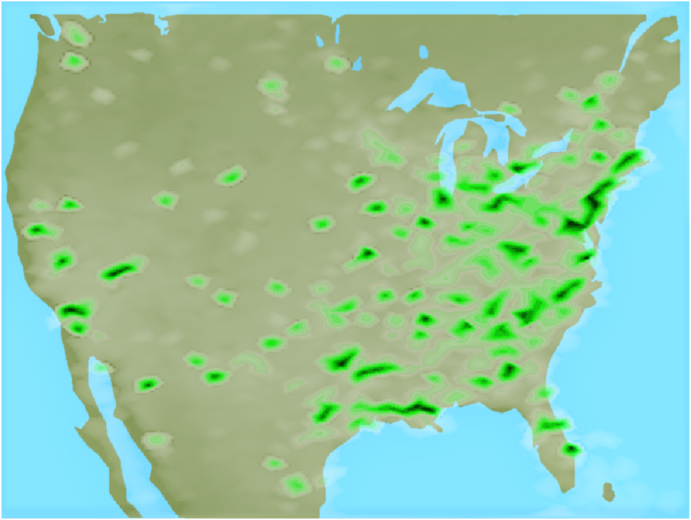


# Evolution of $\phi_t(s, z)$ $(t = 19)$

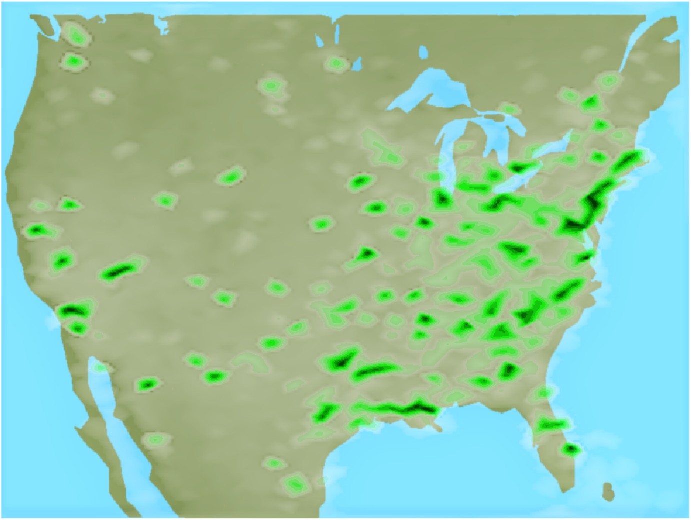


# Evolution of $\phi_t(s, z)$ $(t = 20)$

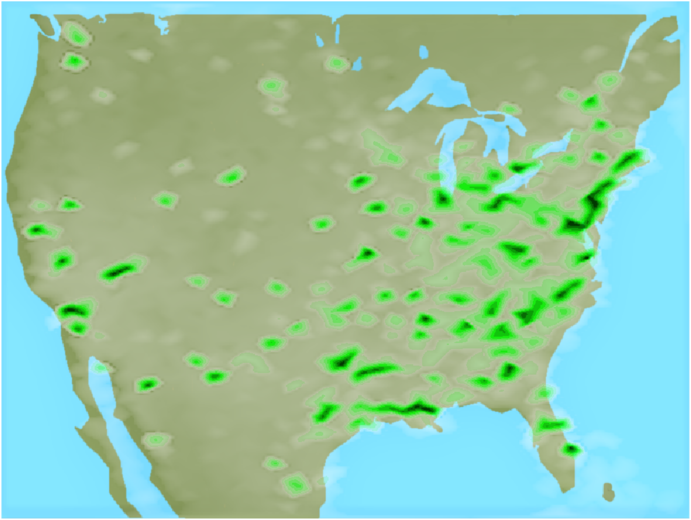




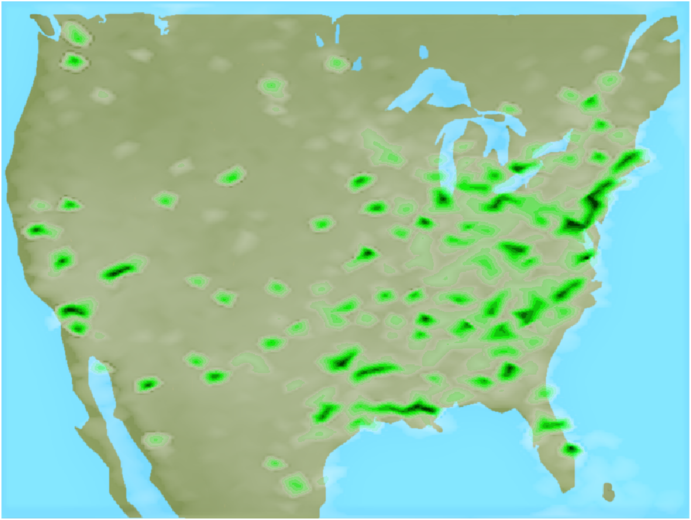
# Evolution of $\phi_t(s, z)$ $(t = 22)$



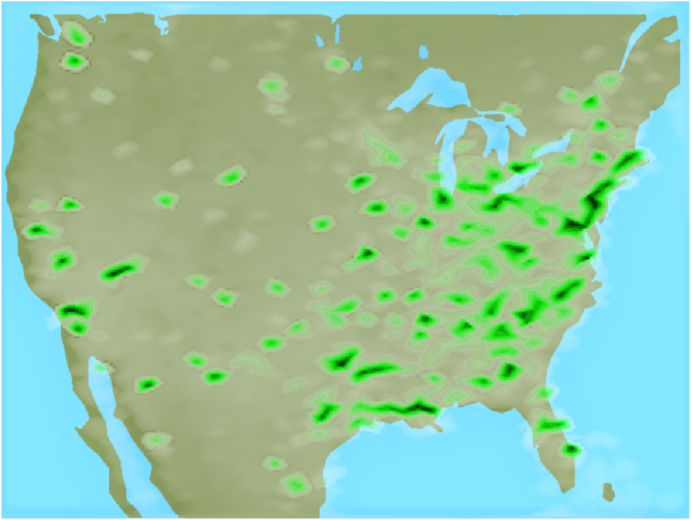
# Evolution of $\phi_t(s, z)$ $(t = 23)$



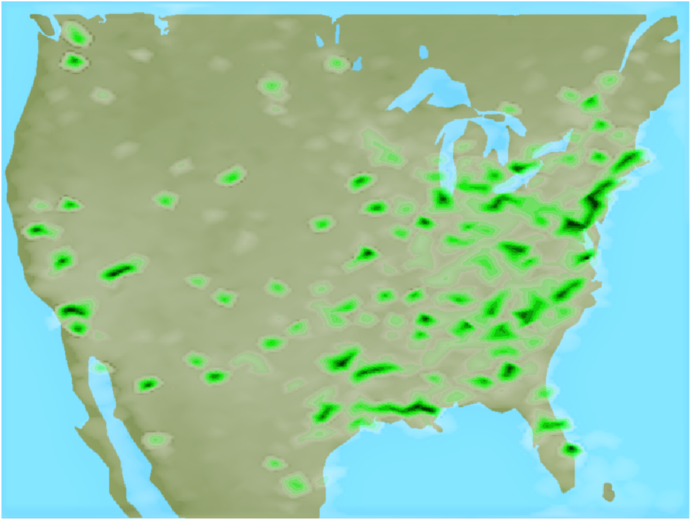
# Evolution of $\phi_t(s, z)$ $(t = 24)$



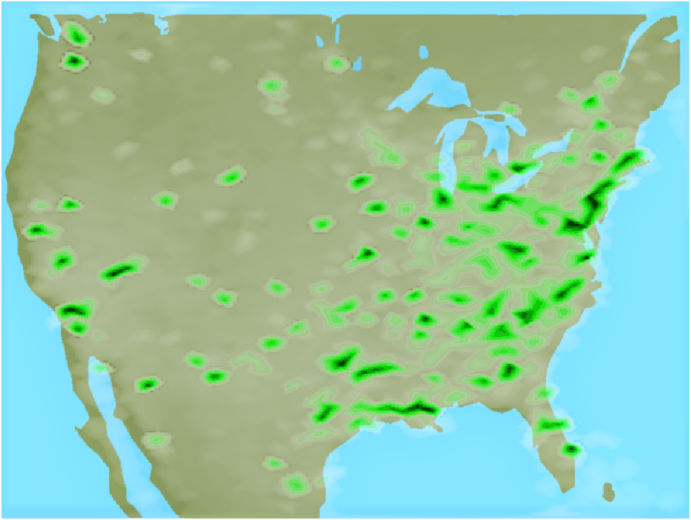
# Evolution of $\phi_t(s, z)$ $(t = 25)$



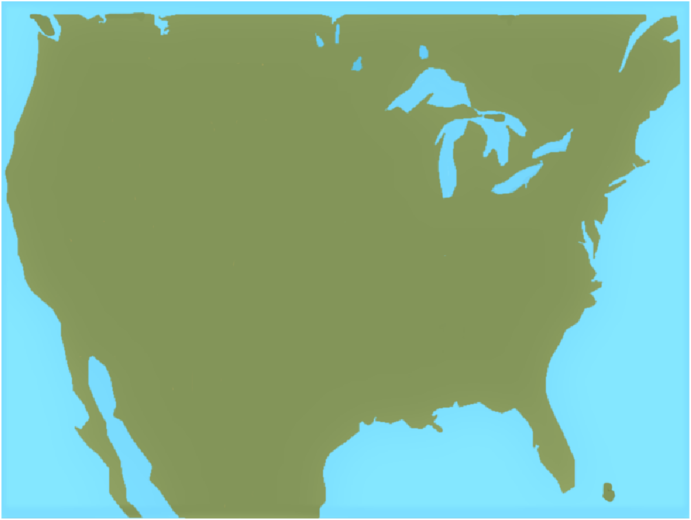
# Evolution of $\phi_t(s, z)$ $(t = 26)$



# Evolution of $\phi_t(s,z)$ $(t = \infty)$

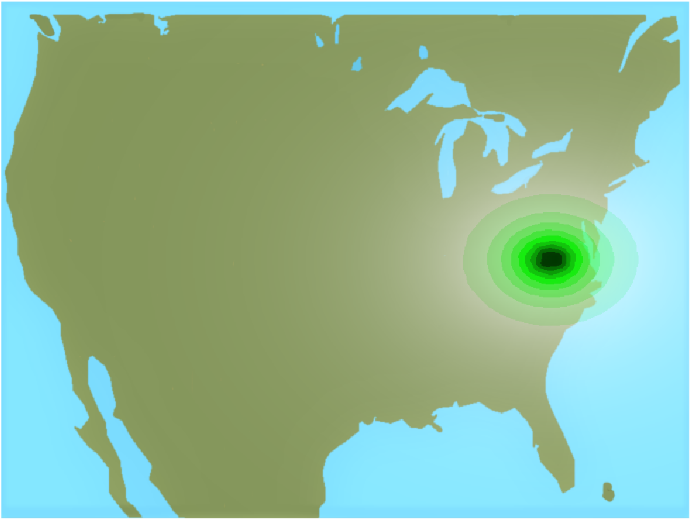


# When the landscape is in equilibrium

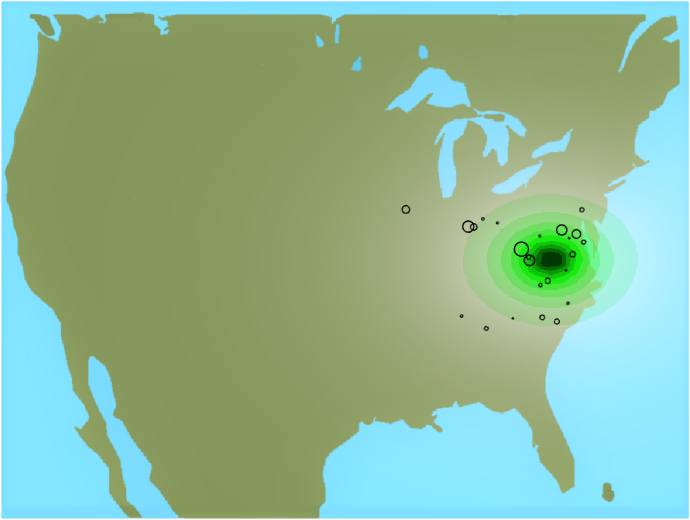


# Simulation ($t = 0$) - initial occupancy $\boldsymbol{X}_0^{(n)}$

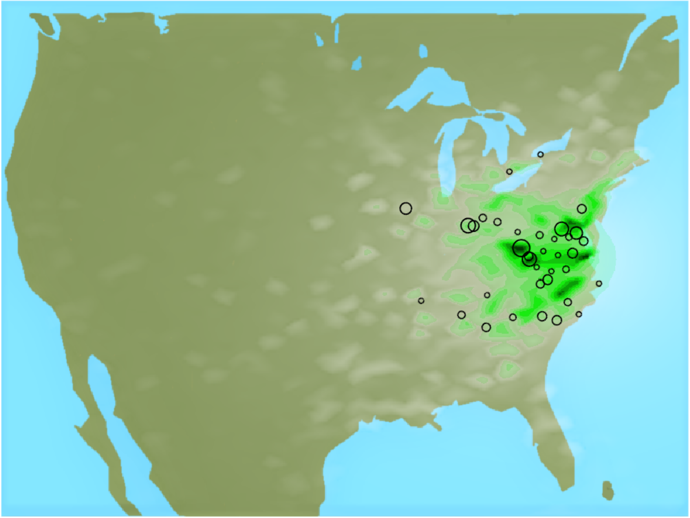
# Simulation ($t = 0$) - initial occupancy probability $\phi_0(s, z)$



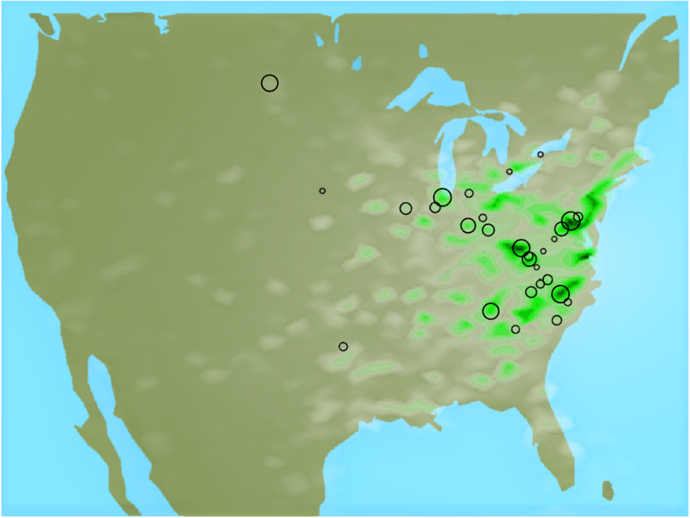
# Simulation ($t = 0$)



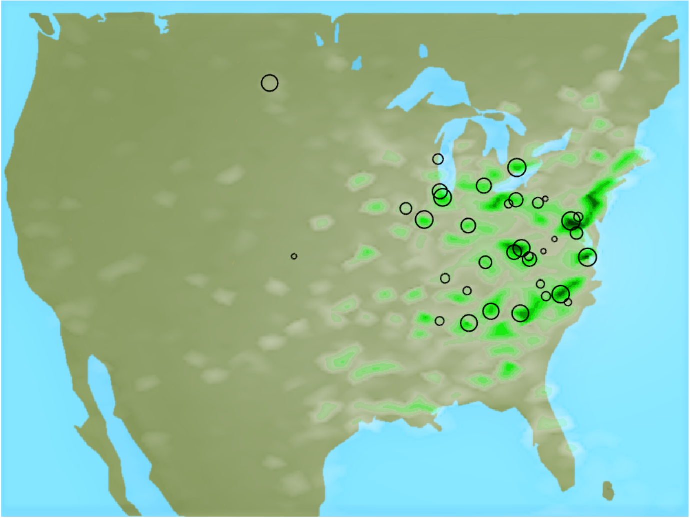
# Simulation ($t = 1$)



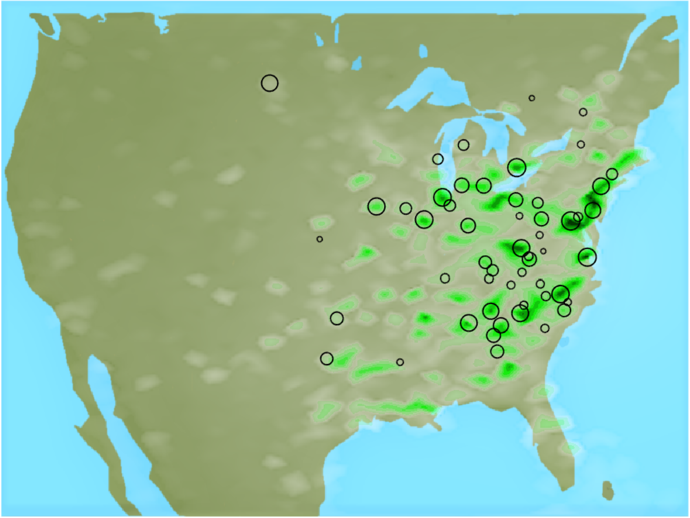
# Simulation ($t = 2$)



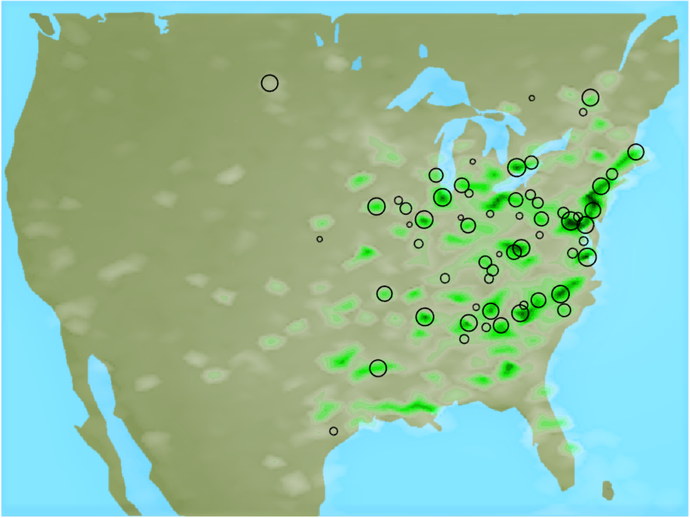
# Simulation ($t = 3$)



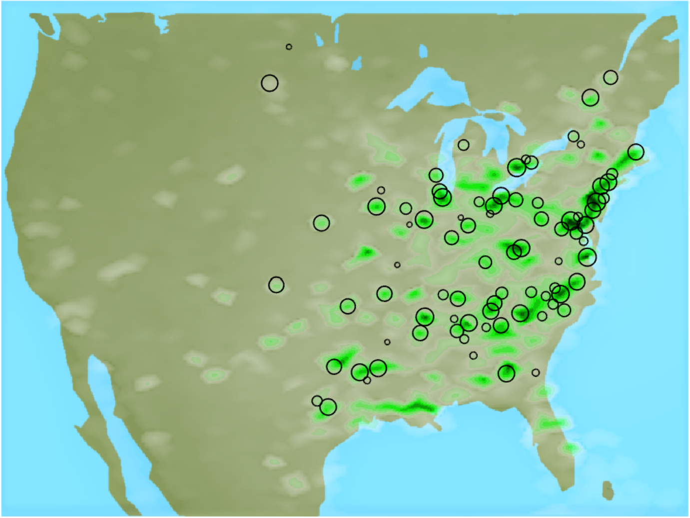
# Simulation ($t = 4$)



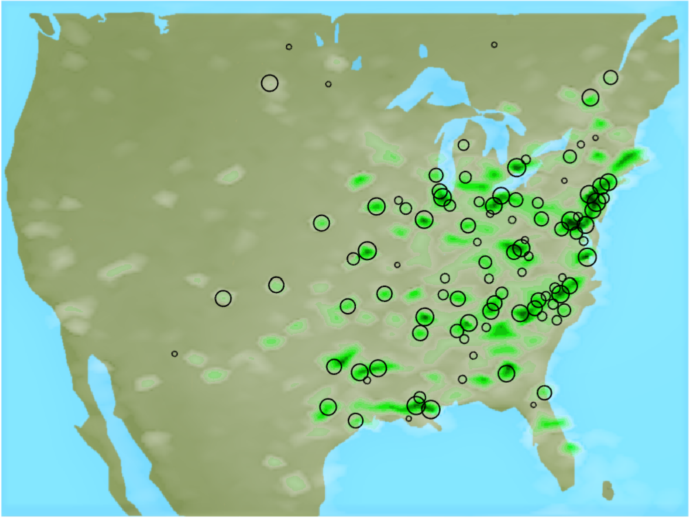
# Simulation ($t = 5$)



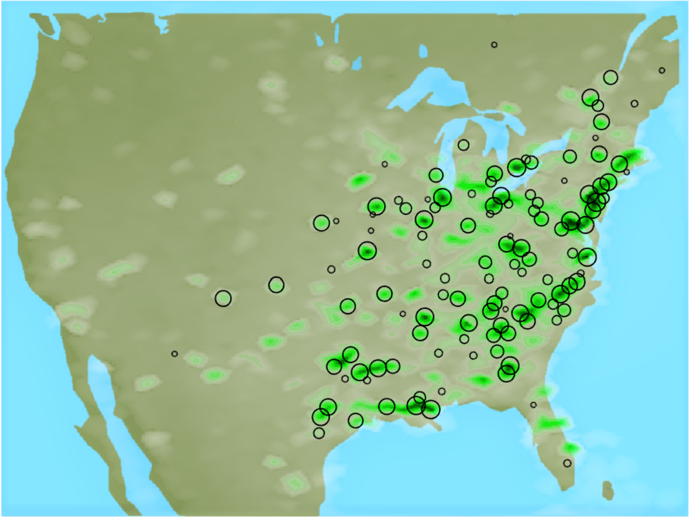
# Simulation ($t = 6$)



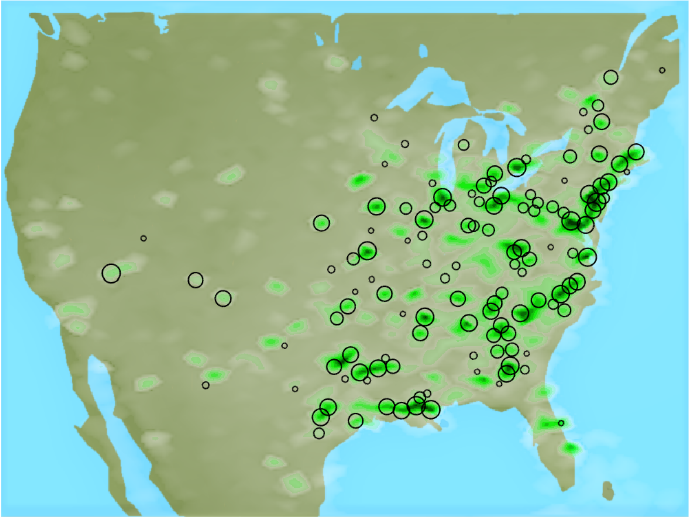
# Simulation ($t = 7$)



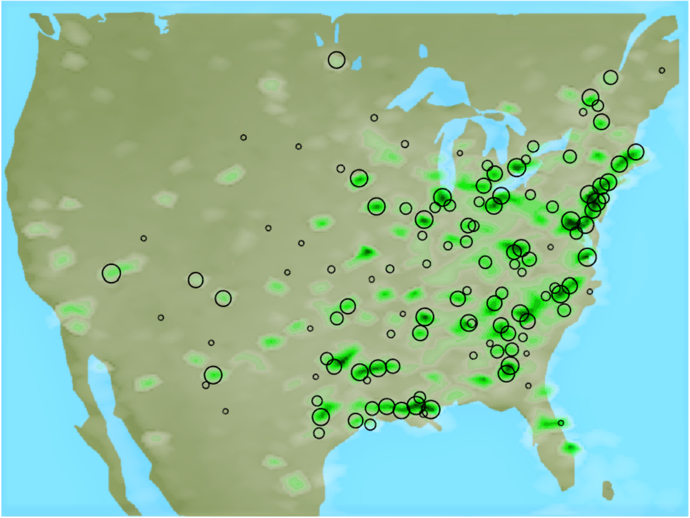
# Simulation ($t = 8$)



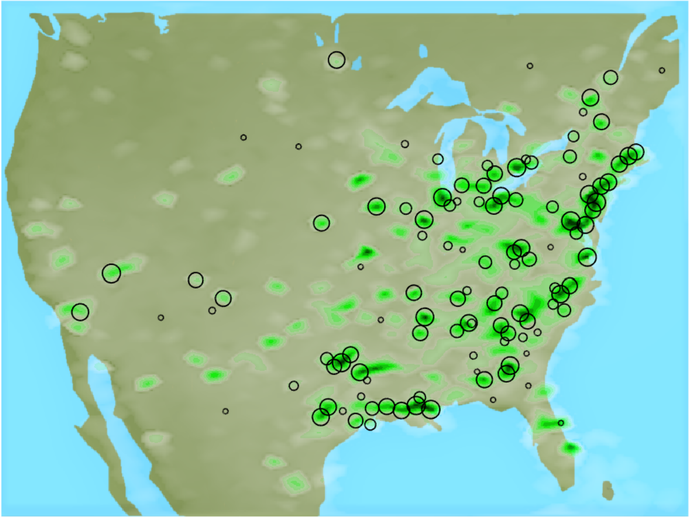
## Simulation ($t = 9$)



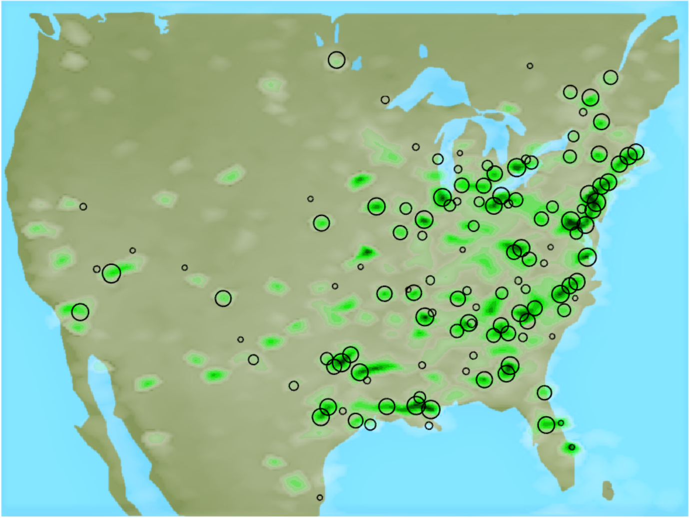
# Simulation ($t = 10$)



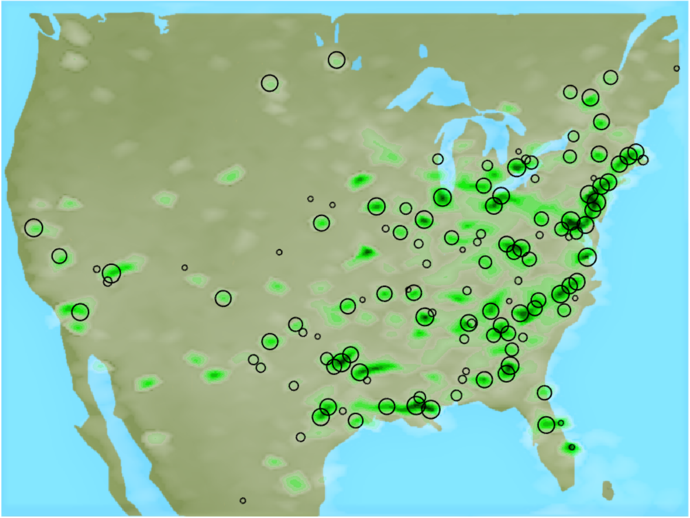
# Simulation ($t = 11$)



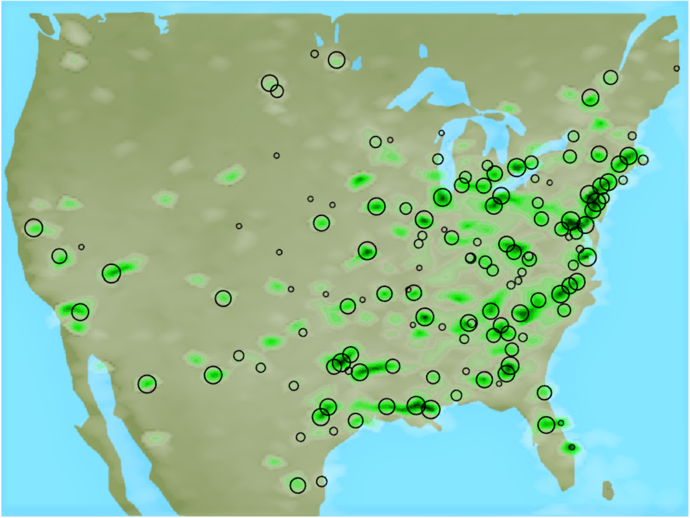
## Simulation ($t = 12$)



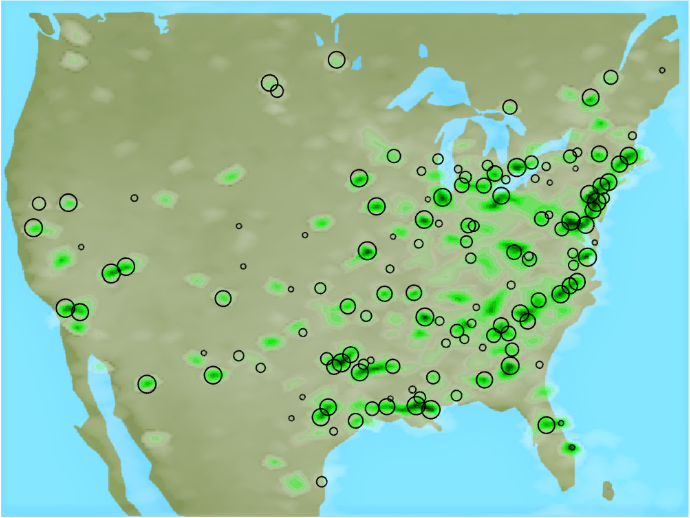
# Simulation ($t = 13$)



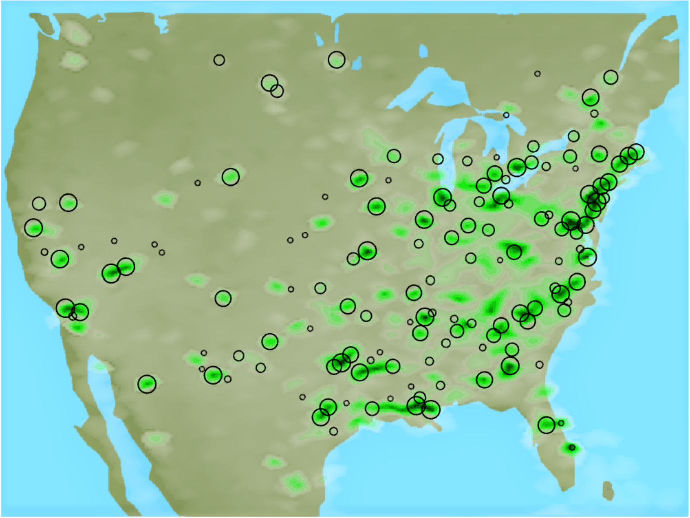
# Simulation ($t = 14$)



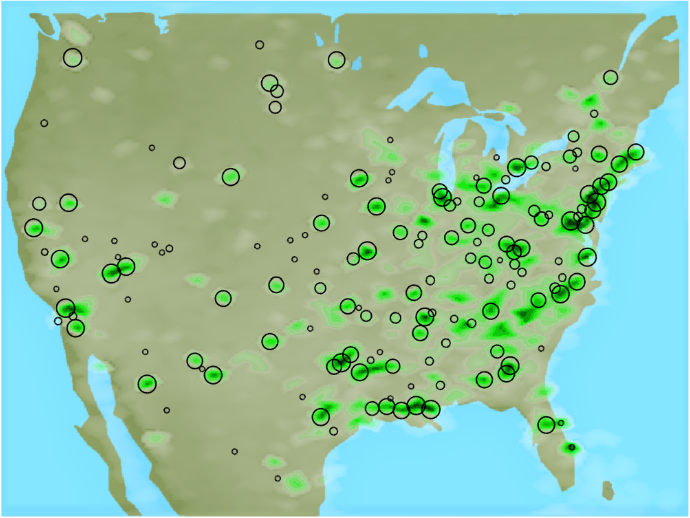
# Simulation ($t = 15$)

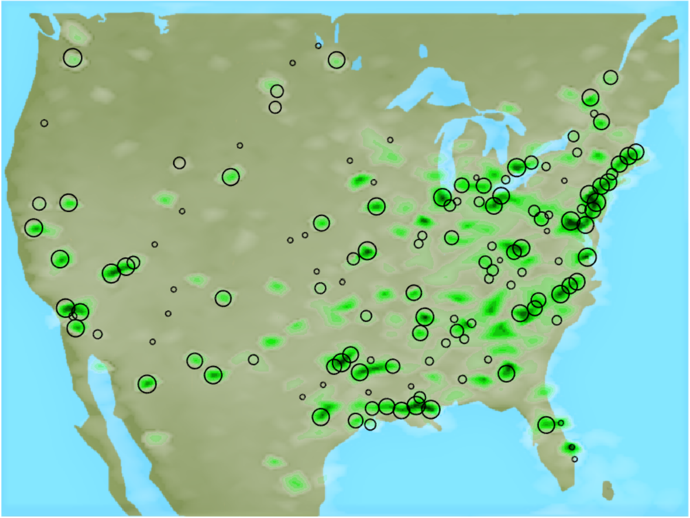


# Simulation ($t = 16$)

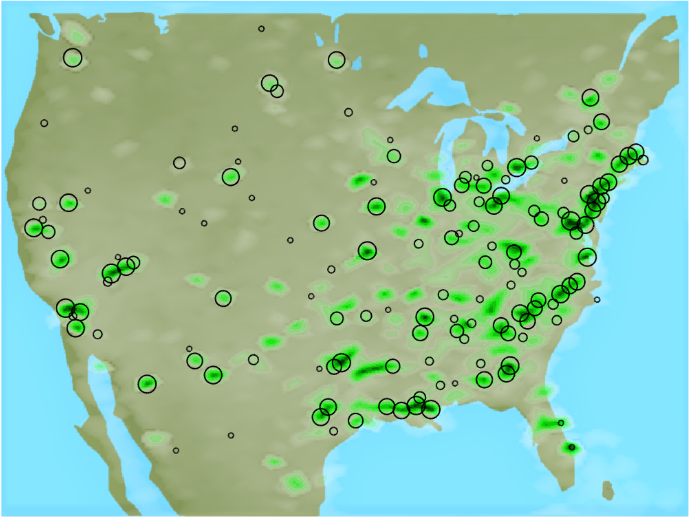


# Simulation ($t = 17$)

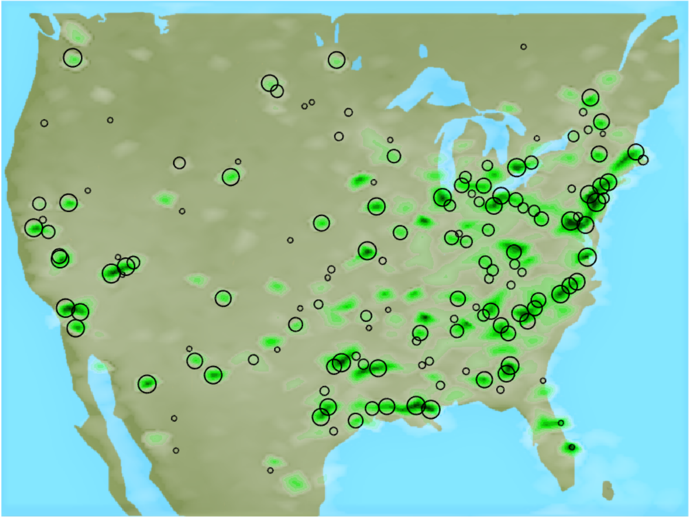




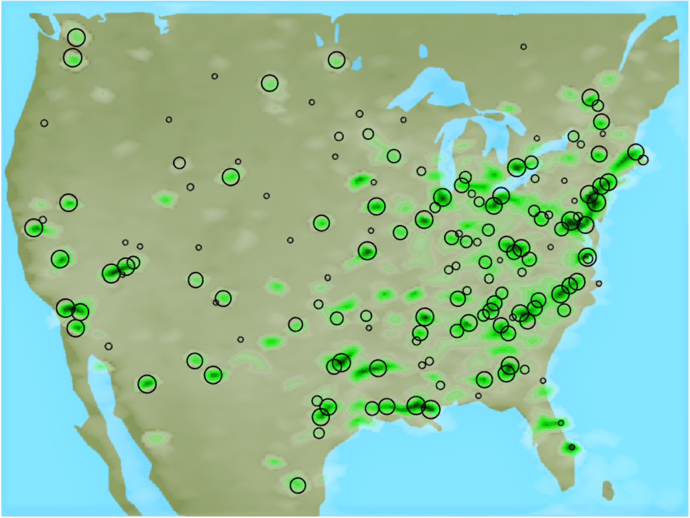
# Simulation ($t = 19$)



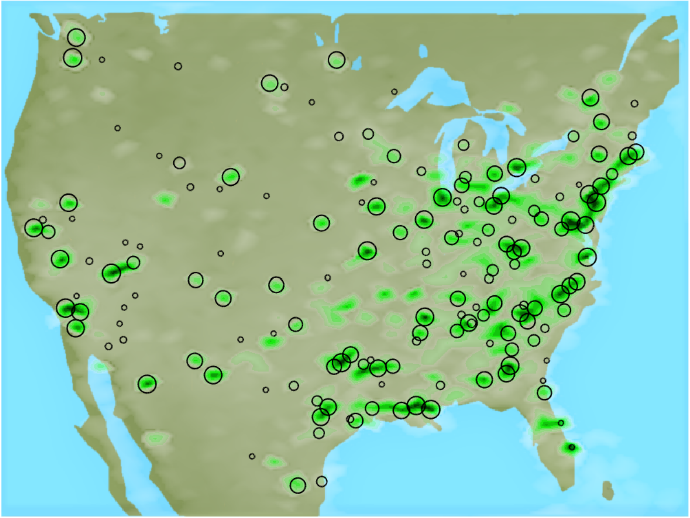
# Simulation ($t = 20$)



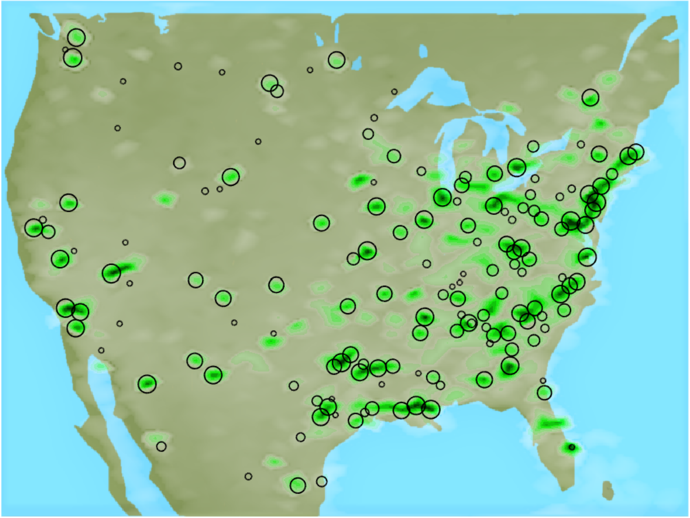
# Simulation ($t = 21$)



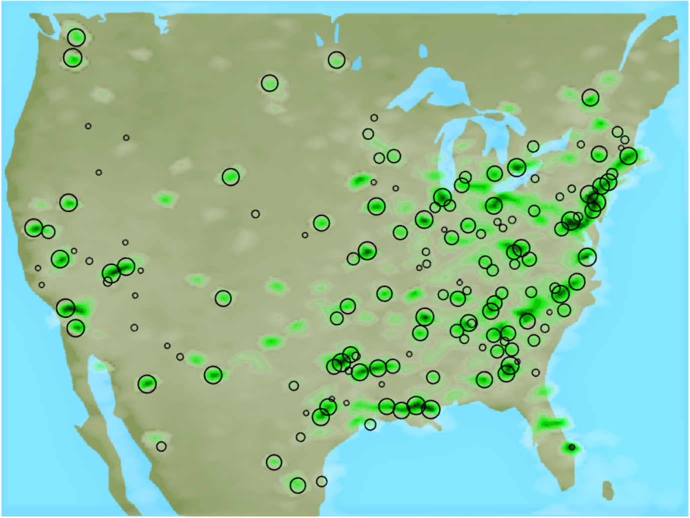
# Simulation ($t = 22$)



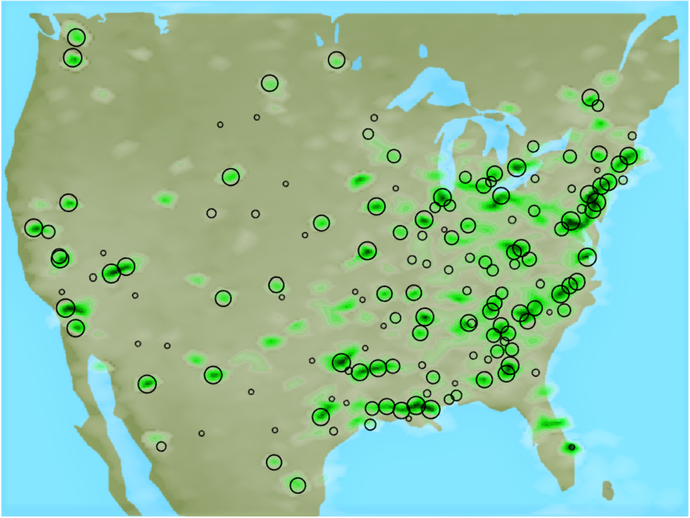
## Simulation ($t = 23$)



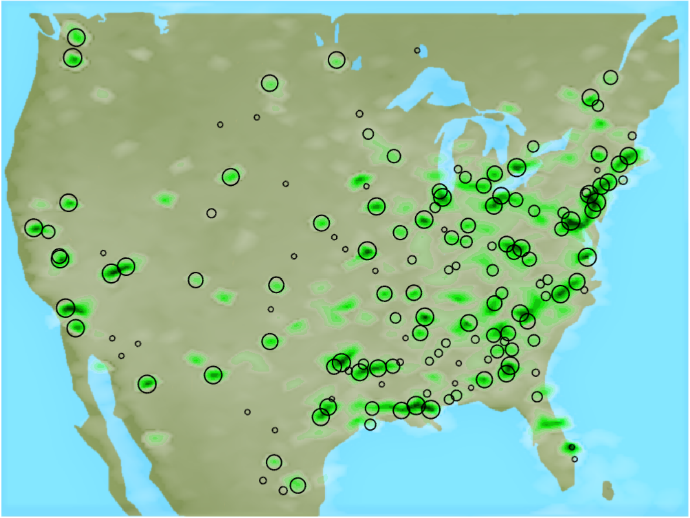
# Simulation ($t = 24$)



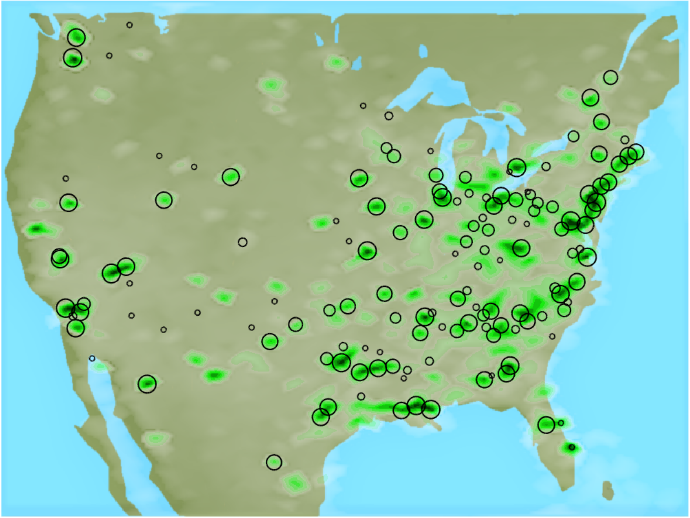
# Simulation ($t = 25$)



# Simulation ($t = 26$)



# Simulation ($t$ large)



# The limiting metapopulation in equilibrium

The fixed points $\phi_\infty := \partial \mu_\infty / \partial \sigma$ of the simplified recursion satisfy

$$\phi_\infty(s,z) = c\,(\psi(z)) \int r\, P^*(s,dr) + (1 - c\,(\psi(z))) \int r\, \phi_\infty(r,z) P^*(s,dr),$$

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

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

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

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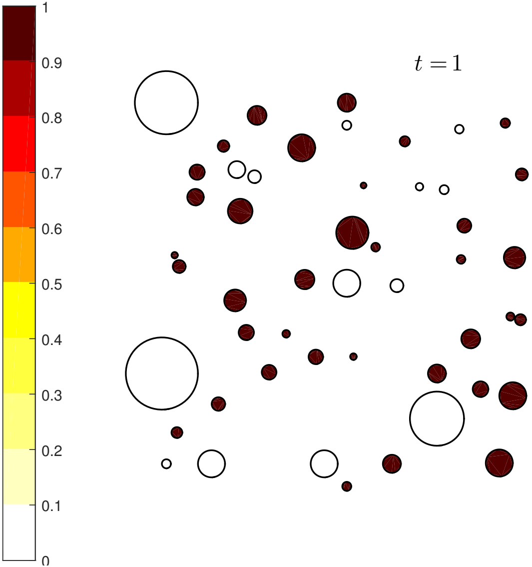
Think of $\psi(z)$ as being the equilibrium large-metapopulation connectivity for a patch located at $z$, and $c\,(\psi(z))$ as being the corresponding equilibrium potential of the population to colonize that patch.

Based on the spectral radius of a certain bounded linear operator, we are able to distinguish between the (complementary) cases (i) where the simplified recursion has only the trivial fixed point $\partial\mu_\infty/\partial\sigma(s,z) = 0$, this fixed point being globally stable (*evanescence*), and (ii) where it has a unique non-zero fixed point and all non-zero trajectories converge to this fixed point (*persistence*).

# Occupancy simulation - proportion of time occupied




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

Tweaked spatial Poisson process.

**Ease of movement**:

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

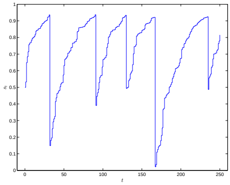
**Areas**:

$a_i = 6\pi R_i^2$, where $R_i^2 \sim \exp(5000)$.
$\mathbb{E}a_i \simeq 0.00377$.

**Colonization function**:

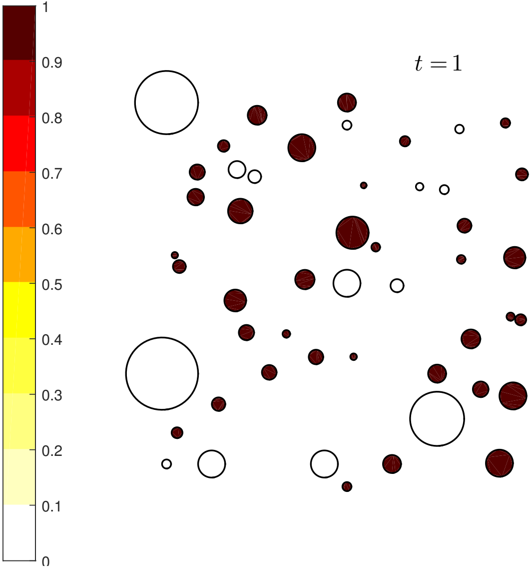
$c(x) = 1 - \exp(-5x)$.

**Survival probabilities**:

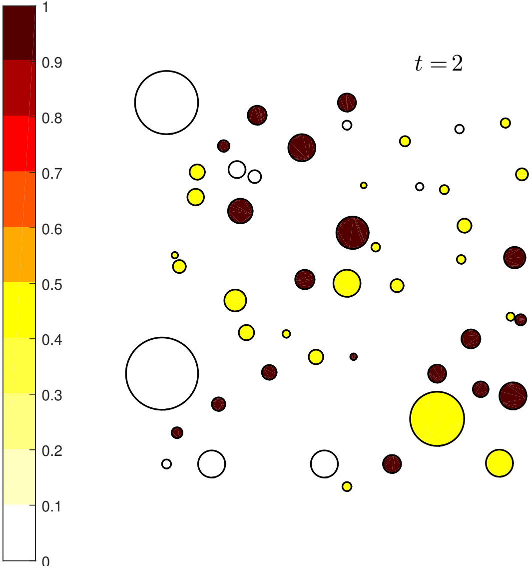


**Initial occupancy**: 70%

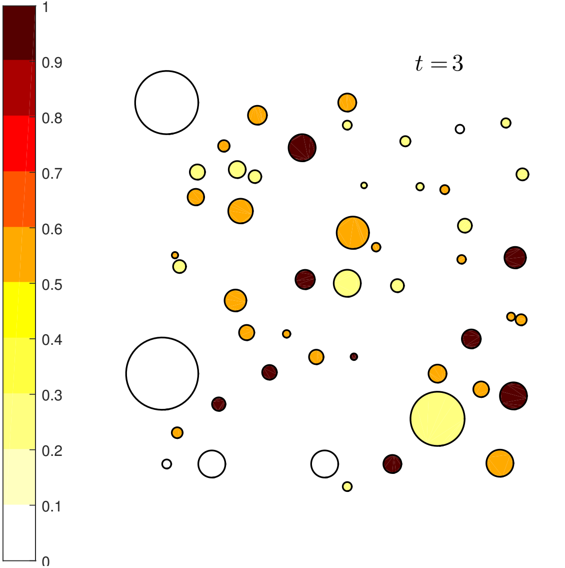
# Occupancy simulation - proportion of time occupied



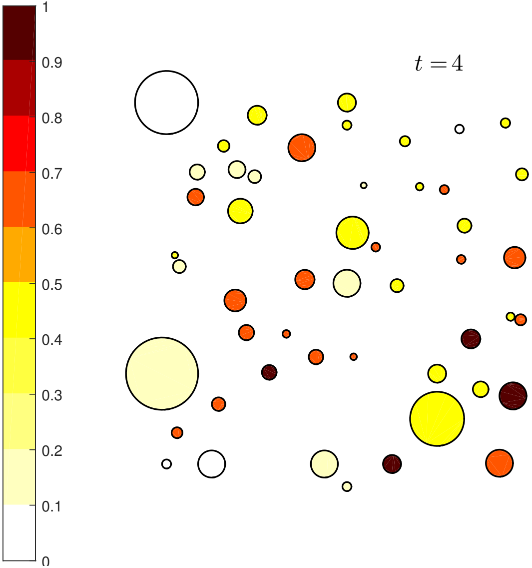
# Occupancy simulation - proportion of time occupied



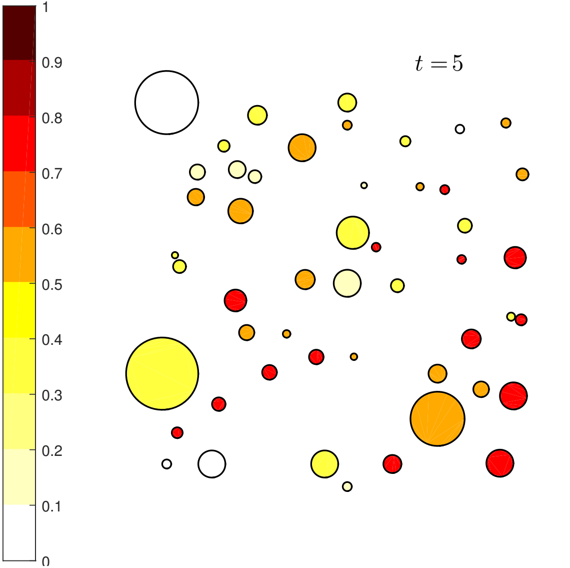
# Occupancy simulation - proportion of time occupied



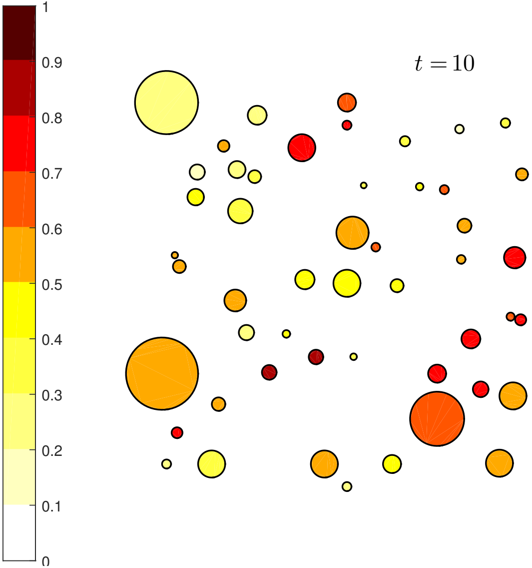
# Occupancy simulation - proportion of time occupied



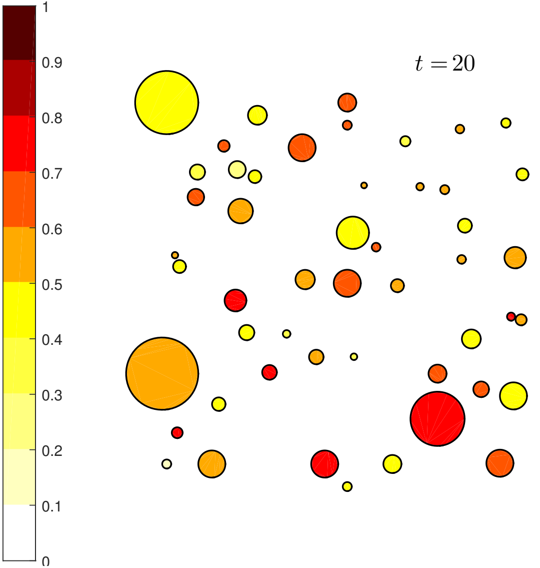
# Occupancy simulation - proportion of time occupied



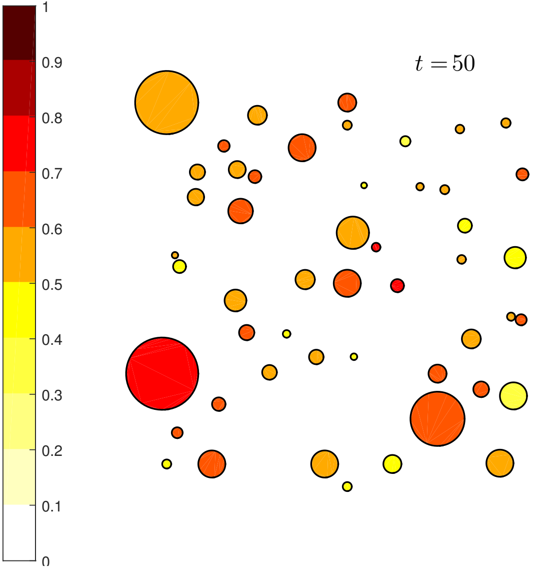
# Occupancy simulation - proportion of time occupied



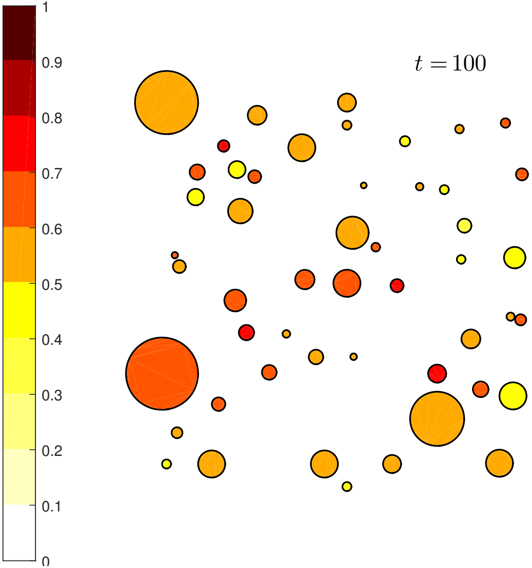
## Occupancy simulation - proportion of time occupied



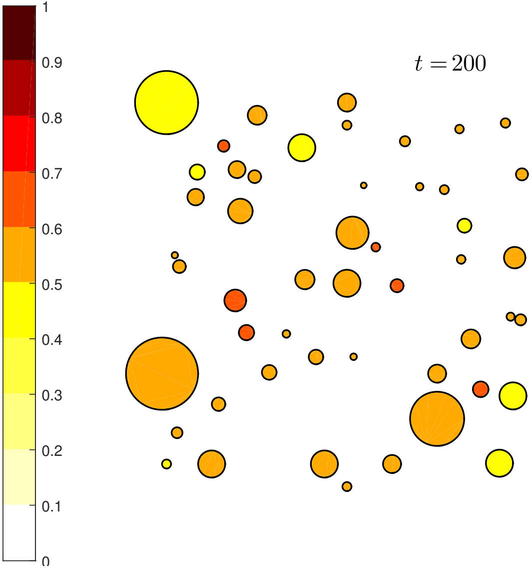
# Occupancy simulation - proportion of time occupied



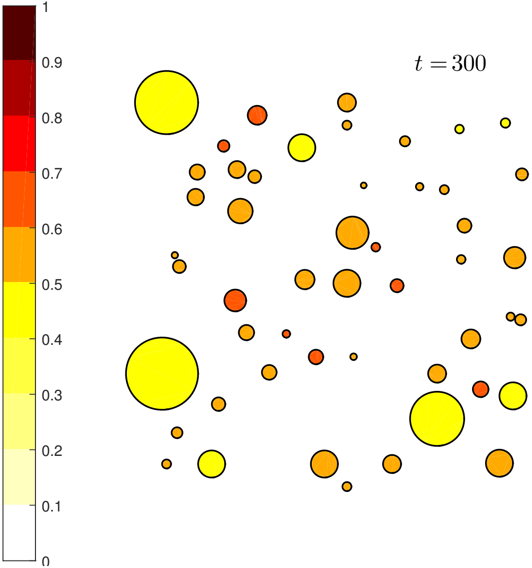
# Occupancy simulation - proportion of time occupied



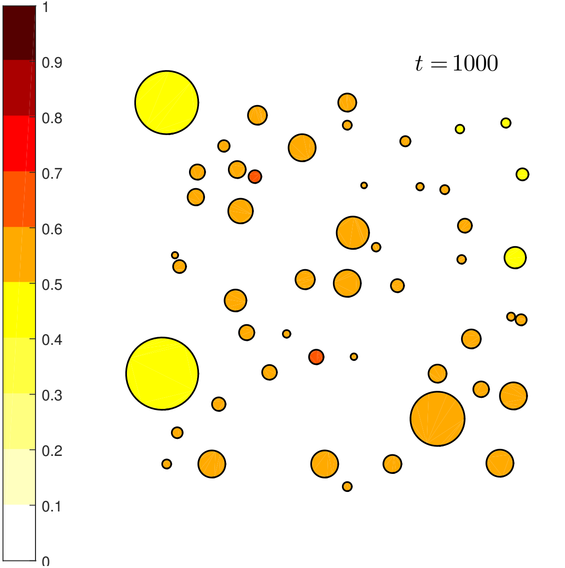
# Occupancy simulation - proportion of time occupied



# Occupancy simulation - proportion of time occupied



# Occupancy simulation - proportion of time occupied



# Theoretical - proportion of time occupied