# Metapopulations in evolving landscapes

Phil. Pollett

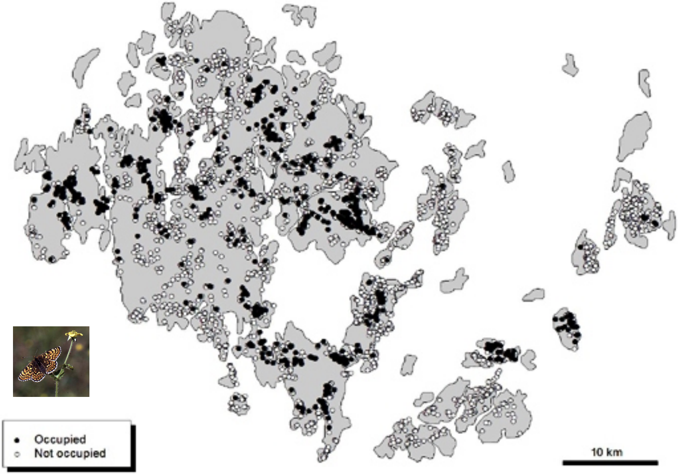
The University of Queensland

61st Annual Meeting of the
Australian Mathematical Society

Macquarie University, 14 December 2017

ACEMS
AUSTRALIAN RESEARCH COUNCIL CENTRE OF EXCELLENCE FOR
MATHEMATICAL AND STATISTICAL FRONTIERS

# Metapopulations



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

# Collaborators

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

Buckley, F.M. and Pollett, P.K. (2010) Analytical methods for a stochastic mainland-island metapopulation model. *Ecol. Modelling* **221**, 2526–2530.

McVinish, R. and Pollett, P.K. (2010) Limits of large metapopulations with patch dependent extinction probabilities. *Adv. Appl. Probab.* **42**, 1172–1186.

McVinish, R. and Pollett, P.K. (2012) The limiting behaviour of a mainland-island metapopulation. *J. Math. Biol.* **64**, 775–801.

McVinish, R. and Pollett, P.K. (2012) A central limit theorem for a discrete-time SIS model with individual variation. *J. Appl. Probab.* **49**, 521–530.

McVinish, R. and Pollett, P.K. (2013) Interaction between habitat quality and an Allee-like effect in metapopulations. *Ecol. Modelling* **249**, 84–89.

McVinish, R. and Pollett, P.K. (2013) The limiting behaviour of a stochastic patch occupancy model. *J. Math. Biology* **67**, 693–716.

McVinish, R. and Pollett, P.K. (2013) The deterministic limit of a stochastic logistic model with individual variation. *Math. Biosci.* **241**, 109–114.

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

Smith, A., McVinish, R. and Pollett, P.K. (2014) A model for a spatially structured metapopulation accounting for within patch dynamics. *Math. Biosci.* **247**, 69–79.

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

McVinish, R., Pollett, P.K. and Chan, Y.S. (2016) A metapopulation model with Markovian landscape dynamics. *Theoretic. Pop. Biol.* **112**, 80–96.

McVinish, R. Pollett, P.K. and Shausan A. (2016) Limiting the spread of disease through altered migration patterns. *J. Theoretic. Biol.* **393**, 60–66.

McVinish, R., Barbour, A.D. and Pollett, P.K. Local approximation of a metapopulation's equilibrium. Submitted.

Hodgkinson, L., McVinish, R. and Pollett, P.K. Approximations and limit theorems for a class of discrete-time occupancy processes. Submitted.

## SPOM

A *stochastic patch occupancy model* (SPOM)

# SPOM

A *stochastic patch occupancy model* (SPOM)

Suppose that there are $n$ patches.

Let $\boldsymbol{X}_t^{(n)} = (X_{1,t}^{(n)}, \ldots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch $i$ is occupied at time $t$.

# SPOM

A *stochastic patch occupancy model* (SPOM)

Suppose that there are $n$ patches.

Let $\boldsymbol{X}_t^{(n)} = (X_{1,t}^{(n)}, \ldots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch $i$ is occupied at time $t$.

Assume that colonization and extinction happen in distinct, successive phases.

# SPOM

A *stochastic patch occupancy model* (SPOM)

Suppose that there are $n$ patches.

Let $\boldsymbol{X}_t^{(n)} = (X_{1,t}^{(n)}, \ldots, X_{n,t}^{(n)})$, where $X_{i,t}^{(n)}$ is a binary variable indicating whether or not patch $i$ is occupied at time $t$.

Assume that colonization and extinction happen in distinct, successive phases.

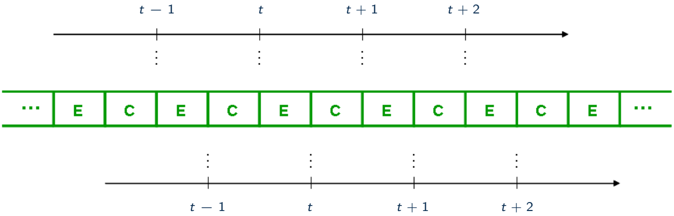
For many species the propensity for colonization and local extinction is markedly different in different phases of their life cycle. Examples:

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

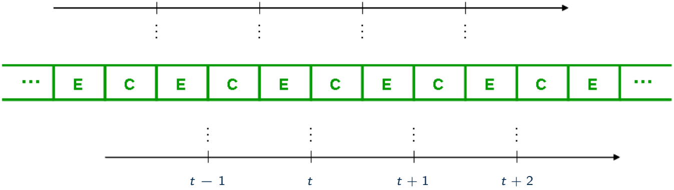
# SPOM - Phase structure

Colonization and extinction happen in distinct, successive phases.



## SPOM - Phase structure

Colonization and extinction happen in distinct, successive phases.



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

## SPOM - Phase structure

*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*).

# SPOM - Phase structure

*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*).

**Examples**: $D(z, \tilde{z}) = \exp(-\beta\|z - \tilde{z}\|)$ and $c(x) = 1 - \exp(-\alpha x)$, where $\alpha, \beta > 0$.

# SPOM - Phase structure

*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*).

**Examples**: $D(z, \tilde{z}) = \exp(-\beta\|z - \tilde{z}\|)$ and $c(x) = 1 - \exp(-\alpha x)$, where $\alpha, \beta > 0$.

**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 $c'(0) > 0$.

# SPOM - Phase structure

*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*).

# SPOM - Phase structure

*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*).

*Extinction*: occupied patch $i$ remains occupied with probability $s_{i,t}$.

# SPOM - Phase structure

*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*).

*Extinction*: occupied patch $i$ remains occupied with probability $s_{i,t}$.

Then, given the current state $\boldsymbol{X}_t^{(n)}$ and survival probabilities $\boldsymbol{S}_t^{(n)} = (s_{i,t},\ i = 1, \ldots, n)$, the $X_{i,t+1}^{(n)}$ $(i = 1, \ldots, n)$ are independent with transitions

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

# SPOM - Phase structure

*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*).

*Extinction*: occupied patch $i$ remains occupied with probability $s_{i,t}$.

Then, given the current state $\boldsymbol{X}_t^{(n)}$ and survival probabilities $\boldsymbol{S}_t^{(n)} = (s_{i,t},\ i = 1, \ldots, n)$, the $X_{i,t+1}^{(n)}$ $(i = 1, \ldots, n)$ are independent with transitions

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

(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 $P(s, dr)$.

# Examples of the survival probability model $(s_t)_{t=0}^{\infty}$

**Example 1** Patches are classified as being suitable or unsuitable for occupancy:

$$s_{t+1} = \begin{cases} s^* & \text{with probability } p(s_t) \\ 0 & \text{with probability } 1 - p(s_t), \end{cases}$$

where $p : [0,1] \mapsto [0,1]$ is a continuous function, so that

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

# Examples of the survival probability model $(s_t)_{t=0}^{\infty}$

**Example 1** Patches are classified as being suitable or unsuitable for occupancy:

$$s_{t+1} = \begin{cases} s^* & \text{with probability } p(s_t) \\ 0 & \text{with probability } 1 - p(s_t), \end{cases}$$

where $p : [0,1] \mapsto [0,1]$ is a continuous function, so that

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

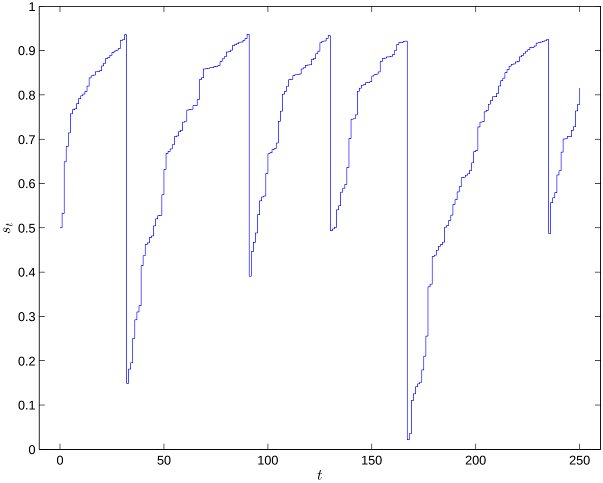
**Example 2** Following McKinlay and Borovkov[†], suppose that

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

where $p : [0,1] \mapsto [0,1]$ is continuous, and $(D_t)$ and $(U_t)$ are sequences of independent and identically distributed random variables on $[0,1]$ with distributions $F_D$ and $F_U$.

[†] McKinlay, S. and Borovkov, K. (2016) On explicit form of the stationary distributions for a class of bounded Markov chains. *Journal of Applied Probability* 53, 231–243.

# Climax community species



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

# SPOM - Homogeneous case - Law of Large Numbers

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

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

$$N_t^{(n)}/n \xrightarrow{p} x_t, \quad \text{for all } t \geq 1,$$

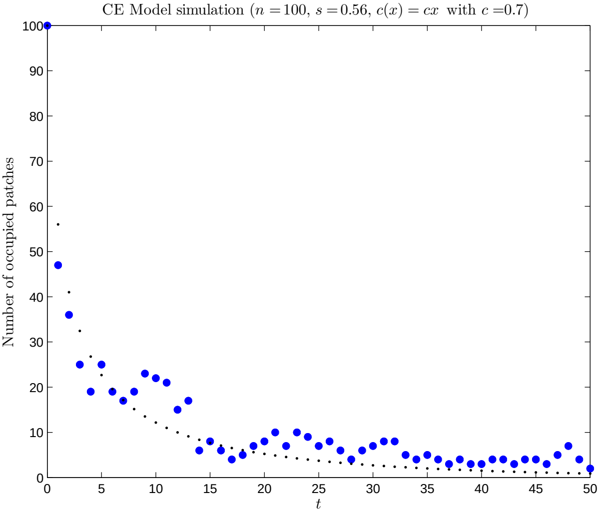
with $(x_t)$ determined by $x_{t+1} = f(x_t)$, where

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

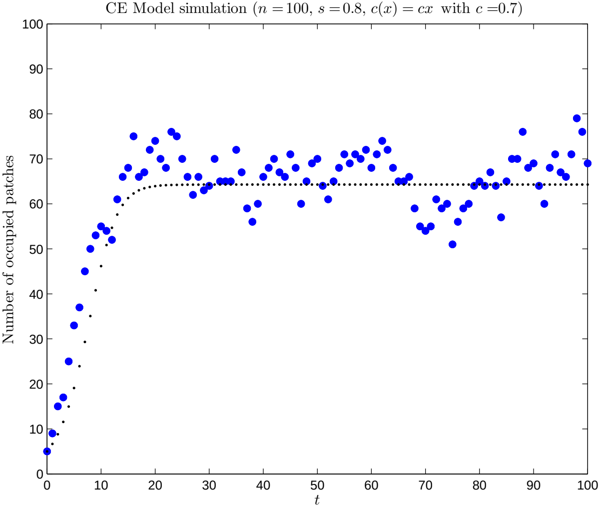
Survival probability

Colonization probability

# CE Model - Evanescence



# CE Model - Quasi stationarity



# Stability

**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

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

*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).

# Stability

**Proposition 1** If $N_0^{(n)}/n \xrightarrow{p} x_0$ (a constant), then

$$N_t^{(n)}/n \xrightarrow{p} x_t, \quad \text{for all } t \geq 1,$$

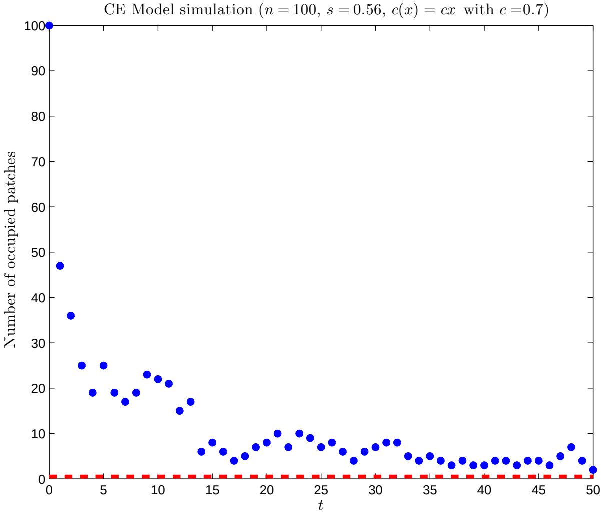
with $(x_t)$ determined by $x_{t+1} = f(x_t)$, where

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

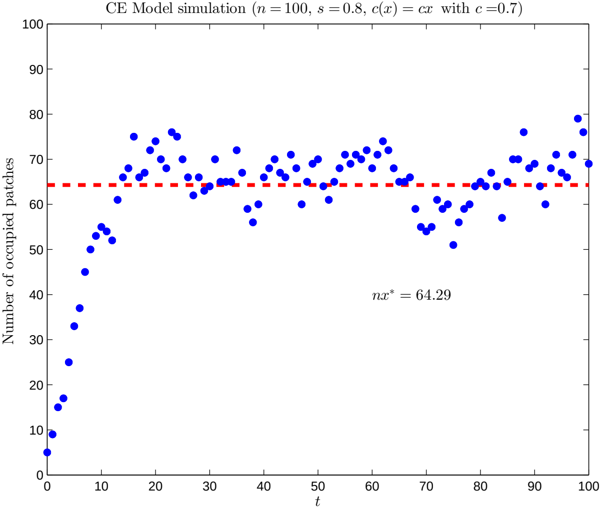
*Evanescence*: $1 + c'(0) \leq 1/s$. 0 is the unique fixed point in $[0, 1]$. It is stable.

*Quasi stationarity*: $1 + c'(0) > 1/s$. There are two fixed points in $[0, 1]$: 0 (unstable) and $x^* \in (0, 1)$ (stable).

# CE Model - Evanescence



# CE Model - Quasi stationarity



# SPOM - General case

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

$$\Pr\left(X_{i,t+1}^{(n)} = 1 \,\middle|\, \boldsymbol{X}_t^{(n)}, \boldsymbol{S}_t^{(n)}\right) = s_{i,t} X_{i,t}^{(n)} + s_{i,t}\, c \left(\frac{1}{n}\sum_{j=1}^{n} X_{j,t}^{(n)} D(z_i, z_j) a_j\right)\left(1 - X_{i,t}^{(n)}\right).$$

# Our approach - random measures

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

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

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

where $C^+(\mathcal{D})$ is the space of continuous functions $h : \mathcal{D} \mapsto [0,\infty)$.

# Our approach - random measures

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

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

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

where $C^+(\mathcal{D})$ is the space of continuous functions $h : \mathcal{D} \mapsto [0,\infty)$.

# Our approach - random measures

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

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

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

where $C^+(\mathcal{D})$ is the space of continuous functions $h : \mathcal{D} \mapsto [0,\infty)$.

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.

# Executive summary

The landscape $(s_{i,t}^{(n)}, a_i, z_i;\ i = 1, \dots, n)$ at time $t$ is summarized by $\sigma_{n,t}$. The metapopulation (occupancy process) is summarized by $\mu_{n,t}$.

# Executive summary

The landscape $(s_{i,t}^{(n)}, a_i, z_i;\ i = 1, \ldots, n)$ at time $t$ is summarized by $\sigma_{n,t}$. The metapopulation (occupancy process) is summarized by $\mu_{n,t}$.

**Large metapopulation**. First we let $n$ get large.

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 $\mu_{t+1} = \mathcal{H}(\mu_t, \sigma_t)$.

# Executive summary

The landscape $(s^{(n)}_{i,t}, a_i, z_i;\ i = 1, \ldots, n)$ at time $t$ is summarized by $\sigma_{n,t}$. The metapopulation (occupancy process) is summarized by $\mu_{n,t}$.

**Large metapopulation**. First we let $n$ get large.

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 $\mu_{t+1} = \mathcal{H}(\mu_t, \sigma_t)$.

**Landscape in equilibrium**. Next we see that if the survival probability model $(\boldsymbol{S}^{(n)}_t)$ 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.

# Executive summary

The landscape $(s_{i,t}^{(n)}, a_i, z_i;\ i = 1, \ldots, n)$ at time $t$ is summarized by $\sigma_{n,t}$. The metapopulation (occupancy process) is summarized by $\mu_{n,t}$.

**Large metapopulation**. First we let $n$ get large.

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

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

**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.

**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 $\partial\mu_\infty/\partial\sigma \equiv 0$, being globally stable (*evanescence*), and (ii) where there is a unique non-zero fixed point and all non-zero trajectories converge to it (*persistence*).

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

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

This will be satisfied, for example, if the random vectors $(a_i, s_{i,0}, z_i)$, $i = 1, 2, \ldots$, are iid.

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

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

This will be satisfied, for example, if the random vectors $(a_i, s_{i,0}, z_i)$, $i = 1, 2, \ldots$, are iid.

**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 $(s_{i,t})_{t=0}^{\infty}$, $i = 1, \ldots, n$.]

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

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

This will be satisfied, for example, if the random vectors $(a_i, s_{i,0}, z_i)$, $i = 1, 2, \ldots$, are iid.

**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 $(s_{i,t})_{t=0}^{\infty}$, $i = 1, \ldots, n$.]

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 $h \in C^+([0,1] \times \Omega)$,

$$\int h(s,z)\mu_{t+1}(ds,dz) = \int s\mathcal{P}h(s,z)(1-c(\psi_t(z)))\mu_t(ds,dz) \\ + \int s\mathcal{P}h(s,z)c(\psi_t(z))\sigma_t(ds,dz),$$

where

$$\mathcal{P}h(s,z) = \int h(r,z)P(s,dr) \quad \text{and} \quad \psi_t(z) = \int D(z,\tilde{z})\mu_t(d\tilde{s},d\tilde{z}).$$

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

# 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 $h \in C^+([0,1] \times \Omega)$,

$$\int h(s,z)\mu_{t+1}(ds,dz) = \int s\mathcal{P}h(s,z)(1 - c(\psi_t(z)))\mu_t(ds,dz) + \int s\mathcal{P}h(s,z)c(\psi_t(z))\sigma_t(ds,dz),$$

where

$$\mathcal{P}h(s,z) = \int h(r,z)P(s,dr) \quad \text{and} \quad \psi_t(z) = \int D(z,\tilde{z})\mu_t(d\tilde{s},d\tilde{z}).$$

[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.

# 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 $h \in C^+([0,1] \times \Omega)$,

$$\int h(s,z)\mu_{t+1}(ds,dz) = \int s\mathcal{P}h(s,z)(1-c(\psi_t(z)))\mu_t(ds,dz) + \int s\mathcal{P}h(s,z)c(\psi_t(z))\sigma_t(ds,dz),$$

where

$$\mathcal{P}h(s,z) = \int h(r,z)P(s,dr) \quad \text{and} \quad \psi_t(z) = \int D(z,\tilde{z})\mu_t(d\tilde{s},d\tilde{z}).$$

[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.

# When the landscape is in equilibrium

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

# When the landscape is in equilibrium

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

**Lemma 2** As $t \to \infty$, $\sigma_t$ converges to a product measure $\sigma = \nu \times \bar{\sigma}_0$, where $\bar{\sigma}_0(A) = \sigma_0([0, 1] \times A)$, for measurable $A \subset \Omega$.

# When the landscape is in equilibrium

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

**Lemma 2** As $t \to \infty$, $\sigma_t$ converges to a product measure $\sigma = \nu \times \bar{\sigma}_0$, where $\bar{\sigma}_0(A) = \sigma_0([0,1] \times A)$, for measurable $A \subset \Omega$.

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

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

# When the landscape is in equilibrium

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

**Lemma 2** As $t \to \infty$, $\sigma_t$ converges to a product measure $\sigma = \nu \times \bar{\sigma}_0$, where $\bar{\sigma}_0(A) = \sigma_0([0,1] \times A)$, for measurable $A \subset \Omega$.

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

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

**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

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

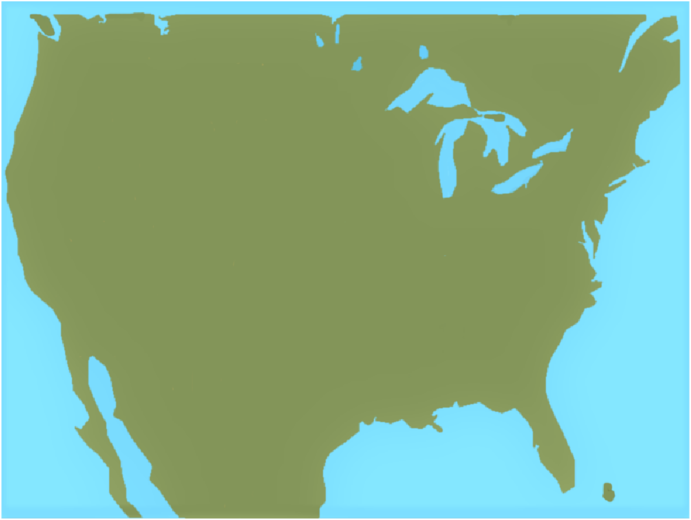
and, if

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

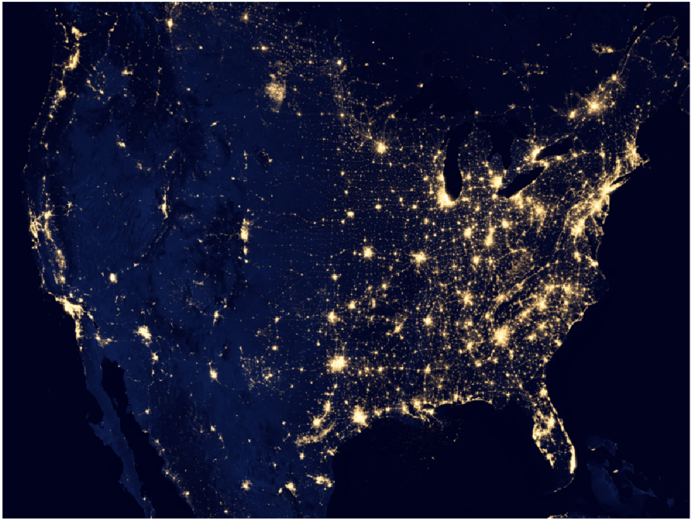
then

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

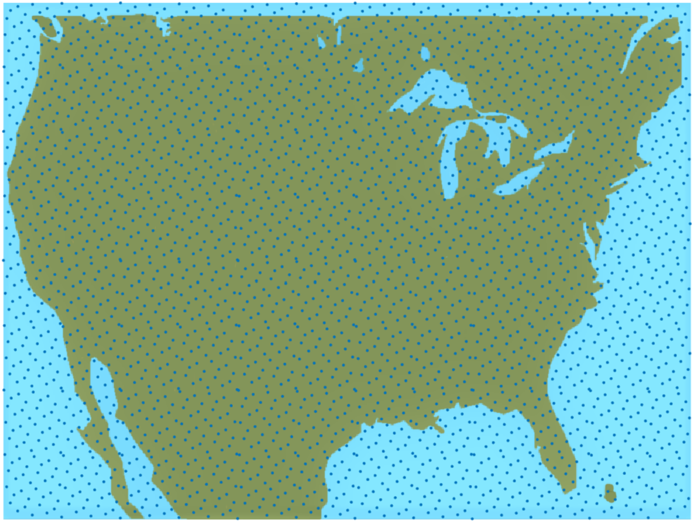
## When the landscape is in equilibrium



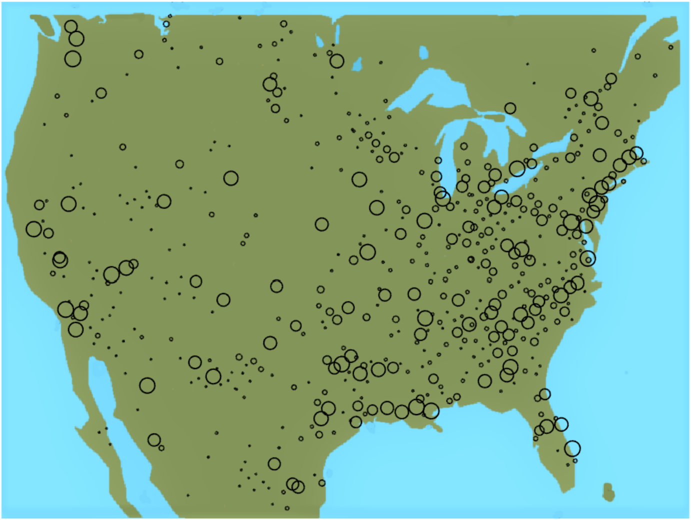
# USA light polution - proxy for patch weight



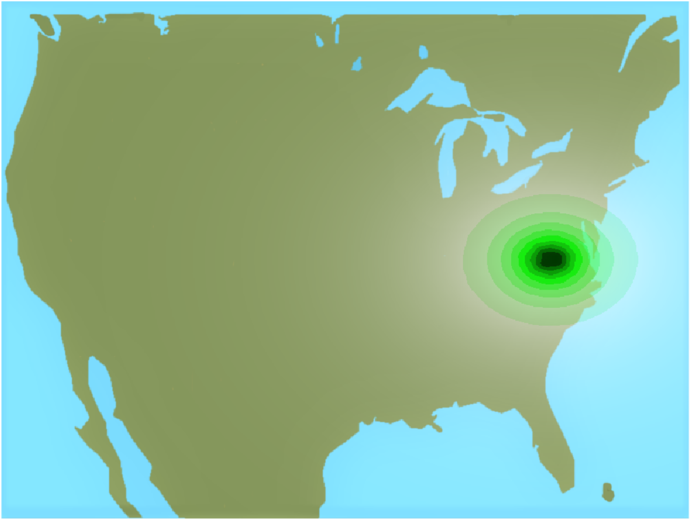
# Potential patch positions ($z_i$)



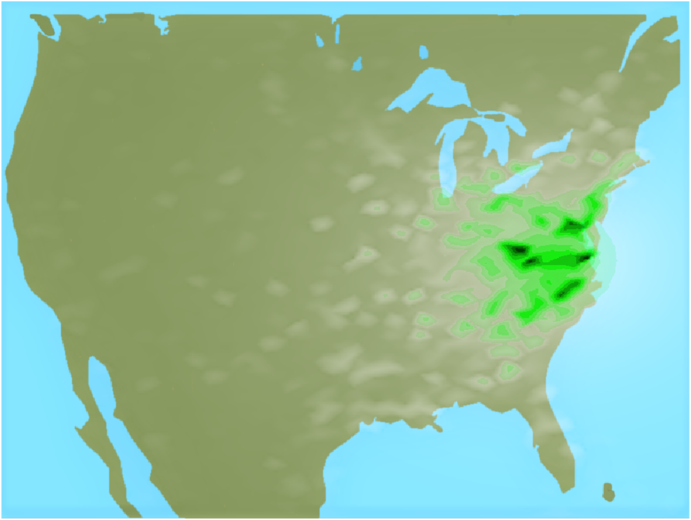
# Patch weights ($n = 540$)



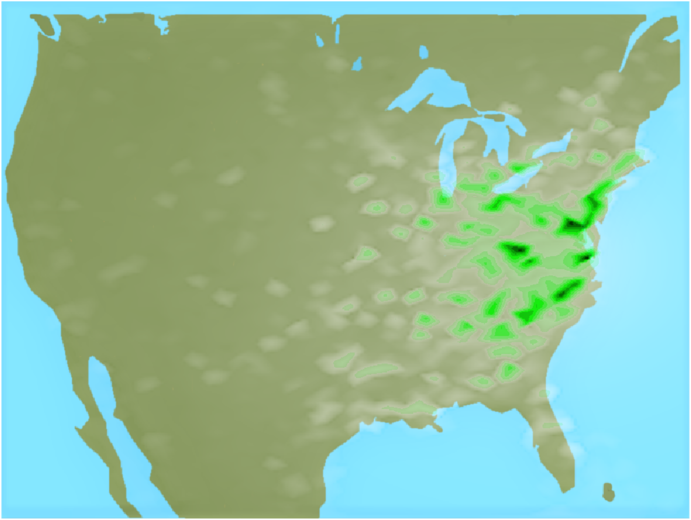
# Evolution of $\phi_t(s,z)$ $(t=0)$



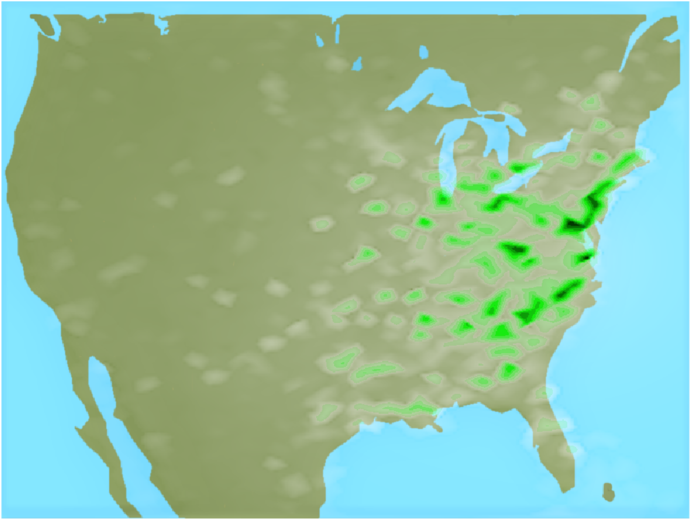
# Evolution of $\phi_t(s,z)$ $(t=1)$



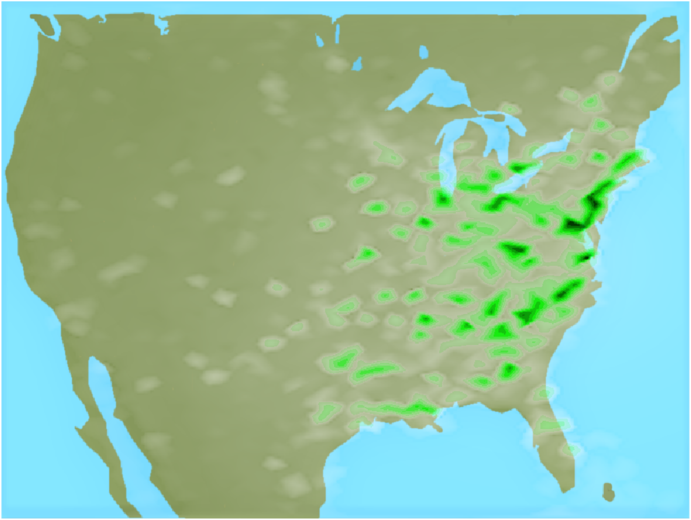
# Evolution of $\phi_t(s, z)$ $(t = 2)$



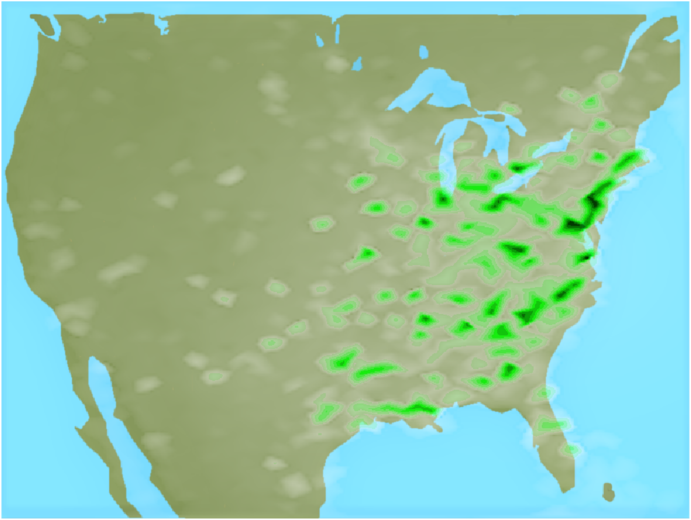
# Evolution of $\phi_t(s, z)$ $(t = 3)$



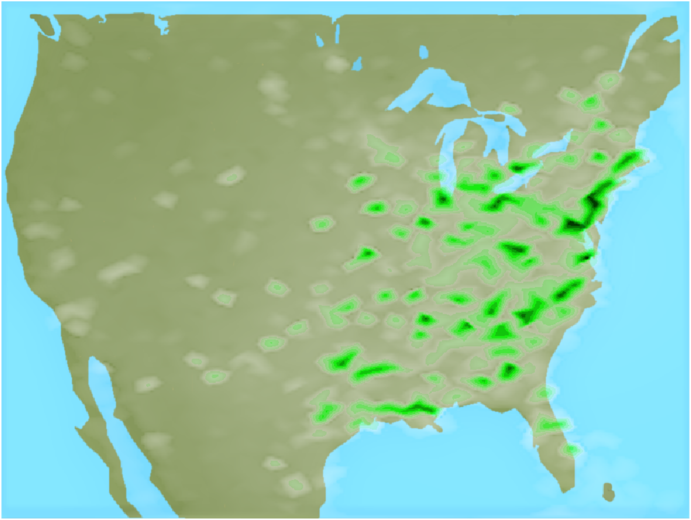
# Evolution of $\phi_t(s, z)$ $(t = 4)$



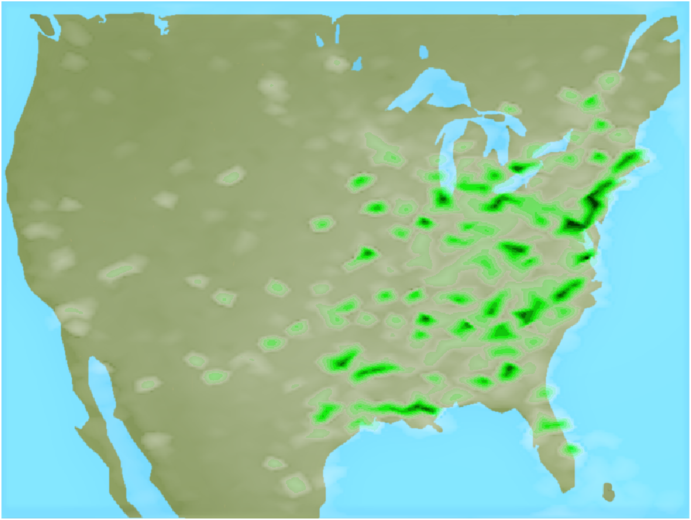
# Evolution of $\phi_t(s, z)$ $(t = 5)$



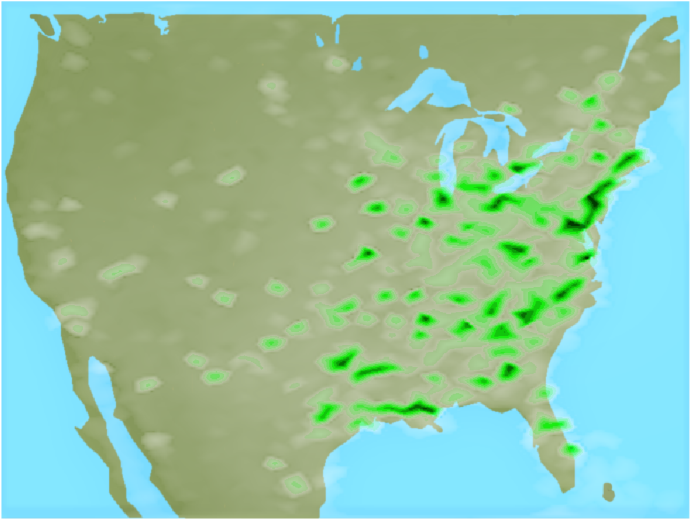
# Evolution of $\phi_t(s,z)$ $(t=6)$



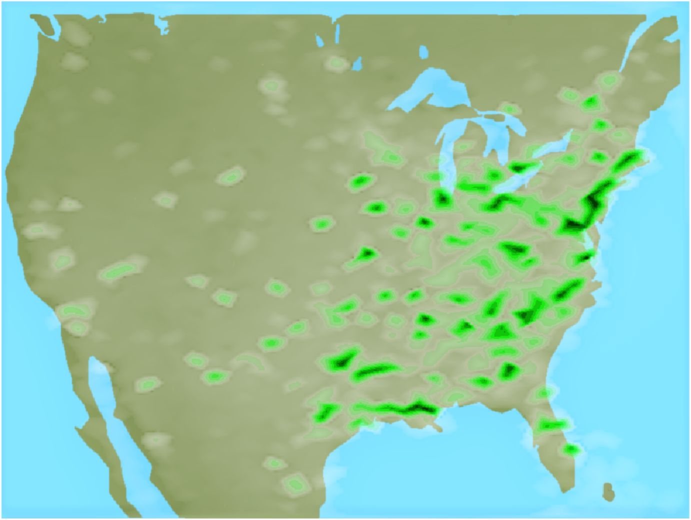
# Evolution of $\phi_t(s, z)$ $(t = 7)$



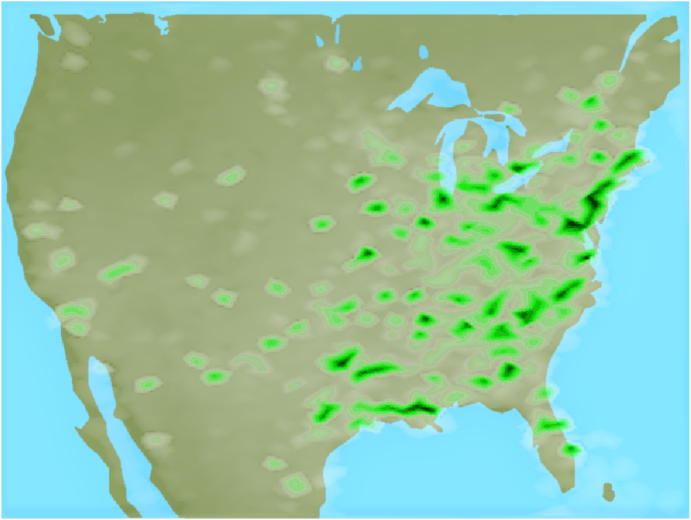
# Evolution of $\phi_t(s,z)$ $(t=8)$



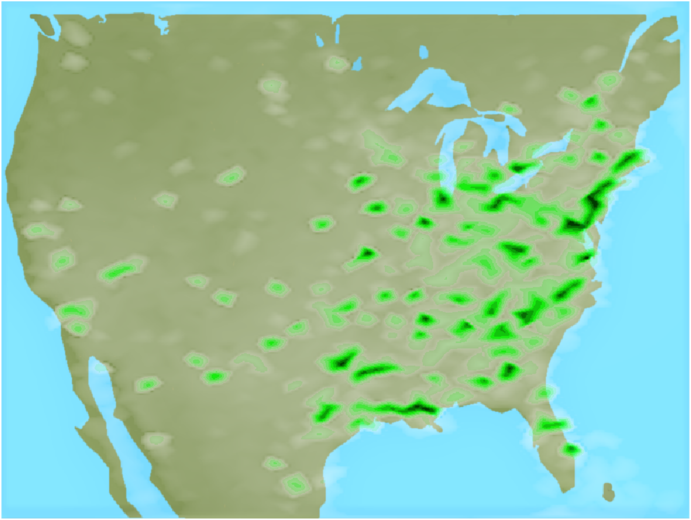
# Evolution of $\phi_t(s, z)$ $(t = 9)$



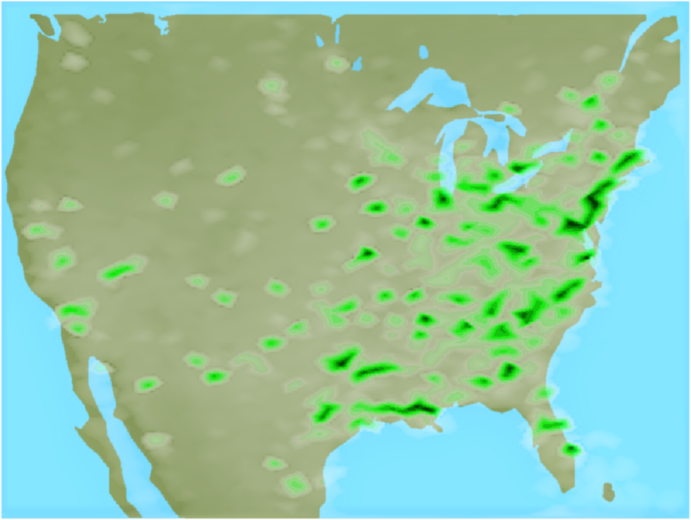
# Evolution of $\phi_t(s, z)$ $(t = 10)$



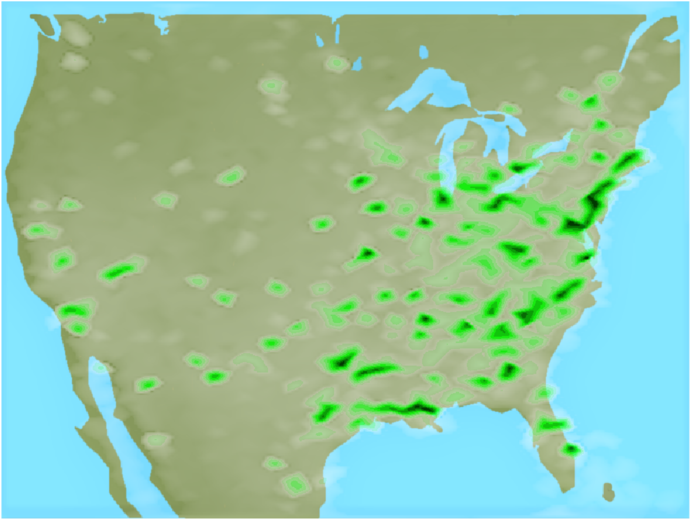
# Evolution of $\phi_t(s,z)$ $(t = 11)$



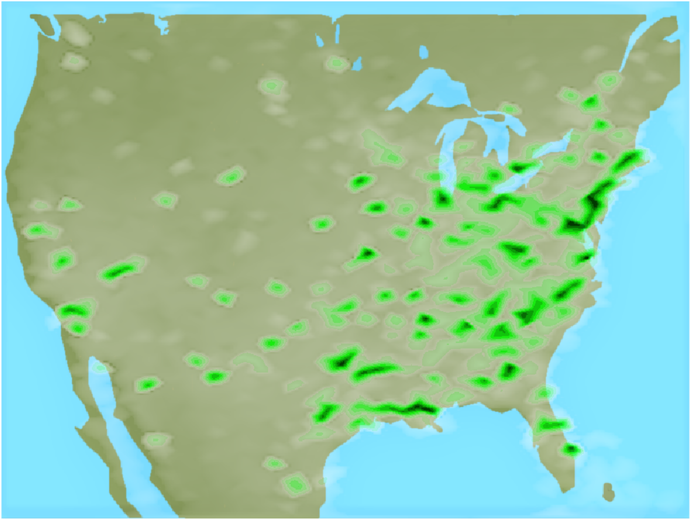
# Evolution of $\phi_t(s,z)$ $(t=12)$



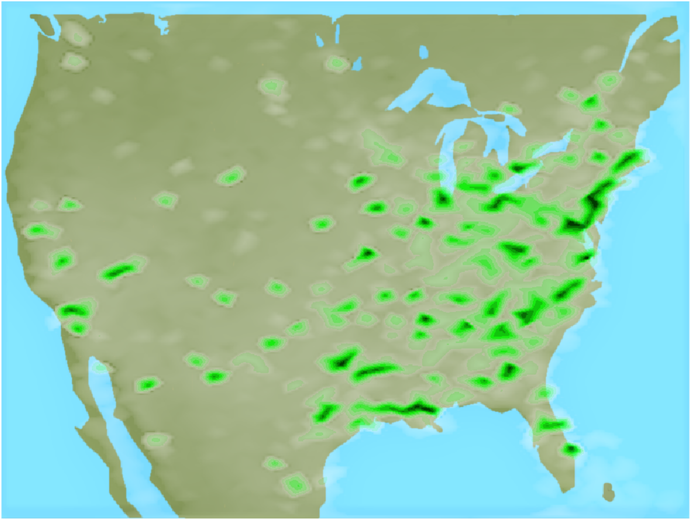
# Evolution of $\phi_t(s, z)$ $(t = 13)$



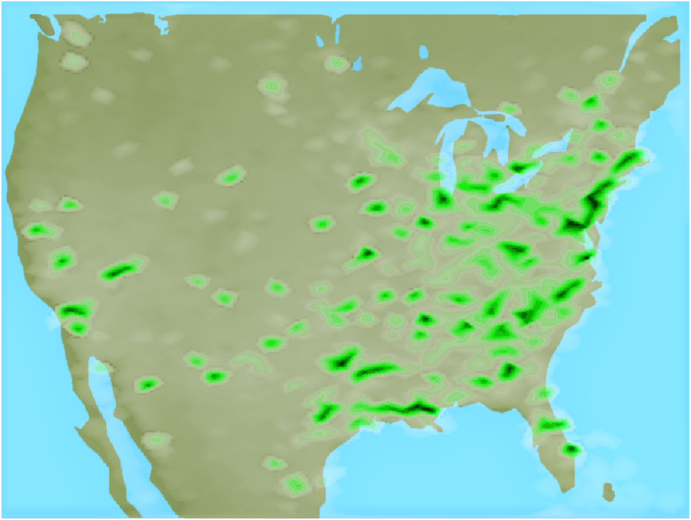
# Evolution of $\phi_t(s, z)$ $(t = 14)$



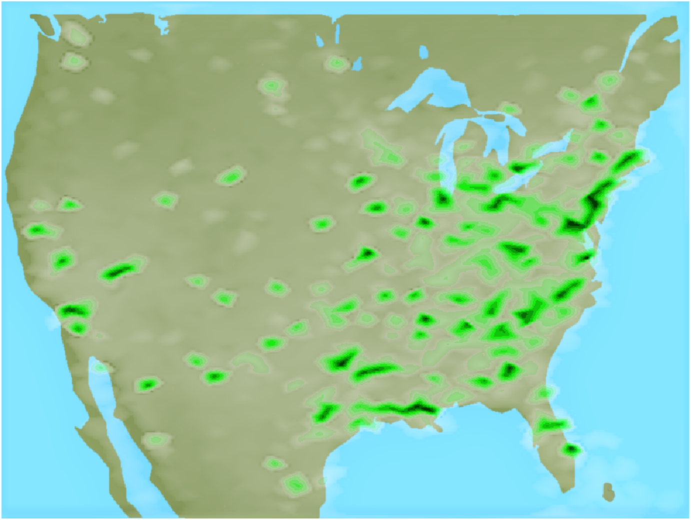
# Evolution of $\phi_t(s, z)$ $(t = 15)$



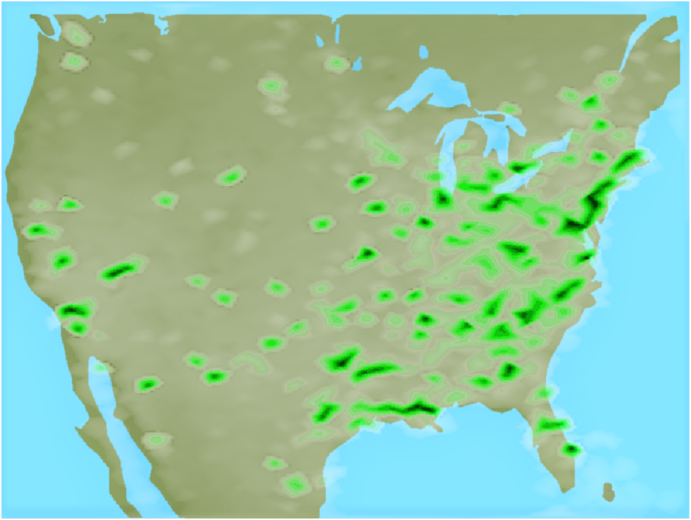
# Evolution of $\phi_t(s,z)$ $(t = 16)$



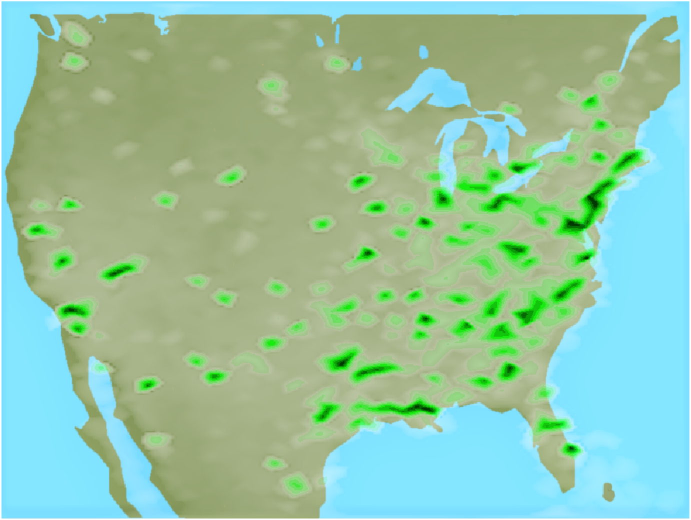
# Evolution of $\phi_t(s, z)$ $(t = 17)$



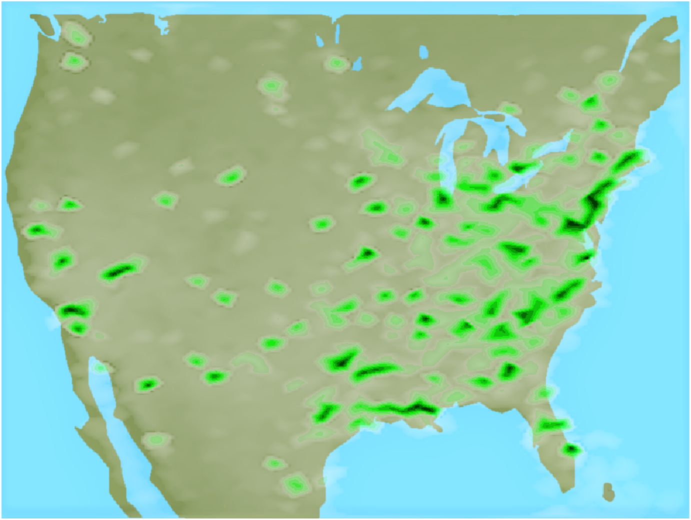
## Evolution of $\phi_t(s,z)$ $(t = 18)$



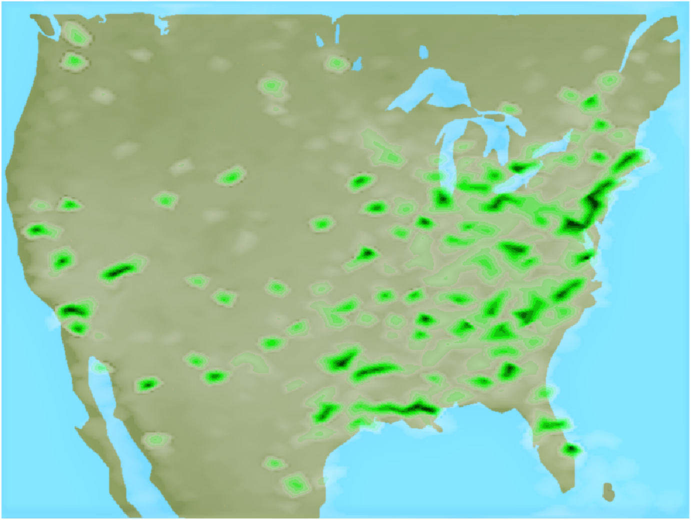
# Evolution of $\phi_t(s, z)$ $(t = 19)$



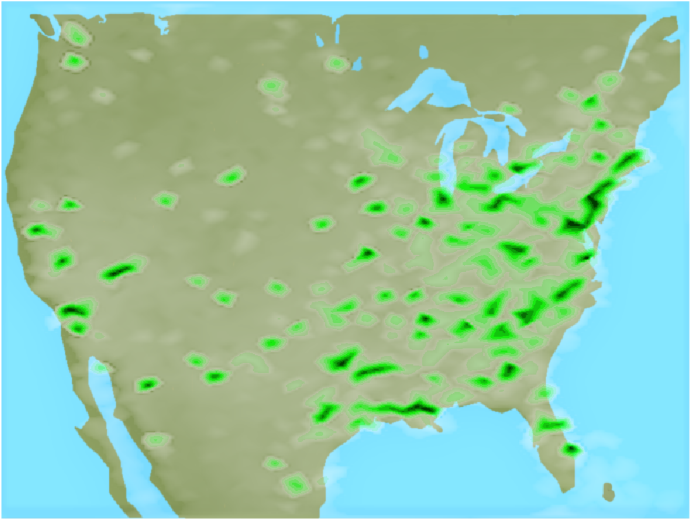
# Evolution of $\phi_t(s,z)$ $(t = 20)$



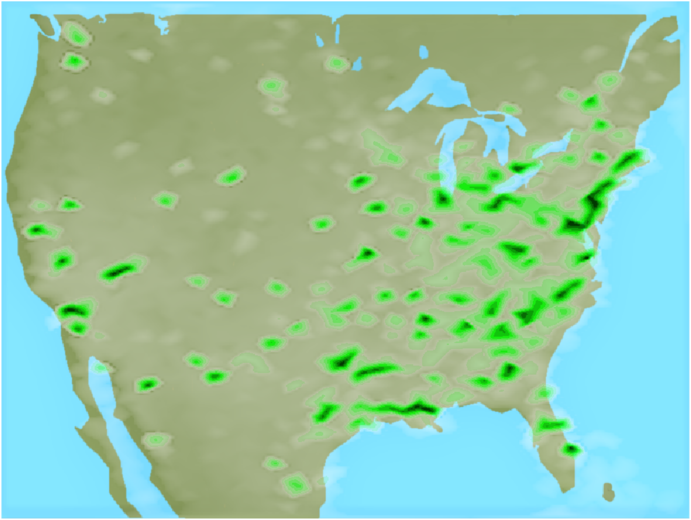
# Evolution of $\phi_t(s,z)$ $(t = 21)$



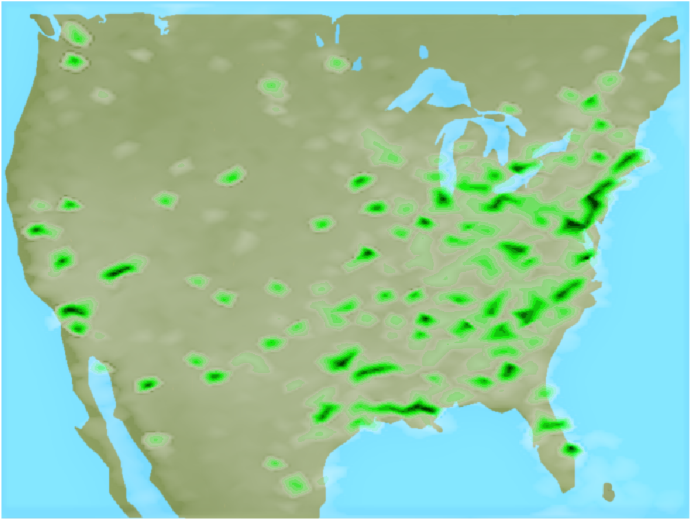
# Evolution of $\phi_t(s,z)$ ($t = 22$)



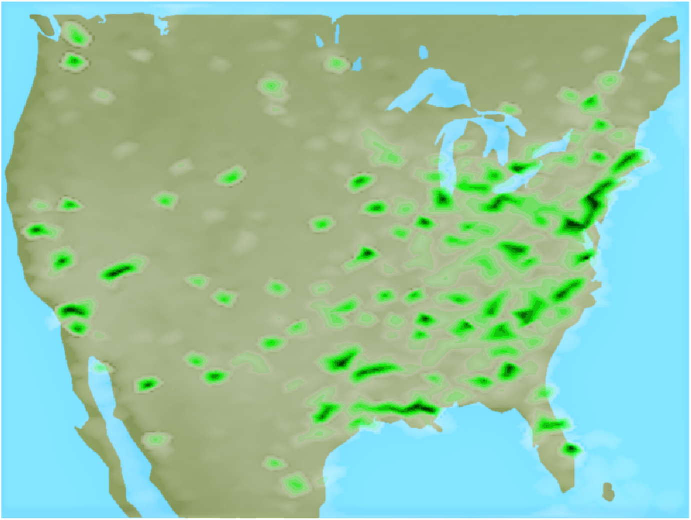
# Evolution of $\phi_t(s, z)$ $(t = 23)$



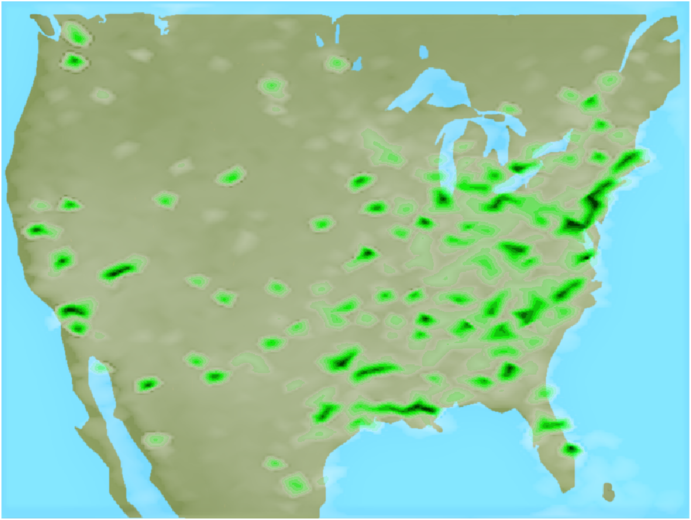
# Evolution of $\phi_t(s, z)$ $(t = 24)$



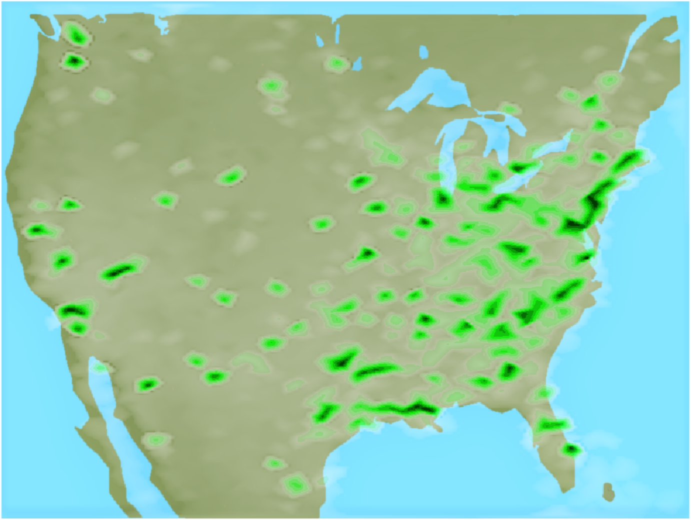
# Evolution of $\phi_t(s, z)$ $(t = 25)$



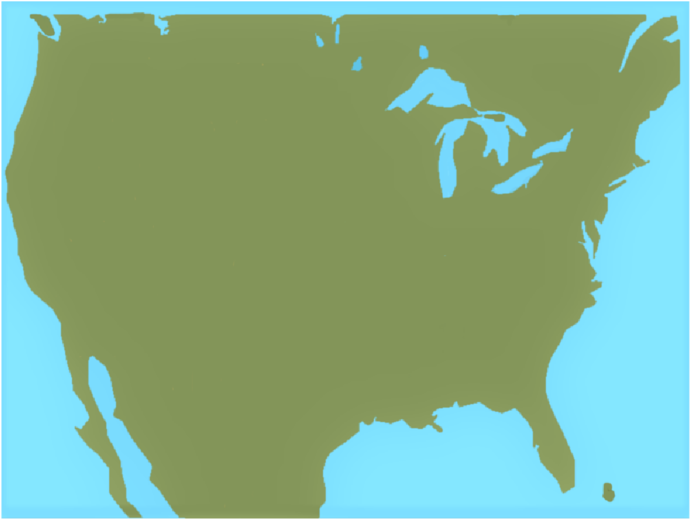
# Evolution of $\phi_t(s, z)$ $(t = 26)$



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

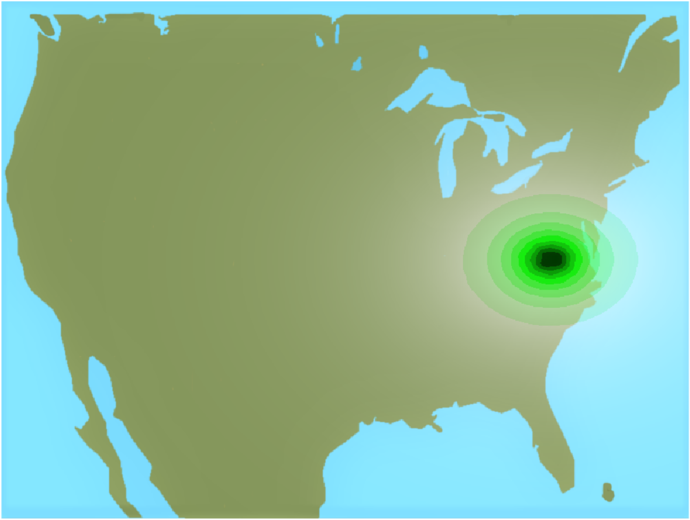


# When the landscape is in equilibrium

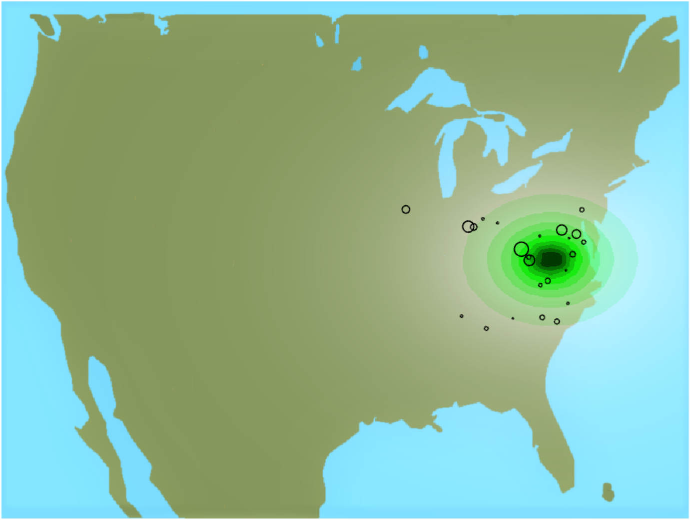


# Simulation ($t = 0$) - initial occupancy $\boldsymbol{X}_0^{(n)}$

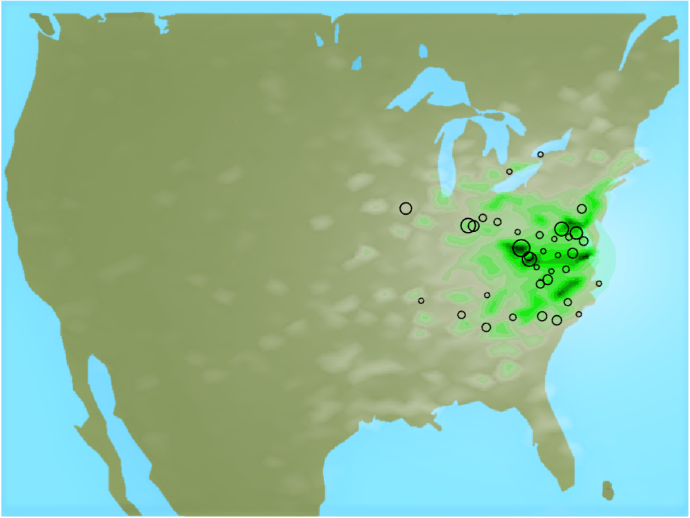
# Simulation ($t = 0$) - initial occupancy probability $\phi_0(s, z)$



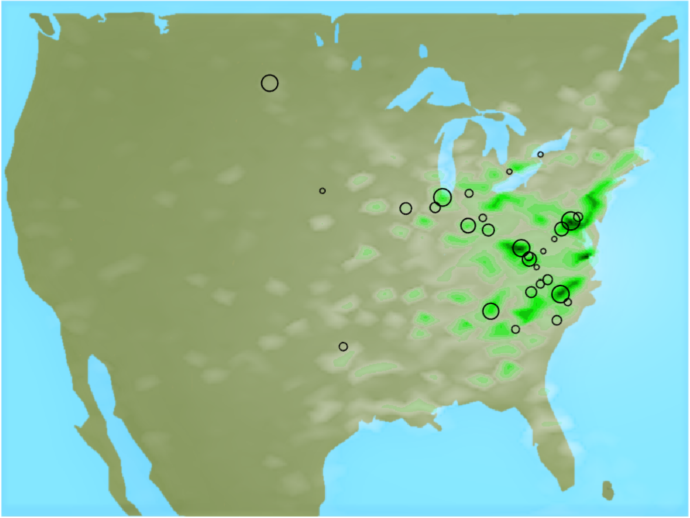
# Simulation ($t = 0$)



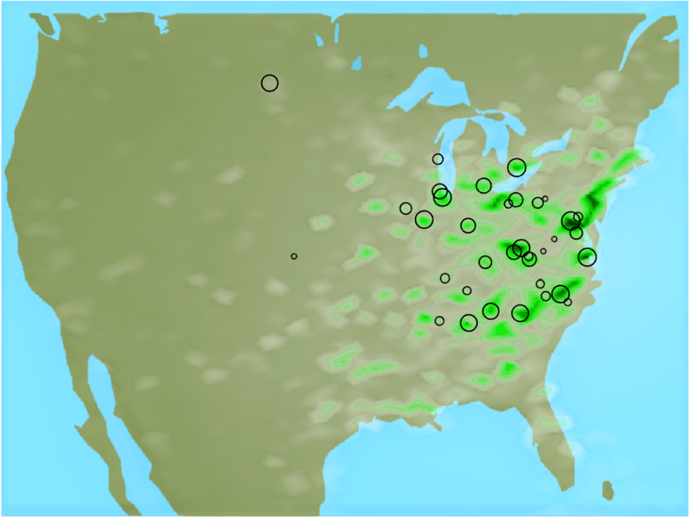
# Simulation ($t = 1$)



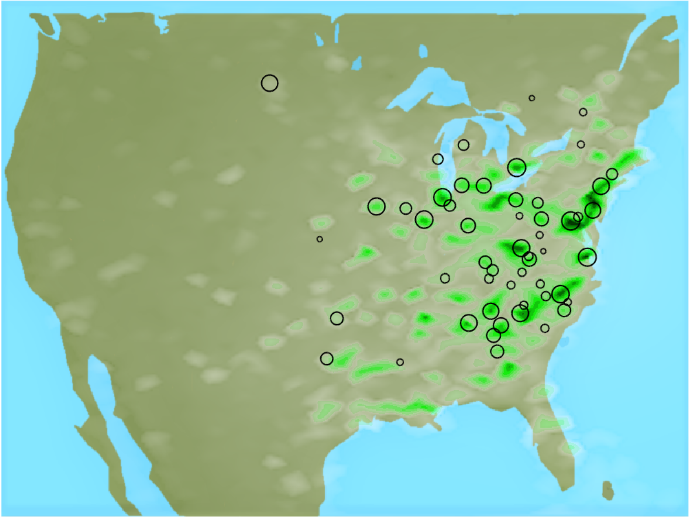
# Simulation ($t = 2$)



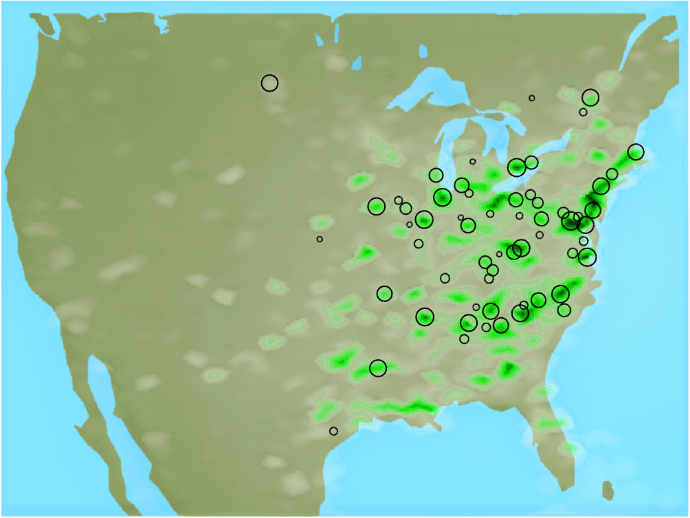
# Simulation ($t = 3$)



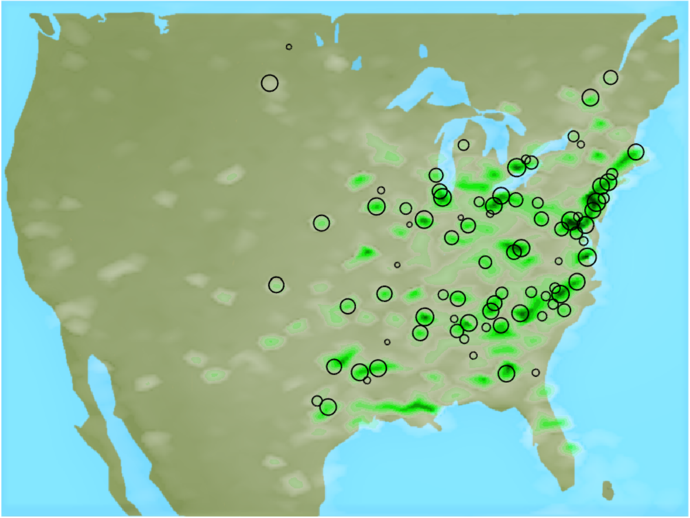
# Simulation ($t = 4$)



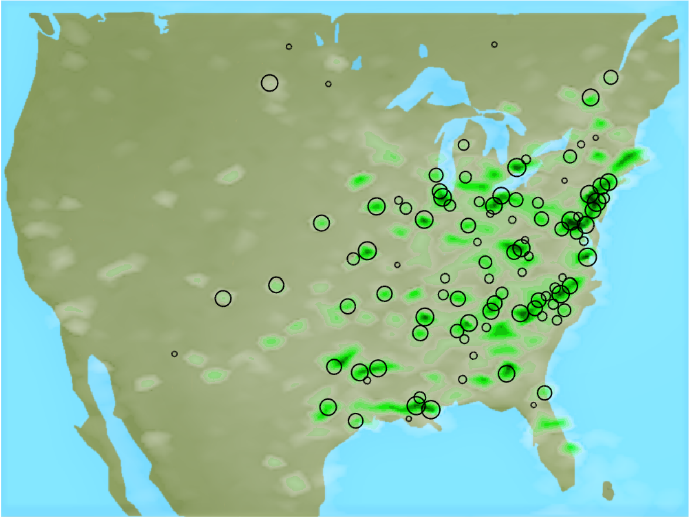
# Simulation ($t = 5$)



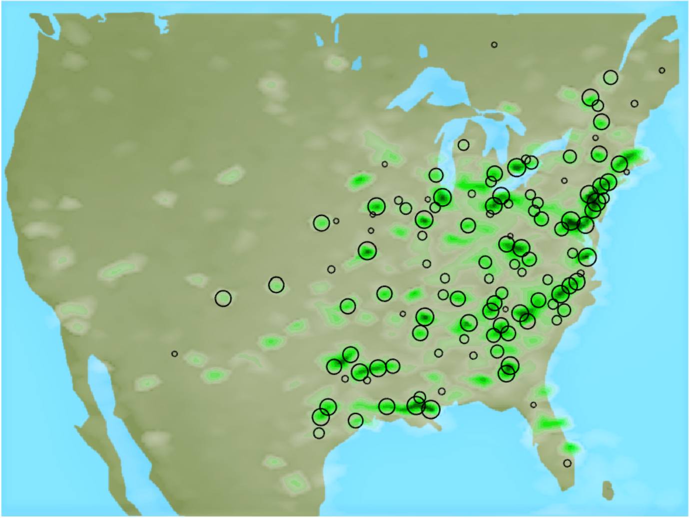
# Simulation ($t = 6$)



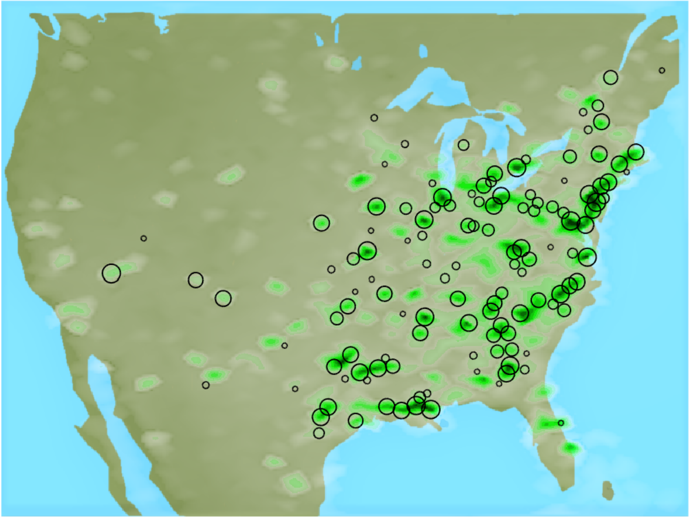
# Simulation ($t = 7$)



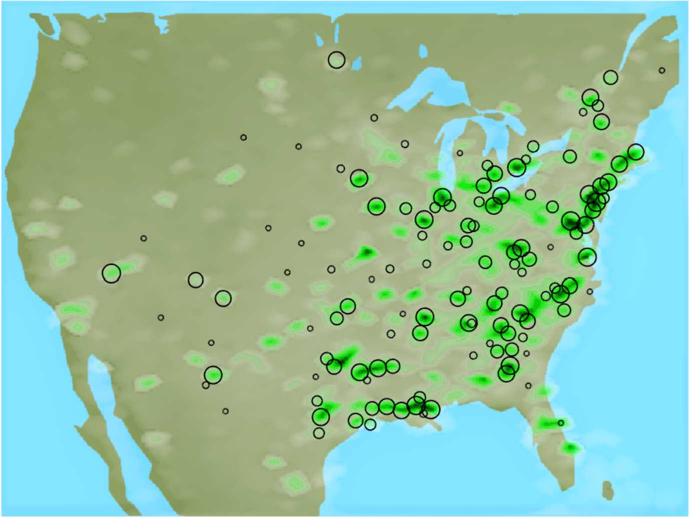
# Simulation ($t = 8$)



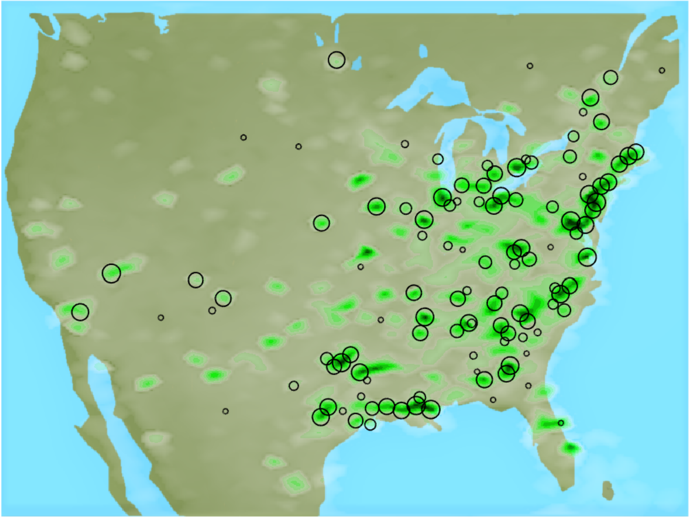
# Simulation ($t = 9$)



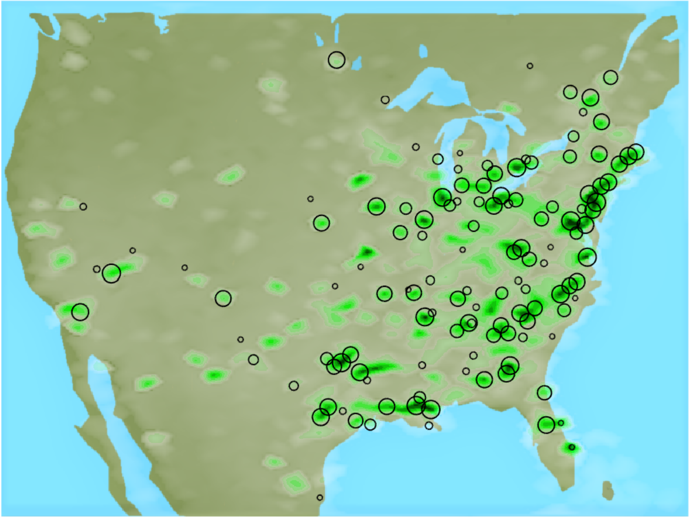
# Simulation ($t = 10$)



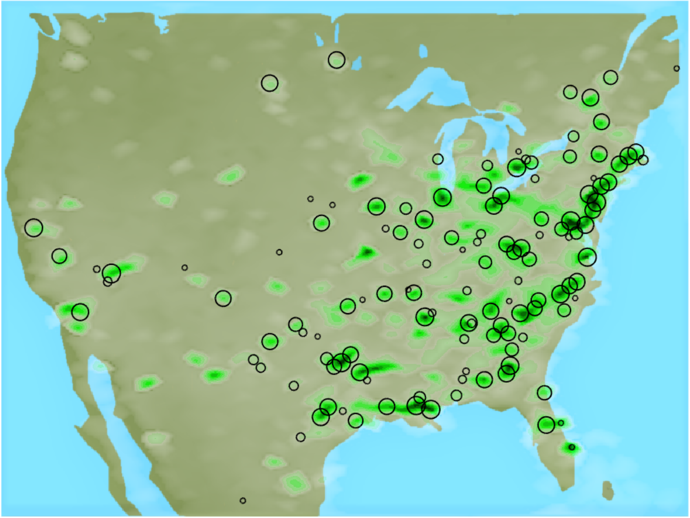
# Simulation ($t = 11$)



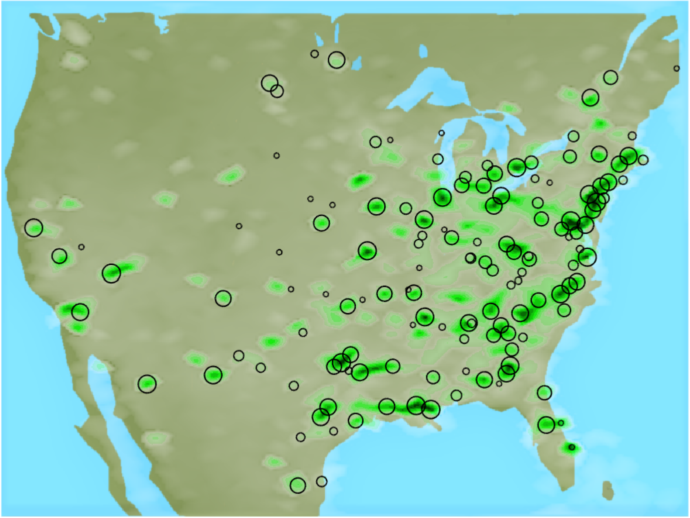
# Simulation ($t = 12$)



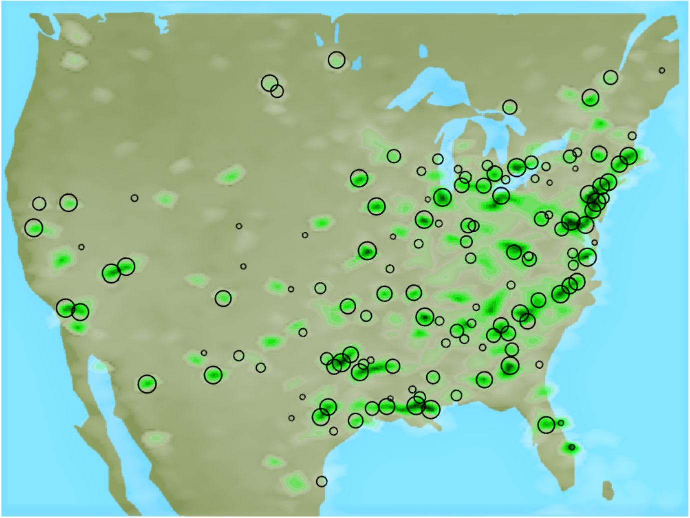
# Simulation ($t = 13$)



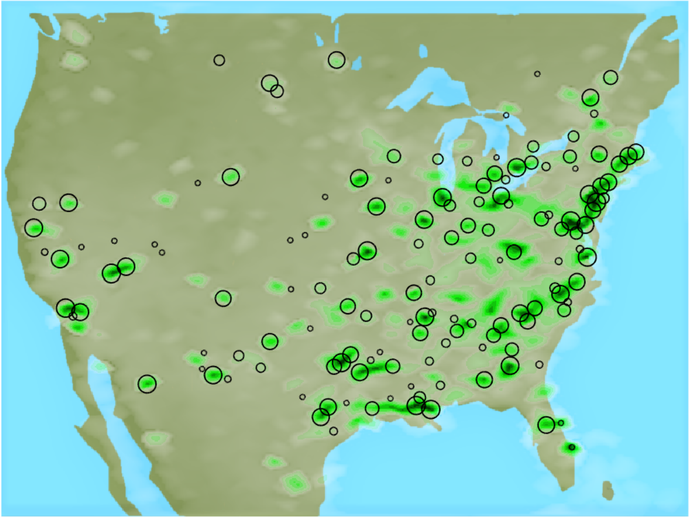
# Simulation ($t = 14$)



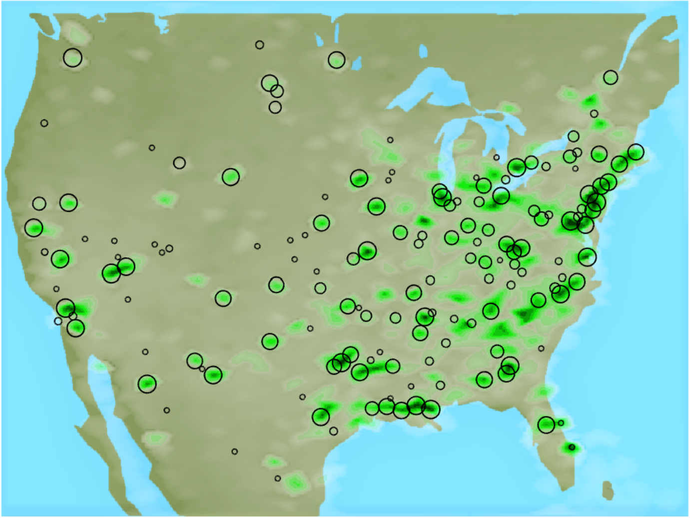
# Simulation ($t = 15$)



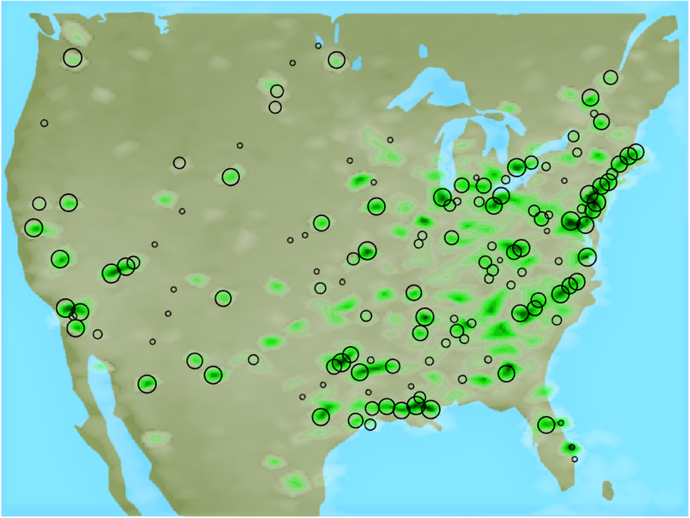
# Simulation ($t = 16$)



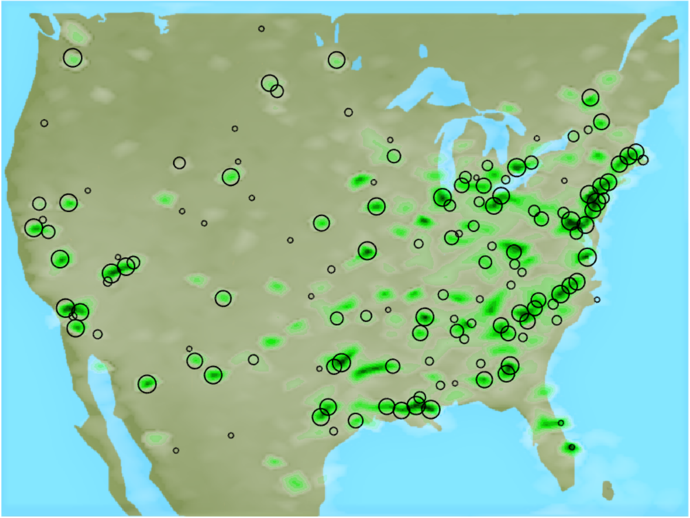
# Simulation ($t = 17$)



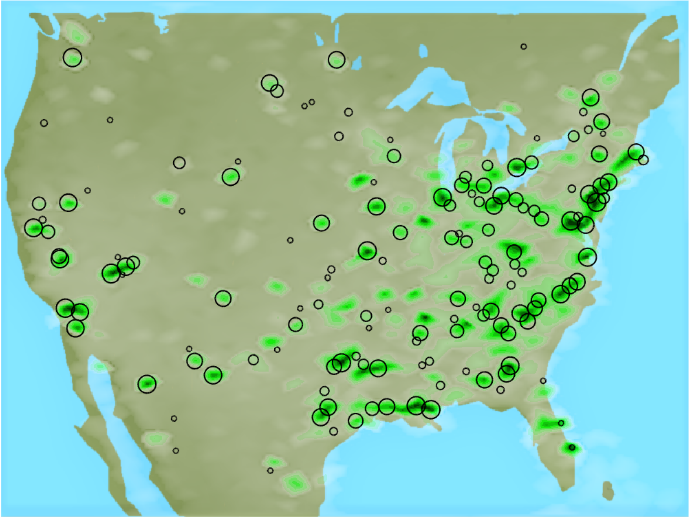
# Simulation ($t = 18$)



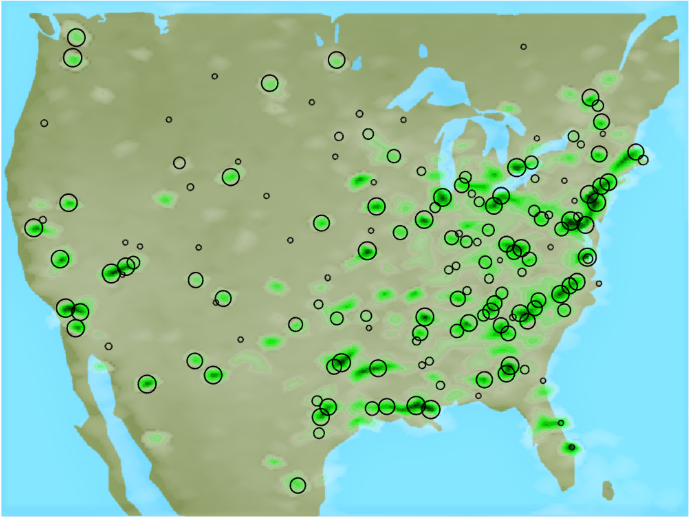
# Simulation ($t = 19$)



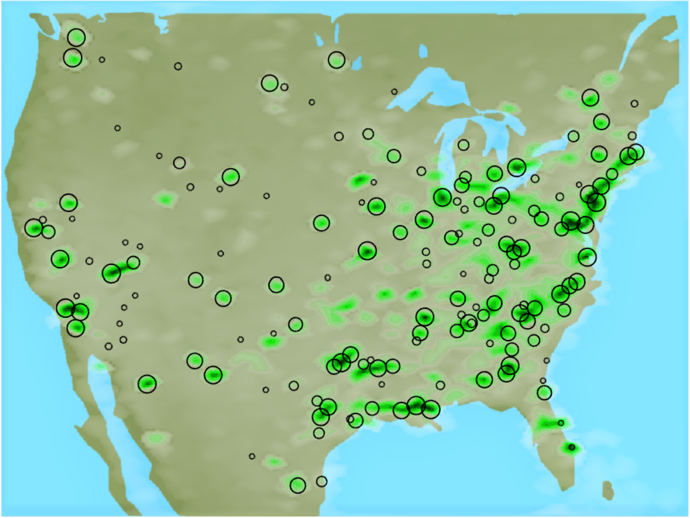
## Simulation ($t = 20$)



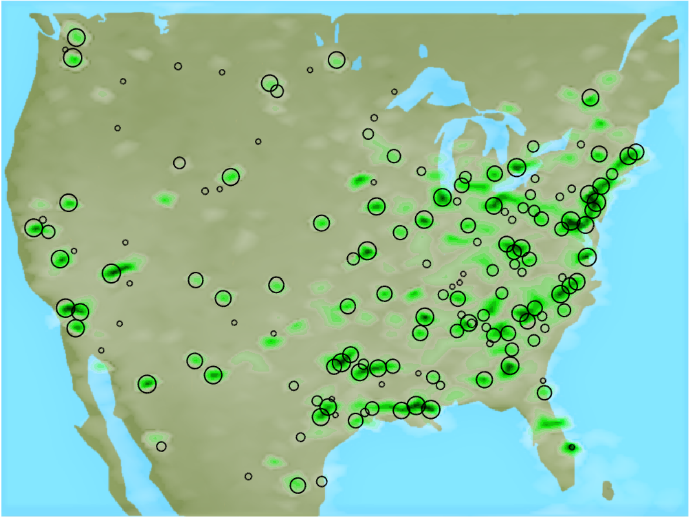
# Simulation ($t = 21$)



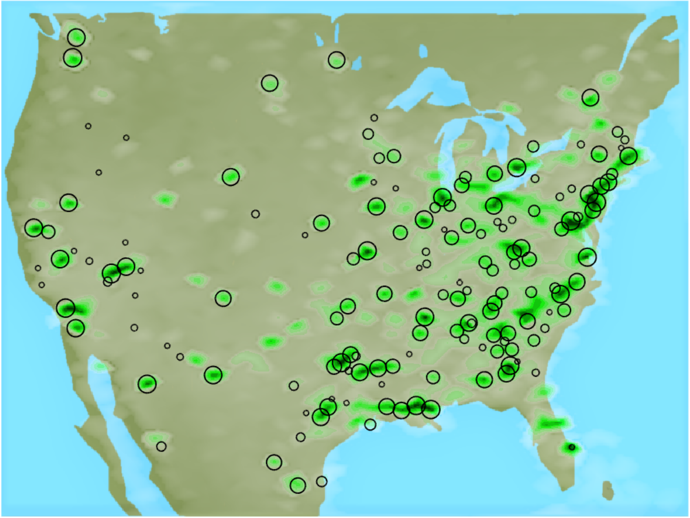
# Simulation ($t = 22$)



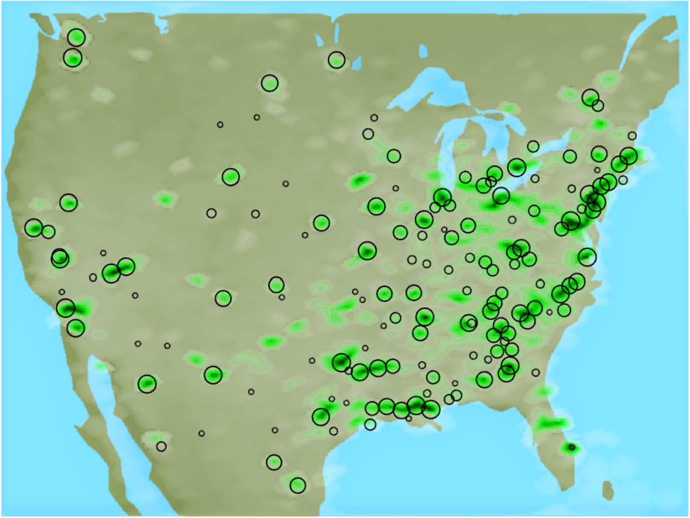
# Simulation ($t = 23$)



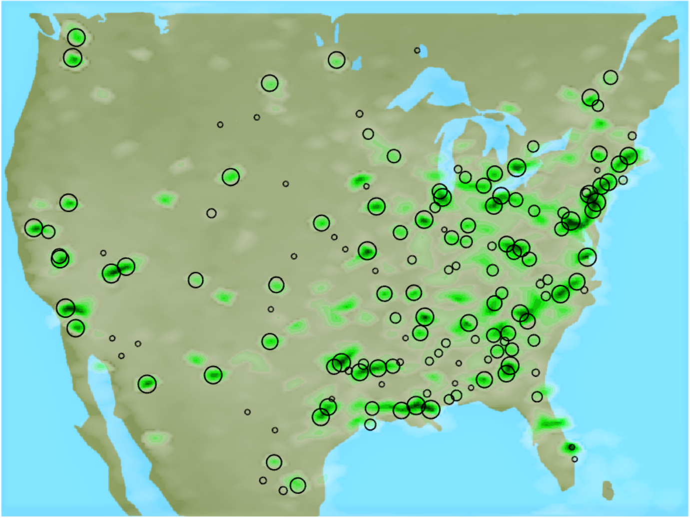
# Simulation ($t = 24$)



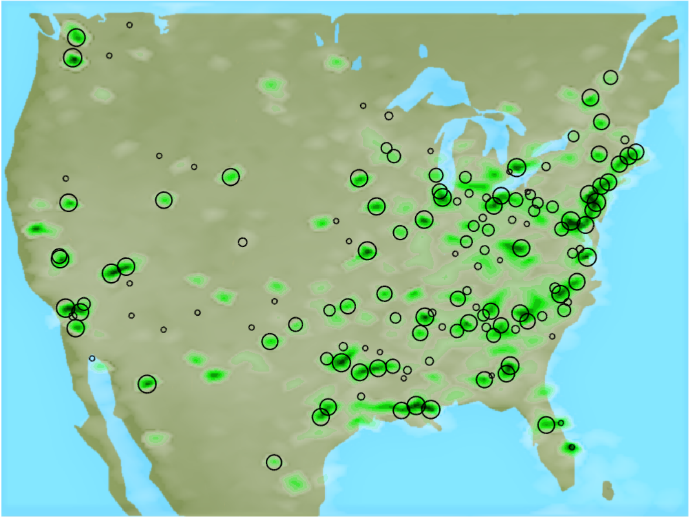
# Simulation ($t = 25$)



# 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

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

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

# The limiting metapopulation in equilibrium

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

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

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

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

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

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 $\partial\mu_\infty/\partial\sigma \equiv 0$, 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*).