# Diffusion approximation for a spatially realistic structured metapopulation model

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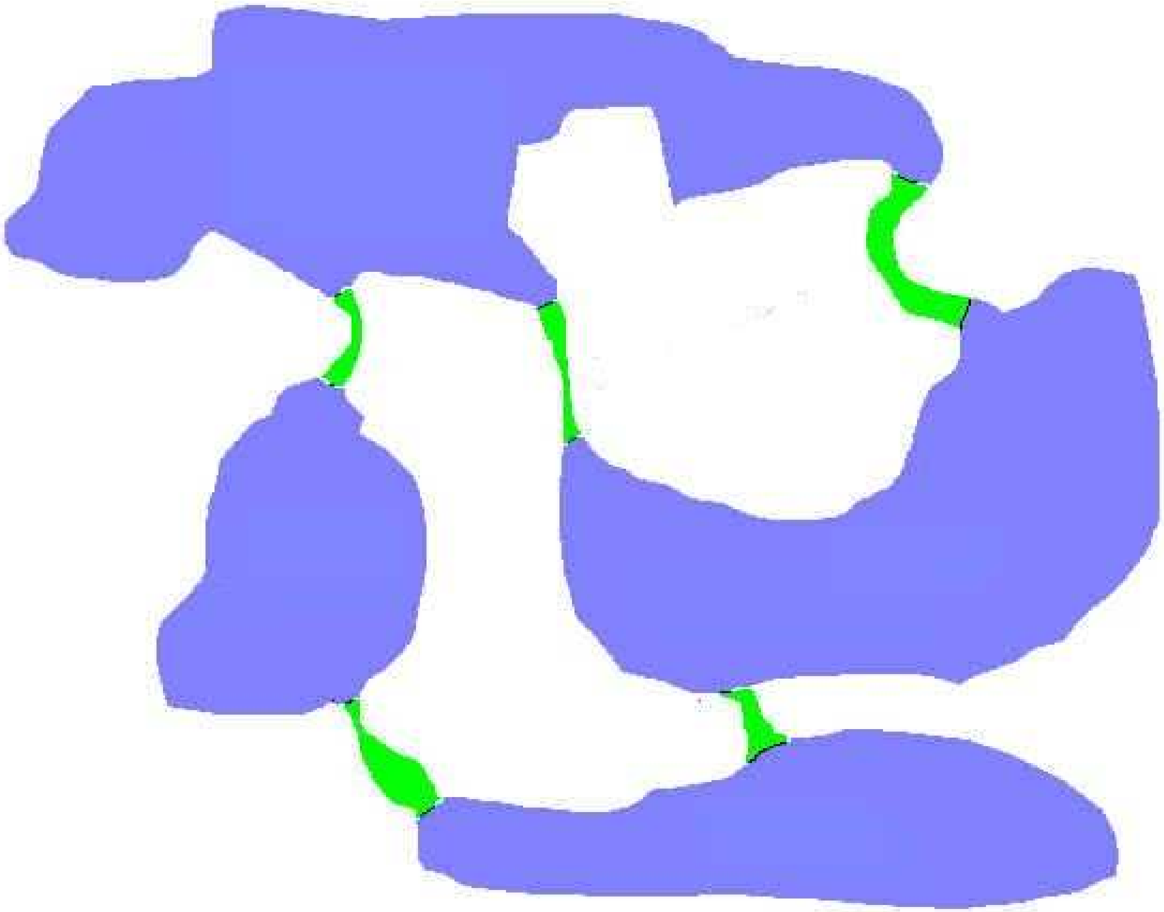
# What is a metapopulation?



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- - Heterogenous landscape

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- No spatial structure - homogenous mixing

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- But...

  - does not account for local population dynamics

  - computationally intensive ($2^k \times 2^k$ for a $k$-patch system)

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- Surprise surprise... a continuous-time Markov chain!

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- Patch abundance - local population dynamics?

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- $e_i$ - $i$-th unit vector

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$$Q = (q(i,j), i, j \in S),$$

so that $q(i,j)$ represents the rate of transition from state $i$ to state $j$, for $j \neq i$, and $q(i,i) = -q(i)$, where

$$q(i) := \sum_{j \neq i} q(i,j) \; (< \infty)$$

represents the total rate out of state $i$.

# The model - transition rates

Birth

$$q(n, n + e_i) = b\frac{n_i}{N_i}(N_i - n_i),\ \forall\, i \in K$$

Migration

$$q(n, n - e_i + e_j) = \gamma_{ij}\frac{n_i}{N_j}(N_j - n_j),\ \forall\, i \neq j, i, j \in K$$

Death

$$q(n, n - e_i) = \mu n_i,\ \forall\, i \in K$$

where $K = \{1, \ldots, k\}$.

# Density-dependence

*Definition*: A one-parameter family of Markov chains $\{P_\nu, \nu > 0\}$ with state space $S_\nu \subset \mathbb{Z}^D$ is called density dependent if there exists a set $E \subseteq \mathbb{R}^D$ and a continuous function $f : E \times \mathbb{Z}^D \to \mathbb{R}$, such that

$$q_\nu(k, k+l) = \nu f\left(\frac{k}{\nu}, l\right), \qquad l \neq 0.$$

[Kurtz (1970)]

# Functional law of large numbers

*Theorem*: Suppose that $f(x,l)$ is bounded for each $l$ and that $F$, where $F(x) = \sum_l l f(x,l)$, is Lipschitz continuous on $E$. Then, if

$$\lim_{\nu \to \infty} X_\nu(0) = x_0,$$

we have, for fixed $\tau > 0$ and for all $\epsilon > 0$, that

$$\lim_{\nu \to \infty} \mathit{Pr} \left( \sup_{t \le \tau} |X_\nu(t) - X(t, x_0)| > \epsilon \right) = 0,$$

where $X(\cdot, x)$ is the unique trajectory satisfying

$$X(0,x) = x, \quad X(t,x) \in E, \ 0 \le t \le \tau, \quad \frac{\partial}{\partial t} X(t,x) = F(X(t,x)).$$

[Kurtz (1970)]

# Functional central limit theorem

$$\sqrt{\nu}\,(X_\nu(t) - X(t, x_0)) \to \text{Gaussian Diffusion}$$

$$\sqrt{\nu}\,(X_\nu(t) - x^*) \to N(0, \Sigma_t)$$

Long-term

$$\mathsf{E}(X_\nu) \approx x^*$$

$$\mathsf{Var}(X_\nu) \approx \frac{1}{\nu}\Sigma \quad \text{where } \Sigma = \lim_{t\to\infty} \Sigma_t.$$

[Kurtz (1971)]

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$$f(x, x + e_i) = b\frac{x_i}{\rho_i}(\rho_i - x_i), \ \forall i \in K$$

$$f(x, x - e_i + e_j) = \gamma_{ij}\frac{x_i}{\rho_j}\left(\rho_j - x_j\right), \ \forall i \neq j, i, j \in K$$

$$f(x, x - e_i) = \mu x_i, \ \forall i \in K.$$

# Deterministic approximation

The functional law of large numbers gives us

$$\frac{dx}{dt} = F(x)$$

Therefore we have a system of $k$ differential equations with the $i$-th given by

$$\frac{dx_i}{dt} = \left( b - \mu - \sum_{j \neq i} \gamma_{ij} \right) x_i + \sum_{j \neq i} \gamma_{ij} x_j + \frac{x_i}{\rho_i} \left[ \sum_{j \neq i} \frac{\gamma_{ij}}{\rho_j} x_j (\rho_i - \rho_j) - b x_i \right]$$

# Special case - 2 equal patches

$$\frac{dx_1}{dt} = \left(b - \mu - \gamma - \frac{b}{\rho}x_1\right)x_1 + \gamma x_2$$

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Fixed points and stability

Trivial fixed point: $(0, 0)$
Stable if $b - \mu < 0$, saddle if $0 < b - \mu < 2\gamma$ and unstable if $b - \mu > 2\gamma$.

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SL fixed point: $\left(\frac{1}{2b}(b-\mu), \frac{1}{2b}(b-\mu)\right)$
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Another pair: Real and saddles if $|b - \mu| > 2\gamma$.

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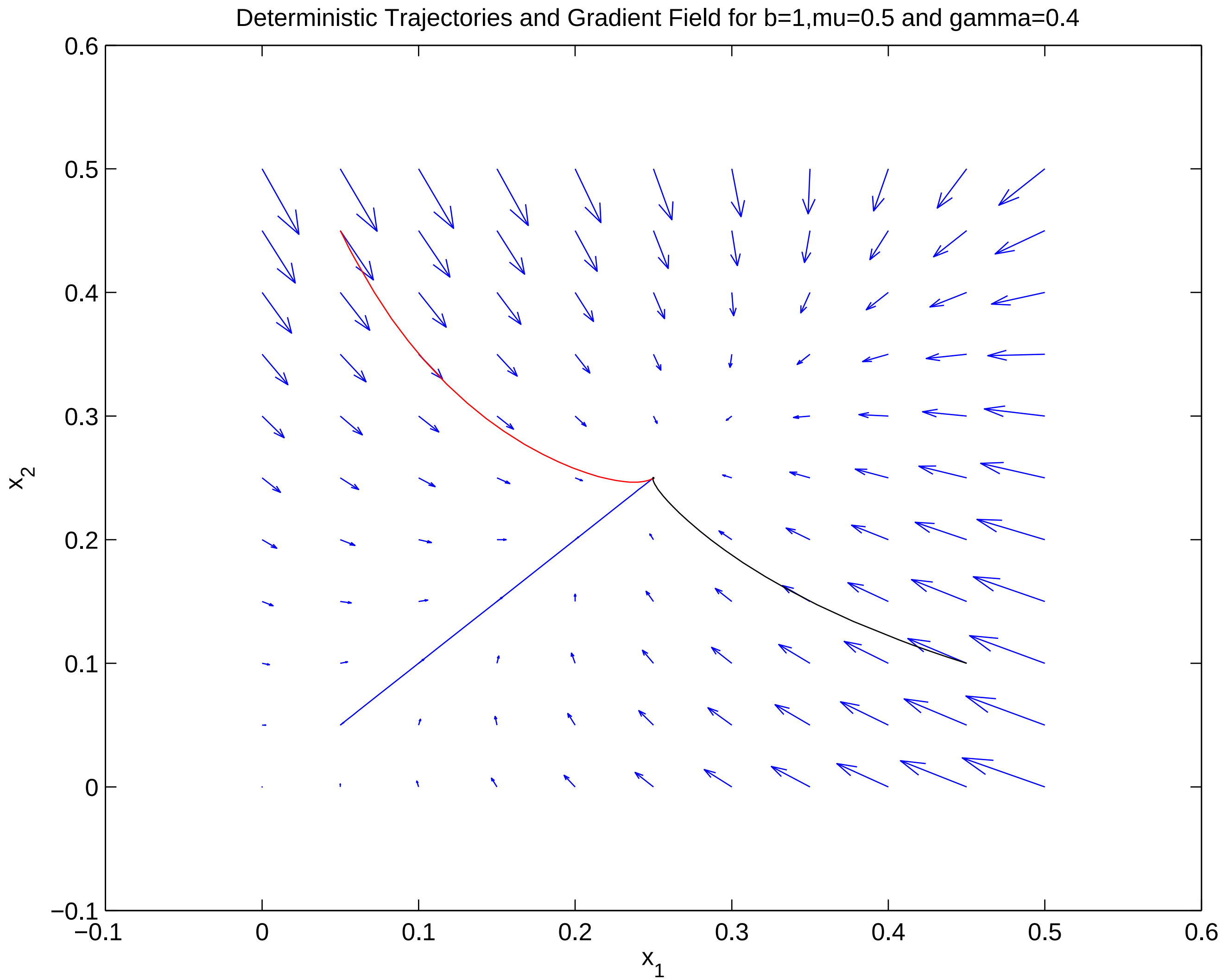

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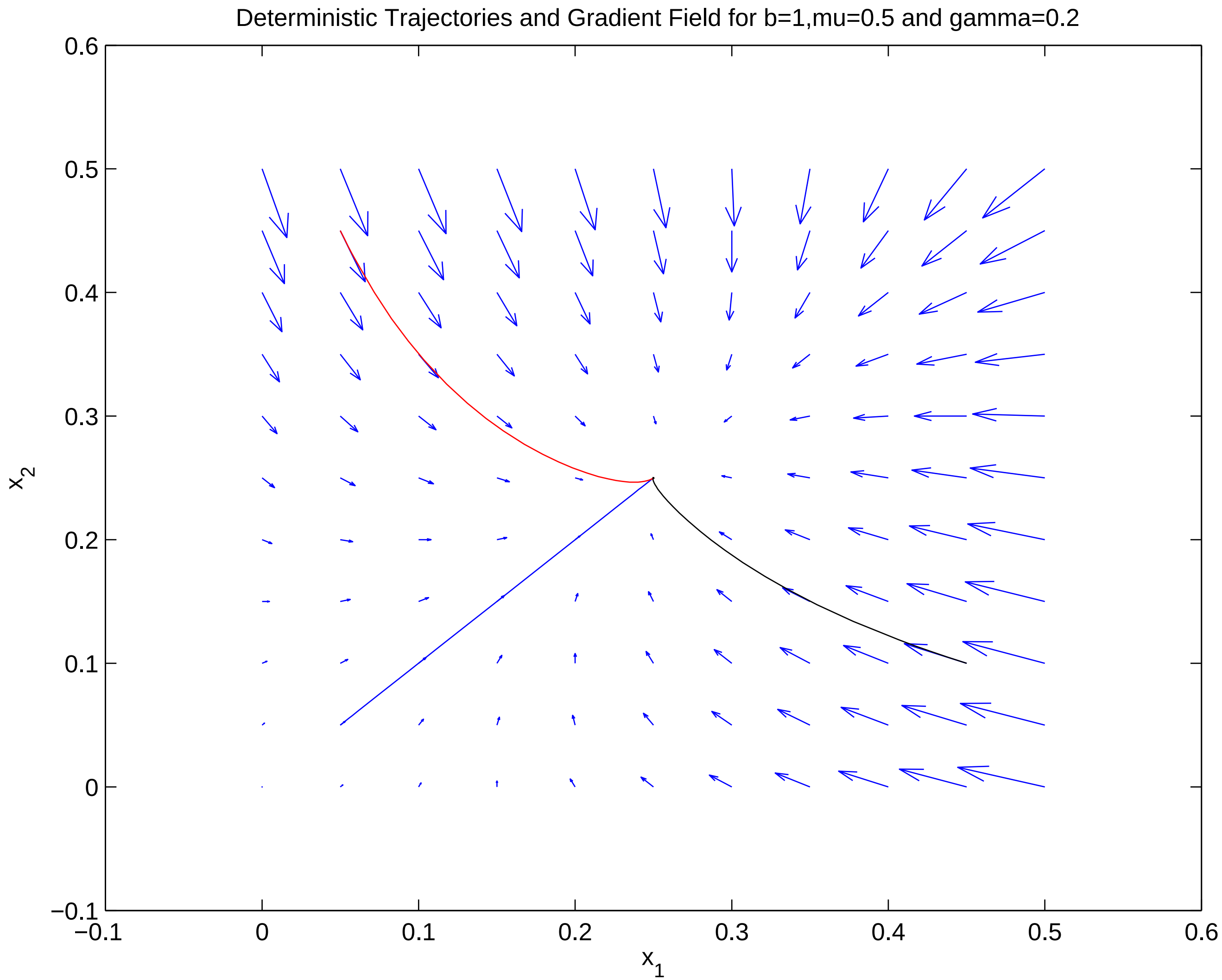

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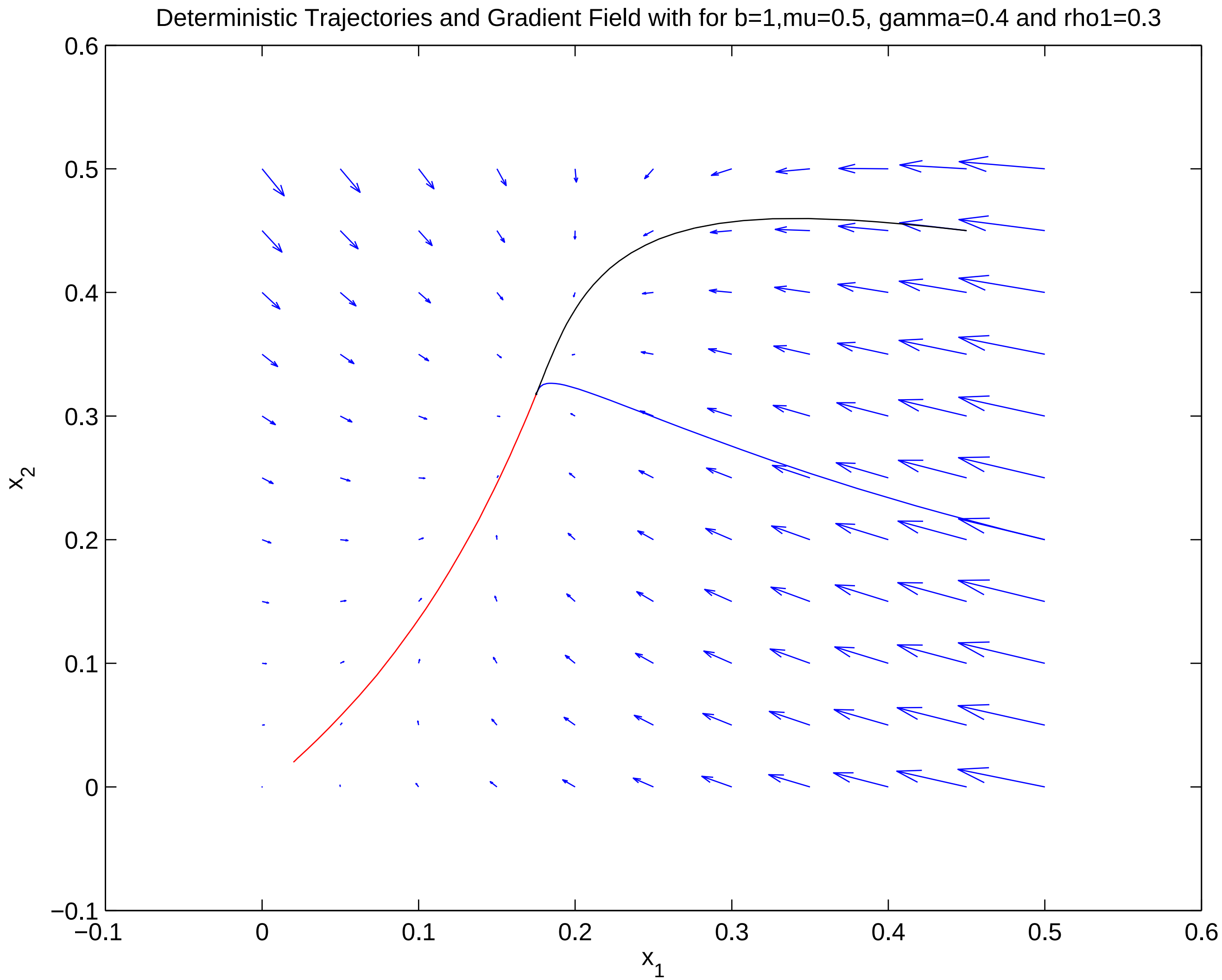

# General stability analysis

The nonlinear system can be written in the linearised form

$$\frac{d\underline{x}}{dt} = A\underline{x} + h(\underline{x})$$

where

$$A = \Gamma + (b - \mu)I$$

in which $\Gamma$ is a q-matrix with diagonal entries given by $-\sum_{j \neq i} \gamma_{ij}$ and off-diagonal entries $\gamma_{ij}$, and $h(\underline{x})$ consists of higher order terms such that $||h(\underline{x})|| = o(||\underline{x}||)$, as $||\underline{x}|| \to 0$.

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Determine stability by considering the eigenvalues $\sigma$ of $A$

$$A\underline{\mathsf{x}} = \sigma\underline{\mathsf{x}}$$

so we have

$$(b - \mu)\underline{\mathsf{x}} + \Gamma\underline{\mathsf{x}} = \sigma\underline{\mathsf{x}}$$

and therefore

$$\Gamma\underline{\mathsf{x}} = [\sigma - (b - \mu)]\,\underline{\mathsf{x}}$$

so finally we have

$$\sigma_i = \lambda_i + b - \mu$$

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where $\lambda_i$ is the $i$-th eigenvalue of $\Gamma$. Therefore, SL fixed point is always stable if

$$b > \mu.$$

# One-dimensional summary

If the patches are close to homogenous in size, we can approximate the equilibrium mean population density by using the logistic model [Verhulst (1838)]

$$\frac{dy}{dt} = by(1-y) - \mu y$$

with equilibrium $y^* = \frac{1}{b}(b-\mu)$, which is stable if $b > \mu$, where $y = \sum_{i=1}^{k} x_i$.

The equilibrium density at each patch will then be given by

$$x_i^* = \frac{1}{kb}(b-\mu), \quad i = \{1, 2, \ldots, k\}$$

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- Diffusion approximation - investigate the variances and covariances
- Listen to Michael’s talk and then have some pizza!

# Acknowledgements

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and

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