McMaster University

Mathematics and Statistics

$$\int_M d\omega = \int_{\partial M} \omega$$

Mathematics 4MB3/6MB3
Mathematical Biology

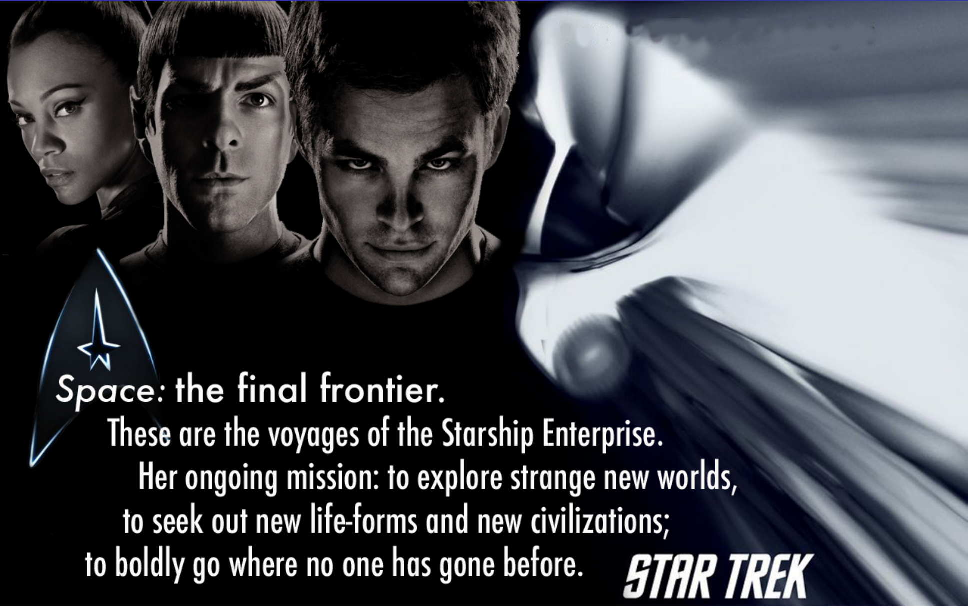
Instructor: David Earn

Lecture 7
Space
Monday 28 October 2019

Announcments

- **Midterm test:**
  - *Date:* Monday 4 November 2019
  - *Time:* 11:30am–1:30pm
  - *Location:* in class, ETB-237
- **Assignment 4** is due the day of the midterm.
  Due Monday 4 November 2019 before class.
  - Make sure *you personally* can do the question on calculating $\mathcal{R}_0$ on this assignment *before* the midterm test.

Spatial Epidemic Dynamics



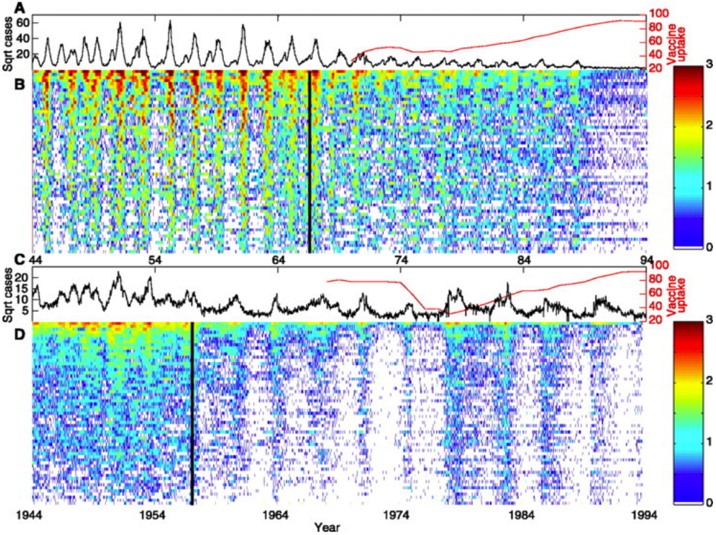
Something to think about

- All of our analysis has been of temporal patterns of epidemics
- What about spatial patterns?
- What problems are suggested by observed spatial epidemic patterns?
- Can spatial epidemic data suggest improved strategies for control?
- Can we reduce the eradication threshold below $p_{\rm crit} = 1 - \frac{1}{\mathcal{R}_0}$?

Measles and Whooping Cough in 60 UK cities

Measles

Whooping Cough



Rohani, Earn & Grenfell (1999) *Science* **286**, 968–971

Better Control? Eradication?

- The term-time forced SEIR model successfully predicts past patterns of epidemics of childhood diseases
- Can we manipulate epidemics predictably so as to increase probability of eradication?
- Can we eradicate measles?

Idea for eradicating measles

- Try to re-synchronize measles epidemics in the UK and, moreover, synchronize measles epidemics worldwide: synchrony is good
- Devise new vaccination strategy that tends to synchronize...
- Avoid spatially structured epidemics...
- Time to think about the mathematics of synchrony...
- But analytical theory of synchrony in a periodically forced system of differential equations is mathematically demanding...
- So let's consider a much simpler biological model...

The Logistic Map

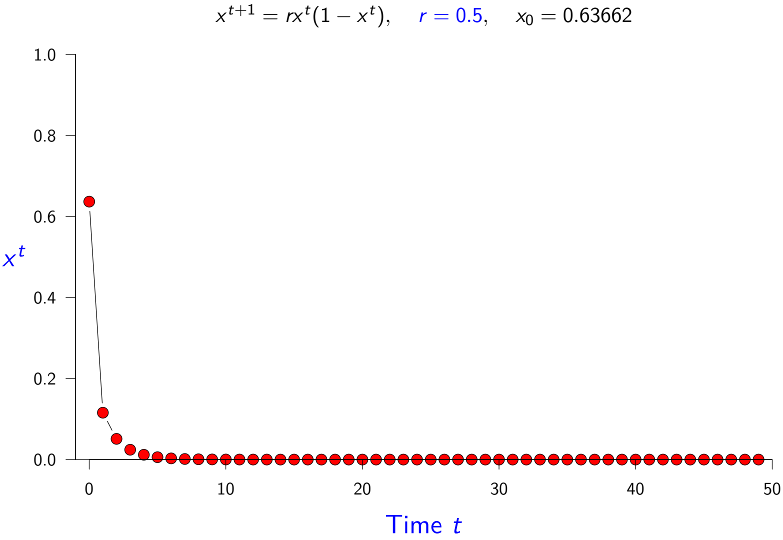
Logistic Map

- Simplest non-trivial *discrete time* population model for a single species (with *non-overlapping generations*) in a *single habitat patch*.
- Time: $t = 0, 1, 2, 3, \ldots$
- State: $x \in [0,1]$ (population density)
- Population density at time t is x^t. Solutions are sequences:

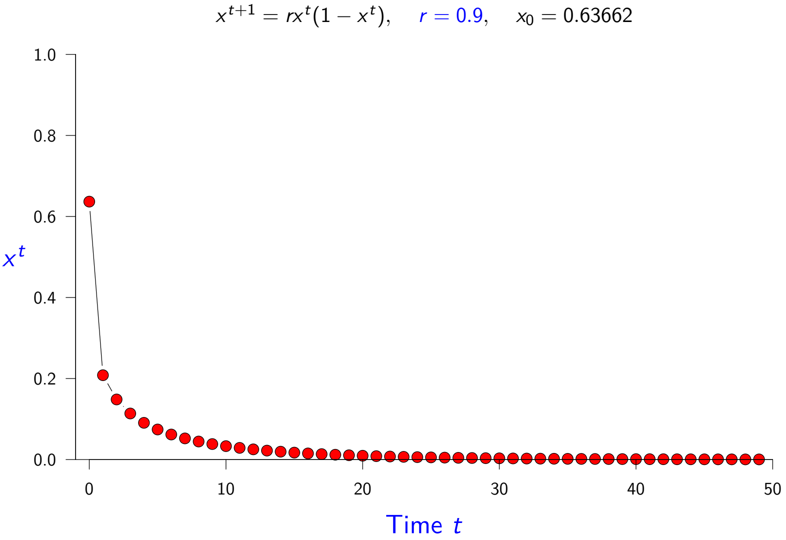
$$x^0,\ x^1,\ x^2,\ \ldots$$

- $x^{t+1} = F(x^t)$ for some *reproduction function* $F(x)$.
- For logistic map: $F(x) = rx(1-x)$, so $x^{t+1} = rx^t(1-x^t)$. $x^{t+1} = [r(1-x^t)]x^t \implies r$ is *maximum fecundity* (which is achieved in limit of very small population density).
- What kinds of dynamics are possible for the Logistic Map?

Logistic Map Time Series, $r = 0.5$

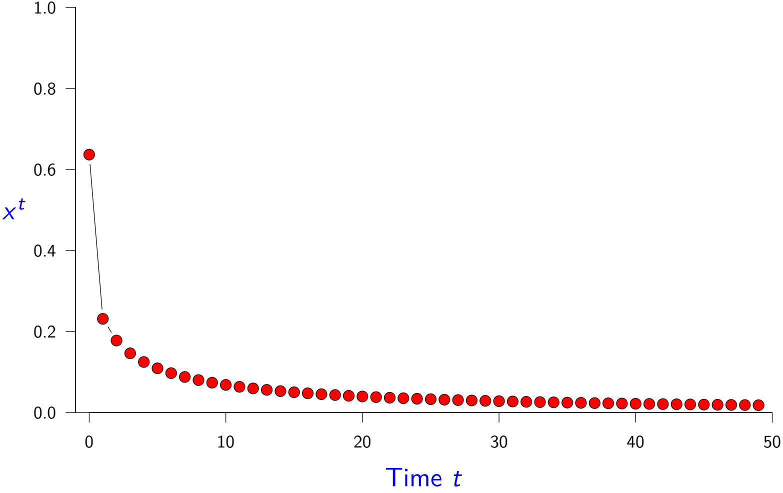


Logistic Map Time Series, $r = 0.9$

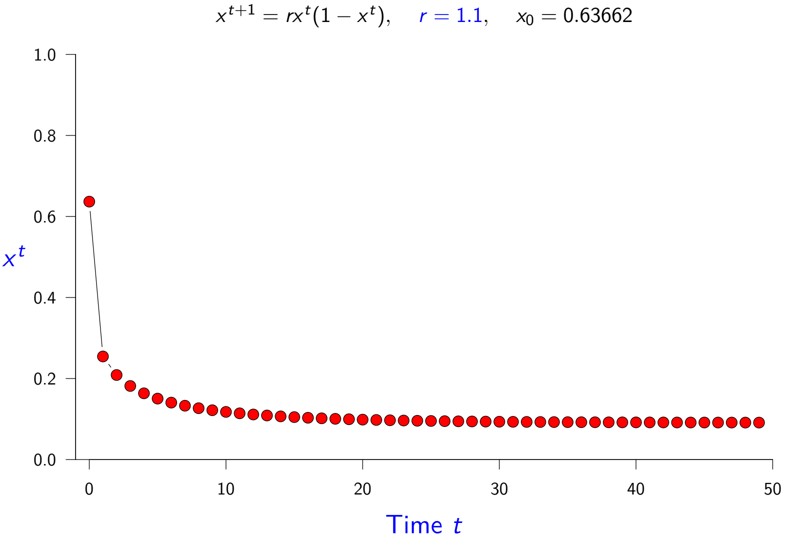


Logistic Map Time Series, $r = 1$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 1, \quad x_0 = 0.63662$$

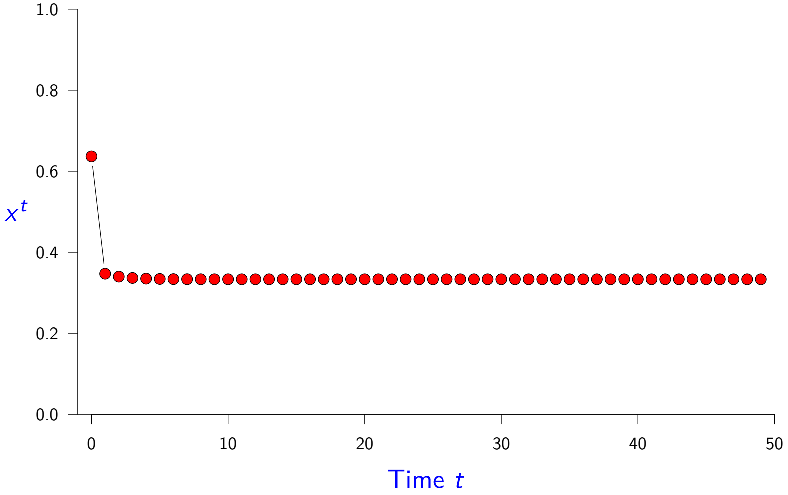


Logistic Map Time Series, $r = 1.1$

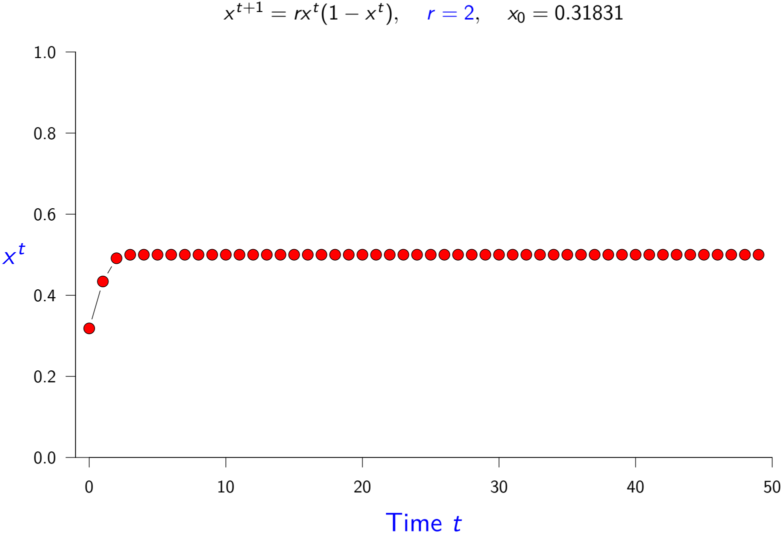


Logistic Map Time Series, $r = 1.5$

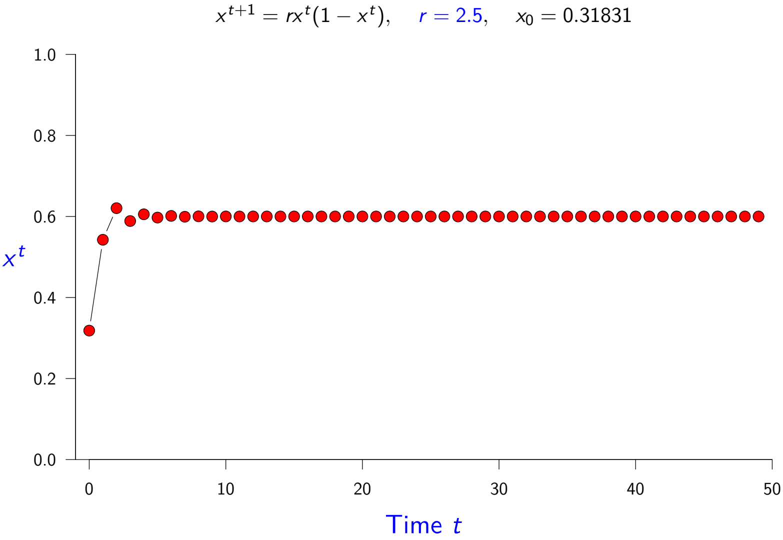
$$x^{t+1} = rx^t(1 - x^t), \quad r = 1.5, \quad x_0 = 0.63662$$



Logistic Map Time Series, $r = 2$

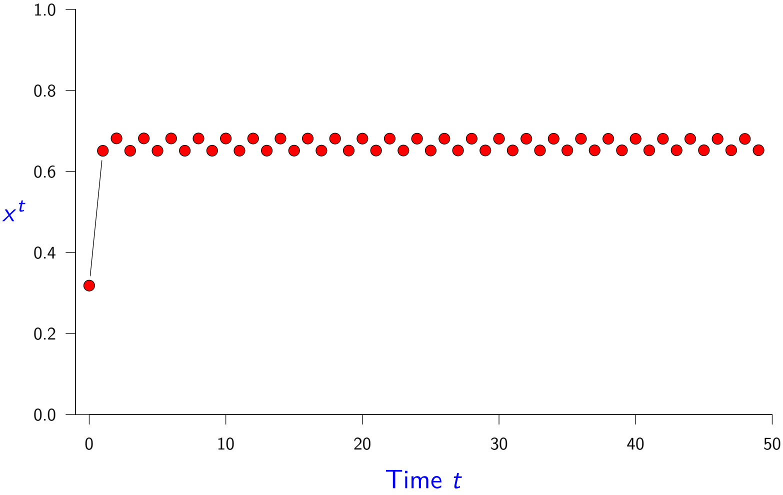


Logistic Map Time Series, $r = 2.5$

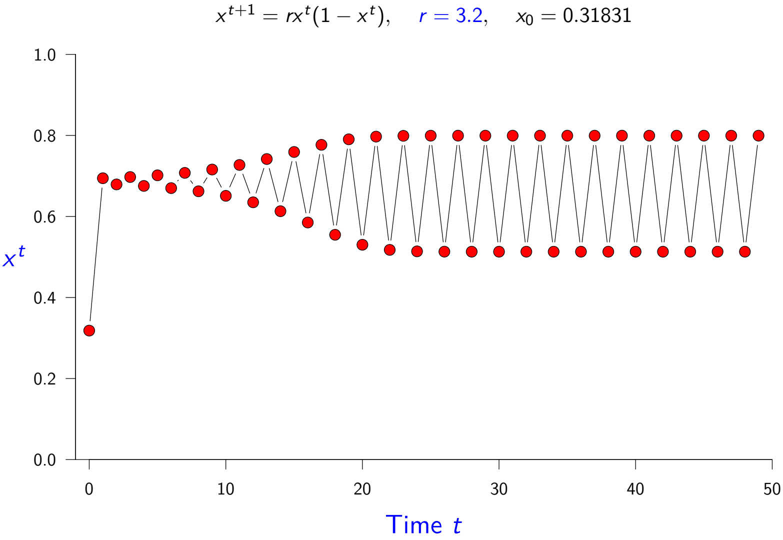


Logistic Map Time Series, $r = 3$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 3, \quad x_0 = 0.31831$$

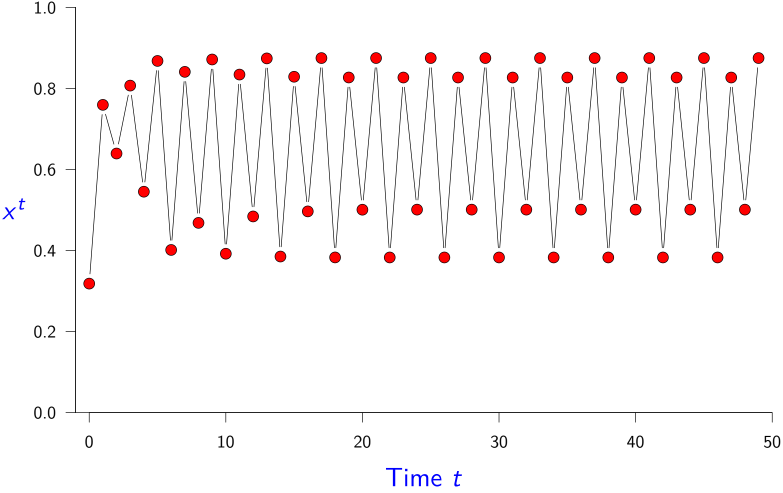


Logistic Map Time Series, $r = 3.2$

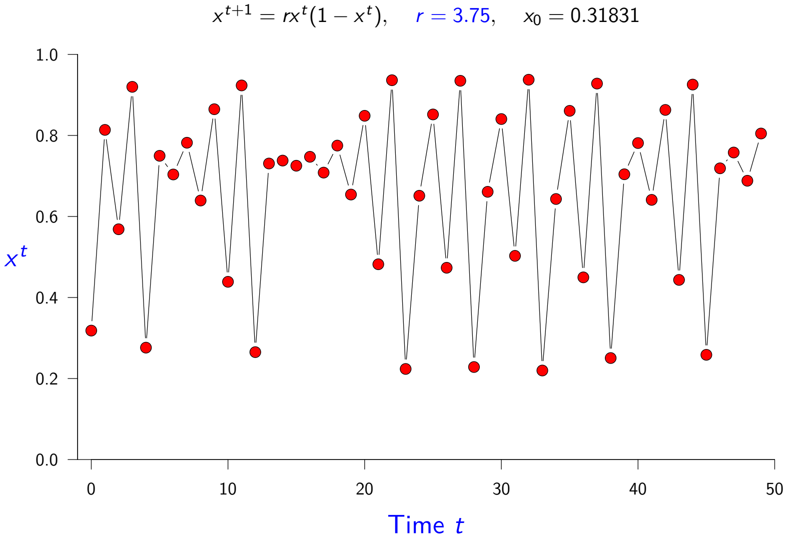


Logistic Map Time Series, $r = 3.5$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 3.5, \quad x_0 = 0.31831$$

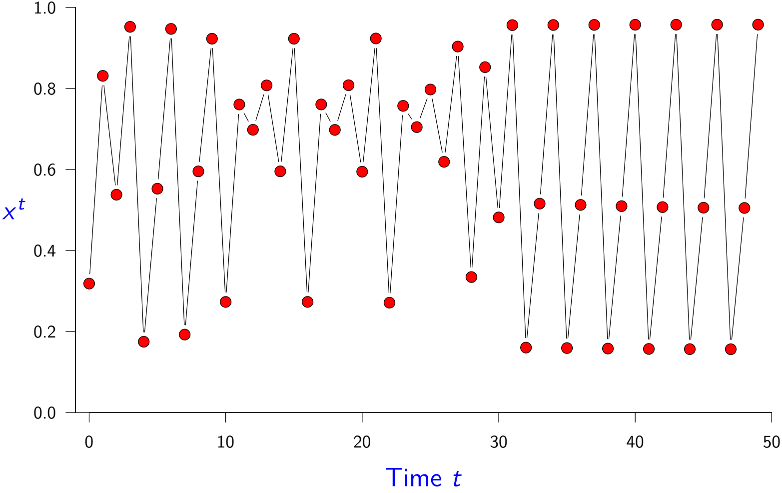


Logistic Map Time Series, $r = 3.75$

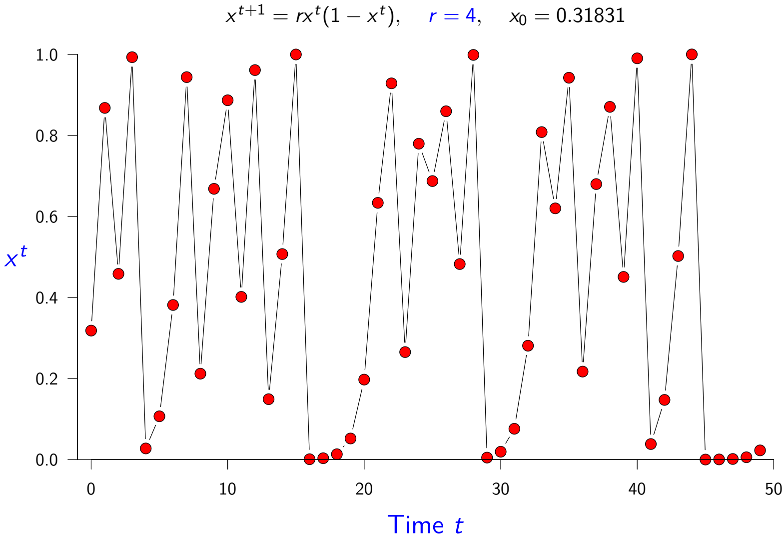


Logistic Map Time Series, $r = 3.83$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 3.83, \quad x_0 = 0.31831$$



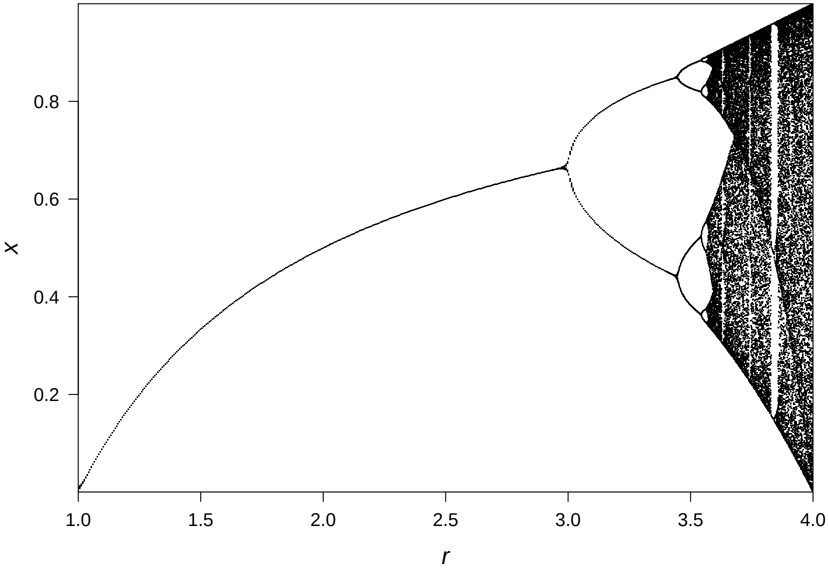
Logistic Map Time Series, $r = 4$



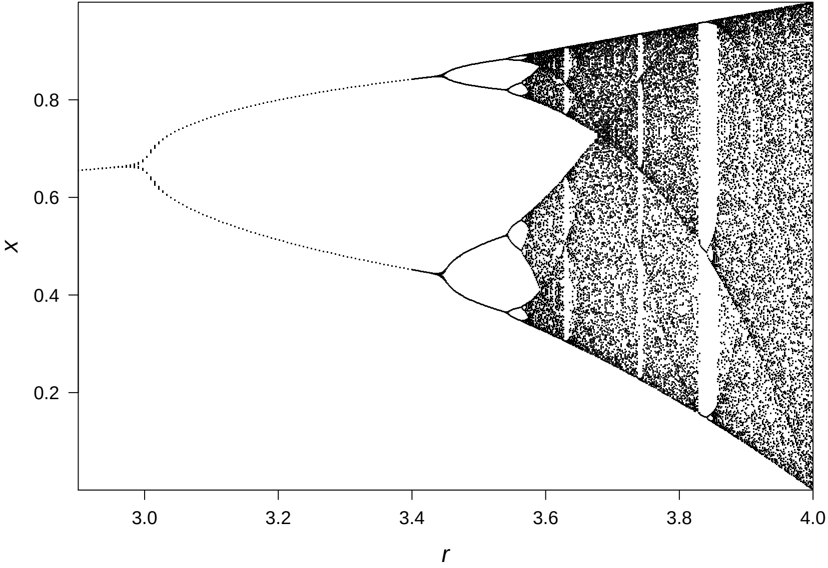
Logistic Map Summary

- Time series show:
  - $r \leq 1 \implies$ Extinction.
  - $1 < r < 3 \implies$ Persistence at equilibrium.
  - $r > 3 \implies$ period doubling cascade to chaos, then appearance of cycles of all possible lengths, and more chaos, ...
- How can we summarize this in a diagram?
  - Bifurcation diagram (wrt r).
  - Ignore transient behaviour: just show attractor.

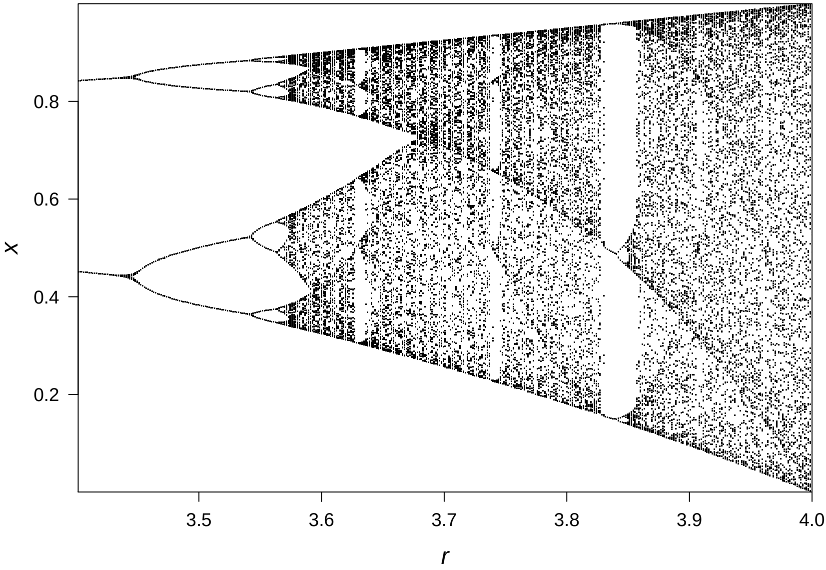
Logistic Map, $F(x) = rx(1 - x)$, $1 \le r \le 4$



Logistic Map, $F(x) = rx(1-x)$, $\quad 2.9 \le r \le 4$



Logistic Map, $F(x) = rx(1 - x)$, $3.4 \leq r \leq 4$



Logistic Map as a Tool to Investigate Synchrony

- Very simple single-patch model: only one state variable.
- Displays all kinds of dynamics from GAS equilibrium, to periodic orbits, to chaos.
  - This was *extremely surprising* to population biologists and mathematicians in the 1970s.

May RM (1976) "Simple mathematical models with very complicated dynamics" *Nature* **261**, 459–467

- Easier to work with logistic map as single patch dynamics than SIR or SEIR model.
- Can still understand how synchrony works conceptually.
- Now we are ready for the ...

... *Mathematics of Synchrony* ...

Mathematics of Synchrony

- System comprised of isolated *patches*
  e.g., cities, labelled $i = 1, \ldots, n$

- *State* of system in patch i specified by $\mathbf{x}_i$
  e.g., $\mathbf{x}_i = (S_i, E_i, I_i, R_i)$

- Connectivity of patches specified by a *dispersal matrix*
  $\mathrm{M} = (m_{ij})$

- System is *coherent* (perfectly synchronous) if the state is the same in all patches
  i.e., $\mathbf{x}_1 = \mathbf{x}_2 = \cdots = \mathbf{x}_n$

Illustrative example: logistic metapopulation

- *Single patch model:* $x^{t+1} = F(x^t)$
- *Reproduction function:* $F(x) = rx(1-x)$
- *Multi-patch model:* $x_i^{t+1} = \sum_{j=1}^{n} m_{ij} F(x_j{}^t)$

$$\text{i.e.,} \quad \begin{pmatrix} x_1^{t+1} \\ \vdots \\ x_n^{t+1} \end{pmatrix} = \begin{pmatrix} m_{11} & \cdots & m_{1n} \\ \vdots & \ddots & \vdots \\ m_{n1} & \cdots & m_{nn} \end{pmatrix} \begin{pmatrix} F(x_1^t) \\ \vdots \\ F(x_n^t) \end{pmatrix}$$

where $\mathrm{M} = (m_{ij})$ is *dispersal matrix*.

- *Colour coding of indices:*
  - row indices are red
  - column indices are cyan

Basic properties of dispersal matrices $M = (m_{ij})$

Discrete-time *metapopulation* model:

$$x_i^{t+1} = \sum_{j=1}^{n} m_{ij} F(x_j^t), \qquad i = 1, 2, \ldots, n.$$

- m_{ij} = *proportion* of population in patch j that disperses to patch i.
- $\therefore\ 0 \le m_{ij} \le 1$ for all i and j (*each m_{ij} is non-negative and at most 1*)
- Total proportion that leaves or stays in patch j: $\sum_{i=1}^{n} m_{ij}$ (*sum of column j*)
- $\therefore\ \sum_{i=1}^{n} m_{ij} \le 1$ (*every column sums to at most 1*)

Could be < 1 if some individuals are lost (die) while dispersing.

Basic properties of dispersal matrices $M = (m_{ij})$

Discrete-time *metapopulation* model:

$$x_i^{t+1} = \sum_{j=1}^{n} m_{ij} F(x_j^t), \qquad i = 1, 2, \ldots, n.$$

Definition (No loss dispersal matrix)

An $n \times n$ matrix $M = (m_{ij})$ is said to be a ***no loss dispersal matrix*** if all its entries are non-negative ($m_{ij} \geq 0$ for all i and j) and its column sums are all 1, *i.e.*,

$$\sum_{i=1}^{n} m_{ij} = 1\,, \qquad \text{for each } j = 1, \ldots, n.$$

- The dispersal process is "conservative" in this case.
- A no loss dispersal matrix is also said to be "column stochastic".

Notation for coherent states

Discrete-time *metapopulation* model:

$$x_i^{t+1} = \sum_{j=1}^{n} m_{ij} F(x_j^t), \qquad i = 1, 2, \ldots, n.$$

- State at time t is $\mathbf{x}^t = (x_1^t, \ldots, x_n^t) \in \mathbb{R}^n$.
- If state $\mathbf{x}$ is *coherent*, then for some $x \in \mathbb{R}$ we have

$$\begin{aligned} \mathbf{x} &= (x_1, x_2, \ldots, x_n) \\ &= (x, x, \ldots, x) = x(1, 1, \ldots, 1) \end{aligned}$$

- For convenience, define

$$\boldsymbol{e} = (1, 1, \ldots, 1) \in \mathbb{R}^n$$

so any coherent state can be written $x\boldsymbol{e}$, for some $x \in \mathbb{R}$.

Constraint on row sums of dispersal matrix M

Lemma (Row sums are the same)

If all initially coherent states remain coherent then the row sums of the dispersal matrix are all the same.

Proof.

Suppose initially coherent states remain coherent, *i.e.*,
$\mathbf{x}^t = a\boldsymbol{e} \implies \mathbf{x}^{t+1} = b\boldsymbol{e}$ for some $b \in \mathbb{R}$.
Choose a such that $F(a) \neq 0$. Then

$$x_i^{t+1} = b = \sum_{j=1}^{n} m_{ij} F(x_j^t) = \sum_{j=1}^{n} m_{ij} F(a) = F(a) \sum_{j=1}^{n} m_{ij}$$

$$\implies \sum_{j=1}^{n} m_{ij} = \frac{b}{F(a)} \qquad \text{(independent of } i\text{)}$$

□

Constraint on row sums of dispersal matrix M

Lemma (Row sums are all 1)

If every solution $\{x^t\}$ of the single patch map $F(x)$ yields a coherent solution $\{x^t e\}$ of the full map then the row sums of the dispersal matrix are all 1.

Proof.

Suppose $\mathbf{x}^t = ae \implies \mathbf{x}^{t+1} = F(a)e$ and $F(a) \neq 0$. Then

$$x_i^{t+1} = F(a) = \sum_{j=1}^{n} m_{ij} F(x_j^t) = \sum_{j=1}^{n} m_{ij} F(a) = F(a) \sum_{j=1}^{n} m_{ij}$$

$$\implies \sum_{j=1}^{n} m_{ij} = 1 \qquad \text{(independent of } i\text{)}$$

□

Project

You should be thinking about your **Project**. . .

- Remember your group must give an oral presentation of your project as well (in the last class).
- Classes after the midterm are NOT optional. Your group is expected to meet in class and take advantage of the instructor's presence to solve issues with your project.
- Project Notebook template is posted on project page.
- Movie night?

Midterm Test

Student Name: ____________________ Student Number: _______________

MATHEMATICS 4MB3/6MB3

Midterm Test, Monday 11 March 2019

Special Instructions and Notes:

(i) This test has **12** pages. Verify that your copy is complete. Note that the final two pages are blank to provide additional space if needed.

(ii) Clearly write your name and student number at the top of each page.

(iii) **Answer all questions in the space provided.**

(iv) It is possible to obtain a total of 50 marks. There are 10 multiple choice questions (2 marks each) and 10 short answer questions (total of 30 marks).

(v) **For multiple choice questions, circle only one answer.**

(vi) No calculators, notes, or aids of any kind are permitted.

(vii) PHAC refers to the Public Health Agency of Canada.

GOOD LUCK

Midterm Test

- The test will cover everything from lectures and assignments/solutions up to and including today.
- Material connected with time series analysis and synchrony/coherence will occur only in multiple choice questions.
- You are assumed to be comfortable with:
  - Elementary algebra, including finding the eigenvalues of 2×2 matrices.
  - Stability analyses of differential equations.
  - Finding $\mathcal{R}_0$ by biological and mathematical [$\rho(FV^{-1})$] methods.
  - Converting flow charts or verbal descriptions into compartmental ODE models.
- You will be presented with scenarios including graphs, and asked to write explanations that would be understandable by people at PHAC.

Let's review what we've done so far on spatial models. . .

- Logistic metapopulation model
- Notion of coherence
- No-loss dispersal matrix M: column sums are all 1
- To retain homogeneous solutions: row sums are all 1

Simple examples of no loss dispersal matrices

- *Equal coupling:* a proportion m from each patch disperses uniformly among the other $n-1$ patches:

$$m_{ij} = \begin{cases} 1-m & i=j \\ m/(n-1) & i \neq j \end{cases}$$

- *Nearest-neighbour coupling:* a proportion m go to the two nearest patches:

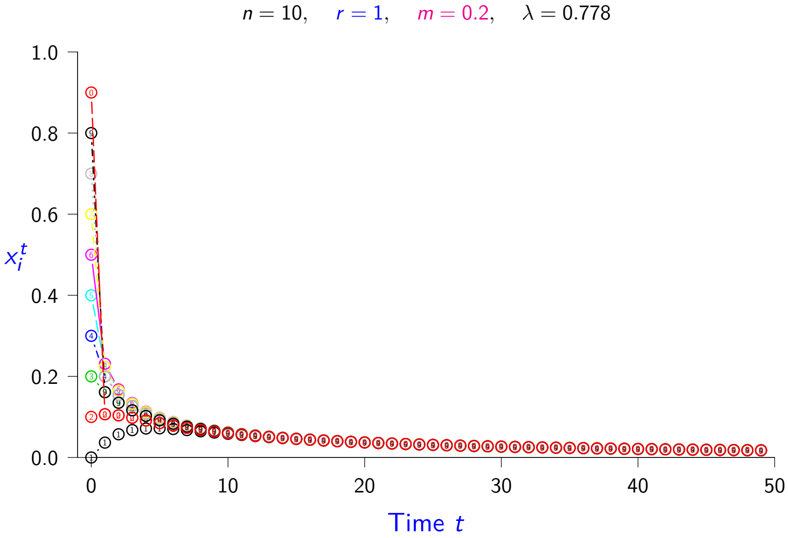
$$m_{ij} = \begin{cases} 1-m & i=j \\ m/2 & i=j-1 \text{ or } j+1 \pmod{n} \\ 0 & \text{otherwise} \end{cases}$$

- Real dispersal patterns generally between these two extremes

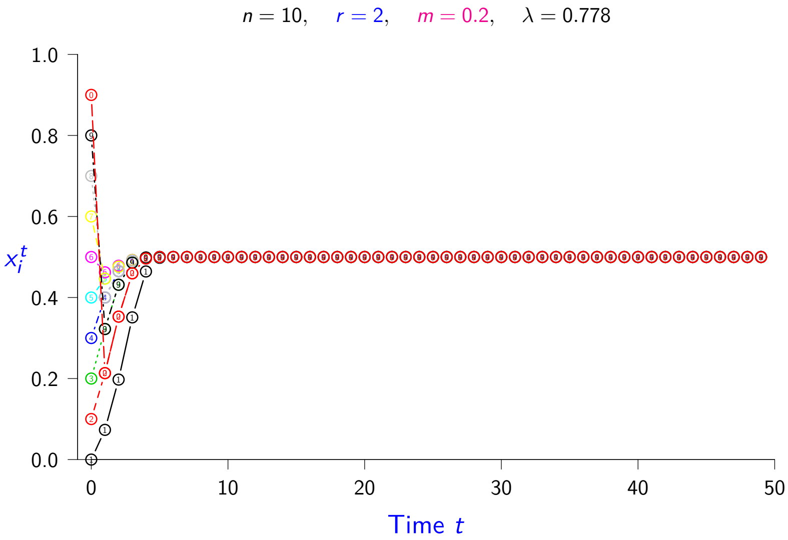
Key Question

- Can we find conditions on the dispersal matrix M, and/or the single patch reproduction function F, that guarantee (or preclude) coherence asymptotically (as $t \to \infty$)?
  - If so, then this sort of analysis should help to identify synchronizing vaccination strategies.

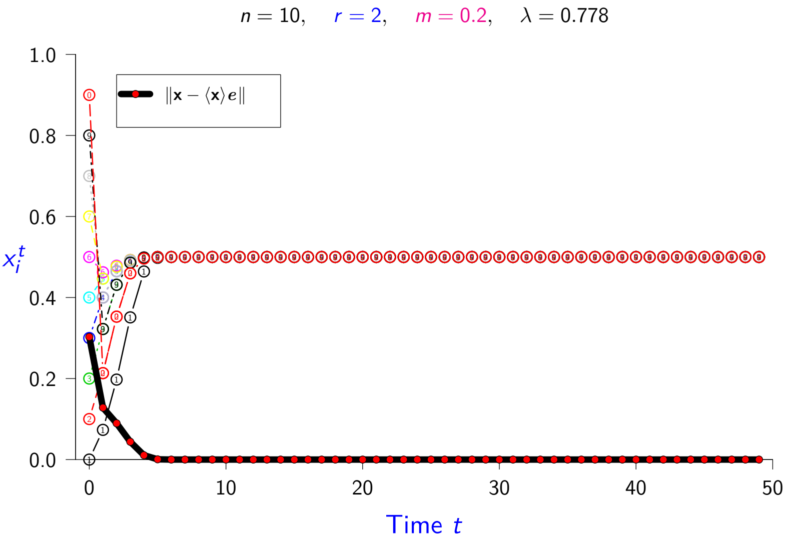
Logistic Metapopulation Simulation ($r = 1$, $m = 0.2$)



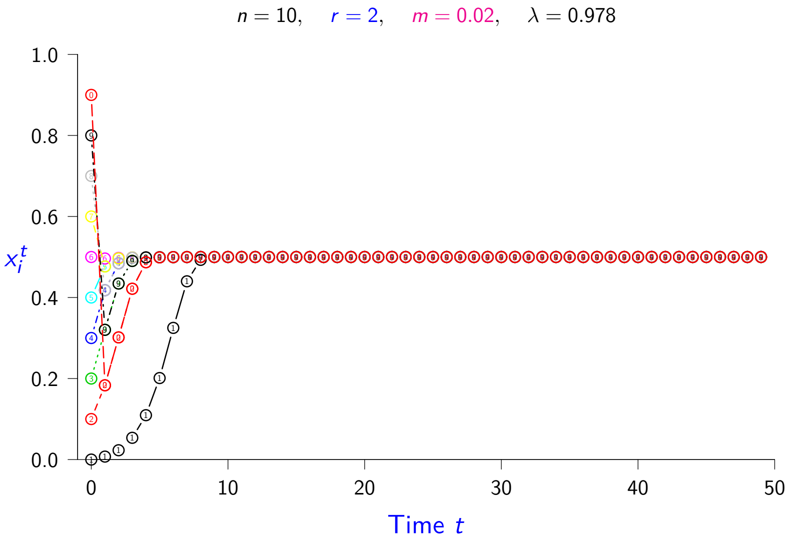
Logistic Metapopulation Simulation ($r = 2$, $m = 0.2$)



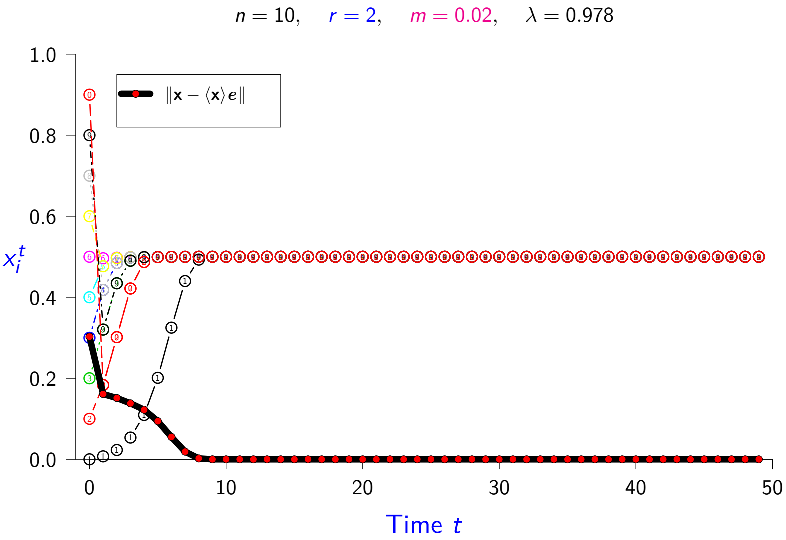
Logistic Metapopulation Simulation ($r = 2,\ m = 0.2$)



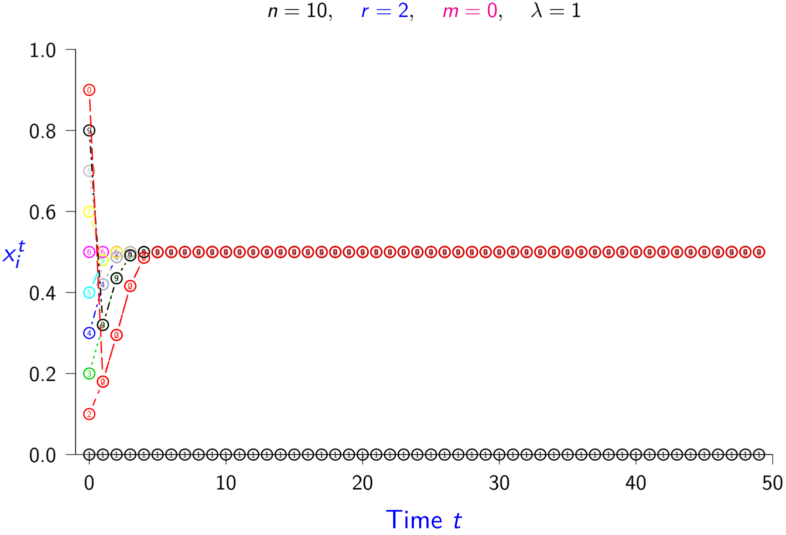
Logistic Metapopulation Simulation ($r = 2,\ m = 0.02$)



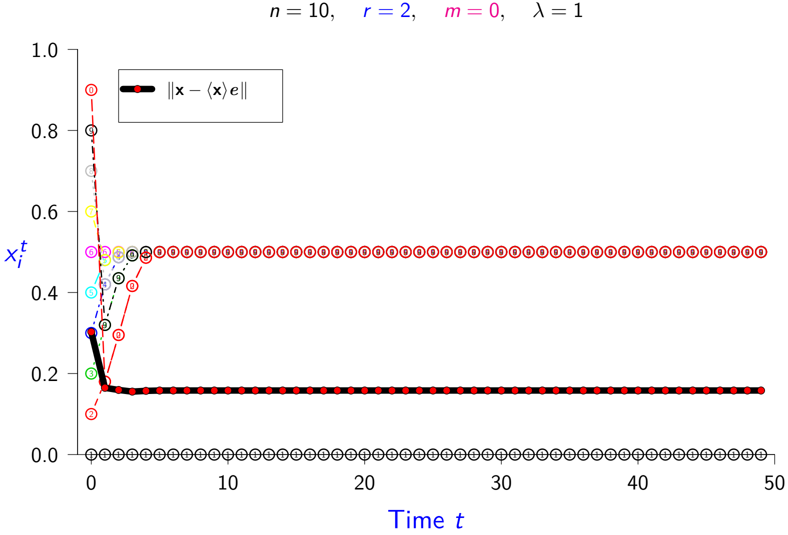
Logistic Metapopulation Simulation ($r = 2,\ m = 0.02$)



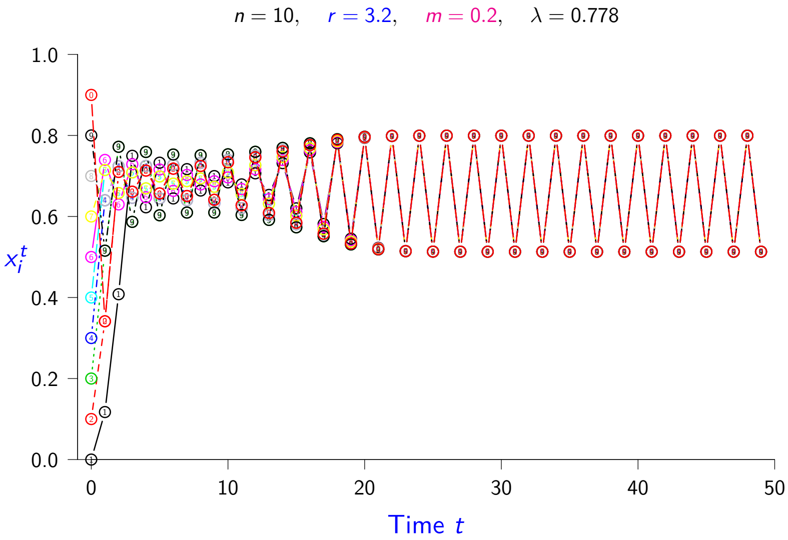
Logistic Metapopulation Simulation ($r = 2$, $m = 0$)



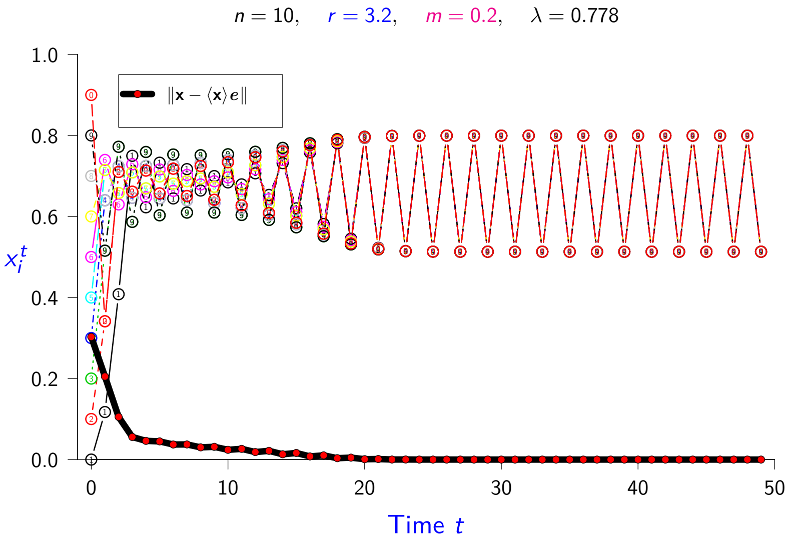
Logistic Metapopulation Simulation ($r = 2$, $m = 0$)



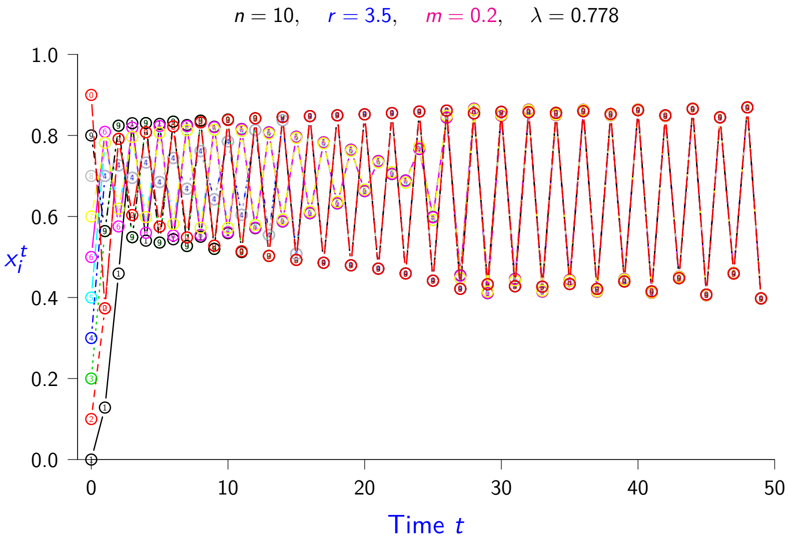
Logistic Metapopulation Simulation ($r = 3.2$, $m = 0.2$)



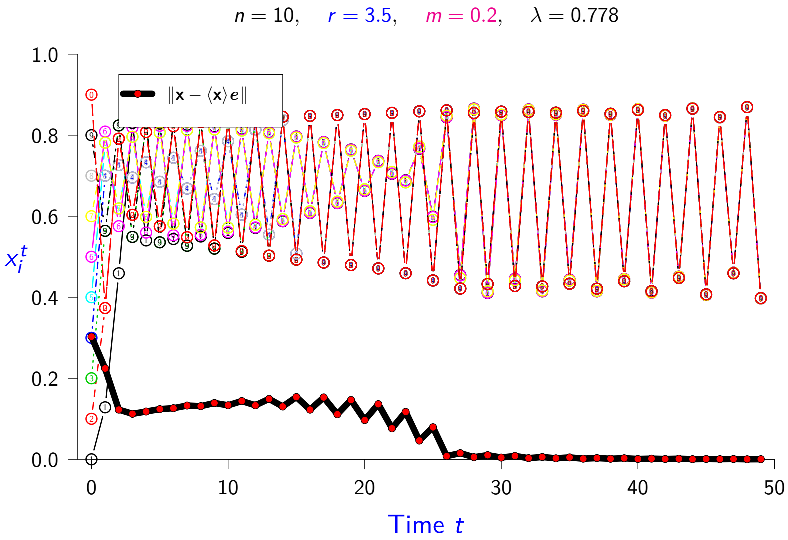
Logistic Metapopulation Simulation ($r = 3.2,\ m = 0.2$)



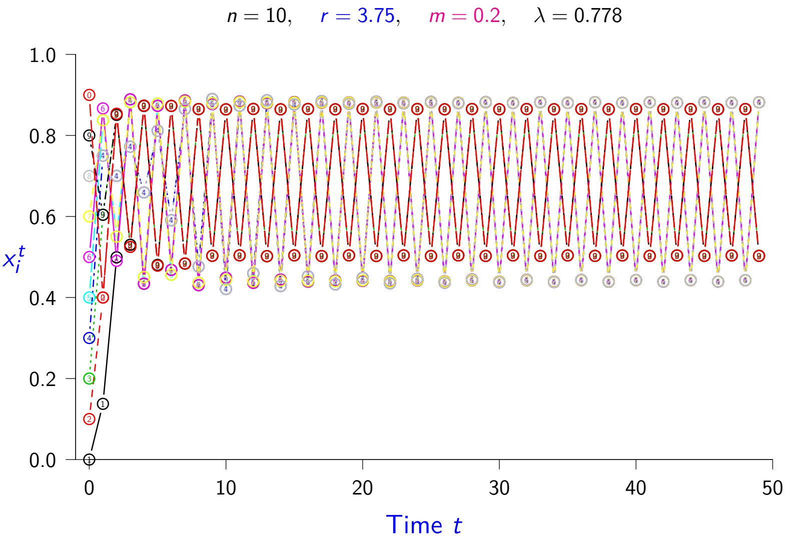
Logistic Metapopulation Simulation ($r = 3.5$, $m = 0.2$)



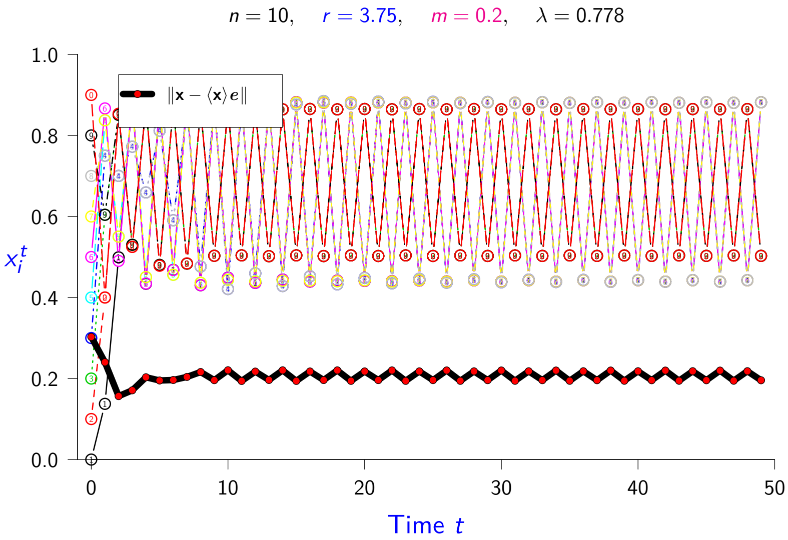
Logistic Metapopulation Simulation ($r = 3.5,\ m = 0.2$)



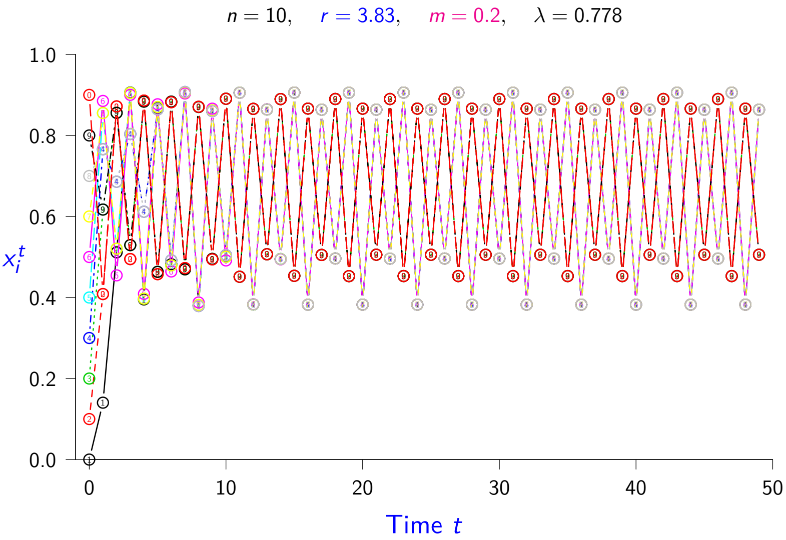
Logistic Metapopulation Simulation ($r = 3.75$, $m = 0.2$)



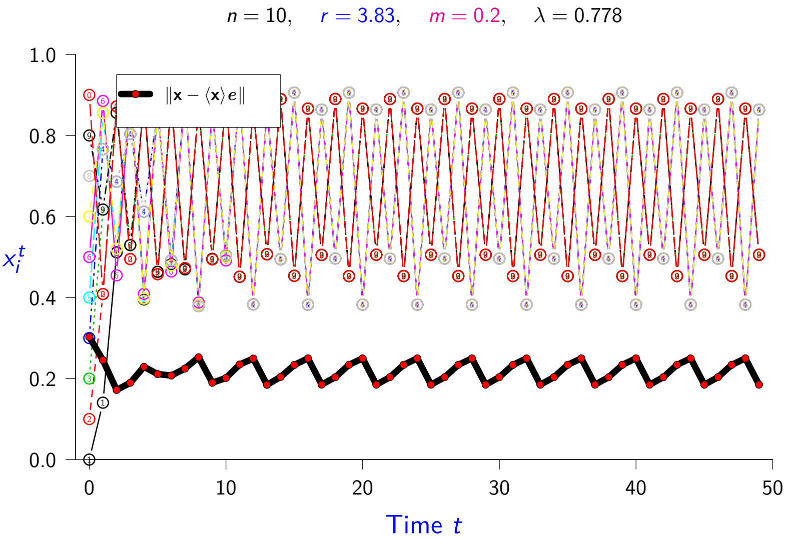
Logistic Metapopulation Simulation ($r = 3.75$, $m = 0.2$)



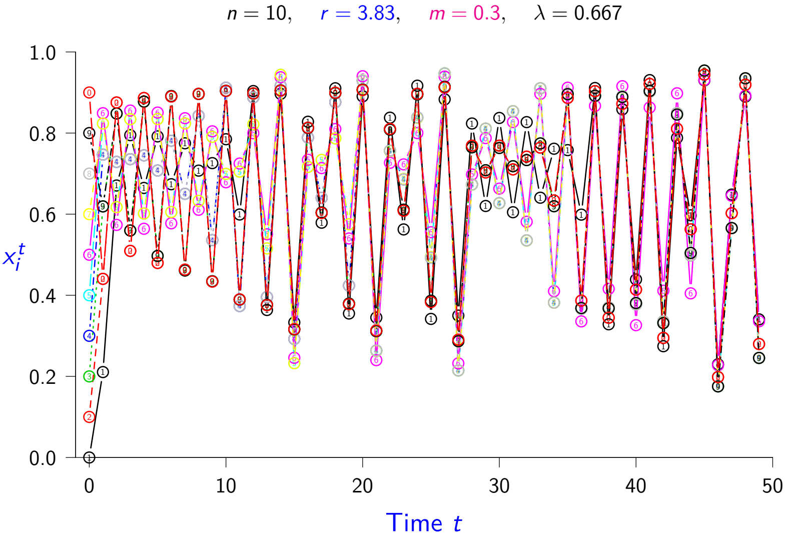
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.2$)



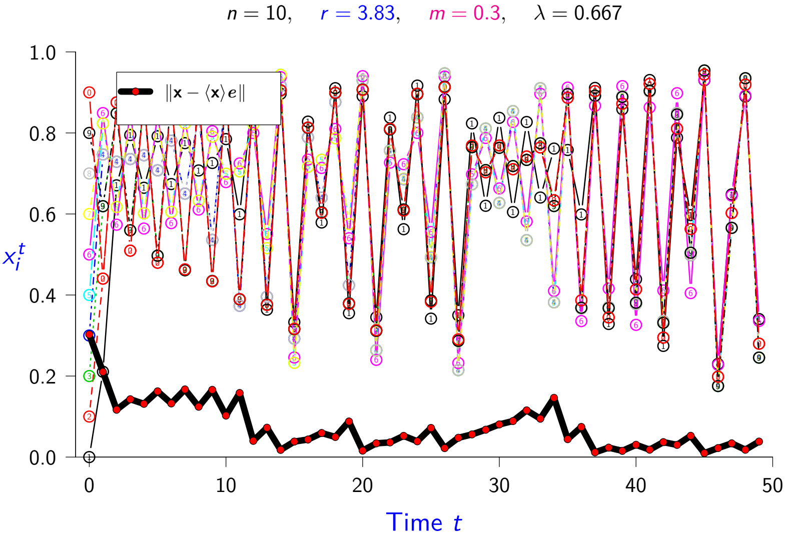
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.2$)



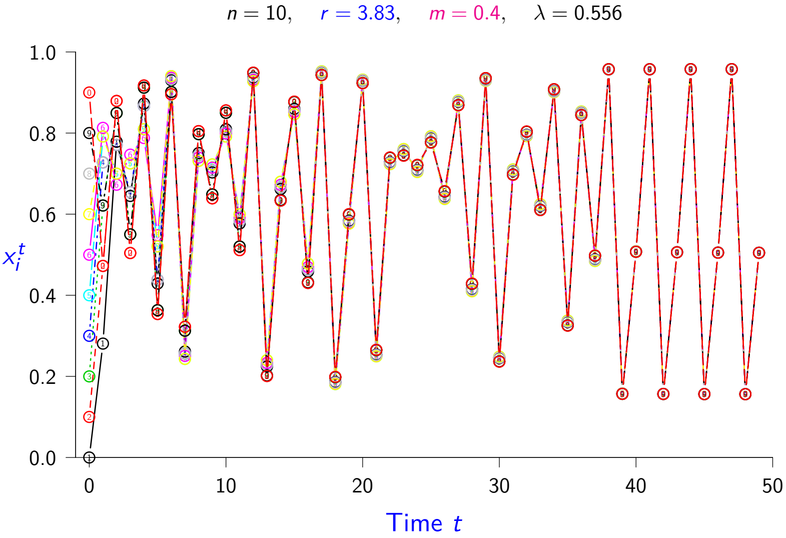
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.3$)



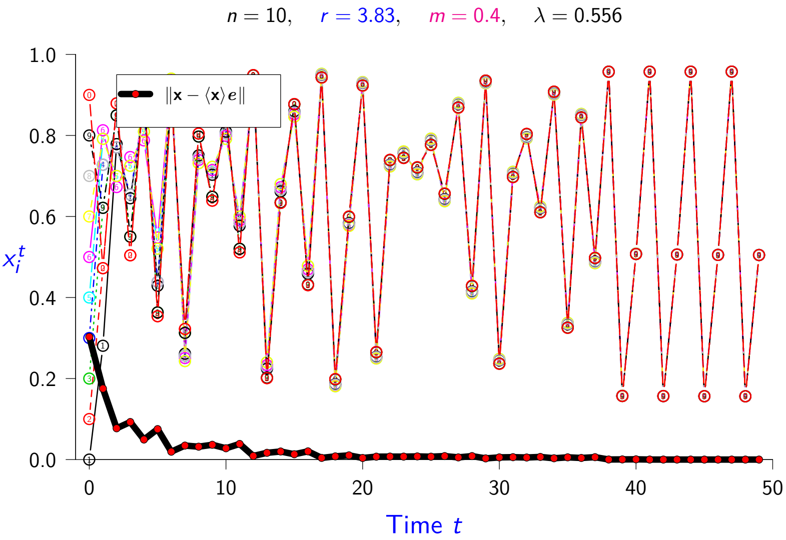
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.3$)



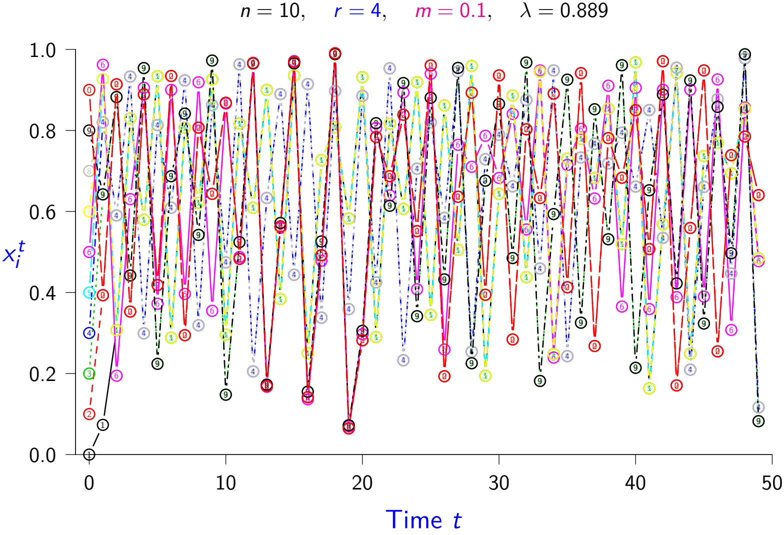
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.4$)



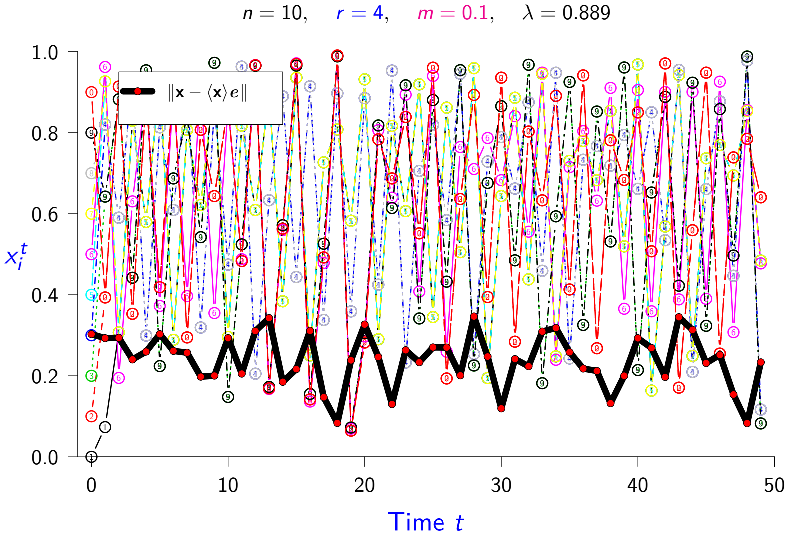
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.4$)



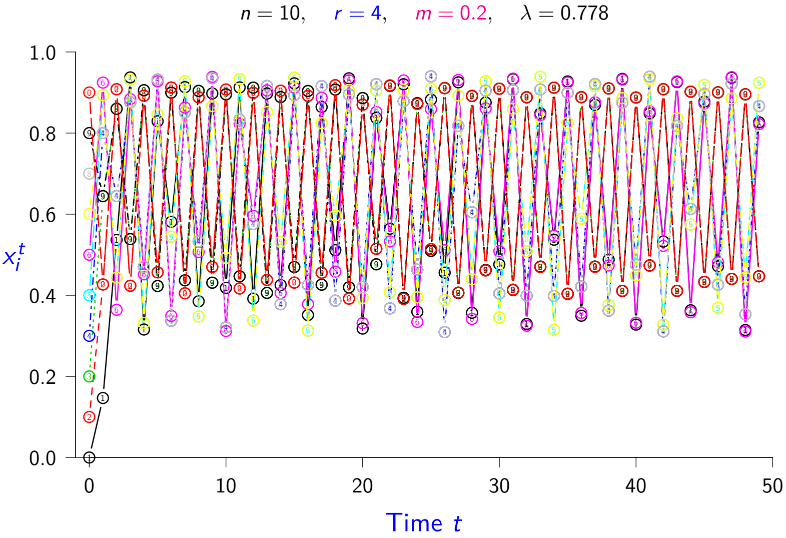
Logistic Metapopulation Simulation ($r = 4$, $m = 0.1$)



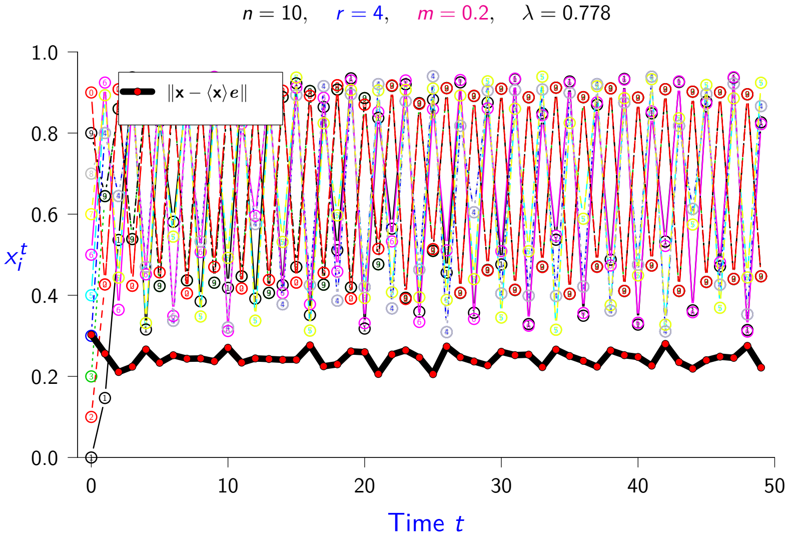
Logistic Metapopulation Simulation ($r = 4$, $m = 0.1$)



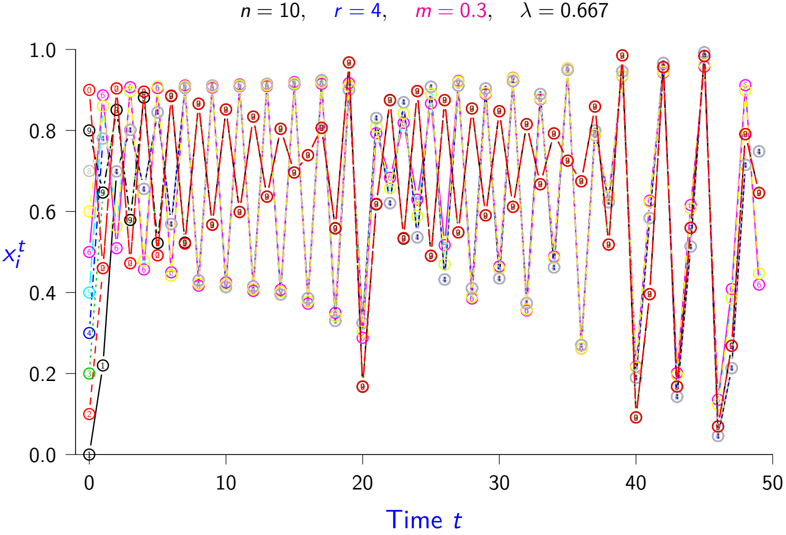
Logistic Metapopulation Simulation ($r = 4$, $m = 0.2$)



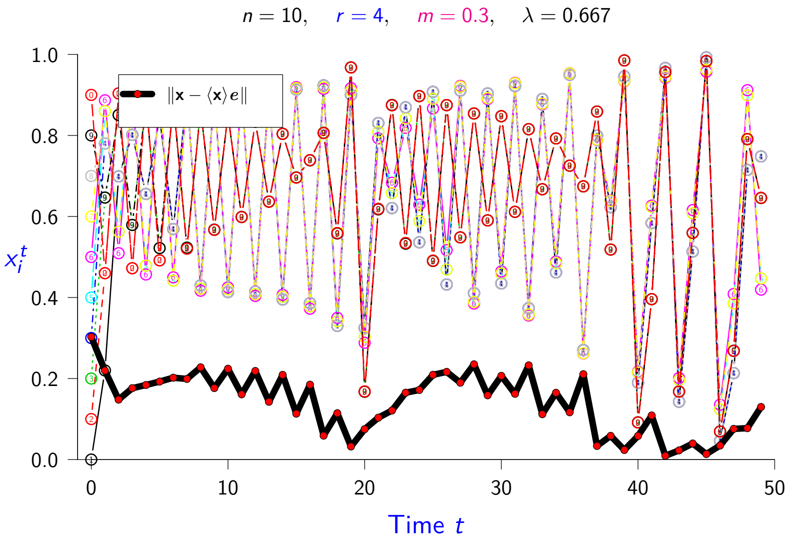
Logistic Metapopulation Simulation ($r = 4$, $m = 0.2$)



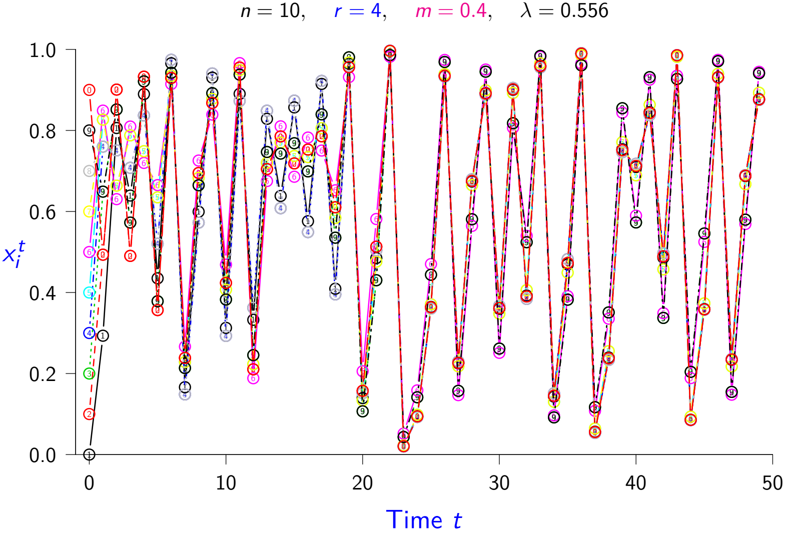
Logistic Metapopulation Simulation ($r = 4$, $m = 0.3$)



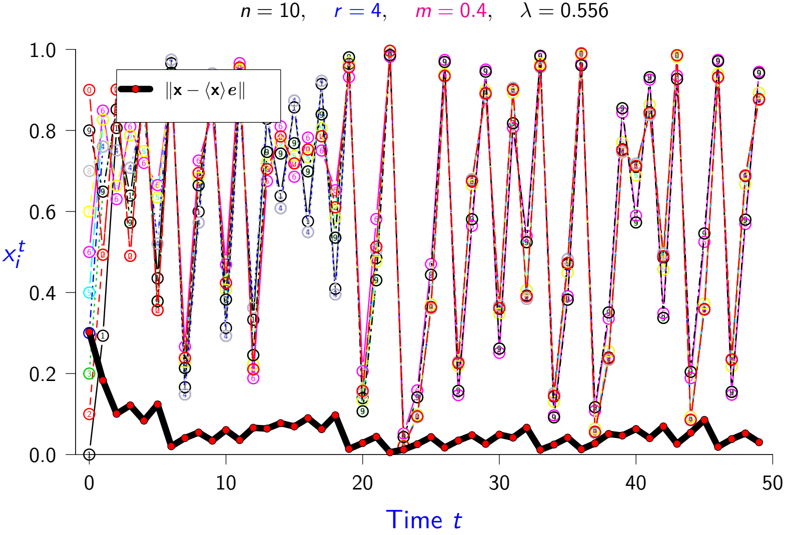
Logistic Metapopulation Simulation ($r = 4$, $m = 0.3$)



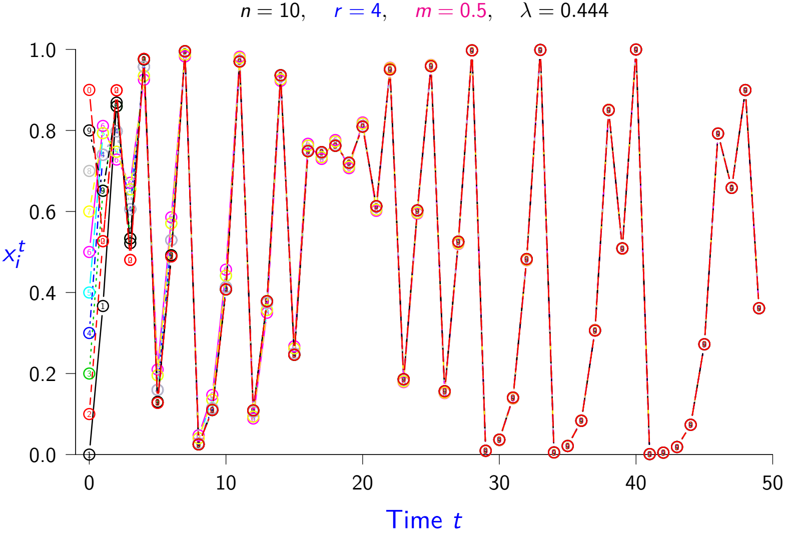
Logistic Metapopulation Simulation ($r = 4$, $m = 0.4$)



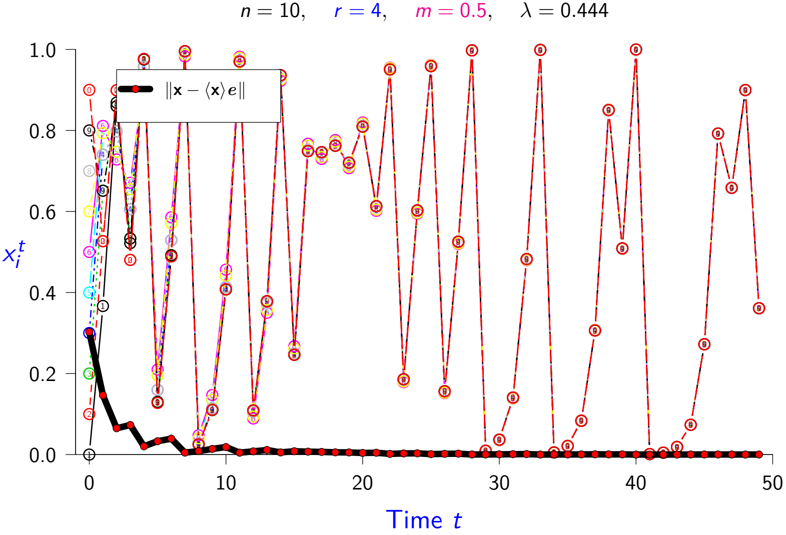
Logistic Metapopulation Simulation ($r = 4$, $m = 0.4$)



Logistic Metapopulation Simulation ($r = 4$, $m = 0.5$)



Logistic Metapopulation Simulation ($r = 4$, $m = 0.5$)



Metapopulation dynamics: what we've seen so far

- Examples of connectivity matrices
  - equal coupling
  - nearest-neighbour coupling on a ring
- Logistic Metapopulation Simulations (10 patches)

- $r = 1,\ m = 0.2$
- $r = 2,\ m = 0.2$
- $r = 2,\ m = 0.02$
- $r = 2,\ m = 0$
- $r = 3.2,\ m = 0.2$
- $r = 3.5,\ m = 0.2$
- $r = 3.75,\ m = 0.2$
- $r = 3.83,\ m = 0.2$
- $r = 3.83,\ m = 0.3$
- $r = 3.83,\ m = 0.4$
- $r = 4,\ m = 0.1$
- $r = 4,\ m = 0.2$
- $r = 4,\ m = 0.3$
- $r = 4,\ m = 0.4$
- $r = 4,\ m = 0.5$

Quantities that affect coherence

Degree of spatial coupling:

- Determined by dispersal matrix $M = (m_{ij})$.
- Do we need to worry about about all matrix entries? n^2 parameters?
- Are eigenvalues enough?
- Dominant eigenvalue is always 1. Why?
  - Next slide...
- Coherence is affected by magnitude $|\lambda|$ of *subdominant eigenvalue* λ.

Dominant eigenvalue of dispersal matrix M is always 1

Definition (Positive vector)

A vector is ***positive*** if each of its components is positive.

Definition (Dominant eignvalue)

λ is a ***dominant eigenvalue*** of a matrix A if no other eigenvalue of A has larger magnitude.

Theorem

Let A be a nonnegative matrix. If A has a positive eigenvector then the corresponding eigenvalue λ is nonnegative and dominant, i.e., $\rho(A) = \lambda$.

Proof.

See Horn & Johnson (2013) *Matrix Analysis*, Corollary 8.1.30, p. 522. □

Dominant eigenvalue of dispersal matrix M is always 1

Corollary

Consider a discrete-time metapopulation map,

$$x_i^{t+1} = \sum_{j=1}^{n} m_{ij} F(x_j^t), \quad i = 1, \ldots, n. \qquad (\heartsuit)$$

If solutions of the single patch system, $x^{t+1} = F(x^t)$, yield coherent solutions of ($\heartsuit$) then 1 is a dominant eigenvalue of M*.*

Proof.

We found earlier that if solutions of the single patch map yield coherent solutions of ($\heartsuit$) then $\sum_{j=1}^{n} m_{ij} = 1$ for all i.

This is equivalent to the statement that $\mathrm{M}\boldsymbol{e} = \boldsymbol{e}$, *i.e.*, 1 is an eigenvalue of M with eigenvector $\boldsymbol{e}$.

But $\boldsymbol{e}$ is a positive vector, hence by the lemma on the previous slide, 1 is a dominant eigenvalue of M. □

Quantities that affect coherence

Maximum "reproductive rate":

- Maximum fecundity = maximum reproduction per individual per time step.
- For (single patch) logistic map, $F(x) = rx(1-x)$, maximum fecundity is r. *Note:* $r = \max_x \big(F'(x)\big)$.
- Maximum fecundity for any one-dimensional single species map F is $r = \max_x \big(F'(x)\big)$.
- More generally, single patch map can be multi-dimensional: could represent multiple species (*e.g.*, predator, prey, ...) and/or multiple states per species (*e.g.*, S, E, I, R).
- We can think of $r = \max_{\mathbf{x}} \|D_{\mathbf{x}}F\|$ as the maximum "reproductive rate" for a multi-dimensional single-patch map.
- r is relevant to coherence.

Quantities that affect coherence

Average "reproductive rate":

- Mean "reproductive rate" over T time steps is $\frac{1}{T}\sum_{t=0}^{T-1}\|D_{\mathbf{x}_t}F\|$.

- Geometric mean turns out to be more important:

$$\left[\prod_{t=0}^{T-1}\|D_{\mathbf{x}_t}F\|\right]^{1/T} = \left[\,\|D_{\mathbf{x}_0}F\|\,\|D_{\mathbf{x}_1}F\|\cdots\|D_{\mathbf{x}_{T-1}}F\|\,\right]^{1/T}$$

$$= \left[\,\|D_{\mathbf{x}_0}F\cdot D_{\mathbf{x}_1}F\cdots D_{\mathbf{x}_{T-1}}F\|\,\right]^{1/T}$$

$$= \left[\left\|D_{\mathbf{x}_0}F^T\right\|\right]^{1/T}$$

$$\therefore \log\left[\prod_{t=0}^{T-1}\|D_{\mathbf{x}_t}F\|\right]^{1/T} = \frac{1}{T}\log\left\|D_{\mathbf{x}_0}F^T\right\|$$

Quantities that affect coherence

Average "reproductive rate":

- We actually want the average over the entire trajectory, so we would like to consider

$$\lim_{T\to\infty} \frac{1}{T} \log \left\| D_{\mathbf{x}_0} F^T \right\| = \lim_{T\to\infty} \frac{1}{T} \log \left\| \prod_{t=0}^{T-1} D_{\mathbf{x}_t} F \right\|$$

$$= \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log \| D_{\mathbf{x}_t} F \| \ .$$

- But this limit may not exist! So consider

$$\chi_{\mathbf{x}_0} = \limsup_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log \| D_{\mathbf{x}_t} F \| \ .$$

which always exists if $\| D_{\mathbf{x}} F \|$ is bounded
(true for us because we assume $r = \max_{\mathbf{x}} \| D_{\mathbf{x}} F \|$ exists).

Quantities that affect coherence: Summary

- *Degree of spatial coupling:*
  Magnitude $|\lambda|$ of *subdominant eigenvalue* λ of dispersal matrix M
- *Maximum "reproductive rate":*

$$r = \max_{\mathbf{x}} \|D_{\mathbf{x}} F\|$$

- *Average "reproductive rate":*

$$\chi_{\mathbf{x}_0} = \limsup_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log \|D_{\mathbf{x}_t} F\| \ .$$

This is called the maximum (Lyapunov) *characteristic exponent* of the single patch map.

Criteria for asymptotic coherence

- *Coherence inevitable:*
  Global asymptotic coherence: system will eventually synchronize regardless of initial conditions:

$$r|\lambda| < 1$$

- *Coherence possible:*
  Local asymptotic coherence: system will synchronize if sufficiently close to a coherent attractor:

$$e^{\chi}|\lambda| < 1 \qquad \textit{i.e.},\ \chi + \log|\lambda| < 0$$

  Note: χ is the same for "almost all" initial states $\mathbf{x}$ (non-trivial to prove)

- *Coherence impossible:*

$$\chi + \log|\lambda| > 0$$

Earn, Levin & Rohani (2000) *Science* **290**, 1360–1364

Mathematics and Statistics

$$\int_M d\omega = \int_{\partial M} \omega$$

Mathematics 4MB3/6MB3 Mathematical Biology

Instructor: David Earn

Lecture 9
Space II
Monday 11 November 2019

Fall 2019
Course Evaluations

Open: Thursday November 21, 10:00AM

Close: Thursday December 5, 11:59PM

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Coherence: what we've seen so far

- Quantities that affect coherence
- Coherence criteria

Global asymptotic coherence (GAC) for equal coupling

Theorem: $r|\lambda| < 1 \implies$ GAC.

Proof in case of equal coupling:

Dispersal matrix:

$$m_{ij} = \begin{cases} 1 - m & i = j \\ m/(n-1) & i \neq j \end{cases}$$

Subdominant eigenvalue:

$$\lambda = 1 - \left(\frac{n}{n-1}\right) m$$

General map:

$$x_i' = \sum_{j=1}^{n} m_{ij} F(x_j)$$

Equal coupling case in terms of λ:

$$= \lambda F(x_i) + (1-\lambda) \langle F(x_j) \rangle$$

Global asymptotic coherence (GAC) for equal coupling

Difference in density between any two patches at next iteration:

$$x_i' - x_k' = \lambda[F(x_i) - F(x_k)]$$

$$= \lambda F'(\xi)(x_i - x_k) \qquad \text{(Mean Value Theorem)}$$

Hence $|x_i' - x_k'| \leq r|\lambda||x_i - x_k|$ *because* $r = \max_x |F'(x)|$.

Therefore, $r|\lambda| < 1$ *implies* $|x_i - x_k| \to 0$.

Q.E.D.

Note: Actually true for very general connectivity matrices M and multi-dimensional single-patch dynamics $F(\mathbf{x})$.

Earn & Levin (2006) *PNAS* **103**, 3968-3971

Theory of local asymptotic coherence (LAC)

- Requires measure theory (*e.g.*, Math 4A03), which allows us to make precise statements like "χ is the same for almost all initial states".
- More significant theoretically than practically, because it yields only *possibility* rather than *probability* of coherence.
- Quasi-global theory attempts to bridge the gap between "probability $= 1$" and "probability > 0".

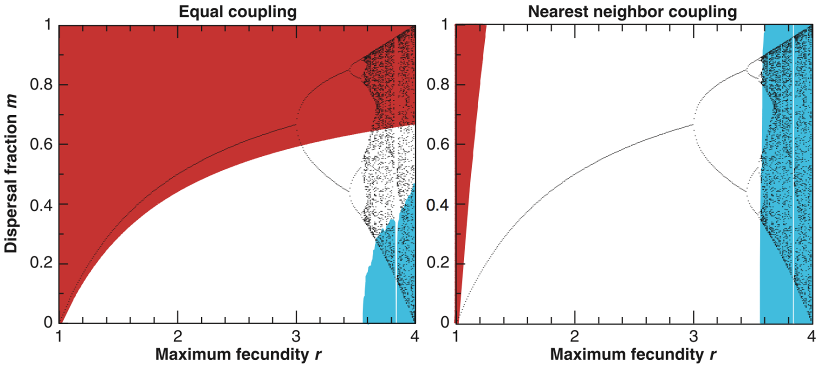
McCluskey & Earn (2011) *J. Math. Biol.* **62**, 509–541

Application of simple coherence criteria

10 patch logistic metapopulation

$r|\lambda| < 1$ (coherence inevitable)

$e^{\chi}|\lambda| > 1$ (coherence impossible)



Earn, Levin & Rohani (2000) *Science* **290**, 1360–1364

Comments on coherence theory

Global theory is limited in applicability:

- Nice theorem guarantees global asymptotic coherence (GAC)

  Earn & Levin (2006) *PNAS* **103**, 3968-3971
- But hypotheses quite restrictive

Local theory is limited in practical power:

- Applies very generally and aids understanding
- But coherence *possible* doesn't tell how *probable*

Quasi-global theory promising:

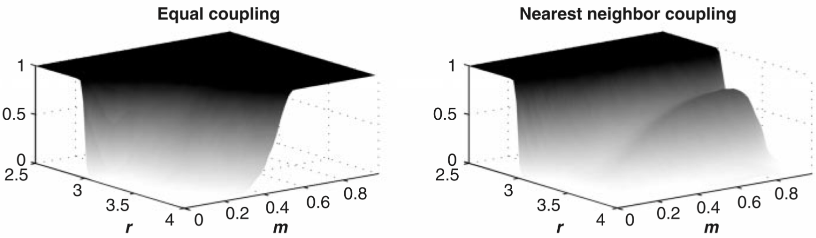
- Show asymptotic approach to coherent manifold from anywhere nearby (rather than just near attractor)
- Via Lozinskii measures

  McCluskey & Earn (2011) *J. Math. Biol.* **62**, 509–541

Coherence in "numerical experiments" (simulations)

10 patch logistic metapopulation

- Systematically explore representative set of initial conditions and determine probability of coherence within some tolerance, within some specified time
  - *e.g.*, coherence to within 10% within 10 iterations



Earn, Levin & Rohani (2000) *Science* **290**, 1360–1364

- *Extremely demanding computationally. . .*

Connecting coherence to extinction

- Strictly deterministic simulations reveal conditions (model parameter regions) that tend to lead to coherence.
- Coherence $\neq$ extinction, but intuitively predict:

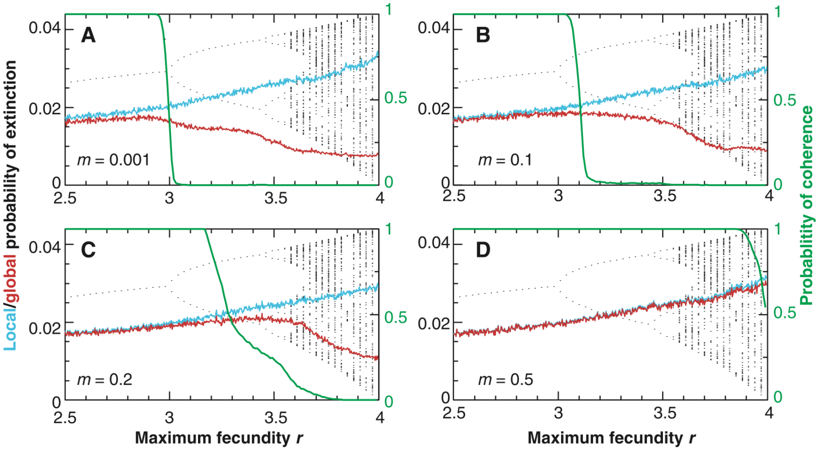
  higher probability of coherence $\Longrightarrow$

  - higher probability of global extinction
  - smaller difference between probabilities of local and global extinction

- Test these predictions by adding *global noise* (randomly occurring events that affect all patches equally) to the deterministic simulations.
- Global noise models *environmental stochasticity* (*e.g.*, weather), which presents a large risk of global extinction because the noise is correlated across all patches.

Effects of global events that affect all patches equally

10 patch logistic metapopulation subject to "global noise"



Earn, Levin & Rohani (2000) *Science* **290**, 1360–1364

Comments on coherence “experiments”

10 patch logistic metapopulation

- Relationship between model parameters (r, m) and probability of coherence is complicated.
- Predicted relationship between probabilities of coherence and extinction verified.
- Experiments we’ve discussed ignore *demographic stochasticity*:
  - number of individuals in a population is always an integer.
  - number of offspring an individual produces is a stochastic process.
- Better model would use a stochastic demographic process rather than a deterministic map based on population densities.
- Population models like logistic metapopulation are most relevant to situations where we want to prevent extinctions (conservation of endangered species).

Relationship to conservation

- For species that we want to conserve, *synchrony is bad!*
- Synchrony prevents *rescue effects*
- Coherence criteria yield method for estimating *risk of synchronization* in ecological systems

Earn, Levin & Rohani (2000) "Coherence and Conservation" *Science* **290**, 1360–1364

Current Coherence Research

Mathematical challenges

- Strengthen theorems
- Work out details of illustrative examples

Biological goals

- Why do measles and whooping cough have opposite patterns of synchrony?
- What kinds of vaccination strategies can synchronize epidemics worldwide?
- Are such strategies practical to implement?
- Example: global pulse vaccination

Global pulse vaccination

Basic idea

- International vaccination day each year (or in alternate years, *etc.*)
- Probably combined with continuous vaccination in countries that already have almost complete coverage

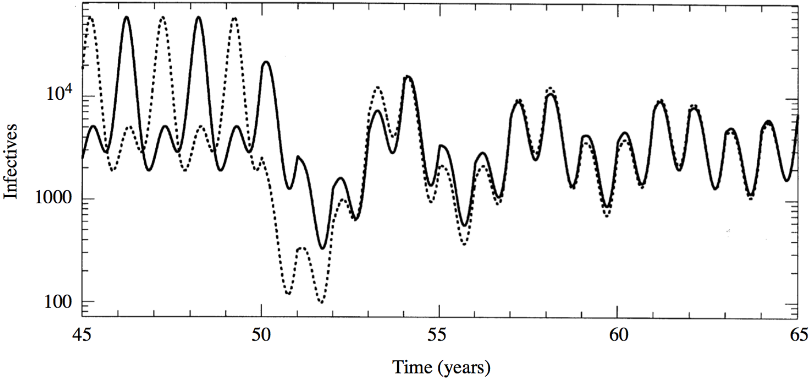
Why might this help?

- Introduce a synchronized periodic forcing
- Has potential to synchronize epidemic troughs
- Pathogen more likely to go extinct globally during synchronized trough

Why might this fail?

- Periodic forcing can have complex dynamical effects. . .

Example of Synchronization via Pulse Vaccination



SEIR model: $N_1 = N_2 = 5 \times 10^7$, $\mathcal{R}_0 = 17$, $\sigma^{-1} = 8$ days, $\gamma^{-1} = 5$ days, $\alpha = 0.15$, $\epsilon = 0.001$.

- Immunization started in year 50. Then 20% of susceptible population vaccinated on 1 January each year.

Earn, Rohani & Grenfell (1998) *Proc. R. Soc. Lond.* **265**, 7–10