



Faculty of Science Graduate Studies Open House

Get a head start on grad school & learn about everything from **#Gradlife** to crafting the perfect application

Tuesday, March 12th 2019
CIBC Hall
5:00PM - 6:30PM

Contact: trepanr@mcmaster.ca

20 Space I

21 Space II

22 Space III

23 TEST

24 Space IV



Mathematics
and Statistics

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

Mathematics 4MB3/6MB3 Mathematical Biology

Instructor: David Earn

Lecture 20

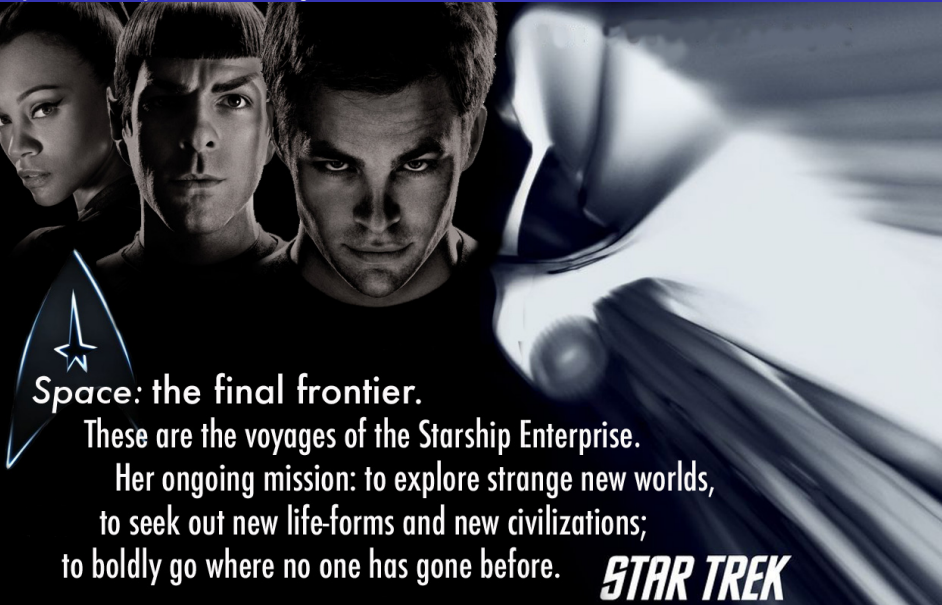
Space I

Monday 4 March 2019

Announcements

- **Midterm test:**
 - *Date:* Monday 11 March 2019
 - *Time:* 9:30am–11:20am
 - *Location:* Hamilton Hall 410
- **Assignment 4** is due after the midterm, but do it before the midterm! Due Wednesday 13 March 2019 at 10:30am
 - Make sure to complete the question on calculating \mathcal{R}_0 on this assignment *before* the midterm test.
- **Draft Project Description Document** has been posted.
 - Questions?

Spatial Epidemic Dynamics



Space: the final frontier.

These are the voyages of the Starship Enterprise.

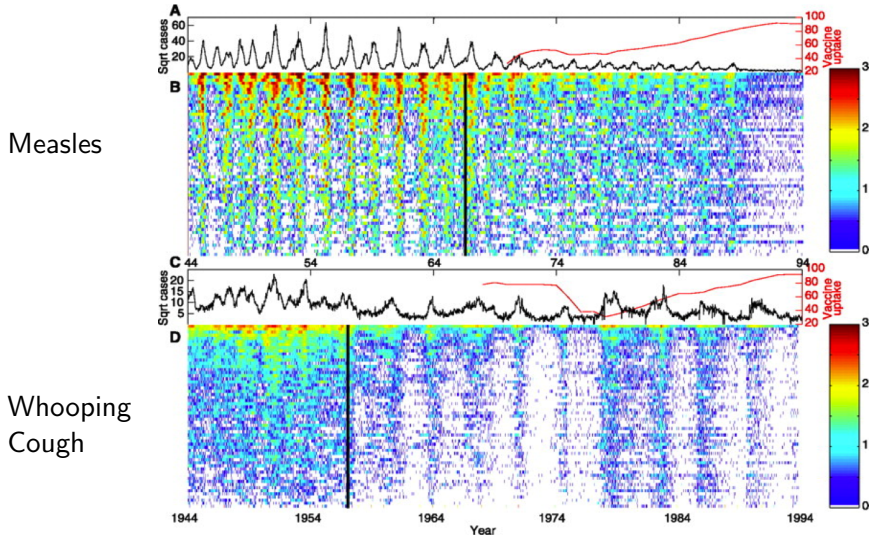
**Her ongoing mission: to explore strange new worlds,
to seek out new life-forms and new civilizations;
to boldly go where no one has gone before.**

STAR TREK

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 $p_{\text{crit}} = 1 - \frac{1}{\mathcal{R}_0}$?

Measles and Whooping Cough in 60 UK cities



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

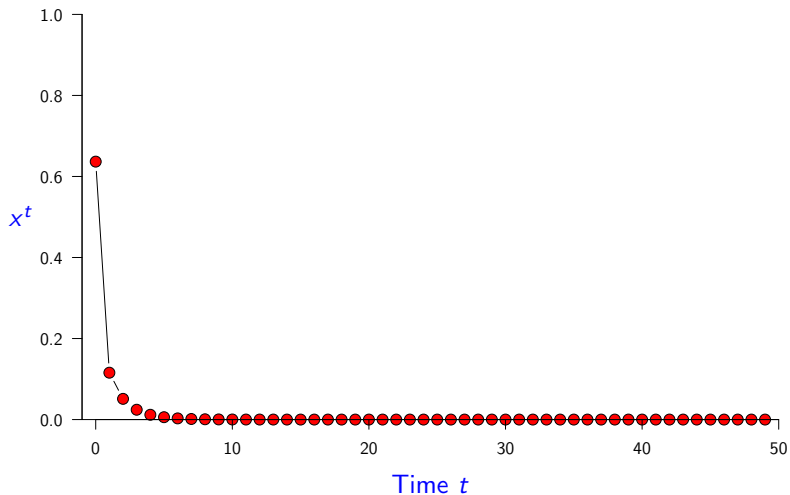
- Simplest non-trivial *discrete time* population model for a single species (with *non-overlapping generations*) in a *single habitat patch*.
- Time: $t = 0, 1, 2, 3, \dots$
- State: $x \in [0, 1]$ (population density)
- Population density at time t is x^t . Solutions are sequences:

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

- $x^{t+1} = F(x^t)$ 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?

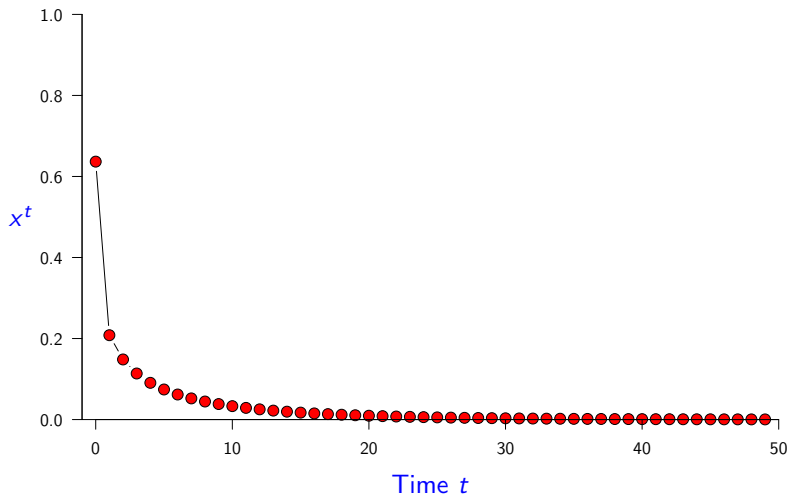
Logistic Map Time Series, $r = 0.5$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 0.5, \quad x_0 = 0.63662$$



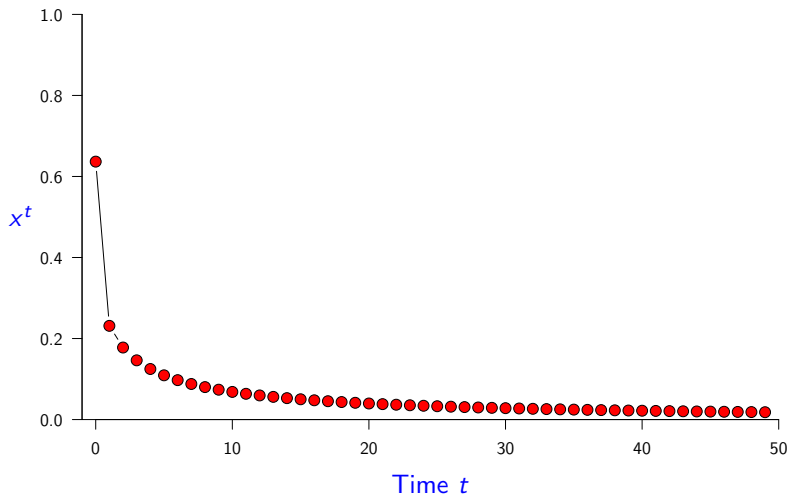
Logistic Map Time Series, $r = 0.9$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 0.9, \quad x_0 = 0.63662$$



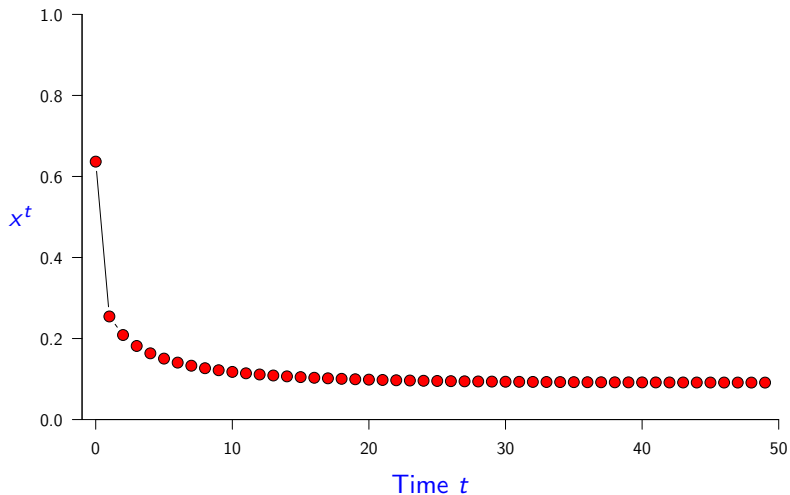
Logistic Map Time Series, $r = 1$

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



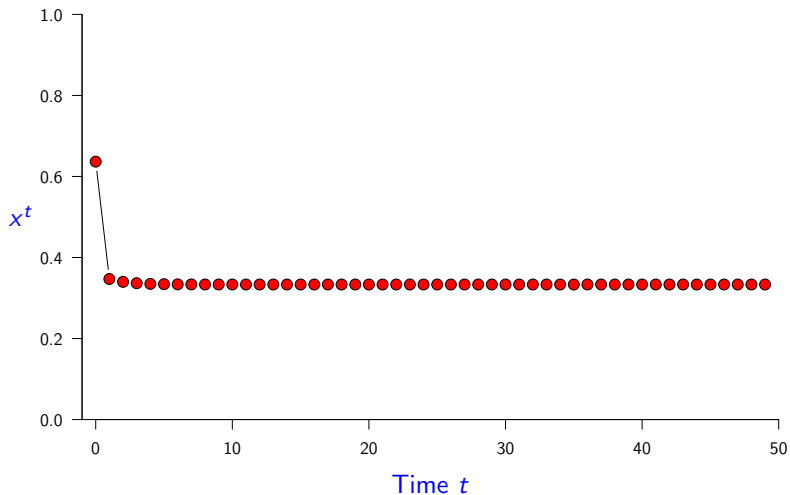
Logistic Map Time Series, $r = 1.1$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 1.1, \quad x_0 = 0.63662$$



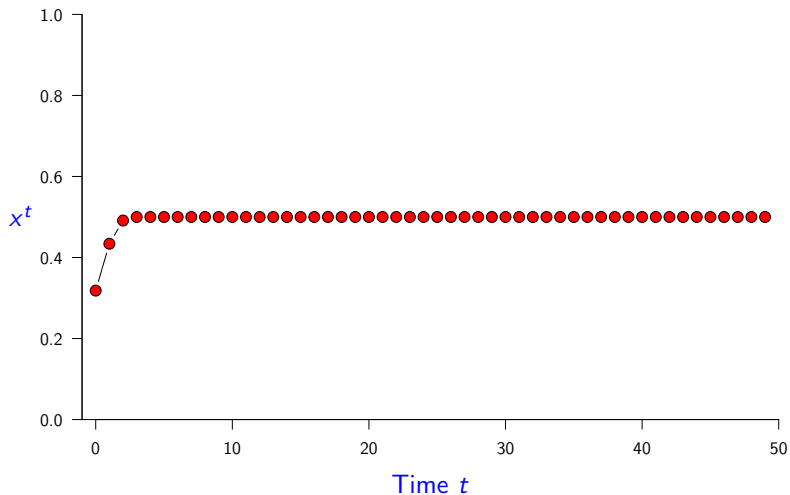
Logistic Map Time Series, $r = 1.5$

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



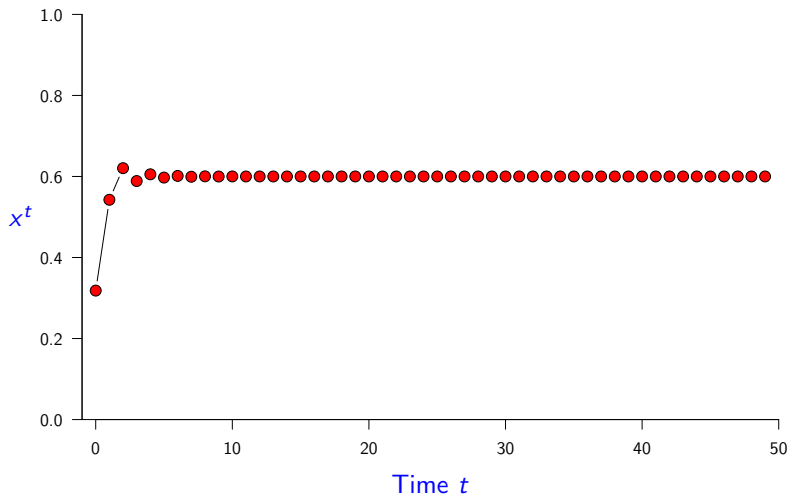
Logistic Map Time Series, $r = 2$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 2, \quad x_0 = 0.31831$$



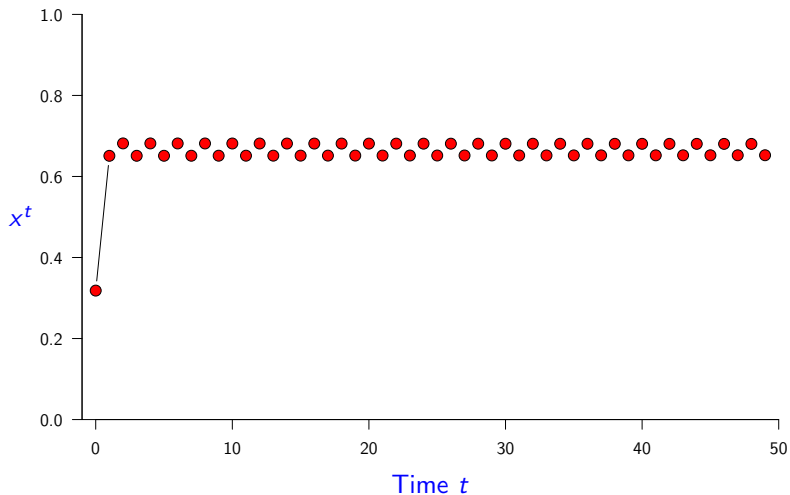
Logistic Map Time Series, $r = 2.5$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 2.5, \quad x_0 = 0.31831$$



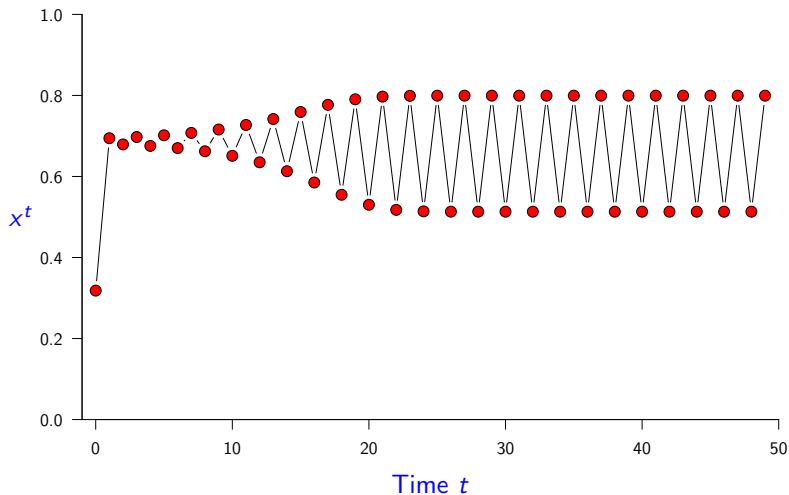
Logistic Map Time Series, $r = 3$

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



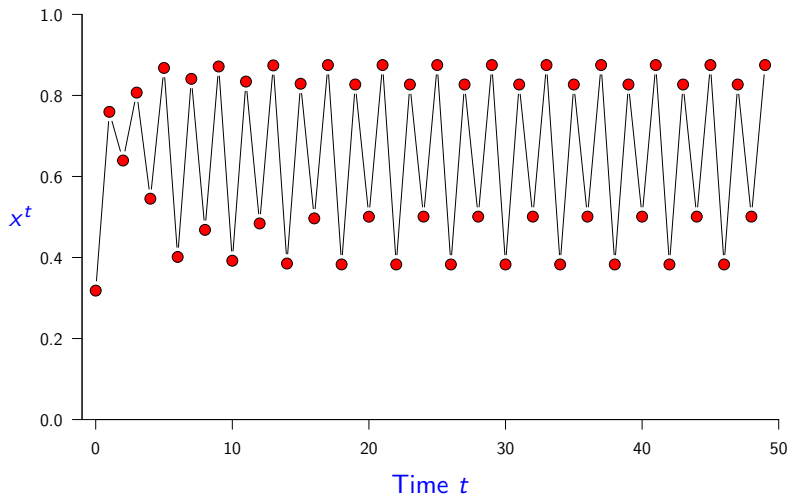
Logistic Map Time Series, $r = 3.2$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 3.2, \quad x_0 = 0.31831$$



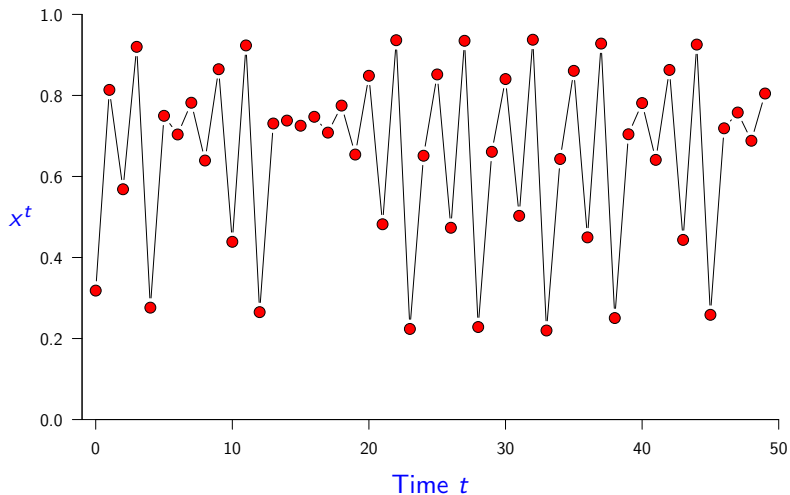
Logistic Map Time Series, $r = 3.5$

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



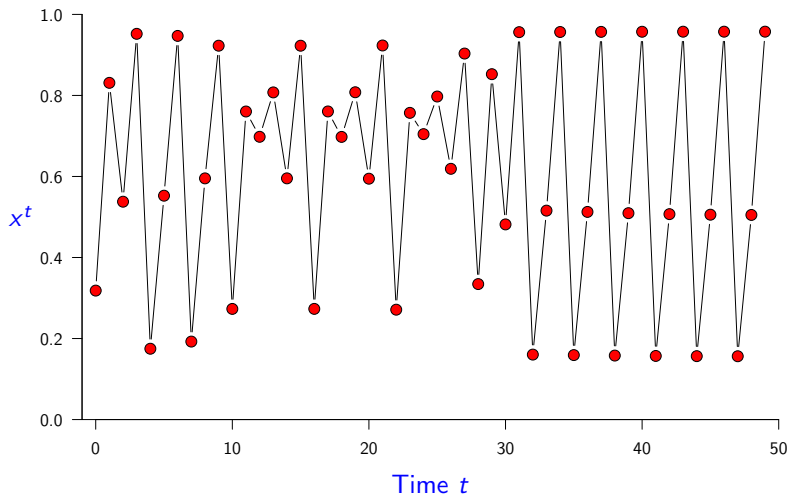
Logistic Map Time Series, $r = 3.75$

$$x^{t+1} = rx^t(1 - x^t), \quad r = 3.75, \quad x_0 = 0.31831$$



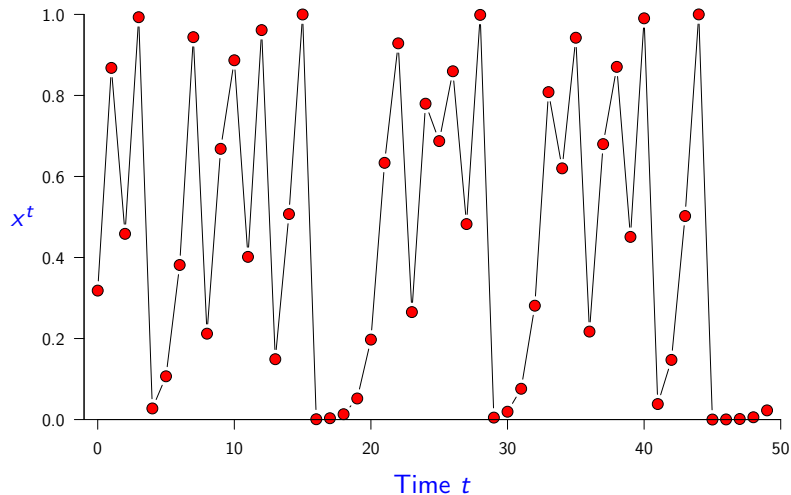
Logistic Map Time Series, $r = 3.83$

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



Logistic Map Time Series, $r = 4$

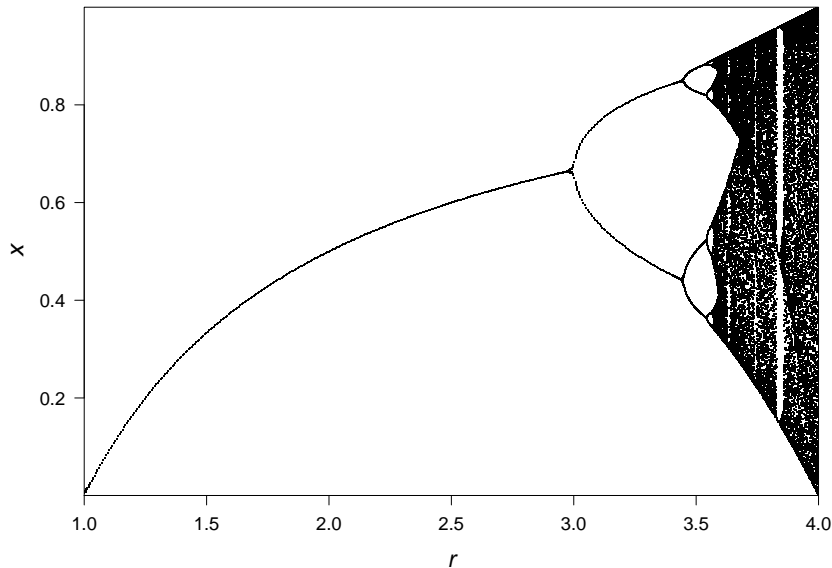
$$x^{t+1} = rx^t(1 - x^t), \quad r = 4, \quad x_0 = 0.31831$$



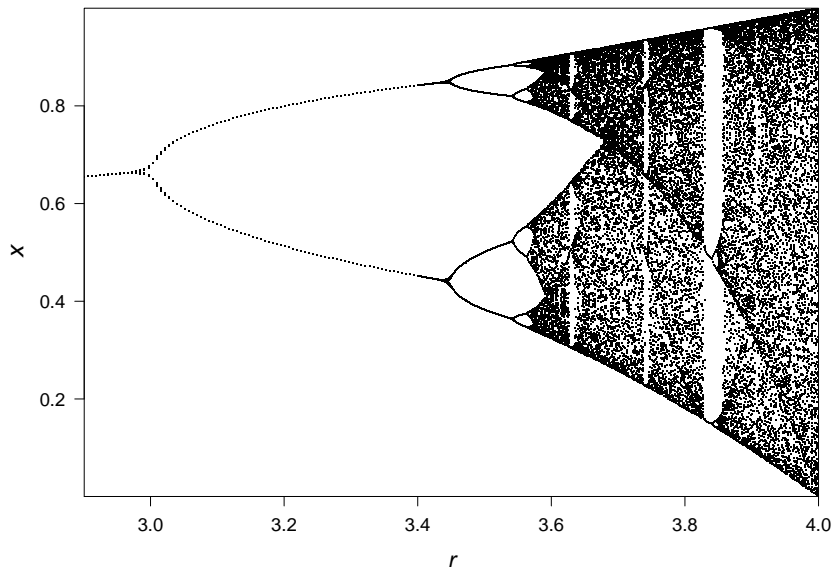
Logistic Map Summary

- 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.

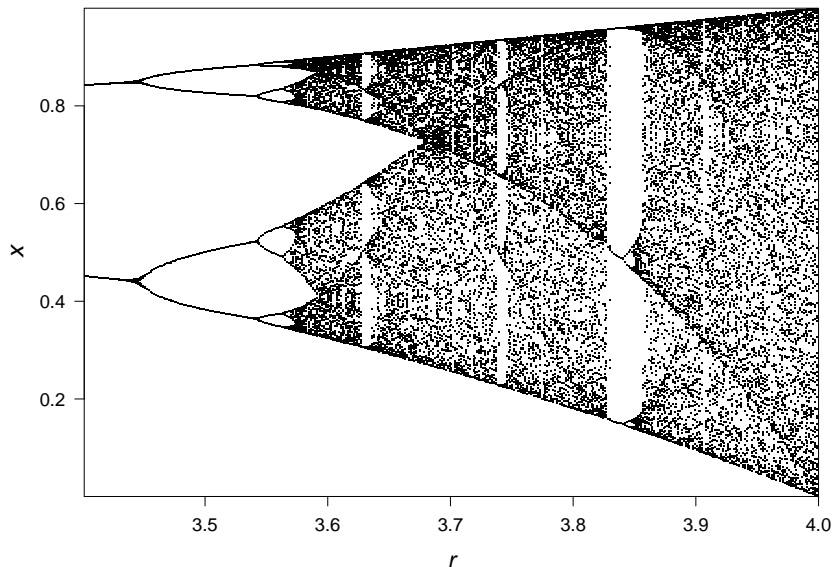
Logistic Map, $F(x) = rx(1 - x)$, $1 \leq r \leq 4$



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



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





Mathematics
and Statistics

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

Mathematics 4MB3/6MB3 Mathematical Biology

Instructor: David Earn

Lecture 21

Space II

Monday 4 March 2019

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 $i = 1, \dots, n$
- *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*
 $M = (m_{ij})$
- System is *coherent* (perfectly synchronous) if the state is the same in all patches
i.e., $\mathbf{x}_1 = \mathbf{x}_2 = \dots = \mathbf{x}_n$

Illustrative example: logistic metapopulation

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

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

where $M = (m_{ij})$ 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:

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

- m_{ij} = *proportion* of population in patch j that disperses to patch i .

- $\therefore 0 \leq m_{ij} \leq 1$ 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)

- $\therefore \sum_{i=1}^n m_{ij} \leq 1$ (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:

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

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.*,

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

- 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:

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

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

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

- For convenience, define

$$\mathbf{e} = (1, 1, \dots, 1) \in \mathbb{R}^n$$

so any coherent state can be written $x\mathbf{e}$, 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.,

$\mathbf{x}^t = a\mathbf{e} \implies \mathbf{x}^{t+1} = b\mathbf{e}$ for some $b \in \mathbb{R}$.

Choose a such that $F(a) \neq 0$. Then

$$\begin{aligned}x_i^{t+1} = b &= \sum_{j=1}^n m_{ij} F(x_j^t) = \sum_{j=1}^n m_{ij} F(a) = F(a) \sum_{j=1}^n m_{ij} \\ \implies \sum_{j=1}^n m_{ij} &= \frac{b}{F(a)} \quad (\text{independent of } i)\end{aligned}$$



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

$$\begin{aligned}x_i^{t+1} &= F(a) = \sum_{j=1}^n m_{ij} F(x_j^t) = \sum_{j=1}^n m_{ij} F(a) = F(a) \sum_{j=1}^n m_{ij} \\ &\implies \sum_{j=1}^n m_{ij} = 1 \quad (\text{independent of } i)\end{aligned}$$





Mathematics
and Statistics

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

Mathematics 4MB3/6MB3 Mathematical Biology

Instructor: David Earn

Lecture 22

Space III

Wednesday 6 March 2019

Announcements

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 - *Date:* Monday 11 March 2019
 - *Time:* 9:30am–11:20am
 - *Location:* Hamilton Hall 410
- **Assignment 4** is due after the midterm, but do it before the midterm! Due Wednesday 13 March 2019 at 10:30am
 - Make sure to complete the question on calculating \mathcal{R}_0 on this assignment before the midterm test.
- **Draft Project Description Document** has been posted.
 - Questions?

Project

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

- Remember your group must give an oral presentation of your project as well (in the last couple of classes).
- 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. This is part of your participation mark.
- 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 4 March 2019.
- Material connected with time series analysis and discrete time models 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.

Last time...

- 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:

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

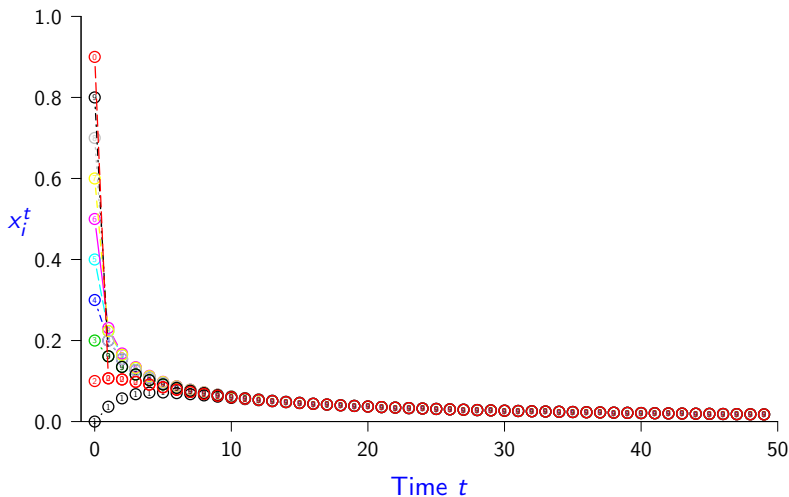
- Real dispersal patterns generally between these two extremes

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 $t \rightarrow \infty$)?
 - If so, then this sort of analysis should help to identify synchronizing vaccination strategies.

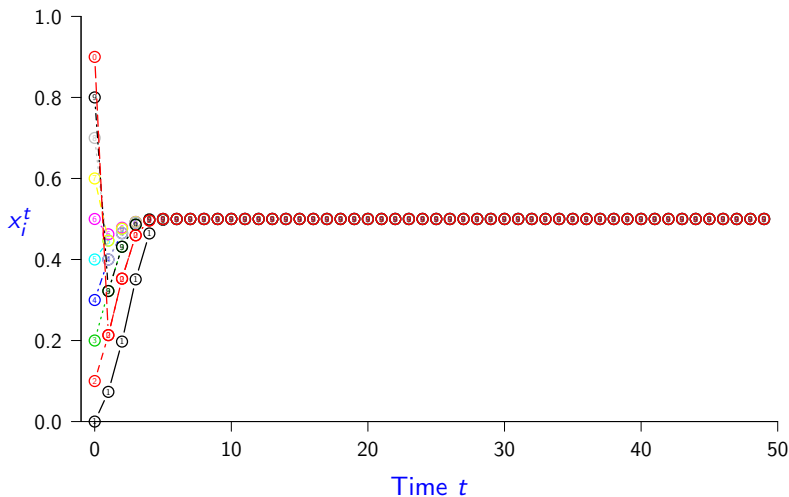
Logistic Metapopulation Simulation ($r = 1, m = 0.2$)

$$n = 10, \quad r = 1, \quad m = 0.2, \quad \lambda = 0.778$$



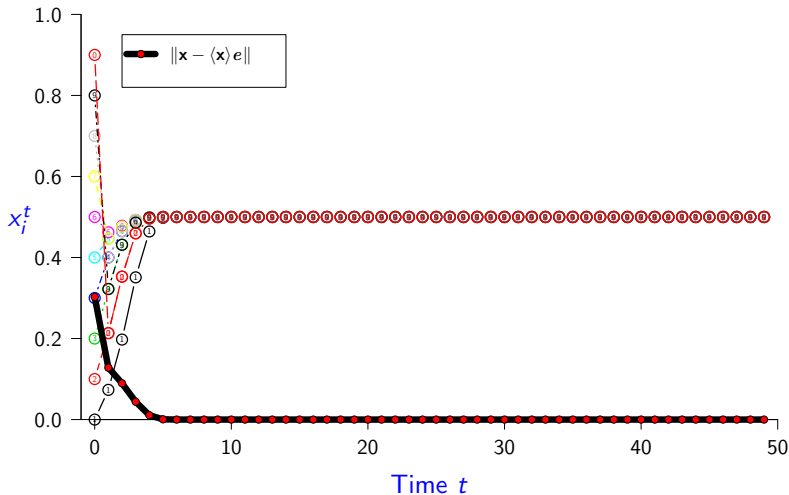
Logistic Metapopulation Simulation ($r = 2, m = 0.2$)

$$n = 10, \quad r = 2, \quad m = 0.2, \quad \lambda = 0.778$$



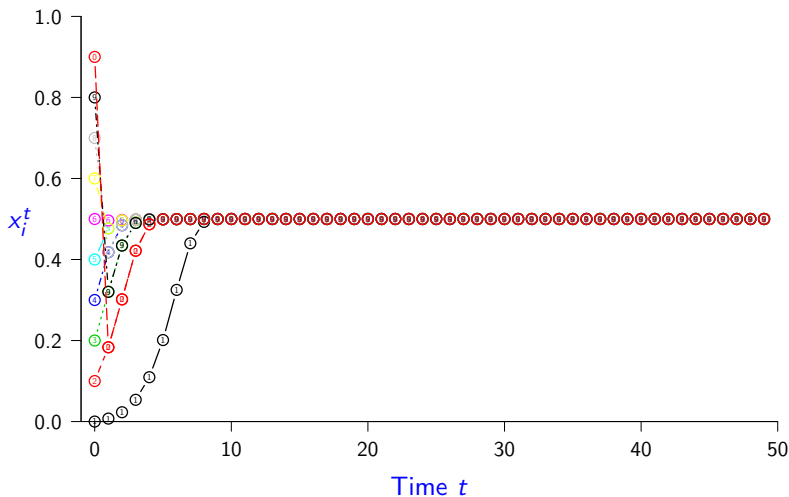
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$$n = 10, \quad r = 2, \quad m = 0.2, \quad \lambda = 0.778$$



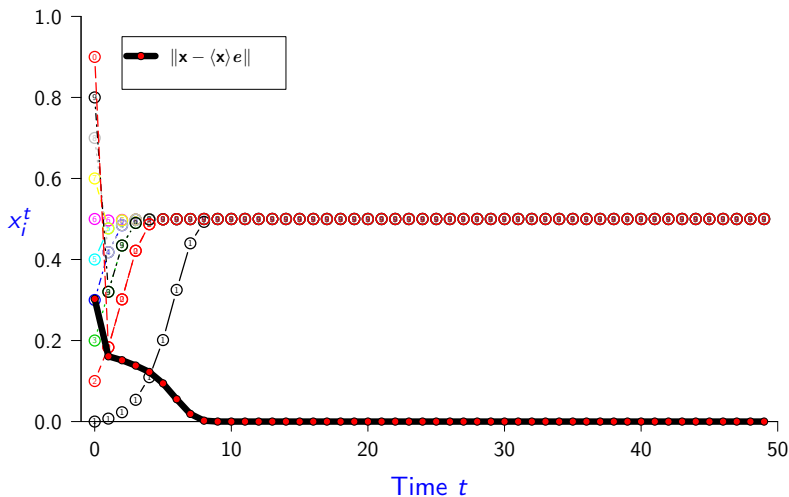
Logistic Metapopulation Simulation ($r = 2$, $m = 0.02$)

$$n = 10, \quad r = 2, \quad m = 0.02, \quad \lambda = 0.978$$



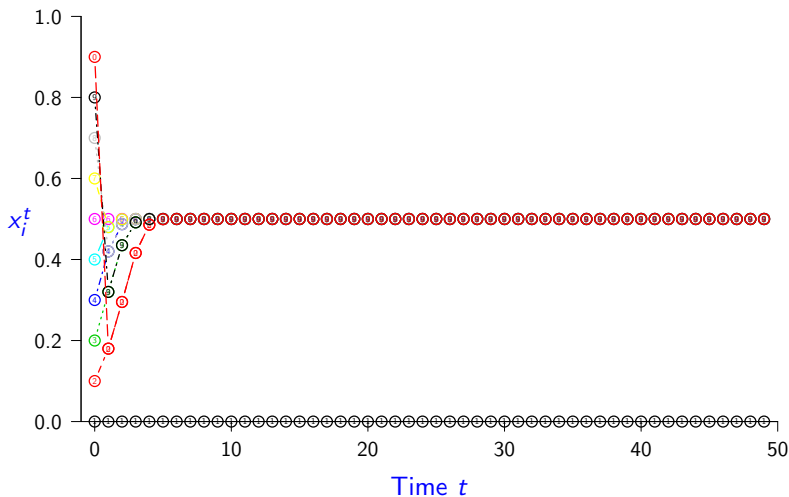
Logistic Metapopulation Simulation ($r = 2$, $m = 0.02$)

$$n = 10, \quad r = 2, \quad m = 0.02, \quad \lambda = 0.978$$



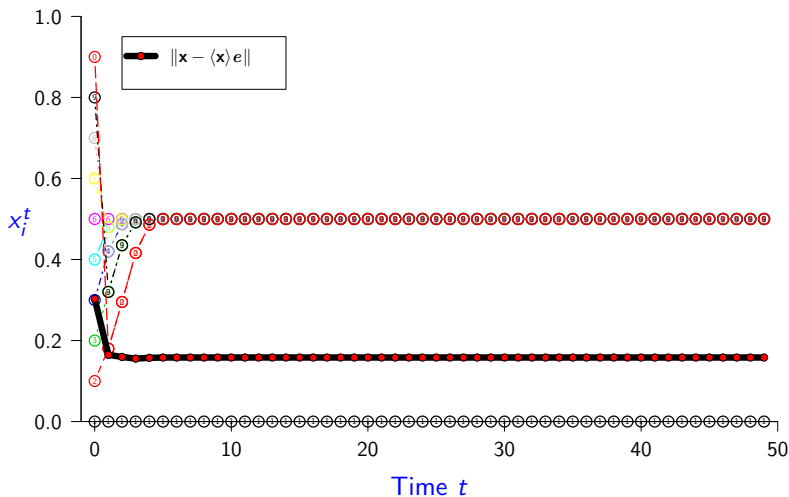
Logistic Metapopulation Simulation ($r = 2, m = 0$)

$$n = 10, \quad r = 2, \quad m = 0, \quad \lambda = 1$$



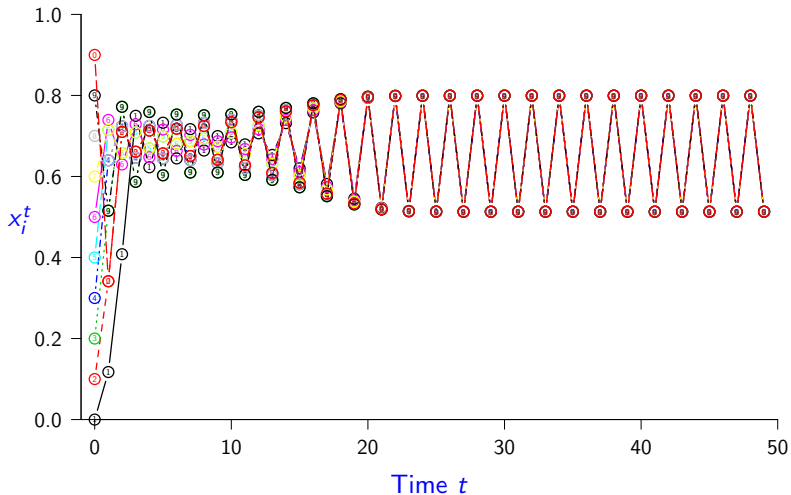
Logistic Metapopulation Simulation ($r = 2, m = 0$)

$$n = 10, \quad r = 2, \quad m = 0, \quad \lambda = 1$$



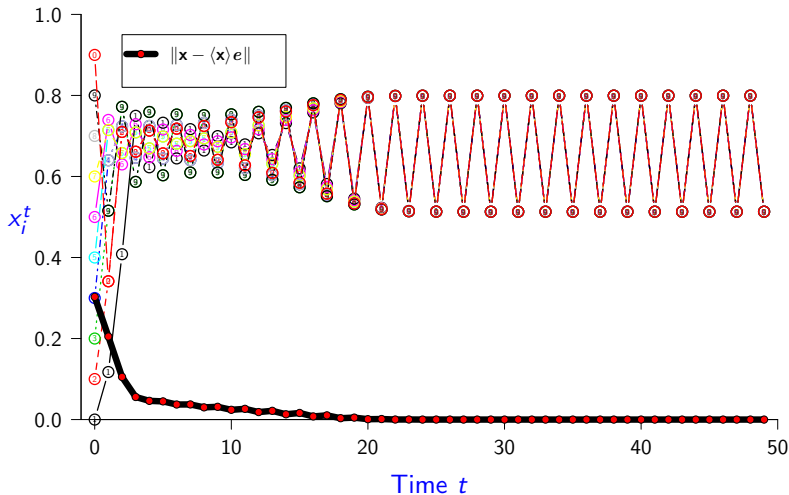
Logistic Metapopulation Simulation ($r = 3.2, m = 0.2$)

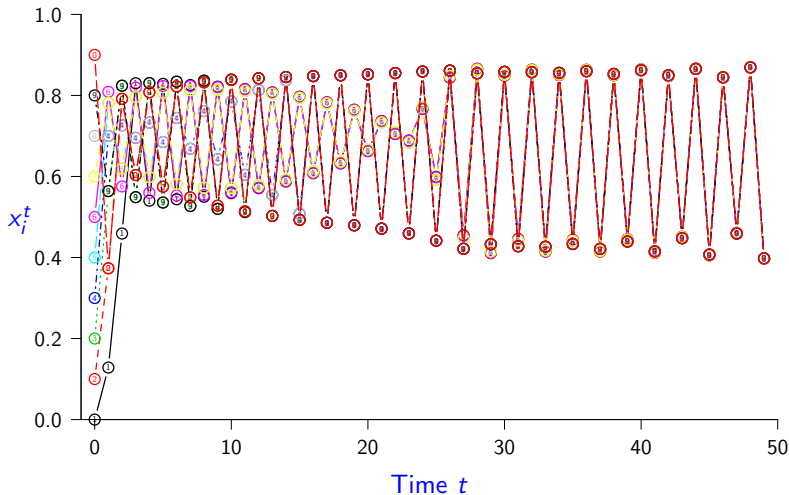
$n = 10, \quad r = 3.2, \quad m = 0.2, \quad \lambda = 0.778$



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

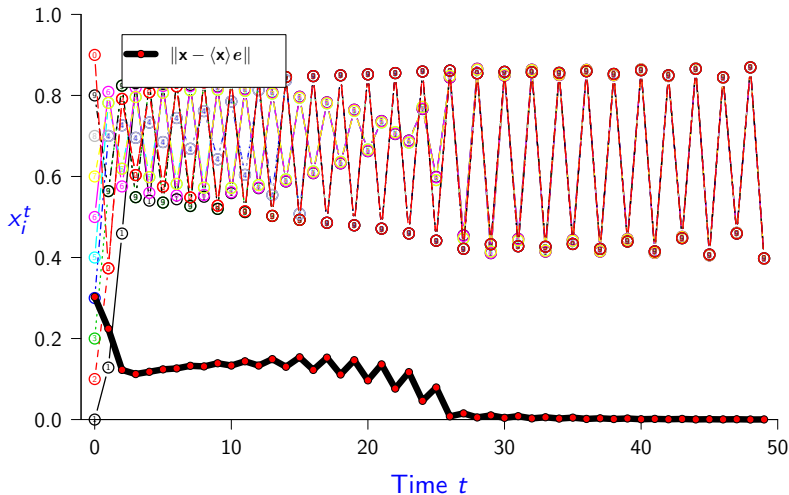
$n = 10, \quad r = 3.2, \quad m = 0.2, \quad \lambda = 0.778$



Logistic Metapopulation Simulation ($r = 3.5$, $m = 0.2$) $n = 10$, $r = 3.5$, $m = 0.2$, $\lambda = 0.778$ 

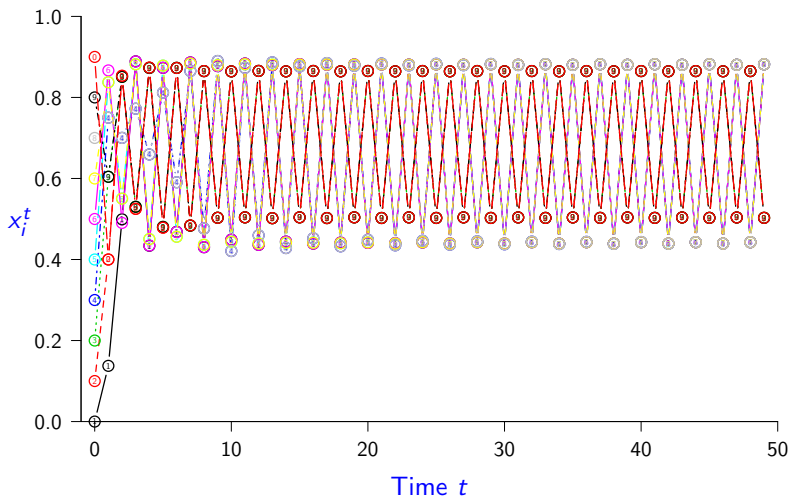
Logistic Metapopulation Simulation ($r = 3.5$, $m = 0.2$)

$n = 10$, $r = 3.5$, $m = 0.2$, $\lambda = 0.778$



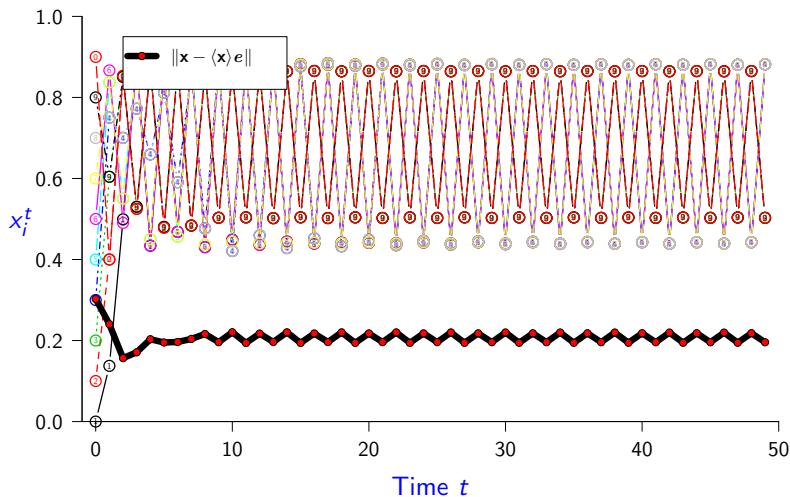
Logistic Metapopulation Simulation ($r = 3.75$, $m = 0.2$)

$n = 10$, $r = 3.75$, $m = 0.2$, $\lambda = 0.778$



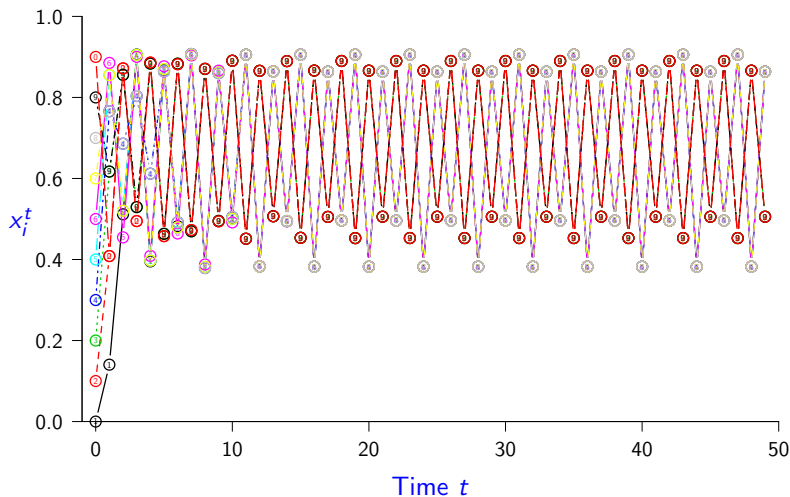
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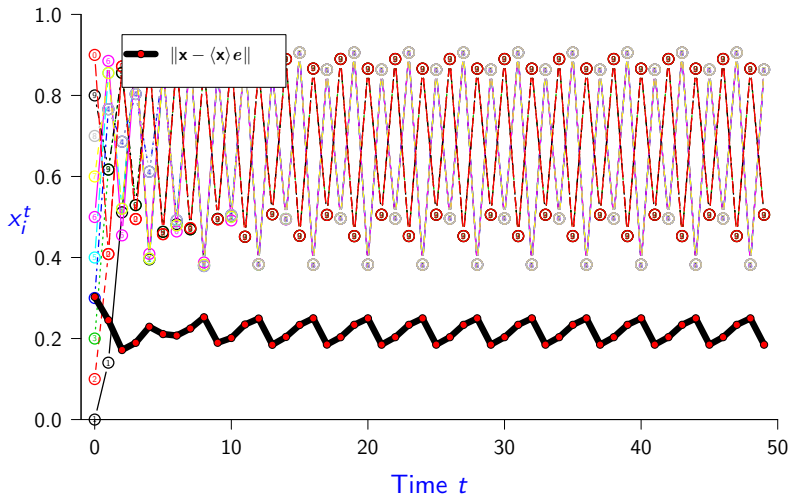
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.2$)

$n = 10$, $r = 3.83$, $m = 0.2$, $\lambda = 0.778$



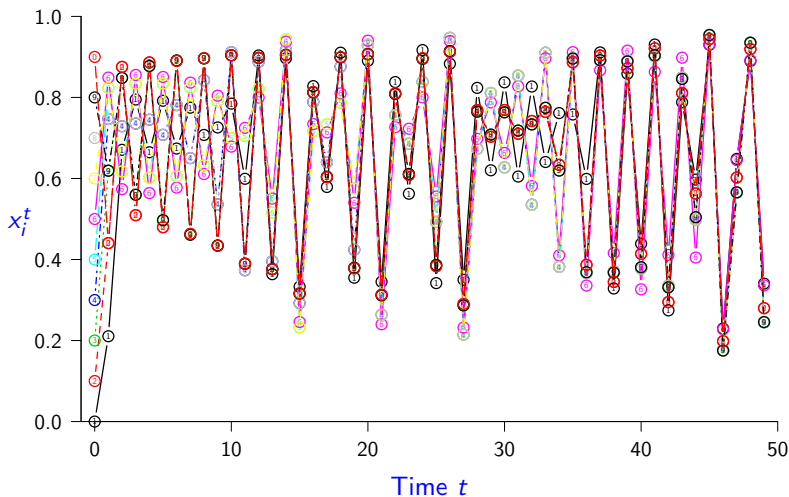
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.2$)

$n = 10$, $r = 3.83$, $m = 0.2$, $\lambda = 0.778$



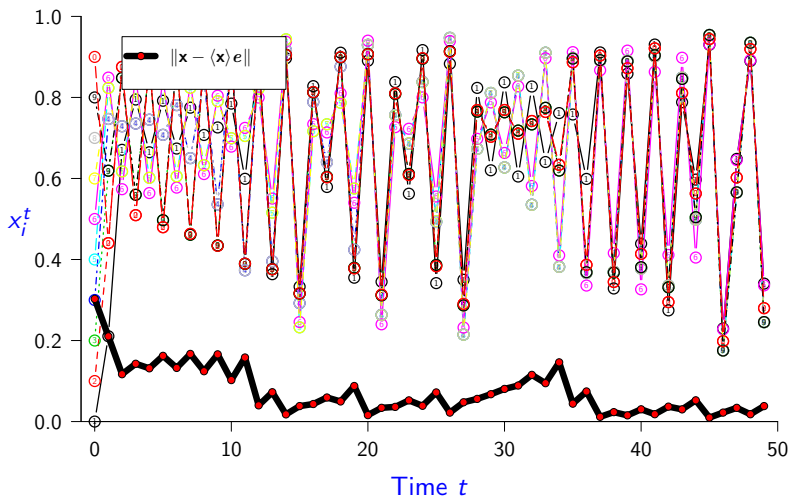
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.3$)

$n = 10$, $r = 3.83$, $m = 0.3$, $\lambda = 0.667$



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

$n = 10$, $r = 3.83$, $m = 0.3$, $\lambda = 0.667$





Mathematics
and Statistics

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

Mathematics 4MB3/6MB3 Mathematical Biology

Instructor: David Earn

Lecture 23

TEST

Monday 11 March 2019



Mathematics
and Statistics

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

Mathematics 4MB3/6MB3 Mathematical Biology

Instructor: David Earn

Lecture 24

Space IV

Wednesday 13 March 2019

Announcements

- **Assignment 4** due TODAY.
- Do the group contribution survey as soon as you receive the e-mail invitation.
- Test will be returned by e-mail, hopefully by end of the day today.

Comments from TA on assignment 3

Comments on assignment 3 (all \LaTeX).

- 1 Use `\log` instead of *log*
- 2 Make sure when referencing equations that the reference actually shows up, *i.e.*, not ??
- 3 Use `\big`, `\bigg`, `\Bigg`, *etc.*, to get bigger brackets for tidier work.
- 4 Check over what your group mates have done to make sure the \LaTeX looks good. There are still people using R_0 , not \mathcal{R}_0 , *etc.*

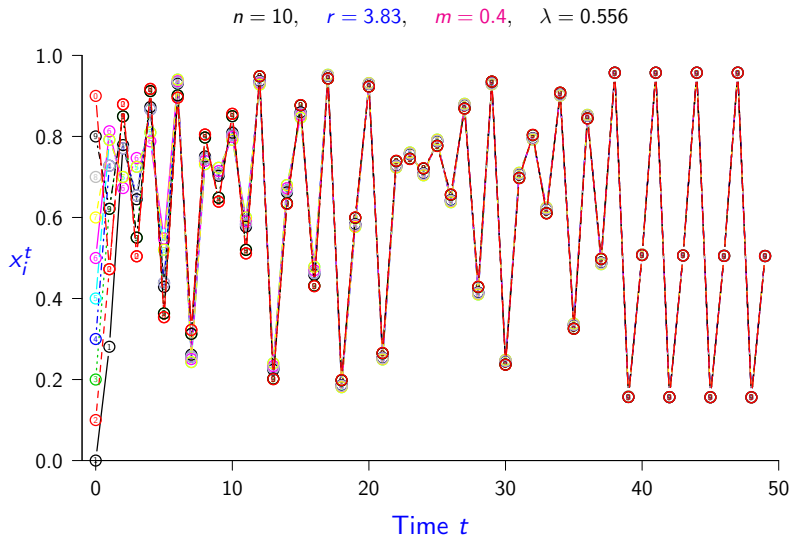
Project

- Remaining classes 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. This is part of your participation mark.
- Details on [Project](#) page.
- Project Notebook template is posted on [project](#) page.
- Preliminary draft and project notebook due Mon 25 March 2019, 9:30am.
- Final version and project notebook due in last class, Mon 8 April 2019, 9:30am.
- Presentations will occur either in last couple of classes or in an evening (preferences?).
- Movie night:
 - Date? Time?
 - Who would like to volunteer to be responsible for pizza order?

Metapopulation dynamics: what we've seen so far

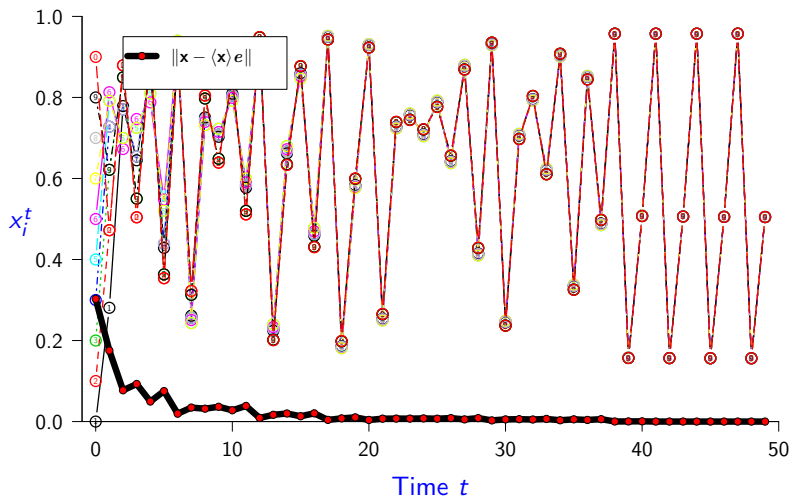
- Examples of connectivity matrices
 - equal coupling
 - nearest-neighbour coupling on a ring
- Logistic Metapopulation Simulations (10 patches)
 - $r = 1, m = 0.2$
 - $r = 2, m = 0.2$
 - $r = 2, m = 0.02$
 - $r = 2, m = 0$
 - $r = 3.2, m = 0.2$
 - $r = 3.5, m = 0.2$
 - $r = 3.75, m = 0.2$
 - $r = 3.83, m = 0.2$
 - $r = 3.83, m = 0.3$

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



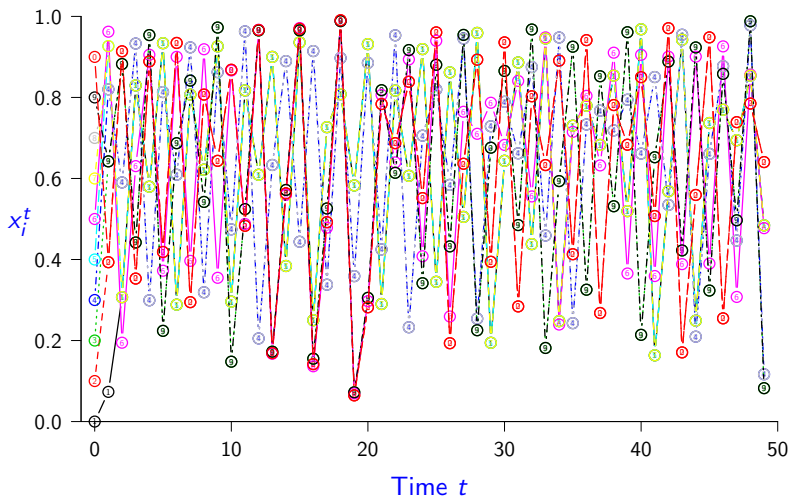
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.4$)

$n = 10$, $r = 3.83$, $m = 0.4$, $\lambda = 0.556$



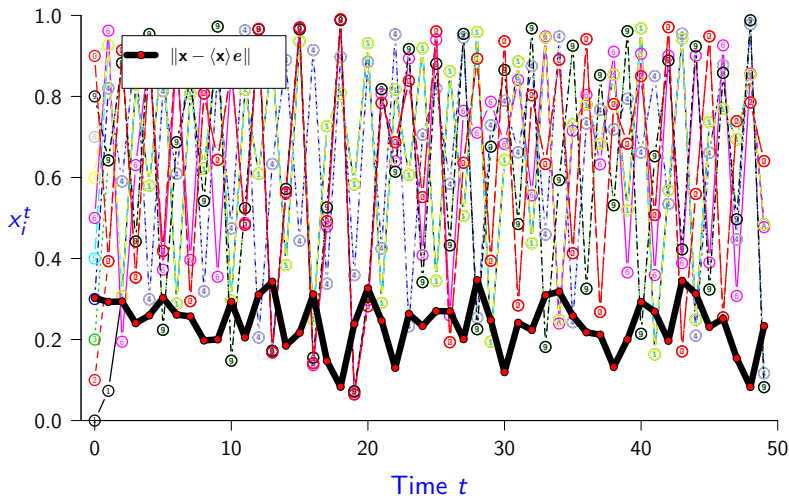
Logistic Metapopulation Simulation ($r = 4, m = 0.1$)

$n = 10, r = 4, m = 0.1, \lambda = 0.889$



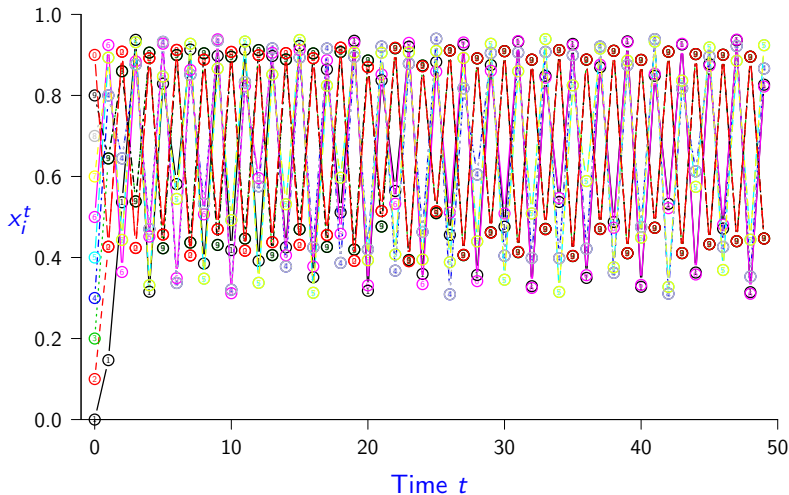
Logistic Metapopulation Simulation ($r = 4, m = 0.1$)

$n = 10, r = 4, m = 0.1, \lambda = 0.889$



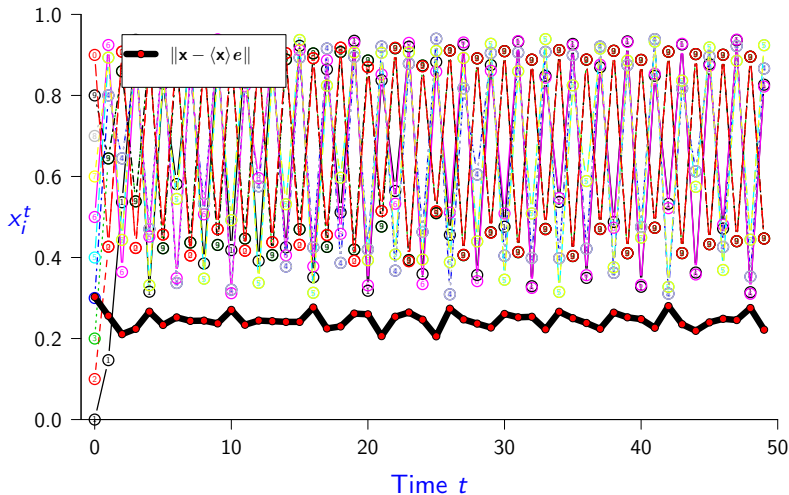
Logistic Metapopulation Simulation ($r = 4, m = 0.2$)

$n = 10, r = 4, m = 0.2, \lambda = 0.778$



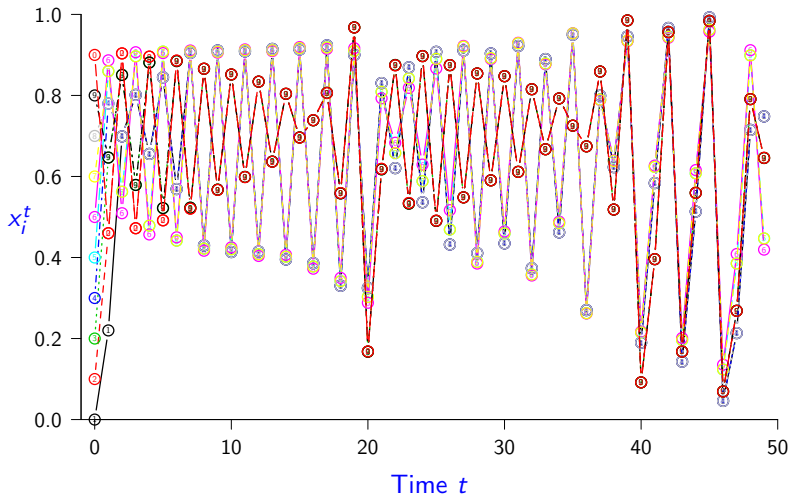
Logistic Metapopulation Simulation ($r = 4, m = 0.2$)

$n = 10, r = 4, m = 0.2, \lambda = 0.778$



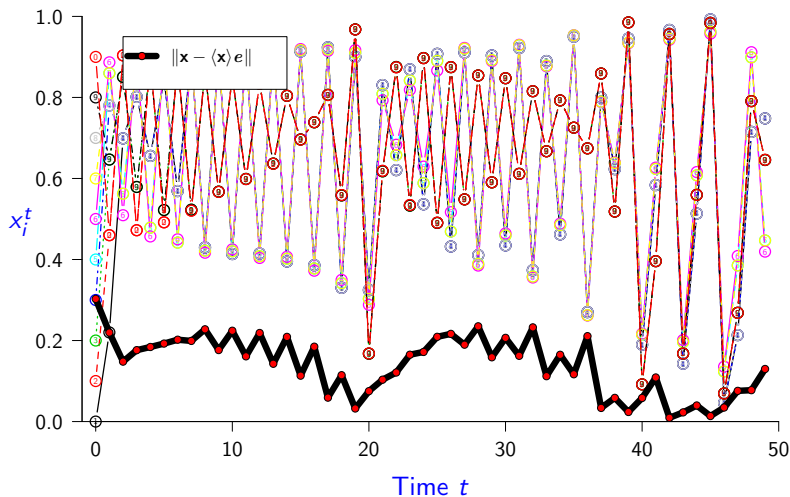
Logistic Metapopulation Simulation ($r = 4, m = 0.3$)

$n = 10, r = 4, m = 0.3, \lambda = 0.667$



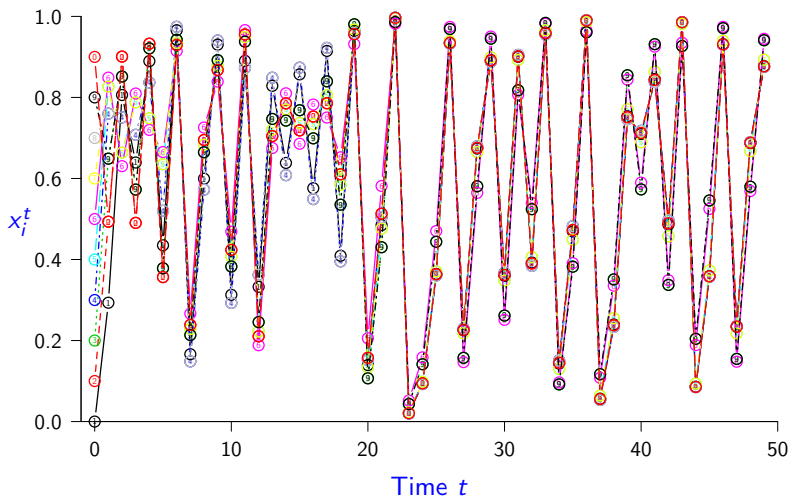
Logistic Metapopulation Simulation ($r = 4, m = 0.3$)

$n = 10, r = 4, m = 0.3, \lambda = 0.667$



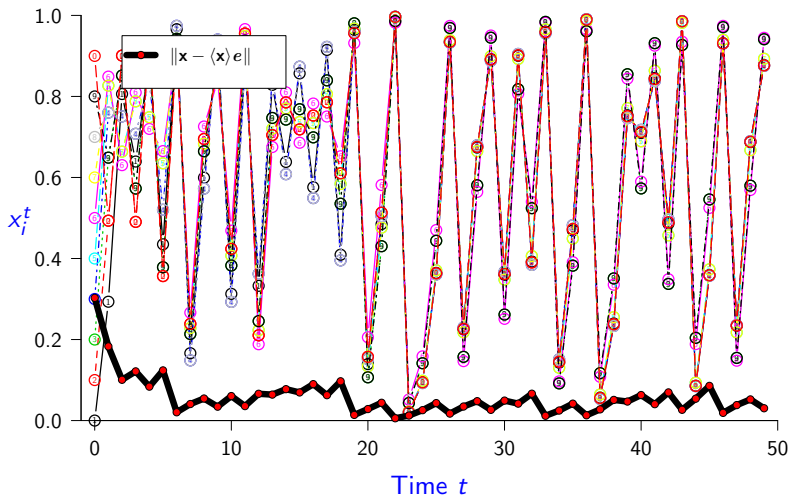
Logistic Metapopulation Simulation ($r = 4, m = 0.4$)

$n = 10, r = 4, m = 0.4, \lambda = 0.556$



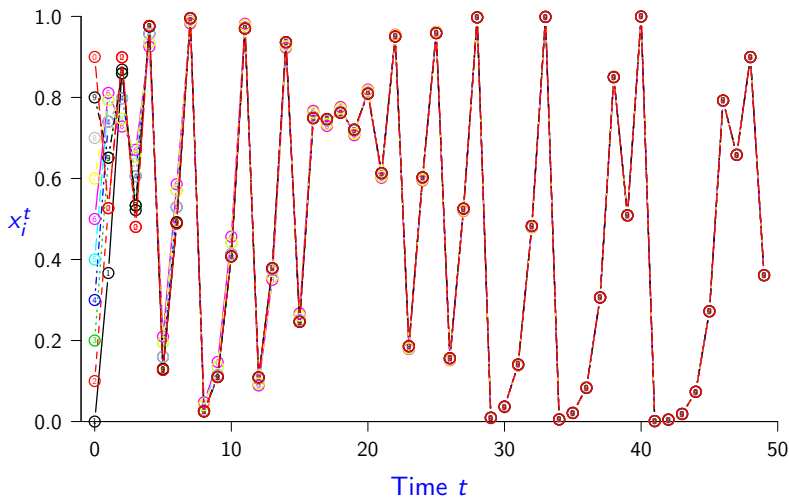
Logistic Metapopulation Simulation ($r = 4, m = 0.4$)

$n = 10, r = 4, m = 0.4, \lambda = 0.556$



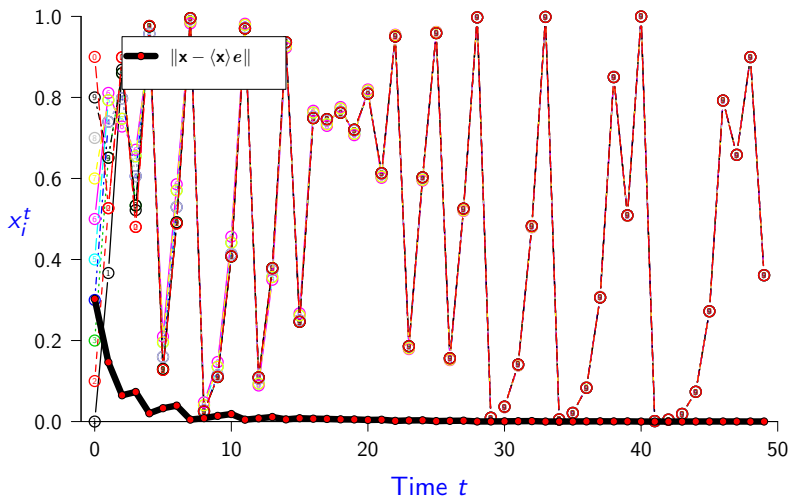
Logistic Metapopulation Simulation ($r = 4, m = 0.5$)

$n = 10, \quad r = 4, \quad m = 0.5, \quad \lambda = 0.444$



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

$n = 10, \quad r = 4, \quad m = 0.5, \quad \lambda = 0.444$



Last time...

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

■ $r = 1, m = 0.2$

■ $r = 3.5, m = 0.2$

■ $r = 4, m = 0.1$

■ $r = 2, m = 0.2$

■ $r = 3.75, m = 0.2$

■ $r = 4, m = 0.2$

■ $r = 2, m = 0.02$

■ $r = 3.83, m = 0.2$

■ $r = 4, m = 0.3$

■ $r = 2, m = 0$

■ $r = 3.83, m = 0.3$

■ $r = 4, m = 0.4$

■ $r = 3.2, m = 0.2$

■ $r = 3.83, m = 0.4$

■ $r = 4, m = 0.5$