19 Space

20 Space II

Mathematics and Statistics

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

Mathematics 4MB3/6MB3 Mathematical Biology

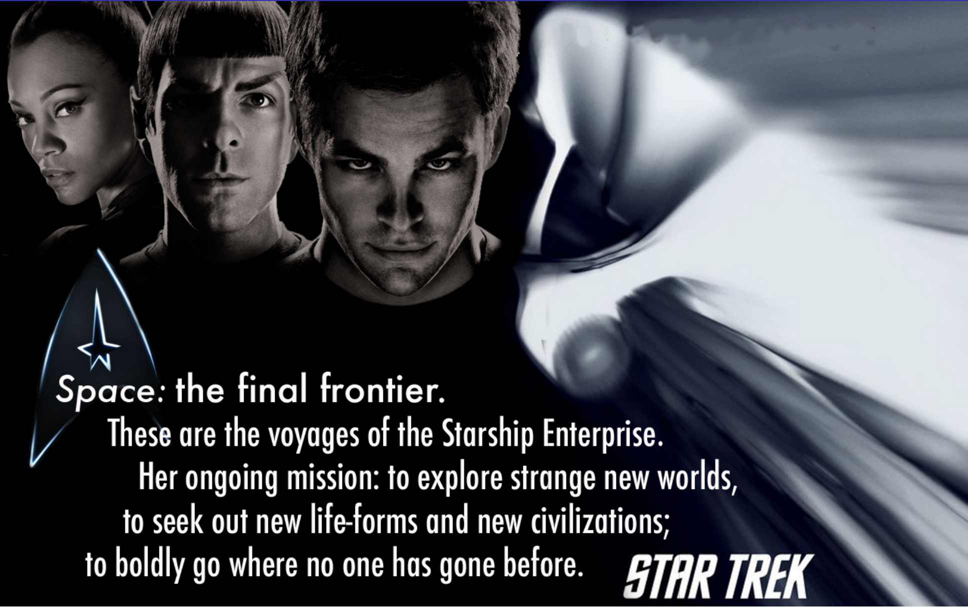
Instructor: David Earn

Lecture 19
Space
Wednesday 28 February 2018

Announcments

- **Assignment 3** due today.
  - Do group contribution survey TODAY!!
- **Assignment 4** due Wednesday 14 March 2018, 11:30am.
- **Midterm test:**
  - *Date:* Thursday 8 March 2018
  - *Time:* 7:00pm to 9:00pm
  - *Location:* BSB-B154

Spatial Epidemic Dynamics



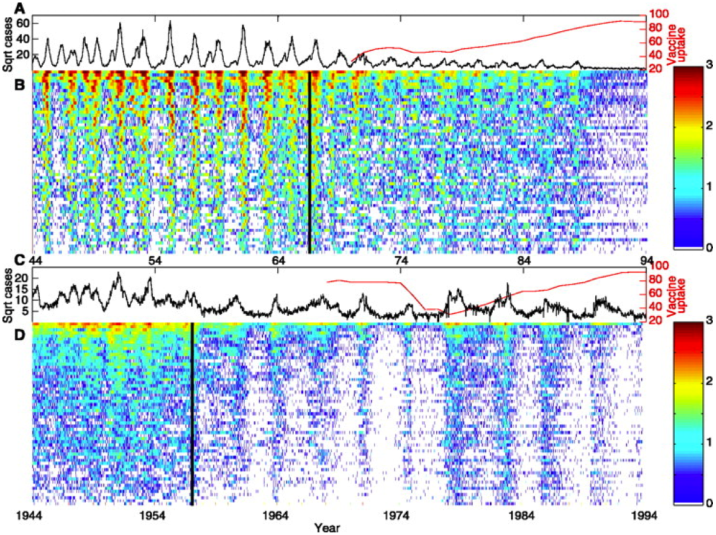
Something to think about

- 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

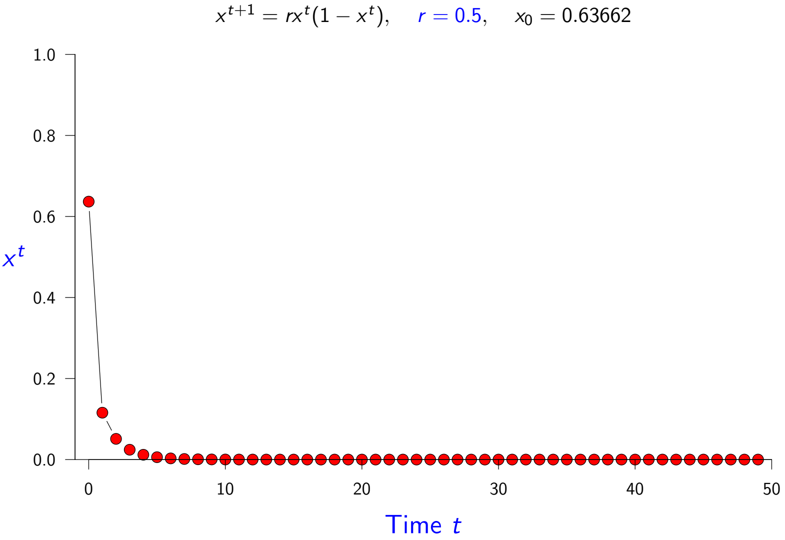
Logistic Map

- 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:

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

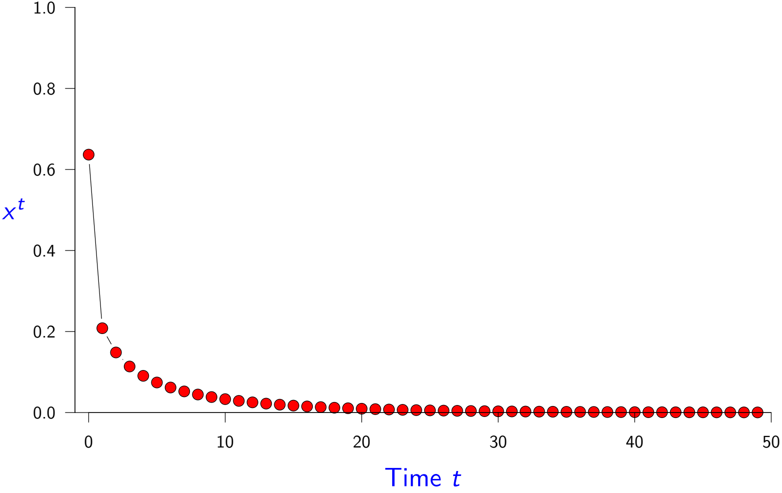
- $x^{t+1} = F(x^t)$ for some *reproduction function* $F(x)$.
- For logistic map: $F(x) = rx(1-x)$, so $x^{t+1} = rx^t(1-x^t)$. $x^{t+1} = [r(1-x^t)]x^t \implies r$ is *maximum fecundity* (which is achieved in limit of very small population density).
- What kinds of dynamics are possible for the Logistic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

Logistic Map Time Series, $r = 0.5$

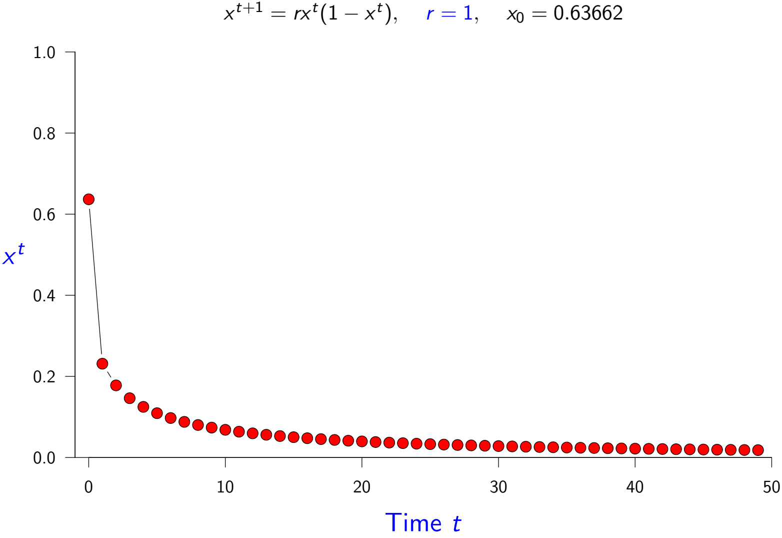


Logistic Map Time Series, $r = 0.9$

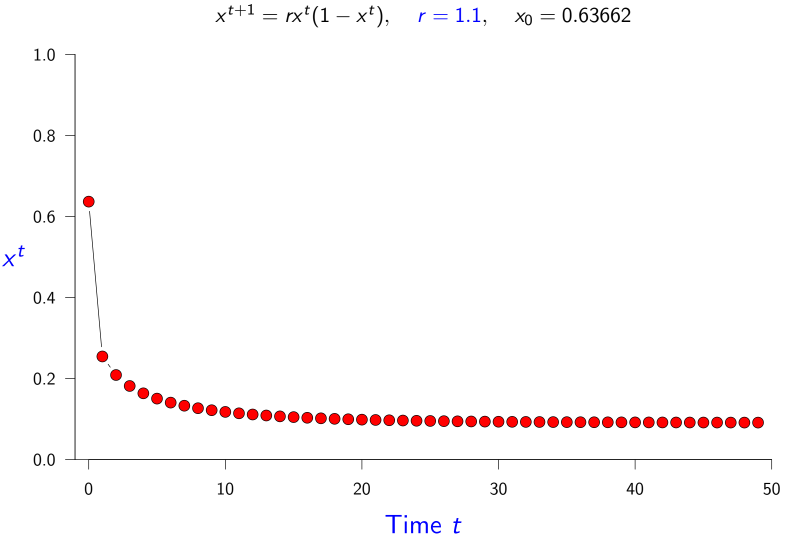
$$x^{t+1} = rx^t(1 - x^t), \quad r = 0.9, \quad x_0 = 0.63662$$



Logistic Map Time Series, $r = 1$

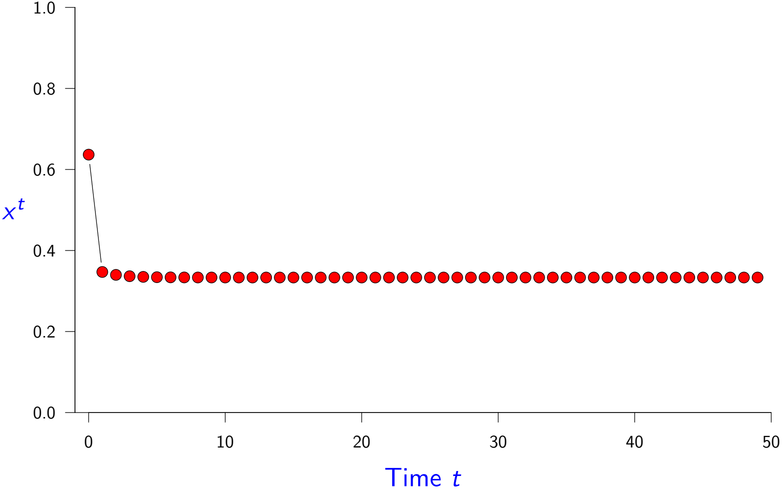


Logistic Map Time Series, $r = 1.1$

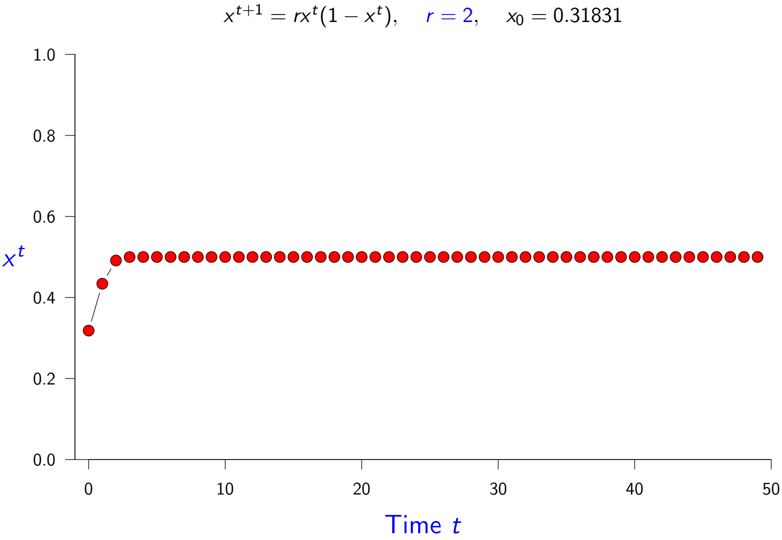


Logistic Map Time Series, $r = 1.5$

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

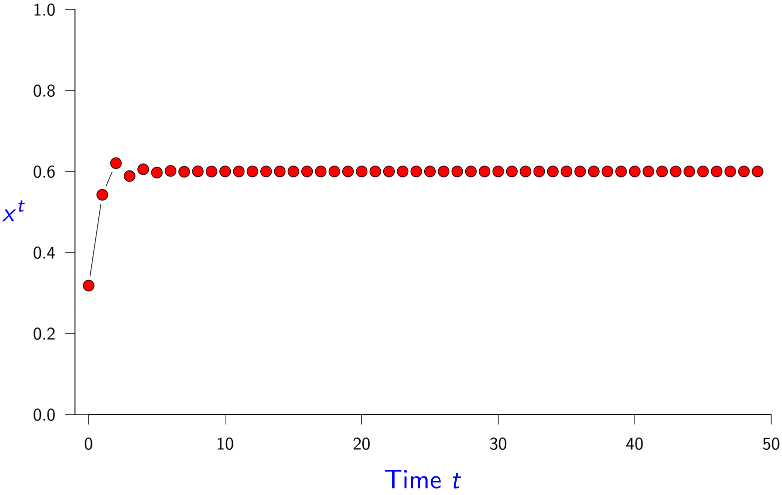


Logistic Map Time Series, $r = 2$



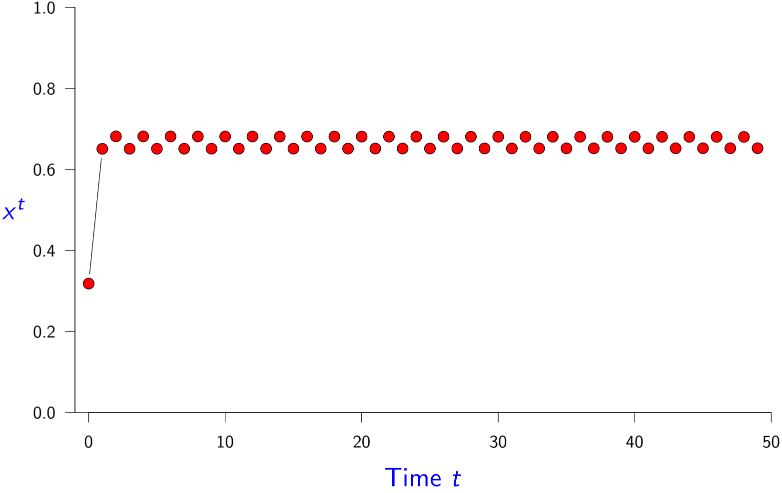
Logistic Map Time Series, $r = 2.5$

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

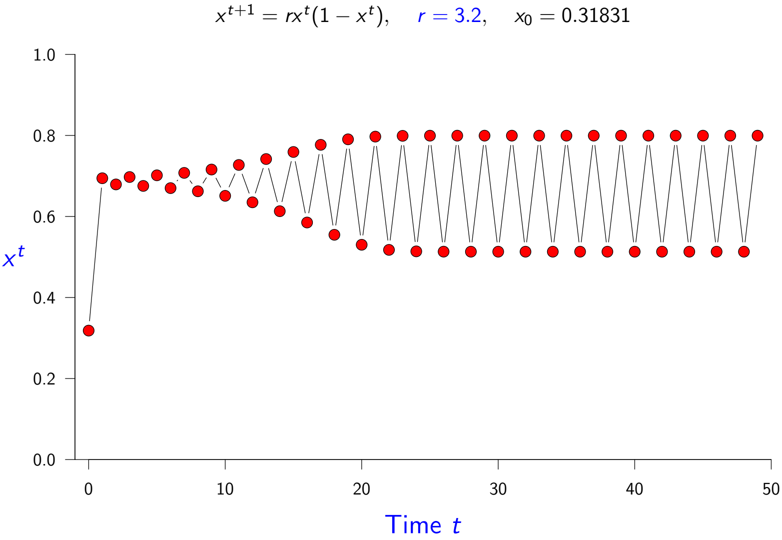


Logistic Map Time Series, $r = 3$

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

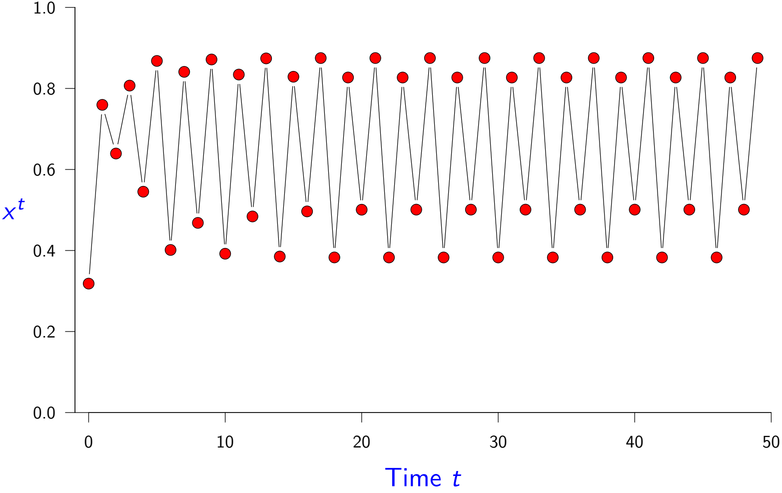


Logistic Map Time Series, $r = 3.2$

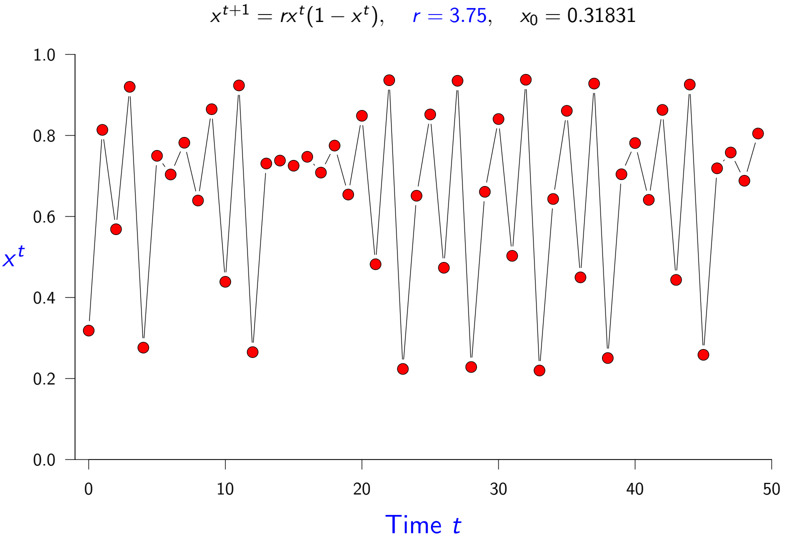


Logistic Map Time Series, $r = 3.5$

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

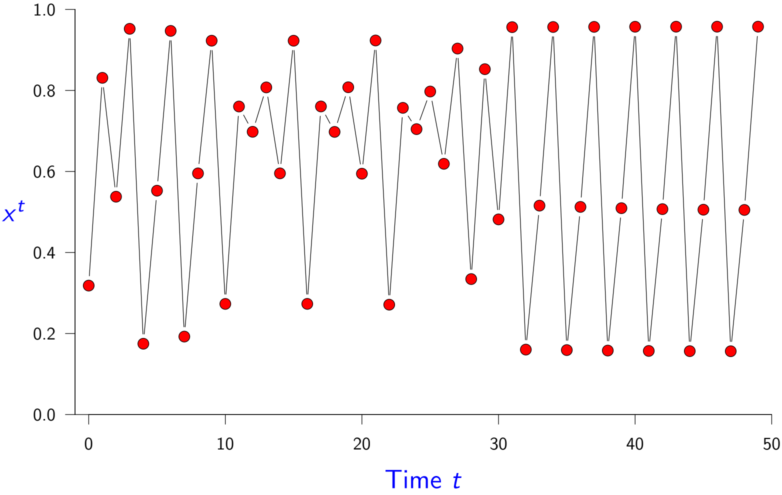


Logistic Map Time Series, $r = 3.75$

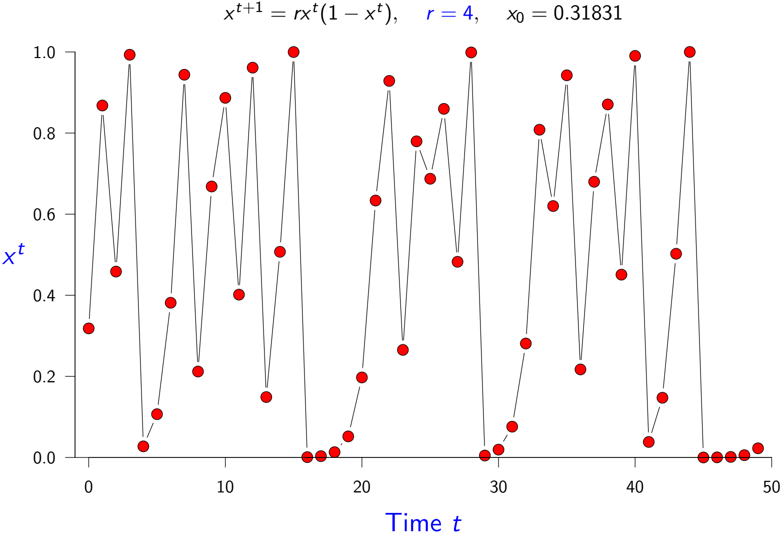


Logistic Map Time Series, $r = 3.83$

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



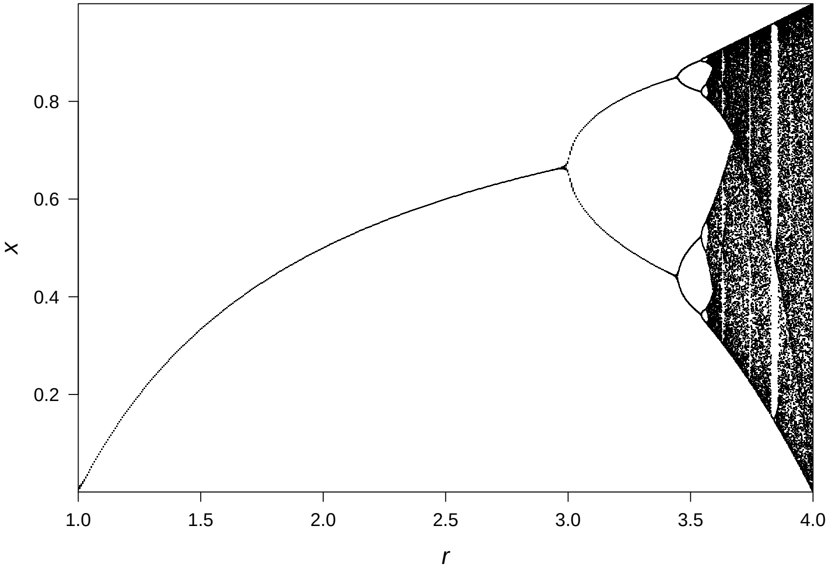
Logistic Map Time Series, $r = 4$



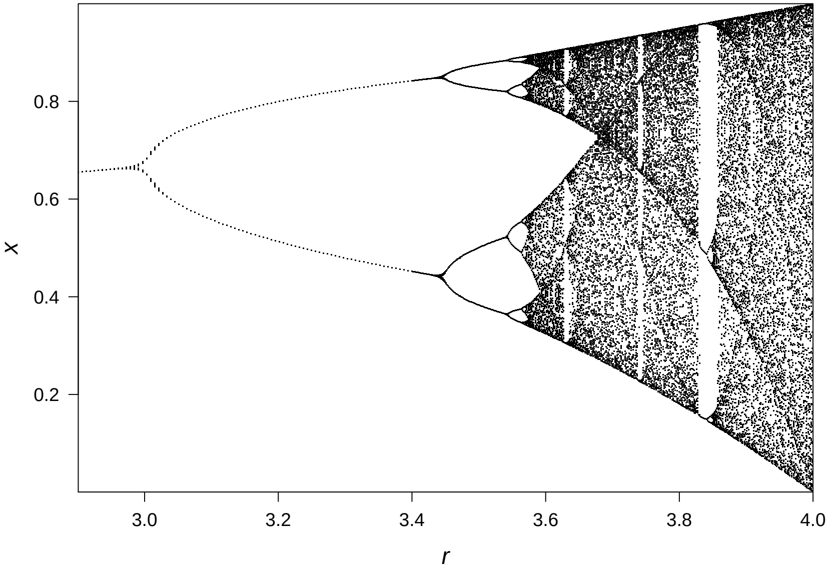
Logistic Map Summary

- 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.

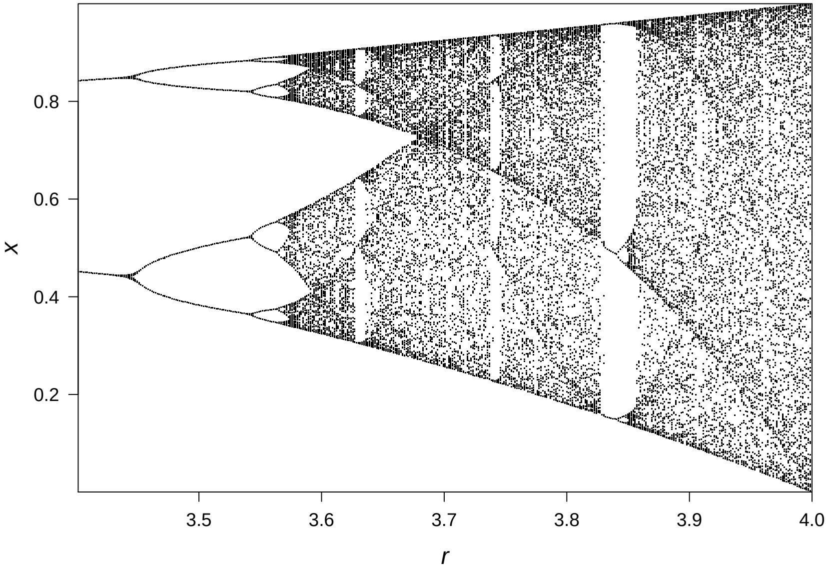
Logistic Map, $F(x) = rx(1-x)$, $\quad 1 \le r \le 4$



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



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



Mathematics
and Statistics

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

Mathematics 4MB3/6MB3
Mathematical Biology

Instructor: David Earn

Lecture 20
Space II
Friday 2 March 2018

Announcments

- **Assignment 3**.
  - Thanks for doing the group contribution survey.
- **Assignment 4** due Wednesday 14 March 2018, 11:30am.
- **Midterm test:**
  - *Date:* Thursday 8 March 2018
  - *Time:* 7:00pm to 9:00pm
  - *Location:* BSB-B154

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

  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 $\mathrm{M} = (m_{ij})$ is *dispersal matrix*.
- *Colour coding of indices:*
  - row indices are red
  - column indices are cyan

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

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.
- $\therefore\ 0 \leq m_{ij} \leq 1$ 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 $\mathrm{M} = (m_{ij})$

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 $\mathrm{M} = (m_{ij})$ 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.*,
$\mathbf{x}^t = ae \implies \mathbf{x}^{t+1} = be$ 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

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

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

□

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:

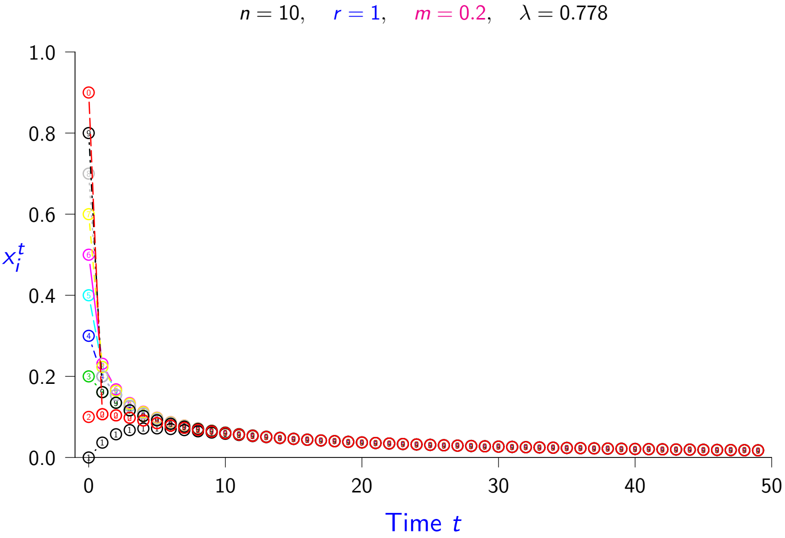
$$m_{ij} = \begin{cases} 1-m & i=j \\ m/2 & i=j-1 \text{ or } j+1 \pmod{n} \\ 0 & \text{otherwise} \end{cases}$$

- Real dispersal patterns generally between these two extremes

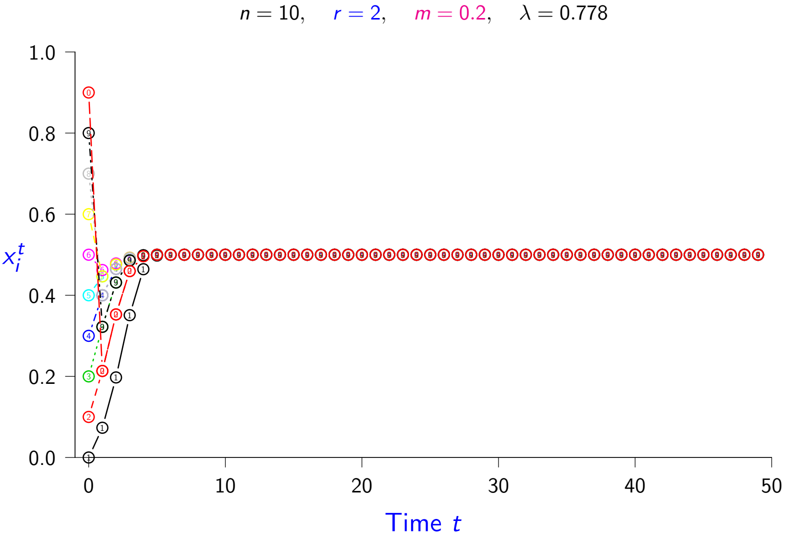
Key Question

- 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.

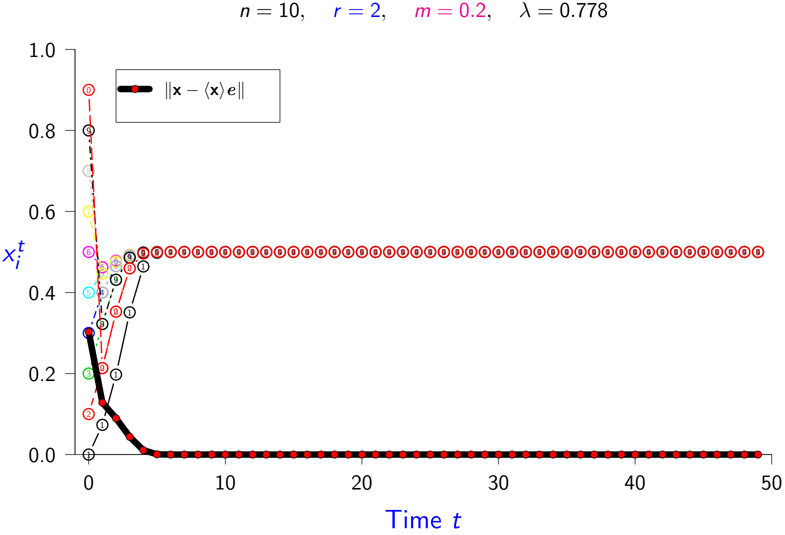
Logistic Metapopulation Simulation ($r = 1$, $m = 0.2$)



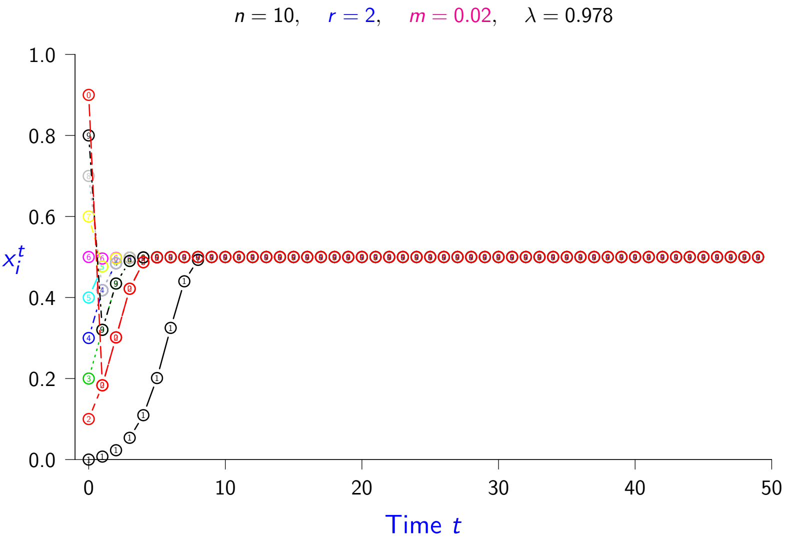
Logistic Metapopulation Simulation ($r = 2$, $m = 0.2$)



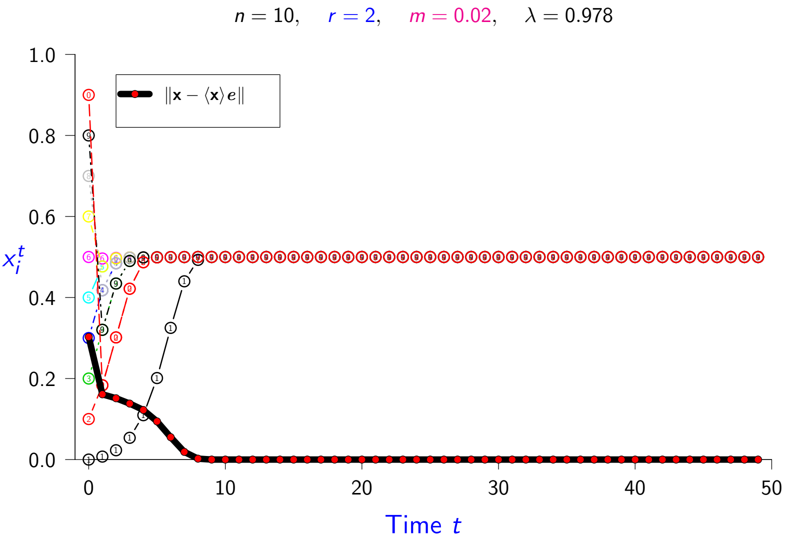
Logistic Metapopulation Simulation ($r = 2,\ m = 0.2$)



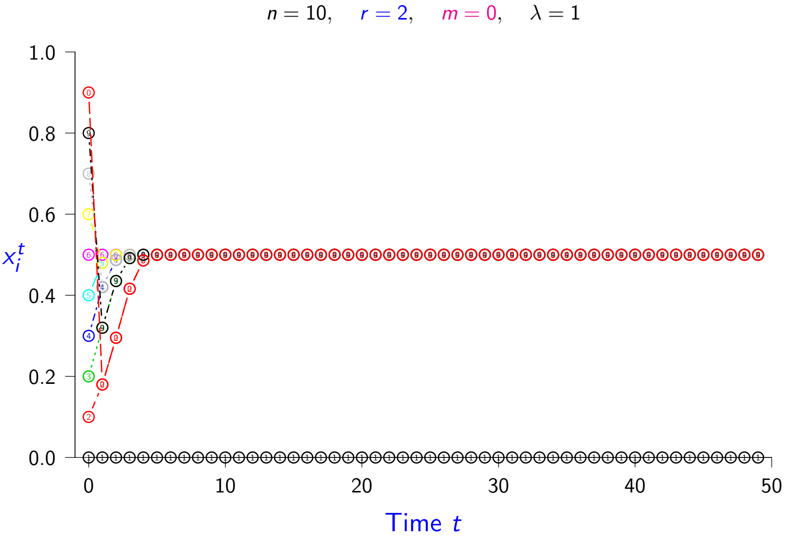
Logistic Metapopulation Simulation ($r = 2,\ m = 0.02$)



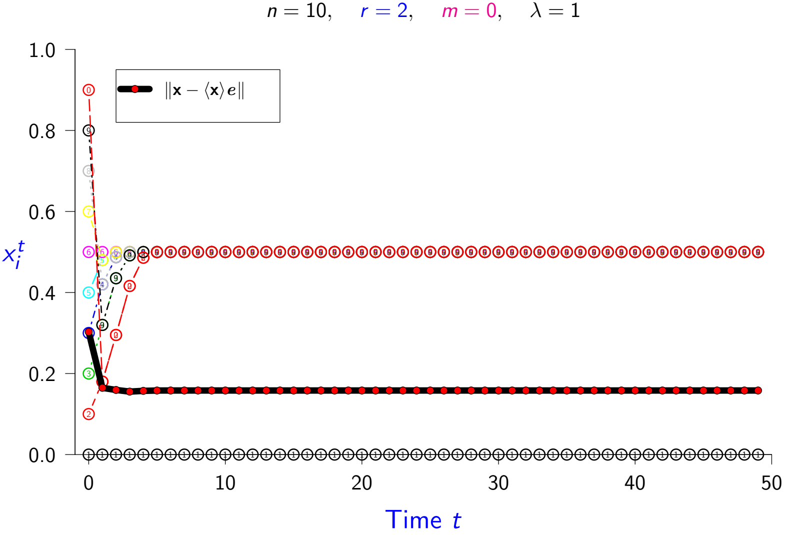
Logistic Metapopulation Simulation ($r = 2,\ m = 0.02$)



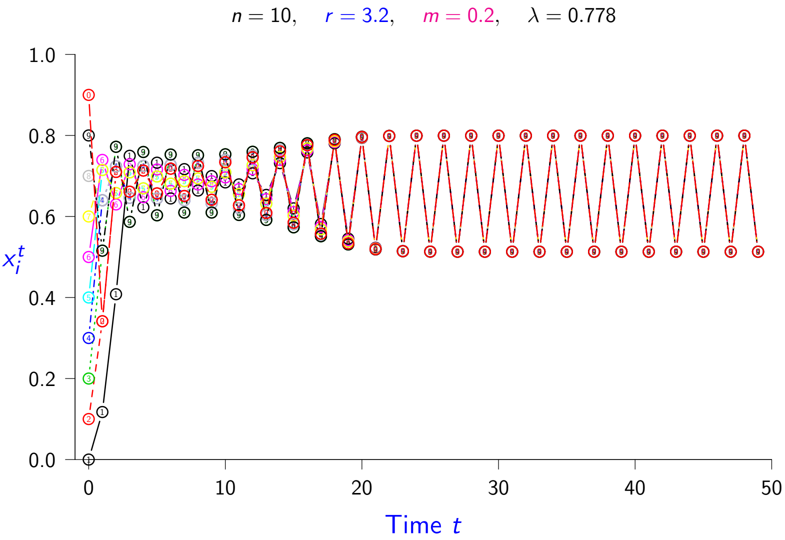
Logistic Metapopulation Simulation ($r = 2,\ m = 0$)



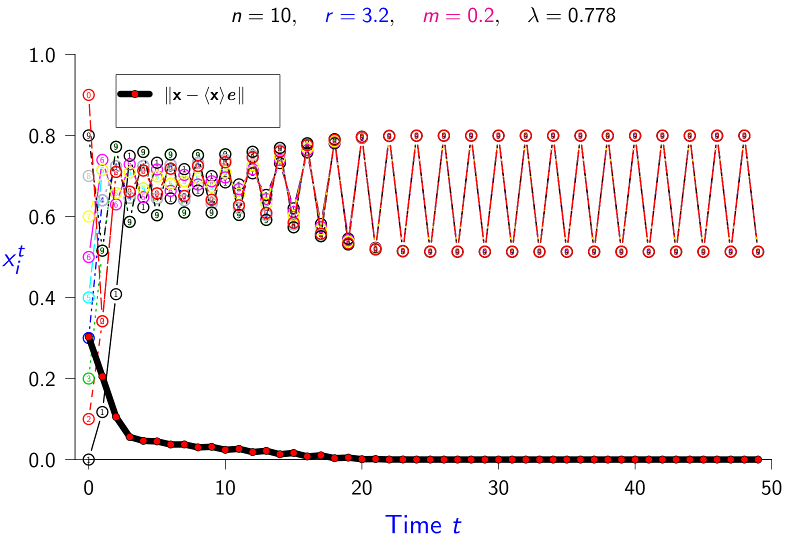
Logistic Metapopulation Simulation ($r = 2$, $m = 0$)



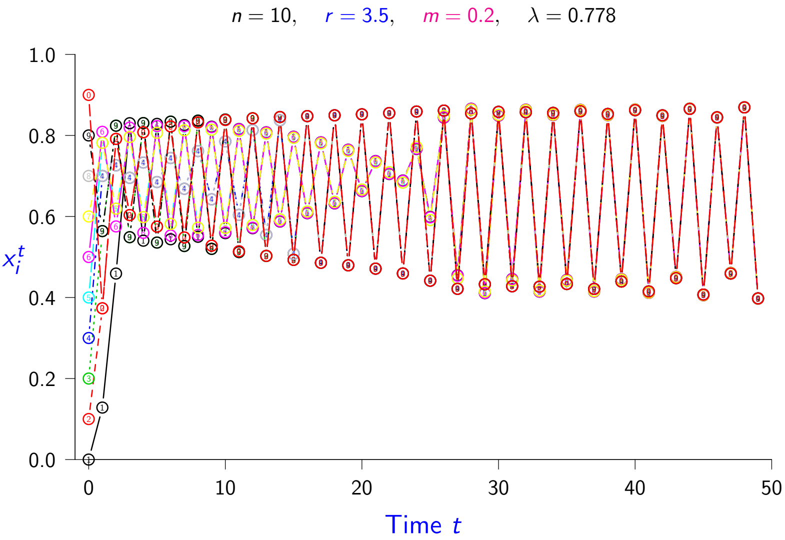
Logistic Metapopulation Simulation ($r = 3.2,\ m = 0.2$)



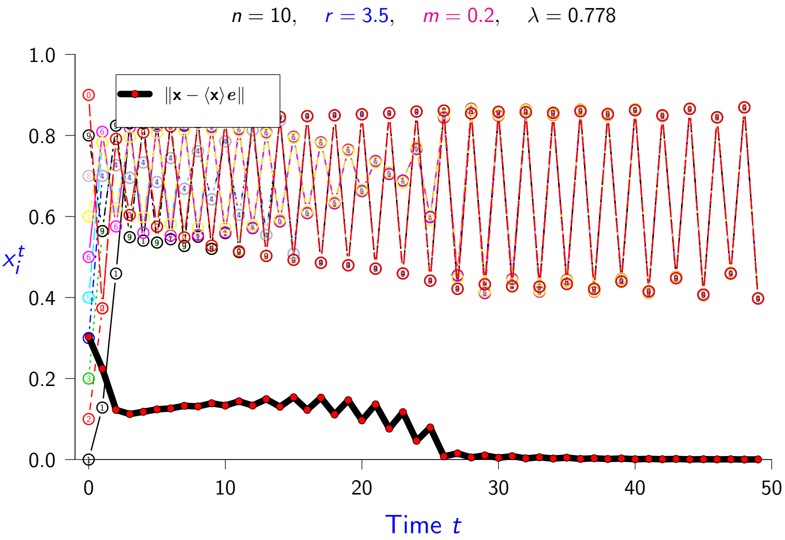
Logistic Metapopulation Simulation ($r = 3.2,\ m = 0.2$)



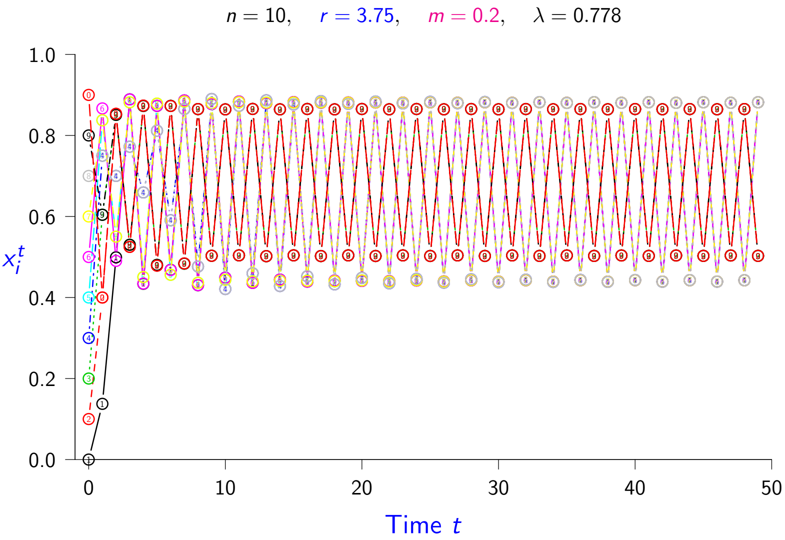
Logistic Metapopulation Simulation ($r = 3.5$, $m = 0.2$)



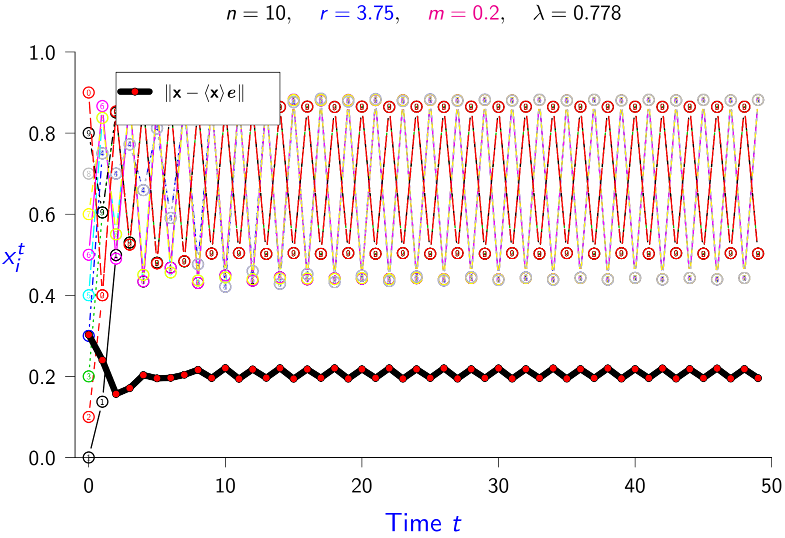
Logistic Metapopulation Simulation ($r = 3.5,\ m = 0.2$)



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

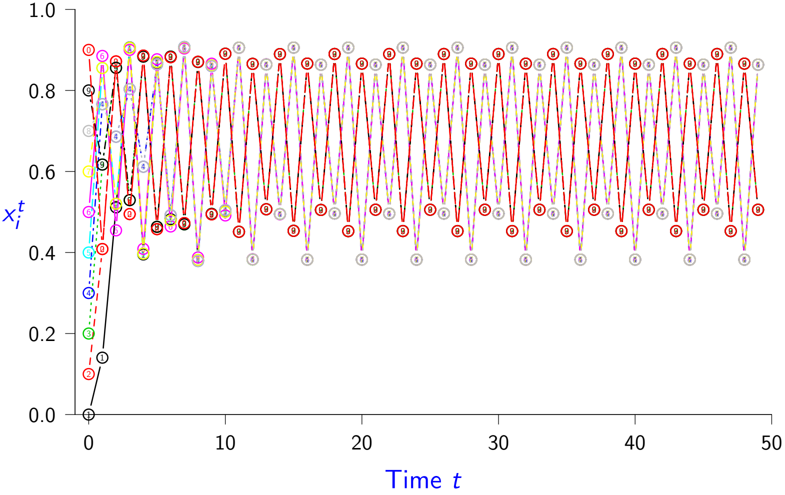


Logistic Metapopulation Simulation ($r = 3.75$, $m = 0.2$)

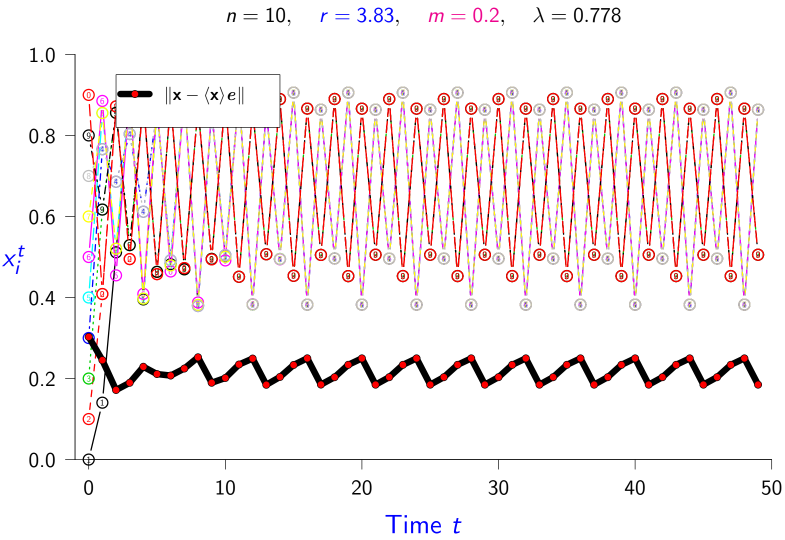


Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.2$)

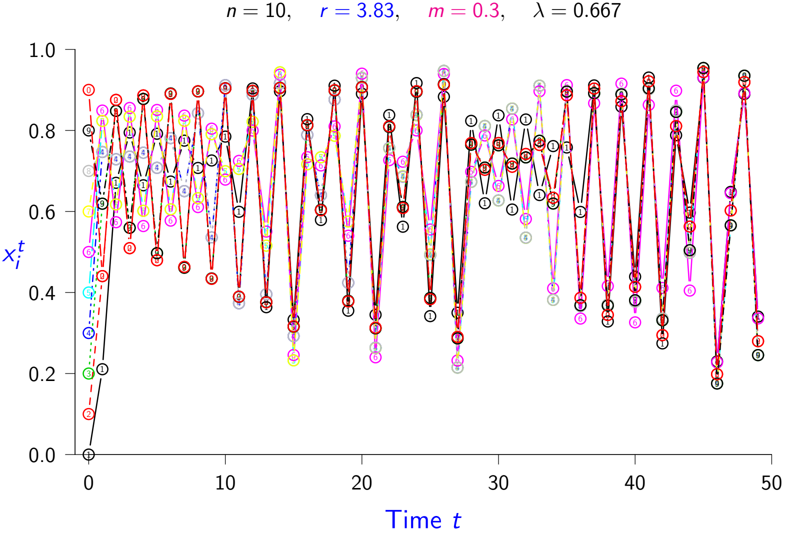
$n = 10$, $r = 3.83$, $m = 0.2$, $\lambda = 0.778$



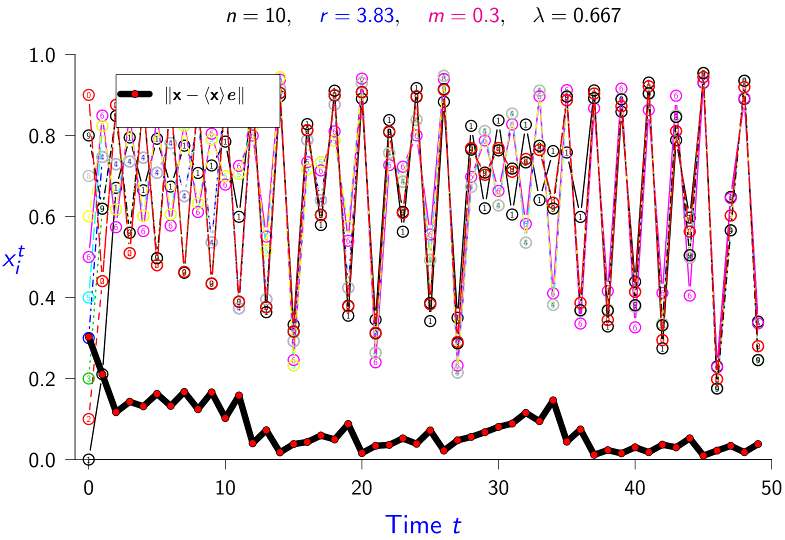
Logistic Metapopulation Simulation ($r = 3.83,\ m = 0.2$)



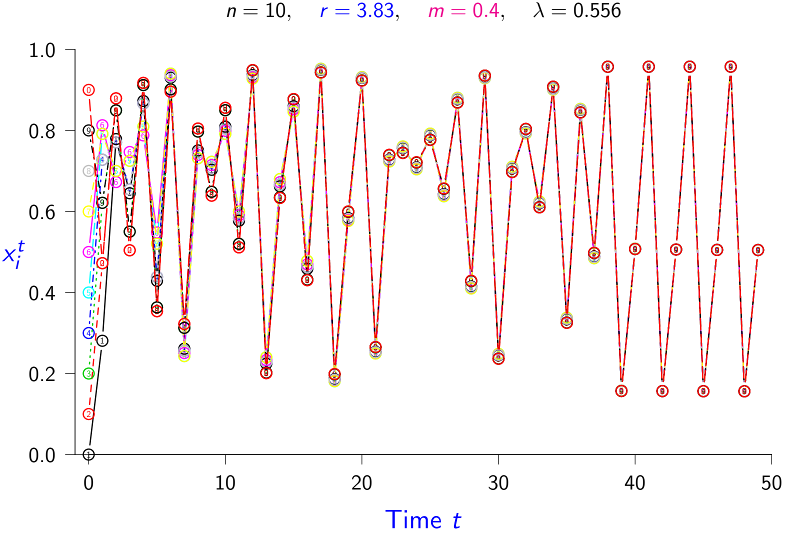
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.3$)



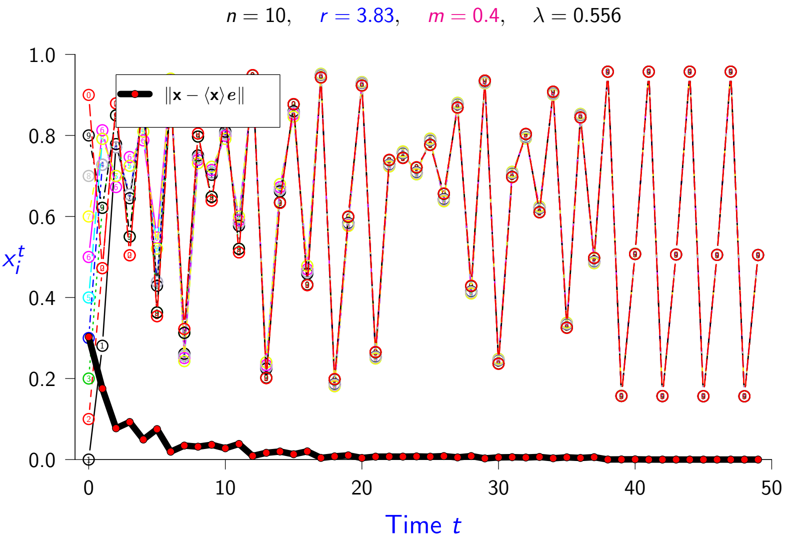
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.3$)



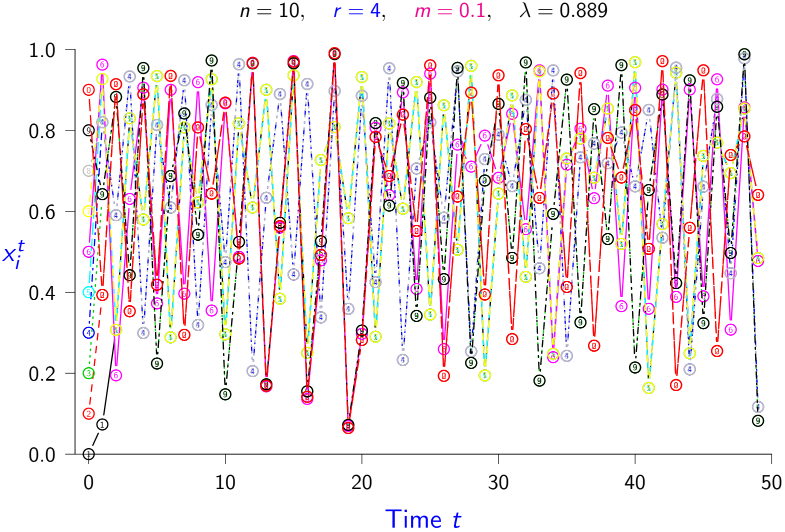
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.4$)



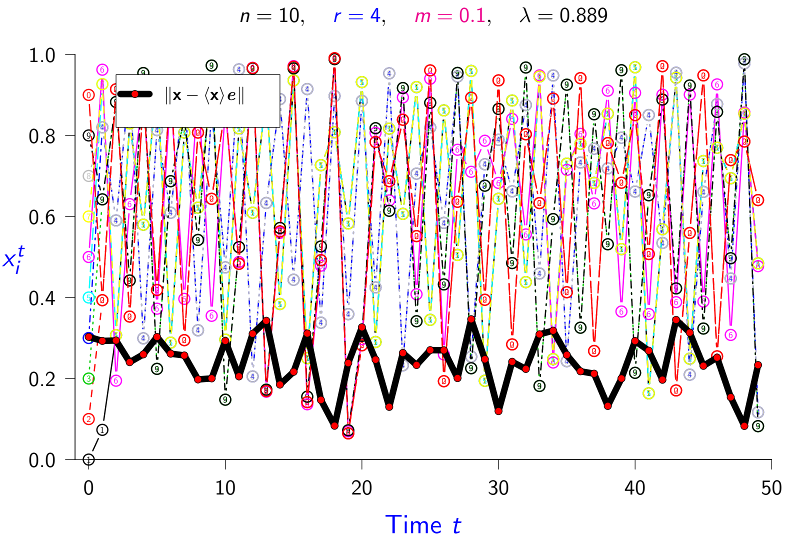
Logistic Metapopulation Simulation ($r = 3.83$, $m = 0.4$)



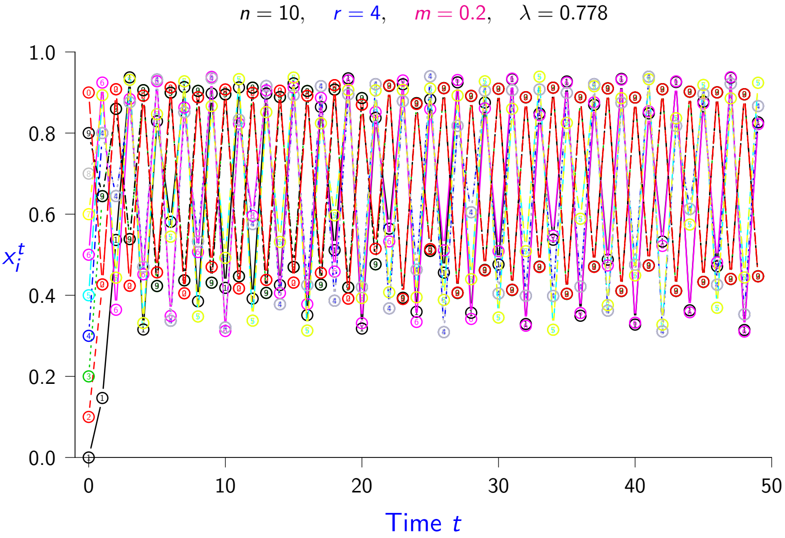
Logistic Metapopulation Simulation ($r = 4$, $m = 0.1$)



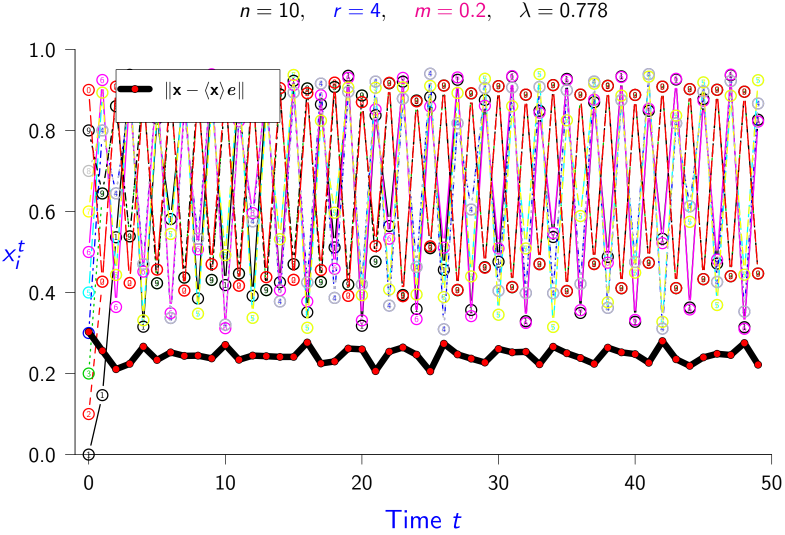
Logistic Metapopulation Simulation ($r = 4$, $m = 0.1$)



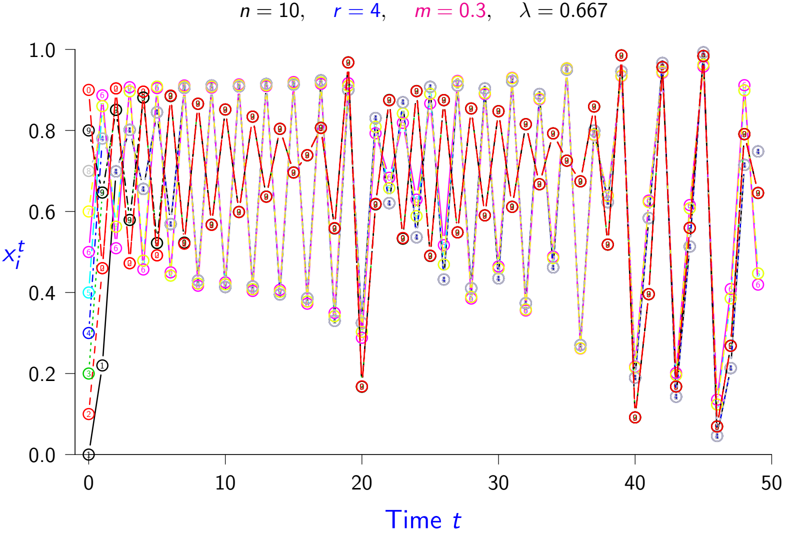
Logistic Metapopulation Simulation ($r = 4$, $m = 0.2$)



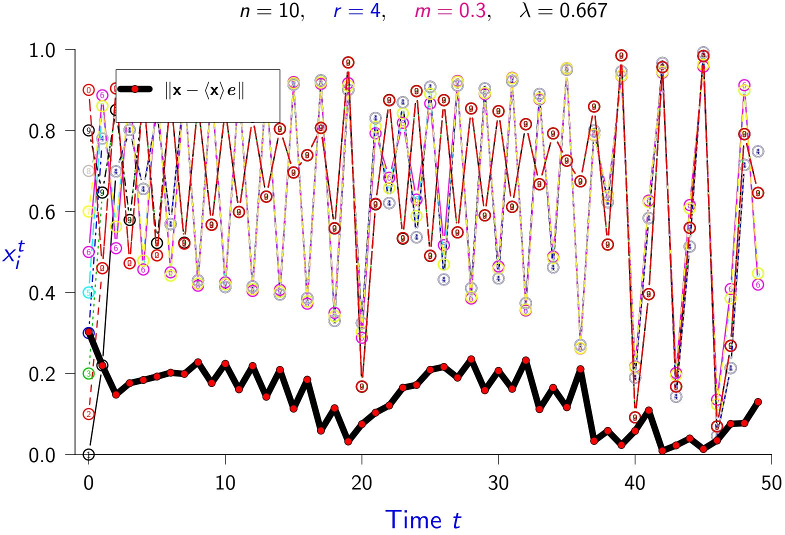
Logistic Metapopulation Simulation ($r = 4$, $m = 0.2$)



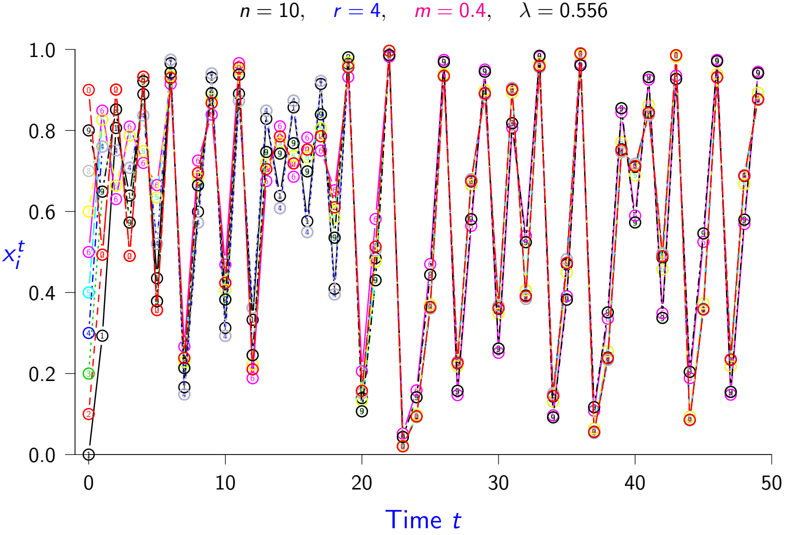
Logistic Metapopulation Simulation ($r = 4$, $m = 0.3$)



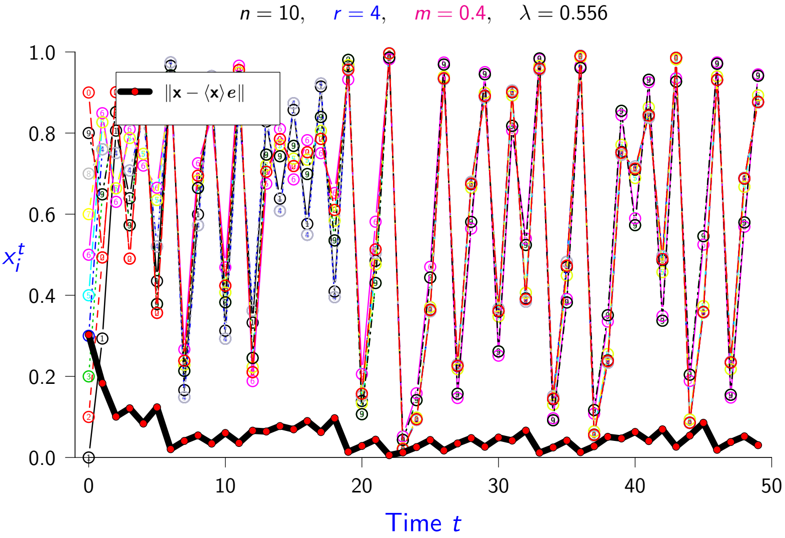
Logistic Metapopulation Simulation ($r = 4$, $m = 0.3$)



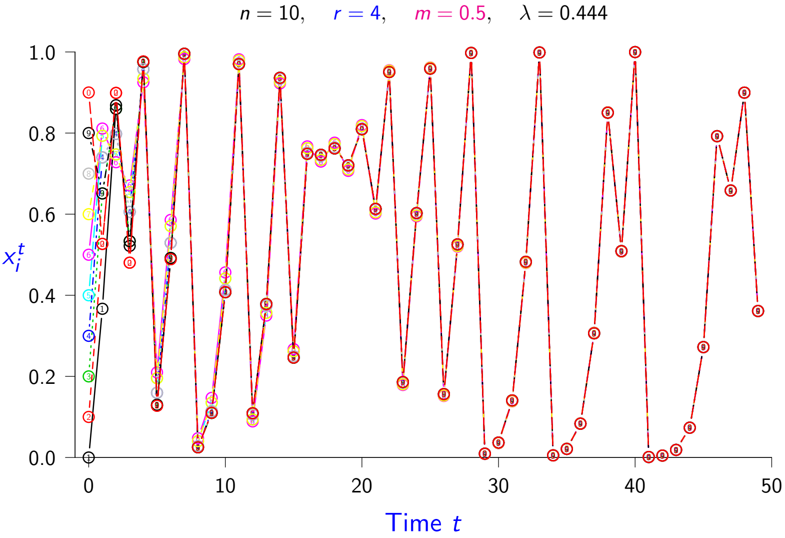
Logistic Metapopulation Simulation ($r = 4$, $m = 0.4$)



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



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



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