

SCIENCE

McMaster  
University 

# 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 12<sup>th</sup> 2019**  
**CIBC Hall**  
**5:00PM - 6:30PM**

**Contact:** trepanr@mcmaster.ca

**20** Space I

**21** Space II



Mathematics  
and Statistics

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

## Mathematics 4MB3/6MB3 Mathematical Biology

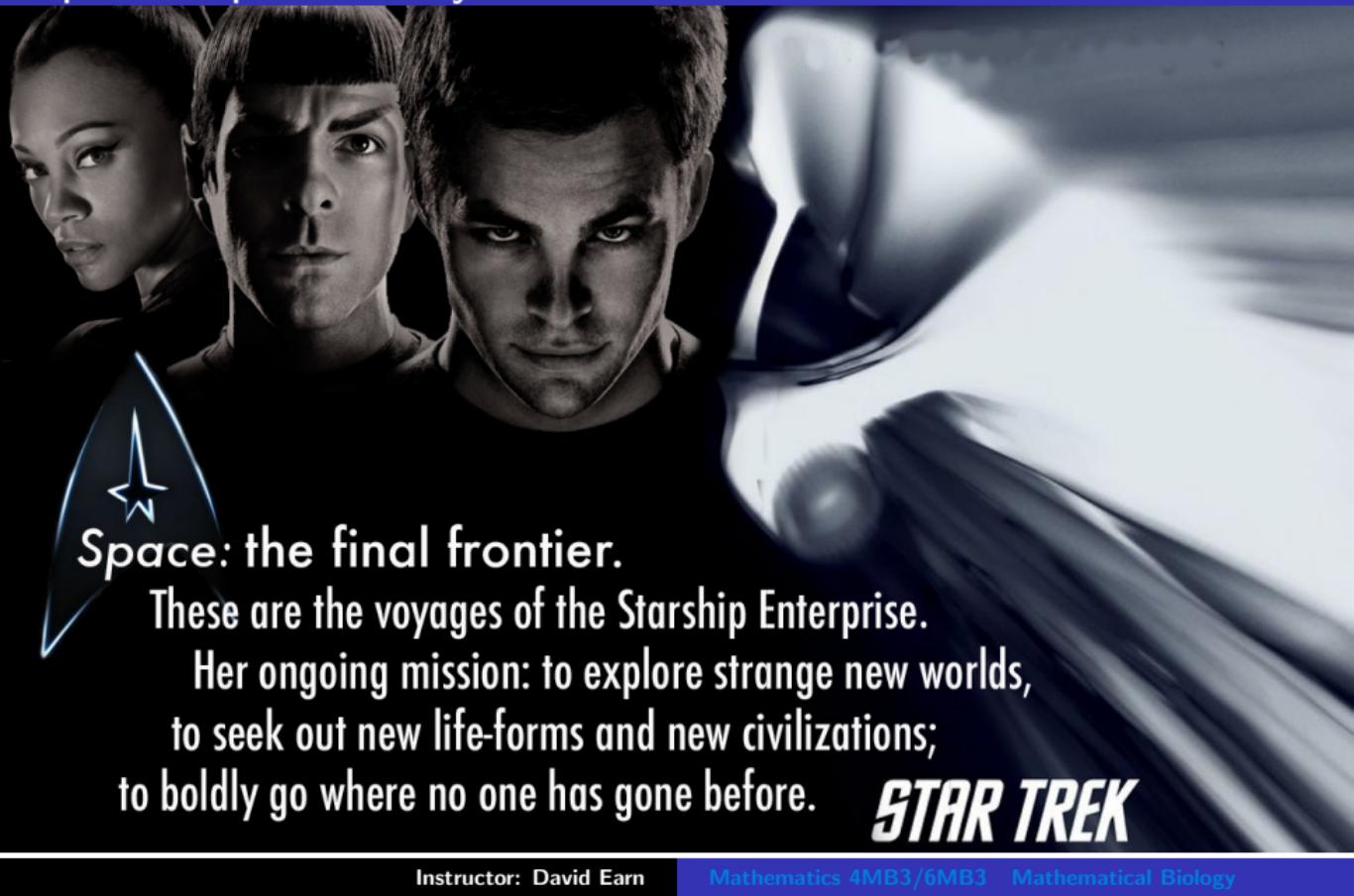
Instructor: David Earn

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.

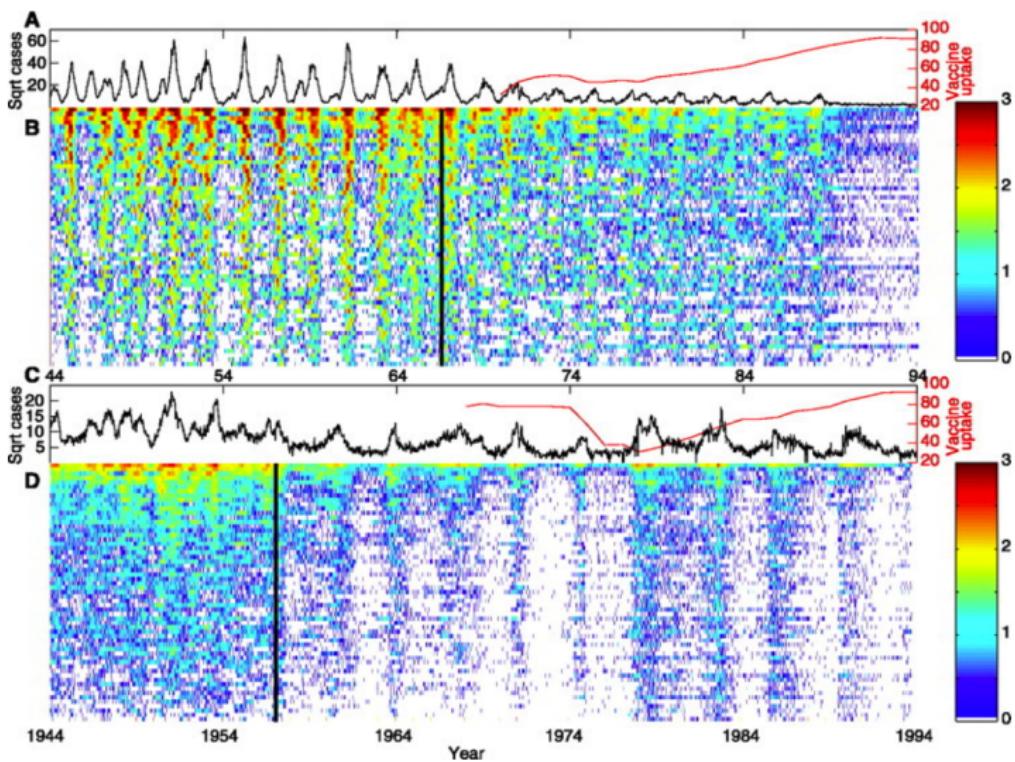
**STAR TREK**

## 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

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

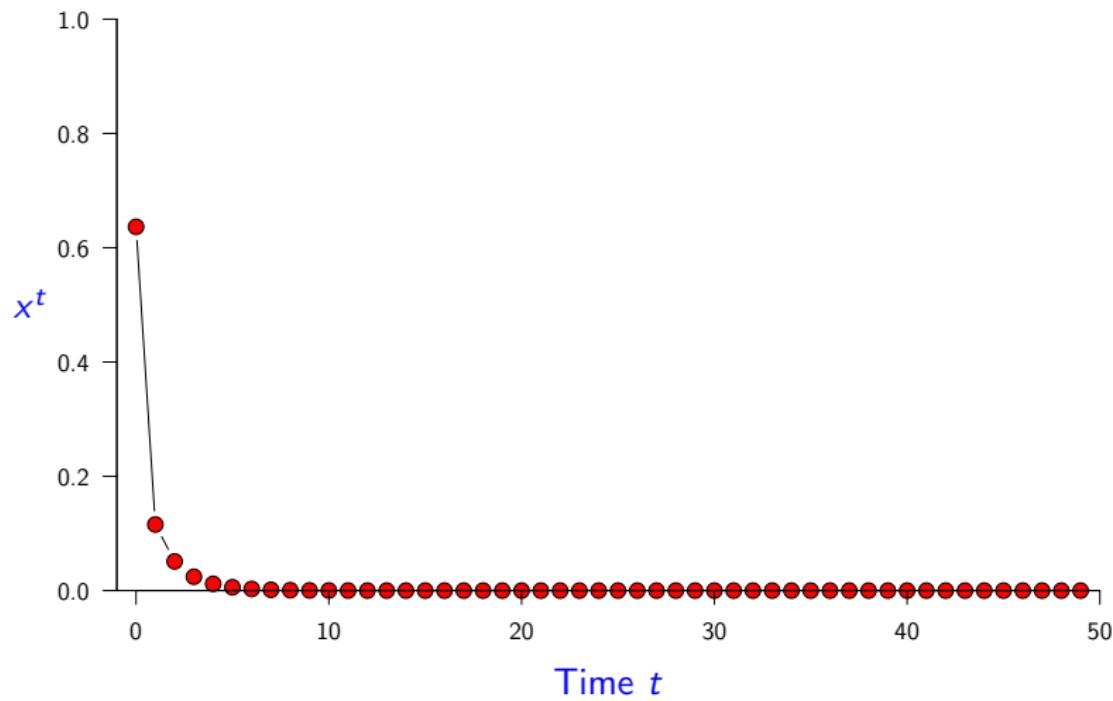
- Simplest non-trivial *discrete time* population model for a single species (with *non-overlapping generations*) in a *single habitat patch*.
- Time:  $t = 0, 1, 2, 3, \dots$
- State:  $x \in [0, 1]$  (population density)
- Population density at time  $t$  is  $x^t$ . Solutions are sequences:

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

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

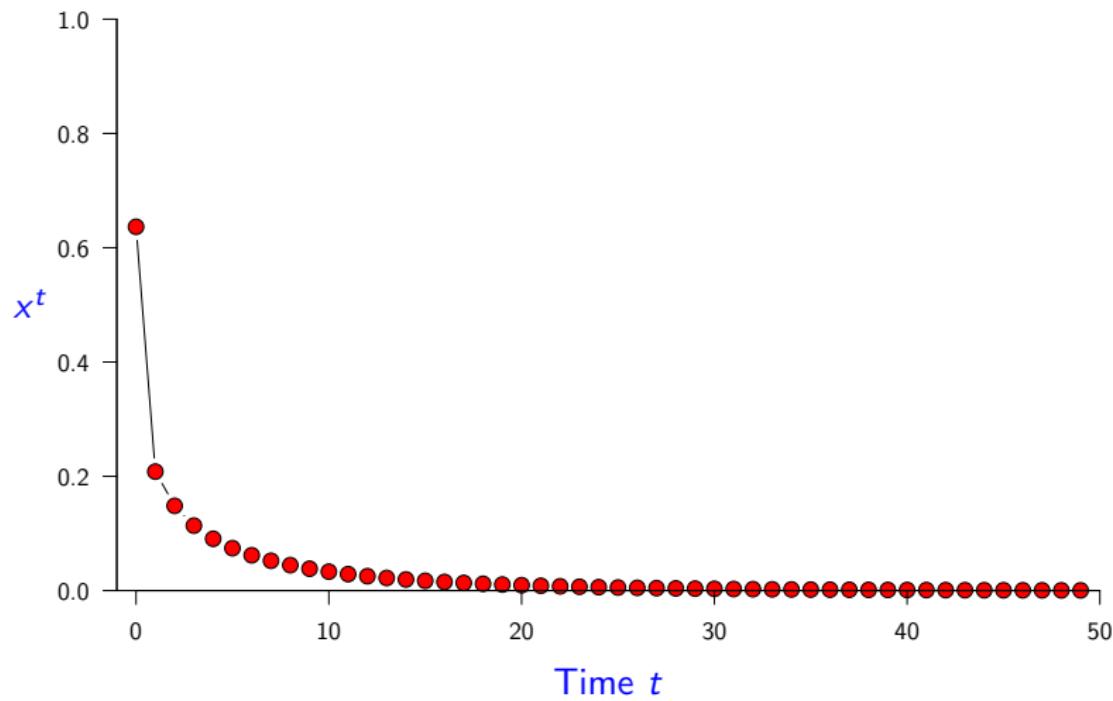
# Logistic Map Time Series, $r = 0.5$

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



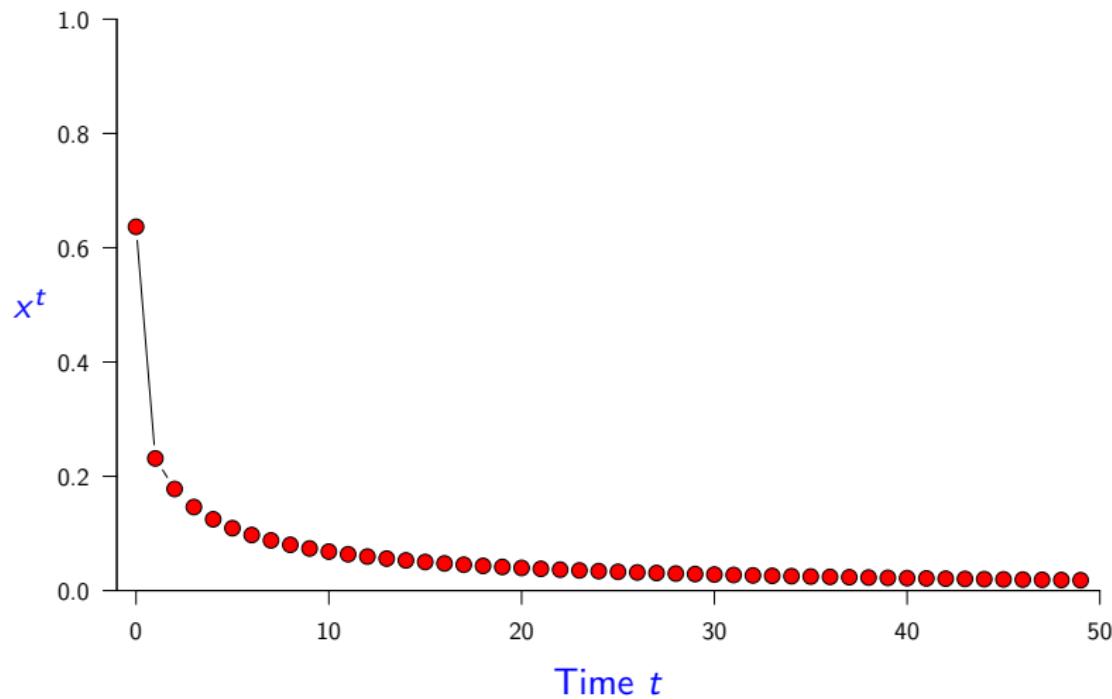
# Logistic Map Time Series, $r = 0.9$

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



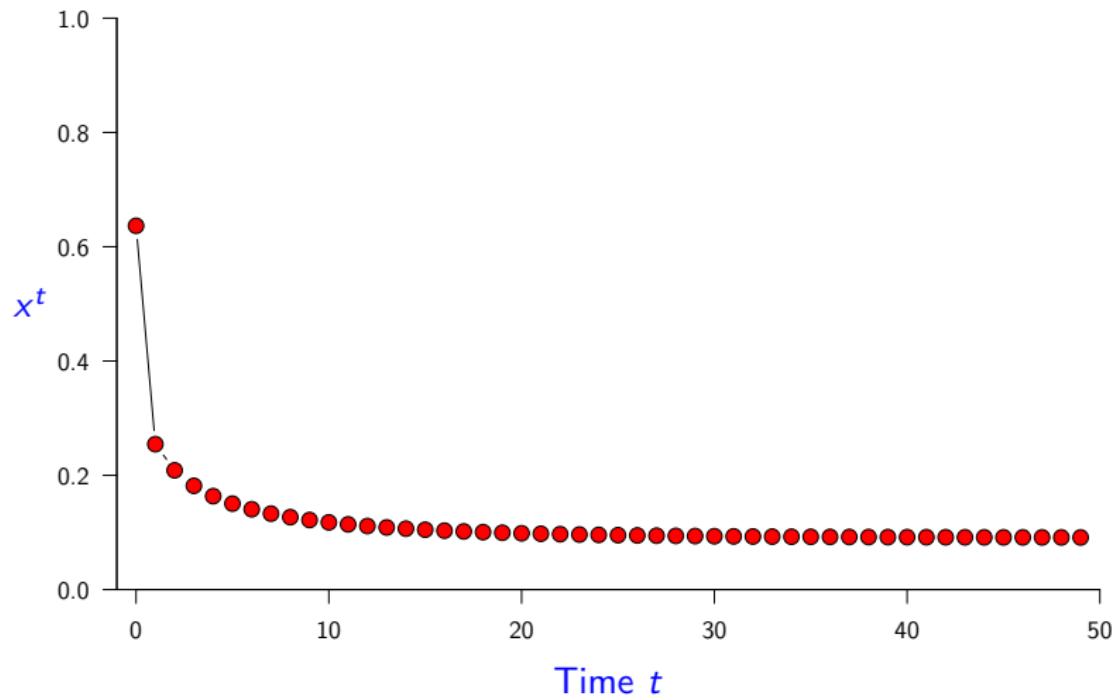
# Logistic Map Time Series, $r = 1$

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



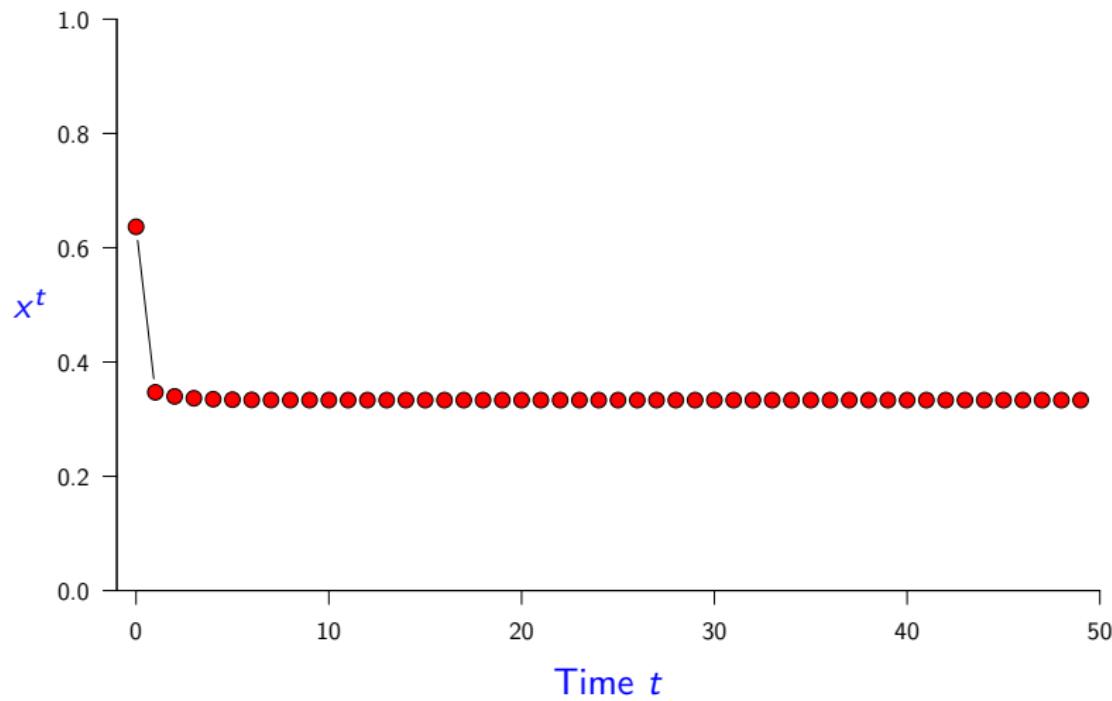
# Logistic Map Time Series, $r = 1.1$

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



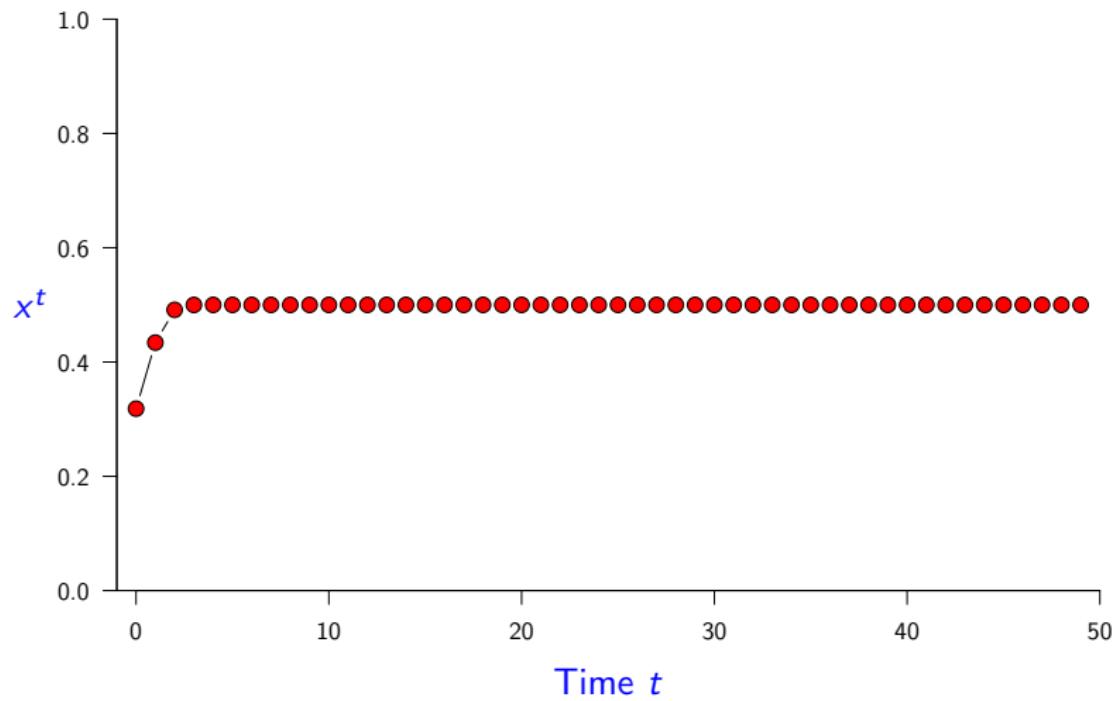
# Logistic Map Time Series, $r = 1.5$

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



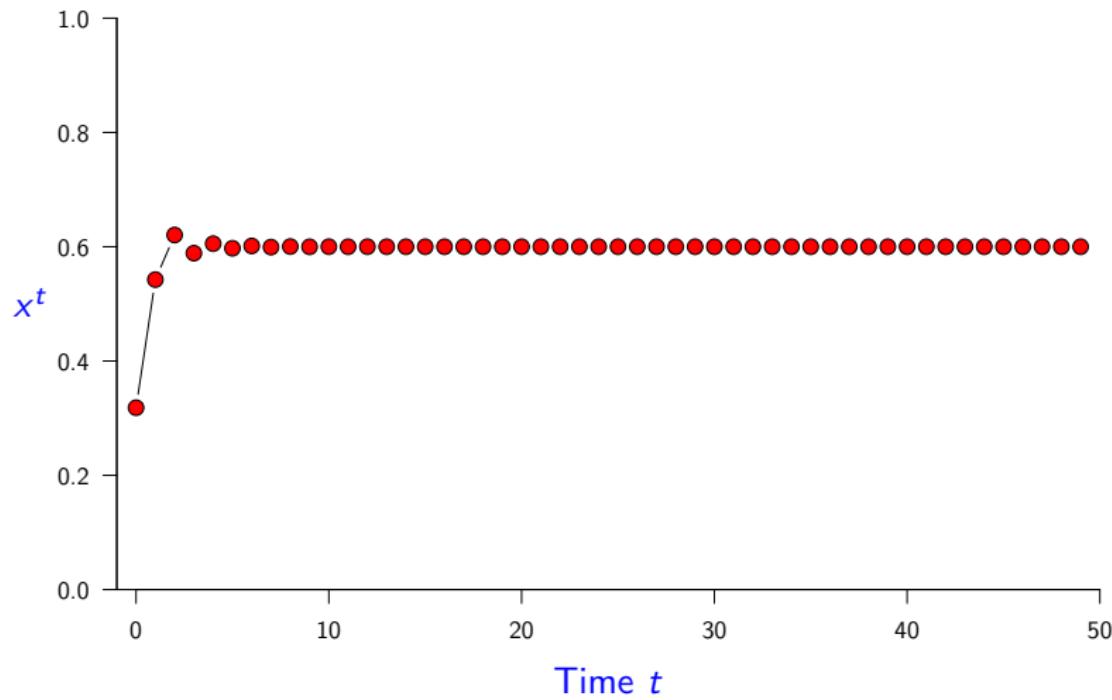
# Logistic Map Time Series, $r = 2$

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



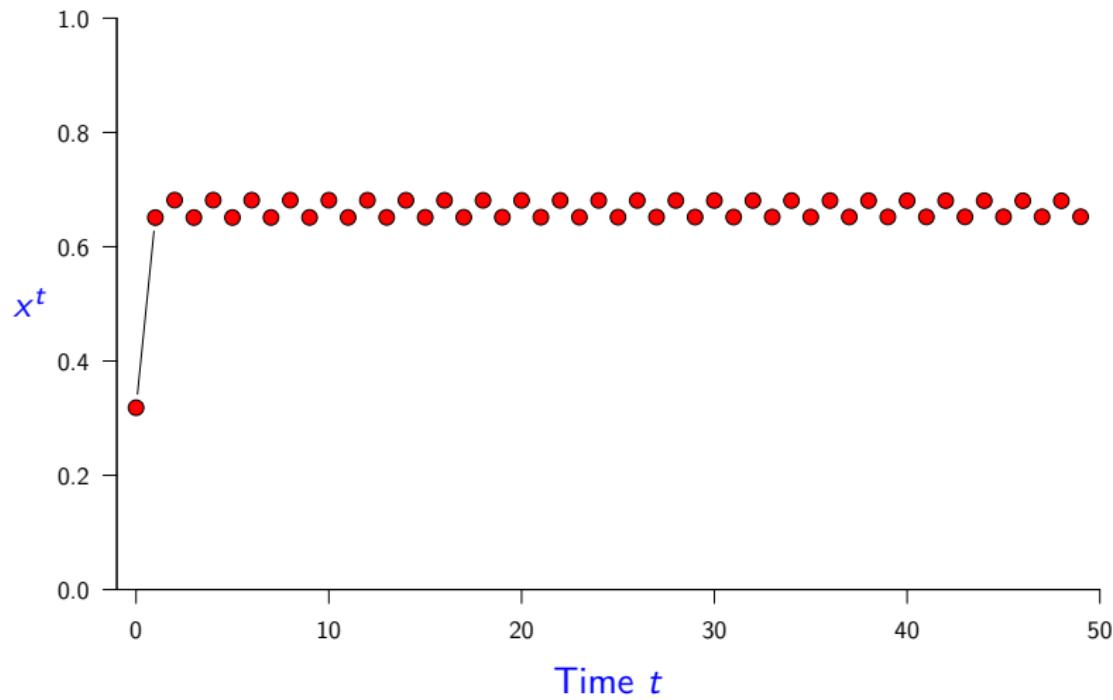
# Logistic Map Time Series, $r = 2.5$

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



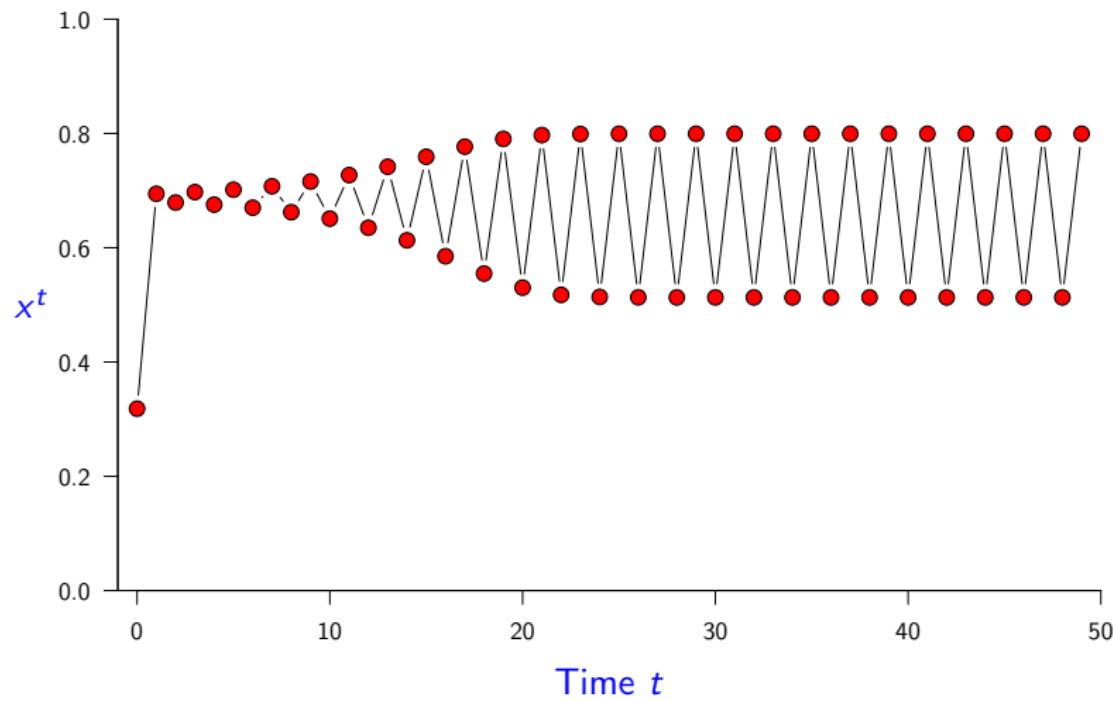
# Logistic Map Time Series, $r = 3$

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



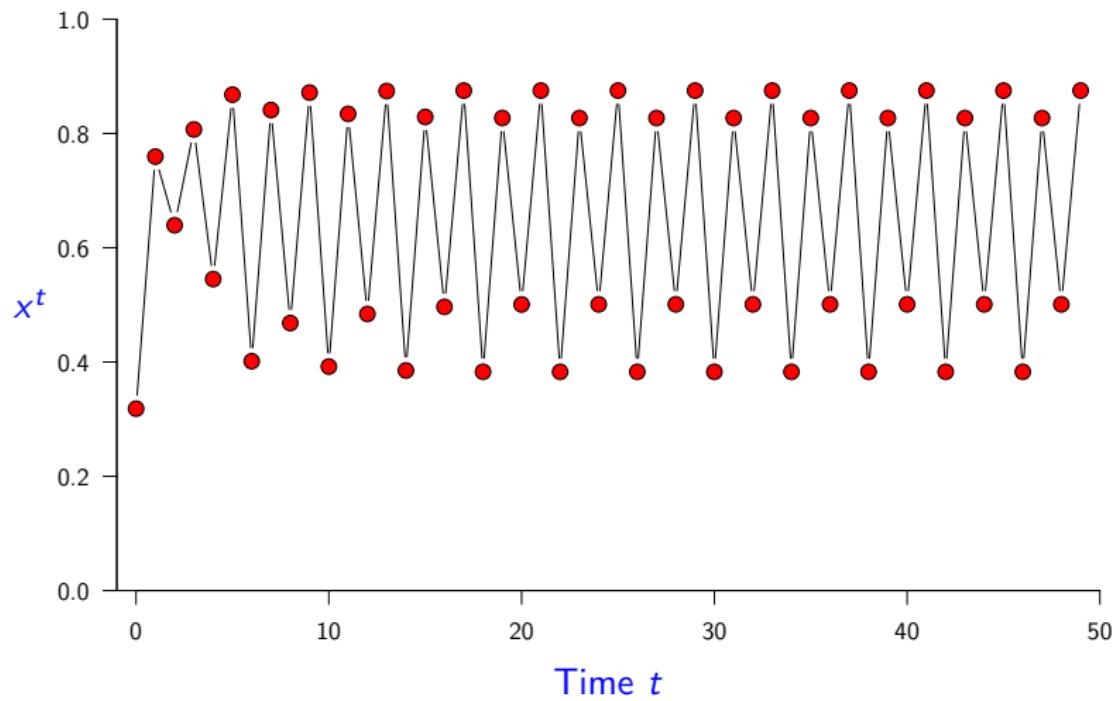
# Logistic Map Time Series, $r = 3.2$

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



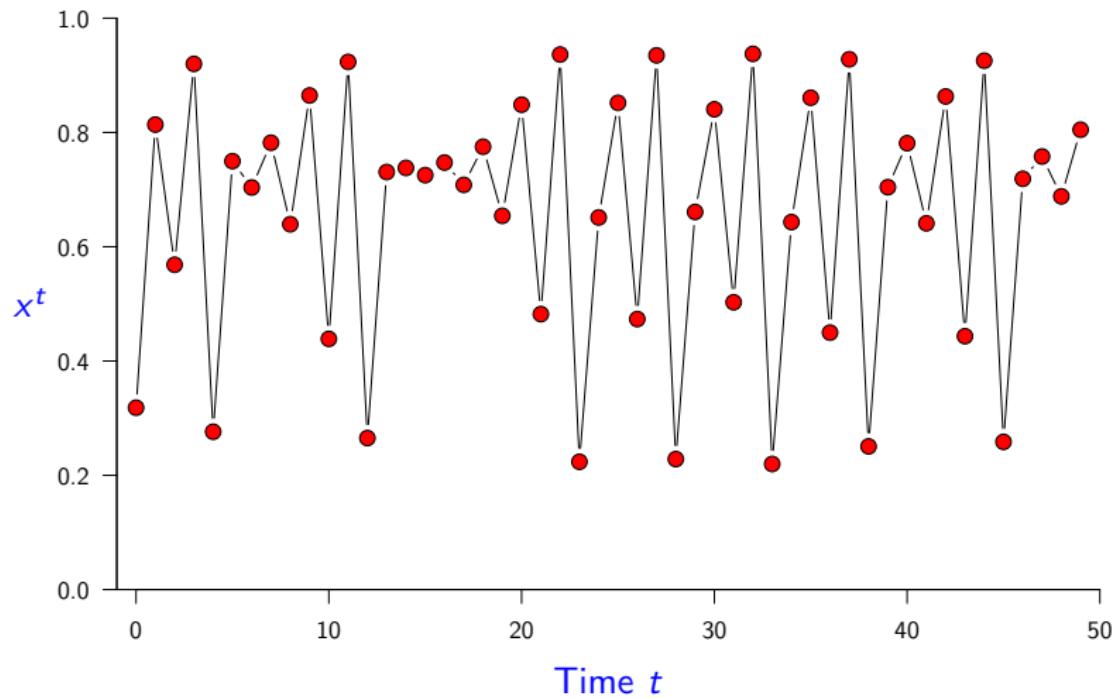
# Logistic Map Time Series, $r = 3.5$

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



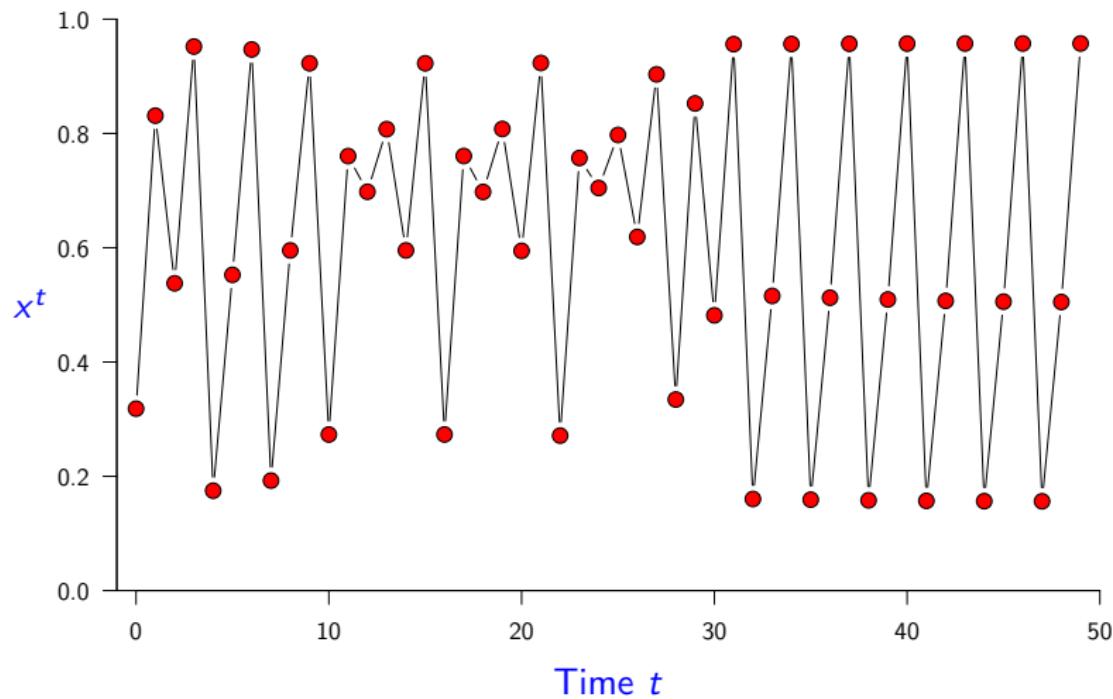
# Logistic Map Time Series, $r = 3.75$

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



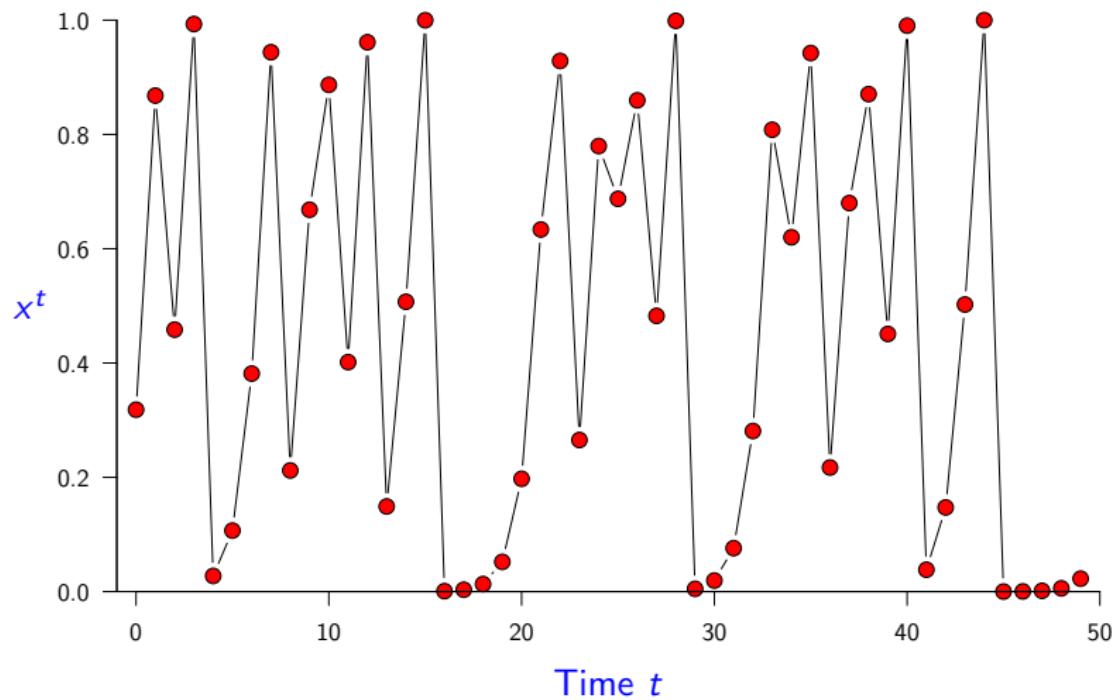
# Logistic Map Time Series, $r = 3.83$

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



Logistic Map Time Series,  $r = 4$ 

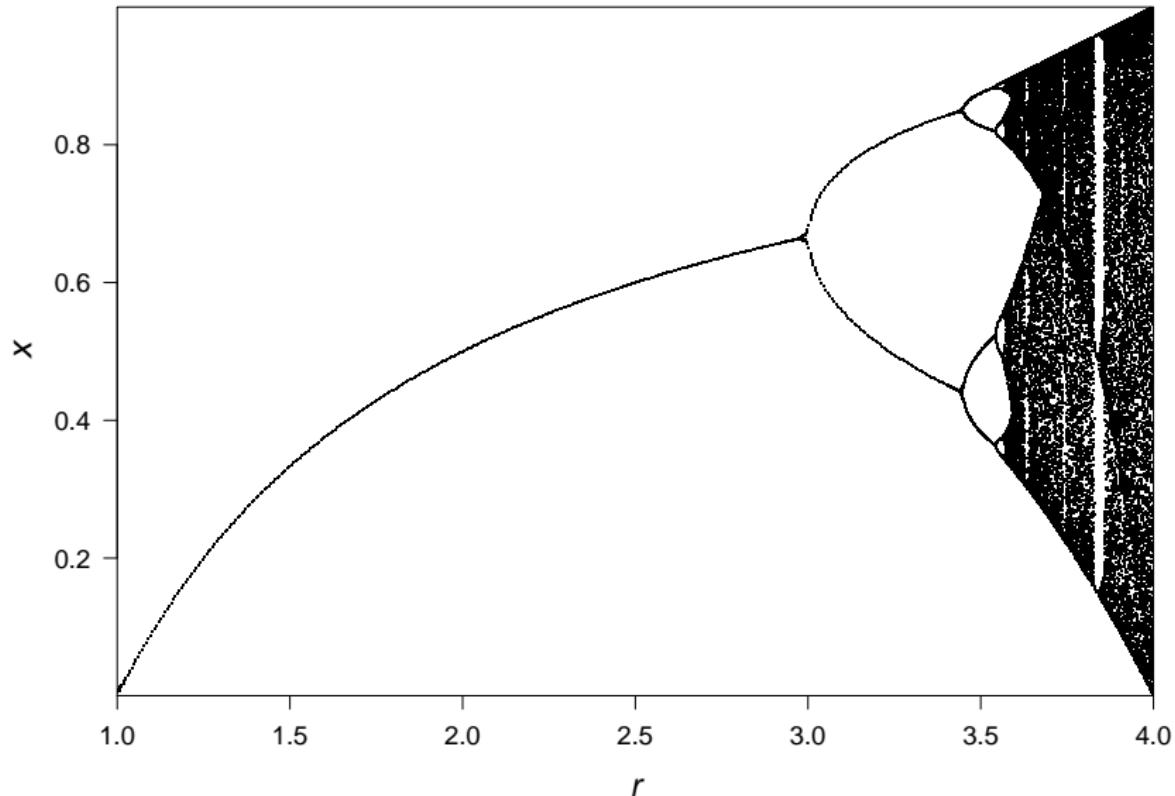
$$x^{t+1} = rx^t(1 - x^t), \quad r = 4, \quad x_0 = 0.31831$$



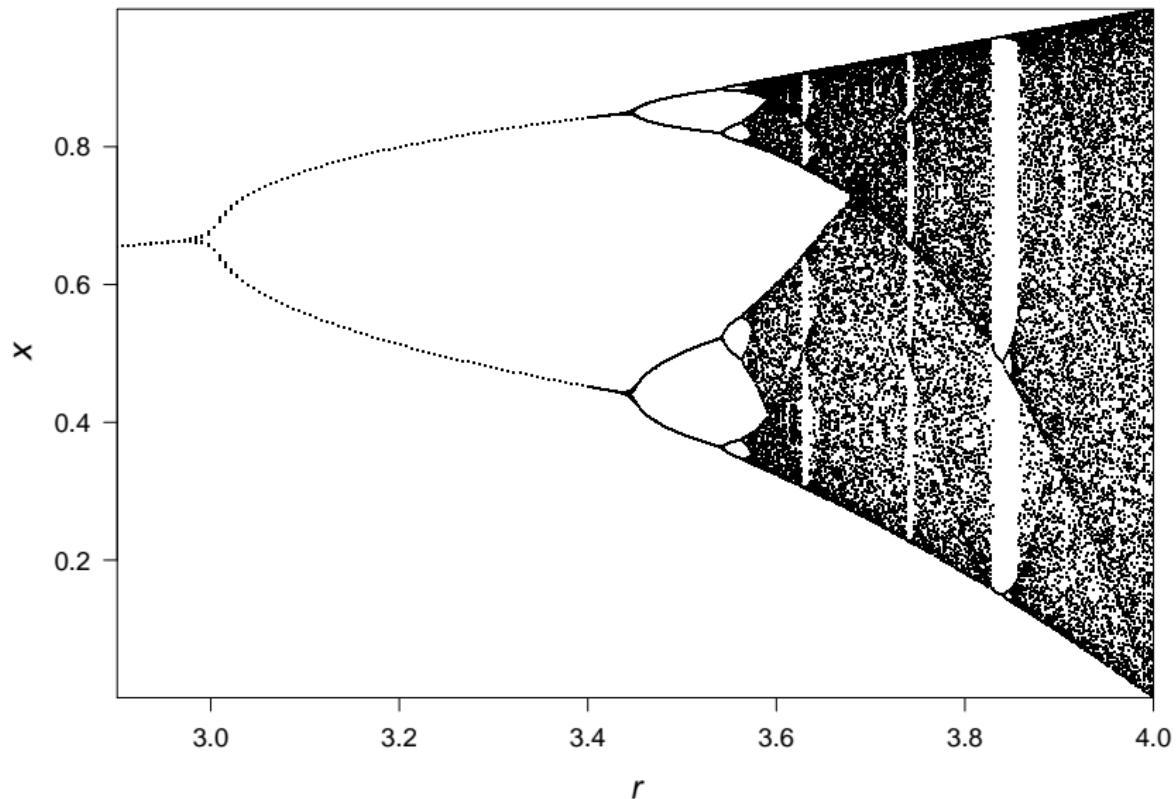
# Logistic Map Summary

- 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.

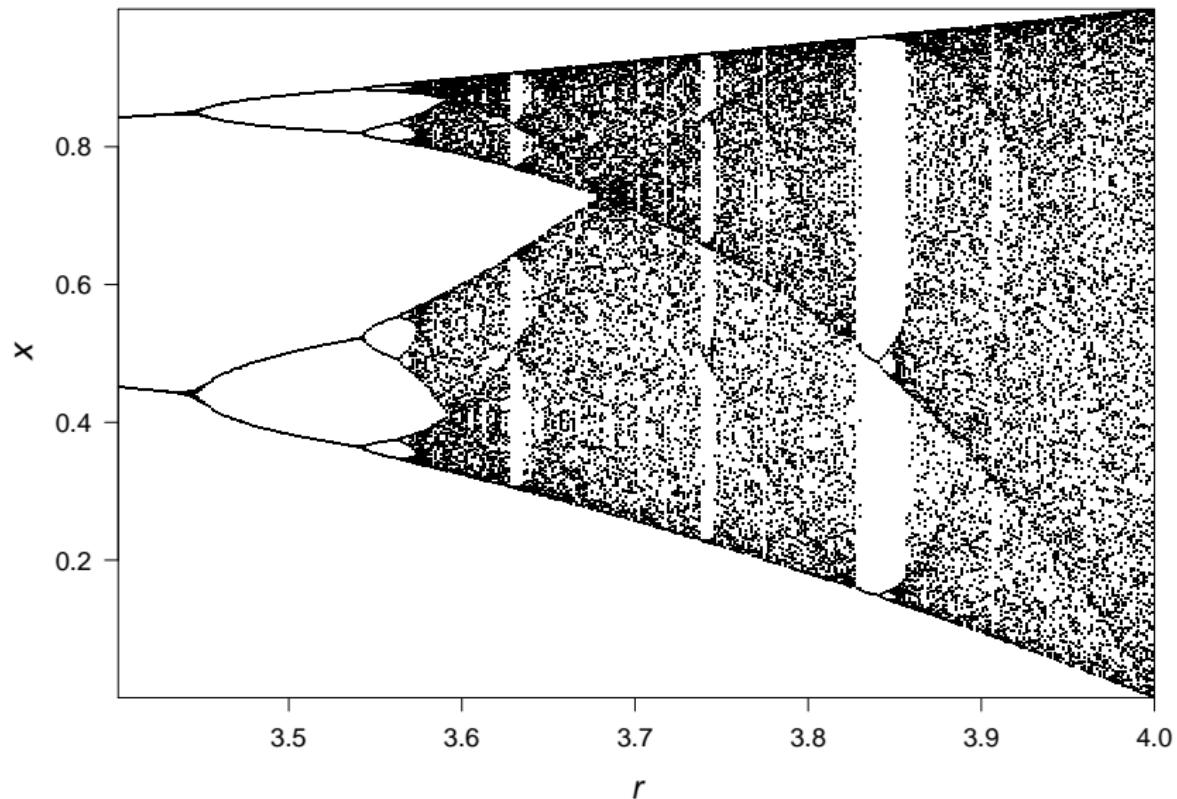
Logistic Map,  $F(x) = rx(1 - x)$ ,  $1 \leq r \leq 4$



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.,

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

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

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

□