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# MATHEMATICAL MODELS : ANALYSIS AND APPLICATIONS

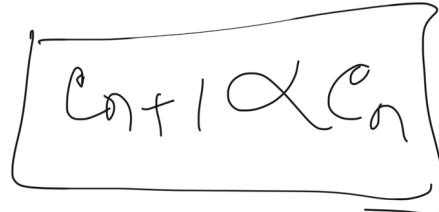
## Lecture 6 : Discrete Time Non – Linear Models in Population Dynamics - I

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# Contents:

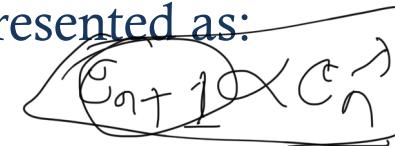
- Non-Linear Cell Division Model.
- Cob-web Graphs for Non-Linear Cell Models.
- Non-Linear Stability Analysis.
- Logistic Growth Function.



# Non-Linear Cell Division Model:

- In the previous lectures, we have studied about the analytical and graphical solution of linear models of cell division. Mathematically (considering no migration) they were represented as:

$$C_{n+1} = \alpha C_n.$$



- The meaning associated with this basic model is that each cell will survive till end. **But does it happen in actual ? No !** To survive each cell, they need to fight for resources. So, there is a need to include the survival rate.
- Again, **on which factor(s) should this survival function depend on?** And what should be the nature of this function?

# Non-Linear Cell Division Model:

- To answer previous questions, let's model out the cell division process with the survival function  $S(C)$ ,

$$C_n = \alpha C_{n-1} S(C_{n-1}) \text{ where } n \in \mathbb{N}$$

- Now, let's analyze this survival function  $S(C)$

1. **No Competition:** If  $S(C) = 1$  for all  $C$ .



2. **Contest Competition:** Here there are finite number of resources. The cells which are able to take one resource will survive and take part in next generation. So

$$\begin{cases} S(C) = 1 \\ S(C) = C_{\text{critical}} / C \end{cases}$$

for  $C \leq C_{\text{critical}}$   
for  $C > C_{\text{critical}}$

3. **Scramble Competition:** Here each individual is assumed to share equal amount of limited resource. If this quantity is sufficient, they will survive otherwise not. Hence,

$$\begin{cases} S(C) = 1 \\ S(C) = 0 \end{cases}$$

for  $C \leq C_{\text{critical}}$   
for  $C > C_{\text{critical}}$

# Non-Linear Cell Division Model:

- Now, practically it's not possible for critical value to be fixed. Also, 0 survival seems unrealistic at-least for large populations ! Then how should this survival function to act?
- Let us assume that  $f(C) = CS(C)$ .
- Now, the contest competition describes the exact compensation as  $\lim_{C \rightarrow \infty} f(C) = l$  where  $l$  is a constant. This represents the situation of compensating any numbers of new cells with already extinct cells. Hence  $s(c) \sim \frac{1}{c}$  for large  $C$ .
- Now, let's consider the in-general case for  $s(C) \sim \frac{l}{C^b}$ 
  - when  $0 < b < 1$  it's called under compensation – resources are less utilized
  - when  $b > 1$  it's called over compensation – resources are over utilized.

# Non-Linear Cell Division Model:

- Now, if  $b \approx 1$  then there is contest competition which means  $f(C)$  eventually levels out a non-zero level for large population hence population will be stabilized by avoiding too many newborns.

- Again, come back to the model equation

$$C_n = \alpha C_{n-1} S(C_{n-1}) = \alpha f(C_{n-1}) \text{ where } n \in \mathbb{N}.$$

- For exhibition of compensatory behavior,  $f(C) \sim \text{constant}$  and  $S(C) \sim 1$  for small  $C$  assuming very small competition among cells. Hence growth must be exponential with growth rate  $\alpha$ .

- One of the simple functions of  $S(C)$  can be

$$S(C) = \frac{1}{1 + ac}, \text{ where } a \text{ is any constant.}$$

# Non-Linear Cell Division Model:

- This leads to the model equation as,

$$C_n = \alpha \frac{C_{n-1}}{1 + aC_{n-1}} \text{ where } n \in N$$

- If we assume the carrying capacity of environment is  $E$ , and the population reached  $E$  will stay there i.e. if  $C_k = E$  for some  $E$  then  $C_{k+m} = E$  for all  $m \geq 0$  and for some  $k$ .
- By substituting in model equation will lead to  $a = \frac{\alpha-1}{E}$ , and the resulting model is given as follows. It's also known as **Beverton-Holt Model**.

$$C_k = \alpha \frac{C_{k-1}}{1 + \frac{\alpha-1}{E} C_{k-1}}$$



# Non-Linear Cell Division Model:

- This model can further be generalized as:

$$C_k = \alpha \frac{C_{k-1}}{(1 + \bar{a}C_{k-1})^b}$$

- This is also known as **Hassel Model**. Depending on b, it compensates both contest competition (for  $b=1$ ) and scramble competition (for  $b>1$ ).



# Stability of Non-Linear System:

- There are relatively very few cases where analytical solution of non-linear difference equations can be computed directly.
- A general non-linear difference equation is in form of:
$$x_{n+1} = f(x_n, x_{n-1}, \dots) \text{ where } n \in N.$$
- Thus, we must have to be satisfied with the nature of system (**stability analysis**) or with the computer generated solution (**numerical analysis**).
- In order to study the nature of system, let's consider a general first order equation (because higher order equations can be converted into system of first order equations. **How?**).



# Stability of First Order Non-Linear Equation:

- The general first order difference equation is:

$$x_{n+1} = f(x_n) \text{ where } n \in \mathbb{N}.$$

- There are a lot of importance of steady state solution especially in problems of dynamics where growth, propagation or reproduction takes place.

- An equilibrium or a steady state relates to the absence of change in system.

- In context of difference equation, a steady state solution  $\lambda$  is defined as:  $x_{n+1} = x_n = (\lambda)$  which describes no change from generation  $n$  to  $n+1$ .

- This implies  $\lambda = f(\lambda)$ . Mathematically, this point  $\lambda$  is referred as fixed point of function  $f(\cdot)$  (the value that function  $f$  leaves unchanged).

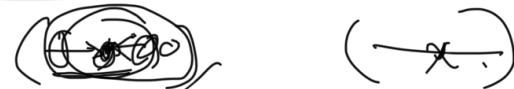
- Invariant

- Quite often, solving for fixed point is simpler/easier than solving non-linear difference equation for general solution.



# Stability of First Order Non-Linear Equation:

- A steady state is termed to be stable if all the neighboring states are attracting to it. If it is not so, steady state is unstable.



- If the system is unstable, population may crash or the number of competing group may shift in favor of few one.



- Now, let us take any arbitrary point  $x_n$  and we want to study that whether this point move away or move towards the steady state. (remember cob-web? The same thing was done graphically.)

- Let's assume  $x_n = \lambda + \varepsilon_n$ , where  $\varepsilon_n$  is a very small quantity termed as perturbation of steady state.

$$\begin{aligned} \rightarrow x_{n+1} &= \lambda + \varepsilon_{n+1}, \quad x_{n+1} = f(x_n) \rightarrow \lambda = f(\lambda) \\ \rightarrow \varepsilon_{n+1} &= x_{n+1} - \lambda, \\ \rightarrow \varepsilon_{n+1} &= f(x_n) - \lambda, \quad (\text{from fixed point equation}) \end{aligned}$$
$$\begin{aligned} \lambda &= \alpha_0 + h = f(x_0 + h) \\ &= f(x_0) + hf'(x_0) \end{aligned}$$

# Stability of First Order Non-Linear Equation:

→  $\varepsilon_{n+1} = f(\lambda + \varepsilon_n) - \lambda = f(\lambda) + \lambda \frac{dy}{dx} \Big|_{x=\lambda} + O(\lambda^2).$

Since  $\varepsilon_n$  is very small, so we can expand function  $f$  by Taylor's series. After neglecting 2<sup>nd</sup> and higher order terms,

→  $\varepsilon_{n+1} = f(\lambda) - \lambda + \lambda \frac{dy}{dx} \Big|_{x=\lambda} = \lambda \frac{dy}{dx} \Big|_{x=\lambda}$

- This equation is in form of:

$$\varepsilon_{n+1} = a\varepsilon_n \text{ where } n \in \mathbb{N} \text{ and } a = \frac{dy}{dx} \Big|_{x=\lambda}$$

- Recall from previous lectures, the system will be stable if  $|a| < 1$  and unstable if  $|a| > 1$ .

# Stability of Beverton Holt Model of Cell Division:

- Consider the Beverton Holt model of cell division process and assume parameter  $a = 1/p$  and  $\alpha = k/p$  where both  $k$  and  $p$  are positive. Now the model will be in form of:

$$C_{n+1} = k \frac{C_n}{p + C_n}$$

$$\lambda = K \frac{\lambda}{p + \lambda} \Rightarrow \lambda(1 - \frac{K}{p + \lambda}) = 0$$

- To calculate the steady state, substitute  $C_{n+1} = C_n = \lambda$ . There are two steady states:

$$\lambda = 0 \text{ and } \lambda = k - p.$$

$$\frac{K}{p + \lambda} = 1$$

$\lambda = k - p$

- Obviously,  $k > p$  because there is no meaning of negative population. To check for stability find the differentiation of function on right hand side of equation at both steady state points.

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$$f(C_n) = \frac{\lambda}{p + \lambda}$$

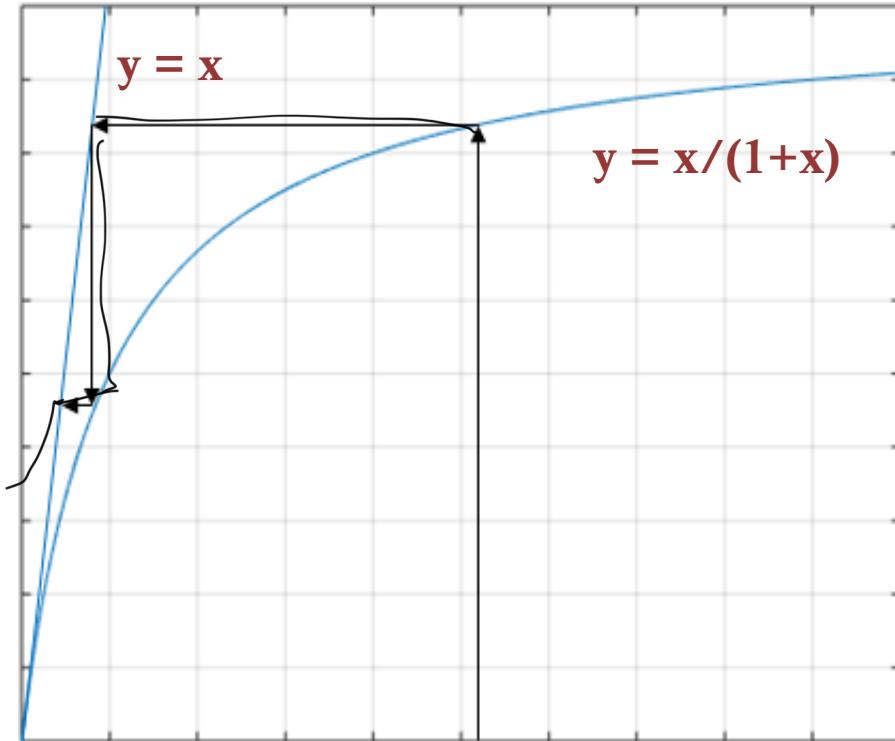
$$\text{and } f'(C_n) = k \frac{p}{(p + \lambda)^2}$$

- Clearly,  $\lambda = 0$  is stable when  $k < p$  and  $\lambda = k - p$  is stable when  $k > p$ .



# Stability of Beverton Holt Model of Cell Division:

- Now's let's verify the same result by cob-web graphs.
- As one can verify that, all the vertical and horizontal motions are monotonically decreasing, hence the model is stable.
- (Exercise) Observe the nature of cob-web for Hassel model for  $b=0.5$  and  $2$ .



# Logistic Difference Equation:

- We have already discussed several discrete time models in population dynamics. All these model were specific to problem. **Can't we think of a model which can govern many classes of systems?** E.g. different populations, distinct species, one species at different stage of evolution or development.
- The model can have variety of meaning depending on the parameters involved in it.
- Now, let's consider a particular type of first order difference equation.

$$y_{n+1} = y_n(r - dy_n).$$

- This equation has 2 parameters  $r$  and  $d$ . **Can we reduce the parameters? YES!**. The method used to reduce the parameters is called as **non-dimensionalization**.
- **Why do we need to get rid of parameters?** Because, the number of computations are directly proportional to the number to parameters. So, if we are reducing the parameters means we are reducing the computations almost proportionally.



# Logistic Difference Equation:

- Now put  $x_n = (d/r) x_n$ . This leads to the following form which is also known as **Pearl-Verhulst equation**.

$$x_{n+1} = r x_n (1 - x_n) . \quad \text{---}$$

- We are left with only one parameter  $r$ . To find the steady state solution, let's substitute  $x_{n+1} = x_n = \lambda$ .
- There are two steady states,  $\lambda = 0$  and  $\lambda = 1 - 1/r$ .
- For the stability,  $F(x_n) = r x_n (1 - x_n)$  so  $F'(x_n) = r(1 - 2x_n)$ . At  $\lambda = 0$ ,  $F'(\lambda) = r$  and at  $\lambda = 1 - 1/r$ ,  $F'(\lambda) = 2 - r$ .
- The steady state  $\lambda = 0$  is stable for  $|r| < 1$  and  $\lambda = 1 - 1/r$  is stable for  $|2 - r| < 1$  or  $1 < r < 3$ .



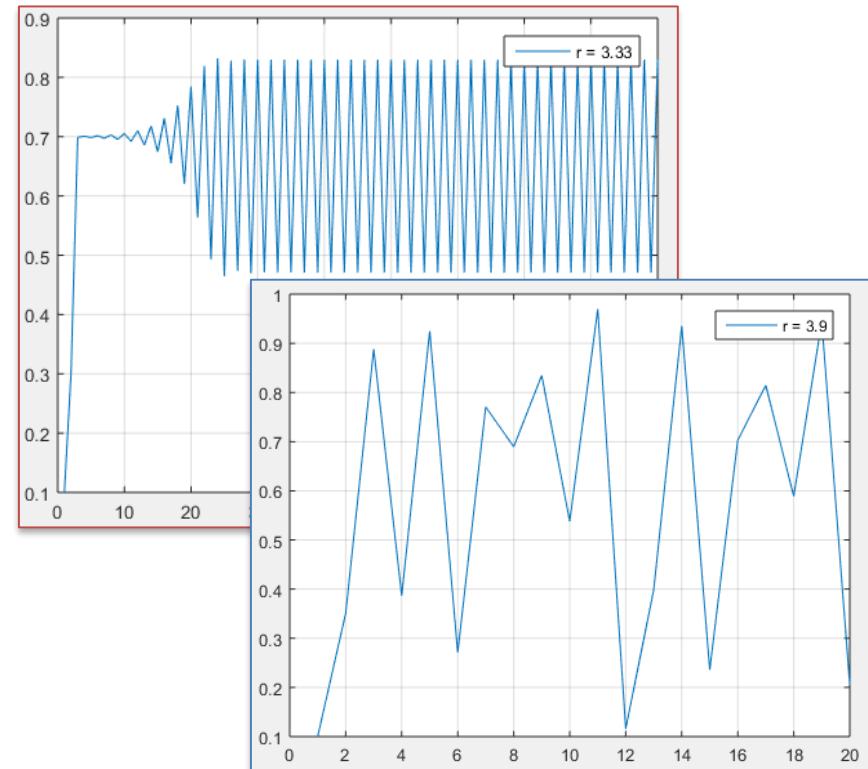
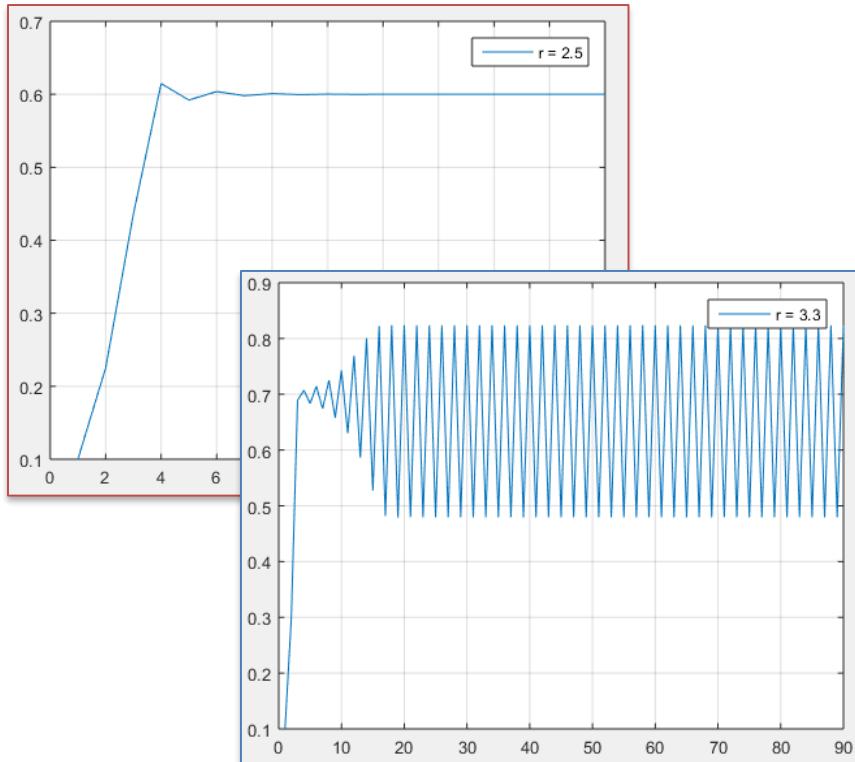
# Observation on Logistic Difference Equation:

- (Exercise) For  $x_0 = 0.1$ , perform 20 iterations for  $r=2.5$ ,  $r=3.3$ ,  $r=3.33$  and  $r=3.9$ . Observe the pattern of numbers. Are you able to find anything interesting?
- $r = 2.5$  Steady State.
- $r = 3.3$  Periodic Oscillations with period = 2.
- $r = 3.33$  Periodic Oscillations with period = 2.
- $r = 3.9$  Chaos.

| S. No. | $r = 2.5$ | $r = 3.3$ | $r = 3.33$ | $r = 3.9$ |
|--------|-----------|-----------|------------|-----------|
| 1      | 0.1000    | 0.1000    | 0.1000     | 0.1000    |
| 2      | 0.2250    | 0.2970    | 0.2997     | 0.3510    |
| 3      | 0.4359    | 0.6890    | 0.6989     | 0.8884    |
| 4      | 0.6147    | 0.7071    | 0.7008     | 0.3866    |
| 5      | 0.5921    | 0.6835    | 0.6983     | 0.9249    |
| 6      | 0.6038    | 0.7139    | 0.7016     | 0.2710    |
| 7      | 0.5981    | 0.6740    | 0.6972     | 0.7705    |
| 8      | 0.6010    | 0.7251    | 0.7030     | 0.6896    |
| 9      | 0.5995    | 0.6577    | 0.6953     | 0.8348    |
| 10     | 0.6002    | 0.7429    | 0.7055     | 0.5379    |
| 11     | 0.5999    | 0.6303    | 0.6918     | 0.9694    |
| 12     | 0.6001    | 0.7690    | 0.7100     | 0.1157    |
| 13     | 0.6000    | 0.5863    | 0.6857     | 0.3992    |
| 14     | 0.6000    | 0.8004    | 0.7177     | 0.9353    |
| 15     | 0.6000    | 0.5271    | 0.6747     | 0.2358    |
| 16     | 0.6000    | 0.8226    | 0.7309     | 0.7029    |
| 17     | 0.6000    | 0.4816    | 0.6550     | 0.8145    |
| 18     | 0.6000    | 0.8239    | 0.7525     | 0.5892    |
| 19     | 0.6000    | 0.4788    | 0.6202     | 0.9439    |
| 20     | 0.6000    | 0.8235    | 0.7844     | 0.2064    |



# Observation on Logistic Difference Equation:



# Summary:

- Different non-linear cell division models.
- Formulation based on survival rate function.
- Non-linear stability analysis.
- Logistic growth difference equation.
- Observation of logistic growth function with a set of parameter values.
- Steady and transient behaviors.





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