

Lecture slides

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Lecture 1

- ▶ Introduction to nonlinear difference equations
- ▶ The Malthusian model
- ▶ The Ricker model

Why difference equations?

A general model

Consider the first order difference equation

$$N_{t+1} = N_t f(N_t) = H(N_t), \quad (1)$$

where $f(N_t)$ is a function that defines the per capita growth rate.
The function $H(N_t)$ describes the total (net) growth rate.

The Malthusian model

The population size at time $t + 1$ is

$$N_{t+1} = N_t + bN_t - dN_t = rN_t,$$

Exercise: solve the Malthusian model and classify qualitative behaviours

Nonlinear models

- ▶ Beverton-Holt

$$N_{t+1} = \frac{rN_t}{1 + \frac{N_t}{K}},$$

- ▶ Hassell model

$$N_{t+1} = \frac{rN_t}{(1 + \frac{N_t}{K})^b},$$

- ▶ Ricker model

$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})}.$$

Numerical simulation of the Ricker model

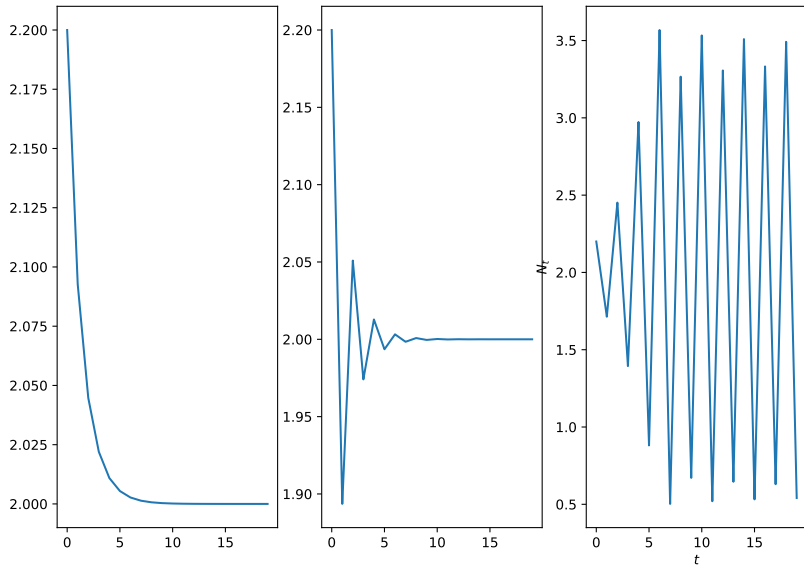


Figure 1: A plot of numerical solutions of the Ricker model. (a) $r=0.5$.

Summary

- ▶ Motivated use of difference equation models
- ▶ Introduced general model for one population
- ▶ Solved the Malthusian model
- ▶ Introduced nonlinear models

Lecture 2 - General techniques for solving nonlinear difference equations

$$N_{t+1} = N_t f(N_t) = H(N_t), \quad (2)$$

- ▶ Computational solutions
- ▶ Fixed points
- ▶ Linear stability of fixed points
- ▶ Cobweb diagrams
- ▶ Bifurcation diagrams
- ▶ Identify how model solutions depend on model parameters

Fixed points

Suppose the solution at the next iteration is equal to that at a given iteration, i.e. there exists some N^* such that

$$N^* = N_{t+1} = N_t$$



Fixed point definition

$$N^* = H(N^*), N^* \geq 0$$

Biological relevance: non-negative solutions

Linear stability analysis - how do small perturbations about N^* behave?

Linear stability analysis (ctd)

💡 Linear stability is determined by the derivative of H evaluated at N^*

$$|H'(N^*)| < 1 \implies \text{linear stability of } N^*.$$

Exercise

Identify the fixed points of the Malthusian model

$$N_{t+1} = rN_t$$

and identify their linear stability.

Cobweb diagrams

Definition

A cobweb diagram is a technique for computing graphical solutions of a difference equation.

Use previous analyses to identify different qualitative cases (one cobweb diagram for each fixed point).

For each case:

- ▶ Sketch a graph of H to evaluate iterative solutions
- ▶ Compute an iterative solution

Example

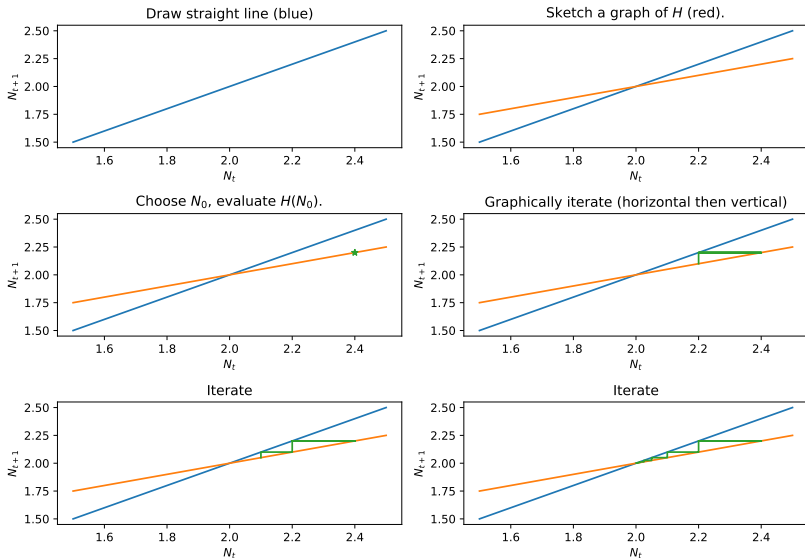


Figure 2: Generating a cobweb plot.

Bifurcation diagrams - Plot fixed points against a parameter and annotate their stability

Exercise

Draw cobweb diagrams for the Malthusian model.

$$N_{t+1} = rN_t$$

and identify their linear stability.

Lecture 3 - Preparation for tutorial 3

- Curve sketching nonlinear functions in qualitatively distinct cases

Example:

Sketch a graph of

$$f(x) = xe^{-r(1-\frac{x}{K})}, \quad r, K \in \mathfrak{R}^+, \quad x \in \mathfrak{R}, x \geq 0$$

Approach

Identify properties of H to distinguish qualitatively distinct cases

Roots

Turning points

Limit as $x \rightarrow \infty$

Limiting behaviour as $x \rightarrow 0$

Tutorial sheet 1

Lecture 4

Consider the model

$$N_{t+1} = \frac{\gamma N_t}{1 + N_t^2}, \quad \gamma \in \mathfrak{R}^+.$$

Fixed points

Linear stability

Cobweb diagrams

Bifurcations

Symbolic computations

The FPs are:

[{N: 0}, {N: -sqrt(gamma - 1)}, {N: sqrt(gamma - 1)}]

The derivative of H is:

$\text{gamma} \cdot (1 - N^2) / (N^2 + 1)^2$

The derivative evaluated at FP 1 is:

gamma

The derivative evaluated at FP 2 is:

$(2 - \text{gamma}) / \text{gamma}$

Lecture 4 .. A model with harvesting

$$N_{t+1} = \frac{\gamma N_t}{1 + N_t^2} - hN_t, \quad \gamma > 0, \quad h \geq 0 \quad (3)$$

Numerical simulation

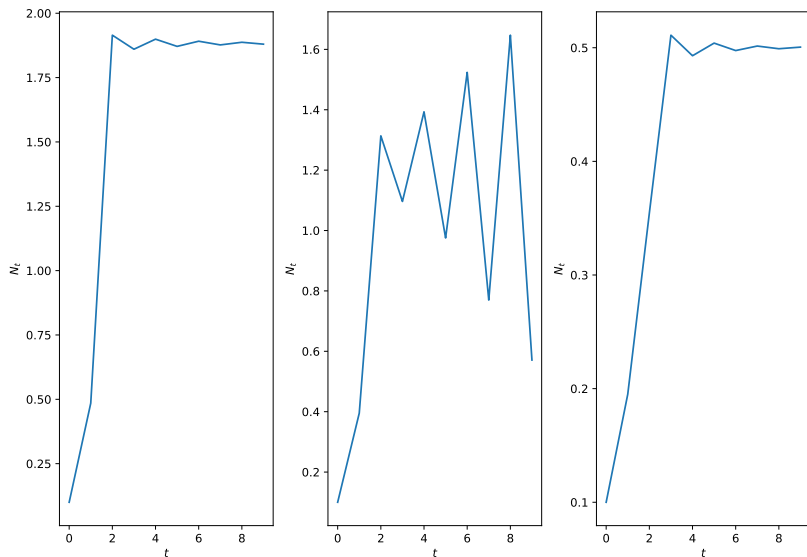


Figure 3: Time series solution for different values of h .

Computing FPs

Linear stability

Deriving expressions for linear stability boundaries in the $h\gamma$ plane

Sketch of stability boundaries

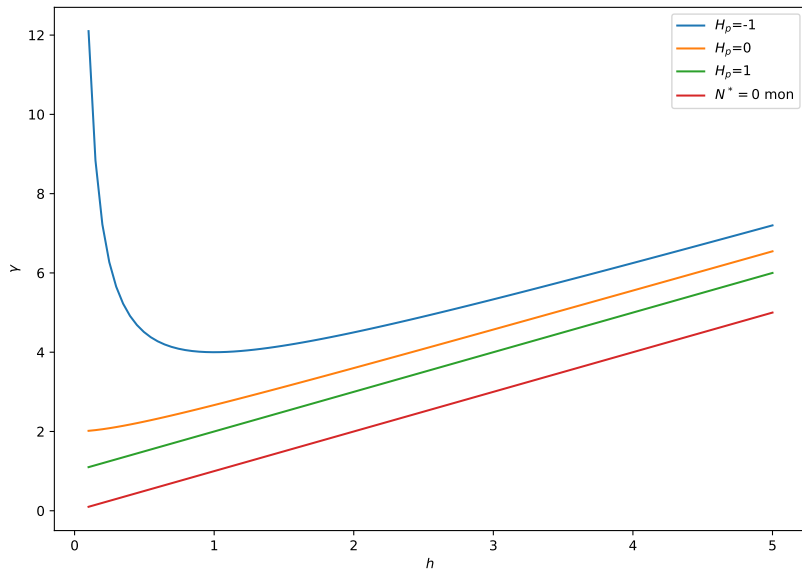
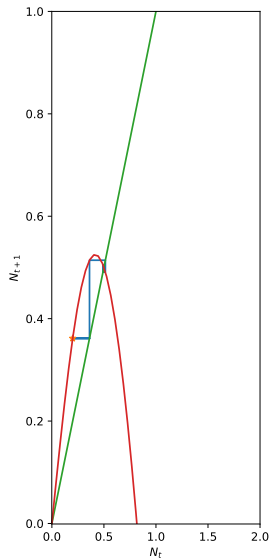
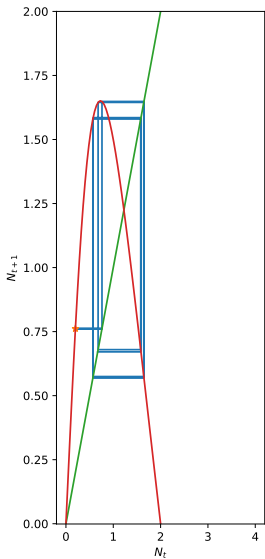
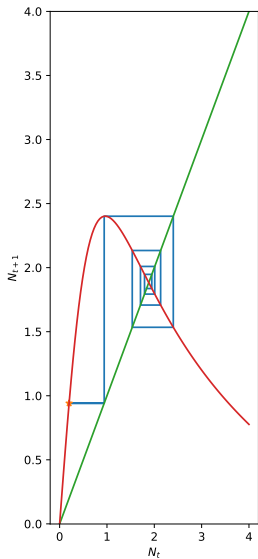


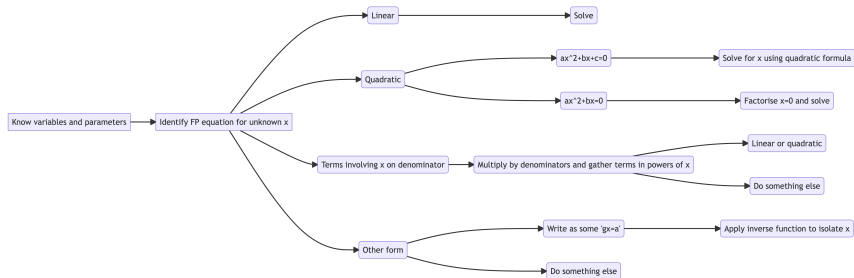
Figure 4: Stability regions for the harvesting model.

Cobweb diagrams



Lecture 5

Quiz review



Oscillatory solutions

$$N_{t+1} = H(N_t) \tag{4}$$

A solution to Equation 4 is defined to be periodic with period T if

$$N_{t+T} = N_t \quad \forall t, N_{t+\tau} \neq N_t \quad \forall t, \quad \tau < T.$$

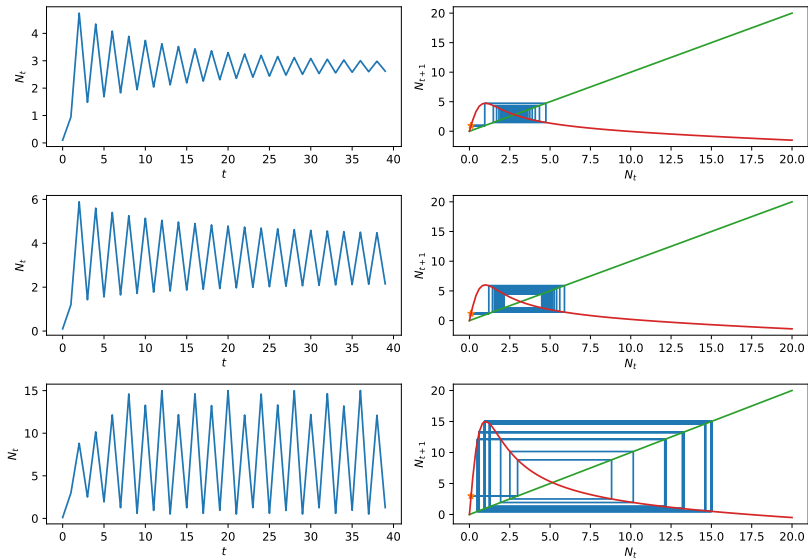


Figure 5: Transition from period 2 to period 4 solutions in the harvesting model

Exercise: identify an equation satisfied by period 2 solutions of the logistic map

$$N_{t+1} = rN_1(1 - N_t).$$

Systems of coupled difference equations

General form of model

We consider governing equations of the form

$$\begin{aligned}N_{t+1} &= f(N_t, P_t), \\ P_{t+1} &= g(N_t, P_t).\end{aligned}$$

Fixed points

The fixed points (N^*, P^*) satisfy

$$N^* = g(N^*, P^*)$$

$$P^* = f(N^*, P^*).$$

Example

Compute the fixed points of the model

$$N_{t+1} = P_t$$

$$P_{t+1} = N_t + P_t.$$

Linear stability analysis

Let

$$N_t = N^* + \hat{N}_t,$$

$$P_t = P^* + \hat{P}_t.$$

Eigenvalues of the Jacobian matrix determine stability

Recap

We are studying equations of the form

$$\begin{aligned}N_{t+1} &= f(N_t, P_t), \\ P_{t+1} &= g(N_t, P_t).\end{aligned}$$

The solution of the linearised system takes the form

$$\mathbf{w}_t = \sum_{i=1}^2 C_i \lambda_i^t \mathbf{c}_i,$$

where λ_i $i = 1, 2$ are eigenvalues of the Jacobian matrix and \mathbf{c}_i corresponding eigenvector.

i Note

For linear stability - real part of both eigenvalues is less than 1 in magnitude

Example

Compute the Jacobian matrix of the model

$$N_{t+1} = P_t$$

$$P_{t+1} = N_t + 2P_t.$$

and hence determine linear stability of the FP (0,0).

Trace determinant form

Suppose

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.$$

The characteristic equation is

$$|A - \lambda \mathbf{1}| = 0$$

Hence

$$\lambda^2 - \lambda(a_{11} + a_{22}) + (a_{11}a_{22} - a_{12}a_{21}) = 0.$$

This can be written as

$$\lambda^2 - \lambda(\operatorname{tr} A) + \det A = 0.$$

The eigenvalues are

$$\lambda = \frac{-\operatorname{tr} A \pm \sqrt{(\operatorname{tr} A)^2 - 4 \det A}}{2}$$

When the eigenvalues cannot be easily explicitly computed

i Jury conditions

Consider the characteristic equation

$$P(\lambda) = \lambda^2 + a\lambda + b = 0,$$

where $a, b \in \mathfrak{R}$.

The Jury conditions state that $|\lambda_i| < 1 \quad \forall \quad i$ if, and only if,

- ▶ $b < 1$,
- ▶ $1 + a + b > 0$,
- ▶ $1 - a + b > 0$.

- ▶ Testing of the Jury conditions is sufficient to determine linear stability.
- ▶ This is often easier than explicitly working out the eigenvalues.

Jury conditions in trace-determinant form

i Jury conditions

Consider the characteristic equation

$$P(\lambda) = \lambda^2 - \operatorname{tr} A \lambda + \det A = 0,$$

where $a, b \in \Re$.

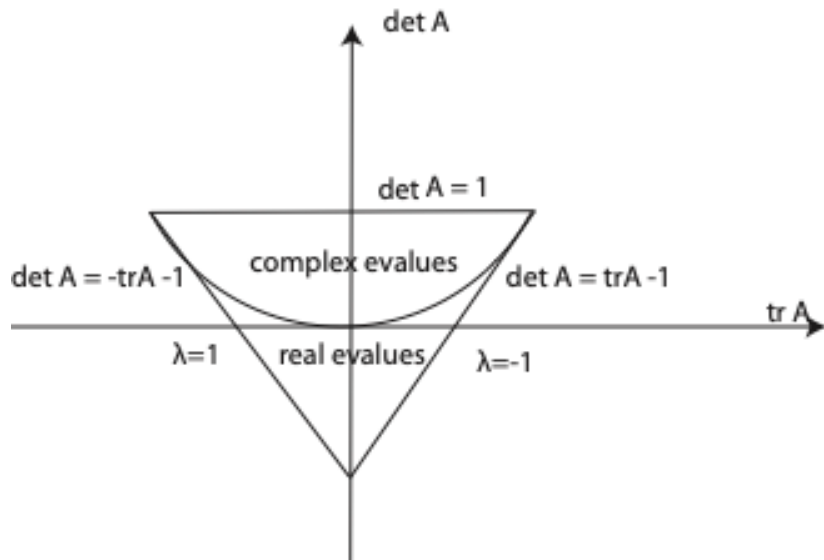
The Jury conditions state that $|\lambda_i| < 1 \quad \forall \quad i$ if, and only if,

- ▶ $\det A < 1$,
- ▶ $1 - \operatorname{tr} A + \det A > 0$,
- ▶ $1 + \operatorname{tr} A + \det A > 0$.

- ▶ Compute the trace and determinant of the Jacobian
- ▶ Testing the Jury conditions to determine linear stability
- ▶ This is often easier than explicitly working out the eigenvalues.

Interpretation in the trace-determinant plane

$$P(\lambda) = \lambda^2 - \text{tr} A \lambda + \det A = 0,$$



Proof of the Jury conditions

Consider the characteristic equation

$$P(\lambda) = \lambda^2 + a\lambda + b = 0,$$

The roots of $P(\lambda)$ are

$$\lambda_{1,2} = \frac{-a \pm \sqrt{a^2 - 4b}}{2}.$$

Complex roots - $a^2 - 4b < 0$

JC 1

$$b = \lambda_1 \lambda_2 = |\lambda_1|^2 = |\lambda_2|^2$$

JC 2 and 3

$$(a^2 - 4b) = (|a|^2 - 2)^2 + \dots$$

Real roots - $a^2 - 4b \geq 0$

Define the largest of the roots to be

$$R = \max\{|\lambda_1|, |\lambda_2|\} = \frac{|a| + \sqrt{a^2 - 4b}}{2}.$$

Consider $R = 1$.

Lecture 7 - The Nicholson-Bailey model

$$\begin{aligned}N_{t+1} &= R_0 N_t f(N_t, P_t), \\ P_{t+1} &= C N_t (1 - f(N_t, P_t)).\end{aligned}$$

Numerical solution

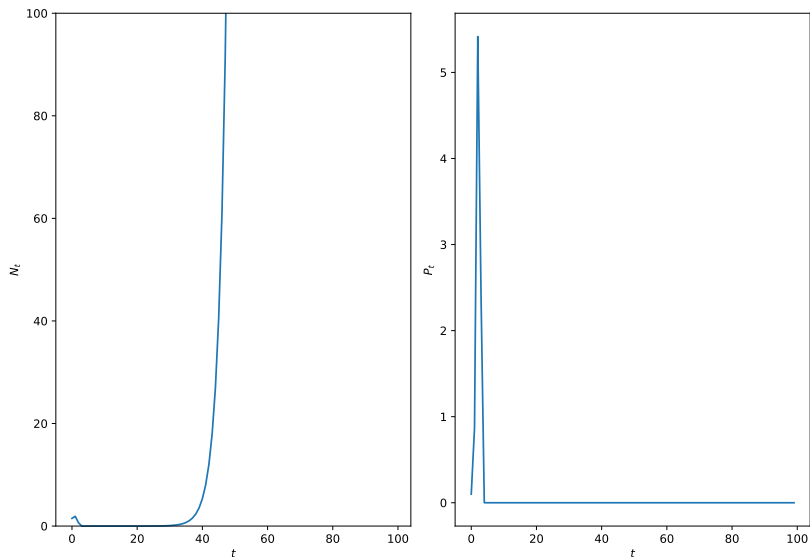


Figure 6: A plot of the Nicholson Bailey model solution.

Fixed points

The fixed points satisfy

$$\begin{aligned}N^* &= R_0 N^* e^{-aP^*}, \\P^* &= CN^*(1 - e^{-aP^*}).\end{aligned}$$

FPS ctd

Linear stability

The Jacobian matrix is given by

$$A_{(N_t, P_t)} = \begin{pmatrix} R_0 e^{-aP_t} & -R_0 a N_t e^{-aP_t} \\ c(1 - e^{-aP_t}) & aC N_t e^{-aP_t} \end{pmatrix}.$$

At (0,0) ... 5cm

Linear stability of the nontrivial FP

The Jacobian matrix is given by

$$A_{(N_t, P_t)} = \begin{pmatrix} R_0 e^{-aP_t} & -R_0 a N_t e^{-aP_t} \\ c(1 - e^{-aP_t}) & aC N_t e^{-aP_t} \end{pmatrix}.$$

The FP is

$$\left(\frac{R_0 \ln R_0}{aC(R_0 - 1)}, \frac{1}{a} \ln R_0 \right).$$

5cm

Applying the Jury conditions

Symbolic computation in Python

The FPs are:

{N: 0, P: 0}

{N: $R_0 \log(R_0) / (C \cdot a \cdot (R_0 - 1))$, P: $\log(R_0) / a$ }

The Jacobian of H is:

$[[R_0 \exp(-P \cdot a), -N \cdot R_0 \cdot a \cdot \exp(-P \cdot a)], [C - C \cdot \exp(-P \cdot a), C \cdot \exp(-P \cdot a)]]$

The Jacobian evaluated at FP 0 is:

$[[R_0, 0], [0, 0]]$

The Jacobian evaluated at FP 1 is:

$[[1, -R_0 \log(R_0) / (C \cdot (R_0 - 1))], [C \cdot (1 - 1/R_0), \log(R_0)]]$