Discrete-Time Models

Linear stability analysis

Computational Biology

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Steady state

- Consider a model

$$x_{n+1} = f(x_n), \quad n = 0, 1, \ldots$$

- Any intersection of the curve $y = f(x)$ and the diagonal line $y = x$ represents a special point.
- Steady state (or fixed point or equilibrium point) of the model: a point x^* that satisfy

$$x^* = f(x^*).$$

- If any iterate is x^*, then all subsequent iterates also are x^*.

Cobwebbing

Cobwebbing: a graphical method of exploring the behaviour of repeatedly applying a function $f(x)$ beginning at an initial point x_0.

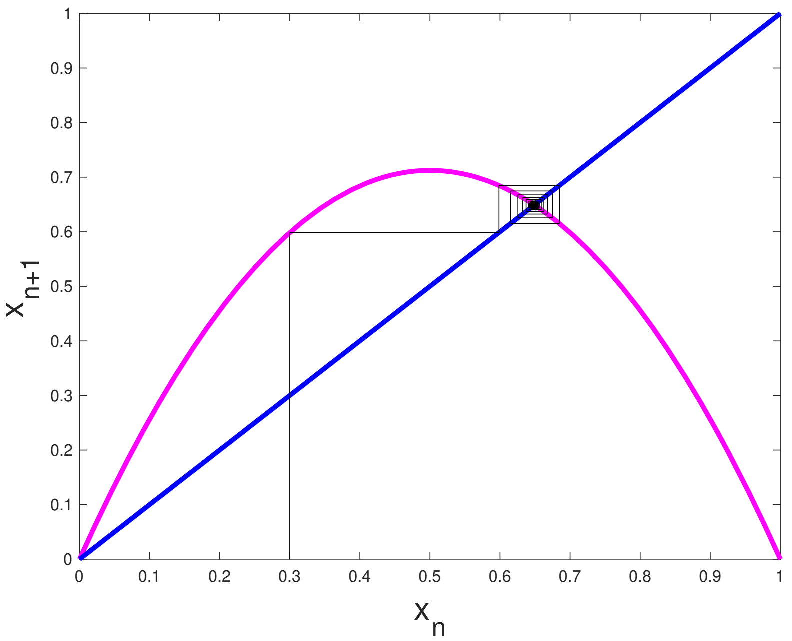


Figure: Cobwebbing for the discrete logistic model.

Cobwebbing process

- We consider our first iterate, x_0, on the horizontal axis.
- Then we calculate the next iterate $x_1 = f(x_0)$. Visually, we represent a vertical line from $(x_0, 0)$ on the horizontal axis to the point (x_0, x_1) lying on the curve $y = f(x)$.
- Then we have to locate x_1 on the horizontal axis. We already have x_1 on the vertical axis, and the easiest way to get it onto the horizontal axis is to reflect it through the diagonal line $y = x$. Visually, this is shown by a horizontal line from (x_0, x_1) to point (x_1, x_1) on the diagonal line.
- Then we calculate the next iterate $x_2 = f(x_1)$ and draw a vertical line from point (x_1, x_1) on the diagonal line to (x_1, x_2).
- This process is repeated for subsequent iterates.

Cobwebbing vs. time evolution

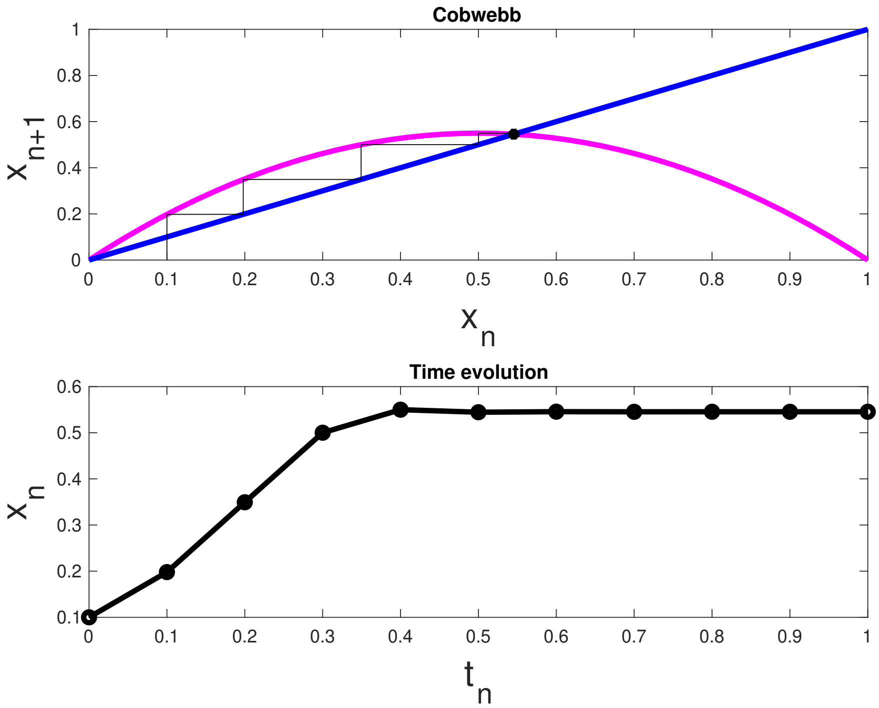


Figure: Graphical determination of the steady state (top); time evolution of the population growth (bottom).

Linear stability

Relevant question: What happens when an iterate is close to, but not exactly at, a fixed point?

- If the subsequent iterates move closer to the fixed point, the fixed point is said to be stable/attracting.
- If the subsequent iterates move further away the fixed point, the fixed point is said to be unstable/repelling.

Strategy: iterate near to a fixed point x^* and study the behaviour of the subsequent iterates.

Linear stability analysis

- Define
$$\eta_n = x_n - x^*, \ n = 1, 2, \dots$$
- Using a Taylor series about x^*, with remainder $R_2(\eta_n)$
$$x^* + \eta_{n+1} = f(x^* + \eta_n) = \underbrace{f(x^*)}_{= x^*} + f'(x^*)\eta_n + R_2(\eta_n).$$
- Linearization: neglect all the term $R_2(\eta_n)$
$$\eta_{n+1} = f'(x^*)\eta_n = \lambda\eta_n, \quad \text{with } \lambda = f'(x^*).$$
- The parameter $\lambda = f'(x^*)$ generally is referred to as the eigenvalue of the map at x*.
- Given the initial condition η_0, the deviations are
$$\eta_n = \lambda^n \eta_0.$$

Linear stability analysis

The behaviour of the deviation η_n, and the subsequent conclusion regarding the stability of the fixed point x^*, can be summarized as follows:

- $\lambda > 1$: geometric growth; fixed point x^* is unstable;
- $0 < \lambda < 1$: geometric decay; fixed point x^* is stable;
- $-1 < \lambda < 0$: geometric decay with sign switch; fixed point x^* is stable;
- $\lambda < -1$: geometric growth with sign switch; fixed point x^* is unstable;
- $\lambda = \pm 1$: carefull analysis of $R_2(\eta_n)$.

Theorem: Let x^* be a fixed point of $x_{n+1} = f(x_n)$. Then x^* is stable if $|f'(x^*)| < 1$ and unstable if $|f'(x^*)| > 1$.

A fixed point x^* is called hyperbolic if $|f'(x^*)| > 1$ and non-hyperbolic if $|f'(x^*)| = 1$.

Dynamics of the Ricker' model

$$N_{n+1} = N_n e^{r\left(1-\frac{N_n}{K}\right)}, \quad r > 0, K > 0$$

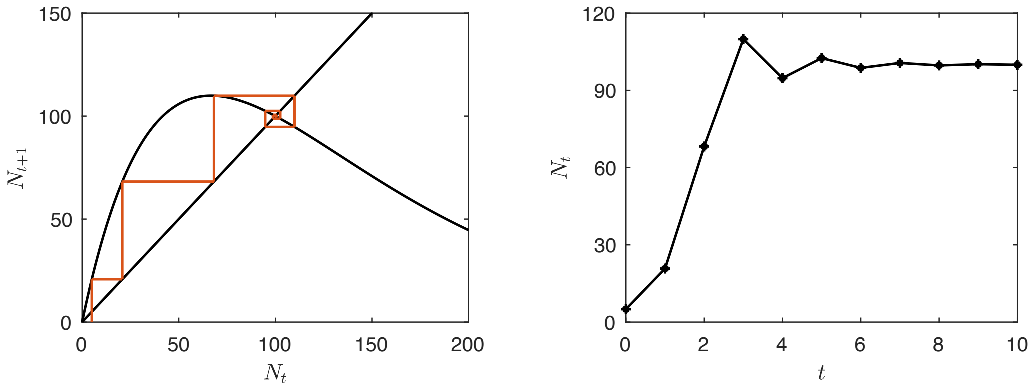
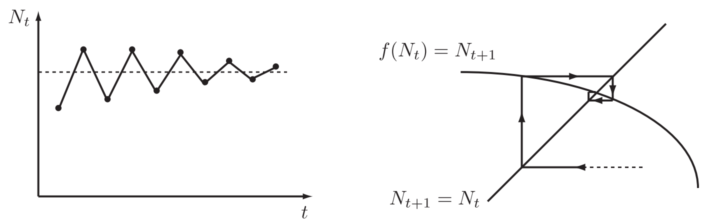


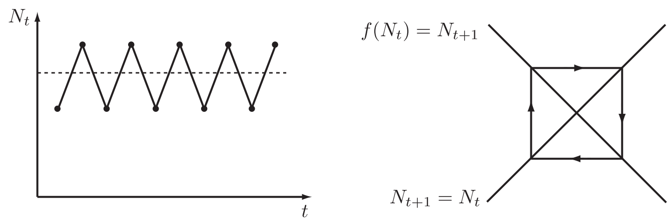
Figure: Ricker' model with $N_0 = 5$, $r = 1.5$, $K = 100$. Cobwebbing (left); time evolution (right).

Dynamics of the Ricker' model

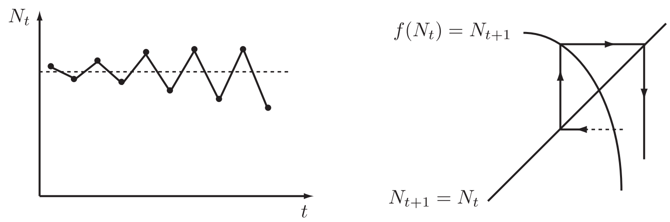
- $-1 < f'(N_s) < 0$



- $f'(N_s) = -1$



- $f'(N_s) < -1$



Bifurcation

A bifurcation point is, in the current context, a point in parameter space where the number of steady states, or their stability properties, or both, change.

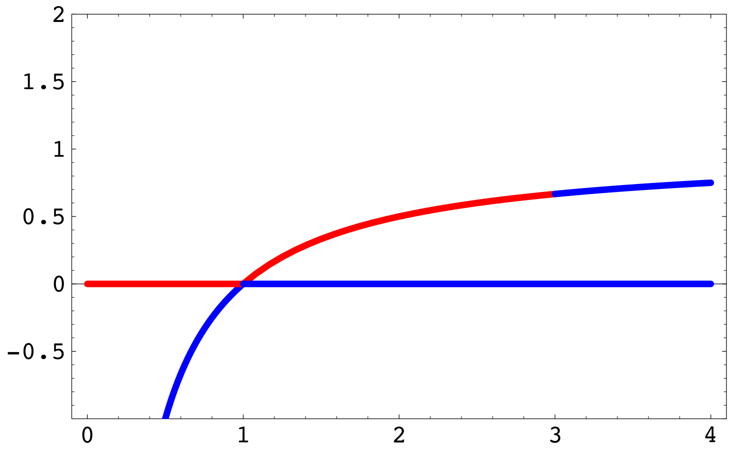


Figure: Bifurcation diagram for the non-dimensional discrete-time logistic model. The non-zero steady state is given, for $r > 1$, by $x^* = (r-1)/r$.

Linear stability analysis: discrete logistic model

Discrete logistic model (Verhulst model)

$$x_{n+1} = r\left(1 - \frac{x_n}{K}\right)x_n, \quad n = 0, 1, \dots, \quad \text{with } r, K > 0.$$

Eliminating the parameter K: let $\bar{x}_n = x_n/K$ to obtain (after dropping the overbars)

$$x_{n+1} = f(x_n) = r\,x_n(1 - x_n), \quad n = 0, 1, \dots, \quad \text{with } r > 0.$$

Note: If $x_n > 1$ then $x_{n+1} < 0$. To avoid this, note that:

- the maximum value of $f(x) = rx(1-x)$ is $f(1/2) = r/4$;
- if $x_0 \in [0, 1]$ and $0 \leqslant r \leqslant 4$ then $x_n \in [0, 1]$ for all n.

Steady states and stability analysis

$$f(x) = rx(1 - x)$$

Steady states and corresponding eigenvalues λ:

- $x^* = 0$, $\lambda = f'(0) = r$,
- $x^* = \dfrac{r-1}{r}$ (positive when $r > 1$), $\lambda = f'(\frac{r-1}{r}) = 2 - r$.

Stability analysis:

- $0 < r < 1$: as r increases the only realistic (non-negative) steady state is $x^* = 0$ which is stable ($0 < \lambda < 1$).
- $r = 1$: first bifurcation, since $x^* = 0$ becomes unstable ($\lambda > 1$ for $r > 1$).
- $1 < r < 3$: the positive steady state $x^* = (r-1)/r > 0$ is stable ($-1 < \lambda < 1$).
  Note: this is the case for the population of *Paramecium aurelia* discussed before, where $r = 1 + 0.0015 \times 540 = 1.81$.
- $r = 3$: second bifurcation, where $\lambda = -1$.

Bifurcation diagram: discrete logistic model ($0 < r \leqslant 3$)

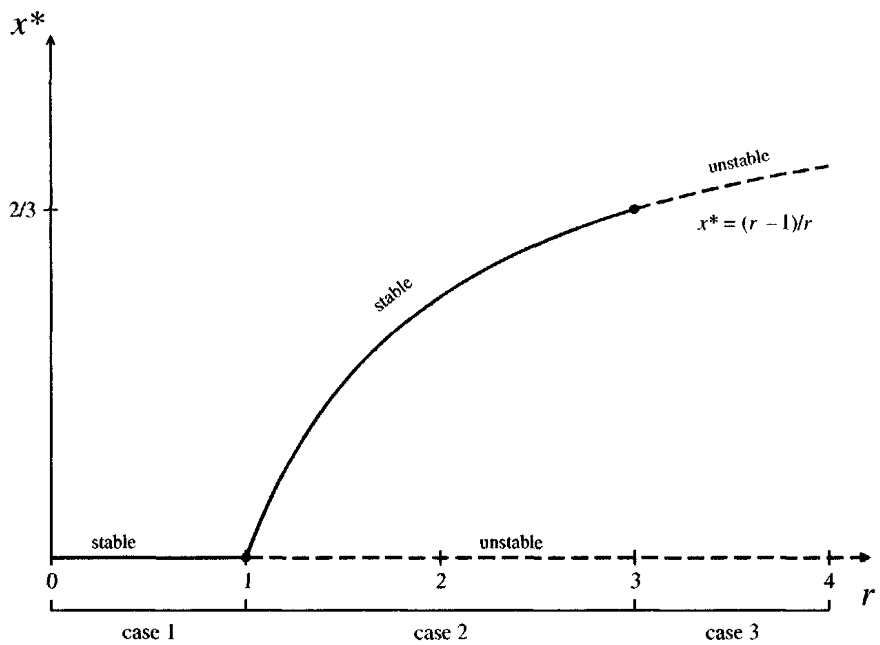


Figure: Fixed points and their stability as a function of the model parameter r. Solid lines indicate stability of the fixed point, and dashed lines indicate instability. The filled circles represent bifurcation points.

Stability analysis: discrete logistic model ($0 < r \leqslant 3$)

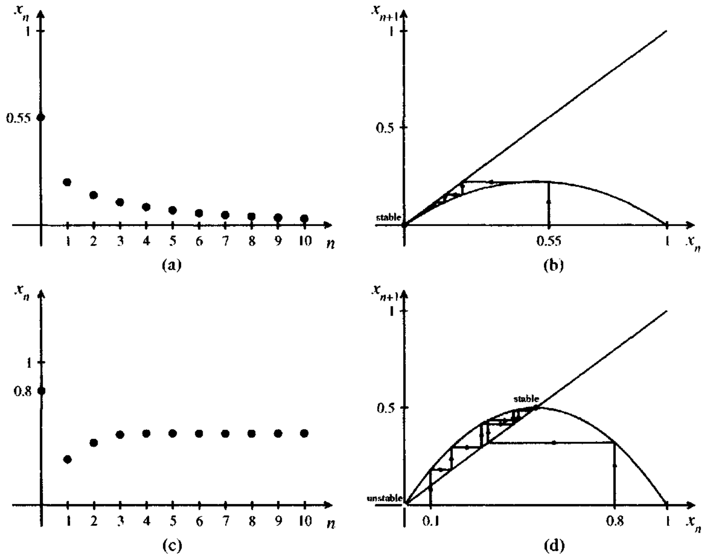


Figure: Case 1 ($0 < r < 1$), for $r = 0.9$ ((a) and (b)): the only faced point $x = 0$ is stable, and the population goes extinct. Case 2 ($1 < r < 3$), for $r = 2$ ((c) and (d)): the faced point $x = 0$ is unstable, the nontrivial fixed point is stable, and the population size stabilizes.

Two-cycle, four-cycle and chaos ($r > 3$)

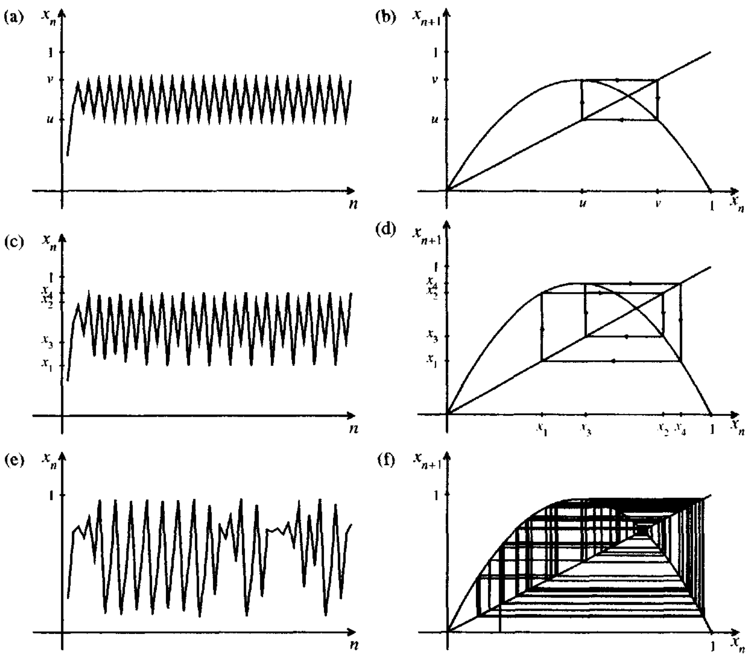


Figure: Case 3 ($3 < r < 4$): two-cycle with $r = 3.2$ ((a) and (b)); four-cycle with $r = 3.55$ ((c) and (d)); chaos with $r = 3.88$ ((e) and (f)).

Bifurcation diagram: discrete logistic equation ($0 < r < 4$)

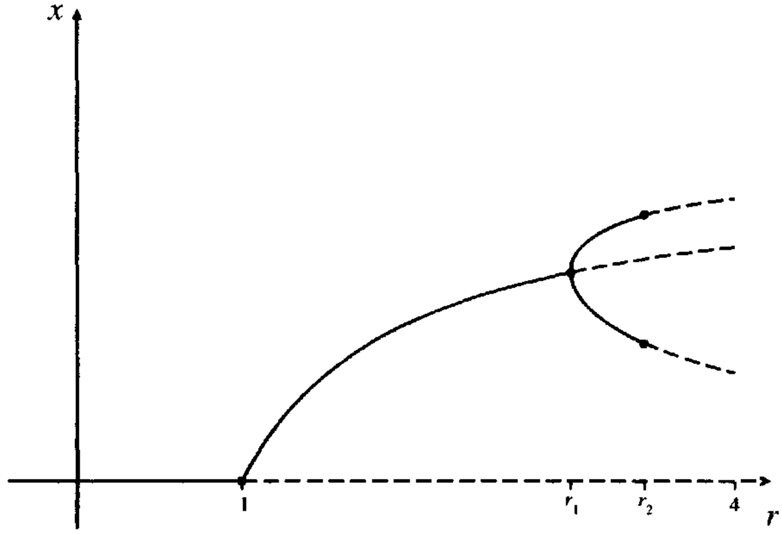


Figure: Fixed points, as well as the 2-cycle for values of $r > 3$. The 2-cycle is stable up to $r = 1 + \sqrt{6}$, and unstable thereafter.

Bifurcation diagram: discrete logistic equation ($0 < r < 4$)

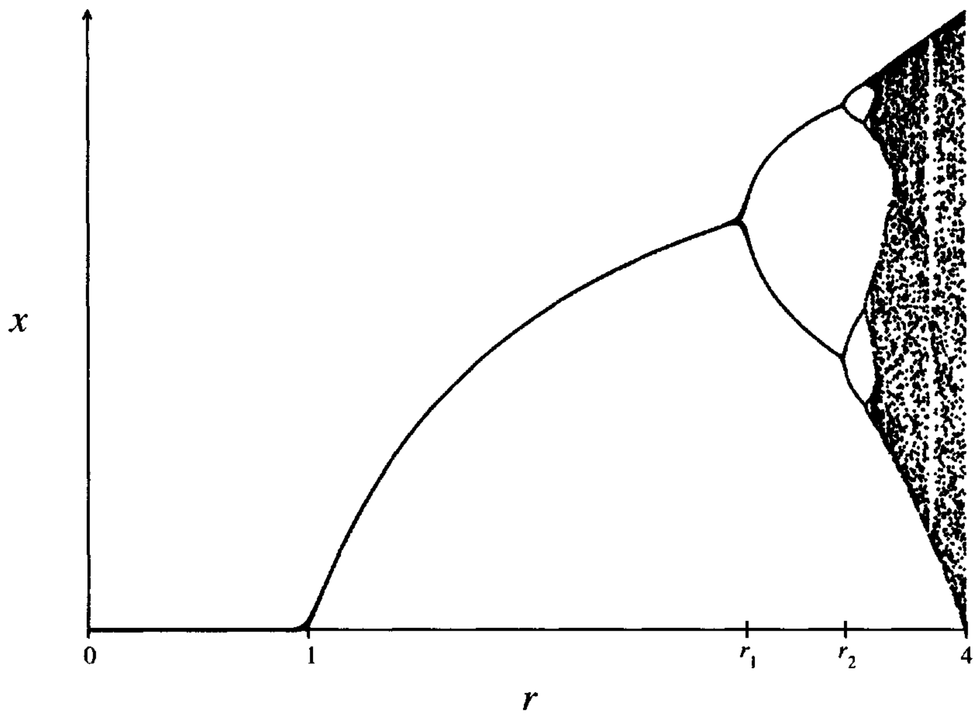


Figure: Orbital bifurcation diagram for the discrete logistic equation.

Homework #2

Exercise 1.3: Suppose that the evolution of a population can be described by a discrete-time Hassel model of the form

$$x_{n+1} = \frac{R_0 x_n}{(1+x_n)^b}.$$

1. Determine any non-negative steady state.
2. Study the linear stability of the steady states.
3. Construct a cobweb map the model and discuss the global qualitative behaviour of the solutions.

Homework #2

Exercise 1.4: Suppose that the evolution of a population can be described by a discrete-time Ricker model of the form

$$N_{n+1} = N_n e^{r\left(1-\frac{N_n}{K}\right)},$$

with $0 < r < 2$ and $K > 0$.

1. Describe the biological interpretation of the model.
2. Determine any non-negative steady states and their linear stability.
3. Construct a cobweb map the model and discuss the global qualitative behaviour of the solutions.

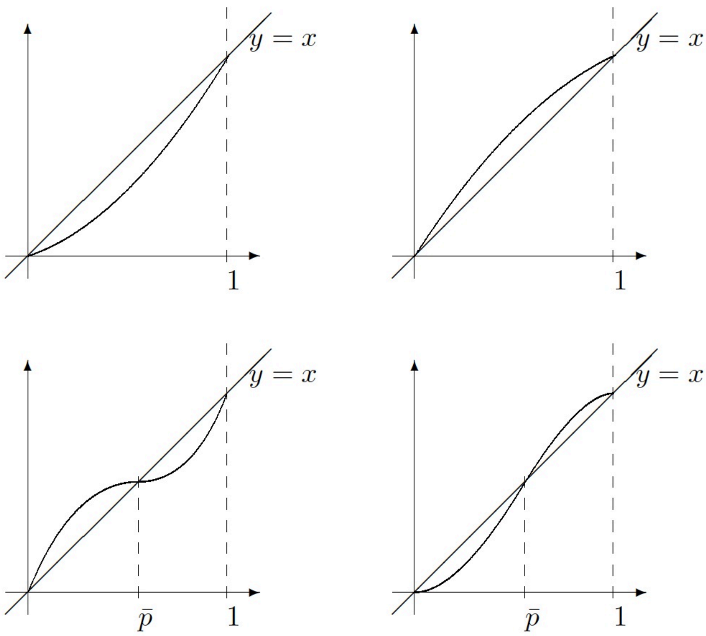
Homework #2

Exercise 1.5: This exercise deals with the second-iterate map, $f^2(x)$, for the logistic map, $f(x) = rx(1-x)$.

1. Compute $f^2(x)$.
2. Find the fixed points of $f^2(x)$. Verify that a nontrivial 2-cycle exists only for $r > 3$.
3. Verify that the nontrivial 2-cycle is stable for $3 < r < 1 + \sqrt{6}$, and unstable for $r > 1 + \sqrt{6}$.

Homework #2

Exercise 1.6: Consider the discrete model $N_{t+1} = f(N_t)$. The graphs of the function $y = f(x)$ and the straight line $y = x$ are shown in the figures, for different definitions of f.



For each case, find the fixed points and their stability.