MATH 372: Difference Equations

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1 Introduction

In this chapter, we use *discrete models* to describe dynamical phenomena in biology. Discrete models are appropriate when one can think about the phenomenon in terms of discrete time steps, or when one wishes to describe experimental measurements that have been collected at fixed time intervals.

In general, we are concerned with a sequence of quantities,

$$x_0, x_1, x_2, x_3, x_4, \ldots,$$

where x_i denotes the quantity at the i-th measurement or after i time steps. For example, x_i may represent

- the size of a population of mosquito insects in year i;
- the proportion of individuals in a population carrying a particular gene in the i-th generation;
- the number of cells in a bacterial culture on day i;
- the concentration of oxygen in the lung after the i-th breath;
- the concentration in the blood of a drug after the i-th dose.

You can undoubtedly think of many more such examples. Note that the time step may or may not be constant. In the example of the bacterial culture, the time step is fixed to be a day, but in the example of the oxygen concentration in the lung, the time step is variable from breath to breath. Also, time steps can be anywhere from milliseconds to years, depending on the biological problem at hand.

We can now ask ourselves, what does it mean to build a discrete model? In the context of our sequence of quantities x_i, a discrete model is a rule describing how the quantities change. In particular, a discrete model describes how x_{n+1} depends on x_n (and perhaps x_{n-1}, x_{n-2}, $\ldots$). Restricting ourselves to the case where x_{n+1} depends on x_n alone, a model then is a sort of "updating function" [1], of the form

$$x_{n+1} = f(x_n), \tag{1}$$

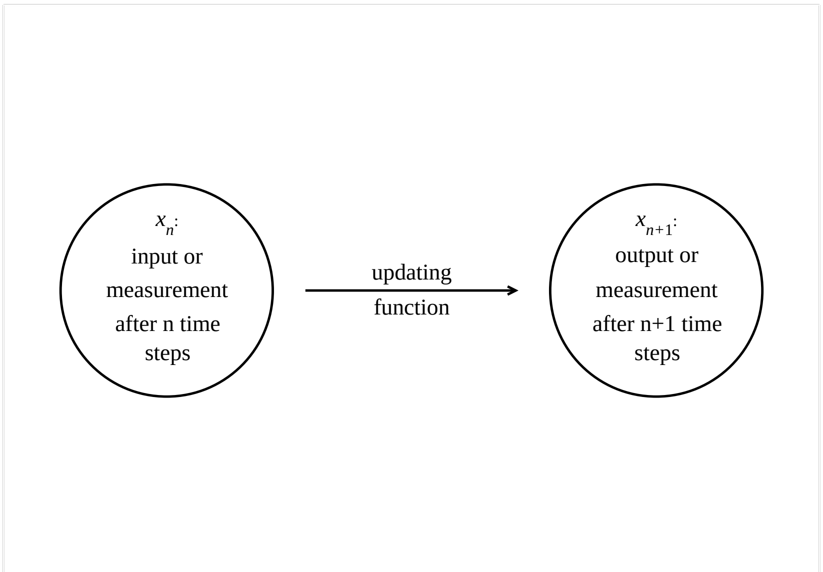

Figure 1: This is the updating function

as shown in Figure 1. The equation $x_{n+1} = f(x_n)$ often is referred to as a **map**.

Finding the precise function f that describes a set of experimental data or that gives a certain desired type of behaviour is not always straightforward. In fact, it is often said that modelling (finding the right function f) is more of an art than a science. In any case, it generally is an iterative process. One starts with a particular function f, and then makes adjustments. Insight into how a function f should be adjusted can often be obtained from knowledge of the behaviour of the current model. The remainder of this chapter discusses techniques that can aid in the analysis of a discrete model.

2 Simple population models

We begin by analyzing one of the simplest maps, with $f(x_n) = rx_n$, giving the linear map

$$x_{n+1} = rx_n. \tag{2}$$

For concreteness, let us think of x_n as the size of an insect population after n years, or during the n-th generation. Here, $r > 0$ is a model **parameter** representing the net reproduction rate of the population. The model thus says that next year's population is proportional to this year's population. If we let x_0 be the population of insects at the start of the study, then

$$\begin{aligned} x_1 &= rx_0, \\ x_2 &= rx_1 = r(rx_0) = r^2x_0, \\ &\vdots \\ x_n &= r^nx_0. \end{aligned}$$

The resulting sequence $x_0,\ x_1,\ x_2, ...$ is called an **orbit** of the map (starting with different initial populations x_0 gives different orbits).

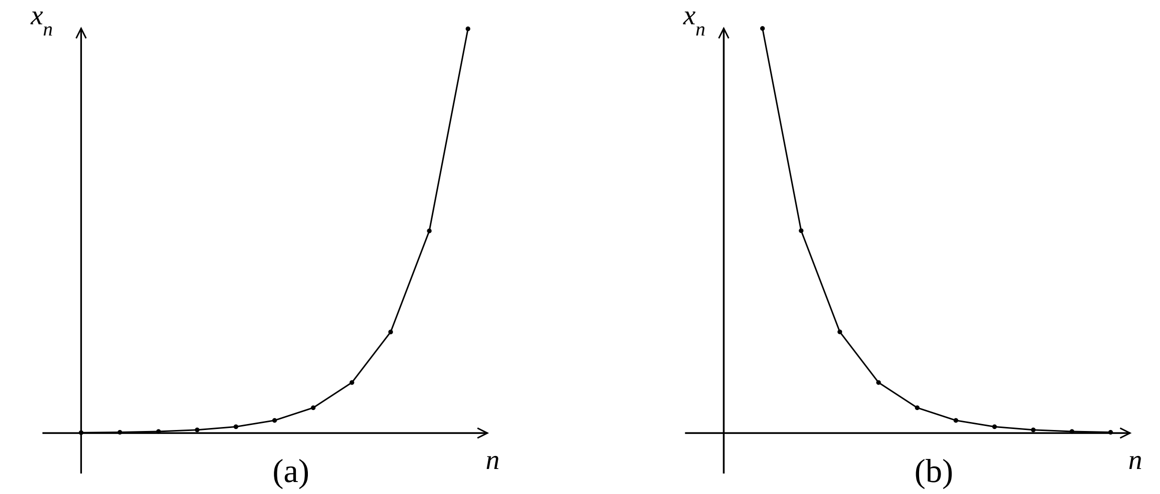

Figure 2: (a) Geometric growth for $r > 1$; (b) Geometric decay for $0 < r < 1$.

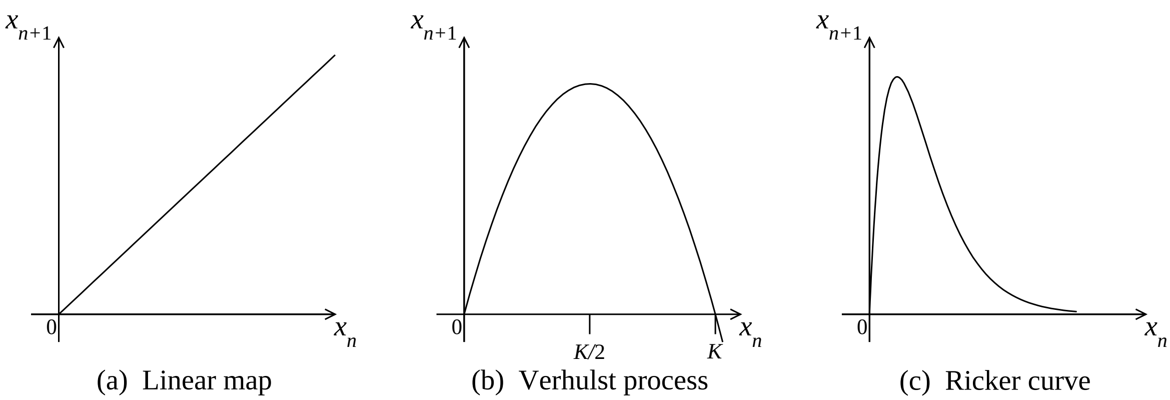

Figure 3: (a) Linear map; (b) Verhulst process; (c) Ricker curve.

It should be clear that the insect population grows without bound if $r > 1$ (for example, if $r = 2$, we obtain the sequence $x_0, 2x_0, 4x_0, 8x_0, \ldots$), as shown in Figure 2(a). Similarly, the insect population shrinks and eventually goes extinct if $0 < r < 1$ (for example, if $r = \frac{1}{2}$, we obtain the orbit $x_0,\ \frac{1}{2}x_0,\ \frac{1}{4}x_0,\ \frac{1}{8}x_0, \ldots$), as shown in Figure 2(b). When the value of r is precisely 1, the population neither grows nor shrinks, but stays constant at its initial value x_0.

Of course, this simple model is not very realistic for describing the longterm growth of any population. There is not a population whose growth will not stagnate eventually due to competition for limited resources among the individuals. The problem with this simple model is that it is based on the assumption that the reproduction rate always is the same, no matter whether the population is large or small.

Figure 3(a) shows the graph of x_{n+1} versus x_n for our current model, (2). The graph is a straight line with slope r. To take into account the effects of overcrowding, we require a graph with a local maximum. A possibility is shown in Figure 3(b), corresponding to the following equation:

$$x_{n+1} = r x_n \left(1 - \frac{x_n}{K}\right), \tag{3}$$

with $r > 0$ and $K > 0$. The graph of this equation is a concave-down parabola, with roots at

$x_n = 0$ and $x_n = K$, and the maximum at $x_n = K/2$, as shown in Figure 3(b). This model of population growth is referred to as the Verhulst process, or the discrete logistic equation (we will encounter the continuous version of the logistic equation in Chapter XXX). It should be clear that if the population during any year exceeds $K/2$, the population a year later is less than $K/2$. That is, the population is self-regulating. One complication with this model is that if the population during any year exceeds K, the population a year later is negative.

To ensure that the population always remains nonnegative, another adjustment can be made to the model. Figure 3(c) shows the Ricker curve [2], given by

$$x_{n+1} = x_n \exp\left[r\left(1 - \frac{x_n}{K}\right)\right], \tag{4}$$

with $r > 0$ and $K > 0$. We can think of the factor $\exp(r)$ as a constant reproduction factor, and of the factor $\exp(-rx_n/K)$ as a mortality factor. The larger the population x_n, the more severe the mortality factor. As before, this population is self-regulating.

Both the Verhulst process and the Ricker model are examples of nonlinear models. In contrast to the linear map from the beginning of this section, the dynamical behaviour of these models is much more interesting, and often unintuitive. There are many tools that allow us to predict the dynamical behaviour of these models, and most of the rest of this chapter is devoted to developing and exploring such tools in the context of the Verhulst process. The Ricker model will be encountered again in the Maple section of this book, in Chapter XXX.

3 Cobwebbing, Fixed Points, and Stability Analysis

For all the models we have looked at so far, if we know the values of the model parameters, plus an initial condition x_0, then we can sequentially find the entire orbit, that is, the iterates x_1, x_2, x_3, ..., one after the other. With the fast computers of today, it is easy to generate many orbits and deduce the dynamics of the model. However, it is easy to miss some subtle behaviour. We often can gain valuable insight into the model dynamics from sophisticated, but easy to learn, mathematical techniques. We will examine a few of such techniques in this section.

One of the questions we would like to address is the longterm dynamics of the model. In the case of the linear map 2, we can easily predict the n-th iterate, namely $x_n = r^n x_0$, and deduce that there is exponential growth when $r > 1$ and exponential decay if $0 < r < 1$. In general, it is not possible to write down a formula for x_n if the model is nonlinear. However, we can obtain an answer to our question from **cobwebbing**. Cobwebbing is a graphical solution method, a method for visualizing the orbits and their longterm behaviour without explicitly calculating each and every iterate along the way.

We demonstrate the cobwebbing technique in Figure 4. Figure 4 shows the graphs of a function $x_{n+1} = f(x_n)$ and the straight line $x_{n+1} = x_n$. We choose our first iterate, x_0, on the horizontal axis. The next iterate is $x_1 = f(x_0)$, which we can just read off the parabola. Visually, this is shown by a vertical line from x_0 on the horizontal axis to the point (x_0, x_1) on the parabola. The next iterate, x_2, can be obtained in a similar way from x_1. We first need 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

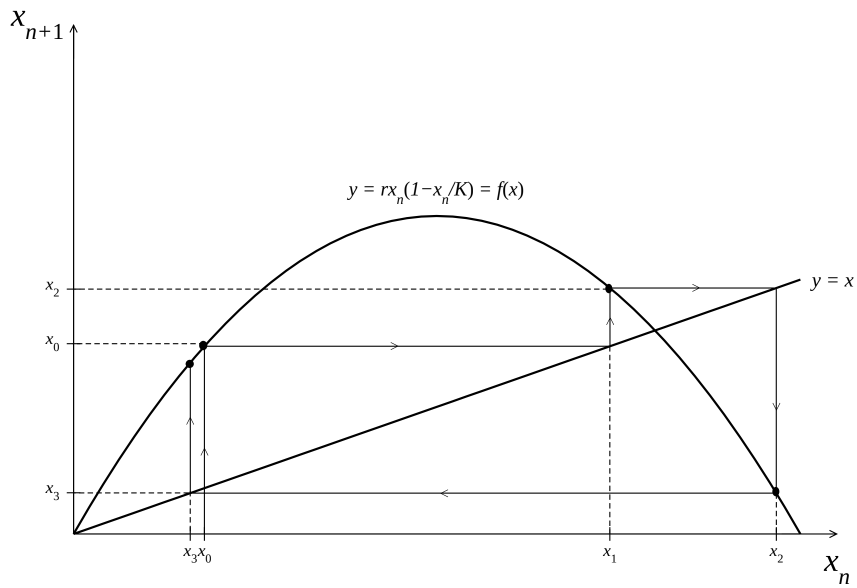

Figure 4: Cobwebbing for the logistic equation, (3). This figure should be changed slightly - choose r between 1 and 3 so that the nontrivial fixed point is stable, and the cobwebbing procedure gives a nice staircase as in the next figure.

axis is to reflect it through the diagonal line $x_{n+1} = x_n$. Visually, this is shown by a horizontal line from x_1 on the vertical axis to the point (x_1, x_1) on the diagonal line, and then a vertical line from the point (x_1, x_1) on the diagonal line to x_1 on the horizontal axis. In summary, one starts by travelling from x_0 vertically to the parabola, then horizontally to the diagonal line, vertically to the parabola, and so on, as indicated by the solid portion of the vertical and horizontal lines on the cobwebbing diagram in Figure 4. In this particular case, the orbit converges to the intersection of the parabola and the diagonal line.

Any intersection of the parabola and the diagonal line represents a special point. Let x^* be such a point. Then $f(x^*) = x^*$. We call any such point a **fixed point** or an **equilibrium point** of the model. If any iterate is x^*, then all subsequent iterates also are x^*. A question of interest is what happens when an iterate is close to, but not exactly at, a fixed point. Do subsequent fixed points move closer to the fixed point or further away? In the former case, the fixed point is said to be **stable**, whereas in the latter case, the fixed point is said to be **unstable**. Examples of both stable and unstable fixed points are shown in Figure 5. The three fixed points shown are x_1^*, x_2^*, and x_3^*. Choosing an initial condition x_0 just to the left of x_2^*, we see that the orbit moves away from x_2^*, and towards x_1^*. Similarly, choosing an initial condition x_0 just to the right of x_2^*, we see tha the orbit again moves away from x_2^*, but now towards x_3^*. We say that x_1^* and x_3^* are stable fixed points, and x_2^* is an unstable fixed point of the model $x_{n+1} = f(x_n)$.

From Figure 5, it appears that the slope of f at the fixed point has something to do with the stability of that fixed point. In particular, the slope of f at the stable fixed points x_1^* and x_3^* is less than 1 (the slope of the straight diagonal line), whereas the slope of f at the unstable fixed point x_2^* is greater than 1. We can formalize these ideas via a **linear stability analysis**, as follows:

We choose the n-th iterate to be close to a fixed point x^* of (1),

$$x_n = x^* + y_n, \tag{5}$$

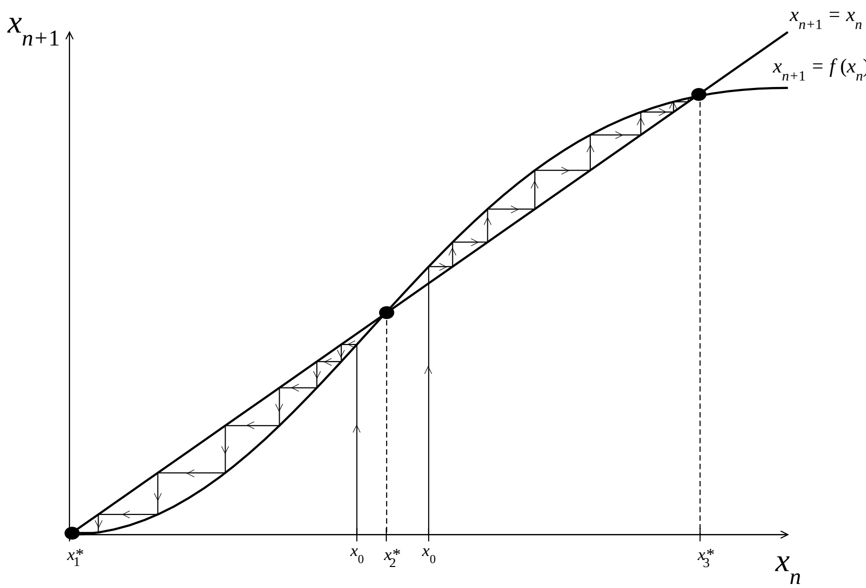

Figure 5: Illustration of stable and unstable fixed points of the difference equation $x_{n+1} = f(x_n)$. The fixed points x_1^* and x_3^* are stable, and the fixed point x_2^* is unstable.

with y_n small, so that x_n can be thought of as a perturbation of x^*. The question of interest now is what happens to y_n, the deviation of x_n from x^*, as the map is iterated. If the deviation grows, then the fixed point x^* is unstable, and if the deviation shrinks, then it is stable. We can find the map for the deviation by substituting (5) into (1) to obtain

$$x^* + y_{n+1} = f(x^* + y_n). \tag{6}$$

We expand the right hand side using a Taylor series about x^* to obtain

$$x^* + y_{n+1} = f(x^*) + f'(x^*)y_n + \mathcal{O}(y_n^2). \tag{7}$$

Since x^* is a fixed point, we can replace $f(x^*)$ on the right hand side by x^*. If, in addition, we can safely neglect all the terms in the Taylor series that have been collected in the term $\mathcal{O}(y_n^2)$, then we are left with a map for the deviation,

$$y_{n+1} = f'(x^*)y_n. \tag{8}$$

We recognize that $f'(x^*)$ is some constant, λ say. The map for the deviation thus is the linear map

$$y_{n+1} = \lambda y_n. \tag{9}$$

We've already looked at the linear map in the context of population growth, (2). There, we restricted the growth parameter to be > 0. Here, $f(x^*)$ can take on any value, depending on the map f, and so there are no restrictions on λ. The behaviour of the deviation y_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.

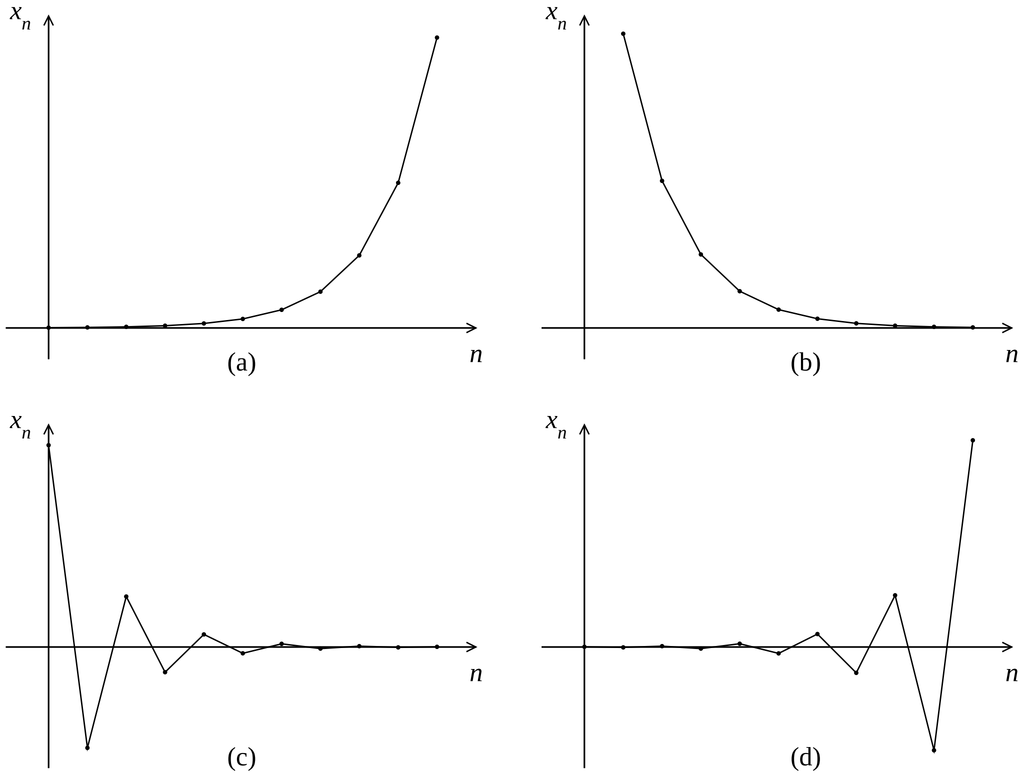

Figure 6: Behaviour of the general linear map, (9), for the cases (a) $\lambda > 1$; (b) $0 < \lambda < 1$; (c) $-1 < \lambda < 0$; (d) $\lambda < -1$.

The four cases are illustrated in Figure 6. Note that no conclusion can be reached when $\lambda = \pm 1$. These two cases require advanced treatment, involving a careful examination of the neglected terms collecting in the term $\mathcal{O}(y_n^2)$ in (7), which is beyond the scope of this book. For treatment of these cases, the reader is referred to a textbook on discrete equations, for example CITE SOMETHING HERE.

More generally, we can summarize the results of the analysis as follows:

x^* is stable when $|\lambda| = |f'(x^*)| < 1$,
x^* is unstable when $|\lambda| = |f'(x^*)| > 1$,
there is no conclusion about the stability of x^* when $|\lambda| = |f'(x^*)| = 1$.

That is, the linear stability of a fixed point x^* is determined by the slope of the map at the fixed point, $\lambda = f(x^*)$. The parameter λ is generally referred to as the **eigenvalue** of the map at x^*.

4 Analysis of the Discrete Logistic Map

We now return to the logistic map, (3), and apply the tools discussed in the previous section to this map. We begin with applying the transformation $\bar{x}_n = \frac{x_n}{K}$ to eliminate the parameter K, and

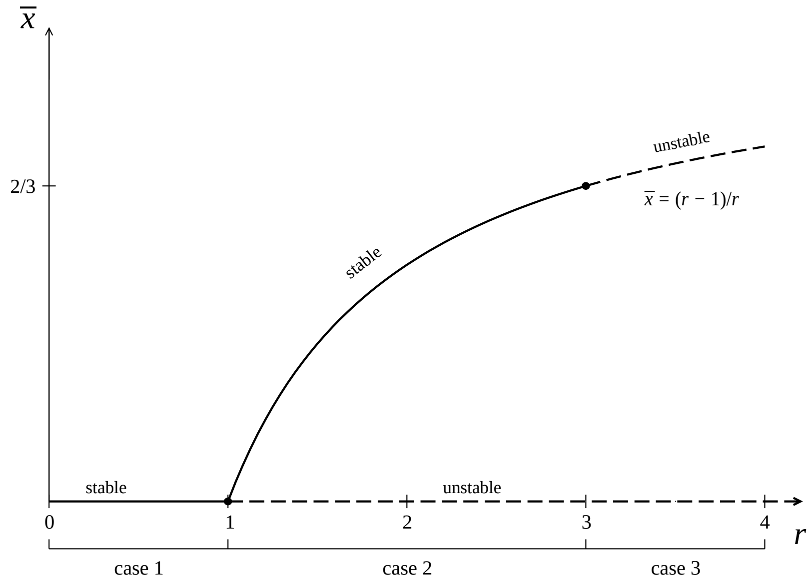

Figure 7: Partial bifurcation diagram for the rescaled logistic map, (10). Shown are the fixed points and their stability as a function of the model parameter r. Solid lines indicate stability of the fixed point, and dashed lines indicate instability.

obtain

$$x_{n+1} = f(x_n) = rx_n(1 - x_n) \tag{10}$$

after dropping the overbars. Note that if we have $x_n > 1$, then $x_{n+1} < 0$. To avoid such situations, we impose the restriction $0 \leq r \leq 4$, so that $x \in [0, 1]$.

The fixed points of the map can be found exactly by setting $f(x^*) = x^*$ and solving for x^*. There are two fixed points. The trivial fixed point, $x^* = 0$, always exists, while the nontrivial fixed point, $x^* = \frac{r-1}{r}$, exists only when $r > 1$.

To determine the stability of the fixed points, we need $f'(x)$, which is

$$f'(x) = r(1 - 2x). \tag{11}$$

At the trivial fixed point, $x^* = 0$, the derivative is $f'(0) = r$. That is, the trivial fixed point is stable for $0 \leq r < 1$, and unstable for $1 < r \leq 4$. At the nontrivial fixed point, $x^* = \frac{r-1}{r}$, we have $f'(\frac{r-1}{r}) = 2 - r$. That is, the nontrivial fixed point is stable for $1 < r < 3$, and unstable for $3 < r \leq 4$. The existence and stability of the fixed points is summarized in the **bifurcation diagram** of the fixed points versus the parameter r, shown in Figure 7. Reading the diagram from left to right, note that the trivial fixed point becomes unstable as soon as the nontrivial fixed points come onto the scene at $r = 1$. The nontrivial fixed point is stable initially, but loses its stability at $r = 3$. The two points $r = 1$ and $r = 3$ are known as **bifurcation points**. A bifurcation point is a parameter value at which there is a qualitative change in the dynamics of the map. The bifurcation at $r = 1$ is called a transcritical bifurcation. There are many other types of bifurcations. A detailed discussion of bifurcation theory is beyond the scope of this course, as is a detailed discussion of the dynamics of the logistic model for the case $3 < r <= 4$. The interested reader is referred to [3].

References

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[3] S. Strogatz, *Nonlinear Dynamics and Chaos: with Applications to Physics, Biology, Chemistry, and Engineering*, Addison-Wesley Publishing Company, Reading, MA, 1994.