Discrete Population Models for Single Species

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Abstract

The author presents a review of *Discrete Population Models for Single Species*. He describes their relevance and applications, gives a graphical approach to solving non-linear models, presents some of the details around *Equilibrium*, *Stability*, and *Chaos*, looks rigorously at the technique of *Linearisation* around equilibrium points, and then reviews *Discrete Models with Delay*.

Chapter 1

Discrete Models

1.1 Introduction

Discrete models, as opposed to continuous models, use difference equations
(rather than differential equations) to model biological phenomena, such as pop-
ulations, when it makes sense to measure the interval of time between events as
discrete or fixed. It also makes sense where successive measurements occur at
fixed time intervals - such as census data. We are interested in models of the
form:

$$x_{t+1} = f(x_t)$$

Where f is a linear or non-linear function of x_t. The sequence $\{x_0, x_1, x_2, \ \ldots\ \}$
is called the *orbit*.

As an example, consider a population that changes over time through births
and deaths only. Let us denote the population at time t to be x_t, and the
population at time $t + 1$ to be x_{t+1}. With a birth rate r_b and a death rate r_d,
we can describe the rate of change of the population as follows:

$$\begin{aligned} x_{t+1} - x_t &= r_b x_t - r_d x_t \\ &= (r_b - r_d)x_t \\ x_{t+1} &= x_t + (r_b - r_d)x_t \\ &= (1 + r_b - r_d)x_t \\ &= rx_t \end{aligned}$$

where $r = 1 + r_b - r_d$. From here it is easy to show that:

$$\begin{aligned} x_t &= rx_{t-1} \\ &= r(rx_{t-2}) \\ &= r^2 x_{t-2} \\ &= r^2(rx_{t-3}) \\ &= r^3 x_{t-3} \\ &\vdots \\ &= r^t x_0 \end{aligned}$$

and for this simple model it is clear to see that when $|r| < 1$ then the population decays to zero, and if $|r| > 1$ then the population grows without bound. If $|r| = 1$ then the population exhibits no growth or decay at all, remaining constant at it's initial value.

1.2 Applications

Some examples where discrete models may be used are:

- plant population (annual reproduction)

- insect population (where there is no overlap in generations)

- cell population (within a culture)

1.3   Solutions

Solving a linear discrete model - coming up with a formula that expresses the n-th iterate of our model in terms of the parameters of the model - is easy, and allows us to make long-term predictions about the behaviour of our model. In the non-linear case it is not possible to do this, and hence difficult to make predictions about the long-term model behaviour, population dynamics, etc.
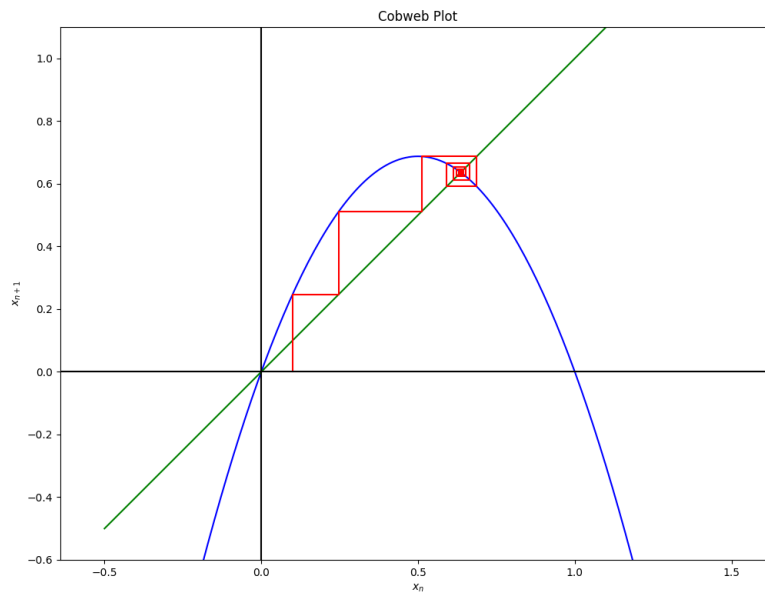

Figure 1.1: Cobweb plot of $x_{t+1} = x_t r(1 - x_t)$

One technique for helping us to understand non-linear discrete models is *cobwebbing*, which is a graphical method for finding equilibrium points. The technique is as follows:

- construct a set of axes with x_t along the horizontal and x_{t+1} along the vertical

- draw the curve of the function $x_{t+1} = f(x_t)$

- draw the line $x_{t+1} = x_t$

- draw a line vertically up from $(x_0, 0)$ on the horizontal till it meets the curve of the function

- this point is (x_0, x_1)

- draw a line horizontally from (x_0, x_1) till it meets the line $x_{t+1} = x_t$

- call this point (x_1, x_1)

- with this point we repeat the above process until we either converge to an equilibrium point or diverge

Equilibrium points are located where the curve and the line intersect - usually denoted x^*.

Chapter 2

Discrete Logistic Growth

2.1 Basics

Consider the Logistic growth model:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

where r is the growth rate, and K is the carrying capacity. We can turn this into a discrete model as follows:

$$
\begin{aligned}
N_{t+1} - N_t &= rN_t\left(1 - \frac{N_t}{K}\right) \\
N_{t+1} &= N_t + rN_t\left(1 - \frac{N_t}{K}\right) \\
&= N_t\left(1 + r - \frac{rN_t}{K}\right) \\
&= N_t(1+r)\left(1 - \frac{rN_t}{(1+r)K}\right)
\end{aligned}
$$

by making a transformation we have:

$$x_{t+1} = f(x_t) = x_t r'(1 - x_t) \quad \text{where} \quad r' = 1 + r \quad \text{and} \quad x_t = \frac{rN_t}{(1+r)K}$$

2.2 Equilibrium

we now investigate the equilibrium states of this model, with $0 \leq r \leq 4$ for simplicity:

$$
\begin{aligned}
x^* &= x^* r(1 - x^*) \\
r(1 - x^*) &= 1 \\
1 - x^* &= \frac{1}{r} \\
x^* &= \frac{r-1}{r}
\end{aligned}
$$

so we have two equilibrium points - $x^* = 0$ and $x^* = (r-1)/r$ with $r > 1$ (as we are not interested in negative populations). In order to understand the behaviour of the equilibrium points we need to look at the first derivative of $f(x)$:

$$
\begin{aligned}
f(x) &= xr(1 - x) \\
f'(x) &= r(1 - 2x)
\end{aligned}
$$

2.3 Stability

Examining both these equilibrium points with $|f'(x)| < 1$ denoting stability, and $|f'(x)| > 1$ denoting instability:

$$
\begin{aligned}
f'(0) &= r \\
f'\left(\frac{r-1}{r}\right) &= 2 - r
\end{aligned}
$$

so $x^* = 0$ is stable for $r < 1$, and unstable for $r > 1$, and $x^* = (r-1)/r$ is stable for $1 < r < 3$, and does not exist for $0 < r < 1$:

	$0 < r < 1$	$1 < r < 3$
$x^* = 0$	stable	unstable
$x^* = \frac{r-1}{r}$	does not exist	stable

Table 2.1: Stability of discrete logistic growth model

2.4 Chaos

$r = 1$ and $r = 3$ are known as *bifurcation points* and represent parameter values where our model's behaviour changes. In order to understand the model's behaviour for $r > 3$ first we observe the following:

$$\begin{aligned}
x_{t+1} &= f(x_t) \\
&= f(f(x_{t-1})) = f^2(x_{t-1}) \\
&= f^2(f(x_{t-2})) = f^3(x_{t-2}) \\
&\vdots \\
&= f^{t+1}(x_0)
\end{aligned}$$

and in particular, looking at the second order difference equation:

$$\begin{aligned}
x_{t+2} &= f^2(x_t) \\
&= f(f(x_t)) \\
&= f(x_t)r(1 - f(x_t)) \\
&= x_t r^2(1 - x_t)(1 - x_t r(1 - x_t))
\end{aligned}$$

setting $x_{t+2} = x_t = x^*$ we find:

$$\begin{aligned}
x^* &= x^* r^2(1 - x^*)(1 - x^* r(1 - x^*)) \\
1 &= r^2(1 - x^*)(1 - x^* r(1 - x^*)) \\
1 &= r^2(1 - x^* r + (x^*)^2 r - x^* + (x^*)^2 r - (x^*)^3 r) \\
1 &= r^2 - x^* r^3 + (x^*)^2 r^3 - x^* r^2 + (x^*)^2 r^3 - (x^*)^3 r^3 \\
0 &= 1 - r^2 + x^* r^3 - (x^*)^2 r^3 + x^* r^2 - (x^*)^2 r^3 + (x^*)^3 r^3
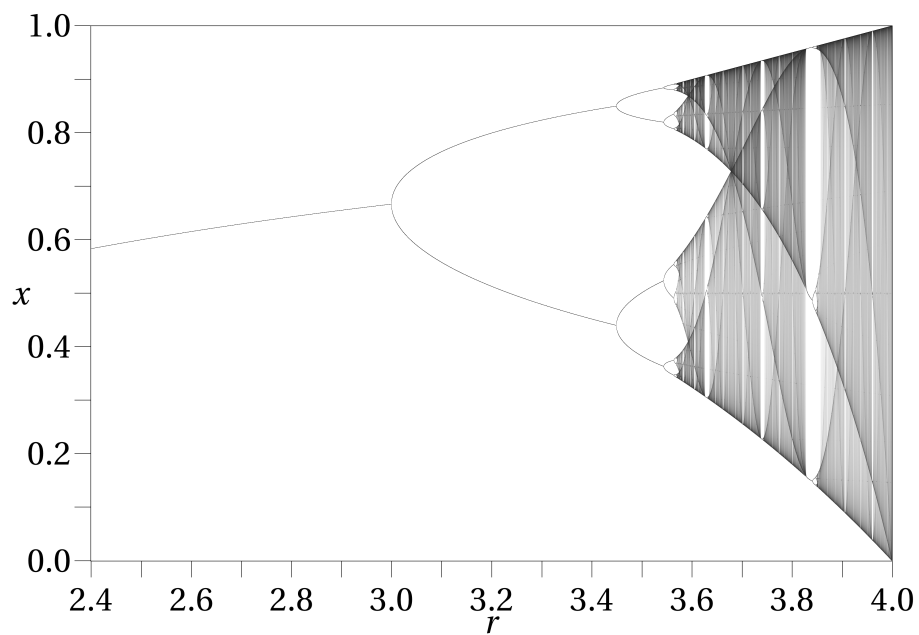\end{aligned}$$

after some manipulation this reduces to:

Figure 2.1: Bifurcations

$$(rx^* - (r+1))(r^2(x^*)^2 - r(r+1)x^* + (r+1)) = 0$$

here $rx^* - (r+1) = 0$ gives us one of our original equilibrium points, so instead we look at:

$$r^2(x^*)^2 - r(r+1)x^* + (r+1) = 0$$

this quadratic will give us two real roots if the discriminant is positive:

$$
\begin{aligned}
r^2(r+1)^2 - 4r^2(r+1) &> 0 \\
r^2 + 2r + 1 - 4r - 4 &> 0 \\
r^2 - 2r - 3 &> 0 \\
(r+1)(r-3) &> 0
\end{aligned}
$$

as we have restricted ourselves to $r > 0$, we have $r > 3$, and our solutions are:

$$
x^* = \frac{(r+1) \pm \sqrt{(r+1)(r-3)}}{2r}
$$

so the next solution is said to have period 2 as there are two possible values. This process continues for increasing r. So p-periodic solutions become $2p$-periodic solutions, and so on.

If an odd periodic solution $(p \geq 3)$ exists for some value of r, say r_c, then there is said to be *aperiodic* or *chaotic* solutions for $r > r_c$. Chaotic solutions are solutions that oscillate in random, or unpredictable, ways.

2.5   Analysis

We now investigate the stability of our Logistic growth model analytically through linearisation about an equilibrium point:

$$
x_t = x^* + u_t, \qquad |u_t| \ll 1
$$

substituting this into our function we get:

$$x^* + u_{t+1} = f(x^* + u_t)$$

Taylor expanding around the equilibrium point we get:

$$x^* + u_{t+1} = f(x^*) + u_t f'(x^*) + \mathcal{O}(u_t^2), \qquad |u_t| \ll 1$$

as x^* is an equilibrium point, $f(x^*) = x^*$, and discarding higher powers of u_t, we get:

$$
\begin{aligned}
u_{t+1} &= u_t f'(x^*) \\
&= \lambda u_t \\
&= \lambda^{t+1} u_0
\end{aligned}
$$

where $\lambda = f'(x^*)$. From this we can draw conclusions about the stability of the equilibrium point. It is clear that:

$$
\begin{aligned}
|\lambda| < 1 &\implies \lim_{t \to \infty} u_t = 0 \\
|\lambda| > 1 &\implies \lim_{t \to \infty} u_t = \pm\infty
\end{aligned}
$$

and hence:

$$
\begin{aligned}
|f'(x^*)| < 1 &\implies x^* \quad \text{is stable} \\
|f'(x^*)| > 1 &\implies x^* \quad \text{is unstable}
\end{aligned}
$$

Chapter 3

Discrete Models with Delay

3.1 Introduction

So far we have assumed that all members of the population at time t contribute to the population at time $t + 1$, but this is not always the case. For example, depending upon the interval of time, some members of a population may not have yet reached sexual maturity, and hence cannot contribute to the population. As a consequence it makes sense in some cases to introduce a delay term to the model.

$$x_{t+1} = f(x_t, x_{t-\tau})$$

3.2 Analysis

We switch now to a different model - Ricker's model:

$$x_{t+1} = x_t \exp(r(1 - x_t))$$

with $r > 0$ - which has equilibrium points $x^* = 0$ and $x^* = 1$. We make a slight change to this model by introducing a delay term:

$$x_{t+1} = x_t \exp(r(1 - x_{t-1}))$$

again, with $r > 0$. Now we linearise around $x^* = 1$:

$$x_t = 1 + u_t, \qquad |u_t| \ll 1$$

substituting into our equation above we get:

$$
\begin{aligned}
1 + u_{t+1} &= (1 + u_t) \exp(r(1 - (1 + u_{t-1}))) \\
&= (1 + u_t) \exp(-ru_{t-1}) \\
&\approx (1 + u_t)(1 - ru_{t-1}) \\
&= 1 - ru_{t-1} + u_t - ru_t u_{t-1} \\
u_{t+1} &= u_t - ru_{t-1}
\end{aligned}
$$

the above using the fact that $\exp(x) \approx 1 + x$ for small x.

3.3   Solutions

We have reduced our model to a second order difference equation:

$$u_{t+1} - u_t + ru_{t-1} = 0$$

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with characteristic equation:

$$z^2 - z + r = 0$$

with solutions:

$$
\begin{aligned}
z_{1,2} &= \frac{1}{2}\left[1 \pm \sqrt{1 - 4r}\right] & 0 < r < \frac{1}{4} \\
z_{1,2} &= \frac{1}{2}\left[1 \pm i\sqrt{4r - 1}\right] & \frac{1}{4} < r < 1
\end{aligned}
$$

for the case of $0 < r < \frac{1}{4}$ we have:

$$u_t = C_1 z_1^t + C_2 z_2^t$$

and because $0 < z_{1,2} < 1$:

$$\lim_{t \to \infty} u_t = 0$$

and hence:

$$\lim_{t \to \infty} x_t = 1$$

therefore $x^* = 1$ is stable for $0 < r < \frac{1}{4}$. For the case of $\frac{1}{4} < r < 1$ we have:

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$$\begin{aligned}
\rho &= |z_{1,2}| = \sqrt{r} \\
\theta &= \tan^{-1}(\sqrt{4r-1}) \\
z_{1,2} &= \rho e^{\pm i\theta}
\end{aligned}$$

which leads to:

$$\begin{aligned}
u_t &= Cz^t + \overline{C}\overline{z}^t \\
&= |A|\, e^{i\gamma}(\rho e^{i\theta})^t + |A|\, e^{-i\gamma}(\rho e^{-i\theta})^t \\
&= 2\,|A|\,\rho^t \left(\frac{e^{i(\theta t+\gamma)} + e^{-i(\theta t+\gamma)}}{2} \right) \\
&= 2\,|A|\,\rho^t \cos(\theta t + \gamma)
\end{aligned}$$

which is stable as $r < 1$. If we take $r_c = 1$, then at r_c we have:

$$\begin{aligned}
\theta_c &= \tan^{-1}(\sqrt{4r_c-1}) \\
&= \tan^{-1}(\sqrt{3}) \\
&= \frac{\pi}{3}
\end{aligned}$$

from which we get:

$$u_t = 2\,|A|\cos(\frac{\pi}{3}t + \gamma)$$

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and hence:

$$\frac{\pi}{3}t_p = 2\pi$$
$$t_p = 6$$

and for $r > r_c$ we have $\rho > 1$ which gives us:

$$\lim_{t \to \infty} u_t = \pm\infty$$

and hence:

$$\lim_{t \to \infty} x_t = \pm\infty$$

Chapter 4

Solutions to problems

4.1 $x_{n+1} = \beta x_n + \alpha x_{n-1}$

This is a linear system. The solution is as follows:

$$
\begin{aligned}
x_{n+1} &= \beta x_n + \alpha x_{n-1} \\
x_{n+1} - \beta x_n - \alpha x_{n-1} &= 0
\end{aligned}
$$

with characteristic equation:

$$\lambda^2 - \beta\lambda - \alpha = 0$$

and solutions:

$$\lambda_{1,2} = \frac{\beta \pm \sqrt{\beta^2 + 4\alpha}}{2}$$

our general solution is of the form:

$$x_n = C_1\lambda_1^n + C_2\lambda_2^n$$

which gives us for $n = 0$ and $n = 1$:

$$
\begin{aligned}
x_0 &= C_1 + C_2 \\
x_1 &= C_1\lambda_1 + C_2\lambda_2
\end{aligned}
$$

taking x_1 we get:

$$
\begin{aligned}
x_1 &= C_1\frac{\beta + \sqrt{\beta^2 + 4\alpha}}{2} + C_2\frac{\beta - \sqrt{\beta^2 + 4\alpha}}{2} \\
&= \frac{\beta}{2}(C_1 + C_2) + \frac{\sqrt{\beta^2 + 4\alpha}}{2}(C_1 - C_2) \\
&= \frac{\beta}{2}x_0 + \frac{\sqrt{\beta^2 + 4\alpha}}{2}(C_1 - C_2)
\end{aligned}
$$

$$
\begin{aligned}
C_1 - C_2 &= \frac{2x_1 - \beta x_0}{\sqrt{\beta^2 + 4\alpha}} \\
C_1 + C_2 &= x_0
\end{aligned}
$$

solving for C_1 and C_2 we get:

$$
\begin{aligned}
C_1 &= \frac{x_0(\sqrt{\beta^2 + 4\alpha} - \beta) + 2x_1}{2\sqrt{\beta^2 + 4\alpha}} \\
\\
C_2 &= \frac{x_0(\sqrt{\beta^2 + 4\alpha} + \beta) - 2x_1}{2\sqrt{\beta^2 + 4\alpha}}
\end{aligned}
$$

so our general solution is:

$$x_n = \left(\frac{x_0(\sqrt{\beta^2 + 4\alpha} - \beta) + 2x_1}{2\sqrt{\beta^2 + 4\alpha}} \right) \left(\frac{\beta + \sqrt{\beta^2 + 4\alpha}}{2} \right)^n$$

$$+ \left(\frac{x_0(\sqrt{\beta^2 + 4\alpha} + \beta) - 2x_1}{2\sqrt{\beta^2 + 4\alpha}} \right) \left(\frac{\beta - \sqrt{\beta^2 + 4\alpha}}{2} \right)^n$$

4.2 $x_{n+1} = x_n \big/ 1 + x_n$

This is a non-linear system.

$$x_{n+1} = \frac{x_n}{1 + x_n}$$

finding the equilibrium points:

$$x^* = \frac{x^*}{1 + x^*}$$

$$\therefore \quad x^* = 0$$

now we look at the stability:

$$f(x) = \frac{x}{1+x}$$

$$f'(x) = \frac{1}{(1+x)^2}$$

$$f'(0) = 1$$

therefore, strictly speaking, we cannot say that $x^* = 0$ is either stable or unstable. Looking at the system graphically (Figure 4.1) starting in the neighbourhood of 1 and cobwebbing, we see that the system tends towards 0 which would imply $x^* = 0$ is stable.
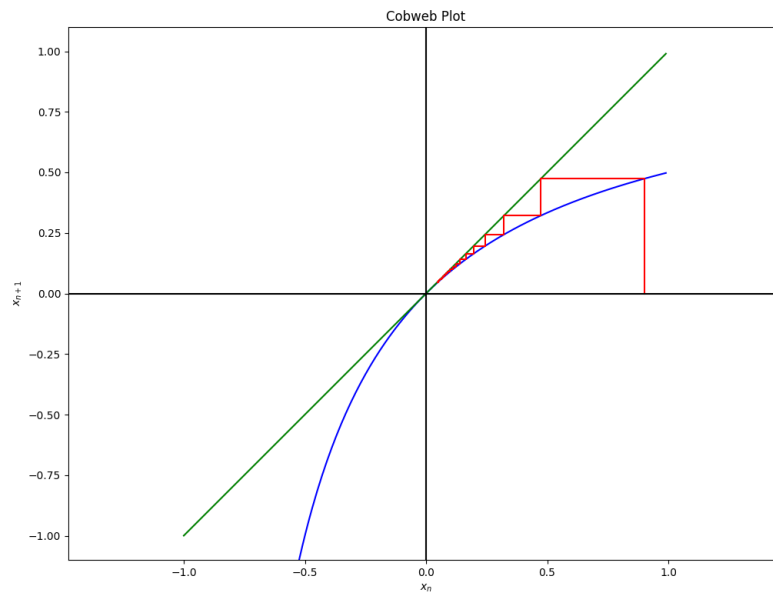

Figure 4.1: Cobweb plot of $x_{n+1} = x_n/1 + x_n$

4.3 $x_{n+1} = 1/2 + x_n$

This is a non-linear system.

$$x_{n+1} = \frac{1}{2 + x_n}$$

finding the equilibrium points:

$$
\begin{aligned}
x^* &= \frac{1}{2 + x^*} \\
2x^* + (x^*)^2 &= 1 \\
(x^*)^2 + 2x^* - 1 &= 0
\end{aligned}
$$

$$x^* = -1 \pm \sqrt{2}$$

we discard $x^* = -1 - \sqrt{2}$ as it is not positive. Now we look at the stability of $x^* = -1 + \sqrt{2}$:

$$
\begin{aligned}
f(x) &= \frac{1}{2 + x} \\
f'(x) &= \frac{-1}{(2 + x)^2}
\end{aligned}
$$

$$\left| f'(-1 + \sqrt{2}) \right| < 1$$

therefore the equilibrium point $x^* = -1 + \sqrt{2}$ is stable.

4.4 $\quad x_{n+1} = x_n e^{\alpha x_n}$

This is a non-linear system.

$$x_{n+1} = x_n e^{\alpha x_n}$$

finding the equilibrium points:

$$
\begin{aligned}
x^* &= x^* e^{\alpha x^*} \\
\therefore \quad x^* &= 0
\end{aligned}
$$

now we look at the stability:

$$
\begin{aligned}
f(x) &= x e^{\alpha x} \\
f'(x) &= (1 + \alpha x) e^{\alpha x} \\
f'(0) &= 1
\end{aligned}
$$

therefore, strictly speaking, we cannot say that $x^* = 0$ is either stable or unstable. Looking at the system graphically (Figure 4.2) starting in the neighbourhood of 0 and cobwebbing, we see that the system tends towards ∞, i.e. is unbounded, which would imply $x^* = 0$ is unstable.
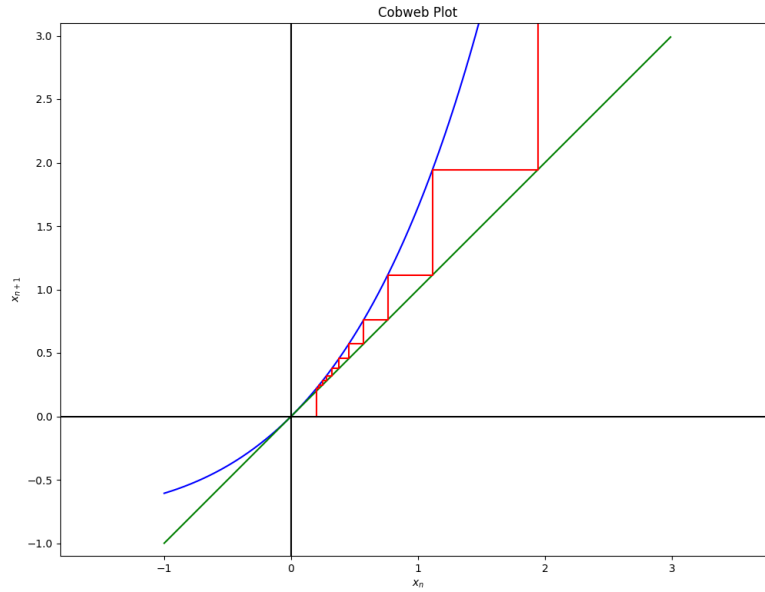
Figure 4.2: Cobweb plot of $x_{n+1} = x_n e^{\alpha x_n}$

4.5 $x_{n+1} = x_n \ln(x_n^2)$

This is a non-linear system.

$$x_{n+1} = x_n \ln(x_n^2)$$

finding the equilibrium points:

$$\begin{aligned} x^* &= x^* \ln((x^*)^2) \\ &= 2x^* \ln(x^*) \end{aligned}$$

$$\begin{aligned} 2\ln(x^*) &= 1 \\ \ln(x^*) &= \frac{1}{2} \\ x^* &= \sqrt{e} \\ \therefore \quad x^* &= 0 \quad \text{or} \quad \sqrt{e} \end{aligned}$$
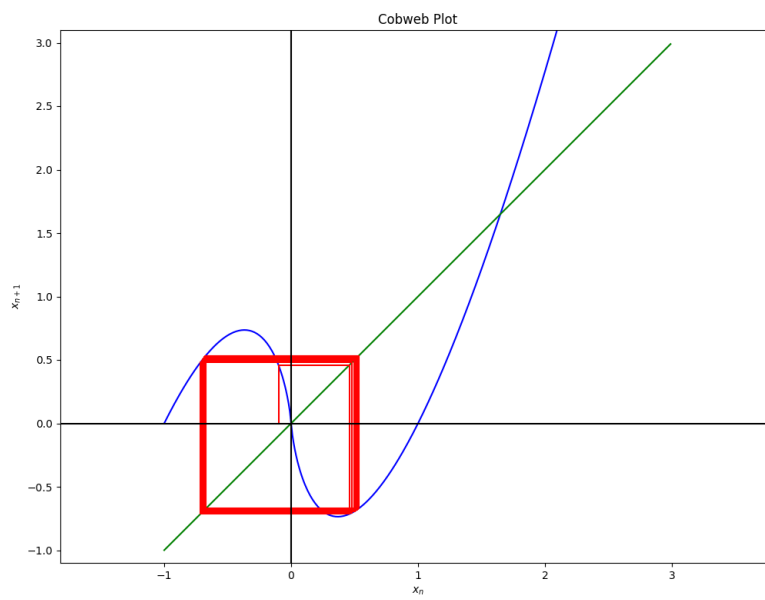
now we look at the stability:

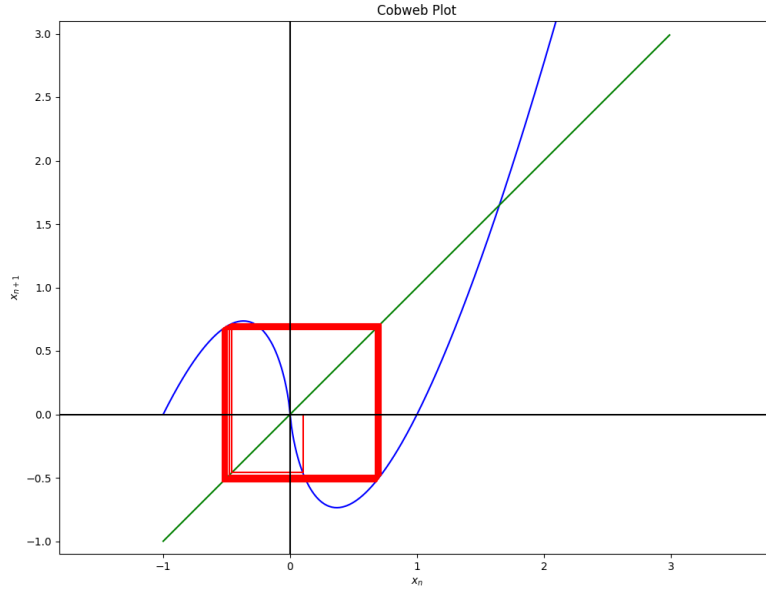Figure 4.3: Cobweb plot of $x_{n+1} = x_n \ln(x_n^2)$ starting from -0.1

Figure 4.4: Cobweb plot of $x_{n+1} = x_n \ln(x_n^2)$ starting from 0.1

$$
\begin{aligned}
f(x) &= 2x\ln(x) \\
f'(x) &= 2(\ln(x) + 1)
\end{aligned}
$$

$$
\begin{aligned}
f'(0) &= -\infty \\
f'(\sqrt{e}) &= 3
\end{aligned}
$$

therefore both $x^* = 0$ and $x^* = \sqrt{e}$ are unstable. But looking at the system graphically and cobwebbing starting at -0.1 (Figure 4.3) and then starting at 0.1 (Figure 4.4) - i.e. in the neighbourhood of 0 - we see periodic oscillations that would suggest a periodic solutions to the system.

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4.6 $(x_{n+1} - \alpha)^2 = \alpha^2(x_n^2 - 2x_n + 1)$

This is a combination of linear systems.

$$
\begin{aligned}
(x_{n+1} - \alpha)^2 &= \alpha^2(x_n^2 - 2x_n + 1) \\
&= \alpha^2(x_n - 1)^2 \\
x_{n+1} - \alpha &= \pm\alpha(x_n - 1) \\
x_{n+1} &= \alpha \pm \alpha(x_n - 1) \\
&= \alpha \pm (\alpha x_n - \alpha)
\end{aligned}
$$

this results in two linear systems, the first:

$$
\begin{aligned}
x_{n+1} &= \alpha x_n \\
&= \alpha^{n+1} x_0
\end{aligned}
$$

and the second:

$$
\begin{aligned}
x_{n+1} &= 2\alpha - \alpha x_n \\
&= 2\alpha - \alpha(2\alpha - \alpha x_{n-1}) \\
&= 2\alpha - 2\alpha^2 + \alpha^2 x_{n-1} \\
&= 2\alpha - 2\alpha^2 + \alpha^2(2\alpha - \alpha x_{n-2}) \\
&= 2\alpha - 2\alpha^2 + 2\alpha^3 - \alpha^3 x_{n-2} \\
&\vdots
\end{aligned}
$$

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$$= 2\alpha\Big(\sum_{i=0}^{n}(-\alpha)^i\Big) + (-\alpha)^{n+1}x_0$$

$$= 2\alpha\Big(\frac{1-(-\alpha)^{n+1}}{1+\alpha}\Big) + (-\alpha)^{n+1}x_0$$

$$= \Big(x_0 - \frac{2\alpha}{1+\alpha}\Big)(-\alpha)^{n+1} + \frac{2\alpha}{1+\alpha}$$

$$= (-1)^{n+1}\Big(x_0 - \frac{2\alpha}{1+\alpha}\Big)\alpha^{n+1} + \frac{2\alpha}{1+\alpha}$$

both systems converge for $|\alpha| < 1$, the first system converges to 0, the second to $2\alpha/1 + \alpha$.

4.7 $x_{n+1} = \sqrt{x_n + 2}$

This is a non-linear system.

$$x_{n+1} = \sqrt{x_n + 2}$$

finding the equilibrium points:

$$
\begin{aligned}
x^* &= \sqrt{x^* + 2} \\
(x^*)^2 &= x^* + 2 \\
(x^*)^2 - x^* - 2 &= 0
\end{aligned}
$$

$$\therefore \quad x^* = -1 \quad \text{or} \quad 2$$

we discard $x^* = -1$ as it is not positive. Now we look at the stability of $x^* = 2$:

$$
\begin{aligned}
f(x) &= \sqrt{x+2} \\
f'(x) &= \frac{1}{2\sqrt{x+2}} \\
f'(2) &= \frac{1}{4}
\end{aligned}
$$

therefore the equilibrium point $x^* = 2$ is stable.

Bibliography

[1] F. Brauer and C. Castillo-Chavez. *Mathematical Models in Population Biology and Epidemiology.* Texts in Applied Mathematics. Springer New York, 2012.

[2] J.D. Murray. *Mathematical Biology: I. An Introduction.* Interdisciplinary Applied Mathematics. Springer New York, 2002.