An introduction to discrete dynamical systems: difference equation models

The basic idea here is to consider systems with changes which may be thought of as occuring discretely. One example would be cells which divide synchronously and which you follow at some fixed set of times following cell division. Other examples include any organism with discrete generations (e.g. many insects, annual plants, etc.) in which you follow either population size or some measure of genetic structure such as allele frequencies. The key here is that there are relatively short and synchronized actions (e.g. breeding seasons) which allows one to ignore the within-time period behavior for the purpose of the model.

An alternative view of discrete models is that they are discretizations of continuous-time models. That is, we can’t really observe organisms continuously, so we just monitor the quantities of interest at discrete intervals. An example would be locations of individuals (which move continuously, but we only observe at discrete intervals). This is the basic idea of time series analysis, which are statistical approaches to describing, predicting and controlling the behavior of a time-dependent system.

I would argue that the appropriate formulation of a model depends upon:

> The question you are trying to address and the appropriate temporal (and spatial scale at which to focus that question
>
> The limitations of the available data to develop the model and then evaluate it

A general form for a first-order difference equation is

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

where the function f determines the new value of the variable at the next time step from the previous value. This is an iteration scheme and if you know the function f and an initial x_0 then you can just iterate the function through time to calculate successive values of x_n. However, the objective of mathematical analysis is to provide some general understanding of models such as this, so that you can determine how the system behaves without having to iterate it numerically. Numerical iteration tells us only what one particular trajectory of the system will be through time. We'd potentially have to do many iterations to get a general picture of the behavior of the system, and mathematical analysis saves us from having to do this.

There are a few basic concepts that apply to analysis of dynamical systems in general:

1. Equilibrium - finding a state of the system which does not change in time (and/or space if the problem is spatial). This is typically found by setting the variables at one time step to be the same as that at the next time step

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

where here n represents the nth time interval or in the continuous case setting the derivatives = 0

$$\frac{dx}{dt} = 0$$

Note that there may be many different equilibria arising in a particular model, with one example being a population model in which 0 and some carrying capacity, K, are both equilibria.

2. Stability - determining whether there is a long-term approach to some regular pattern in the system. The simplest case of this is if the system approaches a single equilibrium through time

$$\lim_{n \to \infty} x_n = x^*$$

But there are quite a few different notions of stability. The usual one is **local asymptotic stability** , meaning that following a small perturbation of the system from an equilibrium, through time the system will approach that equilibrium. Note that in many situations, the system may not ever equal the equilibrium value, but rather $x_n - x^*$ gets as small as you would like as n increases. Another notion of stability is **global stability** , meaning that following any perturbation, not just small, local ones, the system approaches an equilibrium.

3. Dynamic equilibria - here the system has some dynamic pattern that, if it starts in this pattern, stays in this pattern forever. If the pattern is stable, then the system approaches this dynamical pattern. One example is a limit cycle in the continuous case, and a 2-cycle in the discrete case:

$$x_n = x^* \text{ for } n \textit{ even}$$

and

$$x_n = x^{**} \text{ for } n \textit{ odd}$$

4. Domain of stability - this is the region (in either the state space of the system, or in some parameter space if the equations are a function of some parameters which affect stability) within which an equilibrium is stable. Thus if values of x_0 in the interval [a , b] guarantee that

$$\lim_{n \to \infty} x_n = x^*$$

and this interval is the largest interval for which this holds, then this interval is the domain of stability. Similarly, if the system depends upon some parameter, so that say

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

and an equilibrium is x^* which may depend upon α, then if

$$\lim_{n \to \infty} x_n = x^*$$

for α in $[a , b]$ then this is the domain of stability for the parameter α.

5. Linearization - here we approximate a function by a line segment (if it's a function of one variable) or by a piece of a plane (if it's a function of 2 variables). Such an approximation will generally be accurate (e.g. not too far from the original function) only for small ranges of the variable. This is very useful in determining local stability of an equilibrium, because we can approximate the functions determining the dynamics near the equilibrium and from such an approximation determine whether the equilibrium is approached through time or not.

The simplest difference equations - Linear case

The first-order linear difference equation is

$$x_{n+1} = a\ x_n + b \tag{1}$$

where a and b are constants. If b = 0, then this is the simplest model for growth, corresponding to geometric growth with

$$x_n = x_0\ a^n \tag{2}$$

where x_0 is the initial number of cells. Note that unless a is an integer, x_n is not necessarily an integer, so it is more typical to interpret x_n as measuring not the number of cells but some density, which is not then limited to integer values. The b term in (1) can be thought of as an immigration term, if it is positive, or a density independent death term if it is negative. If b > 0, then the solution becomes a little more complicated. This is the simplest case of a non-homogeneous equation, meaning that it has a term that does not depend upon the variable x_n. In general, for linear systems such as this, the general solution is found by adding the general solution of the homogeneous equation

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

to a particular solution (e.g. any solution we can find) to (1). The general solution for linear homogeneous equations is always of the form

$$x_n = c\ \lambda^n$$

where we already know from (2) that in this case $\lambda = a$. To find a particular solution, we typically would try a constant - so assume $x_n = A$ for all n and plug this into (1) to get

$$A = \frac{b}{1 - a}$$

which holds as long as $a \neq 1$. Then the solution of (1) is

$$x_n = C\ a^n + \frac{b}{1 - a}$$

where C is a constant based upon the initial conditions

$$C = x_0 - \frac{b}{1 - a}$$

For the case a = 1, the solution is

$$x_n = x_0 + n\ b$$

Note that in this model there is an equilibrium value which we already found by setting x_n to a constant, it is the value A. Note that if b > 0, then this equilibrium is negative unless a < 1. If a < 1 then the population is declining, and there is an equilibrium which arises when immigration (measured by b) just balances decline. If $b < 0$, and $a > 1$, then there is an equilibrium where growth just balances death. What we next want to investigate is the stability of these.

Stability for the linear case

Here we want to determine whether the equilibrium A found for (1) is stable, by which we mean that if we start off with x_0 near A, will X_n approach A as n increases. The way we do this in general is to define a new variable, call it y_n, which gives the distance of x_n from the equilibrium A

$$y_n = x_n - A$$

and the equilibrium will be stable if y_n decreases towards 0 as n increases. By a simple substitution, we can change (1) to an equation in y_n

$$y_{n+1} = a\ y_n \tag{3}$$

which arises since we chose A to be an equilibrium. But the solution of (3) is just geometric growth

$$y_n = y_0\ a^n$$

and so y_n will decline towards 0 only if $a < 1$. This means that the only case in which A is a stable equilibrium occurs when $b > 0$ and $a < 1$, when the populaion inherently is dying out, and is maintained at an equilibrium only when there is immigration. In the case $b < 0$ and $a > 1$, the equilibrium at A is not stable. If $x_0 > A$ the population grows without bound.

Everything that we did here generalizes to difference equations of a much more general form. The general m-th order difference equation is

$$a_0\ x_n + a_1\ x_{n-1} + \cdots + a_m\ x_{n-m} = b_n \tag{4}$$

where the order m gives the number of previous time steps (generations) which affect the current value of the variable (population size). The case that is a simple extension of the above is the constant coefficient one, in which the a_i terms are constants, with $b_n = 0$, being the homogeneous case. Here what happens is that the general solution is found by looking for geometric growth assuming

$$x_n = c\ \lambda^n$$

and plugging this into (4) in the case $b_n = 0$ gives

$$a_0\ \lambda^m + a_1\ \lambda^{m-1} + \cdots + a_m = 0 \tag{5}$$

which is called the characteristic equation for (4). There will in general be m solutions for λ which satisfy (5) and the general solution is then given by

$$x_n = c_1\ \lambda_1^n + c_2\ \lambda_2^n + \cdots + c_m\ \lambda_m^n$$

where the λ_i are different solutions of (5). What determines the behavior here is the λ_i of the largest magnitude - if it is greater than 1 in magnitude then solutions grow without bound, if it is between 0 and 1 then solutions decline to 0, if it is between -1 and 0 then solutions decline to zero but with oscillations.

Note: an alternative way to view the above higher-order difference equation is as a system of equations, and this leads to the use of linear algebra and matrices.

So what good is all this linear theory? The main advantage is that if we can linearize a more complicated non-linear system (typically near an equilibrium) then we can use the above theory to state whether or not the equilibrium in the non-linear system is locally stable. In general, all we have to do is to examine the solutions of the characteristic equation (5) for the linearize system, and this will tell us whether solutions grow (move away from the equilibrium) or decline (move towards the equilibrium, so it is then locally stable.

Non-linear Models

All biological systems are non-linear, since growth/change cannot continue in a linear manner for very long without causing reduction in available resources. Feedbacks occur which limit components of systems due to their own values or values of other components. The simplest discrete non-linear models are those which have the next higher-order term (e.g. a second power)

$$x_{n+1} = a\ x_n + bx_n^2 + c \tag{6}$$

but just as analyzing a quadratic equation in algebra was quite a bit more difficult that a linear one, analyzing (6) is quite a bit more difficult than the linear case. In fact, even quite simple non-linear difference equations including (6), may be impossible to solve in any simple closed form. This means that either one is limited in analyzing them to doing numerical simulations and generalizing from the limited number of these which can be done, or else using the general themes of analysis for dynamical systems mentioned above to produce a general picture of what happens in the system. Also, in most cases analysis of discrete equations, such as (6), can be much more difficult than analysis of a similar looking differential equation such as

$$\frac{dx}{dt} = a\ x + bx^2 + c$$

So the usual approach in analyzing non-linear discrete equations is to:

1. Look for equilibria, including ones which are not simple, such as cycles

2. Analyze the stability of the equilibria, by doing a local linearization

3. Investigate the paarmeters of the model equations to determine how changes in parameters affect the location and stability of equilibria.

So if we consider the first-order difference equation

$$x_{n+1} = f(x_n) \tag{7}$$

then the above steps correspond to first setting

$$x^* = f(x^*) \tag{8}$$

to find any equilibria and then to determine if an equilibrium is stable, defining the distance from equilibrium

$$y_n = x_n - x^*$$

and substituting this into (7). However to do this we need to use the linearization of the function f near the equilibrium x^*, which makes use of Taylor's Theorem which says that we can approximate a function near a point on the graph of that function by a line through the point wth slope the derivative of the function at that point. This says

$$f(x + x^*) = f(x^*) + x \frac{df}{dx}(x^*) + o(x^2)$$

where x is sufficiently small and the o( ) represents terms that are small (e.g. die out at least as fast as x^2). So then we substitute the y_n into the linearization to get

$$y_{n+1} + x^* = f(x^*) + y_n \frac{df}{dx}(x^*)$$

which neglects the small terms and then using (8) and letting $a = \frac{df}{dx}(x^*)$ we get

$$y_{n+1} = a\ y_n$$

which is a linear equation. This means that y_n decreases towards 0, and thus the equilibria x^* is locally stable, if |a| < 1 and is not stable if |a| > 1. If a = 1 or a = -1, then we can't tell from this procedure what happens - it depends upon the terms we neglected as small.

Now if we wanted to look for equilibria that repeat (say a 2-cycle which repeats every two time periods) then we look at the iterated function g(x)=f(f(x)) since

$$x_{n+2} = f(x_{n+1}) = f(f(x_n)) = g(x_n)$$

and repeat the same analysis only using the g(x) function.

We'll illustrate this now with what is often considered the appropriate discrete analog to the continuous logistic growth equation

$$\frac{dx}{dt} = r\ x\ (1 - \frac{x}{K})$$

namely the hyperbolic equation

$$x_{n+1} = \frac{k\ x_n}{b + x_n} \tag{8}$$

Here we set $x_n = x^*$ and get two solutions $x^* = k - b$ and $x^* = 0$. So for the population to be positive at these, we need k > b. Then to determine stability we need the derivative of $\frac{k\ x_n}{b + x_n}$ which is simply $\frac{k\ b}{(b+x)^2}$ and evaluating this at each of the two equilibria, we see that $x^* = k - b$ is stable when $\frac{b}{k} < 1$ which means k > b so that this equilibrium is stable whenever it exists. If you plug in 0 to the derivative, you get the condition $\frac{k}{b} < 1$ which means that the 0 equilibrium (population extinction) is never stable when the other equilibrium exists.

The next difference equation to look at is the discrete logistic

$$x_{n+1} = x_n \, (\, r - a \; x_n \,)$$

where r and a are constants. First we illustrate the nondimensionalization here by noting that for this equation to make dimensional sense, r must be dimensionless and a must have units $\frac{1}{units \; of \;\; x}$. It thus makes sense to rescale the equation so that it is dimensionless and one reasonable choice for this is to let $y_n = \frac{a}{r} \; x_n$ in which case the y_n are dimensionless and we get a new equation

$$y_{n+1} = r \; y_n \, (\, 1 - y_n \,)$$

Analysis of this equation follows in a similar way to that of the above, except it has lots more interesting dynamics. The simple equilibria are 0 and $1 - \frac{1}{r}$ and the second of these is stable if 1 < r < 3 and the 0 solution is stable if 0 < r < 1. It gets interesting when r is greater than 3 - we’ll look at this numerically.