Dynamics of a single population in discrete time

Erol Akçay
Bio 417 Spring 2017

January 25, 2017

In the previous lecture, we looked at continuous time models that can be represented as $\frac{dN}{dt} = f(N)$, which have many properties that are nice in some ways but also constraining in others. For example, dynamics in single dimension in continuous time cannot exhibit any cycling. Furthermore, as long as $f(N)$ is continuous, the equilibria of a single-dimensional flow must follow in an alternating stability pattern (stable-unstable-stable-...). As we will see, these properties are not true for discrete-time dynamics.

Why do discrete-time? For one thing, in many real-life cases, we have observations in discrete time. We usually cannot monitor populations in the wild continuously; most of our population and environmental data comes from seasonal, yearly, or even lower frequency surveys. So, if our models are to be used in conjunction with real-world data, discrete-time representation is a natural framework. One way to interpret discrete-time dynamics, then, is to regard them as "summaries" of what happened to a population (which lives in continuous time) over a given time period.

Another reason is that funky things tend to happen in discrete-time dynamics that don't happen in continuous time, for reasons that are sometimes biologically very interesting, as we shall see. But first, we start with a very innocuous discrete time dynamic.

Geometric growth

The simplest discrete time model is the following:

$$N_{t+1} = \lambda N_t \ , \tag{1}$$

where N_t is the population size at time t, and λ is a constant; it is called the **geometric growth rate** of the population. If $\lambda > 1$, then the population at $t+1$ is greater than at t, so the population is always growing, and vice versa. This is like the exponential growth in continuous time, and in fact the two are closely related: consider a continuously growing population that is censused yearly. Suppose the intrinsic growth rate r in the continuous population is measured in units of $1/\text{years}$ (so the time-units match up with the census period). Then, after a year from time t, at time $t + 1$, the new population is:

$$N_{t+1} = N_t \exp[r] \tag{2}$$

Comparing this last equation to (1), we can see that $\exp[r] = \lambda$, or equivalently $r = \log(\lambda)$. The scales of λ and r can sometimes get confusing. Any $r > 0$ will lead to an infinitely growing population, and any $r < 0$ will lead to an ever-shrinking one that asymptotically goes extinct. But with λ, the relevant threshold between growth and decline is 1 ($\exp(0) = 1$). Also, whereas r is a true *rate*, in units of individuals per time, λ is a ratio of two population sizes, and therefore dimensionless. The "per time" aspect of rate is instead accounted implicitly in the discrete time intervals, so if one changes the duration of intervals, λ must necessarily change as well, so that we would have to recalculate $\exp[r * \Delta t]$, were Δt is the length of the new discrete time interval.

The logistic map

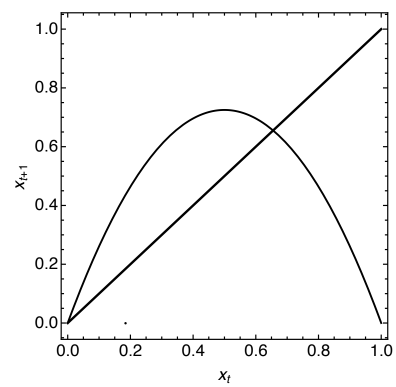
Geometric growth is a bit boring (except possibly it describes your investment portfolio). We had the logistic growth dynamics in continuous time as a toy-model of density dependence; why not do the same in discrete time? Let us simply take the discrete version of the logistic equation, given by

$$N_{t+1} = \lambda \left(1 - \frac{N_t}{K}\right) N_t \ . \tag{3}$$

Here λ is again a constant, the geometric growth rate. It is customary to scale the population size by K, so that we express it as a fraction of the carrying capacity, $x_t = N_t/K$:

$$x_{t+1} = \lambda \left(1 - x_t\right) x_t \ . \tag{4}$$

Now, first let's try to represent the dynamics of this map as we did with the continuous-time dynamics. Instead of plotting the instantaneous *change* in population size, the dynamics now gives us the population size at the next time step, x_{t+1}, so let's plot that against the population size now, x_t. This function is called a map, and the one in equation (4) is called a "logistic map". It is shown in the figure at the margin.

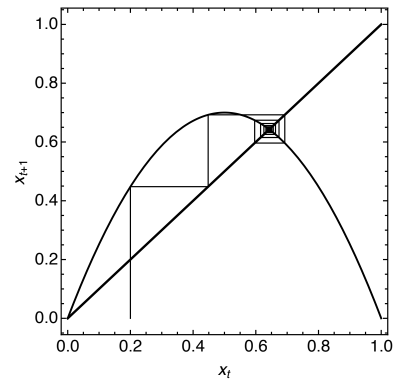


The plot of x_{t+1} against x_t for $\lambda = 2.9$. The straight line depicts $x_{t+1} = x_t$.

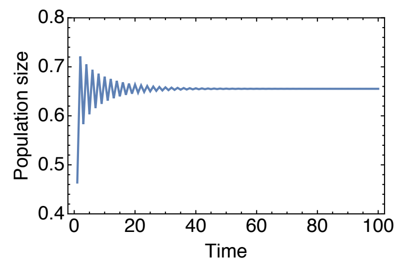
In this plot, we have also included the line on which $x_{t+1} = x_t$. The intersection of this line with the map gives us the value of x that stays unchanged when the map is applied, in other words, a fixed point, or equilibrium, of the map. Just like in continuous time, equilibria can be stable or unstable, depending on whether small deviations from them will grow or shrink. As can be seen in the figure, the logistic map has two equilibria: one at zero, and one at a positive value of x. We will look at its stability shortly.

This representation of the map gives us a way to look at the dynamics graphically. The basic idea is that when you start at a given value of x, say, x_1, you find x_2 by going vertically up until you hit the curve depicting the map. To find the next value, x_3, you need to find x_2 on the $x - axis$, which you can do by going from the map's curve to the 45° line; then going back up (or down) to the map, you find x_3, and so on. The resulting vertical and horizontal trips between the map and the 45° line are called a cobweb diagram (for obvious reasons), and are a graphical way to represent discrete time dynamics in a single dimension.

The figures on the margin depict the dynamics of the logistic map in cobweb and time-trajectory forms, for $\lambda = 2.9$. For this parameter value, there is a single, stable equilibrium. However, convergence to this equilibrium is not monotonic (i.e., not from one side only): the dynamics keep overshooting and undershooting the equilibrium, albeit by progressively diminishing amounts, resulting in damped oscillations. This is a kind of behavior that a continuous time system would never exhibit (in a single dimension)! But there is even funkier stuff happening in the logistic map, as we'll see.



Example of a cobweb diagram for the logistic map with $\lambda = 2.9$. Convergence to the equilibrium point can be seen, but the convergence is not monotonic: the dynamics over- and under-shoot the equilibrium, resulting in damped oscillations.



The same dynamics as in the prvious figure $\lambda = 2.9$), with x_t plotted against t, showing damped oscillations converging to a stable equilibrium.

Linear stability analysis in discrete time

Like in the continuous time dynamics, one can determine the stability of equilibria using this graphical method, but for discrete time, this becomes pretty tedious already in a single dimension. Luckily, we again have an analytical method for determining the stability of an equilibrium. Consider a map $x_{t+1} = g(x_t)$ with equilibrium x^* (i.e., $x^* = g(x^*)$). Suppose at time t, we start with a small deviation δ_t from x^*, i.e., $x_t = x^* + \delta_t$. The question again is whether δ_t will grow or shrink.[1] We can write:

$$x_{t+1} = x^* + \delta_{t+1} = g(x^* + \delta_t) \tag{5}$$

Again, assuming δ_t is small, we write the Taylor expansion of $g(\cdot)$ and ignore terms quadratic or higher order in δ_t, so that we have: e for δ_{t+1}:

$$x_{t+1} = x^* + \delta_{t+1} \approx g(x^*) + g'(x^*)\delta_t = x^* + g'(x^*)\delta_t \ , \tag{6}$$

where the last step follows from x^* being an equilibrium of the map. Thus $\delta_{t+1} \approx g'(x^*)\delta_t$. Hence, the magnitude of δ will grow if the absolute value of $g'(x^*)$ is greater than 1, i.e. $|g'(x^*)| > 1$. Conversely, δ will shrink if $|g'(x^*)| < 1$, or $-1 < g'(x^*) < 1$.

Let's apply this condition to the logistic map. First, let's find the equilibrium of the map (equation (4)):

$$\begin{aligned} x^* &= \lambda x^*(1 - x^*) \\ 1 &= \lambda(1 - x^*) \\ x^* &= 1 - \frac{1}{\lambda} = \frac{\lambda - 1}{\lambda} \end{aligned} \tag{7}$$

This equilibrium is between 0 and 1 for $\lambda > 1$. Now, let's evaluate the stability

[1] Since we know that the dynamics can jump from one side of the equilibrium to the other, we have to pose this question in terms of magnitudes now, i.e., we are interested in whether the absolute value of δ, $|\delta|$ will grow or shrink.

of the equilibrium:

$$\begin{aligned} g'(x^*) &= \lambda[(1-x^*) - x^*] = \lambda(1-2x^*) \\ &= \lambda\left(1 - 2\frac{\lambda-1}{\lambda}\right) \\ &= 2-\lambda\,, \end{aligned} \tag{8}$$

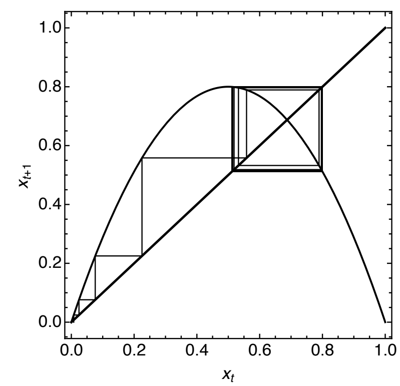
which is greater than -1 for $\lambda < 3$,[2] therefore we can conclude that the equilibrium will be stable for $\lambda < 3$, and unstable otherwise.

[2] It is always less than 1 if $\lambda > 1$.

Next up: what happens when the equilibrium is unstable in the logistic map?

Mischief in the logistic map: cycles, period doubling, and chaos

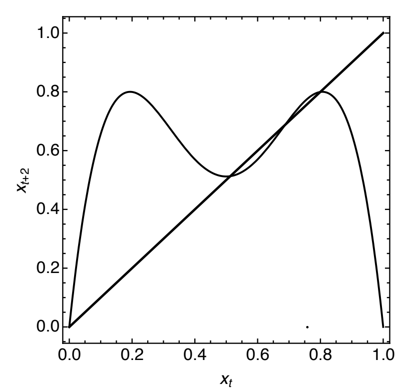
Let's go back to the cobweb diagram, and plot the dynamics for a value of $\lambda > 3$, as we do on the margin. We can see that we still have a convergence, but this time not to a stable point, but to a cycle consisting of two points. This is an instance of what is called *a bifurcation* in dynamical systems theory: a transition in the parameter space where equilibria (or cycles) appear, disappear, or change stability properties.



Dynamics of the logistic map with $\lambda = 3.2$. The cobweb diagram shows convergence to a cycle, where the dynamics oscillate between two values of x.

One way to see the existence of the cycle is to look at the "two-step map", or the map applied twice:

$$x_{t+2} = g(x_{t+1}) = g(g(x_t)) = h(x_t) \tag{9}$$



The map that arises from applying the logistic map twice in succession, i.e., x_{t+2} in the logistic map plotted against x_t ($\lambda = 3.2$). The fixed point of the logistic map itself is still present, but this map has two more fixed points, which corresponds to a cycle with period two.

As the plot of $h(x_t)$ shows, there are two points now that the dynamics return to in two periods: these points constitute the stable cycle that we found in the cobweb diagram. How do we know that the cycle is stable? Label the two points on the cycle as a and b, and suppose you start at a. The stability of the cycle is determined by the stability of the two-step map $h(x_t)$, which we can treat as any other map, i.e., check if its derivative has magnitude less than 1. By virtue of the chain rule, we have

$$h'(a) = g'(g(a))g'(a) = g'(b)g'(a) \tag{10}$$

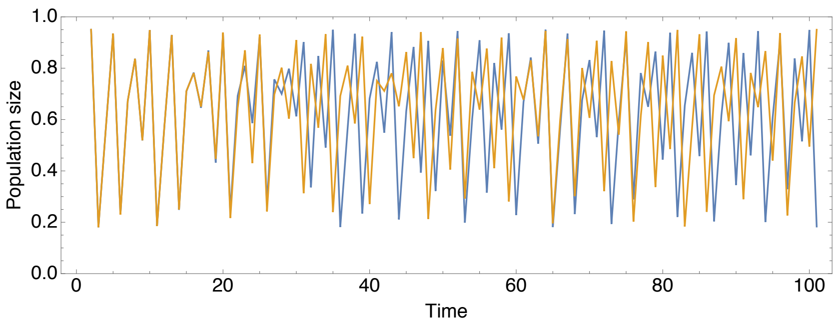
Hence, the derivative of the two-step map at its fixed point is the product of the derivatives of the single-step map evaluated at the points on the cycle. If this product has magnitude less than 1, the cycle is stable.[3]

[3] It is left as an exercise to check if this condition holds.

What happens as lambda grows further? On the margin in the next page, you can see population trajectories with different λs. The succession of figures show that as λ increases, the two-point cycle becomes unstable at some point, and a four-point cycle appears (at $\lambda \approx 3.449$); an eight-point cycle appears at $\lambda \approx 3.544$), and the period of the stable cycle keeps doubling as λ increases. But importantly, the increase in λ required for each successive doubling diminishes geometrically with a constant factor in the limit of large periods. If one denoted with λ_n the value of λ at which the cycle with period 2^n appears, we have:

$$\lim_{n->\inf} \frac{\lambda_n - \lambda_{n-1}}{\lambda_{n+1} - \lambda_n} = 4.669\cdots . \tag{11}$$

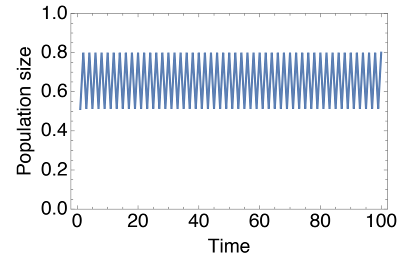
This geometric convergence means that there is a finite λ that the system will have a period of infinity before reaching it. Indeed, that value of λ is $3.569946\cdots$ for the logistic map. For values of λ above this value, the system never returns to the same point ever again, and keeps bounding around: the logistic map becomes chaotic![4]



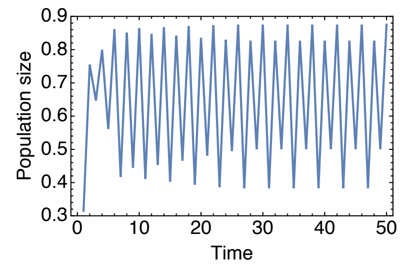
We should stress that the chaotic behavior is entirely deterministic: if one knows exactly what the initial conditions were, one could predict the future trajectory with 100% accuracy. But chaotic dynamics also are extremely sensitively dependent on initial conditions, meaning even populations that start out with only slightly different initial conditions will have very different trajectories. Given that our estimates of initial conditions are always subject to measurement error, a really chaotic population would also be unpredictable in practice except in the short term. The figure below illustrates this problem. It shows the trajectories of two populations, both with $\lambda = 3.8$. One population has $x_0 = 0.5$, the other $x_0 = 0.5001$. The graph depicts the initial agreement between the trajectories, which later diverge and become uncorrelated.

Amazingly, it later turned out that the constant in (11) is actually not a property of just the logistic map, but is universal to any map of the form $x_{t+1} = \lambda f(x_t)$, where $f(x_t)$ has the same qualitative shape as the logistic map (i.e., is smooth, concave down and has a single maximum). This property, called universality, indicates that chaos might be a widespread property of a class of systems, regardless of the details of the mechanisms (regardless of whether they describe population growth, electronic circuits, etc.).

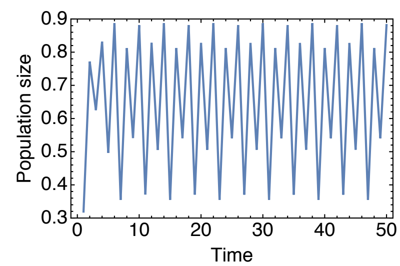
One final property of the logistic map (and all other unimodal maps like it) can be seen in a plot called the orbit diagram, which plots the points the systems visits in its steady-state (i.e., when the initial transient dynamics have passed) for a given value of the parameter λ. The orbit diagram shows the successive bifurcations leading to cycles with doubling periods giving way to



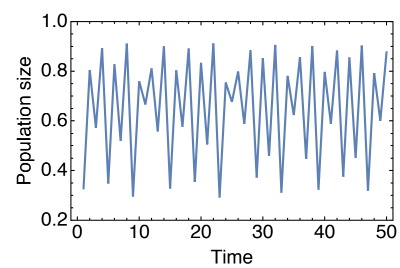
The population trajectory with $\lambda = 3.2$, showing a stable two-point cycle.



The population trajectory with $\lambda = 3.45$, where the system has a stable cycle consisting of four points.



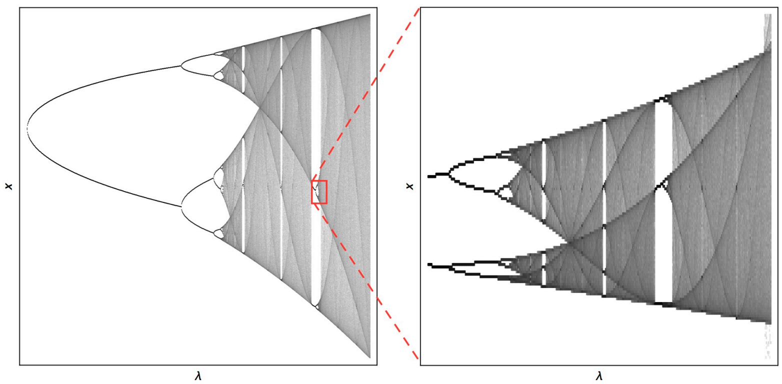
The population trajectory with $\lambda = 3.55$, showing again a stable cycle, with 8 points.



The population trajectory with $\lambda = 3.65$, showing where the cycles are no more, and the dynamics are chaotic (which never goes through the same point twice).

[4] This was famously pointed out by May et al. (1976), who made a strong plea for using simple discrete time models to capture complex population dynamics. More information about the behavior of the logistic map can be found in Strogatz (2001, Ch. 10).

chaos where the system seems to spend time in all points within given intervals (the gray regions), that then give way to "windows" of periodicity with different periods that then undergo doubling again, giving rise to chaos, and so on. More strikingly, even if one zooms in to a very small region of the orbit diagram, one recovers the same type of pattern, regardless of scale. In other words, there is no way to know which scale you are looking at from the figures themselves.



The orbit diagram for the logistic map. The panel on the left shows λ ranging from 3 to 4, while the panel on the right magnifies the region in the red box. The two plots look very similar to each other (except for the pixellation which is not essential). The orbit diagram has fractal property. Another feature that can be seen in the plot is that the behavior or the logistic map beyond the point at which chaos starts to appear consists of periods of chaotic behavior interspersed with windows of periodicity (not necessarily powers of two).

References

May, R. M., et al. 1976. Simple mathematical models with very complicated dynamics. Nature 261:459–467.

Strogatz, S. H. 2001. Nonlinear dynamics and chaos: with applications to physics, biology and chemistry. Westview Press.