The logistic difference equation and the route to chaotic behaviour

Level 1 module in "Modelling course in population and evolutionary biology"

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1 Introduction

1.1 Difference equations versus differential equations

Frequently population dynamical models assume continuous time. Models in continuous time are usually appropriate for organisms that have overlapping generations. However, many biological populations are more accurately described by non-overlapping generations (such as insect populations with one generation per year or annual plants). The dynamics of these populations are often more appropriately expressed by so-called *difference equations*. Here, the population size of the next generation $t+1$ is expressed as a function of the population size in the current generation t.

In general a single species difference equation can be expressed as

$$n_{t+1} = C(n_t)n_t$$

In analogy to the exponential equation the simplest difference equation is obtained if $C(n_t)$ is a constant:

$$n_{t+1} = Rn_t \tag{1}$$

It is easy to see (by iteration of the above equation) that the solution is given by

$$n_t = n_0 R^t \tag{2}$$

where n_0 is the population size in generation $t = 0$. This equation is the analogue of the exponential function in discrete time.

In R, such a single species difference equation can be coded as

```
model <- function(r,n0,time) {
         output <- numeric(time+1)
         output[1] <- n <- n0
         for (t in c(1:time)) {
             n <- r * n
             output[t+1] <- n
         }
         output
}


### Run the model
out  <- model(1.2,1,10)
### Plot the model
plot(1:length(out)-1,out,xlab="time",ylab="population size")
```

1.2 Logistic difference equation

The logistic difference equation is given by

$$x_{t+1} = x_t e^{r(1-x_t)} \tag{3}$$

It can be derived as a discrete time analogy to the logistic differential equation, which is given by

$$\frac{dx}{dt} = rx(1-x) \tag{4}$$

where x is the population density (scaled by its carrying capacity) and r is the maximal growth rate of the population at low values of x. For more information on the logistic difference equation and its relation to the logistic differential equation, please, see the lecture script “Ecology and Evolution II: Populations” by Sebastian Bonhoeffer. Another equation that is often referred to as the logistic difference equation or logistic map is given by $x_{t+1} = rx_t(1-x_t)$, where $1 \leq r \leq 4$ and $0 \leq x \leq 1$. This equation displays analogous dynamical behaviour as Eq. 3.

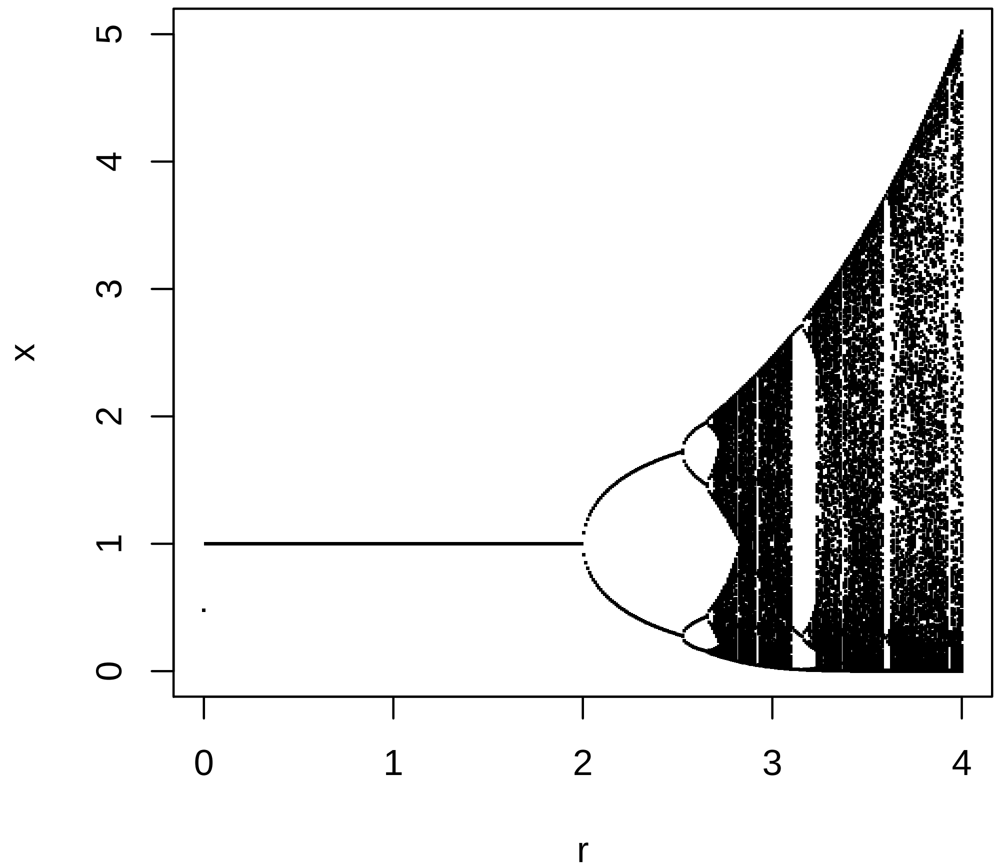

Figure 1: The bifurcation diagram of the logistic difference equation for $0 < r < 4$.

1.3 Implementing the logistic difference equation

Modify the supplied R script to implement the logistic difference equation. Run it from any initial value between 0 and 1 until $t = 30$, with three different values of r: 1.5, 2.2 and 3.5. Plot the obtained time series. What sort of behaviour do you observe for the different values of r? Experiment with other values for r, different initial conditions and different series lengths.

1.4 The route to chaos as illustrated by the bifurcation diagram

Figure 1 shows a *bifurcation diagram*. This plot is obtained in the following way. For each value of r, the logistic difference equation is iterated for n steps (starting from a random initial number) to attain stable behaviour (if there is any). Then a further m iteration steps are performed and x_t is plotted at the resulting time points $n < t < n + m$. Figure 1 was generated with $n = 1000$ and $m = 300$. For $r < 2$ the dynamics are similar to that of the logistic differential equation in that the population always converges to the steady state $x_t = 1$ for large t (which implies that the population n_t is always at its carrying capacity K). At $r = 2$ there is the first bifurcation (period doubling) as the solution begins to oscillate between two values for this value of r. As r increases further there are further period doublings, resulting in cycles of period 4, 8, 16, and so on. Eventually, for even larger values of r the logistic differential equation shows chaotic behaviour, which means that the population behaviour cannot be predicted accurately for longer periods of time. Two trajectories starting from nearly identical values will diverge further and further away from each other.

1.5 Phase diagrams and stable cycles

Another way to explore the dynamical behaviour of the logistic difference equation are phase diagrams in which the value of x_{t+k} is plotted against x_t for a given time series and a given choice of k. Figure 2 shows the phase diagrams for several values of k. If (after a transient phase of equilibration) $x_{t+k} = x_t$ for all values of t, then the system shows stable cycles with period k. (The bifurcation diagram in Figure 1 indicates that there are parameter values of r for which the system shows stable cycles.) If for a given value of r the system converges to a stable cycle with period k, then the trajectory should converge to a point in the phase diagram plotting x_{t+k} against x_t.

1.6 General message

The important message is that simple models can show complex behaviour. Hence, if we observe a complex dynamic behaviour of a natural population in the field, this does not necessarily imply that the underlying rules determining the dynamics have to be complex too. Moreover, the complex behaviour of the logistic difference equation is in strong contrast with the comparatively simple behaviour of the logistic differential equation. As a rule of thumb difference equations show more complicated behaviour than the corresponding models in continuous time[a].

[a]The discovery of the role of deterministic chaos in biology largely goes back to Robert May. Being a native of Australia, Robert May was first a theoretical physicist. Becoming the successor to Robert McArthur as a theoretical ecologist at Princeton University, Robert May moved on later to Oxford University. As one of very few scientist Robert May was made a Lord by the British Queen in 2001. Robert May has also received an honorary doctorate from the ETH Zurich.

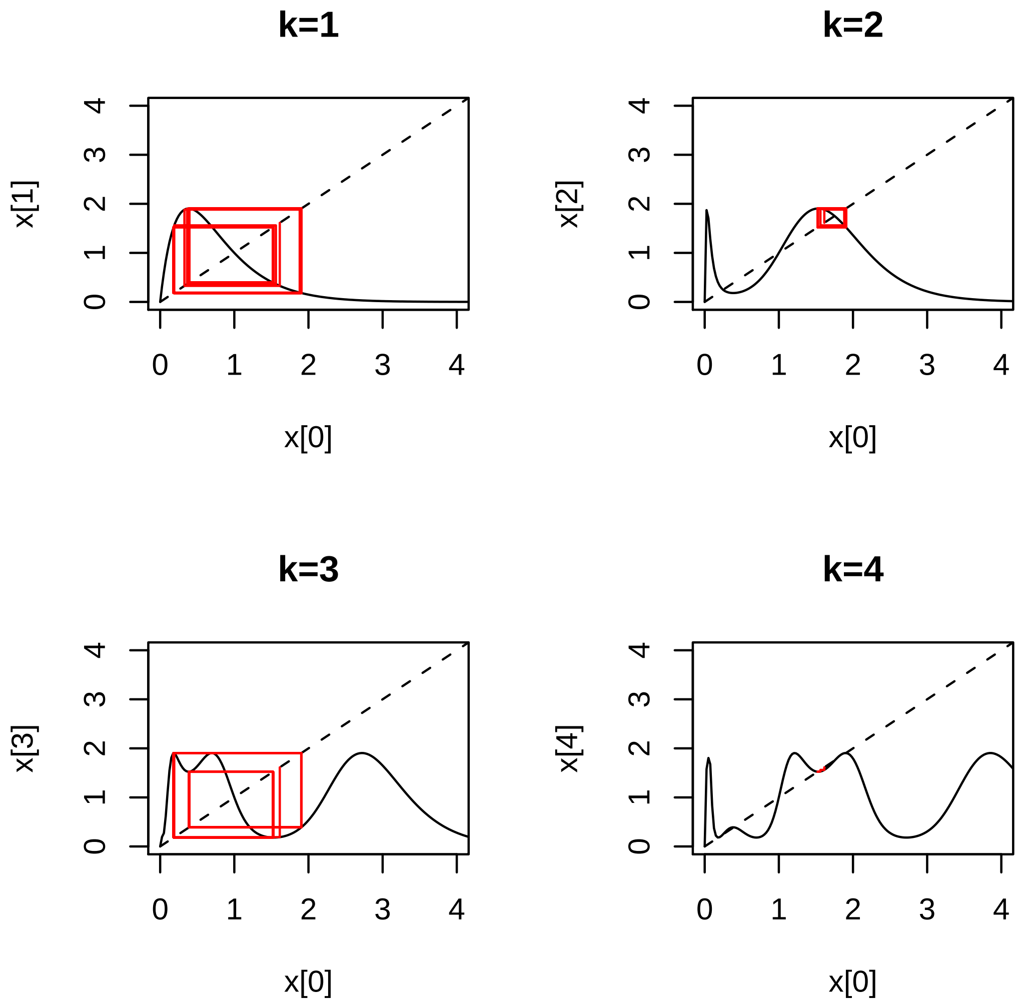

Figure 2: Phase diagrams plotting x_{t+k} against x_t for $k = 1, 2, 3$ and 4. The black solid line shows for a given k the values x_{t+k} for $0 \leq x_t \leq 4$. The dashed line represents the diagonal. Hence the intersection of the dashed line and the solid line gives the points where $x_{t+k} = x_t$, indicating that at these points the system shows periodicity with period k. However, this periodic behaviour can be stable or unstable. The red line represents the trajectory (time course) of the system in the phase plane. (The red line connects the points $(x_0, x_0), (x_0, x_k), (x_k, x_k), (x_k, x_{2k}), \ldots, (x_{i\times k}, x_{i\times k}), (x_{i\times k}, x_{(i+1)\times k})$ etc. A stable cycle of period k is manifest as a convergence of the redline to a point in the phase diagram of (x_t, x_{t+k}). In the plots shown here $r = 2.6$ and the panel with $k = 4$ shows that we have a stable cycle with period 4 for this value of r.

2 Exercises

2.1 Basic exercises

Eb1. Generate bifurcation plots as in Figure 1. Amplify interesting sections of the plot by constraining the range of r and using smaller increments. Generate time series plots for interesting values of r.

Eb2. Generate chaotic time series (e.g. take $r = 3.5$) and look at the distribution of x values attained in the series. Is it completely random (i.e. uniformly distributed)? Hint: use the `hist()` function to visualize the distribution. You can use long time series and high resolution histograms for best effect.

Eb3. Are there windows of periodic behaviour within chaotic regimes? Try to develop a method that computes the periodicity of a time series. (A periodicity of k means that $x_{t+k} = x_k$ for all t that are sufficiently large such that the dynamic behaviour has stabilized). Are there parameter values of r for which the LDE shows dynamic behaviour with uneven periodicity? Advanced option: plot periodicity as a function of r.

2.2 Advanced/additional exercises

Ea1. Plot the dynamic behaviour of the LDE in a phase diagram (see section 1.5 and Figure 2). When are periodic solutions stable? What are the graphical conditions for stability? (Hint: look at the slopes of the intersecting lines.)

Ea2. How can one define chaotic behaviour? What characterizes chaotic versus non-chaotic regimes? Try to develop a quantitative measure that allows you to distinguish between both regimes, and approximate the critical value of r at which chaotic behaviour appears.

Ea3. Start two simulation runs from slightly different population sizes. Check whether the two trajectories are diverging from each other, or converging into a single trajectory. Do this for different regimes of the growth rate (stable, periodic, chaotic behaviour).

Ea4. Develop a spatial extension of the LDE (along the lines of the spatial Nicholson-Bailey model, see corresponding module). Assume that a certain fraction of individuals migrates to neighbouring fields. How does space affect chaotic dynamics? Note that this may be a work-intensive (but fun) extension to the LDE!