Evolutionary Dynamics

Tutorial 1

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21st September 2017

1 Discrete time

Suppose you have a difference equation

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

where $t \in \mathbb{N}$. The system does not change iff $x_{t+1} = x_t = x^*$. The resulting *equilibrium* or *fixed* points x^* are determined by the intersection of the bisectrix and f, that is the criterion:

$$x^* = f(x^*). \tag{2}$$

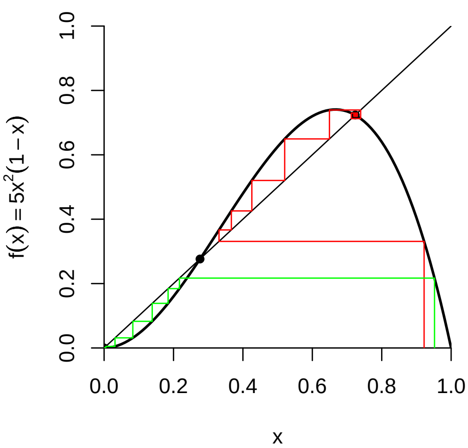
A fixed point can be either attractive, repelling, or neutral. This can be determined from the derivative f' at the fixed point. One finds that x^* **is attractive if** $|f'(x^*)| < 1$**, and** x^* **is repelling if** $|f'(x^*)| > 1$. To understand these criteria, suppose we are at a position close to the fixed point, $x_t = x^* + \varepsilon_t$. We analyze the evolution of the distance ε_t. As ε_t is small, we use a Taylor expansion

$$\varepsilon_{t+1} = f(x^* + \varepsilon_t) - f(x^*) \approx f'(x^*)\varepsilon_t. \tag{3}$$

From this equation we see that the increment will only decrease if $|f'(x^*)| < 1$, which is exactly the criterion for stability.

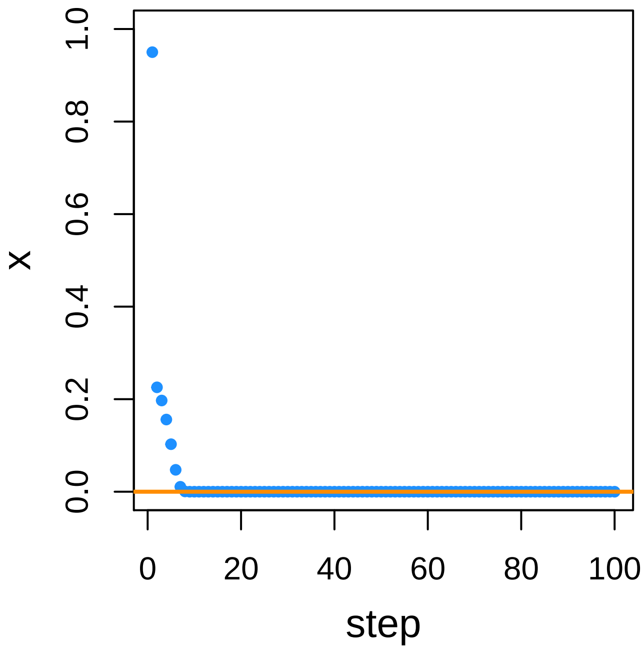
1.1 An example

Suppose we have $f(x) = 5x^2(1-x)$. Solving $f(x) = x$ yields the fixed points $x_1^* = 0$, $x_2^* = \frac{1}{2} - \frac{\sqrt{5}}{10} \approx 0.28$, and $x_3^* = \frac{1}{2} + \frac{\sqrt{5}}{10} \approx 0.72$. As shown below, however, only x_1^* and x_3^* are attractive.



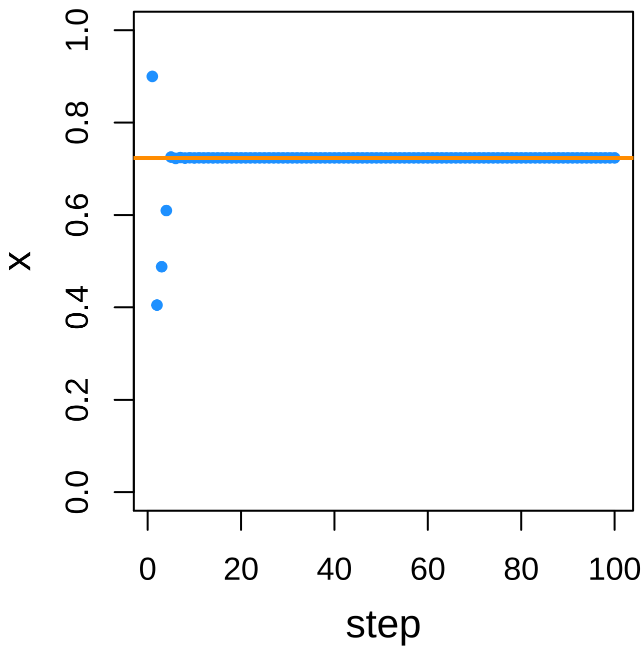
```r
steps <- 100
xs <- rep(0, steps)
xs[1] <- 0.95  # initial condition
for (ii in 2:steps) {
    xs[ii] <- 5 * xs[ii - 1]^2 * (1 - xs[ii - 1])
}
```

```r
par(mar = c(4, 4, 0.5, 0.5))
par(mgp = c(2.5, 1, 0))
par(cex.lab = 1.25)
plot(xs, xlab = "step", ylab = "x", main = "", col = "dodgerblue",
    pch = 20, ylim = c(0, 1))
abline(h = 0, col = "#ff8c00", lwd = 2)
```



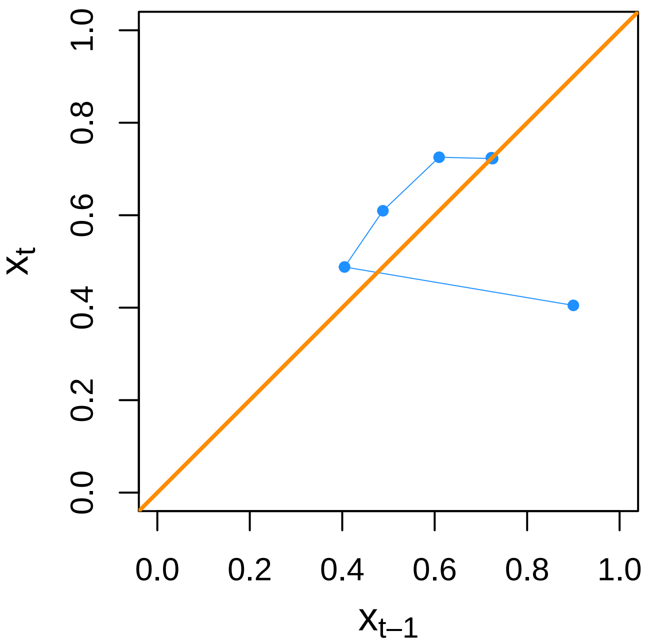

```r
xs[1] <- 0.9  # initial condition
for (ii in 2:steps) {
    xs[ii] <- 5 * xs[ii - 1]^2 * (1 - xs[ii - 1])
}
```

```r
plot(xs, xlab = "step", ylab = "x", main = "", col = "dodgerblue",
    pch = 20, ylim = c(0, 1))
abline(h = 1/2 + sqrt(5)/10, col = "#ff8c00", lwd = 2)
```



On the Poincaré plot of x_t against x_{t-1} we can trace the path to the stable fixed point

```
xstm1 <- xs[-length(xs)]
xst <- xs[-1]
plot(xstm1, xst, xlab = expression(x[t - 1]), ylab = expression(x[t]),
    main = "", col = "dodgerblue", pch = 20, xlim = c(0, 1), ylim = c(0,
        1))
lines(xstm1, xst, col = "dodgerblue", lwd = 0.5)
abline(b = 1, a = 0, col = "#ff8c00", lwd = 2)
```



2 Continuous time: Single variable models

We consider a dynamical system which is described by the single function of time x. The quantity $x(t)$ represents the value of x as a function of the continuous time variable t. The dynamical behaviour of the system is described by the differential equation

$$\frac{dx}{dt} = f(x(t)). \tag{4}$$

2.1 Finding equilibrium points

An equilibrium point of the system is a value for the variable such that the state of the system does not change any more. The condition for the equilibrium is that

$$\dot{x} = \frac{dx}{dt} = 0.$$

Thus, one has to solve the equation

$$f(x) = 0. \tag{5}$$

We denote the equilibrium point by x^*. Note that the equation 5 can in general have more than one solution, each corresponding to a different equilibrium.

2.2 Determining the stability of equilibria

If we plug the equilibrium point in the equation describing the dynamics of the system, we will find that it will not change. But what if the system starts from a point close but not exactly equal to an equilibrium point? This is the subject of stability analysis.
Let's suppose that the system at time t is in a position $x(t) = x^* + \varepsilon(t)$, *i.e.* displaced by a quantity ε from an equilibrium point. How will the system evolve? Will the displacement increase or decrease? To answer this question, we can write the evolution of the displacement $\varepsilon(t)$

$$\frac{d\varepsilon}{dt} = \frac{d}{dt}(x(t) - x^*) = f(x(t)) = f(x^* + \varepsilon(t)). \tag{6}$$

Taking the Taylor expansion of $f(x)$ around the point x^* we can write

$$\frac{d\varepsilon}{dt} = f(x^*) + \underbrace{\frac{df}{dx}|_{x=x^*}}_{=r} \varepsilon(t) = 0 + r\varepsilon(t). \tag{7}$$

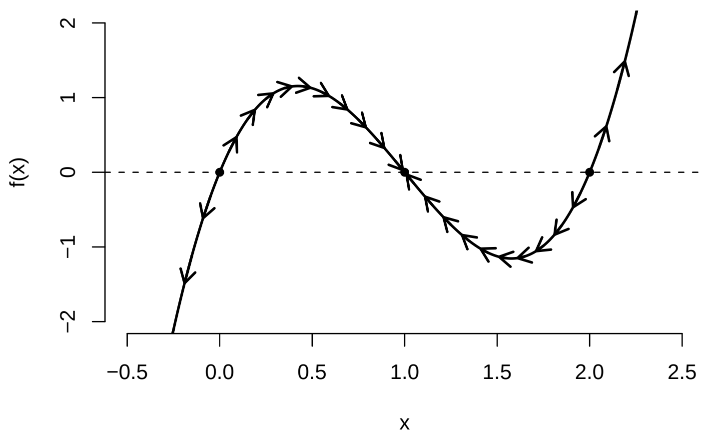
Solving this differential equation we obtain

$$\varepsilon(t) = e^{rt}\varepsilon(t = 0). \tag{8}$$

It is easy to see that **the condition for the stability of the equilibrium is** $r = \frac{df}{dx}|_{x=x^*} < 0$.

2.3 An example

Consider the case $f(x) = 3x(x-1)(x-2)$. The third degree polynomial f has three zero. Thus, the fixed points are given by $x_1^* = 0$, $x_2^* = 1$, $x_3^* = 2$.



Which of them are stable? The derivative of f is $f'(x) = 3(x-1)(x-2) + 3x(x-2) + 3x(x-1)$. We find that $f'(x_1^*) = 6$, $f'(x_2^*) = -3$, and $f'(x_3^*) = 6$. That is x_1^* and x_3^* are unstable, and x_2^* is stable ($f'(x_2^*) < 0$).

```
library(deSolve)
parms <- c()
my.atol <- c(1e-06)
times <- c(0:100)/25
sdiffeqns <- function(t, s, parms) {
    sd1 <- 3 * s[1] * (s[1] - 1) * (s[1] - 2)
    list(c(sd1))
}
```

We can check this by numerically integrating the differential equation starting at $x^* \pm \varepsilon$

```
initconds <- c(0 - 1e-06)  # just below 0
out0m <- lsoda(initconds, times, sdiffeqns, rtol = 1e-10, atol = my.atol)

DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 2.00327e-16

DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
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     (H = step size). Solver will continue anyway.
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      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 2.00327e-16

DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 1.64605e-16

DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 1.64605e-16

DLSODA-  Above warning has been issued I1 times.
     It will not be issued again for this problem.
In above message, I1 = 10

DLSODA-  At current T (=R1), MXSTEP (=I1) steps
      taken on this call before reaching TOUT
In above message, I1 = 5000

In above message, R1 = 2.18389
```

```
initconds <- c(0 + 1e-06)  # just above 0
out0p <- lsoda(initconds, times, sdiffeqns, rtol = 1e-10, atol = my.atol)
initconds <- c(1 - 1e-06)  # just below 1
out1m <- lsoda(initconds, times, sdiffeqns, rtol = 1e-10, atol = my.atol)
initconds <- c(1 + 1e-06)  # just above 1
out1p <- lsoda(initconds, times, sdiffeqns, rtol = 1e-10, atol = my.atol)
initconds <- c(2 - 1e-06)  # just below 2
out2m <- lsoda(initconds, times, sdiffeqns, rtol = 1e-10, atol = my.atol)
initconds <- c(2 + 1e-06)  # just above 2
out2p <- lsoda(initconds, times, sdiffeqns, rtol = 1e-10, atol = my.atol)
```

```
DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 2.00258e-16

DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 2.00258e-16

DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 2.00258e-16

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      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 1.64549e-16

DLSODA-  Warning..Internal T (=R1) and H (=R2) are
      such that in the machine, T + H = T on the next step
     (H = step size). Solver will continue anyway.
In above message, R1 = 2.18389, R2 = 1.64549e-16

DLSODA-  Above warning has been issued I1 times.
```

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     It will not be issued again for this problem.
In above message, I1 = 10

DLSODA-  At current T (=R1), MXSTEP (=I1) steps
      taken on this call before reaching TOUT
In above message, I1 = 5000

In above message, R1 = 2.18389
```

```
plot(out0p, xlab = "time", ylab = "x", main = "", col = "dodgerblue",
    lty = 1, lwd = 2, ylim = c(-2, 4), xlim = c(0, 4))
lines(out0m, col = "#ff8c00", lty = 3, lwd = 3)
lines(out2m, col = "dodgerblue", lty = 1, lwd = 2)
lines(out2p, col = "#ff8c00", lty = 3, lwd = 3)
lines(out1m, col = "#68228b", lty = 2, lwd = 2)
lines(out1p, col = "#cd2626", lty = 3, lwd = 3)
```