Univariate non-linear continuous-time deterministic models

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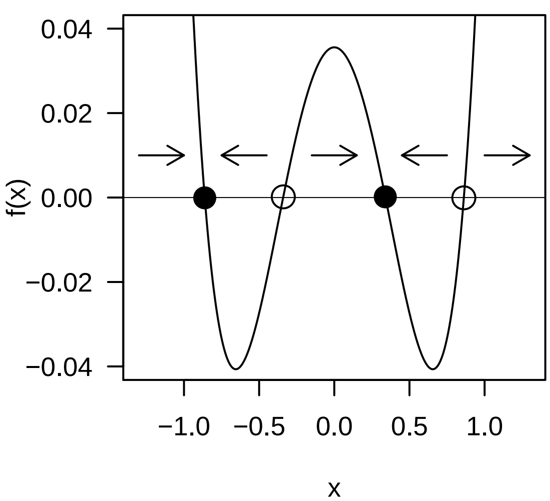
Basic model: $\frac{dx(t)}{dt} = f(x(t))$. For example, $f(N) = rN(1 - \frac{N}{K})$ is the logistic model in continuous time.

Fixed points and stability

In general, as usual, fixed points are found by setting $\frac{dx}{dt} = f(x) = 0$ and solving for x. A fixed point $x^\star$ is stable if $f'(x^\star) < 0$, because this ensures that the state will return to $x^\star$ for sufficiently small perturbations from $x^\star$.

Graphical methods



Which points are stable? Why?

Example: logistic model

There are two solutions to $f(N^\star) = 0 = rN^\star(1 - \frac{N^\star}{K})$, which are $N^\star = 0, K$. For stability we evaluate $f'(N) = r(1-\frac{2N}{K})$ at the fixed points. $f'(0) = r$ and $f'(K) = -r$. Therefore, if $r > 0$, the fixed point at zero is unstable whereas that at K is stable. How do these stability properties compare with discrete time?

Example: constant harvest model

$f(N) = rN(1-\frac{N}{K})-h$. Fixed points obey, $-\frac{r}{K}(N^\star)^2 + rN^\star - h = 0$. Using the quadratic formula $N^\star = \frac{-r\pm\sqrt{r^2-r(\frac{-r}{K})(-h)}}{2(\frac{-r}{K})}$. A non-dimensional form is easier to understand. Let $\nu = \frac{h}{rK}$ be a dimensionless harvest rate and $n = \frac{N}{K}$ be a dimensionless state variable. This yields $f(n) = r(n(1-n)-\nu)$. Fixed points, $n^\star = \frac{1}{2}(1 \pm \sqrt{1-4\nu})$. If $\nu > 1/4$ there are no FPs, with $\nu = 1/4$ there is one FP ($n^\star = 1/2$), and with $\nu < 1/4$ there are two. For stability: $f'(n) = r(1-2n)$, $f'(n^\star) = \mp r\sqrt{1-4\nu}$. Why did the $\pm$ sign change to $\mp$? Draw a picture to help understand this model.

Time-dependent solution

Two approaches: (1) general solution using differential equation methods or (2) simulate special cases using numerical methods.

General solutions

A more general model is $g(x, \frac{dx}{dt}, \frac{d^2x}{dt^2}, ...) = f(t)$. In this class we will only be doing general solutions for first-order homogeneous (i.e. $f(x) = \frac{dx}{dt}$) and first-order non-homogeneous (i.e. $f(x,t) = \frac{dx}{dt}$).

For homogeneous we go back to the logistic, which can be done with separation of variables. $\frac{dN}{N(1-\frac{N}{K})} = r\,dt$. Using the partial fractions trick the left hand side is $\frac{dN}{N} + \frac{dN}{K-N}$. Check my work! The indefinite integrals are $\int \frac{dN}{N} = \log(N) + C$, $\int \frac{dN}{N-K} = -\log(N-K) + C$, and $r \int dt = rt + C$. Finish the job. For non-homogeneous check out the drugs in the body example (Mooney and Swift p. 252).

Numerical solutions

The simplest approach is *Euler's method*: convert into a difference equation. There is a trade-off here: if you make the step-size too large the approximation will be poor, but if you make the step-size too small computations will take a long time (watch out for computation times longer than the age of the universe!). Although Euler's method is easy to understand, In general you are better off using smarter software (e.g. `scipy.integrate.odeint`)

```python
import numpy as np
import scipy.integrate
import matplotlib.pyplot as plt
def gradfun(x, t, params):
    """gradient function
       parameters in order
          (state, time, parameters)
       x, params are tuples
    """
    r, K = params   ## unpack parameters
    N,   = x        ## unpack states
    ## return result as an array
    return(np.array([r*N*(1-N/K)]))

t_vec = np.arange(0,10,step=0.1)
params = (1,10)
desol = scipy.integrate.odeint(
    gradfun,
    y0 = (0.1,), ## tuple (1 element)
    t = t_vec,
    args = (params,)) ## tuple-in-tuple!
plt.plot(desol)
```

Example: plant and animal growth

Start with a conservation of energy law (1)

$$B = B_c N_c + E_c \frac{dN_c}{dt}$$

B, rate of energy intake (e.g. via food); B_c, rate of intake required to maintain a single cell; N_c, number of cells; E_c, energy required to create a new cell. By (1) defining m and m_c as the masses of the entire organism and of a single cell, and (2) using the empirical relationship, $B = am^b$ (constants $b \approx 3/4$ and a), we have a differential equation for the mass of an organism (derive this),

$$\frac{dm}{dt} = \underbrace{\frac{am_c m^b}{E_c}}_{\text{supply}} - \underbrace{\frac{B_c m}{E_c}}_{\text{demand}}$$

When the supply of energy exceeds the demand, the organism can grow (sketch the supply and demand curves). There is a trivial fixed point at $m^\star = 0$ and an interesting one at $m^\star = \left(\frac{am_c}{B_c}\right)^{\frac{1}{1-b}}$. Note equilibrium mass is larger for organisms with cells that are larger and have smaller energy requirements. Interestingly, the equilibrium mass is independent of the energy required to make a new cell, E_c (although it does influence the rate of approach to equilibrium).

Time dependent solution can be found by a change of variables $\mu = 1 - \left(\frac{m}{m^\star}\right)$, which leads to a simple exponential decay model (note that μ is dimensionless). By the chain rule,

$$\frac{d\mu}{dt} = \left(\frac{dm}{d\mu}\right)^{-1} \frac{dm}{dt}$$

By finding the derivative $\frac{dm}{d\mu}$ and substituting in the new variable for n into the differential equation above we have,

$$\frac{d\mu}{dt} = -a(m^\star)^{b-1}(1-b)\mu$$

This is a simple exponential decay model, which you can solve (do it and back transform to get the time dependent solution for m).

More generally, this is an example of Bernoulli differential equation.

References

[1] S. A. L. M. Kooijman. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, Mar. 2000. Google-Books-ID: Z3VWvByKrWwC.