Mathematical modelling in biology

Some models

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June 7, 2023

Contents

1 The bathtub

Imagine a container in which there exists an input of water $I(t)$ and an output $O(t)$. Let $V(t)$ be the volume of water in the bathtub. The varation in time of the volume of water is:

$$\frac{dV(t)}{dt} = I(t) - O(t)$$

1.1 Constant input

Assume that the input is constant $I(t) = \Lambda$ and that the output depends on $V(t)$ through a constant γ. The problem then becomes:

$$\frac{dV(t)}{dt} = \Lambda - \gamma V(t)$$

This can be solved thorugh the variation of constants method. First solve the associated homogeneous equation:

$$\begin{aligned}
\frac{du(t)}{dt} &= -\gamma u(t) \\
\frac{du(t)}{u(t)} &= -\gamma dt \\
\int \frac{du(t)}{u(t)} &= -\gamma \int dt \\
\ln(u(t)) &= -\gamma t + c \\
u(t) &= e^{-\gamma t + c} \\
u(t) &= Ce^{-\gamma t}
\end{aligned}$$

Then we can write $V(t) = C(t)e^{-\gamma t}$. Computing its derivative:

$$\frac{dV(t)}{dt} = \frac{dC(t)}{dt}e^{-\gamma t} - \gamma C(t)e^{-\gamma t}$$

Posing it equal to the starting one:

$$\begin{aligned}
\Lambda - \gamma V(t) &= \frac{dC(t)}{dt}e^{-\gamma t} - \gamma C(t)e^{-\gamma t} \\
\Lambda - \cancel{\gamma V(t)} &= \frac{dC(t)}{dt}e^{-\gamma t} - \cancel{\gamma V(t)} \\
\frac{dC(t)}{dt} &= \Lambda e^{\gamma t} \\
C(t) &= \int \Lambda e^{\gamma t} dt \\
C(t) &= \frac{\Lambda}{\gamma}e^{\gamma t} + c
\end{aligned}$$

So that the solution then becomes:

$$\begin{aligned}
V(t) &= \left[\Lambda \frac{e^{\gamma t}}{\gamma} + c\right] e^{-\gamma t} \\
&= \frac{\Lambda}{\gamma} + ce^{-\gamma t}
\end{aligned}$$

The same thing can be done using an integrating factor:

$$\begin{aligned}
\frac{dV(t)}{dt} &= \Lambda - \gamma V(t) \\
\frac{dV(t)}{dt} + \gamma V(t) &= \Lambda \\
e^{\int \gamma dt}\frac{dV(t)}{dt} + \gamma e^{\int \gamma dt} V(t) &= \Lambda e^{\int \gamma dt} \\
e^{\gamma t}\frac{dV(t)}{dt} + \gamma e^{\gamma t} V(t) &= \Lambda e^{\gamma t} \\
\frac{d}{dt}\left[e^{\gamma t} V(t)\right] &= \Lambda e^{\gamma t} \\
e^{\gamma t} V(t) &= \int \Lambda e^{\gamma t} dt \\
e^{\gamma t} V(t) &= \frac{\Lambda}{\gamma} e^{\gamma t} + c \\
V(t) &= \frac{\Lambda}{\gamma} + c e^{-\gamma t}
\end{aligned}$$

1.2 Constant input and no output

In the case in which there is no output the problem then becomes:

$$\frac{dV(t)}{dt} = \Lambda$$

This is easy to solve:

$$V(t) = \Lambda t + c$$

1.3 Varying input

Let now the input be a function of time $I(t) = \Lambda(t)$. The equation becomes:

$$\frac{dV(t)}{dt} = \Lambda(t)$$

The solutions of this is found by integrating both sides:

$$V(t) + \int_0^t \Lambda(u) du + c$$

1.4 Output flux but no input

Let now the input be a function of time $O(t) = \gamma V(t)$. The variation in time becomes:

$$\frac{dV(t)}{dt} = -\gamma V(t)$$

This does not explicitly depends on t: it is autonomous. This can be solved thourgh the separation of variable methods:

$$\frac{dV(t)}{dt} = -\gamma V(t)$$
$$\frac{dV(t)}{V(t)} = -\gamma dt$$
$$\int \frac{dV(t)}{V(t)} = -\gamma \int dt$$
$$\ln(V(t)) = -\gamma t + c$$
$$V(t) = e^{-\gamma t + c}$$
$$V(t) = e^{-\gamma t} e^{c}$$
$$V(t) = kre^{-\gamma t}$$

k in this context is the volume in the bathtub at time 0, wich could be computed if the volme at time 0 was given:

$$\begin{cases} \frac{dV(t)}{dt} = -\gamma V(t) \\ V(0) = V_0 \end{cases}$$

So that $V(0)$ can be computed:

$$V(0) = kre^{-\gamma 0}$$
$$V(0) = k$$

2 Malthus equation

The Malthus equation is a model for the growth of a population. It neglets difference amond individuals and migrations. It represents a population through its size that will increase thru reproduction and decrease through death:

$$\frac{dN(t)}{dt} = B(t) - D(t)$$

The number of births can deaths are linked to the current population. A death rate μ can be introduced ($\frac{1}{\mu}$ is the average lifespan) and a birth rate β (the average number of newborn generated during a lifespan). Both are non-negative constants:

$$\frac{dN(t)}{dt} = \beta N(t) - \mu N(t)$$
$$\frac{dN(t)}{dt} = (\beta - \mu)N(t)$$
$$\frac{dN(t)}{dt} = rN(t)$$

Where $r = \beta - \mu$ is the instantaneous growth rate or Malthus parameter or biological potential of the population. The equation can be solved through the separation of variables method:

$$\begin{aligned}
\frac{dN(t)}{dt} &= rN(t) \\
\frac{dN(t)}{N(t)} &= rdt \\
\int \frac{1}{N(t)} dN(t) &= \int rdt \\
\ln(N(t)) &= rt + c \\
N(t) &= e^{rt+c} \\
N(t) &= ke^{rt} \\
N(t) &= ke^{(\beta-\mu)t}
\end{aligned}$$

Where k is the population size at time 0. If $r < 0$ the population will go extint, while if $r > 0$ it will grow exponentially. If $r = 0$ the population is constant. The basic reproduction number $R_0 = \frac{\beta}{\mu}$ can be considered. $r < 0$ is equivalent to $R_0 < 1$, while $R_0 > 1$ is equivalent to $r > 0$. Now, the equilibria and stability can be computed:

$$\begin{aligned}
rN(t) &= 0 \\
N(t) &= 0
\end{aligned}$$

This is the only equilibrium point.

3 The logistic equation

The logistic equation introduces into the Malthus' one a term that limits the growth of the population. The simplest way to do so is to modify the rates, supposing that fertility decreses and mortailtiy inreases inearly with $N(t)$:

$$\begin{aligned}
\beta(N(t)) &= \beta_0 - \tilde{\beta}N(t) \\
\mu(N(t)) &= \mu_0 + \tilde{\mu}N(t)
\end{aligned}$$

Where $\beta_0, \tilde{\beta}, \mu_0, \tilde{\mu}$ are positive constants. Now the equation becomes:

$$\begin{aligned}
\frac{dN(t)}{dt} &= \beta(N(t))N(t) - \mu(N(t))N(t) \\
&= (\beta_0 - \tilde{\beta}N(t))N(t) - (\mu_0 + \tilde{\mu}N(t))N(t) \\
&= \beta_0 N(t) - \tilde{\beta}N^2(t) - \mu_0 N(t) - \tilde{\mu}N^2(t) \\
&= N(t)\left[\beta_0 - \tilde{\beta}N(t) - \mu_0 - \tilde{\mu}N(t)\right] \\
&= N(t)\left[(\beta_0 - \mu_0) - (\tilde{\beta} - \tilde{\mu})N(t)\right] \\
&= N(t)(\beta_0 - \mu_0)\left[1 - \frac{N(t)(\tilde{\beta} - \tilde{\mu})}{\beta_0 - \mu_0}\right]
\end{aligned}$$

Now $(\beta_0 - \mu_0) = r$, the Malthus parameter, and $\frac{(\beta_0 - \mu_0)}{(\tilde{\beta} - \tilde{\mu})} = K$, the carrying capacity:

$$\frac{dN(t)}{dt} = rN(t)\left[1 - \frac{N(t)}{K}\right]$$

If both $\tilde{\beta}$ and $\tilde{\mu}$ are 0 the equation goes back to the Malthus one. For very large $N(t)$ and $\tilde{\beta} > 0$, the birth rate could go negative. This does not cause mathamtical problems and the conditions are which it happens do not occur, so it is neglected. Generally it is assumed that $r > 0$, since the population is growing over time. So if $r > 0$, and considering all the other assumptions $K > 0$.

3.1 Solution

To solve the equation we solve for its reciprocal:

$$u(t) = \frac{1}{N(t)}$$

This implies that:

$$\begin{aligned}
\frac{du(t)}{dt} &= -\frac{1}{N^2(t)}\frac{dN(t)}{dt} \\
&= \frac{-rN(t)\left[1 - \frac{N(t)}{K}\right]}{N^2(t)} \\
&= \frac{-r\left[1 - \frac{N(t)}{K}\right]}{N(t)} \\
&= -r\left[\frac{1}{N(t)} - \frac{1}{K}\right] \\
&= -ru(t) + \frac{r}{K}
\end{aligned}$$

This is a linear non-homoeneous differential euqation that can be solved with the variation of constants method. Solving first the associated homogeneous problem thorugh sepration of variables:

$$\begin{aligned}
\frac{du(t)}{dt} &= -ru(t) \\
\frac{du(t)}{u(t)} &= -rdt \\
\int \frac{1}{u(t)} du(t) &= \int -rdt \\
\ln(u(t)) &= -rt + c \\
u(t) &= e^{-rt+c} \\
u(t) &= Ce^{-rt}
\end{aligned}$$

Let C be a function of t:

$$u(t) = C(t)e^{-rt}$$

And derive it:

$$\frac{du(t)}{dt} = C'(t)e^{-rt} - rC(t)e^{-rt}$$

Considering that:

$$\frac{du(t)}{dt} = -ru(t) + \frac{r}{K}$$

So that:

$$\begin{aligned}
-ru(t) + \frac{r}{K} &= \frac{dC(t)}{dt}e^{-rt} - rC(t)e^{-rt} \\
\cancel{-rC(t)e^{-rt}} + \frac{r}{L} &= \frac{dC(t)}{dt}e^{-rt} - \cancel{rC(t)e^{-rt}} \\
\frac{dC(t)}{dt}e^{-rt} &= \frac{r}{K} \\
\frac{dC(t)}{dt} &= \frac{r}{K}e^{rt} \\
C(t) &= \frac{r}{K}\int e^{rt}dt \\
C(t) &= \frac{\cancel{r}}{K\cancel{r}}e^{rt} + c
\end{aligned}$$

$$C(t) = \frac{1}{K}e^{rt} + c$$

Subsitituting back into $u(t)$:

$$u(t) = \left[\frac{e^{rt}}{K} + c\right] e^{-rt}$$
$$u(t) = \frac{1}{K} + ce^{-rt}$$

So that:

$$N(t) = \frac{1}{\frac{1}{K} + ce^{-rt}}$$

Now, solving the Cauchy problem where $N(0) = N_0$:

$$\frac{1}{\frac{1}{K} + ce^{-r0}} = N_0$$
$$\frac{1}{\frac{N_0}{K} + cN_0} = 0$$
$$\frac{N_0}{K} + cN_0 = 1$$
$$cN_0 = 1 - \frac{N_0}{K}$$
$$c = \frac{1}{N_0} - \frac{1}{K}$$

So that, substituting:

$$N(t) = \frac{1}{\frac{1}{K} + \left[\frac{1}{N_0} - \frac{1}{K}\right] e^{-rt}} = \frac{K}{1 + \left[\frac{K-N_0}{N_0}\right] e^{-rt}}$$

3.2 Equilibria and stability

Assume $r > 0$ and $K > 0$:

$$rN(t)\left[1 - \frac{N(t)}{K}\right] = 0$$
$$N(t) = 0 \qquad \wedge \qquad N(t) = K$$

The first equilibrium is unstable, since the population is growing, while the second is stable.

4 Logistic equation with periodic carrying capacity

The logistic model can be modified by assomng that the carrying capacity K is a periodic, always positive function of t. For example:

$$k(t) = K_0(1 + \epsilon \cos(\omega t)) \qquad\qquad 0 < \epsilon < 1$$

The model then becomes:

$$\begin{aligned}
\frac{dN(t)}{dt} &= rN(t)\left[1 - \frac{N(t)}{K(t)}\right] \\
&= rN(t)\left[1 - \frac{N(t)}{K_0(1 + \epsilon \cos(\omega t))}\right]
\end{aligned}$$

Which makes the equation not autonomous anymore.

4.1 Solution

The equation can be solved with the same reciprocal trick:

$$u(t) = \frac{1}{N(t)}$$

$$\begin{aligned}
\frac{du(t)}{dt} &= -\frac{1}{N^2(t)}\frac{dN(t)}{dt} \\
&= \frac{-r\cancel{N(t)}\left[1 - \frac{N(t)}{K(t)}\right]}{N^{\cancel{2}}(t)} \\
&= \frac{-r\left[1 - \frac{N(t)}{K(t)}\right]}{N(t)} \\
&= -r\left[\frac{1}{N(t)} - \frac{1}{K(t)}\right] \\
&= -ru(t) + \frac{r}{K(t)}
\end{aligned}$$

Now this can be solved with the Variation of constants. Solving the associated homogeneous problem:

$$u(t) = Ce^{-rt}$$

Now let C a function of t and compute the derivative:

$$\frac{du(t)}{dt} = \frac{dC(t)}{dt}e^{-rt} - rC(t)e^{-rt}$$

So now, substituting what we now:

$$
\begin{aligned}
\frac{dC(t)}{dt}e^{-rt} - rC(t)e^{-rt} &= -ru(t) + \frac{r}{K(t)} \\
\frac{dC(t)}{dt}e^{-rt} - rC(t)e^{-rt} &= -ru(t) + \frac{r}{K(t)} \\
\frac{dC(t)}{dt}e^{-rt} - \cancel{rC(t)e^{-rt}} &= -\cancel{rC(t)e^{-rt}} + \frac{r}{K(t)} \\
\frac{dC(t)}{dt}e^{-rt} &= \frac{r}{K(t)} \\
\frac{dC(t)}{dt} &= \frac{r}{K(t)}e^{rt} \\
C(t) &= r\int \frac{e^{rt}}{K(t)}dt \\
C(t) &= r\int \frac{e^{rt}}{K_0(1+\epsilon\cos(\omega t))}dt \\
C(t) &= \frac{r}{K_0}\int \frac{e^{rt}}{1+\epsilon\cos(\omega t)}dt
\end{aligned}
$$

Which has no analyitical solution. So now:

$$u(t) = e^{-rt}\frac{r}{K_0}\int \frac{e^{rt}}{1+\epsilon\cos(\omega t)}dt$$

And:

$$N(t) = \frac{e^{rt}K_0}{r\int \frac{e^{rt}}{1+\epsilon\cos(\omega t)}dt}$$

4.2 Equilibria

Assuming still $r > 0$ and $K_0 > 0$, the equilibria can be computed:

$$
\begin{aligned}
rN(t)\left[1 - \frac{N(t)}{K(t)}\right] &= 0 \\
N(t) = 0 \qquad \wedge \qquad N(t) &= K(t)
\end{aligned}
$$

The first equlibria is unstable. The second is an asymptotically stable periodic equilibria with period $T = \frac{2\pi}{\omega}$.

5 Predator-Prey system

The predator-prey system is a non-linear system of two differential equations:

$$\begin{cases} \frac{dH(t)}{dt} &= rH(t)\left[1 - \frac{H(t)}{K}\right] - \alpha H(t)P(t) \\ \frac{dP(t)}{dt} &= -\mu P(t) + \gamma\alpha H(t)P(t) \end{cases}$$

Estimating now the parameters:

$$\begin{cases} \frac{dH(t)}{dt} &= 2H(t)\left[1 - H(t)\right] - 2H(t)P(t) \\ \frac{dP(t)}{dt} &= -\frac{1}{2}P(t) + 3H(t)P(t) \end{cases}$$

5.1 Equilibrium points

$$\begin{cases} 2H(t)\left[1 - H(t)\right] - 2H(t)P(t) &= 0 \\ -\frac{1}{2}P(t) + 3H(t)P(t) &= 0 \end{cases}$$

$$\begin{cases} H(t) = 0 \qquad \wedge \qquad H(t) &= 1 - P(t) \\ -\frac{1}{2}P(t) + 3H(t)P(t) &= 0 \end{cases}$$

There are two solution for the first equation. Considering the first:

$$\begin{cases} H(t) &= 0 \\ -\frac{1}{2}P(t) + 3H(t)P(t) &= 0 \end{cases}$$

$$\begin{cases} H(t) = 0 & \\ -\frac{1}{2}P(t) &= 0 \end{cases}$$

$$\begin{cases} H(t) = 0 & \\ P(t) &= 0 \end{cases}$$

So the first equilibrium point is $E_1 = (0, 0)$.
Considering now the second:

$$\begin{cases} H(t) & = 1 - P(t) \\ -\frac{1}{2}P(t) + 3H(t)P(t) & = 0 \end{cases}$$

$$\begin{cases} H(t) & = 1 - P(t) \\ -\frac{1}{2}P(t) + 3(1 - P(t))P(t) & = 0 \end{cases}$$

$$\begin{cases} H(t) & = 1 - P(t) \\ -\frac{1}{2}P(t) + 3P(t) - 3P^2(t) & = 0 \end{cases}$$

$$\begin{cases} H(t) & = 1 - P(t) \\ P(t)\left[-\frac{1}{2} + 3 - 3P(t)\right] & = 0 \end{cases}$$

$$\begin{cases} H(t) & = 1 - P(t) \\ P(t) & = 0 \qquad \wedge \qquad P(t) = \frac{5}{6} \end{cases}$$

So there are two equilibrium points: $E_2 = (1, 0)$ and $E_3 = \left(\frac{1}{6}, \frac{5}{6}\right)$. The vector field will be enriched adding the equilibrium points and the null isoclines, the curves where the derivatives are posed equal to zero one at a time:

$$2H(t)\left[1 - H(t)\right] - 2H(t)P(t) = 0$$
$$H(t) = 0 \qquad \wedge \qquad H(t) = 1 - P(t)$$

And:

$$-\frac{1}{2}P(t) + 3H(t)P(t) = 0$$
$$P(t)\left[-\frac{1}{2} + 3H(t)\right] = 0$$
$$P(t) = 0 \qquad \wedge \qquad H(t) = \frac{1}{6}$$

Furhtermore the phase plane will be filled with vectors having components:

$$[f(H(t), P(t)), g(H(t), P(t))]$$

Solutions will be tangent to these vectors, although there will not be any information about the evolution in time (there is no t axis). The three equilibrium will be consant in time. Since now the objective is qualitative it is enouch, instead of evaluating the points, to study the sign of the derivatives in the regions identified by the isoclines. In each region the sign will be constant: the isoclines are points in which derivatives change sign, so:

$$
\begin{aligned}
\frac{dH(t)}{dt} &> 0 \\
2H(t)[1 - H(t)] - 2H(t)P(t) &> 0 \\
2H(t) - 2H^2(t) - 2H(t)P(t) &> 0 \\
H(t)[2 - 2H(t) - 2P(t)] &> 0 \\
(H(t) > 0 \wedge 2 - 2H(t) - 2P(t) > 0) \vee (H(t) < 0 \wedge 2 - 2H(t) - 2P(t) < 0) &> 0
\end{aligned}
$$

Since the second solution is not comptaible with the biological domain, $\frac{dH(t)}{dt} > 0$:

$$H(t) > 0 \wedge H(t) < 1 - P(t)$$

Now, considering the second equation:

$$
\begin{aligned}
\frac{dP(t)}{dt} &> 0 \\
-\frac{1}{2}P(t) + 3H(t)P(t) &> 0 \\
P(t)\left[-\frac{1}{2} + 3H(t)\right] &> 0 \\
(P(t) > 0 \wedge -\frac{1}{2} + 3H(t) > 0) \vee (P(t) < 0 \wedge -\frac{1}{2} + 3H(t) < 0) &> 0
\end{aligned}
$$

The second solution is again not compatible with the biological domain, $\frac{dP(t)}{dt} > 0$:

$$P(t) > 0 \wedge H(t) > \frac{1}{6}$$

From this the direction field can be populated with vectors with unitary coordinates and negative horizontal when over the $H(t)+1-P(t)$ isocline and positive under it. Morever vectors to the left of $H(t) = \frac{1}{6}$ wil have negative vertical component and positive to the right. All vectors on an isocline will have the corresponding component equal to 0. From this E_1 and E_2 are unstable, whie it is hard to make predictions about E_3.

5.2 Stability

To compute the stability of the equilibria first the Jaciobian needs to be computed:

$$
\begin{aligned}
J &= \begin{bmatrix} \frac{\partial f}{\partial H(t)} & \frac{\partial f}{\partial P(t)} \\ \frac{\partial g}{\partial H(t)} & \frac{\partial g}{\partial P(t)} \end{bmatrix} \\
&= \begin{bmatrix} 2 - 4H(t) - 2H(t) & -2H(t) \\ 3P(t) & -\frac{1}{2} + 3H(t) \end{bmatrix}
\end{aligned}
$$

Now inserting the value of the equilibrium in the Jacobian. For E_1:

$$J \ddagger [$$