From the Lotka-Volterra model to bi-stability in a short crash course.

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The Lotka Volterra model can be written as

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{k}\right) - axy \quad \text{and} \quad \frac{\mathrm{d}y}{\mathrm{d}t} = axy - dy \ , \tag{1}$$

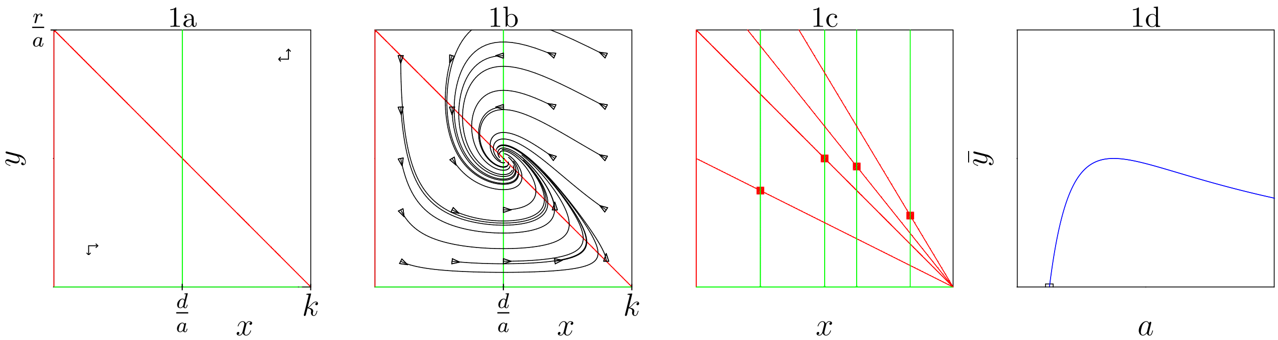
where x could be a prey and y its predator, or x could be tumor and y an immune response, or x could susceptible individuals in a population and y infected individuals, or x could be target cells and y a virus infecting these target cells. Indeed, this model is used in many areas of biology. At low densities of x and y the population x grows exponentially (at rate r), and in the absence of y the x population approaches the steady state $\bar{x} = k$ (which in ecology is called the carrying capacity). $\mathrm{d}x/\mathrm{d}t = rx(1 - x/k)$ is called logistic growth. The parameter a is the interaction parameter of the mass action term, and d is the death rate of y.

Setting $\mathrm{d}y/\mathrm{d}t = 0$ and $\mathrm{d}x/\mathrm{d}t = 0$ gives

$$\bar{x} = \frac{d}{a} \quad \text{and} \quad y(x) = \frac{r}{a}\left(1 - \frac{x}{k}\right) \quad \text{, respectively, and hence} \quad \bar{y} = \frac{r}{a}\left(1 - \frac{d}{ak}\right) \ , \tag{2}$$

where $\bar{x}$ was solved from $\mathrm{d}y/\mathrm{d}t = 0$, which implies that the steady state of x is completely determined by the parameters of y. Since changing r or k fails to affect the steady of x, we observe that decreasing the growth rate of a tumor, x, e.g., by chemotherapy, or increasing the carrying capacity of a prey, x, e.g., by feeding, does not have any effect on $\bar{x}$, and only changes $\bar{y}$. This simple toy model comes with unexpected predictions.

We study the model further by phase plane analysis. The "nullcline" or "zero-isocline" $\mathrm{d}x/\mathrm{d}t = 0$ is given by Eq. (2)b, and since this is a function of x we sketch a space having x on the horizontal and y on the vertical axis. The x-nullcline is a straigth line from $(x = 0, y = r/a)$ to $(x = k, y = 0)$. The y-nullcline is given by Eq. (2)a and is a vertical line at $x = d/a$:



The vector field indicated by the arrows can be obtained by considered extreme values in the phase plane. When $x \to 0$ and $y \to 0$ we see that $\mathrm{d}x/\mathrm{d}t \simeq rx > 0$ and $\mathrm{d}y/\mathrm{d}t \simeq -dy < 0$. When $x \geq k$ we see that $\mathrm{d}x/\mathrm{d}t < 0$ and $\mathrm{d}y/\mathrm{d}t/y = ak - d$,which will be positive whenever the maximum birth rate, ak, is larger than the death rate d. Trajectories in the phase plane intersect the nullclines horizontally or vertically. There are three steady states in this phase plane: the origin, $(0, 0)$, is a saddle point because there is an unstable horizontal direction, x at carrying capacity, $(k, 0)$, is also a saddle point but with an unstable vertical direction, and the non-trivial state $(\bar{x}, \bar{y})$ as defined in Eq. (2). The stability of the non-trivial steady state can be seen from the trajectories.

One can also linearize the model around the steady state by writing $\mathrm{d}x/\mathrm{d}t = f(x, y)$ and $\mathrm{d}y/\mathrm{d}t = g(x, y)$ and taking the partial derivatives to write the Jacobian matrix

$$J = \begin{pmatrix} \partial_x f & \partial_y f \\ \partial_x g & \partial_y g \end{pmatrix} = \begin{pmatrix} r - 2r\bar{x}/k - a\bar{y} & -a\bar{x} \\ a\bar{y} & a\bar{x} - d \end{pmatrix} = \begin{pmatrix} -rd/a & -d \\ a\bar{y} & 0 \end{pmatrix} \quad \text{or} \quad J_s = \begin{pmatrix} - & - \\ + & 0 \end{pmatrix} , \quad (3)$$

where J_s is a qualitative Jacobian giving the signs of the full Jacobi matrix. J has a negative trace, $\text{tr} = -rd/a < 0$, and positive determinant, $\det = ad\bar{y} > 0$, implying that both eigenvalues are negative, and that the steady state is stable. Note that the signs of this Jacobian matrix can also be read from the vector field around the steady state.

There is another unexpected outcome of the Lotka Volterra model because $\bar{y}$ depends non-monotonically on a (see Fig. 1c, 1d, and Eq. (2)c). Increasing a in the phase plane moves the vertical x-nullcline to the left, and rotates the y-nullcline down (Fig. 1c), which has a non-monotonic effect on $\bar{y}$ (Fig. d). Strangely this means that decreasing rate at which a virus, y, infects target cells or hosts, x, can increase the amount of virus $\bar{y}$. Or, that increasing the rate at which a predator, y, kills its prey, x, decreases the predator density.

Finally one can add another level to the Lotka Volterra model and make a 3-dimensional food chain:

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{k}\right) - axy , \quad \frac{\mathrm{d}y}{\mathrm{d}t} = axy - d_y y - byz \quad \text{and} \quad \frac{\mathrm{d}z}{\mathrm{d}t} = byz - d_z z , \quad (4)$$

and observe that $\bar{y} = d_z/b$ is now solved from $\mathrm{d}z/\mathrm{d}t = 0$ and hence that $\bar{x}$ is solved from $\mathrm{d}x/\mathrm{d}t = 0$. This implies that $\bar{x}$ will now dependent on its replication rate, r, and carrying capacity, k. Generally, $\bar{x}$ will only depend on its own parameters, r and k, when the food chain has an odd length.

Saturated interaction. Since the interaction between x and y need not be linear the Lotka-Volterra model can be extended with a saturated interaction term:

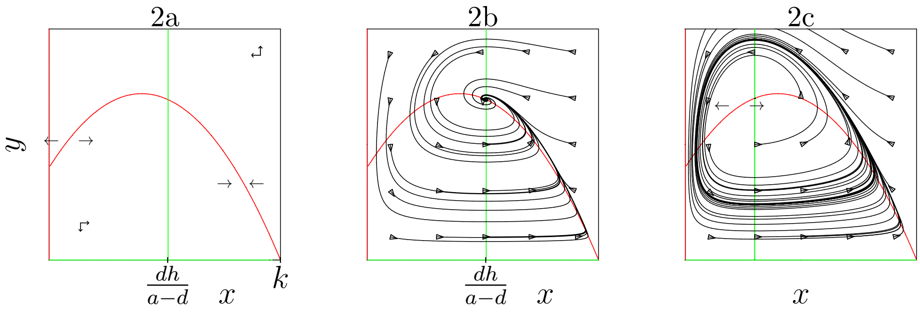
$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{k}\right) - \frac{axy}{h + x} \quad \text{and} \quad \frac{\mathrm{d}y}{\mathrm{d}t} = \frac{axy}{h + x} - dy , \quad (5)$$

where a is the maximum effect of y on x, and h is the density of x where this effect is half maximal (at $x = h$ the interaction term is $(a/2)y$). This is similar to the classical Michaelis Menten function.

We study this model by phase plane analysis. The two nullclines are given by

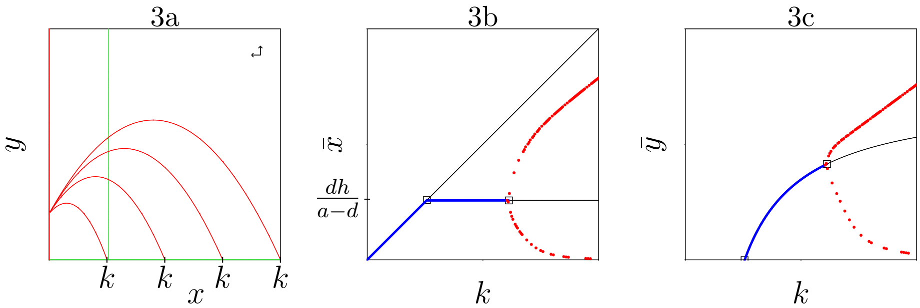
$$y(x) = \frac{r}{a}\left(h + x\right)\left(1 - \frac{x}{k}\right) \quad \text{and} \quad x = \frac{dh}{a - d} . \quad (6)$$

Since the x-nullcline is a function of x we again sketch a plane having x on the horizontal and y on the vertical axis, and observe that the x-nullcline is a parabola crossing the horizontal axis at $x = -h$ and $x = k$. Note that the left side of the nullcline is unstable (horizontal arrows pointing away from it), and it is stable on the right hand side of the maximum:



When the vertical y-nullcline intersects the parabola in its stable region the local vector field around the non-trivial steady resembles that of the Lotka Volterra model, which indeed gives the same signs in the Jacobian, $J_s = \begin{pmatrix} - & - \\ + & 0 \end{pmatrix}$ (Fig. 2a). Hence the steady state is stable and all trajectories approach it (Fig. 2b). When it intersects on the unstable left side, the horizontal vector field points away from the steady state, giving $J_s = \begin{pmatrix} + & - \\ + & 0 \end{pmatrix}$. Since the trace is now positive the steady state is unstable, and we see trajectories approaching a stable limit cycle (Fig. 2c). Thus, the global attractor is periodic behavior of x and y.

The change in stability of the non-trivial steady state is called a Hopf bifurcation. One may visualize this by changing a single parameter of the system, e.g., k, and changing the steady state from stable spiral point (heavy blue lines in Fig. 3b and 3c) to an unstable spiral point (light black lines). At the Hopf bifurcation a limit cycle is born. Close the bifurcation point nothing much happens because a stable spiral point becomes a stable limit cycle with a very small amplitude. This limit cycle grows when one moves further away from the bifurcation (red dots in Fig. 3b and 3c indicate the amplitude of the limit cycle):



Changing the parameter k one can make a bifurcation diagram display all steady states of the model. For low values of k the carrying capacity, $(\bar{x} = k, \bar{y} = 0)$, is the only attractor of the system (Fig. 3a), and this state become unstable when $k = dh/(a - d)$ (black diagonal line in Fig. 3b) and the state $\bar{x} = dh/(a - d), \bar{y})$ becomes the global attractor (horizontal blue line in Fig. 3b and curved blue line in Fig. 3c). When the vertical nullcline crosses the top of the parabola, i.e., when $(k - h)/2 = dh/(a - d)$, this steady state becomes unstable (the line turns black, and a stable limit cycle (red symbols) is born.

A sigmoid interaction term. Several processes in biology have sigmoid saturation functions. Let's rewrite the model into

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{k}\right) - \frac{ayx^2}{h^2 + x^2} \quad \text{and} \quad \frac{\mathrm{d}y}{\mathrm{d}t} = \frac{ayx^2}{h^2 + x^2} - dy \;, \tag{7}$$

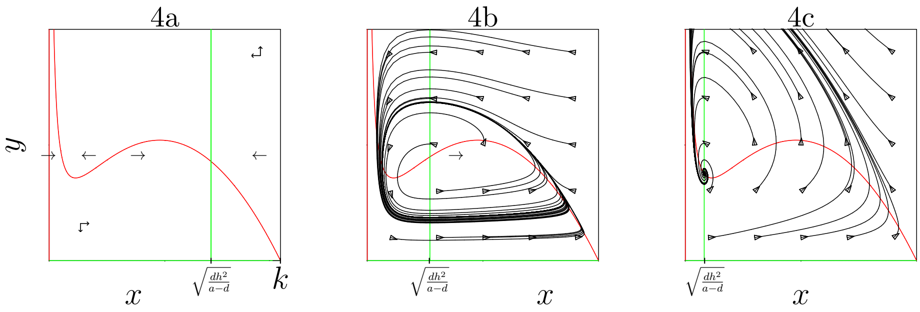
where the $x^2/(h^2+x^2)$ function is called a Hill function. The meaning of the parameters a and h stays the same. The nullclines are now described by

$$y(x) = \frac{r}{a}\,\frac{h^2+x^2}{x}\left(1-\frac{x}{k}\right) \quad \text{and} \quad x = h\sqrt{\frac{d}{a-d}}\ , \tag{8}$$

respectively. The y-nullcline remains a vertical line. We can get an idea of the x-nullcline by considering Eq. (8)a for small and large values of x. For $x \ll h$ and $h \ll x < k$ we obtain

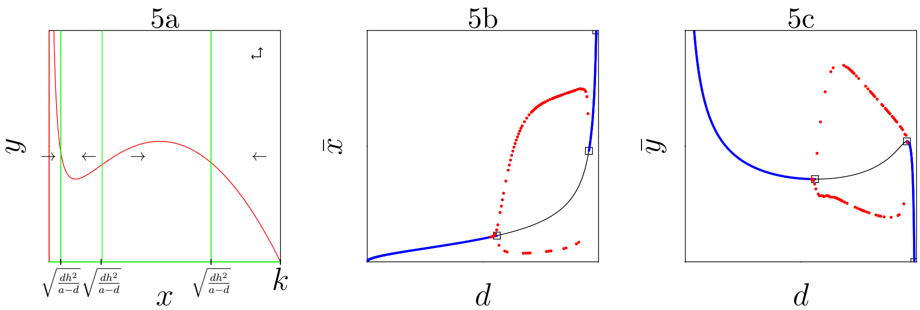
$$y(x) = \frac{r}{a}\,\frac{h^2}{x}\left(1-\frac{x}{k}\right) \quad \text{and} \quad y(x) = \frac{r}{a}\,x\left(1-\frac{x}{k}\right)\ , \tag{9}$$

respectively. The former reveals a vertical asymptote at $x = 0$, and the latter is a parabola intersecting the horizontal axis at $x = 0$ and $x = k$. In combination this may look like the phase plane in Fig. 4a. Note the x-nullcline now has two stable parts and an unstable region in between its minimum and maximum:

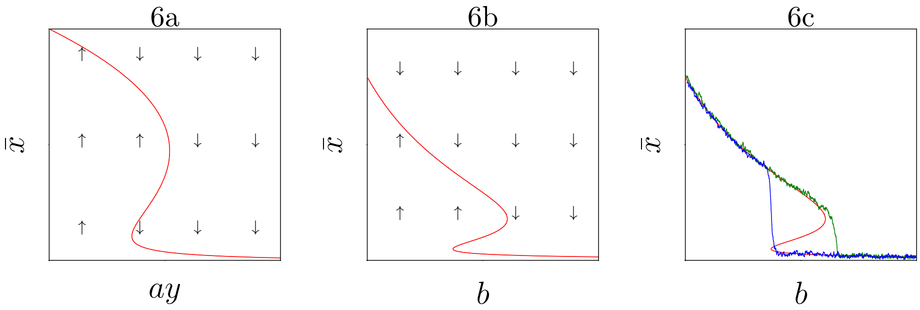


When the vertical y-nullcline intersects on the stable right hand side of the nullcline the situation around the steady state is again like that of the Lotka Volterra model, $J_s = \begin{pmatrix} - & - \\ + & 0 \end{pmatrix}$, and the non-trivial steady state is the global attractor (Fig. 4a). When the y-nullcline intersects in the unstable region between the minimum and the maximum of the x-nullcline the steady state is unstable, $J_s = \begin{pmatrix} + & - \\ + & 0 \end{pmatrix}$, and the trajectories approach a stable limit cycle (Fig. 4b). The new situation, where the y-nullcline intersects on the stable left hand side of the minimum (Fig. 4c), the global attractor of the system is again a stable steady state, with $J_s = \begin{pmatrix} - & - \\ + & 0 \end{pmatrix}$.

One can again summarize the potential behaviors of the model by making a bifurcation diagram. In the figure below we change the death rate, d, to move the vertical y-nullcline to the left or to the right (Fig. 5a). Plotting $\bar{x}$ or $\bar{y}$ as a function of d we obtain the diagrams displayed in Fig. 5b and 5c. Note that $\bar{y} = 0$ at the largest value of d: for larger values of d the system approaches the carrying capacity $\bar{x} = k$. We see two Hopf bifurcation at which a stable limit cycle appears or disappears. The amplitude of the limit cycle (red dots) is maximal somewhere in between these two Hopf bifurcations:



If we were to fix ay as a bifurcation parameter, the x-nullcline with its minimum and maximum would represent the steady state, $\bar{x}$, of Eq. (7)a. Plotting $\bar{x}$ as a function of the "parameter" ay gives the bifurcation diagram shown in Fig. 6a. We observe an intermediate region of ay values where the system is bi-stable. A large value of $\bar{x}$ is separated from a low value of $\bar{x}$ by an unstable value of $\bar{x}$. The two bifurcations in Fig. 6a are called saddle-node bifurcations because a saddle and a node point merge and annihilate each other. This is an example of a catastrophic bifurcation because the system behavior will switch to a completely unrelated attractor.



A simple toy model to make a bifurcation diagram like Fig. 6a is the following

$$\frac{\mathrm{d}x}{\mathrm{d}t} = a - bx + \frac{x^2}{1+x^2} \ , \tag{10}$$

where by changing b one can make the line $y = bx$ intersect the line $y = a + x^2/(1+x^2)$ once or three times. This delivers the bifurcation diagram in Fig. 6b. Starting with a low value of b, and increasing b slowly while drawing normally distributed random values of a, we obtain the noisy green trajectory shown in Fig. 6c. The system switches to the low state of x around the highest saddle-node bifurcation. If one were to turn backwards at the end by slowly decreasing b, one would obtain the noise blue trajectory shown on Fig. 6c, which reverts to the upper branch of x at the lowest saddle-node bifurcation. This "late" switching between alternate attractors around the tipping points is called hysteresis.

Reading more. Background on phase plane analysis and the ecological models of Eqs. (1), (5), and (7) can be found in various textbooks [1, 2]. The review paper [4] or the book by Marten Scheffer [3] gives an excellent introduction into bi-stability and the potential early warning signals in the system behavior around tipping points. All figures in this handout were made with GRIND (`http://tbb.bio.uu.nl/rdb/grind.html`); in the computer practical you will make similar pictures using an R-version of GRIND (`http://tbb.bio.uu.nl/rdb/grindR.html`).

References

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