Sketching nullclines and vector fields in phase spaces.

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This is a short tutorial summarizing the math involved in sketching nullclines and a vector field in a phase space. We will demonstrate an example with simple straight nullclines (the Lotka-Volterra model), and an example with a hyperbolic nullcline. If you have difficulties sketching hyperbolas please read and watch the tutorial on sketching functions. Because our equations are parameter free (i.e., we use letters rather than numbers) we need to consider all qualitatively different situations for each model.

1   Lotka-Volterra model

The model can be written as:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = aR - bR^2 - cRN \quad \text{and} \quad \frac{\mathrm{d}N}{\mathrm{d}t} = dRN - eN \ ,$$

where a, b, c, d, and e are positive parameters (constants), and R and N are the prey and predator densities (variables).

A first step is to sketch nullclines (0-isoclines) in phase space. A nullcline is the set of points (R, N) for which the corresponding population remains constant. Thus, the R-nullcline is the set of points at which $\mathrm{d}R/\mathrm{d}t = 0$, and the N-nullcline is the set of points at which $\mathrm{d}N/\mathrm{d}t = 0$. Setting $\mathrm{d}R/\mathrm{d}t = 0$ and $\mathrm{d}N/\mathrm{d}t = 0$ in one finds

$$R = 0 \ , \quad N = \frac{a - bR}{c} \quad \text{and} \quad N = 0 \ , \quad R = \frac{e}{d} \ ,$$

for the prey nullclines, and the predator nullclines, respectively. The second expression (for the non-trivial prey-nullcline) suggests that we best plot N as a function of R, i.e., we decide that N spans up the vertical axis, and R forms the horizontal axis of the phase space (see Fig. 1). The prey-nullcline intersects the vertical axis at $N = a/c$ and the horizontal axis when $a - bR = 0$, i.e., at the carrying
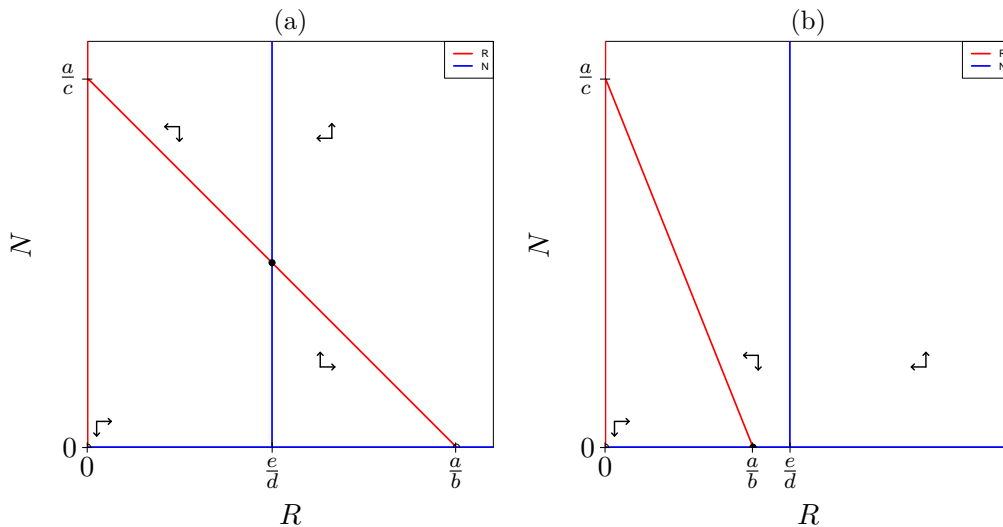

Figure 1: The two qualitatively different phase spaces of the Lotka-Volterra model, with the vector field indicated by arrows.

capacity, $R = a/b$. Since the non-trivial predator predator nullcline is located at $R = e/d$ we have to consider two possibilities, i.e., $a/b > e/d$ and the other way around (see Fig. 1a and b). In Panel (a) the nullclines intersect in three steady states, but when $a/b < e/d$ there are only two steady states $(R, N) = (0, 0)$ and $(a/b, 0)$ (for biological reasons we only consider the positive quadrant).

A second step is to determine the vector field in each phase space. Not knowing the parameter values, one considers an extreme point in phase space. For example, in the neighborhood of the point $(R, N) = (0, 0)$, one can neglect the quadratic bR^2, cRN, and dRN terms, such that

$$\frac{\mathrm{d}R}{\mathrm{d}t} \approx aR , \quad \frac{\mathrm{d}N}{\mathrm{d}t} \approx -eN .$$

Since the former is strictly positive, and the latter strictly negative, we assign the vector $(+-)$ to the local direction of the vector field (see Fig. 1a and b). This means that $\mathrm{d}R/\mathrm{d}t > 0$ below the slanted R-nullcline, i.e., arrows point to the right, and that at the left hand side of the vertical N-nullcline $\mathrm{d}N/\mathrm{d}t < 0$, i.e., arrows point downwards. The derivatives switch sign, and the corresponding arrows switch direction, when crossing a nullcline (precisely on the R and N-nullclines the arrows are vertical and horizontal, respectively). Nullclines therefore separate the phase space into regions where the derivatives have the same sign.

One can also determine the steady states of the system directly from the ODEs. A steady state, or equilibrium, is defined as $\mathrm{d}R/\mathrm{d}t = \mathrm{d}N/\mathrm{d}t = 0$, and solving that system for R and N, one finds

$$(R, N) = (0, 0) , \quad (R, N) = (a/b, 0) \quad \text{and} \quad (R, N) = \left(\frac{e}{d}, \frac{da - eb}{dc} \right)$$

as the three steady states of this system. This confirms that the non-trivial steady state only exists when $\frac{da - eb}{dc} > 0$, i.e., when $da > eb$ or $a/b > e/d$; see Fig. 1. Graphically steady states correspond to the intersects of the nullclines.

Finally, one has to determine the nature of the steady states. For the steady states $(0, 0)$ and $(a/b, 0)$ one can read from the local vector field that they are saddle points. Around $(a/b, 0)$ the vertical component is the unstable direction, and around $(0, 0)$ the horizontal component is the unstable direction. This is not so simple for the non-trivial point. Because there is no stable and unstable direction in the local vector field, the non-trivial steady state cannot be a saddle point, and it therefore has to be a node or a spiral point. To determine its stability one formally has to linearize the model [1, 2].

Fortunately, some of the signs of this Jacobian can be determined graphically (see the accompanying Ebook [2]). One can check for local feedback of the populations onto themselves. Increasing R in the steady state makes $\mathrm{d}R/\mathrm{d}t < 0$, and increasing N in the steady state keeps $\mathrm{d}N/\mathrm{d}t = 0$ because one lands exactly on the $\mathrm{d}N/\mathrm{d}t = 0$ nullcline (see Fig. 1a). Because locally there is no positive feedback this suggests that the non-trivial steady state is stable. Indeed the absence of positive feedback establishes that the trace of the Jacobi matrix is negative, and given that the non-trivial steady state is not a saddle point (corresponding to a negative determinant), we can conclude that the non-trivial steady state is stable.

2 Non-linear nullclines

Consider the following model

$$\frac{\mathrm{d}L}{\mathrm{d}t} = eA - dL(1 + \epsilon A) - mL \quad \text{and} \quad \frac{\mathrm{d}A}{\mathrm{d}t} = mL - \delta A ,$$
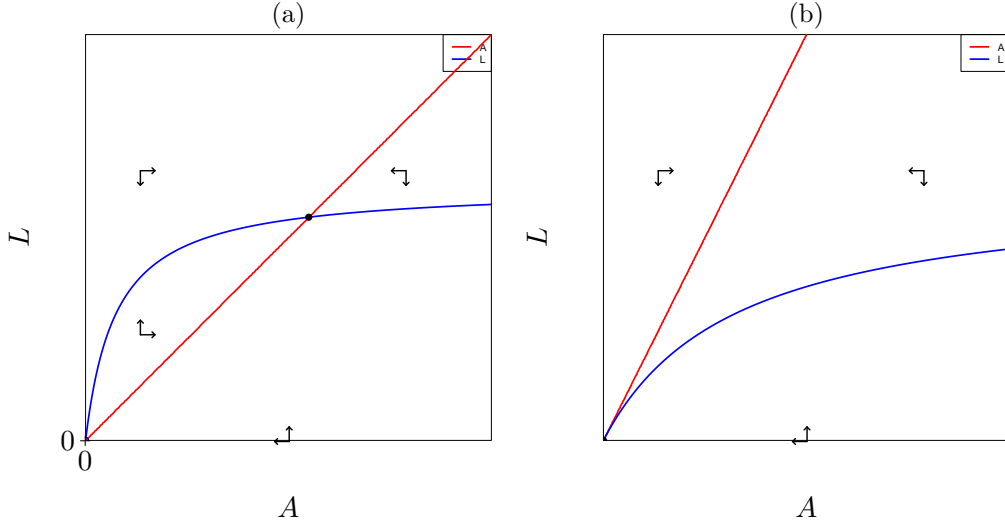
Figure 2: The phase space of the larvae model with the vector field indicated by the arrows.

for larvae, L, maturing, m, into adults, A, that lay eggs, e. The mortality of the larvae increases linearly with the density of the adults. Setting $\mathrm{d}A/\mathrm{d}t = 0$ readily delivers the nullcline $A = mL/\delta$ (or, equivalently, $L = \delta A/m$).

Setting $\mathrm{d}L/\mathrm{d}t = 0$ we choose to solve for L as a function of A (arbitrarily in this case) ,

$$eA - dL - d\epsilon LA - mL = 0 \quad \leftrightarrow \quad eA = L(d + d\epsilon A + m) \quad \leftrightarrow \quad L = \frac{eA}{d + m + d\epsilon A} = \frac{\alpha A}{h + A} \,,$$

where $\alpha = \frac{e}{d\epsilon}$ and $h = \frac{d+m}{d\epsilon}$. Since the final expression is a normal saturation function (i.e., a Hill function), it is fairly easy to sketch sketch L as a function of A, and hence we choose L as the vertical variable and A as the horizontal variable (see Fig. 2). Since both nullclines leave the origin with slopes δ/m and $\alpha/h = \frac{e}{d+m}$, respectively, we have to consider two cases, i.e., (1)

$$\frac{\delta}{m} < \frac{e}{d+m} \quad \leftrightarrow \quad \delta < \frac{em}{d+m} \,,$$

where the death rate of the adults is smaller than number of eggs produced per adult, e, times the maximum fraction of larvae maturing, $\frac{m}{d+m}$, and (2) where this is just the other way around (see Fig. 2a and b, respectively). In the former case (Fig. 2a) the nullclines intersect twice, in the origin and in a non-trivial steady state. In Fig. 2b the nullclines only intersect in the origin.

For the vector field we could in both panels consider $\mathrm{d}L/\mathrm{d}t$ for an intermediate number of adults with no larvae, i.e., $\mathrm{d}L/\mathrm{d}t = eA$, which is positive, meaning the vertical vectors point inwards from the horizontal axis. For the adults we could consider the same region, i.e., $\mathrm{d}A/\mathrm{d}t = -\delta A$, which is negative, meaning that the horizontal vectors point leftwards on (and near) the horizontal axis (see Fig. 2). Completing the vector field by flipping the corresponding vector each time we cross a particular nullcline, we complete the vector field in both panels of Fig. 2. The vector field in Fig. 2a reveals that the origin is unstable (i.e., a saddle point) and that the non-trivial steady state is stable. Conversely, the origin is stable in Fig. 2b: The population cannot maintain itself because the death rate of the adults is faster than the maximum production of novel adults by larvae.

Solving $\mathrm{d}L/\mathrm{d}t = \mathrm{d}A/\mathrm{d}t = 0$ we find that the non-trivial steady state in Fig. 2a is located at

$$\bar{L} = \frac{em - d\delta - m\delta}{m\epsilon d} \quad \text{and} \quad \bar{A} = \frac{m\bar{L}}{\delta} \,,$$

which confirms that $\bar{L} > 0$ when $\delta < \frac{em}{d+m}$.

3

References

[1] **Garfinkel, A., Shevtsov, J., and Guo, Y.**, 2017. Modeling Life: The Mathematics of Biological Systems. Springer, New York.

[2] **Panfilov, A. V., Ten Tusscher, K. H. W. J., and De Boer, R. J.**, 2016. Matrices, Linearization, and the Jacobi matrix. http://tbb.bio.uu.nl/rdb/books/math.pdf, EBook.