

4 Dynamics of interacting populations

So far, we have considered the dynamics of a single species. However, the major part of ecology is really about interactions of species that live in the same ecosystem. And even if we are only interested in a single species, we need to take into account that its dynamics in nature will crucially be influenced by the presence (or absence) of other species. Whenever these other species dynamics on a similar time scale, we need to include them into the model. For a pair of species, there are three basic types of interactions:

1. **Competition** (e.g. for food or for nesting sites). Presence of individuals from the other species reduces population growth.
2. **Mutualism.** Both species profit from the presence of the respective other species. Typical examples are plant-pollinator interactions, or seed-dispersal systems, where plants produce fruit to reward animal-aided dispersal. Another class are the interactions of endosymbionts (bacteria, fungi) and their hosts (most animals).
3. **Host-parasite or predator-prey.** Asymmetric consequences of the interactions. Presence of the host/prey is good for the predator – but not vice-versa.

In these scenarios, the density regulation for a given species will typically not only depend on the total density of individuals across all species, but on the individual densities of all species: for a predator it will matter a lot whether other individuals around are prey or rather competing predators. We therefore cannot use the simplistic modeling scheme of the previous section, where we have assumed that density regulation depends only on the total number of all individuals (in various age classes) and affects all these individuals in the same way. We will therefore introduce a new class of models for the population dynamics of interacting species. We will use the formalism in continuous time, which leads to coupled ordinary differential equations. Let $x_i(t)$ be the density of species i at time t and $1 \leq i \leq n$. Then

$$\dot{x}_i(t) := f_i(x_1(t), x_2(t), \dots, x_n(t)) \quad (1)$$

with f_i continuously differentiable on some subset of \mathbb{R}^n . Collectively, we can write

$$\dot{\mathbf{x}}(t) = \mathbf{f}(\mathbf{x}(t)) \quad (2)$$

defining a time-homogeneous, coupled, first-order ODE system. There is a unique solution for each initial condition \mathbf{x} , which can be represented as a line $\mathbf{x}(t)$ in the phase space, where $\mathbf{f}(\mathbf{x})$ are tangent vectors to $\mathbf{x}(t)$ defining the velocity of the dynamics. In this notation, $\mathbf{x}(t)$, $\mathbf{y}(t)$ etc. are solutions of a system of differential equations $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ with the same f , but with different initial conditions \mathbf{x} and \mathbf{y} . In general, solutions need not exist for all times t (but only for an open time interval). However, if the dynamics keep $\mathbf{x}(t)$ in a compact set, the solution exists for all times $-\infty < t < \infty$. Since population densities are non-negative and also won't increase without bounds, this is always the case for a meaningful biological model.

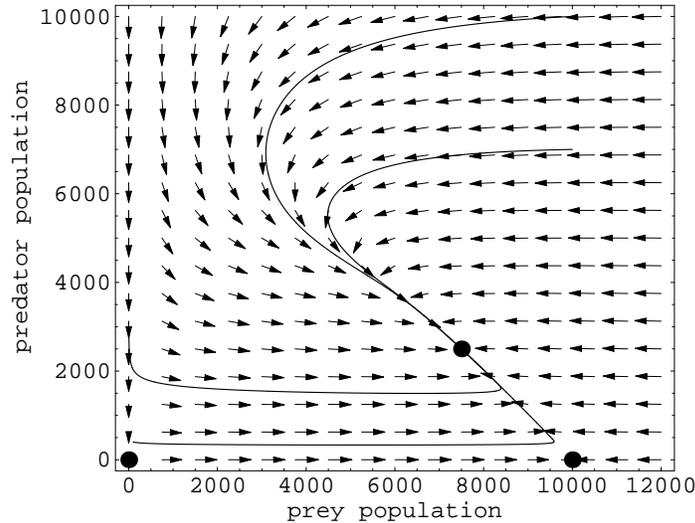


Figure 1: Phase space with vector field for the Lotka-Volterra predator-prey model ($r_x = 1$, $c_x = -10^{-4}$, $c_{xy} = -10^{-4}$, $r_y = -0.05$, $c_y = -10^{-5}$, $c_{yx} = 10^{-5}$) with solutions for various starting conditions.

4.1 Lotka-Volterra model

As our main example, we will consider interactions between two species, $x(t)$ and $y(t)$, following the Lotka-Volterra dynamics,

$$\dot{x} = f_x(x, y) = r_x x + c_x x^2 + c_{xy} x y, \quad (3a)$$

$$\dot{y} = f_y(x, y) = r_y y + c_y y^2 + c_{yx} y x. \quad (3b)$$

The model has the following properties:

- r_x and r_y describe the intrinsic growth rates of both species while rare and in the absence of the other species. These growth rates can be positive or negative, for example for a predator in the absence of prey or for two mutualists that crucially depend on each other.
- The constants c_x and c_y describe the consequences of within-population interactions. These are usually (but not always) dominated by competition, such that c_x and c_y are negative.
- If the interaction parameter c_{xy} (or c_{yx}) is zero, the x (or y) population follows a single-species dynamics. With $c_x = -r_x/K_x$ (resp. $c_y = -r_y/K_y$), we obtain 1-dim. logistic growth.

- In general, the sign of the interaction parameters determines the type of the biological interaction:
 1. For $c_{xy}, c_{yx} < 0$ we obtain a competition model;
 2. $c_{xy} < 0$ and $c_{yx} > 0$ corresponds to an x -host- y -parasite (or x -prey- y -predator) model;
 3. finally, $c_{xy}, c_{yx} > 0$ indicates mutualism.
- The classical Lotka-Volterra model has $r_x > 0$, $r_y < 0$, $c_x = c_y = 0$, $c_{xy} < 0$, and $c_{yx} > 0$. It was designed in the 1920's by Vito Volterra to describe the increased percentage of sharks and rays among all caught fish in the Adriatic Sea after fishing had been interrupted for multiple years due to WW1. The equations were independently derived and analyzed by Alfred Lotka (from Lemberg, Austria-Hungary).

4.2 Equilibria

All points \mathbf{x}^* with $\dot{\mathbf{x}}^* = \mathbf{0}$ are called equilibrium points (or fixed points, rest points, stationary states) of the dynamics. For example, the Lotka-Volterra model has a trivial equilibrium at $\mathbf{x} = 0$. In general, we consider the so-called *isoclines*. The x_i -isocline is the set of all points where $\dot{x}_i = 0$, i.e. where the vector field is vertical to the x_i axis. For the Lotka-Volterra model, we obtain:

- x -isocline for $f_x(x, y) = 0$:

$$x = 0 \quad \text{and} \quad y = -\frac{r_x + c_x x}{c_{xy}} \quad (4)$$

- y -isocline for $f_y(x, y) = 0$:

$$y = 0 \quad \text{and} \quad x = -\frac{r_y + c_{yx} x}{c_y} \quad (5)$$

The equilibria are given by the intersections of the x - and y -isoclines (in general: of all x_i -isoclines). We obtain:

$$(x_1^*, y_1^*) = (0, 0) \quad ; \quad (x_2^*, y_2^*) = (0, -r_y/c_y) \quad ; \quad (x_3^*, y_3^*) = (-r_x/c_x, 0) \quad (6)$$

$$(x_4^*, y_4^*) = \left(\frac{c_{xy}r_y - c_y r_x}{c_x c_y - c_{xy} c_{yx}}, \frac{c_{yx}r_x - c_x r_y}{c_x c_y - c_{xy} c_{yx}} \right). \quad (7)$$

Only equilibrium points with $x_i^*, y_i^* \geq 0$ are attainable and make biological sense. With this information about equilibria and isoclines, we already obtain a qualitative graphical representation of the dynamics in the phase plane. For concreteness, we consider the predator-prey case with $r_x > 0$, $r_y < 0$, $c_x, c_y < 0$, $c_{xy} < 0$, and $c_{yx} > 0$. We see that the (second part of the) x -isocline is monotonically decreasing, starting from $(0, |r_x/c_{xy}|)$ on the y -axis. The second part of the y -isocline is monotonically increasing, starting from the unbiological equilibrium $(0, -|r_y/c_y|)$ on the negative y -axis. It intersects with the x -axis at $\hat{x} = -r_y/c_{yx} > 0$. There are two fundamentally different dynamical regimes.

- For $\hat{x} > x_3^* = -r_x/c_x > 0$, the x and y isoclines intersect in the negative- y half plane and the fourth equilibrium point (x_4^*, y_4^*) is unbiological (and cannot be reached from positive starting values). Adding schematic velocity arrows to the various regions of the phase plane, we quickly see that $(x_3^*, y_3^*) = (-r_x/c_x, 0)$ is the only stable equilibrium of the dynamics: predators cannot be maintained and die out.
- For $\hat{x} < x_3^*$, the x and y isoclines intersect for positive y and the fourth equilibrium point (x_4^*, y_4^*) is biologically meaningful. Adding velocity arrows to the phase plane, we see that $(x(t), y(t))$ trajectories will oscillate around this point, but it remains unclear whether the equilibrium is stable or unstable. A more detailed analysis is needed.

4.3 Stability

Extending the one-dimensional case, we define:

- A fixed point \mathbf{x}^* of an ODE $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ is (Lyapunov) stable iff, for any $\epsilon > 0$ there is a $\delta > 0$, such that

$$\mathbf{x}(0) \in \mathcal{B}(\mathbf{x}^*, \delta) \quad \Rightarrow \quad \mathbf{x}(t) \in \mathcal{B}(\mathbf{x}^*, \epsilon)$$

for all $t \geq 0$.

- A fixed point is asymptotically stable iff it is stable and

$$\lim_{t \rightarrow \infty} |\mathbf{x}(t) - \mathbf{x}^*| = 0$$

for all $\mathbf{x}(0) \in \mathcal{B}(\mathbf{x}^*, \epsilon)$ and some $\epsilon > 0$.

- The set of points $\{\mathbf{x}\}$ with $\mathbf{x}(t) \rightarrow \mathbf{x}^*$ is called the domain (or basin) of attraction of \mathbf{x}^* . The fixed point is said to be globally attracting iff its domain of attraction is the entire state space.
- As generalization of a fixed point, we define the ω -limit of any point \mathbf{x} as the set of all accumulation points of $\mathbf{x}(t)$ for $t \rightarrow \infty$ with $\mathbf{x}(0) = \mathbf{x}$. Obviously, the ω -limit of any point in the domain of attraction of a fixed point \mathbf{x}^* is just \mathbf{x}^* . In general, ω -limits can also be empty, but this is not possible if the dynamics is confined to a compact set.
- Analogous to ω -limits, we define α -limits as accumulation points for $t \rightarrow -\infty$.

As in the one-dimensional case, we can relate stability to local properties of the dynamics in the neighborhood of a fixed point. To this end, we consider the linearized dynamics for some point $\mathbf{x} \in \mathcal{B}(\mathbf{x}^*, \epsilon)$ according to a Taylor expansion

$$f_i(\mathbf{x}) = f_i(\mathbf{x}^*) + \left(\frac{\partial f_i}{\partial x_1} \Big|_{\mathbf{x}=\mathbf{x}^*}, \dots, \frac{\partial f_i}{\partial x_n} \Big|_{\mathbf{x}=\mathbf{x}^*} \right) \cdot (\mathbf{x} - \mathbf{x}^*) + \mathcal{O}[\epsilon^2] \quad (8)$$

and

$$\mathbf{f}(\mathbf{x}) = \mathbf{f}(\mathbf{x}^*) + \mathbf{J} \cdot (\mathbf{x} - \mathbf{x}^*) + \mathcal{O}[\epsilon^2] \quad (9)$$

with the Jacobian matrix

$$\mathbf{J} = \left(\begin{array}{ccc} \frac{\partial f_1}{\partial x_1} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \vdots & & \vdots \\ \frac{\partial f_n}{\partial x_1} & \cdots & \frac{\partial f_n}{\partial x_n} \end{array} \right) \Big|_{\mathbf{x}=\mathbf{x}^*} \quad (10)$$

For a fixed point, we have $\mathbf{f}(\mathbf{x}^*) = \mathbf{0}$ and defining $\mathbf{y} := \mathbf{x} - \mathbf{x}^*$ we obtain the local linear map

$$\dot{\mathbf{y}} = \mathbf{J}\mathbf{y}. \quad (11)$$

Linear ODE's Linear differential equations are not capable of describing meaningful interactions among species. However, as we have seen, any ODE system can be approximated by a linear system locally around a fixed point. It is therefore worthwhile to consider the linear dynamics. Let

$$\dot{\mathbf{x}} = \mathbf{J}\mathbf{x}. \quad (12)$$

with real-valued $n \times n$ matrix \mathbf{J} . Then the solution can be written as

$$\mathbf{x}(t) = \exp[\mathbf{J}t]\mathbf{x}(0) \quad (13)$$

with the matrix exponential

$$\exp[\mathbf{J}t] = \mathbf{I} + \mathbf{J}\frac{t}{1!} + \mathbf{J}^2\frac{t^2}{2!} + \cdots. \quad (14)$$

Eigenvalues of \mathbf{J} can either be real or occur in complex conjugate pairs. Note that if λ is an eigenvalue of \mathbf{J} with corresponding eigenvector \mathbf{v} , then \mathbf{v} is also an eigenvector of $\exp[\mathbf{J}t]$ with eigenvalue $\exp[\lambda t]$. Representing $\mathbf{x}(0)$ as linear combination of (generalized) eigenvectors of \mathbf{J} , we see that the components $x_i(t)$ of the solution $\mathbf{x}(t)$ can be written as linear combinations of the following functions:

- (i) $\exp[\lambda t]$ whenever λ is a real eigenvalue of \mathbf{J} .
- (ii) $\exp[at] \cos[bt]$ and $\exp[at] \sin[bt]$ whenever $a \pm ib$ are eigenvalues of \mathbf{J} .
- (iii) $t^j \exp[\lambda t]$, or $t^j \exp[at] \cos[bt]$ and $t^j \exp[at] \sin[bt]$, with $0 \leq j < m$, whenever the eigenvalue λ or the eigenvalue $a \pm ib$ occurs with (algebraic) multiplicity m .

Obviously, $\mathbf{x}^* = \mathbf{0}$ is a fixed point of the linear ODE (the only one if $\det \mathbf{A} \neq 0$). We can note that positive real parts in the eigenvalues ($\lambda > 0$ or $a > 0$) of \mathbf{J} lead to components in \mathbf{t} that diverge away from $\mathbf{0}$, while negative real parts lead to components that vanish in the limit $t \rightarrow \infty$. Any imaginary part $b \neq 0$ leads to oscillations, which are damped if and only if $a < 0$. We can define the following types of fixed points:

- A fixed point is called *hyperbolic* if none of the eigenvalues has zero real part. A hyperbolic fixed point is...

1. A *sink* if the real parts of all eigenvalues are negative. In this case,

$$\lim_{t \rightarrow \infty} \mathbf{x}(t) = \mathbf{0} \quad (15)$$

for any starting vector $\mathbf{x}(0)$. Hence, $\mathbf{0}$ is globally stable (the ω -limit of every point). A sink can be either a *stable node* (all eigenvalues real) or a *stable spiral/sink focus* (some eigenvalues complex).

2. A *source* if the real parts of all eigenvalues are positive. In this case any orbit $\mathbf{x}(t)$ grows exponentially and $\mathbf{0}$ is the α -limit of every point. A source can be either an *unstable node* (all eigenvalues real) or an *unstable spiral/source-focus* (some eigenvalues complex).

3. A *saddle point* if some eigenvalues have positive real parts and some have negative real parts, but none are on the imaginary axis. The points with ω -limit $\mathbf{0}$ and the points with α -limit $\mathbf{0}$ each form a linear submanifold of \mathbb{R}^n , called the *stable* and *unstable manifold*, respectively, which together span \mathbb{R}^n . Sometimes, saddle points are also further characterized, for example by attaching the word “focus” when there are complex eigenvalues. However, this is only possible in more than two dimensions.

- Eigenvalues on the imaginary axis correspond to degenerate solutions. In particular, an eigenvalue $\lambda = 0$ leads to a manifold of fixed points and a purely imaginary eigenvalue to a manifold of periodic orbits.
- Hyperbolic eigenvalues are structurally stable in the sense that small changes of the parameters lead to (only) small changes of the equilibrium structure. In contrast, non-hyperbolic equilibria are structurally unstable with respect to any perturbation that introduces a small component on the real axis.

Two-dimensional systems. A classification of fixed points depends on the roots of the characteristic polynomial. For a real-valued two-dimensional matrix

$$\mathbf{A} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \quad (16)$$

this can be written in terms of the trace and the determinant as

$$\lambda^2 - \lambda \operatorname{tr}[\mathbf{A}] + \det[\mathbf{A}] \quad (17)$$

and hence

$$\lambda_{1,2} = \frac{\operatorname{tr}[\mathbf{A}] \pm \sqrt{\operatorname{tr}[\mathbf{A}]^2 - 4 \det[\mathbf{A}]}}{2}. \quad (18)$$

According to the so-called *Routh-Hurwitz criterion*, we have

$$\operatorname{Re}(\lambda_{1,2}) < 0 \quad \Leftrightarrow \quad \operatorname{tr}[\mathbf{A}] < 0 \quad \text{and} \quad \det[\mathbf{A}] > 0 \quad (19)$$

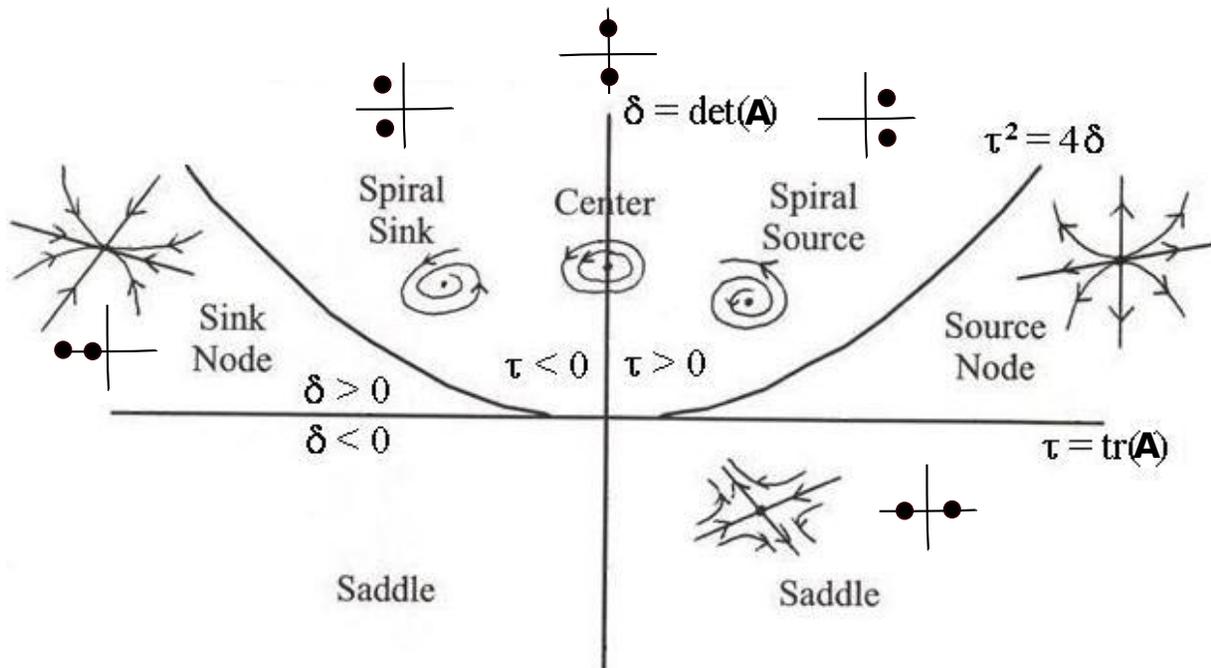


Figure 2: Classification of asymptotic behavior for equilibria in two-dimensional systems of ODEs. For each area in the trace-determinant space, the figure displays the location of eigenvalues in the complex plane (real part on the x -axis and imaginary part on the y -axis) and a representative phase portrait. Modified from <http://www.augustana.ualberta.ca/hackw/mat332/exhibit/fxdpt2d.html>.

(proof immediate). Further, both roots will be real if and only if $\text{tr}[\mathbf{A}]^2 \leq 4 \det[\mathbf{A}]$. We obtain a full classification of possible equilibria of the linear system (Fig. 2).

So far, we have derived a classification framework for equilibria in linear systems of ODEs. The *Hartman-Grobman theorem* guarantees that this classification can also be used to characterize the fixed points of nonlinear ODE system. In particular,

- A fixed point is a sink if all eigenvalues of the corresponding Jacobian have negative real parts. In this case, the fixed point is asymptotically stable.
- Any eigenvalue of the Jacobian with strictly positive real part leads to an unstable fixed point.
- For fixed points, where some (or all) eigenvalues of the Jacobian have real part zero, and all others negative real parts, the Hartman-Grobman theorem does not apply and stability depends on higher order terms.

With this, we can now apply this classification framework to equilibria in the Lotka-Volterra model.

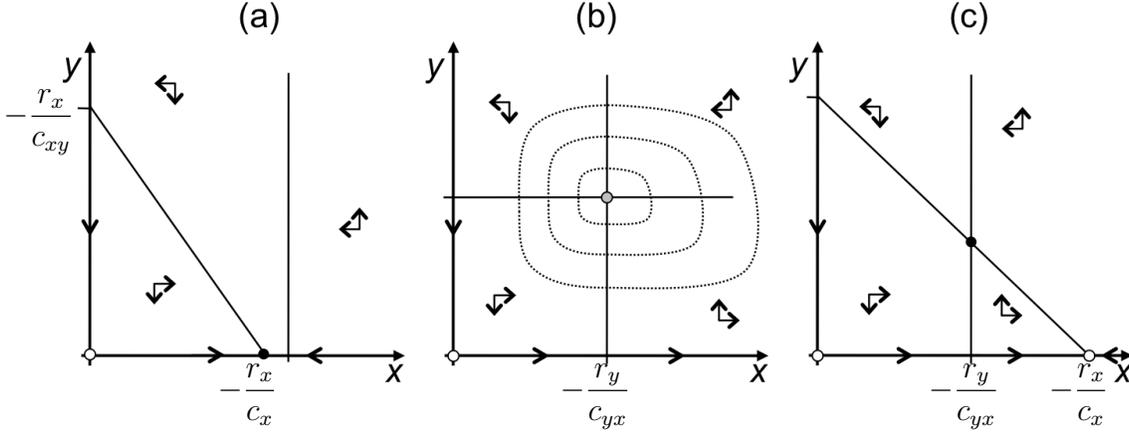


Figure 3: The three isocline configurations for the Lotka-Volterra predator-prey model. (a) Isoclines do not intersect. The point $(-r_y/c_{yx})$ equilibrium is globally stable. (b) Isoclines intersect but prey grows exponentially in the absence of the predator. The interior equilibrium is neither a sink nor a source but a center. The whole interior of the phase plane is filled with periodic orbits (hatched lines). (c) Isoclines intersect. The interior equilibrium (x^*, y^*) is globally stable.

4.4 Stability for the Lotka-Volterra model

We consider the general Lotka-Volterra model. We have the Jacobian

$$\mathbf{J} = \begin{pmatrix} \frac{\partial f_x}{\partial x} = r_x + 2c_x x + c_{xy}y & \frac{\partial f_x}{\partial y} = c_{xy}x \\ \frac{\partial f_y}{\partial x} = c_{yx}y & \frac{\partial f_y}{\partial y} = r_y + 2c_y y + c_{yx}x \end{pmatrix} \quad (20)$$

which can be analyzed for arbitrary parameters. We will discuss the three models for the basic biological interactions in turn.

Predator-prey We start with the predator-prey model, defined by $c_{xy} < 0$ and $c_{yx} > 0$. We assume logistic growth of the prey with $r_x > 0$ and $c_x = -r_x/K_x < 0$. The predator cannot grow on its own. Thus $r_y < 0$. For computational simplicity, we chose $c_y = 0$. For the trivial fixed point $(0, 0)$, we obtain

$$\mathbf{J}(\mathbf{x}_1^*) = \begin{pmatrix} r_x & 0 \\ 0 & r_y \end{pmatrix}. \quad (21)$$

It is thus a saddle point and unstable. The second fixed point is unbiological. For the third one,

$$\mathbf{J}(\mathbf{x}_3^*) = \begin{pmatrix} -r_x & -r_x c_{xy}/c_x \\ 0 & r_y - r_x c_{yx}/c_x \end{pmatrix}, \quad (22)$$

with eigenvalues $-r_x < 0$ and $r_y - r_x c_{yx}/c_x$. This fixed point is stable if and only if

$$K_x = \left| \frac{r_x}{c_x} \right| < \left| \frac{r_y}{c_{yx}} \right|. \quad (23)$$

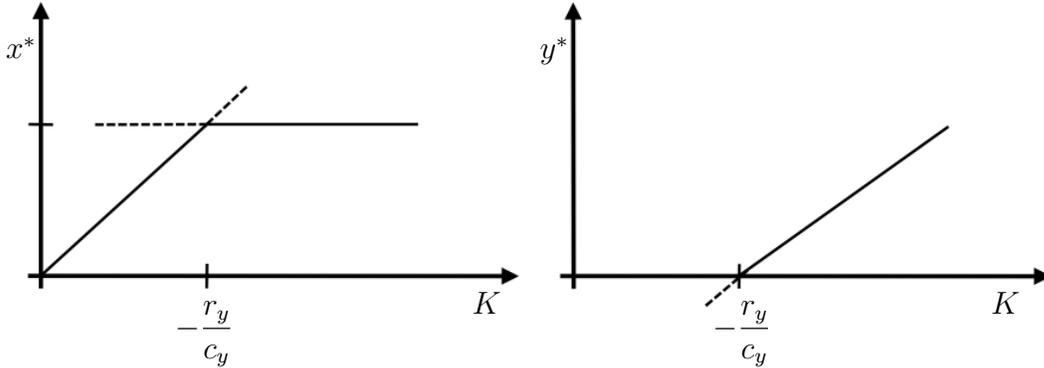


Figure 4: Bifurcation diagram for the prey x^* and predator y^* equilibrium density with bifurcation parameter $K = -r_x/c_x$. Solid lines correspond to asymptotically stable equilibria, hatched lines to unstable equilibria. At $K_x = -r_y/c_y$ a transcritical bifurcation occurs.

This means that the prey carrying capacity is too small to satisfy the needs of the predator, which will then die out. For the fourth equilibrium

$$\mathbf{x}_4^* = \left(-\frac{r_y}{c_{yx}}, -\frac{c_{yx}r_x - c_x r_y}{c_{xy}c_{yx}} \right)$$

we have

$$\mathbf{J}(\mathbf{x}_4^*) = \begin{pmatrix} -c_x r_y / c_{yx} & -c_{xy} r_y / c_{yx} \\ -(c_{yx} r_x - c_x r_y) / c_{xy} & 0 \end{pmatrix}. \quad (24)$$

We have $\text{tr}[\mathbf{J}] = -c_x r_y / c_{yx} < 0$ and

$$\det[\mathbf{J}] = -\frac{r_y(c_{yx}r_x - c_x r_y)}{c_{yx}} > 0 \quad \Leftrightarrow \quad K_x = \left| \frac{r_x}{c_x} \right| > \left| \frac{r_y}{c_{yx}} \right|. \quad (25)$$

Using the Routh-Hurwitz criterion, we see it is stable if and only if the fixed point \mathbf{x}_3^* is unstable. This is the case if and only if there is a positive predator frequency $y_4^* > 0$. The fixed point can be either a node (for $4 \det < \text{tr}^2$) or a spiral. We get spirals for

$$\frac{|c_x|}{c_{yx}} < 2 \left(\sqrt{1 + r_x/|r_y|} - 1 \right), \quad (26)$$

this is, if intraspecific competition for the prey is weak (little self-regulation) relative to the predator's benefit from the prey. In the limit $c_x \rightarrow 0$, we get center-type behavior (Fig. 3b). This is the original model by Volterra. Since it is “on the boundary” between stable and unstable spirals, it is structurally unstable. Note that the prey equilibrium density depends only on growth parameters of the predator. [This holds strictly only for $c_y = 0$.] In particular, only the predator profits from increased growth (large r_x) and carrying capacity (low c_x) of the prey. This served as the explanation of the Adriatic fish-and-shark data after WW1.

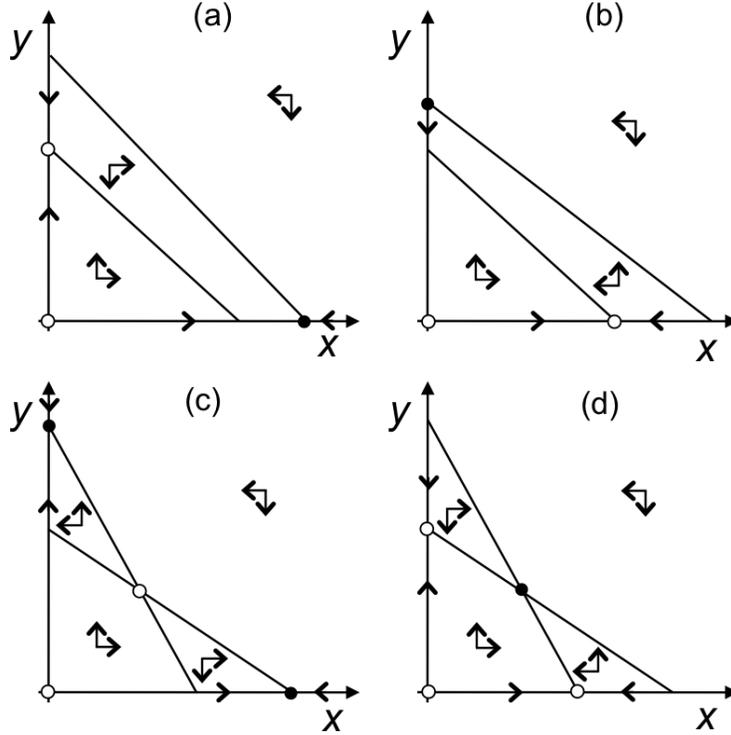


Figure 5: Four possible isocline configurations in the Lotka-Volterra two-species competition model. Open and filled circles indicate unstable and asymptotically stable equilibria, respectively. (a) Species x dominates species y . (b) Species y dominates species x . (c) Each species dominates when frequent. The interior equilibrium is a saddle point. (d) Each species increases in frequency when rare. The interior equilibrium point is asymptotically stable.

Competition With the Lotka-Volterra competition model, we have the parameters $r_x, r_y > 0$, $c_x, c_y < 0$, and $c_{xy}, c_{yx} < 0$. It is easy to determine the whole dynamics purely graphically.

- First, we have simple logistic growth for both species in the absence of the other one. This determines the dynamics on the axes with the carrying capacities $K_x = |r_x/c_x|$ and $K_y = |r_y/c_y|$ as stable equilibria.
- Second, presence of some individuals of the other species contributes to a reduction in the population size that can be maintained. We can conclude that both the x - and y -isoclines have a negative slope. For the Lotka-Volterra model, both isoclines are linear.
- The x -isocline intersects the x axis at K_x . The intersection point $|r_x/c_{xy}|$ with the y axis can either be larger or smaller than K_y . Similarly, the y -isocline extends from K_y to some intersection point $|r_y/c_{yx}|$ with the x axis that may be larger or smaller than

K_x . The direction of the flow in the various domains follows easily from extrapolation of the flow on the axes.

We obtain four different possibilities (see Fig. 5), corresponding to three different patterns:

1. **Dominance** If both isoclines do not cross, one species (with the higher isocline) always dominates the other. (For example: $K_x = |r_x/c_x| > |r_y/c_{yx}|$ and $|r_x/c_{xy}| > |r_y/c_y| = K_y$ for a dominating species x .)
2. **Mutual exclusion** If both isoclines intersect below the carrying capacity of the other species, both species dominate when frequent. Biologically, this is the case if competition against the other species is stronger than competition against conspecifics (weighted by intrinsic growth): $|c_{yx}/r_y| > |c_x/r_x|$ and $|c_{xy}/r_x| > |c_y/r_y|$. As a result, the intersection of both isoclines corresponds to an unstable saddle point.
3. **Coexistence** If both isoclines intersect above the carrying capacity of the other species, both species dominate when rare. We then obtain a stable equilibrium where both species coexist. Biologically, this means that competition among conspecifics is stronger than competition with the other species, $|c_{yx}/r_y| > |c_x/r_x|$ and $|c_{xy}/r_x| > |c_y/r_y|$. This is possible if both species also have their own “private” resource and only compete for some (shared) resources. We then say that each species has its own ecological niche. To this end, both species must not be “too similar” in an ecological sense. This is known as the *principle of limiting similarity* as condition for coexistence.

Mutualism See Exercise 5.

4.5 Global stability

So far, we have analyzed only local stability of equilibria. To complete our understanding of the qualitative behavior of the LV equation we need to know whether an asymptotically stable equilibrium has the whole interior of the state space as basin of attraction, in which case it is *globally stable*, or whether the basin of attraction is a subset of the interior of the state space (local stability). From the graphical analysis of the LV competition and mutualism scenario it appears to be clear that asymptotic stability implies global stability. The same is true for \mathbf{x}_3^* in the predator-prey scenario given that the interior equilibrium does not exist. It remains the case of \mathbf{x}_4^* in the predator-prey scenario. Given our current knowledge, we cannot exclude that in this case there are for example periodic orbits in the interior of the state space. To demonstrate global stability, we need to know the ω -limit for each point in the interior of the state space.

In the following, we will again use the short-hand notation that $\mathbf{x}(t), \mathbf{y}(t)$ etc. are solutions of a system of differential equations $\dot{\mathbf{x}} = f(\mathbf{x})$ with the same f , but with different initial conditions $\mathbf{x} \equiv \mathbf{x}(0)$ and $\mathbf{y} \equiv \mathbf{y}(0)$. In addition to fixed points \mathbf{x}^* with $\dot{\mathbf{x}}^* = 0$, ω -limits can contain periodic points \mathbf{x} such that $\mathbf{x}(T) = \mathbf{x}$ for some $T > 0$, but $\mathbf{x}(t) \neq \mathbf{x}$

for $0 < t < T$. Then all other points on the orbit $\mathbf{x}(t)$ are also periodic points and together they form a periodic orbit γ . A periodic orbit γ is called

- *limit cycle* if $\exists \mathbf{x} \notin \gamma$ s.t. $\omega(\mathbf{x}) = \gamma$ and
- *attractor* if $\omega(\mathbf{x}) = \gamma \forall \mathbf{x}$ in some neighborhood of γ .

It is also possible for ω -limits to contain points that are neither fixed points nor periodic points (e.g., with chaotic behavior).

For the Lotka-Volterra model and most other biological models of interest, we do not know the full solution $\mathbf{x}(t)$ of the nonlinear system of ODEs. Therefore, we cannot simply obtain ω -limits as accumulation points of the solution. Fortunately, there are two results that allow us to determine, or at least narrow down, ω -limits even without knowing the full solution. Importantly, these theorems also apply in cases where the Jacobian matrix has eigenvalues with zero real part such that the Hartmann-Grobmann theorem does not apply.

Theorem: Every ω -limit is invariant: $\mathbf{y} \in \omega(\mathbf{x}) \Rightarrow \mathbf{y}(t) \in \omega(\mathbf{x})$.

Proof Let \mathbf{y} be in $\omega(\mathbf{x})$. Then $\mathbf{x}(t_k) \rightarrow \mathbf{y}$ for some sequence t_k . Since solutions are continuous functions of their initial condition, we have $\mathbf{x}(t_k + t) \rightarrow \mathbf{y}(t)$ for arbitrary t 's and for $k \rightarrow \infty$. Therefore, $\mathbf{y}(t)$ belongs to $\omega(\mathbf{x})$. \square

The second result is based on the concept of *Lyapunov functions*. The idea is as follows. We construct a function V of \mathbf{x} that has a maximum at \mathbf{x}_4^* . Thus, the “peak of a mountain” in the plane spanned by \mathbf{x} is located at \mathbf{x}_4^* . The aim is to construct this function V such that a solution of the dynamical system under consideration can only travel in an uphill direction on this landscape. Alternatively, we can construct V in such a way that we travel always downhill and the focal equilibrium is a minimum.

Theorem: Lyapunov Let $\dot{\mathbf{x}} = f(\mathbf{x})$ be a time-independent ODE defined on some subset G of \mathbb{R}^n . Let $V : G \rightarrow \mathbb{R}$ be continuously differentiable. If the derivative \dot{V} of the map $t \rightarrow V(\mathbf{x}(t))$ satisfies the inequality $\dot{V} \geq 0$ (or $\dot{V} \leq 0$) for all solutions $\mathbf{x}(t)$, then $\omega(\mathbf{x}) \cap G$ is contained in the set $\{\mathbf{x} \in G : \dot{V}(\mathbf{x}) = 0\}$ (and so is $\alpha(\mathbf{x}) \cap G$). In particular, if this set only contains a single point, this point is a globally stable equilibrium.

Proof Let $\mathbf{y} \in \omega(\mathbf{x}) \cap G$. Then there exists a sequence $t_k \rightarrow +\infty$ with $\mathbf{x}(t_k) \rightarrow \mathbf{y}$. Since $\dot{V} \geq 0$ along the orbit of \mathbf{x} , we have $\dot{V}(\mathbf{y}) \geq 0$ by continuity. Also by continuity, $V(\mathbf{x}(t_k))$ converges to $V(\mathbf{y})$, and hence

$$V(\mathbf{x}(t)) \leq V(\mathbf{y}) \tag{27}$$

for every $t \in \mathbb{R}$. To prove the statement by contradiction, assume $\dot{V}(\mathbf{y}) > 0$. Since the value of V can never decrease along the orbit, this implies

$$V(\mathbf{y}(t)) > V(\mathbf{y}) \quad (28)$$

for $t > 0$. From $\mathbf{x}(t_k) \rightarrow \mathbf{y}$ it follows by continuity that $\mathbf{x}(t_k + t) \rightarrow \mathbf{y}(t)$ and hence

$$V(\mathbf{x}(t_k + t)) \rightarrow V(\mathbf{y}(t)). \quad (29)$$

With Eq. (28) it follows that

$$V(\mathbf{x}(t_k + t)) > V(\mathbf{y}) \quad (30)$$

for k sufficiently large. This is in contradiction to Eq. (27). \square

Lyapunov's theorem does not tell us how to find a *Lyapunov function* V and unfortunately no general recipe exists. In mechanical or electrical systems, energy is often a Lyapunov function. We will now attempt to construct a Lyapunov function to determine whether or not the interior equilibrium of the LV model given by Eq. (3) is globally stable. For this, we look for a function V that has a maximum at

$$\mathbf{x}_4^* = (x_4^*, y_4^*) = \left(\frac{c_{xy}r_y - c_yr_x}{c_xc_y - c_{xy}c_{yx}}, \frac{c_{yx}r_x - c_xr_y}{c_xc_y - c_{xy}c_{yx}} \right).$$

We do some reverse engineering. A simple function would have the form

$$V(x, y) = aH(x) + bG(y) \quad (31)$$

for some $a, b > 0$. To get a maximum at \mathbf{x}_4^* , we then need

$$0 = \left. \frac{dV}{dx} \right|_{\mathbf{x}=\mathbf{x}^*} \quad (32)$$

$$0 = \left. \frac{dV}{dy} \right|_{\mathbf{x}=\mathbf{x}^*}, \quad (33)$$

which, in case of Eq. (31), implies

$$0 = \left. \frac{dH}{dx} \right|_{x=x^*} \quad (34)$$

$$0 = \left. \frac{dG}{dy} \right|_{y=y^*}. \quad (35)$$

Simple derivatives fulfilling these requirements are

$$\frac{dH}{dx} = \frac{x^*}{x} - 1 \quad \text{and} \quad \frac{dG}{dy} = \frac{y^*}{y} - 1$$

resulting in

$$H(x) = x^* \ln x - x \quad \text{and} \quad G(y) = y^* \ln y - y,$$

which is defined on \mathbb{R}_+^2 . Checking the second derivatives shows that this choice produces indeed a maximum. Does this V do the job? The derivative of the function $t \rightarrow V(x(t), y(t))$ is

$$\dot{V}(x, y) = \frac{\partial V}{\partial x} \dot{x} + \frac{\partial V}{\partial y} \dot{y} \quad (36)$$

$$= a \left(\frac{x^*}{x} - 1 \right) x (r_x + c_x x + c_{xy} y) + b \left(\frac{y^*}{y} - 1 \right) y (r_y + c_y y + c_{yx} x) \quad (37)$$

Recall that the nontrivial isoclines of Eq. (3) are given by

$$r_x = -c_x x - c_{xy} y \quad (38a)$$

$$r_y = -c_y y - c_{yx} x \quad (38b)$$

and that \mathbf{x}_4^* is the solution of Eq. (38). Thus, we can replace r_x and r_y with $-c_x x^* - c_{xy} y^*$ and $-c_y y^* - c_{yx} x^*$, respectively. This yields

$$\begin{aligned} \dot{V}(x, y) &= a(x^* - x)(-c_x x^* - c_{xy} y^* + c_x x + c_{xy} y) + b(y^* - y)(-c_y y^* - c_{yx} x^* + c_y y + c_{yx} x) \\ &= -ac_x(x - x^*)^2 - bc_y(y - y^*)^2 + (ac_{xy} + bc_{yx})(x - x^*)(y - y^*). \end{aligned} \quad (39)$$

The sign of (39) is not obvious. However, if we choose $a = c_{yx}$ and $b = -c_{xy}$, then the last term in (39) becomes zero and we have

$$\dot{V}(x, y) = -c_x c_{yx} (x - x^*)^2 + c_y c_{xy} (y - y^*)^2 \geq 0. \quad (40)$$

We may therefore apply Lyapunov's theorem. The ω -limit of every orbit in \mathbb{R}_+^2 is contained in the set $K = \{(x, y) : \dot{V}(x, y) = 0\}$. We will now distinguish three different versions of the LV predator-prey model:

1. For $c_y < 0$, K consists only of the point \mathbf{x}_4^* . All trajectories in \mathbb{R}_+^2 converge to \mathbf{x}_4^* . This point is globally stable.
2. For $c_y = 0$ (no self limitation in the predator, the case studied above), $K = \{(x, y) \in \mathbb{R}_+^2 : x = x_4^*\}$. But the ω -limit must be an invariant subset of K , and therefore reduces to \mathbf{x}_4^* . This point is again globally stable.
3. If both $c_y = 0$ and $c_x = 0$ (Lotka's original model in which also the prey is not self-regulated), then $K = \mathbb{R}_+^2$

$$\dot{V} = dV(x(t), y(t))/dt = 0 \quad \text{and} \quad V(x(t), y(t)) = \text{const.}$$

for any point $\mathbf{x} \in \mathbb{R}_+^2$. The function V remains constant along the orbits. In this case, V is called a *constant of motion*. V has a unique maximum at \mathbf{x}_4^* and approaches $-\infty$ along every half-line starting at \mathbf{x}_4^* . The constant level sets $\{(x, y) \in \mathbb{R}_{>0}^2 : V(x, y) = \text{const.}\}$ are closed curves around \mathbf{x}_4^* . Hence, the orbits are periodic and \mathbf{x}_4^* is a center (Fig. 3 b). It is neither locally nor globally stable.

In summary, it is now clear that limit cycles are impossible in the LV competition, mutualism and predator-prey system. This also holds true for versions of the LV model that do not have a biological interpretation:

Theorem The two-dimensional Lotka-Volterra Eq. (3) has either no periodic orbits or a continuum of periodic orbits. [For a proof see Hofbauer & Sigmund, 1998, p. 33].