5 The Dynamics of Two Interacting Populations: Beyond the Lotka-Volterra model

Many insights into the dynamics of interacting species rely on the Lotka-Volterra framework. This raises the question how reliable and general these results can be. Indeed, the model makes several rather restrictive assumptions, such as a linear dependence of per capita birth rates on the densities (e.g. no Allee effect) and no density dependence of the pair interaction parameters (c_x, c_y, c_{xy}, c_{yx} do not depend on x or y). This can have unbiological consequences, e.g. for mutualism, where populations can grow without bounds for some parameter choices. In more general, we should ask for any model whether changes in the modeling assumptions can lead to qualitatively new effects.

5.1 A general two-species competition model

A general model of interacting populations (without immigration) is of the form

$$\dot{x} = x \, F(x, y) \tag{1a}$$
$$\dot{y} = y \, G(x, y), \tag{1b}$$

with continuously differentiable functions $G(x, y)$ and $F(x, y)$. For most natural systems it will be impossible to determine the exact functional form of F and G. It is therefore desirable to obtain results without specifying F and G but only constraining them by certain boundary conditions. Here, we follow this approach for the case of competition between two populations. We make the following assumptions:

1. Competing populations affect each others growth rates negatively. Therefore,

$$\frac{\partial F(x, y)}{\partial y} < 0 \qquad \text{and} \qquad \frac{\partial G(x, y)}{\partial x} < 0. \tag{2}$$

2. Competition occurs due to shared resources (e.g., food, nesting sites). Here, we assume that the two competing types both require the same essential resource. Thus, if one competitor is very common both species have a negative growth rate: there exists a $K > 0$ so that $F(x, y) < 0$ and $G(x, y) < 0$ if $x > K$ or $y > K$.

In the following we derive the qualitative dynamics of a competition model based on assumptions (1) and (2). The following statements can be made about the isoclines.

- The non-trivial x-isocline is given by

$$\bar{F} = \{(x, y) \in \mathbb{R}^2_{>0} : F(x, y) = 0\}. \tag{3}$$

Above $\bar{F}$ we have $\dot{x} < 0$ and below $\bar{F}$ we have $\dot{x} > 0$. Indeed, for x fixed, $F(x, y)$ decreases as a function of y (cf. Eq. 2). Therefore, a vertical line through a point (x, y) intersects with $\bar{F}$ at most once.
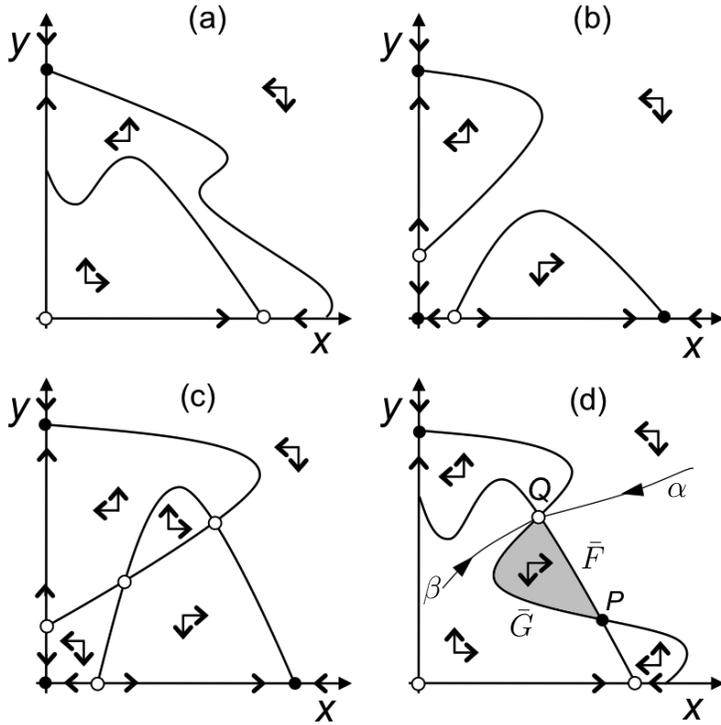
Figure 1: Four examples for possible isocline configurations in the general two-species competition model. Open and filled circles indicate unstable and asymptotically stable equilibria, respectively. (a&b) Isoclines do not intersect. (b&c) Both species show an Allee effect. (d) Example with a stable interior equilibrium point P. The gray area B is positively invariant: all orbits that cross its ordinary boundary points go into B. The isocline for the x-species is labelled $\bar{F}$. It passes through the equilibria that lie on the x-axis. The isocline for the y-species is labelled $\bar{G}$. It passes through the equilibria that lie on the y-axis.

- The non-trivial y-isocline is given by

$$\bar{G} = \{(x,y) \in \mathbb{R}^2_{>0} : G(x,y) = 0\}. \tag{4}$$

  To the right of $\bar{G}$ we have $\dot{y} < 0$ and to the left of $\bar{F}$ we have $\dot{y} > 0$. For y fixed, $G(x,y)$ decreases as a function of x (cf. Eq. 2). Therefore, a horizontal line through a point (x,y) intersects with $\bar{G}$ at most once.

Both $\bar{F}$ and $\bar{G}$ are continuous. Due to our second assumption above, they both lie within the square

$$\{(x,y) : 0 \le x \le K, 0 \le y \le K\}.$$

Every orbit in $\mathbb{R}^2_{>0}$ flows into this square.

- The situation is simple if $\bar{F}$ and $\bar{G}$ do not intersect. Then either one or both species go extinct (Fig. 1a,b).

2

- Next, consider the case that $\bar{F}$ and $\bar{G}$ intersect finitely many times (this is the *generic* case). The points of intersection are equilibria of Eq. (1). The isoclines $\bar{F}$ and $\bar{G}$ divide $\mathbb{R}^2_{>0}$ into regions B in which the signs of $\dot{x}$ and $\dot{y}$ do not change. The boundary of these regions consists of equilibrium points, of segments of the coordinate axes, and of points that belong to $\bar{F}$ or $\bar{G}$, but not to both. Let us call the latter *ordinary boundary points*.

Lemma For each region B, either all orbits passing through its ordinary boundary points enter B, or all orbits passing through its ordinary boundary points leave B.

Proof Four cases have to be distinguished: (i) $\dot{x} > 0$, $\dot{y} > 0$; (ii) $\dot{x} > 0$, $\dot{y} < 0$; (iii) $\dot{x} < 0$, $\dot{y} > 0$; (iv) $\dot{x} < 0$, $\dot{y} < 0$. Consider (ii), a region B with $\dot{x} > 0$ and $\dot{y} < 0$ (gray region in Fig. 1d) . This means that B lies below $\bar{F}$ (this is where we have $\dot{x} > 0$) and to the right of $\bar{G}$ (this is where we have $\dot{y} < 0$). Next we consider an ordinary boundary point P. If $P \in \bar{F}$, then P is to the right of $\bar{G}$: the orbit through P goes vertically downwards into B. If $P \in \bar{G}$, then P is below $\bar{F}$: the orbit through P goes horizontally to the right into B. In this case, all orbits passing ordinary boundary points P of B go into B. The argument is analogous for the other three cases. We find that regions of type (ii) and (iii) can never be left again: they are *positive invariant*. Conversely, regions of type (i) and (iv) can never be entered from outside (*negative invariant*). $\qquad\square$

For the asymptotic behavior, we can conclude the following:

- Because the signs of $\dot{x}$ and $\dot{y}$ are constant in the interior of a region B, the ω-limit of any orbit $\boldsymbol{x}(t)$ can never be contained in the interior of a single region. In the positive invariant regions all orbits converge toward an equilibrium. In regions of type (i) and (iv), orbits either also converge to an equilibrium or they enter a positive invariant region through an ordinary boundary point. In conclusion, in the general competition model the dynamics always converges towards an equilibrium.

- Which equilibria are asymptotically stable? It is easy to see that equilibria at which both $\bar{F}$ and $\bar{G}$ have a negative slope with $\bar{F}$ steeper than $\bar{G}$ are asymptotically stable (Fig. 1d). An investigation of all other cases in which $\bar{F}$ and $\bar{G}$ can intersect each other shows that the only other asymptotically stable fixed point is $(K_x, 0)$ when K_x is to the right of $\bar{G}$ and $(0, K_y)$ when K_y is above $\bar{F}$.

- How do ω-limits depend on initial conditions? In Fig. 1(d) point Q is a saddle point. Then exactly two trajectories, α and β, exist that approach Q. These are known as *stable manifolds* of Q or *separatrices* of Q. The separatrix α divides the unbounded region into a part with points $\boldsymbol{x}$ with $\omega(\boldsymbol{x}) = (0, K_y)$ and a part with points $\boldsymbol{x}$ with $\omega(\boldsymbol{x}) = P$. Thus, two points $\boldsymbol{x}$ and $\boldsymbol{x}'$ that are very close to each other but separated by α have different ω-lime sets.

3

Summarizing, we see that the qualitative dynamics of the Lotka-Volterra competition model matches the general competition model in that there are no limit cycles or chaotic orbits. However, in the general case multiple stable equilibria in the interior and on the boundary can exist. Biologically, whether species can coexist or one species goes extinct can depend on the starting conditions.

5.2   Equilibria in 2-dimensional ODEs

In the last section, we have determined which kind of equilibrium behavior can result from a general competition model. Before we try to obtain similar results for other biological scenarios, we should first get a better idea about which types of equilibria are possible at all for a 2-dimensional dynamical system. We thus assume a general ODE

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$$

on an open subset $M \subset \mathbb{R}^2$ and $f \in C^1(M, \mathbb{R}^2)$. Which kind of ω-limits can we get for such a system? In one dimension, all ω-limits are fixed points. In two dimensions, the following theorem shows that the situation is still relatively simple.

Poincaré-Bendixson Theorem   Let $\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$ be a time-independent 2-dimensional ODE as defined above with at most finitely many fixed points. Let $\boldsymbol{x} \in M$ and $\omega(\boldsymbol{x})$ be a non-empty, connected, and compact ω-limit set. Then one of the following applies:

1. $\omega(\boldsymbol{x})$ is a fixed point.

2. $\omega(\boldsymbol{x})$ is a periodic (or closed) orbit.

3. $\omega(\boldsymbol{x})$ consist of finitely many fixed points and orbits connecting these fixed points (with these fixed points as ω- and α-limits).

We note the following

- One can easily show that for any orbit that is bounded forward in time the corresponding ω-limit is non-empty, connected, and compact. Since this should be the case for any realistic population dynamical model, the Poincaré-Bendixson Theorem will apply. For orbits that are bounded backward in time, the analogous result holds for the α-limit.

- A direct consequence of the theorem is that chaotic attractors cannot occur in two dimensions.

- The theorem can be used to demonstrate the existence of periodic orbits: if we can identify a compact *trapping region*, which can only be entered, but never left by any orbit, and if this region does not contain a fixed point, then it must contain at least one periodic orbit.

- Since a periodic orbit and its interior is a compact region that cannot be entered or left (forward and backward invariant), a fixed point must exist in the interior of each closed orbit. (Intuitively: An orbit starting from an internal point must have an ω-limit or α-limit in the interior of the region. This limit is either a fixed point or a closed orbit. If it is a closed orbit, iterate the argument.) This implies that periodic orbits can only occur around fixed points. A compact trapping region to demonstrate the existence of a periodic orbit must therefore always contain a hole (with the fixed point in it).

- One can further show that in 2d dynamical systems all isolated closed orbits are indeed limit cycles. Vice versa, closed orbits that are not isolated (center-type behavior like in the Lotka-Volterra predator-prey model) are not limit cycles.

- For two dynamical variables x_1 and x_2 with derivatives $\dot{x}_1$ and $\dot{x}_2$ given as polynomials of x_1 and x_2 with finite degree n, the question how many (isolated) limit cycles can exist is known as *Hilbert's 16th problem* and no answer is known for $n > 1$ (where no limit cycle can exist). For $n = 2$, systems with up to four limit cycles are known. For general n, it is at least known that the maximal number is always finite.

- A formal proof of the Pointcaré-Bendixson Theorem can be found, for example, in the book by Gerald Teschl *Ordinary Differential Equations and Dynamical Systems*, available form his webpage. The proof relies on the Jordan Curve Theorem, which states that any closed curve divides the plane into two disjoint sets: the interior and the exterior. Any two points in the interior can be connected by a path which never intersects the curve, but every path between interior and exterior has to cross the curve. This seems a trivial observation which, however, is very difficult to prove.

- The theorem uses that solutions of ODEs in the plain are subject to strong geometric constraints. Since the orbits can never cross (uniqueness of the solution) they can easily be trapped in the interior of some region where they can no longer escape. Since this constraint does not exist in higher dimensions, the equilibrium structure of dynamical systems in 3 or more dimensions can be much more complex (including chaotic behavior).

The first step in the analysis of a dynamical system is usually to characterize the fixed points and their stability. In simple cases, we can still do this analytically. For a full characterization of the stationary behavior, we need to account for limit cycles, which is generally a more difficult task. To exclude cycling, we can try to find a Lyapunov function, as explained above. An alternative criterion is provided by the following theorem.

Bendixson-Dulac Theorem   Let $\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$ be an ODE defined on a simply connected set (i.e., a set without holes) $G \subset \mathbb{R}^2$. Let B be a positive scalar function defined on G. If the divergence of the vector field $B\boldsymbol{f}$,

$$\operatorname{div}[B\boldsymbol{f}](\boldsymbol{x}) = \frac{\partial B f_1}{\partial x_1}(\boldsymbol{x}) + \frac{\partial B f_2}{\partial x_2}(\boldsymbol{x}) \tag{5}$$

has the same sign (strictly positive or strictly negative) on G *almost everywhere*, then $\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$ admits not periodic orbits in G.

- A function B with the above property is known as *Dulac function*. For $B = 1$, expression (5) equals the divergence of $\boldsymbol{f}$ and is given by the trace of the Jacobian matrix. Indeed, $\operatorname{div} \boldsymbol{f}(\boldsymbol{x}) \neq 0$ means that the flow defined by the ODE is *area expanding* or *contracting*, i.e., averaging over the boundary, leaves or enters every compact and simply connected set. This is not possible with a closed orbit, which defines a region that can neither be entered nor left by the flow.

- The proof of the theorem follows from *Green's theorem*, see *Hofbauer & Sigmund* for details. Note that a positive Dulac function $B(\boldsymbol{x})$ can always be chosen since the transformed ODE

$$\dot{\boldsymbol{x}} = B(\boldsymbol{x})\boldsymbol{f}(\boldsymbol{x})$$

  has the same orbits as the original ODE, with a change in the velocity defined by B. In particular, the stationary behavior of both ODE systems is the same.

5.3 General predator-prey models and Hopf-bifurcations

In this section, we revisit predator-prey models. In the Lotka-Volterra predator-prey model isolated (and stable) limit cycles do not exist. However, predator-prey cycles seem to be common in nature. Famous examples: lynx and snowshoe hare in Canada, many populations of voles and their predators. Is the Lotka-Volterra predator-prey model missing something?

A (somewhat) general predator prey model: the Gause model

Georgy Gause was a Russian biologist who experimentally tested the Lotka-Volterra predator-prey model with protists and yeast. After he was not able to reproduce the predictions of Lotka and Volterra, he proposed modifications to original Lotka-Volterra model. (This is an interaction between theory and empiricism at its best!) As in the case of competition, it is desirable to study a predator-prey model in which not all functional forms are specified. For the Gause model, we study

$$\dot{x} = xg(x) - yf(x) \tag{6a}$$
$$\dot{y} = y\big(c(x) - d\big), \tag{6b}$$

where

1. $g(x)$ is the growth rate of the prey population in the absence of predation. Self-regulation in the prey implies that there exists a $K_x > 0$ so that $g(x) > 0$ for $x < K_x$, $g(K_x) = 0$, and $g(x) < 0$ for $x > K_x$.

2. $f(x)$ is the functional response of the predator, describing the effect of predation on the prey. We require that $f(0) = 0$ and $f(x) > 0$ for $x > 0$.
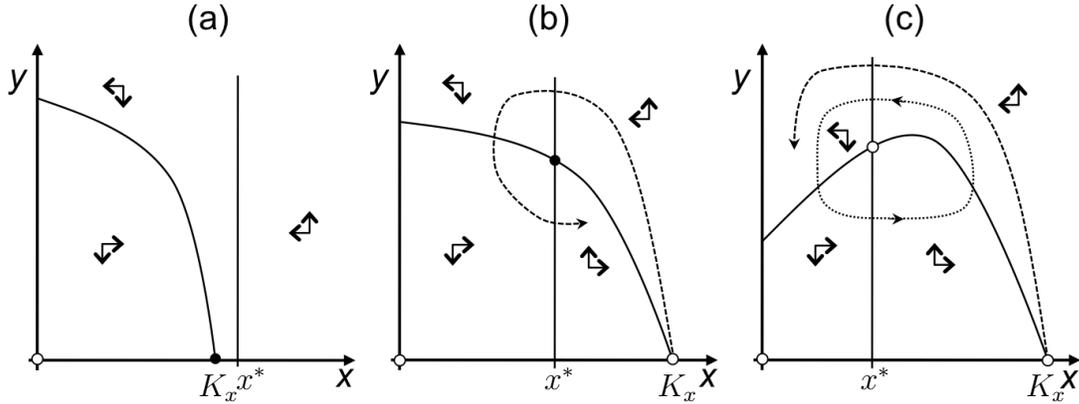
Figure 2: The three generic isocline configurations in the Gause predator-prey model. Open and filled circles indicate unstable and asymptotically stable equilibria, respectively. (a) Isoclines do not intersect. (b) Prey isocline has a negative slope at the interior equilibrium. The equilibrium is then asymptotically stable. (c) Prey isocline has a positive slope at the interior equilibrium. The equilibrium is then unstable. For the special case of the Rosenzweig-MacArthur model we prove that it is then surrounded by a stable limit cycle (dotted line). The hatched line in (b) and (c) represents the unstable manifold of the saddle point $(K_x, 0)$.

3. $c(x)$ describes consumption of prey and conversion into predator individuals. $c(x)$ may be independent of $f(x)$. We require that $c(0) = 0$ and $dc(x)/dx > 0$ for $x > 0$.

4. d is the constant consumer mortality rate. There is thus no self-regulation in the predator. Indeed, the basic assumption of the Gause model is that the predator density remains low, such that its effect on the dynamics is only linear.

We can determine the isoclines for this model.

- Assume x^* exists with $c(x^*) = d$. This simply means that predators can eat enough to exist. The predator-isocline equals to the vertical line $x = x^*$ and the line $y = 0$ (absence of predators).

- The non-trivial part of the prey isocline $\{(x, y) \in \mathbb{R}^2_{>0} : \dot{x} = 0\}$ is determined by the equation

$$y_{\text{iso}} = \frac{xg(x)}{f(x)}.$$

We have $y_{\text{iso}} \geq 0$ (in the biological parameter range) for $x \in]0, K_x]$. This function intersects the predator-isocline at $(K_x, 0)$ (the prey equilibrium in the absence of predators). Furthermore, it may have at most one intersection with the line $x = x^*$.

Two scenarios are relevant:

1. $x^* > K_x$: Isoclines do not intersect (Fig. 2). Then the predator goes extinct.

2. $x^* < K_x$: Isoclines have a unique point of intersection $(x^*, y^*) \in \mathbb{R}^2_{\geq 0}$ (Fig. 2b&c). We focus on this case in the following.

The Jacobian matrix at (x^*, y^*) equals

$$
\mathsf{J} = \begin{pmatrix} H(x^*) & -f(x^*) \\ y^* \dfrac{\mathrm{d}c(x^*)}{\mathrm{d}x} & 0 \end{pmatrix}
$$

where

$$
H(x) = g(x) + x\frac{\mathrm{d}g(x)}{\mathrm{d}x} - \frac{xg(x)}{f(x)}\frac{\mathrm{d}f(x)}{\mathrm{d}x}. \tag{7}
$$

We apply the Routh-Hurwitz criterion (Eq. **??**). We have $\det \mathsf{J} > 0$ and $\text{trace} = H(x^*)$. The point (x^*, y^*) is asymptotically stable if and only if $H(x^*) < 0$. Note that

$$
\frac{\mathrm{d}}{\mathrm{d}x}\frac{xg(x)}{f(x)} = \frac{H(x)}{f(x)}. \tag{8}
$$

Thus, $H(x^*) < 0$ if and only if

$$
\left.\frac{\mathrm{d}}{\mathrm{d}x}\frac{xg(x)}{f(x)}\right|_{x=x^*} < 0. \tag{9}
$$

- In conclusion, the interior equilibrium is a sink when the prey-isocline has a negative slope at the equilibrium and a source when the prey-isocline has a positive slope (Fig. 2b&c).

- We see from the graph (and can easily derive) that the two other equilibria, $(0,0)$ and $(K_x, 0)$, are both are saddle points. Their stable manifolds are given by the x and y axes.

- What can we conclude for the global behavior? Consider, in particular, a point on the unstable manifold that departs from $(K_x, 0)$ (i.e., a point for which $(K_x, 0)$ is the α-limit). The orbit starting from such a point is bounded. Indeed, for a point on the manifold near $(K_x, 0)$, the prey density x is initially declining and must reach x^* at some finite value $\tilde{y} \geq y^*$. At this point, the predator density cannot increase any further and the orbit enters a region that is bounded by the axes, the unstable manifold from $(K_x, 0)$ to $(x^*, \tilde{y})$ and the line $y = \tilde{y}$, that cannot be left anymore. From the Pointcaré-Bendixson theorem, we conclude that there are two possibilities:

  1. If $\omega(\boldsymbol{x})$ contains an equilibrium point it must be (x^*, y^*) (the other two equilibrium points are out of question). In fact, then (x^*, y^*) is even globally stable because all orbits have to circle around (x^*, y^*), but cannot intersect the unstable manifold of $(K_x, 0)$ (Fig. 2b).

  2. If $\omega(\boldsymbol{x})$ contains no equilibrium point, then $\omega(\boldsymbol{x})$ is a periodic orbit γ. This orbit surrounds (x^*, y^*) and is a limit cycle: since other orbit cannot cross the unstable manifold, every point in the exterior converges to γ (Fig. 2c).

8

- One might think that the first scenario applies when (x^*, y^*) is a sink and that the second scenario applies when (x^*, y^*) is a source. However, this need not to be the case. For example, the limit cycle can be an attractor from the outside but not from the inside (*half-stable*) or more than one limit cycle can exist. For the general model the analysis cannot be completed. Below, we therefore specify the functions $g(\boldsymbol{x})$, $f(\boldsymbol{x})$, and $c(\boldsymbol{x})$.

The Rosenzweig-MacArthur model

The easiest choice for competition among prey is the logistic model with linear density dependence in $g(x)$. A natural choice for the interaction between predator and prey is type two functional response, which, in contrast to the Lotka-Volterra model (with type one functional response), assumes a saturation effect for large prey densities x. We then arrive at the following model first studied by Rosenzweig and MacArthur.

$$\dot{x} = f_1(x, y) = x r_x \left(1 - \frac{x}{K_x}\right) - \frac{xy c_{xy}}{a + x} \tag{10a}$$

$$\dot{y} = f_2(x, y) = \frac{xy c_{yx}}{a + x} - dy, \tag{10b}$$

where all parameters are positive.

- From the general model we know that the non-trivial prey isocline is determined by the equation $y_{\text{iso}} = r_x(1 - x/K_x)(a + x)/c_{xy}$.

- The non-trivial predator isocline is given by the vertical line $x^* = ad/(c_{yx} - d)$.

If $K_x \leq ad/(c_{yx} - d)$, the predator goes extinct and $(K_x, 0)$ is globally stable. From now on we focus on the case where an internal equilibrium (x^*, y^*) exists. From Eq. (9) already know that it is a sink if $K_x < a + 2x^*$ and a source if $K_x > a + 2x^*$. A more detailed answer concerning global stability is provided by the following proposition, which makes use of the Bendixson-Dulac theorem.

Proposition   The internal fixed point (x^*, y^*) of Eq. (10) is globally stable if and only if $K \leq a + 2x^*$.

Proof   We consider the Dulac function

$$B(x, y) = \frac{a + x}{x} y^{\gamma - 1}$$

with γ chosen appropriately. We derive

$$\text{div}[B\boldsymbol{f}] = \frac{\partial B f_1}{\partial x} + \frac{\partial B f_2}{\partial y} = \frac{y^{\gamma - 1}}{x} \left(r_x x \left(1 - \frac{a + 2x}{K_x}\right) - \gamma(c_{yx} - d)(x^* - x) \right). \tag{11}$$

We argue as follows:

- The term $r_x x(1 - (a + 2x)/K_x$ defines a parabola in x that opens downwards and intersects the x-axis at $x = 0$ and $x = (K_x - a)/2$. The term $\gamma(c_{yx} - d)(x^* - x)$ describes a line with slope $-\gamma(c_{yx} - d)$ that intersects the x-axis at $x = x^*$.

- If $K_x < a + 2x^*$ then $x^* > (K_x - a)/2$ and the line intersects the x-axis outside the parabola. It is therefore possible to choose an γ so that the parabola lies below the line (Fig. 3).

- Hence, the parabola and the line never cross and $\text{div}[B\boldsymbol{f}]$ always has the same sign (< 0). Due to the Bendixson-Dulac theorem, this excludes cycles and with Pointcaré-Bendixson we conclude that the internal fixed point must be globally attracting in the interior of the parameter range.

- For $K_x = a + 2x^*$, we still find an γ for which the line is tangent to the parabola and thus $\text{div}[B\boldsymbol{f}] < 0$ almost everywhere, but for the point $x = x^*$ where it equals zero. Hence, periodic orbits can still be excluded and the interior fixed point is the global attractor.

- If, $K_x > a + 2x^*$ then we have seen that the internal fixed point is unstable. With the Poincaré-Bendixson theorem and our results for the general Gause model it is clear that in this case a limit cycle around (x^*, y^*) must exist. $\qquad\square$
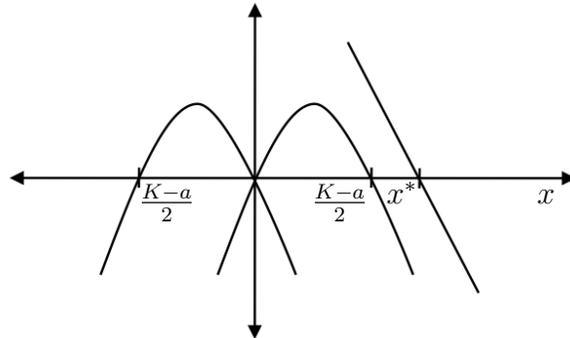

Figure 3: Sketch illustrating the proof that an γ can be chosen so that Expression (11) is negative. The parabola is given by $r_x x(1 - (a + 2x)/K_x)$ and the straight line by $\gamma(c_{yx} - d)(x^* - x)$ for an appropriately chosen value of γ. The right parabola applies for $K > a$ and the left one for $K < a$.

Let us summarize the stationary behavior. The Jacobian matrix J has a pair of complex conjugate eigenvalues $\lambda_{1,2} = \alpha \pm \beta i$ with $\alpha, \beta \in \mathbb{R}$.

- For $K_x < a + 2x^*$ we have $\alpha < 0$. (x^*, y^*) is a sink and is globally stable (Fig. 2b).

- For $K_x = a + 2x^*$ we have $\alpha = 0$. The linearized dynamics has a center at (x^*, y^*). For the nonlinear dynamics, the point (x^*, y^*) is asymptotically stable.

10

- For $K_x > a + 2x^*$ we have $\alpha > 0$. (x^*, y^*) is a source that is surrounded by a limit cycle (Fig. 2c). [In fact, one can prove that in this model only a single limit cycle can exist but such a proof is beyond the scope of this lecture.]
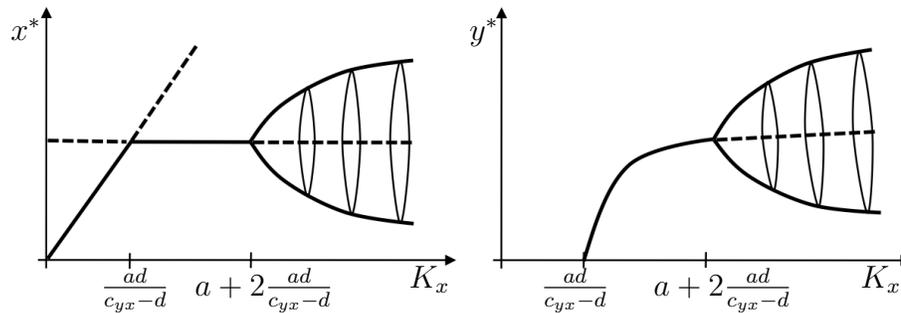

Figure 4: Bifurcation diagram for the prey (x^*) and predator (y^*) equilibrium density with bifurcation parameter K_x. Solid lines correspond to asymptotically stable equilibria, hatched lines to unstable equilibria. At $K_x = ad/(c_{yx} - d)$ a transcritical bifurcation occurs and at $K_x = a - 2ad/(c_{yx} - d)$ as supercritical Hopf bifurcation occurs.

Some remarks on the equilibrium behavior of the Rosenzweig-MacArthur model:

1. It is clear that at $K_x = a + 2x^*$ a bifurcation point of the dynamics has to exist. This type of bifurcation is known as *Hopf bifurcation* and is shown in Fig. 4.

2. Increasing the prey carrying capacity beyond the point $ad/(c_{yx} - d)$ (the minimal density for predators to exist) benefits only the predator, but not the prey. This "extreme" result is due to the vertical predator isocline at $x = x^*$. However, very steep isoclines readily occur in natural systems if the predator is primarily limited by the availability of prey rather than by direct negative density dependence.

3. Increasing the prey carrying capacity even further (beyond the critical point of the Hopf bifurcation) increases the chance for the prey to go extinct due to stochasticity (paradox of enrichment).

4. Form an empirical point of view, it is still still not clear whether these models capture the essence of predator-prey cycles in nature. In particular, it is an active research area to determine whether predator-prey cycles are endogenously driven, i.e., by the interactions of predators and their prey, or by exogenous factors.

Hopf bifurcations

The bifurcation that we have seen in the Rosenzweig-MacArthur model is an example of a general type of bifurcations, where stable or unstable fixed points can split a fixed point plus a (stable or unstable) limit cycle. For ODE systems in arbitrary (finite) dimensions, they are characterized by the following theorem.

Hopf's theorem   Let G be an open subset of $\mathbb{R}^n$ and

$$\dot{\boldsymbol{x}} = \boldsymbol{f}_\mu(\boldsymbol{x})$$

a family of n-dimensional ODEs on G depending on some parameter $\mu \in (-\epsilon, \epsilon)$ and $\boldsymbol{f}_\mu$ analytic (i.e. given by a power series). Let P_μ be an equilibrium point at which all eigenvalues of the Jacobian matrix J have negative real parts but for one pair of complex conjugate eigenvalues

$$\lambda_1 = \alpha(\mu) + \beta(\mu)i$$
$$\lambda_2 = \alpha(\mu) - \beta(\mu)i$$

with $\alpha(\mu), \beta(\mu) \in \mathbb{R}$ and $\text{sign}[\alpha] = \text{sign}[\mu]$ and $\beta(0) \neq 0$. Thus, P_μ is a sink for $\mu < 0$ (and hence asymptotically stable) and a source for $\mu > 0$ (and hence unstable). We also require that $\partial\alpha/\partial\mu > 0$, i.e. the eigenvalues cross the imaginary axis with non-zero speed. We then have:

supercritical Hopf bifurcation If P_0 is asymptotically stable, then, for sufficiently small positive values of μ, the unstable equilibrium point P_μ is surrounded by a periodic attractor (Fig. 5a).

subcritical Hopf bifurcation If P_0 is unstable, then, for sufficiently small negative values of μ, the asymptotically stable equilibrium point P_μ is surrounded by a periodic repellor (Fig. 5b).
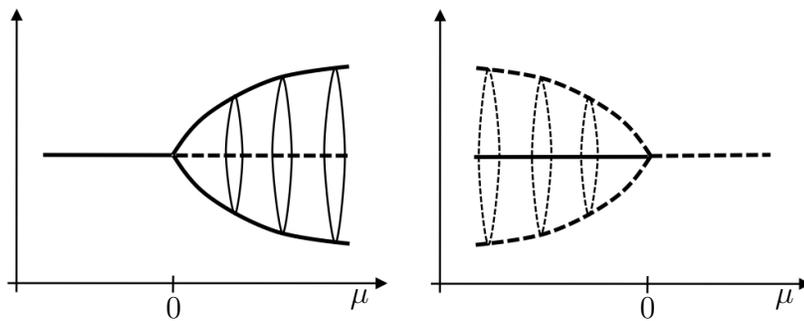

Figure 5: (a) supercritical Hopf bifurcation, (b) subcritical Hopf bifurcation. Solid lines correspond to asymptotically stable equilibria, hatched lines to unstable equilibria.

- At a supercritical Hopf bifurcation, a stable fixed point becomes locally unstable but the flow sufficiently far away does not feel this local change and is still contracting. As a result, a periodic orbit becomes the new attractor. (Analogous for subcritical.)

12

- The direction of the "far flow" is indicated by the stability or instability of the equilibrium point P_0 for $\mu = 0$. With vanishing real parts of $\lambda_{1,2}$, this equilibrium is non-hyperbolic (neither a sink, a source, nor a saddle). Its stability therefore cannot be deduced from linearization but depends on higher-order terms. These terms are weaker than the linear ones in the direct vicinity of the fixed point, but stronger at some distance. A small perturbation by moving μ away from zero will introduce small, but non-zero linear terms, which dominate in a neighborhood, but not at some greater distance.

- In practice, the dependence on higher order terms makes it difficult to determine the stability of P_0. Often only a Lyapunov function or a Dulac function can provide definite answers.

- The diameter of the limit cycle generated at the bifurcation points increases continuously from zero and grows initially proportional to the square root of the bifurcation parameter, $\sqrt{\mu}$.