

## 6 Dynamics of more than two populations

In dynamical systems of dimension three or higher the Jordan curve theorem does not apply and  $\omega$ -limit sets of ODEs need not to be equilibrium points or periodic orbits anymore. Instead, also *strange attractors* can exist and the dynamics can show *chaos*.

### 6.1 The General Lotka-Volterra Equations

The general Lotka-Volterra equation for  $n$  populations reads

$$\dot{x}_i = x_i \left( r_i + \sum_{j=1}^n a_{ij} x_j \right), \quad (1)$$

where  $x_i$  and  $r_i$  denote the density and the intrinsic growth rate of the  $i$ th species, respectively. The  $a_{ij}$  describe the effect of the  $j$ th species on the growth rate of the  $i$ th species. In matrix notation this becomes

$$\dot{\mathbf{x}} = \mathbf{r} \circ \mathbf{x} + \mathbf{x} \cdot \mathbf{A} \mathbf{x}, \quad (2)$$

where  $\circ$  denotes the element-wise multiplication of two vectors (Hadamard product). The matrix  $\mathbf{A}$  is known as *interaction matrix*. While the two-dimensional Lotka-Volterra equations are completely classified, this has not been achieved for the general system due to the potential for more complicated attractors. Indeed, chaotic motion is possible already in the system with three species. Nevertheless, we can state some general results and also obtain explicit solutions for some special cases of biological interest.

#### Equilibria

Note first that all faces of the state space  $x_i = 0$ , which correspond to states where species  $i$  is absent, are invariant under the flow (no individual can immigrate). Consequently, also the flow in the interior of the state space (i.e., for  $x_i > 0, \forall i$ ) is invariant. The density  $x_i(t)$  may approach zero, however, which means extinction. Internal fixed points are solutions of the linear equation system

$$y_i = r_i + \sum_{j=1}^n a_{ij} x_j = 0 \quad i = 1, \dots, n \quad (3)$$

with all components  $x_j = x_j^* > 0$ . Since the restriction of the dynamics to a boundary face  $x_i = 0$  again leads to a Lotka-Volterra system (with one fewer dimension), fixed points on the boundaries can be found in an analogous way.

- In general (i.e., if the linear system is not degenerate), there will be at most a single internal fixed point for the Lotka-Volterra system. In the degenerate case, there is a continuum of fixed points.

- A useful theorem states that if there is no internal fixed point, then there is no  $\alpha$ - or  $\omega$ -limit in the interior of the state space at all. I.e., all orbits either flow to the boundary (extinction of one species) or to infinity. For a proof, note that the convex set  $\mathbf{K}$  defined by the linear system (3) with  $x_j > 0$  is disjoint from  $\mathbf{0}$  if there is no internal fixed point. We then can define a hyperplane  $\mathbf{H}$  through  $\mathbf{0}$  that is disjoint from  $\mathbf{K}$  and a vector  $\mathbf{c} = (c_1, \dots, c_n) \neq \mathbf{0}$  that is orthogonal to  $\mathbf{H}$  such that  $\mathbf{c} \cdot \mathbf{y} > 0$  for all  $\mathbf{y} \in \mathbf{K}$ . Then

$$V(\mathbf{x}) = \sum_i c_i \log x_i$$

is a Lyapunov function (indeed,  $\dot{V} = \sum_i c_i \dot{x}_i/x_i = \sum_i c_i y_i > 0$ ). Since  $V(\mathbf{x})$  has no internal maximum this proves the theorem.

- If there is a unique internal fixed point  $\mathbf{x}^*$ , one can further prove that all orbits that neither converge to the boundary nor to infinity must have  $\mathbf{x}^*$  as their long time average (see Hofbauer & Sigmund, chapter 5 for a proof). Hence, if closed or chaotic attractors exist for an  $n$ -dimensional Lotka-Volterra model, they must always surround a fixed point.

## 6.2 Lotka-Volterra Models for Food Chains

A simplified picture of an ecosystem is that of a *food chain*. Basal species in such a chain are *primary producers*, e.g., plants and algae, that convert solar energy and  $CO_2$  into biomass. Primary producers are eaten by *grazers*. Grazers are eaten by predators which themselves are eaten by larger predators. At top of the chain sits the top-predator. Most ecosystems are more complicated and form food-webs rather than food chains. Nevertheless, food chains are a good starting point to investigate multi-species interactions. The Lotka-Volterra version of a food chain of length  $n$  with self-regulation looks as follows:

$$\dot{x}_1 = x_1(r_1 - a_{11}x_1 - a_{12}x_2) \tag{4a}$$

$$\dot{x}_i = x_i(-r_i + a_{i,i-1}x_{i-1} - a_{ii}x_i - a_{i,i+1}x_{i+1}) \text{ for } i \in \{2, \dots, n-1\} \tag{4b}$$

$$\dot{x}_n = x_n(-r_n + a_{n,n-1}x_{n-1} - a_{nn}x_n), \tag{4c}$$

with  $r_i, a_{ij} > 0$ . For this system we recover the dynamics of the two-dimensional Lotka-Volterra predator-prey model.

**Theorem** If Eq. (4) has an internal equilibrium point  $\mathbf{x}^* > 0$ , then all orbits in  $\mathbb{R}_{>0}^n$  converge to  $\mathbf{x}^*$ . Thus,  $\mathbf{x}^*$  is globally stable and (with the results above) periodic or chaotic attractors cannot exist.

**Proof** We will show that the following function is a Lyapunov function:

$$V(\mathbf{x}) = \sum_{i=1}^n c_i (x_i^* \log x_i - x_i) \tag{5}$$

with  $c_i > 0$  to be specified later. Note first that  $V(\mathbf{x})$  has a unique maximum at  $\mathbf{x} = \mathbf{x}^*$ . Then derive

$$\dot{V}(\mathbf{x}(t)) = \sum_{i=1}^n c_i \frac{\dot{x}_i}{x_i} (x_i^* - x_i). \quad (6)$$

Replacing  $\dot{x}_i$  with corresponding equation from Eq. (4) and using that

$$\begin{aligned} r_1 &= a_{11}x_1^* + a_{12}x_2^* \\ r_i &= a_{i,i-1}x_{i-1}^* - a_{ii}x_i^* - a_{i,i+1}x_{i+1}^* \quad \text{for } i \in \{2, \dots, n-1\} \\ r_n &= a_{n,n-1}x_{n-1}^* - a_{nn}x_n^*, \end{aligned}$$

we get

$$\begin{aligned} \frac{\dot{x}_1}{x_1} &= a_{11}(x_1 - x_1^*) + a_{12}(x_2 - x_2^*) \\ \frac{\dot{x}_i}{x_i} &= a_{i,i-1}(x_{i-1} - x_{i-1}^*) - a_{ii}(x_i - x_i^*) - a_{i,i+1}(x_{i+1} - x_{i+1}^*) \\ \frac{\dot{x}_n}{x_n} &= a_{n,n-1}(x_{n-1} - x_{n-1}^*) - a_{nn}(x_n - x_n^*). \end{aligned}$$

Eq. (6) then becomes

$$\dot{V}(\mathbf{x}(t)) = \sum_{i=1}^n c_i a_{ii} (x_i - x_i^*)^2 - \sum_{i=1}^{n-1} (x_i - x_i^*)(x_{i+1} - x_{i+1}^*)(c_{i+1} a_{i+1,i} - c_i a_{i,i+1}).$$

If we choose  $c_i > 0$  such that  $c_{i+1}/c_i = a_{i,i+1}/a_{i+1,i}$ , then this equation simplifies to

$$\dot{V}(\mathbf{x}(t)) = \sum_{i=1}^n c_i a_{ii} (x_i - x_i^*)^2 \geq 0. \quad (7)$$

With the Lyapunov theorem follows that for all points  $\mathbf{x} \in \mathbb{R}_{>0}^n$  we have  $\omega(\mathbf{x}) = \mathbf{x}^*$ . Note that for the proof it is sufficient if only one species has intraspecific density regulation, i.e.,  $a_{ii} \geq 0 \forall i$  and  $a_{ii} > 0$  for at least one species.  $\square$

### Three-level food chain

Let us have a look at a specific example. A minimal food chain consists of three trophic levels: a primary producer  $x_1$  (plants), a herbivore  $x_2$  and a carnivore  $x_3$ . Here, each level of the food chain need not to consist of only a single species. Instead, each level can represent the whole *functional group*. For simplicity, we assume that intraspecific density regulation on the level of the consumers can be ignored,  $a_{22} = a_{33} = 0$  and obtain

$$\dot{x}_1 = x_1(r_1 - a_{11}x_1 - a_{12}x_2) \quad (8a)$$

$$\dot{x}_2 = x_2(-r_2 + a_{21}x_1 - a_{23}x_3) \quad (8b)$$

$$\dot{x}_3 = x_3(-r_3 + a_{32}x_2). \quad (8c)$$

**Equilibria and stability** The trivial equilibrium at  $\mathbf{0}$  is unstable for any  $r_1 > 0$ . A non-zero single-species equilibrium only exists for the producer, at  $\mathbf{x}^{*1} = (r_1/a_{11}, 0, 0)$ . It is stable for  $r_1/a_{11} < r_2/a_{21}$ , which is the producer minimal density at which a herbivore can persist. In the absence of the carnivore, this result follows from the 2-species LV model (see Eq. ??). The coordinates of the equilibrium with plants and herbivores coexisting can also be taken from there (??),

$$\mathbf{x}^{*2} = \left( \frac{r_2}{a_{21}}, \frac{a_{21}r_1 - a_{11}r_2}{a_{12}a_{21}}, 0 \right).$$

Obviously, there cannot be any other 2-species equilibria.  $\mathbf{x}^{*2}$  is stable until the herbivore density reaches the minimal level for carnivores to invade, at  $x_2 = r_3/a_{32}$ . Finally, the equilibrium  $\mathbf{x}^{*3}$  with all three trophic levels present equals

$$x_1^{*3} = \frac{r_1 a_{32} - r_3 a_{12}}{a_{11} a_{32}} \tag{9a}$$

$$x_2^{*3} = \frac{r_3}{a_{32}} \tag{9b}$$

$$x_3^{*3} = \frac{r_1 a_{21} a_{32} - r_2 a_{11} a_{32} - r_3 a_{12} a_{21}}{a_{11} a_{23} a_{32}}. \tag{9c}$$

Figure 1 shows the bifurcation diagram for the equilibrium densities as a function of system productivity as given by  $r_1$ . A long standing question in population ecology is whether population densities are regulated *top down* or *bottom up*. Based on this simple model the following conclusions can be drawn.

1. System productivity controls total biomass and the number of trophic levels.
2. In a tritrophic food chain, herbivore density is controlled top down. Plants and carnivores benefit from increased system productivity.
3. Increased death rate in the carnivore increases herbivore abundance and thereby suppresses plant abundance (trophic cascade).
4. Adding more trophic levels has the following effect: systems with an odd number of trophic levels release plant growth while systems with an even number of trophic levels control plant growth.

Empirical support for this model comes mainly from aquatic system.

- At the east coast of North America different kelp species, invertebrate grazers such as sea urchins, and sea-otters form a tritrophic food chain. Data from Alaska show that as sea otters became rare, sea urchins became more common and many kelp forests disappeared (and with them a very rich ecosystem of organisms living in the kelp forests). Sea otters apparently became rarer when orca whales increased their hunting pressure on them, possibly due to decreased fish stocks.

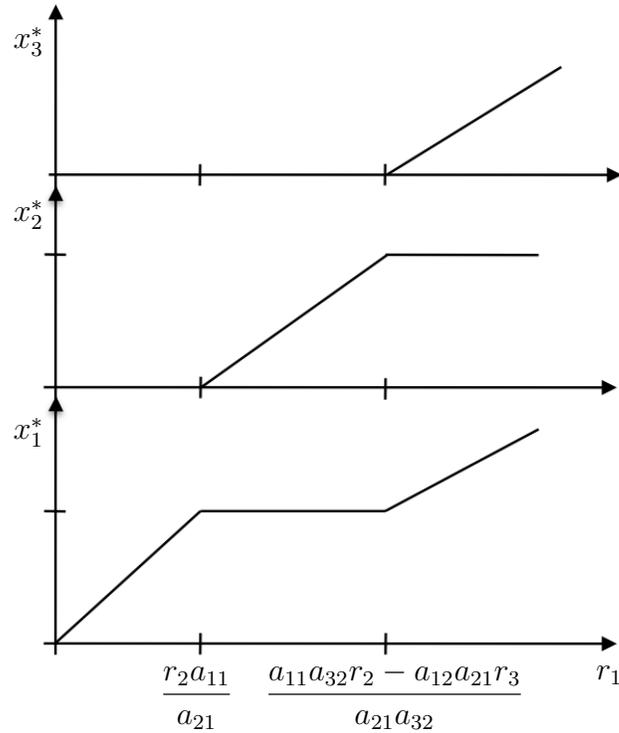


Figure 1: Bifurcation diagram for the equilibrium densities of Eq. (8) with bifurcation parameter  $r_1$ .

- The food web in many fresh water lakes essentially consists of phytoplankton as primary producers, zooplankton, planktivorous fish, and possibly piscivorous fish. Whole-lake manipulation experiments show that lakes that lack piscivorous fish tend to be “green” (trrophic food chain resulting in abundant phytoplankton), whereas “blue” lakes result where piscivorous fish are added as fourth trophic level. This mechanism forms the basis for many lake restoration projects.

### 6.3 Coexistence and Competitive Exclusion

In many natural systems a set of consumer species shares the same resources. Look at the different species of birds at your feeder. But how many consumer species can coexist on a given set of resources? In the Lotka-Volterra competition model we did not model the cause of competition explicitly but only indirectly via the interaction terms  $a_{ij}$ . Two causes of competition can be distinguished. First, competition can be due to direct interactions such as fighting. This is know as *interference competition*. Second, competition can be due to the depletion of shared resources or *exploitation competition*. In the latter case one might want to model the dynamics of the resources explicitly. A minimum model consist of three species: one resource (or prey) and two competing consumers (or predators) and

can be modeled as follows,

$$\dot{x} = r_x x - a_{xx} x^2 - a_{xy_1} x y_1 - a_{xy_2} x y_2 \quad (10a)$$

$$\dot{y}_1 = -r_{y_1} y_1 + a_{y_1 x} x y_1 \quad (10b)$$

$$\dot{y}_2 = -r_{y_2} y_2 + a_{y_2 x} x y_2, \quad (10c)$$

where all parameters are positive. There is no direct interaction among the two types of predators and no direct intraspecific competition in the predators, either. For only a single predator, the system reduces to the Lotka-Volterra predator-prey model that we have discussed above (with intraspecific exploitation competition among predators). For the two predator species to coexist at equilibrium we require

$$\begin{aligned} \dot{y}_1 = 0 &\iff r_{y_1} = a_{y_1 x} x^* \\ \dot{y}_2 = 0 &\iff r_{y_2} = a_{y_2 x} x^*. \end{aligned}$$

This is a system of two linear equations in one unknown and thus overdetermined. In our case, coexistence is only possible if  $r_{y_1}/r_{y_2} = a_{y_1 x}/a_{y_2 x}$ . Thus, coexistence is not robust with respect to perturbations in the parameter values: two consumer species cannot robustly coexist on one resource. This results can be stated much more generally, also beyond the Lotka-Volterra framework.

**Theorem: Competitive Exclusion** In a system of exploitation competition with  $n$  consumer species and  $m < n$  resources, robust coexistence at an equilibrium point is not possible.

**Proof** Let the dynamics of  $m$  resource and  $n$  consumer species be given by

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}, \mathbf{y})$$

and

$$\dot{\mathbf{y}} = \mathbf{y} \circ \mathbf{g}(\mathbf{x}),$$

respectively, where  $\circ$  denotes the Hadamard product. At a point equilibrium  $\mathbf{y}^* \in \mathbb{R}_{>0}^n$  it is required that

$$\mathbf{0} = \mathbf{g}(\mathbf{x}^*).$$

This is a system of  $n$  equations in  $m$  unknowns. It can only have a robust solution when  $m \leq n$ .  $\square$

- Note that the theorem only excludes fixed points. For a general model, there could be closed orbits – we have previously seen that predator-prey systems have a tendency to cycle – or chaotic attractors. Orbits could also diverge to infinity, although this should not occur for a realistic population dynamical model.

- For Lotka-Volterra systems, absence of an internal fixed point implies that other bounded  $\omega$ -limits are also impossible (see our general results above). If the dynamics is bounded, we thus can conclude that all orbits converge to the boundary and at least one species will go extinct.
- A crucial assumption of the theorem is that there is no direct intraspecific competition for the consumer species. It is quite obvious that sufficiently strong intraspecific competition will enable coexistence on even just a single (abundant) resource. However, intraspecific competition usually indicates that there is some other limiting resource (space, nesting places, some other prey species), even if this resource is not explicitly included in the dynamics.
- The exclusion principle is an influential concept in ecology: coexistence requires exclusive resources, which can not (or less easily) be exploited by competing species. However, it is not necessarily easy to apply it in practice. What should be counted as different resource types? E.g., if birds feed on the seeds of a certain plant species this may be counted as a single resource or as infinitely many different resources if the size distribution of the seeds is continuous.

## Cyclic competition

Consider the Lotka-Volterra competition model with two species, following

$$\dot{x}_1 = x_1(1 - x_1 - \alpha x_2) \tag{11}$$

$$\dot{x}_2 = x_2(1 - \beta x_1 - x_2), \tag{12}$$

with  $\alpha, \beta > 0$ . For simplicity, we have set  $r_1 = r_2 = a_{11} = a_{22} = 1$ . The single species thus have carrying capacities  $K_1 = K_2 = 1$ . For  $\alpha, \beta < 1$  both species can coexist, but for  $\alpha, \beta > 1$  they are mutually exclusive, and for  $\alpha < 1$  and  $\beta > 1$  ( $\alpha > 1, \beta < 1$ ) species 1 (species 2) dominates and drives the other one to extinction. Consider a case of dominance, e.g., species 2 dominating over species 1. One can ask whether it is possible to introduce a third competing species such that the system of all three species allows for stable coexistence. Intuitively, if such a species 3 exists, it should “beat” (dominate) species 2, but should be dominated by species 1. An easy symmetric example is provided by the system

$$\dot{x}_1 = x_1(1 - x_1 - \alpha x_2 - \beta x_3) \tag{13}$$

$$\dot{x}_2 = x_2(1 - \beta x_1 - x_2 - \alpha x_3) \tag{14}$$

$$\dot{x}_3 = x_3(1 - \alpha x_1 - \beta x_2 - x_3) \tag{15}$$

with  $0 < \beta < 1 < \alpha$ . Clearly, we find circular dominance on the boundary of the state space: in the  $x_1 - x_2$  plane  $x_2$  dominates and  $\mathbf{e}_2 = (0, 1, 0)$  is globally attracting. Similarly,  $\mathbf{e}_3 = (0, 0, 1)$  and  $\mathbf{e}_1 = (1, 0, 0)$  are the global attractor on the  $x_2 - x_3$  plane and the  $x_3 - x_1$  plane, respectively. In the full three species system, however, the unit vectors  $\mathbf{e}_i, i = 1, 2, 3$

are no longer stable, but are saddle points. The only other fixed point on the boundary is the trivial one  $(0, 0, 0)$ , which is always a source. Finally, there is a unique internal fixed point at

$$\mathbf{m} = \frac{1}{1 + \alpha + \beta} (1, 1, 1). \quad (16)$$

The Jacobian at  $\mathbf{m}$  reads

$$\frac{1}{1 + \alpha + \beta} \begin{pmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{pmatrix}.$$

This is a so-called *circulant* matrix with equal entries in each row (and column), with a circular shift by one from one row to the next. The eigenvalues and eigenvectors of circulants are easy to derive.

**Lemma** The eigenvalues  $\lambda_k$  and eigenvectors  $\mathbf{v}_k$ ,  $k = 0, \dots, n - 1$  of an  $n$ -dimensional circulant matrix

$$\mathbf{J} = \begin{pmatrix} c_0 & c_1 & \dots & c_{n-1} \\ c_{n-1} & c_0 & \dots & c_{n-2} \\ \vdots & & & \vdots \\ c_1 & c_2 & \dots & c_0 \end{pmatrix}$$

are given by

$$\lambda_k = \sum_{j=0}^{n-1} c_j \mu^{j \cdot k}, \quad \mathbf{v}_k = (1, \mu^k, \mu^{2k}, \dots, \mu^{(n-1)k}) \quad (17)$$

where

$$\mu = \exp\left(\frac{2\pi i}{n}\right)$$

is the  $n$ th root of unity. (The proof follows immediately by inserting  $\lambda_k$  and  $\mathbf{v}_k$  into the eigenvalue equation.)

We thus obtain for the Jacobian  $\mathbf{J}$ ,

$$\lambda_0 = -1 \quad , \quad \mathbf{v}_1 = (1, 1, 1), \quad (18)$$

$$\lambda_1 = \bar{\lambda}_2 = \frac{1}{1 + \alpha + \beta} \left( -1 - \alpha \exp[2\pi i/3] - \beta \exp[4\pi i/3] \right). \quad (19)$$

We observe the following

- Since

$$\operatorname{Re}[\lambda_1] = \operatorname{Re}[\lambda_2] = \frac{1}{1 + \alpha + \beta} \left( -1 + \frac{\alpha + \beta}{2} \right)$$

$\mathbf{m}$  is a sink (stable) if  $\alpha + \beta < 2$  and that  $\mathbf{m}$  is a saddle (unstable) if  $\alpha + \beta > 2$ .

- The diagonal  $x_1 = x_2 = x_3$  is invariant under the ODE flow. If  $\mathbf{m}$  is a saddle, it is the stable manifold of the equilibrium.
- All orbits in the interior of a boundary plane have one of the edges  $\mathbf{e}_i$  as  $\omega$ -limit. Each of these points has an unstable manifold on the “next” boundary (e.g.,  $\mathbf{e}_2$  is the  $\omega$ -limit for all orbits in the interior of the  $x_1/x_2$  plane, but has an unstable manifold on the  $x_2/x_3$  plane). The three unstable manifolds connect the three edges. Together with these they form a closed so-called *heteroclinic cycle*.

To analyze the dynamics in the interior of the state space, we consider two functions

$$S = x_1 + x_2 + x_3 \quad ; \quad P = x_1 \cdot x_2 \cdot x_3 . \quad (20)$$

Since we have

$$\dot{S} = x_1 + x_2 + x_3 - (x_1^2 + x_2^2 + x_3^2 + (\alpha + \beta)(x_1 x_2 + x_2 x_3 + x_3 x_1)) \leq \begin{cases} S(1 - S) & \alpha + \beta > 2 \\ S(1 - \frac{\alpha + \beta}{2} S) & \alpha + \beta \leq 2 \end{cases}$$

the  $\omega$ -limits of all orbits are confined to a bounded region  $S \leq \max[1, 2/(\alpha + \beta)]$  and no population can explode. We further derive

$$\dot{P} = \dot{x}_1 x_2 x_3 + x_1 \dot{x}_2 x_3 + x_1 x_2 \dot{x}_3 = P(3 - (1 + \alpha + \beta)S) .$$

We will now show that  $P/S^3$  is a Lyapunov function in the interior of the state space. Indeed, we have

$$\frac{d}{dx_i} \frac{P}{S^3} = \frac{P(S - 3x_i)}{x_i S^4} = 0 \quad \text{for} \quad x_1 = x_2 = x_3 ,$$

where it assumes a maximum. We also have  $P/S^3 \geq 0$  and  $P/S^3 = 0$  (minimum) at the boundary where  $P = 0$ . For the time derivative, we derive

$$\frac{d}{dt} \frac{P}{S^3} = \frac{P}{S^4} \left(1 - \frac{\alpha + \beta}{2}\right) \left( (x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2 \right)$$

and conclude the following

- For  $\alpha + \beta < 2$ , the Lyapunov function is monotonically increasing and we converges to the diagonal  $x_1 = x_2 = x_3$ . We have already seen that on this diagonal convergence to  $\mathbf{m}$  follows, which is thus the global attractor for every orbit in the interior.
- For  $\alpha + \beta > 2$ , the Lyapunov function is monotonically decreasing. Every orbit not on the diagonal  $x_1 = x_2 = x_3$  thus converges to the boundary. at the boundary it must follow the heteroclinic cycle, which is the (almost) globally attracting  $\omega$ -limit in this case.
- Our symmetric example of cyclic competition does not have a real biological motivation. It mainly demonstrates what kind of phenomena can occur in higher dimensional systems. Indeed in Lotka-Volterra models with two consumers and two resources heteroclinic cycles appear quite naturally (see Hofbauer & Sigmund, chapter 16).

- Heteroclinic cycles can also occur in two-dimensional dynamical systems (but not in 2d Lotka-Volterra systems or other typical population dynamical models). This is why we needed to account for a third category for  $\omega$ -limits in the Pointcaré-Bendixson Theorem. See the book by Teschl (chapter 7) for an example.

## Coexistence concepts

At this point we should make precise what we mean by *coexistence*. In systems with (potentially) closed orbits, heteroclinic cycles, or chaotic motion this can be a subtle issue. We can rarely expect to obtain a full description of all  $\omega$ -limits together with their attraction domains. For many purposes, however, the precise asymptotics is less important than the question of *extinction*, i.e., whether all species in the system will survive in the long term or not. We are particularly interested in global concepts, in the sense that survival does not depend on initial conditions (given that all species are initially present). Various mathematical concepts exist, with different biological implications. Consider a dynamical system

$$\dot{x}_i = x_i f_i(\mathbf{x}) \quad i = 1, \dots, n$$

that is defined on  $\mathbb{R}_{\geq 0}^n$ .

### Definition

1. The system is *persistent* if for every orbit with starting value  $\mathbf{x}(0)$  in the interior of the state space

$$\limsup_{t \rightarrow \infty} \mathbf{x}_i(t) > 0 \quad \forall i. \quad (21)$$

2. We say that a system is *invasible* if every attracting  $\omega$ -limit on the boundary of the reduced system (with one or several species removed) can be invaded by a missing species when added in very low density. Formally, we require that averaged per capita growth rate for some missing species  $i$  is positive,

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T f_i(\mathbf{x}(t)) dt > 0.$$

(For chaotic attractors we need to specify whether we require this for every orbit or almost every orbit  $\mathbf{x}(t)$ .)

3. The dynamical system is said to be *permanent* if there exists  $\delta, D > 0$  such that  $x_i(0) > 0$  for  $i \in \{1, \dots, n\}$  implies

$$\liminf_{t \rightarrow +\infty} x_i(t) > \delta \quad \text{for } i \in \{1, \dots, n\}. \quad (22)$$

and

$$\limsup_{t \rightarrow +\infty} x_i(t) \leq D \quad \text{for } i \in \{1, \dots, n\}. \quad (23)$$

Note that  $\delta$  and  $D$  do not depend on the initial condition  $x_i(0)$ . Condition (23) (uniform boundedness) holds whenever populations cannot grow to infinity, thus, for any well-formulated population dynamical model.

- It is clear that permanence implies persistence, but the opposite is not true, even if we consider only uniformly bounded systems. A system with  $\dot{x}_i = 0$  for  $x_i < D$  is persistent, but not invisable or permanent. The same holds for the degenerate Lotka-Volterra predator-prey model with center-type behavior. A system with an attracting heteroclinic cycle like in the 3-species Lotka-Volterra system discussed above is both persistent and invisable, but not permanent.
- For purposes of biological application, *persistence* is usually too weak. There is no force inherent to the system that would protect a species from going extinct. Coexistence is thus not stable. This is different for permanent systems, where the boundary is a repeller. Indeed, a system is permanent if a compact set  $K$  in the interior of the state space exists such that all orbits in the interior end up in  $K$ .
- *Invasibility* guarantees that species can grow from low densities. The concept thus implies better stability than persistence. However, it can still be “tricked” by heteroclinic cycles, where invasion of one species means that another one will eventually die out.
- An advantage of invasibility over permanence as defined her is that it is robust with respect to small perturbations of the system. Indeed, a system can be permanent, but not invisable, if orbits close to the boundary are repelled with zero speed. However, we can extend the definition of permanence to require robustness. A more relevant advantage of invasibility is that the conditions are often easier to check.

### Dynamic coexistence of two predators on a single resource

As an example, let us study the potential for coexistence of two predator species  $y_1$  and  $y_2$  on one resource species  $x$  in the following system:

$$\dot{x} = xr \left(1 - \frac{x}{K}\right) - \frac{y_1 x e_1}{a + x} - y_2 x e_2 \quad (24a)$$

$$\dot{y}_1 = y_1 f_1(x) = y_1 \left( \frac{x c_1}{a + x} - d_1 \right) \quad (24b)$$

$$\dot{y}_2 = y_2 f_2(x) = y_2 (x c_2 - d_2) \quad (24c)$$

We have previously studied the two-species systems (24a) & (24b) and (24a) & (24c) in isolation. For the first system (Rosenzweig-MacArthur, RMA), we have seen that the equilibrium point is either globally stable or, when it is unstable, prey and predator coexist on a limit cycle. For the second system (Lotka-Volterra, LV), the internal equilibrium point is globally stable whenever it exists. We denote the internal equilibrium points of RMA system (24a & 24b) and the LV system (24a & 24c) by  $(x^*, y_1^*)$  and  $(x^{**}, y_2^{**})$ , respectively.

To study coexistence in the three-species system, we first focus on invasibility. It is easy to see that no predator can survive in the presence of the other one if it cannot even survive without its competitor. We then need to distinguish two cases.

1. Assume first that both the RMA and the LV two-species systems have a stable equilibrium point. It is easy to see that the system is not mutually invisable in this case. Indeed, the second predator can invade the stable equilibrium  $(x^*, y_1^*)$  of the RMA system if and only if

$$x^* c_2 - d_2 > 0. \quad (25)$$

Since  $x^{**} c_2 - d_2 = 0$ , this is possible if and only if  $x^* > x^{**}$ , in other words, if predator 2 can survive on fewer resources than predator 1. Vice versa, the first predator can invade the equilibrium  $(x^{**}, y_2^{**})$  of the LV system if and only if

$$\frac{x^{**} c_1}{a + x^{**}} - d_1 > 0. \quad (26)$$

Since  $x^* c_1 / (a + x^*) - d_1 = 0$  and the per-capita growth rate  $f_1(x)$  is strictly monotonic in  $x$ , this is possible if and only if  $x^{**} > x^*$ . These two conditions cannot be satisfied simultaneously: there is no mutual invasibility. Since we have no interior fixed points in the  $(y_1, y_2)$ -plane (we have two equations in one unknown) coexistence is indeed impossible and invasion implies fixation.

2. Since the per-capita growth rates  $f_i(x)$  of both predators are monotonic, there are unique minimal prey densities  $f_1(x^*) = 0$  and  $f_2(x^{**}) = 0$  at which the  $i$ th predator can maintain itself in a constant environment (with constant  $x$ ). Let us now drop the assumption of a stable fixed point in the two-species systems. In particular, we allow that the predator and prey density,  $y_i(t)$  and  $x(t)$ , vary in time but return to their initial value after some time  $\tau$ . The mean prey density over one cycle of period  $\tau$  is given by

$$\bar{x} := \frac{1}{\tau} \int_0^\tau x(t) dt. \quad (27)$$

The mean per-capita predator growth rate over one cycle is

$$\overline{f_i(x)} := \frac{1}{\tau} \int_0^\tau f_i(x(t)) dt. \quad (28)$$

After one period the population size is unchanged:  $y_i(t) = y_i(t + \tau)$ . Therefore,

$$\int_0^\tau f_i(x(t)) dt = \int_0^\tau \frac{1}{y_i} \frac{dy_i}{dt} dt = \ln y_i(\tau) - \ln y_i(0) = 0 \quad (29)$$

and thus

$$\overline{f_i(x)} = 0 \quad (30)$$

has to hold.

A species with a linear functional response (LV system) requires the same average resource density to maintain itself in an environment with cycling  $x$  as it does in a constant environment,  $\bar{x} = x^{**}$ . Indeed, for  $f_2(x) = c_2x - d_2$  we have

$$f_2(\bar{x}) = \frac{c_2}{\tau} \int_0^\tau x(t)dt - d_2 = \frac{1}{\tau} \int_0^\tau (c_2x(t) - d_2)dt = \frac{1}{\tau} \int_0^\tau f_2(x(t))dt = \overline{f_2(x)} = 0, \quad (31)$$

where the last equality follows from Eq. (30). It follows that  $\bar{x} = x^{**}$ .

Next, consider a species with a saturating functional response (RMA system),  $f_1 = xc_1/(a+x) - d_1$ . In this case, the average resource density required for maintenance in a time-varying environment is higher than in a constant environment. This makes intuitive sense: the predator profits only little from times with abundant prey, but suffers a lot from times with rare prey. To verify this, denote with  $l(x)$  the tangent line to  $f_1(x)$  at  $x^*$  (see Fig. 2). Then  $l(x^*) = f_1(x^*) = 0$ , but  $l(x) > f_1(x)$  for  $x \neq x^*$  and therefore  $l(\bar{x}) = \overline{l(x)} > \overline{f_1(x)} = 0$ . Thus,  $l(\bar{x}) > l(x^*)$ , which implies  $\bar{x} > x^*$ .

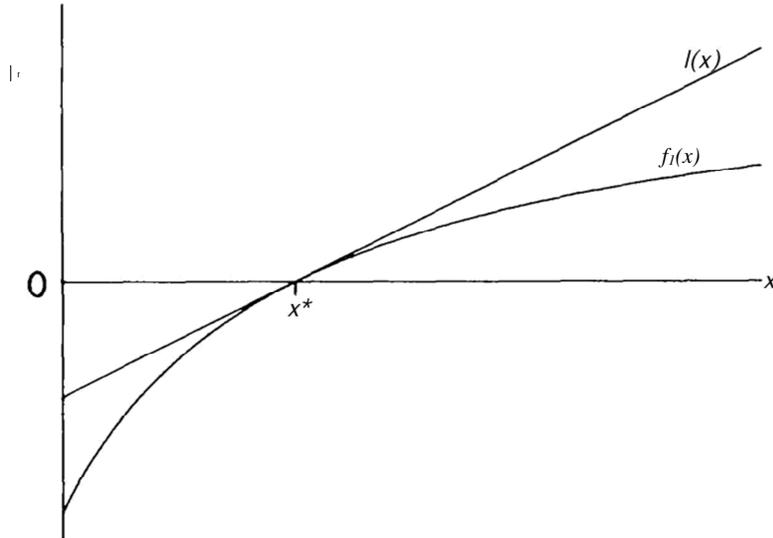


Figure 2: Graphs of the functions  $f_1(x)$  and  $l(x)$ .  $l(x)$  is the tangent line to  $f_1(x)$  at  $x^*$ . (From Armstrong and McGehee 1980.)

Consider now mutual invasibility for parameter values with unstable fixed point  $(x^*, y_1^*)$  for the RMA system, where predator and the prey coexist along a periodic orbit  $\gamma$  with period  $\tau$ . Predator 2 can invade the periodic attractor of predator 1 and the resource if and only if its average per capita growth rate over one cycle (while rare) is positive:

$$\frac{1}{\tau} \int_0^\tau f_2(x(t))dt = \frac{1}{\tau} \int_0^\tau (c_2x(t) - d_2)dt = c_2\bar{x} - d_2 > 0. \quad (32)$$

Hence, invasion is possible if and only if  $\bar{x} > x^{**}$ . We can conclude that the condition for mutual invadability equals

$$x^* < x^{**} < \bar{x}, \quad (33)$$

which can be satisfied for appropriately chosen parameter values. One can show that the three-species community is stable and cycles along a periodic orbit (McGehee & Armstrong, 1977, *J.Diff.Eq.* 23:30-52; Armstrong & McGehee, 1980, *AmNat* 115:151-170).

- Why is coexistence in this model possible, seemingly violating the principal of competitive exclusion? Figure 3(a) shows the per capita growth rates for the two predators for the different prey densities that occur during one cycle. We can see that predator 1 is superior at low resource densities while predator 2 is superior at high resource densities. Thus, which predator is superior regularly changes along the periodic orbit, preventing that one predator excludes the other (Figure 3b).
- One can argue that different densities of the same resource species have to be interpreted as different resources. In this sense, the present model contains infinitely many resources. Accordingly, in principle any number of consumer species can coexist on a single cycling resource. The principle of competitive exclusion can be generalized in a way that it still holds. Of course, more consumers can only coexist if the parameters of their functional response are suitably fine-tuned, making their coexistence less robust to perturbations.
- For stable coexistence in the sense of mutual invasibility we need  $x^* < x^{**}$ . Note that the unstable fixed point  $(x^*, y_1^*)$  of the RMA 2-species system can not be invaded by the second predator under this condition. Indeed,  $(x^*, y_1^*)$  is a saddle with stable manifold pointing into the interior of the state space. As a consequence, there is a single orbit (along the stable manifold) that converges to the boundary and the system is neither permanent nor persistent!

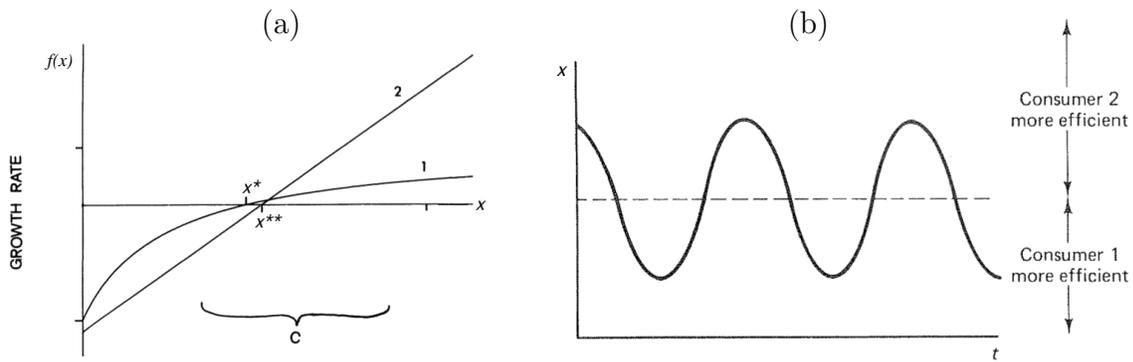


Figure 3: (a) Growth rates of predators of Eq. (24) as a function of prey density  $x$ . The region  $C$  represents the approximate range of variation over  $x$  over one cycle in the three species system (from Armstrong and McGehee 1980). (b) Predator 1 has a higher per capita growth rate at low resource densities whereas Predator 2 has a higher per capita growth rate at high resource densities (from Yodzis 1989).