

Dynamic systems

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Introduction

A dynamic system is a system, biological, physical or more abstract, which changes over time. Examples from ecology are typically a set of interacting populations, which change in abundance over time. Dynamic systems can be described in many different ways, depending on the current application. For instance, in ecology we are often interested in properties like population variance or extinction risk. Also, one might want to be able to predict the future of a system given certain changes in the environment, for example. In any case, it takes knowledge about the particular system, for example the interactions, *and* knowledge about how dynamic systems behave in general. Here, we will deal with the second piece of knowledge.

General features of dynamic systems

State variables and system dimension

A dynamical system is most often described by its *state variables*. The state variables are chosen such that they give enough information about the system to be interesting, but not too much information to make things more complicated than necessary. In the population example, maybe total population size is sufficient to capture the features of a population we are currently interested in. In other situations, one might want to include the age of the individuals in the population description, which leads to an age structured model. In yet other situations, maybe the spatial context is important, and we want to keep track of every single individual as it moves through space and interacts with other individuals of the same or other species.

To conclude, the number of state variables used to describe a particular system depends on the context. The *dimension* of a system is simply defined as the number of state variables. Consequently, a particular real system does not have a fixed dimensionality, but the number of dimensions depends on how we choose to describe the system, and the description in turn depends on the problem or question we want an answer to.

Continuous time systems

Differential equations

A fundamental concept in the theory of dynamic systems is the *differential equation*. A differential equation is a (set of) equation(s) which describes the change per time unit (the *rate of change*) of the state variables of the system. Normally, the rate of change is a function of the state variables themselves, such as:

$$\frac{dx(t)}{dt} = 4x(t) - e^{-x(t-3)} + u(t)$$

Note that the rate of change of the single state variable x is a function of the current state, $x(t)$, but also the state three time units ago, $x(t-3)$, and an external variable $u(t)$. External here means that u is not considered part of the system – there is no feedback from x to u , only a direct influence from u on x . As an ecological example, x could be a population size and u could be an environmental factor, such as temperature.

Given the differential equation and an *initial condition* (plus the possible external input), it is possible to predict the future states of the system. In other words, if we know where the system is right now, we can use the differential equation, which gives the change per time unit, to determine where the system will go. Note that in the example above, one would need not only $x(t)$, but also all the states between $t-3$ and t .

One variable in continuous time

We shall start with one-dimensional systems, i.e. systems where there is only one state variable.

Exponential growth

One of the simplest examples of differential equations is that of exponential growth:

$$\frac{dn(t)}{dt} = rn(t) \quad (\text{A.1})$$

In equation (A.1), $n(t)$ is interpreted as the size of a population, measured as the number of individuals. An alternative way of describing the size of a population is in terms of population *density*, i.e. the number of individuals per unit area or (less common) volume. Here, we shall make little distinction between the two measures, although it may be important in some contexts. The parameter r in (A.1) is the *intrinsic growth rate* of the population. We will discuss it more below.

The growth of the population in (A.1) is solely determined by the size of the population. The bigger the population, the faster the growth (if $r > 0$!!!). The growth per individual, or *the per capita growth rate* is a central concept in population biology. It is defined as the population growth rate divided by the population size: $\frac{dn/dt}{n}$. The

per capita growth rate gives the growth per individual, i.e. how much each individual contributes to the future population size (approximately). In the case of exponential growth, the per capita growth rate is constant, equal to r . If each individual “grows” (i.e. survives and/or reproduces) at the same constant rate, then naturally the growth of the total population will be proportional to the number of individuals, i.e. the size of the population, just like in eq. (A.1).

Given an initial condition, $n(0)$, it is straightforward to solve (A.1):

$$n(t) = n(0)e^{rt} \quad (\text{A.2})$$

Please confirm that (A.2) actually solves (A.1) and that the initial condition is fulfilled.

The solution in (A.2) explains why we called the differential equation (A.1) that of exponential growth in the first place. The population will grow exponentially. If $r > 0$, the population size will grow to infinity. If $r < 0$, the population will go through exponential decline, and reach zero abundance asymptotically. If, finally, $r = 0$, there will be no change. The population will remain the same forever.

Stability in one dimension

The equation of exponential growth may be adequate in some situations, but not for very long time spans, at least not when r is positive. The reason is of course that no population can grow infinitely large. There is some sort of upper boundary to the size of all populations, e.g. due to limited resources. A simple way to incorporate such an upper boundary is to add a factor to eq. (A.1) which decreases with population size:

$$\frac{dn(t)}{dt} = rn(t) \left(1 - \frac{n(t)}{K} \right) \quad (\text{A.3})$$

Equation (A.3) is the *logistic equation* of population growth. The parameter K is called the *carrying capacity* of the environment. K sets the *equilibrium* population size, i.e.

where population growth stops. It is easy to verify that $\frac{dn}{dt} = 0$ in (A.3) when $n = K$. In other words, when $n = K$, there will be no change, the population will stop growing and remain the same size (K) forever.

Equilibria are generally found by setting $\frac{dn}{dt} = 0$ and solving for n . Please note that there is another equilibrium of the logistic growth equation, namely $n = 0$.

The logistic equation can be solved to give:

$$n(t) = \frac{K}{1 + \left(\frac{K}{n(0)} - 1 \right) e^{-rt}} \quad (\text{A.4})$$

It has a sigmoid-shaped growth like:

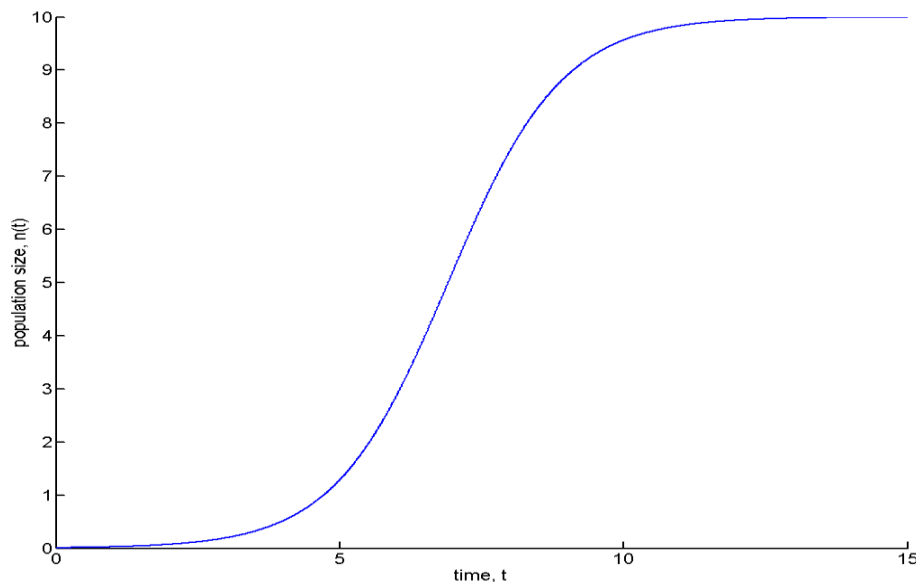


Figure A1. Logistic growth. $r = 1$, $K = 10$, $n(0) = 0.01$.

To further analyse the logistic equation we plot the population rate of change, dn/dt , as a function of population size, n :

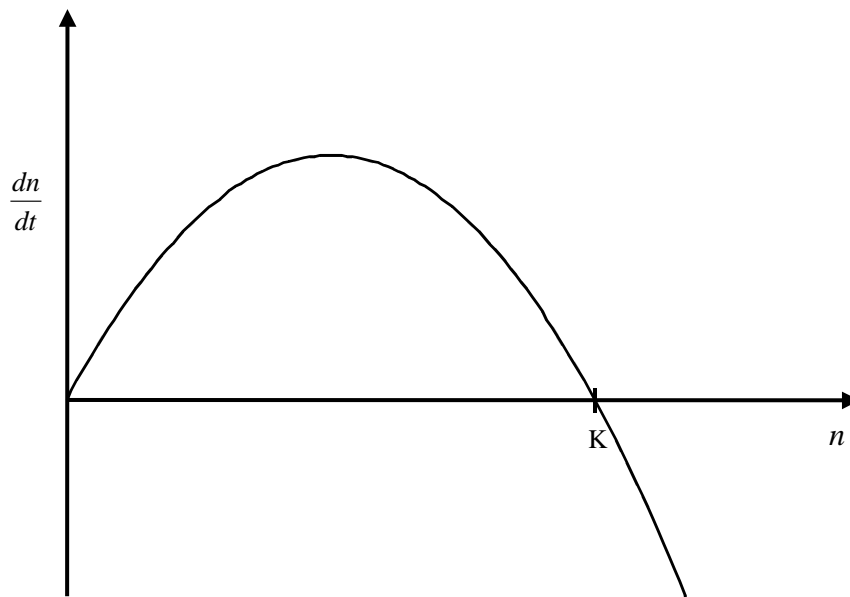


Figure A.2. dn/dt as a function of n according to the logistic equation

First of all, it is obvious that dn/dt equals zero at $n = K$. Thus, it is truly an equilibrium. Further, note that for population sizes below K population growth is positive. In other words, the population will grow if it is below K . However, at population sizes above K the rate of change is negative, which means the population will decrease in numbers if it at any point in time happens to have a population size larger than K . To conclude, the population will grow *towards* K whatever the population size (except $n = 0$!). This makes K a *stable* equilibrium.

To put things in more mathematical terms, we will study a more general case:

$$\frac{dn(t)}{dt} = f(n(t)) \quad (\text{A.5})$$

Here the function f , *the population growth function*, can have in principle any form. We will, however, assume it is continuous and bounded, i.e. it does not change abruptly and can not grow to plus or minus infinity. Equilibrium population sizes, where population growth is zero, are found by solving the equation:

$$f(n^*) = 0 \quad (\text{A.6})$$

We denote equilibria with n^* . Note that there may be several equilibria to the same system. An equilibrium is stable if the population grows at smaller population sizes and decreases at larger population sizes. In other words, the growth rate should be positive below the equilibrium and negative above it. Thus, the growth rate, given by the function f goes from positive to negative values as we pass the equilibrium (where it is zero). It follows that *the slope of f has to be negative at the equilibrium for an equilibrium to be stable*. It is easily verified that the equilibrium is *unstable* if the opposite is true, i.e. if the slope of f is positive at n^* . In other words:

$$\begin{aligned} f'(n^*) < 0 &\Rightarrow \text{stable equilibrium} \\ f'(n^*) > 0 &\Rightarrow \text{unstable equilibrium} \end{aligned} \quad (\text{A.7})$$

One example of an unstable equilibrium is the case of the *Allee effect*. In many species, population growth is hampered at very small population sizes, for instance due to problems finding mates. Consequently, the population growth function can look like this:

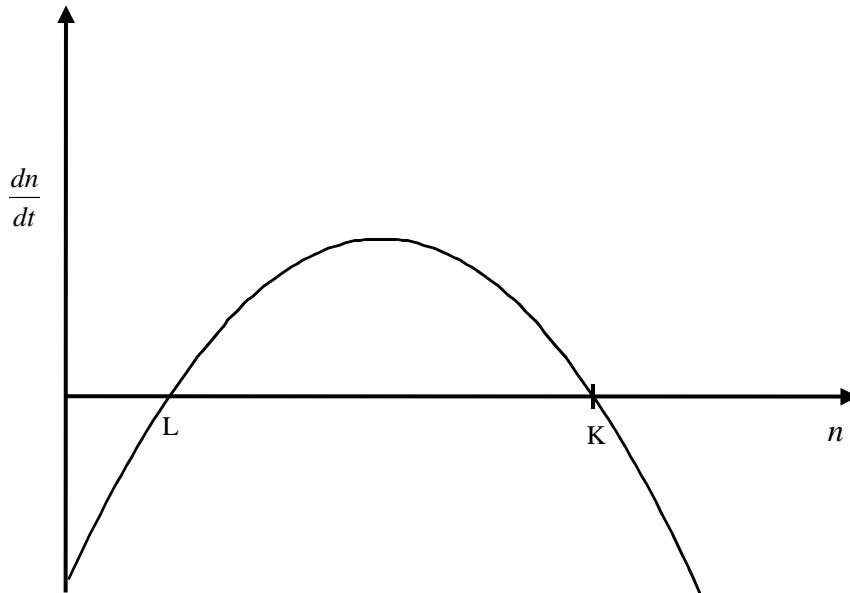


Figure A.3. Population growth with an Allee effect.

In figure (A.3), there is a lower equilibrium, L , below which population growth is negative. Thus, below this critical population size, the population will inevitably go extinct. Above L , however, population growth rate is positive, and the population will grow, much like in figure (A.1), towards the higher equilibrium, K . Conclusively, L is an unstable equilibrium – the population will grow away from it even if the initial population size is very close to L . It is apparent from fig. (A.3) that the slope of the growth function is positive at L (cf. eq. (A.7)).

Several variables in continuous time

Now we turn to dynamic systems with several system variables, i.e. multidimensional systems. First, we shall introduce an important ecological example:

The Lotka-Volterra competition model

The logistic equation (eq. A.3) is a simple way to incorporate *intraspecific competition*, i.e. competition between individuals of the same species, in a population growth function. The larger the population, the more intense is the intraspecific competition. As a consequence, the per capita growth rate, $\frac{dn/dt}{n}$, decreases with n .

For logistic growth the per capita growth rate becomes:

$$\frac{dn(t)/dt}{n(t)} = r \left(1 - \frac{n(t)}{K} \right), \quad (\text{A.8})$$

which is a steadily decreasing function of n .

If populations of several species are competing for the same resources, such as food or nesting places, one would like to include that in the population growth function in a similar way. Competition between individuals of different species is called *interspecific* competition. As a first example, consider two competing populations, population 1 and 2, with population sizes n_1 and n_2 . A straightforward extension of the logistic growth function for population 1 is:

$$\frac{dn_1(t)}{dt} = r_1 n_1(t) \left(1 - \frac{n_1(t) + \alpha_{12} n_2(t)}{K_1} \right) \quad (\text{A.9a})$$

Here, individuals of population 2 “add” to what was earlier the intraspecific competition. Each individual of population 2 competes with population 1 with a fraction α_{12} compared to an individual of population 1. If, for instance, $\alpha_{12} = 0.5$ it means that any individual from population 2 competes half as much with an individual from population 1 as another individual from population 1. The intraspecific competition is usually, but not necessarily, stronger than the interspecific competition. In other words, α_{12} is usually smaller than 1.

The growth of population 2 becomes (with equivalent reasoning):

$$\frac{dn_2(t)}{dt} = r_2 n_2(t) \left(1 - \frac{n_2(t) + \alpha_{21} n_1(t)}{K_2} \right) \quad (\text{A.9b})$$

Together, equations (A.9a,b) comprise the *Lotka-Volterra competition equations* for two populations. It is straightforward to extend them to several populations.

The general case

Generally speaking, we discuss systems of the kind:

$$\begin{cases} \frac{dn_1(t)}{dt} = f_1(n_1(t), n_2(t), \dots, n_k(t)) \\ \frac{dn_2(t)}{dt} = f_2(n_1(t), n_2(t), \dots, n_k(t)) \\ \vdots \\ \frac{dn_k(t)}{dt} = f_k(n_1(t), n_2(t), \dots, n_k(t)) \end{cases} \quad (\text{A.10})$$

which describes a k -dimensional system. It has k state variables, $n_{1..k}$, and consequently k population growth functions, $f_{1..k}$. In a more compact vector format, equation (A.10) may be written:

$$\frac{d\mathbf{n}(t)}{dt} = \mathbf{f}(\mathbf{n}(t)), \quad (\text{A.11})$$

where:

$$\mathbf{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_k(t) \end{pmatrix}, \quad \frac{d\mathbf{n}(t)}{dt} = \begin{pmatrix} \frac{dn_1(t)}{dt} \\ \frac{dn_2(t)}{dt} \\ \vdots \\ \frac{dn_k(t)}{dt} \end{pmatrix} \quad \text{and} \quad \mathbf{f}(\mathbf{n}) = \begin{pmatrix} f_1(n_1, n_2, \dots, n_k) \\ f_2(n_1, n_2, \dots, n_k) \\ \vdots \\ f_k(n_1, n_2, \dots, n_k) \end{pmatrix} \quad (\text{A.12})$$

The Lotka-Volterra example has f_1 and f_2 according to (cf. eqs. A.9a,b):

$$f_1(n_1, n_2) = r_1 n_1 \left(1 - \frac{n_1 + \alpha_{12} n_2}{K_1} \right) \quad (\text{A.13a})$$

$$f_2(n_1, n_2) = r_2 n_2 \left(1 - \frac{n_2 + \alpha_{21} n_1}{K_2} \right) \quad (\text{A.13b})$$

Phase space and trajectories

The current state of a dynamic system is given by the values of the state variables. If the state variables are interpreted as coordinates in n -dimensional space, each state corresponds to a point in that space, which is called the *phase space* of the system. As an example, consider the two-population model above, with population sizes n_1 and n_2 being the state variables. In phase space, n_1 becomes the x -coordinate and n_2 becomes the y -coordinate:

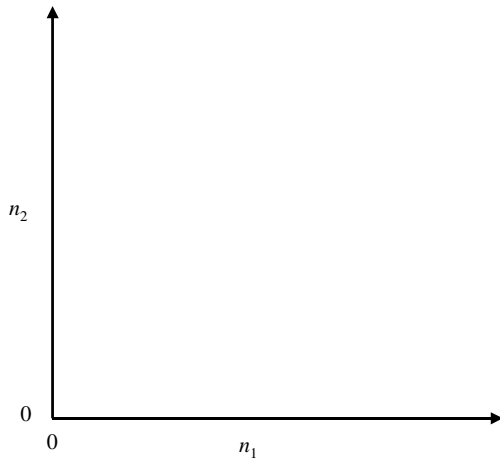


Figure A.4. The phase space of the Lotka-Volterra competition equations of two populations (eqs. A.9a,b).

At any point in time the system is in a certain state, given by the population sizes $n_1(t)$ and $n_2(t)$ (which we have not specified yet, and never will). Thus, for every t , there is a point in phase space which corresponds to the state of the system at that point in time. If we plot the points $(n_1(t), n_2(t))$ for all t within a certain time interval, we get the *trajectory* of the system during that time period:

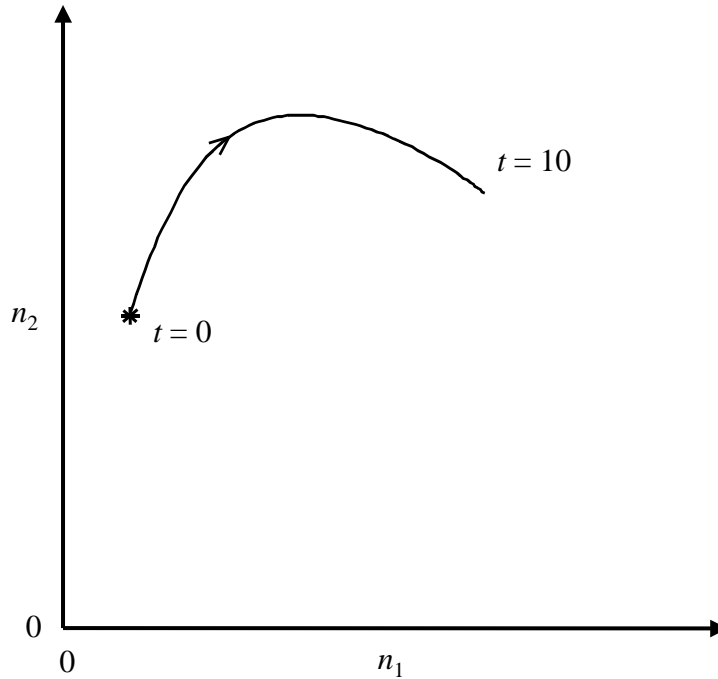


Figure A.5. A sample trajectory of the Lotka-Volterra competition equations. The initial condition is marked with an asterisk and the direction of change over time is indicated with an arrow.

Each trajectory is given by its initial conditions, which determine the whole future development of the system.

Isoclines

A powerful analytical tool of dynamic systems is the concept of population *isoclines*, sometimes referred to as *zero growth isoclines*. The isoclines consist of points in phase space where a particular population has zero growth. To find the isoclines of population i , one simply solves the equation $f_i(\mathbf{n}) = 0$, where f_i is the growth function of population i (cf. A.11 and A.12). For example, the isoclines of population 1 in the Lotka-Volterra equations are found by solving:

$$f_1(n_1, n_2) = r_1 n_1 \left(1 - \frac{n_1 + \alpha_{12} n_2}{K_1} \right) = 0 \quad (\text{A.14})$$

Equation (A.14) has a trivial set of solutions at: $n_1 = 0$. Consequently, the n_2 -axis is one of the isoclines of population 1. It is no surprise that the population does not grow when it is in fact not present. The other solutions to (A.14) are readily calculated as:

$$n_2 = \frac{K_1 - n_1}{\alpha_{12}}, \quad (\text{A.15})$$

which describes a straight line in phase space. The zero growth isoclines of population 2 are found in a similar way to be first of all the n_1 -axis and secondly the line:

$$n_2 = K_2 - \alpha_{21} n_1, \quad (\text{A.16})$$

which gives another straight line in phase space. We have drawn the isoclines below:

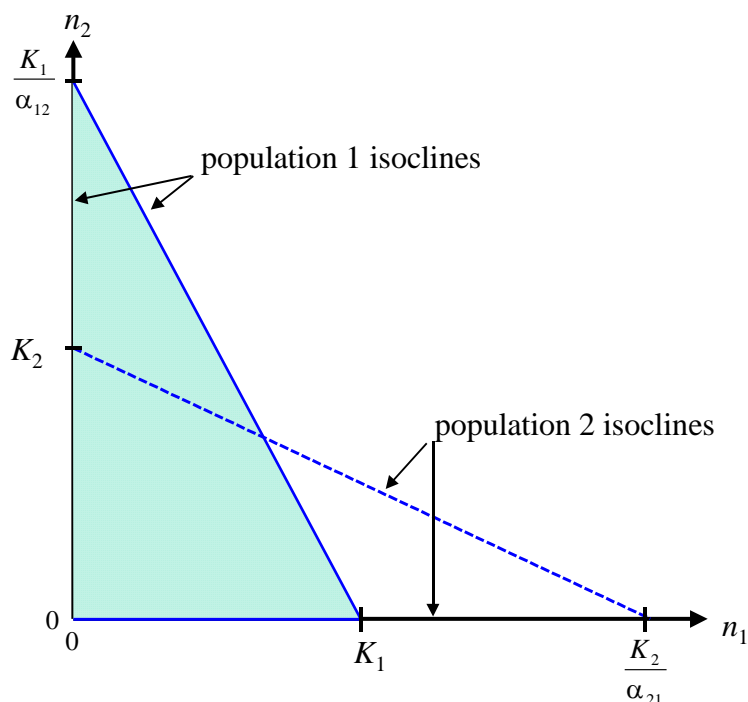


Figure A.6. The zero growth isoclines of the Lotka-Volterra equations.

The isoclines indicate where the growth function of a particular population changes sign, i.e. on one side of the isocline is negative growth and on the other side is positive growth. An analysis of the growth functions will tell where they are positive or negative. In a competition model, small population sizes will always yield little competition. Thus, if all populations are small, all populations will grow, all growth functions will be positive. This gives us the clues we need to determine the direction of growth in the competition case in fig. (A.6). Take the tilting (not vertical) isocline of population 1 above as an example. Below the isocline, i.e. for small population sizes, competition will be low and population 1 will grow. Above the isocline, where we have larger population sizes, population 1 will decrease. The isocline divides the quadrant of positive population sizes into two regions: one triangle close to the origin (shaded above) where population 1 will grow, and the rest (up to the right) where population 1 will decrease. An similar reasoning gives that below the tilted (not horizontal) isocline of population 2, population 2 will increase and above the isocline population 2 will decrease.

Now, we can figure out the principal directions of growth in all regions of phase space. First of all, below *both* isoclines both populations will grow. Above both isoclines both populations will decrease. In addition there are two regions where one population will increase and the other will decrease:

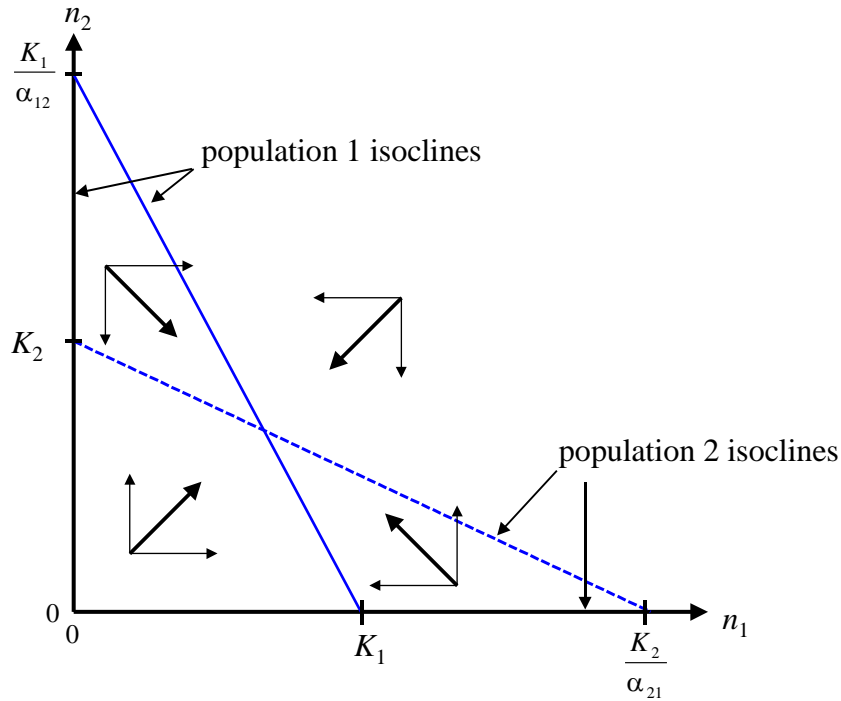


Figure A.7. The principle directions of growth of the Lotka-Volterra competition equations. Parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = 1$, $\alpha_{12} = \alpha_{21} = 0.5$.

Equilibria

An equilibrium of a dynamic system is where all state variables remain constant. Consequently, an equilibrium \mathbf{n}^* is defined by:

$$\mathbf{f}(\mathbf{n}^*) = \mathbf{0} \quad (\text{A.17})$$

In other words: all growth functions equal zero. It follows that equilibria are where isoclines of all populations intersect. In figure (A.7) there are no less than four equilibria. First of all the origin $(0,0)$. Secondly, where the tilted isocline of population 1 meets the n_1 -axis, $(K_1,0)$. This is when population two is totally absent, which makes the growth function of population one (eq. A.9a) collapse to the logistic equation. Consequently, K_1 is the equilibrium. Thirdly, there is the corresponding equilibrium on the n_2 -axis, $(0, K_2)$ where population one is totally absent. Finally, the fourth equilibrium is where the two tilted isoclines intersect, which is the only equilibrium where the two populations *coexist*. The coexistence equilibrium is:

$$\begin{aligned} n_1^* &= \frac{K_1 - \alpha_{12}K_2}{1 - \alpha_{12}\alpha_{21}} \\ n_2^* &= \frac{K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}} \end{aligned} \quad (\text{A.18})$$

Judging from the arrows in figure (A.7), it seems plausible that the equilibrium of coexistence is stable, i.e. if we start somewhere away from the equilibrium, the system will evolve towards it. Below follows a more strict treatment of the stability of an equilibrium.

Stability of equilibria in multidimensional systems

The treatment here is for simplicity given for the two-dimensional case, but is easily extended to several dimensions. Consider an equilibrium $\mathbf{n}^* = (n_1^* \ n_2^*)^T$, which (by definition of an equilibrium) solves eq. (A.17). We are interested in the behaviour of the system in the vicinity of this equilibrium. Close to the equilibrium, at a point $\mathbf{n}^* + \mathbf{x} = (n_1^* + x_1 \ n_2^* + x_2)^T$ the growth functions are well approximated by the linearised equations:

$$\begin{aligned} f_1(n_1^* + x_1, n_2^* + x_2) &\approx f_1(n_1^*, n_2^*) + \frac{\partial f_1}{\partial n_1} x_1 + \frac{\partial f_1}{\partial n_2} x_2 \\ f_2(n_1^* + x_1, n_2^* + x_2) &\approx f_2(n_1^*, n_2^*) + \frac{\partial f_2}{\partial n_1} x_1 + \frac{\partial f_2}{\partial n_2} x_2 \end{aligned} \quad (\text{A.19})$$

where the partial derivatives are taken at the equilibrium densities. By noting that $f_i(n_1^*, n_2^*) = 0$ by the definition of the equilibrium \mathbf{n}^* , the equations in (A.19) simplify to:

$$\begin{aligned} f_1(n_1^* + x_1, n_2^* + x_2) &\approx \frac{\partial f_1}{\partial n_1} x_1 + \frac{\partial f_1}{\partial n_2} x_2 \\ f_2(n_1^* + x_1, n_2^* + x_2) &\approx \frac{\partial f_2}{\partial n_1} x_1 + \frac{\partial f_2}{\partial n_2} x_2 \end{aligned} \quad (\text{A.20})$$

The right hand sides in (A.20) are simply linear combinations of the elements of the vector \mathbf{x} . Consequently, we can write (A.20) as a matrix equation:

$$\mathbf{f}(\mathbf{n}^* + \mathbf{x}) \approx \mathbf{J}\mathbf{x}, \quad (\text{A.21})$$

where \mathbf{J} is the *Jacobian matrix*:

$$\mathbf{J} = \begin{pmatrix} \frac{\partial f_1}{\partial n_1} & \frac{\partial f_1}{\partial n_2} \\ \frac{\partial f_2}{\partial n_1} & \frac{\partial f_2}{\partial n_2} \end{pmatrix} \quad (\text{A.22})$$

The partial derivatives are taken at the equilibrium population sizes (n_1^*, n_2^*) .

Now we can study the approximate dynamics close to the equilibrium. First, assume $\mathbf{n}(t)$ is close to the equilibrium, i.e.:

$$\mathbf{n}(t) = \mathbf{n}^* + \mathbf{x}(t), \quad (\text{A.23})$$

where $\mathbf{x}(t)$ is small.

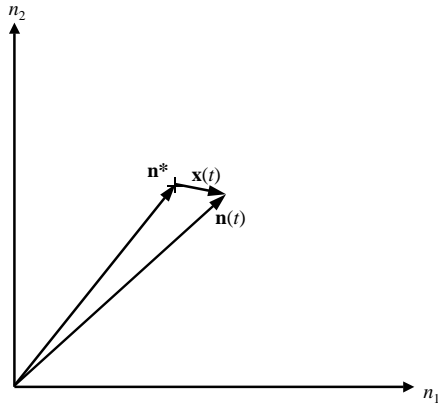
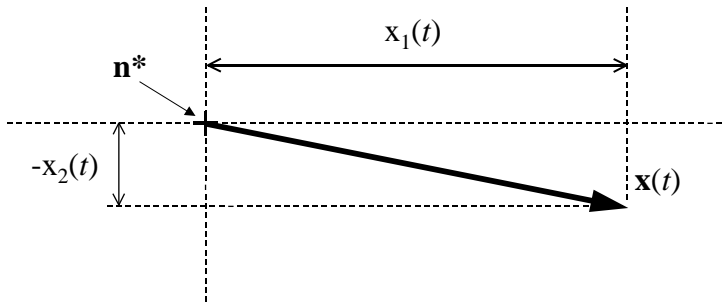


Figure A.8. A small deviation $\mathbf{x}(t)$ from an equilibrium \mathbf{n}^* .

For clarity, we write eq. (A.23) without vector notation:

$$\begin{cases} n_1(t) = n_1^* + x_1(t) \\ n_2(t) = n_2^* + x_2(t) \end{cases} \quad (\text{A.24})$$

Thus, the coordinates x_1 and x_2 give the deviation from the equilibrium along the n_1 - and n_2 -axis, respectively.



As $\mathbf{n}(t)$ swoops through phase space, so will $\mathbf{x}(t)$ and its two elements, x_1 and x_2 , will change accordingly.

The time derivative of (A.23) becomes:

$$\frac{d\mathbf{n}(t)}{dt} = \frac{d}{dt}(\mathbf{n}^* + \mathbf{x}(t)) = \mathbf{0} + \frac{d\mathbf{x}(t)}{dt}, \quad (\text{A.25})$$

which yields that the rate of change of $\mathbf{n}(t)$ is equal to that of $\mathbf{x}(t)$, which is quite logical, if one thinks about it and studies figure (A.8). Nevertheless, we are now ready to approximate the rate of change of $\mathbf{x}(t)$:

$$\frac{d\mathbf{x}(t)}{dt} = \frac{d\mathbf{n}(t)}{dt} = \mathbf{f}(\mathbf{n}(t)) = \mathbf{f}(\mathbf{n}^* + \mathbf{x}(t)) \approx J\mathbf{x}(t), \quad (\text{A.26})$$

where we made use of the approximation in eq. (A.21). Equation (A.26) describes a fully *linear* system, which serves as a good approximation of the full non-linear system in eq. (A.10) or (A.11) close to an equilibrium point. In two dimensions eq. (A.26) looks like (if we change the “ \approx ” to a “ $=$ ”):

$$\begin{cases} \frac{dx_1(t)}{dt} = J_{11}x_1(t) + J_{12}x_2(t) \\ \frac{dx_2(t)}{dt} = J_{21}x_1(t) + J_{22}x_2(t) \end{cases}, \quad (\text{A.27})$$

where J_{ij} are the elements of the Jacobian matrix.

Linear systems are well known and much more easily studied than non-linear systems. They are easy to study in part because one can make a smart *change of coordinates*, which greatly simplifies the system equations. The new coordinate system is given by the eigenvectors of the Jacobian matrix, which we shall denote \mathbf{v}_1 and \mathbf{v}_2 . We define new coordinates, $y_1(t)$ and $y_2(t)$, one per eigenvector, which are given by:

$$\mathbf{x}(t) = y_1(t)\mathbf{v}_1 + y_2(t)\mathbf{v}_2 \quad (\text{A.28})$$

Note that the eigenvectors are not functions of time – they are fixed, given by the Jacobian matrix at the equilibrium, which does not change over time. Given a vector \mathbf{x} , there is only one solution (y_1, y_2) to eq. (A.28). Assuming we have chosen \mathbf{v}_1 and \mathbf{v}_2 to have unit length (and we always can), y_1 and y_2 simply give the projected distances onto the coordinate axes given by the directions of \mathbf{v}_1 and \mathbf{v}_2 . See figure (A.9) below, which in principle is a close-up of figure (A.8) with the eigenvectors added.

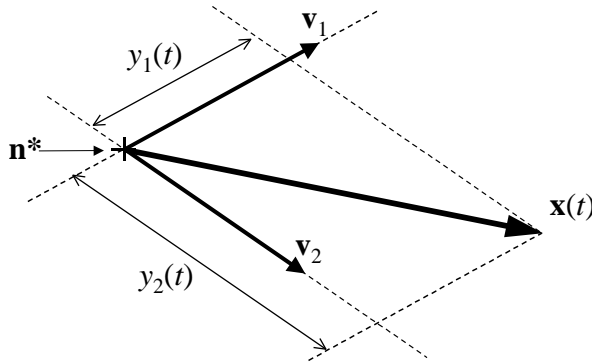


Figure A.9. A change of coordinates to y_1 and y_2 .

To proceed, we take the time derivative of equation (A.28), which yields:

$$\frac{d\mathbf{x}(t)}{dt} = \frac{d}{dt}(y_1(t)\mathbf{v}_1 + y_2(t)\mathbf{v}_2) = \frac{dy_1(t)}{dt}\mathbf{v}_1 + \frac{dy_2(t)}{dt}\mathbf{v}_2 \quad (\text{A.29})$$

A combination of eqs. (A.26), (A.28) and (A.29) gives:

$$\begin{aligned} \frac{d\mathbf{x}(t)}{dt} &= \frac{dy_1(t)}{dt}\mathbf{v}_1 + \frac{dy_2(t)}{dt}\mathbf{v}_2 = \mathbf{J}\mathbf{x}(t) = \mathbf{J}(y_1(t)\mathbf{v}_1 + y_2(t)\mathbf{v}_2) = \\ &= y_1(t)\mathbf{J}\mathbf{v}_1 + y_2(t)\mathbf{J}\mathbf{v}_2 = y_1(t)\lambda_1\mathbf{v}_1 + y_2(t)\lambda_2\mathbf{v}_2 \end{aligned} \quad (\text{A.30})$$

where we also made use of the fact that the vectors \mathbf{v}_1 and \mathbf{v}_2 are eigenvectors of the Jacobian matrix \mathbf{J} , which means $\mathbf{J}\mathbf{v}_1 = \lambda_1\mathbf{v}_1$ and $\mathbf{J}\mathbf{v}_2 = \lambda_2\mathbf{v}_2$, where λ_1 and λ_2 are the eigenvalues of \mathbf{J} .

Equation (A.30) shows something really important. Since the coordinates y_1 and y_2 are unambiguously determined for any given vector, it means that the factors in front of \mathbf{v}_1 in (A.30) must all be the same. Consequently:

$$\frac{dy_1(t)}{dt} = \lambda_1 y_1(t) \quad (\text{A.31a})$$

With equivalent reasoning, we get:

$$\frac{dy_2(t)}{dt} = \lambda_2 y_2(t) \quad (\text{A.31b})$$

This means that *the dynamics of y_1 and y_2 are independent of each other!* Further, the differential equations are particularly simple, namely in the form of exponential growth (cf. eq. A.1). As a consequence, it is easy to solve the differential equations (A.31a,b):

$$\begin{aligned} y_1(t) &= y_1(0)e^{\lambda_1 t} \\ y_2(t) &= y_2(0)e^{\lambda_2 t} \end{aligned} \quad (\text{A.32})$$

To get the solution in our original coordinates x_1 and x_2 , it is sufficient to insert the solutions given in (A.32) into eq. (A.28). However, we need not do that to determine the stability of the equilibrium. It follows from (A.32) that *y_1 and y_2 will approach zero if the eigenvalues of J , λ_1 and λ_2 , are both negative.* If y_1 and y_2 approach zero, so will the whole vector \mathbf{x} . Thus, we can conclude that given a small initial deviation $\mathbf{x}(0)$ from an equilibrium point \mathbf{n}^* , the dynamic system will approach the equilibrium ($\mathbf{x}(t)$ will approach zero) if the eigenvalues of the Jacobian matrix are negative. This leads to the following conclusion:

An equilibrium \mathbf{n}^ is stable if the eigenvalues of the Jacobian matrix, calculated at the equilibrium, are all negative. If any eigenvalue is positive, the equilibrium is unstable.*

Predator-prey models, cycles and complex eigenvalues

We shall continue our investigation of continuous time dynamic systems with yet another example from ecology, namely the *Lotka-Volterra predator prey equations*:

$$\begin{cases} \frac{dn(t)}{dt} = f_n(n(t), p(t)) = rn(t) - an(t)p(t) \\ \frac{dp(t)}{dt} = f_p(n(t), p(t)) = can(t)p(t) - \mu p(t) \end{cases}, \quad (\text{A.33})$$

where $n(t)$ and $p(t)$ denotes prey and predator densities, respectively. In absence of a predator, the prey population exhibits exponential growth with the growth rate r . This assumption may be criticised as unrealistic – in reality there would be an upper limit to the prey population, even in the absence of a predator.

In absence of prey, the predator population exhibits exponential *decline* at a rate μ , the mortality rate of the predator. The number of prey caught per time unit is expressed by the term $an(t)p(t)$, which simply means that the number of prey caught *per predator* per time unit is proportional to the number of prey. Also this assumption is unrealistic – it assumes there is no upper limit to the number of prey a single predator can (and will) catch per unit of time. In reality, of course, predators are limited in the number of prey they can catch and digest per time unit, even if they experience an unlimited number of available prey.

Each caught prey results in c new predators, such that the predator population grows at a rate $can(t)p(t)$ minus the background mortality of the predator.

Despite the apparent flaws of the Lotka-Volterra predator-prey equations, they are still useful for studying some general properties of predator-prey systems. We start our analysis by calculating the isoclines.

For the prey isoclines we solve $dn/dt = 0$, which gives either $n = 0$ or $p = r/a$. The first solution is the p -axis in phase space (the prey population will not grow if no prey are around). The second solution is a horizontal line at a fixed p -value. This determines a predator density (r/a), above which the prey population will start to decrease.

The predator isoclines are given by $dp/dt = 0$, which gives either $p = 0$ or $n = \mu/(ca)$. The first solution is the n -axis in phase space, which trivially means the predator population will not grow if no predators are around. The second solution, $n = \mu/(ca)$, which is a vertical line in phase space at a constant prey density. Below this prey density ($\mu/(ca)$), the predator will suffer from too little food and decrease. Above it, the predators will thrive and increase in numbers.

Below we have drawn the prey and predator isoclines in the predator-prey phase space.

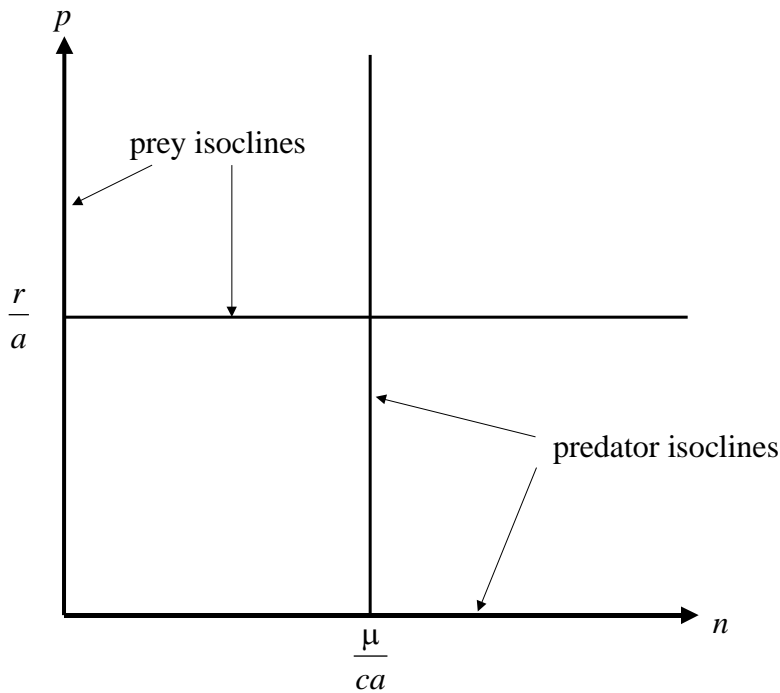


Figure A.10. Isoclines of the Lotka-Volterra predator-prey equations.

It is apparent from figure (A.10) that there are only two possible equilibria, i.e. where a prey isocline intersects with a predator isocline. One (trivial) equilibrium is the origin, $(0,0)$. The other is the point $(\frac{\mu}{ca}, \frac{r}{a})$. To determine the stability of the second, non-trivial, equilibrium we calculate the Jacobian matrix. First, we need the partial derivatives of the growth functions in eq. (A.33):

$$\frac{\partial f_n}{\partial n} = r - ap, \quad \frac{\partial f_n}{\partial p} = -an$$

and

$$\frac{\partial f_p}{\partial n} = cap, \quad \frac{\partial f_p}{\partial p} = can - \mu$$

Inserting the equilibrium $(n^*, p^*) = (\frac{\mu}{ca}, \frac{r}{a})$ gives:

$$J = \left(\begin{array}{cc} \frac{\partial f_n}{\partial n} & \frac{\partial f_n}{\partial p} \\ \frac{\partial f_p}{\partial n} & \frac{\partial f_p}{\partial p} \end{array} \right)_{n=n^*} = \left(\begin{array}{cc} r - a\frac{r}{a} & -a\frac{\mu}{ca} \\ ca\frac{r}{a} & ca\frac{\mu}{ca} - \mu \end{array} \right) = \left(\begin{array}{cc} 0 & -\frac{\mu}{c} \\ cr & 0 \end{array} \right) \quad (\text{A.34})$$

The eigenvalues of J in eq. (A.34) are $\lambda_{1,2} = \pm i\sqrt{\mu r}$, which are imaginary numbers (since μ and r are positive). We have not discussed imaginary or complex eigenvalues above, but in principle all calculations from section (0) are still valid. The problem is that the eigenvector coordinates, y_1 and y_2 , are complex (or imaginary) as well as the eigenvectors, which makes the calculations hard to visualise. Nevertheless, one arrives at expressions equivalent to eqs. (A.31 and A.32). If a particular eigenvalue is complex, say $\lambda_i = a + ib$, eq. (A.32) evaluates to:

$$y_i(t) = y_i(0)e^{\lambda_i t} = y_i(0)e^{(a+ib)t} = y_i(0)e^{at}e^{ibt} = y_i(0)e^{at}(\cos(bt) + i\sin(bt)) \quad (\text{A.35})$$

Equation (A.35) is a sinusoidal oscillation modulated by an exponential factor e^{at} . It follows that it will be a *damped oscillation*, asymptotically approaching zero, if $a < 0$. Thus, the deviations from the equilibrium, given in coordinates y_i , will diminish over time if the real part (a above) of all eigenvalues is negative. Note that this conclusion holds equally true for real eigenvalues, since the real part of a real number is the number itself. Thus, we reach the following conclusion, applicable to all systems:

An equilibrium n^ is stable if all eigenvalues of the Jacobian have negative real parts. If any eigenvalue has a positive real part, the equilibrium is unstable.*

Another conclusion from the above discussion is that complex eigenvalues lead to oscillations. In fact, trajectories close to a stable equilibrium will spiralise into the equilibrium, with ever decreasing radius. If the equilibrium is unstable, the spiral will instead grow to ever larger distance from the equilibrium. In both cases, the cycle period, T (=the time between two peaks), can be approximately calculated from the imaginary part of the eigenvalue:

$$T = \frac{2\pi}{\text{Im}(\lambda)}$$

To finish the predator-prey example above we conclude that it is a borderline case – the real part of the two eigenvalues is exactly zero. This means the equilibrium is *neutrally stable* – trajectories close to the equilibrium will neither diverge from it nor converge to it. In fact, this is true for all phase space. Any initial condition leads to a cyclical motion around the equilibrium and eventually comes back to where it started:

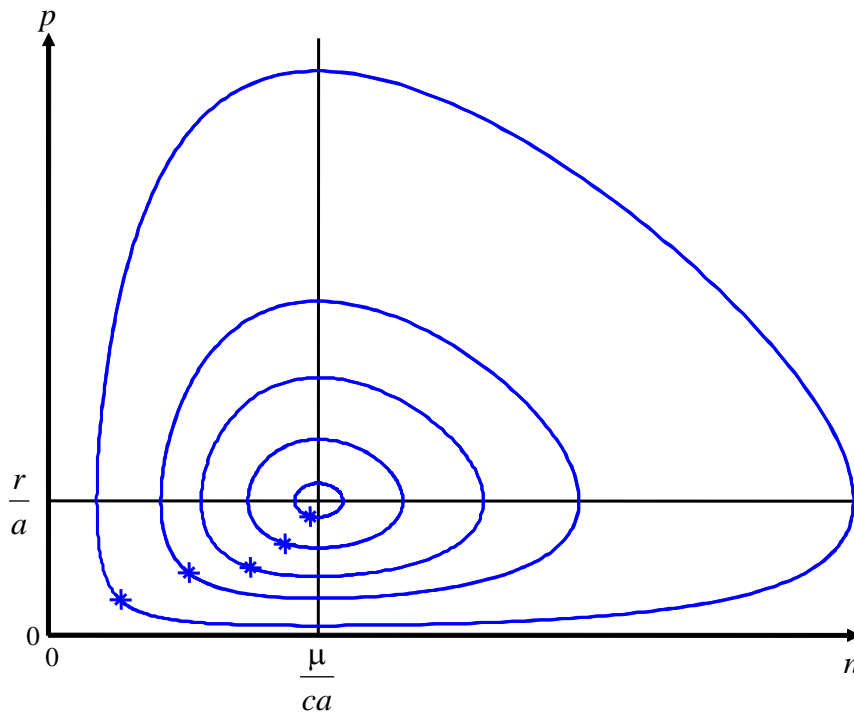


Figure A.11. A few trajectories of the Lotka-Volterra predator-prey equations. Each trajectory is started at an initial condition, marked with an asterisk.

Bonus track: The Jacobian matrix of the Lotka-Volterra competition equations

Model:

$$f_1(n_1, n_2) = r_1 n_1 \left(1 - \frac{n_1 + \alpha_{12} n_2}{K_1} \right)$$

$$f_2(n_1, n_2) = r_2 n_2 \left(1 - \frac{n_2 + \alpha_{21} n_1}{K_2} \right)$$

Non-trivial equilibrium (see above):

$$n_1^* = \frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12} \alpha_{21}}$$

$$n_2^* = \frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12} \alpha_{21}}$$

Partial derivatives:

$$\frac{\partial f_1}{\partial n_1} = r_1 \left(1 - \frac{n_1 + \alpha_{12} n_2}{K_1} \right) + r_1 n_1 \left(-\frac{1}{K_1} \right) = [\text{insert equilibrium and simplify}] =$$

$$= -\frac{r_1}{K_1} n_1^* = -\frac{r_1}{K_1} \left(\frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12} \alpha_{21}} \right)$$

$$\begin{aligned}\frac{\partial f_1}{\partial n_2} &= r_1 n_1 \left(-\frac{\alpha_{12}}{K_1} \right) = [\text{insert equilibrium}] = -\frac{r_1 \alpha_{12}}{K_1} n_1^* = -\frac{r_1 \alpha_{12}}{K_1} \left(\frac{K_1 - \alpha_{12} K_2}{1 - \alpha_{12} \alpha_{21}} \right) \\ \frac{\partial f_2}{\partial n_1} &= \dots = -\frac{r_2 \alpha_{21}}{K_2} n_2^* = -\frac{r_2 \alpha_{21}}{K_2} \left(\frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12} \alpha_{21}} \right) \\ \frac{\partial f_2}{\partial n_2} &= \dots = -\frac{r_2}{K_2} n_2^* = -\frac{r_2}{K_2} \left(\frac{K_2 - \alpha_{21} K_1}{1 - \alpha_{12} \alpha_{21}} \right)\end{aligned}$$

Jacobian matrix:

$$J = \begin{pmatrix} -\frac{r_1}{K_1} n_1^* & -\frac{r_1 \alpha_{12}}{K_1} n_1^* \\ -\frac{r_2 \alpha_{21}}{K_2} n_2^* & -\frac{r_2}{K_2} n_2^* \end{pmatrix}$$