# Appendix I

## Equilibrium stability

### A.1 Local and global stability

Let an ecological community of $S$ species described by an autonomous continuous time model be of the form:

$$\frac{dn_i}{dt} = n_i f_i(n_1, n_2, \ldots, n_S) \equiv n_i f_i(\mathbf{n}) \qquad i = 1, \ldots, S, \tag{I.1}$$

where $f_1(\mathbf{n}), f_2(\mathbf{n}), \ldots, f_S(\mathbf{n})$ are continuous functions in the positive orthant. We can denote the product $n_i f_i(\mathbf{n})$ as $F_i(\mathbf{n})$.

Similarly, we use discrete time, and at time $t$ let $N_i(t)$ denote the density of the $i$th species in an interaction among $S$ species which we represent by a set of nonlinear difference equations:

$$n_i(t+1) = G_i(n_1, n_2, \ldots, n_S) \equiv G_i(\mathbf{n}) \qquad i = 1, \ldots, S, \tag{I.1$'$}$$

where, for convenience, we use $n_i$ in place of $n_i(t)$; but in order to distinguish $n_i(t+1)$ from $n_i(t)$ we shall retain the argument of $n_i(t+1)$.

The simplest way to examine stability in a community model like equation (I.1) is by examining the eigenvalues of the so-called community matrix which is computed at an equilibrium of the model $\mathbf{n}^*$ that, by definition, verifies:

$$f_i(\mathbf{n}^*) = 0 \qquad i = 1, \ldots, S. \tag{I.2}$$

Similarly, for discrete time, we have that an equilibrium $\mathbf{n}^*$, by definition, must verify:

$$G_i(\mathbf{n}^*) = \mathbf{n}^* \qquad i = 1, \ldots, S. \tag{I.2$'$}$$

doi:10.1088/978-0-7503-2432-8ch5

This community matrix is the Jacobian matrix, given by:

$$J_{ij} \equiv \left.\frac{\partial\left(\frac{dn_i}{dt}\right)}{\partial n_j}\right|_{\mathbf{n}^*} = \left.\frac{\partial F_i(\mathbf{n})}{\partial n_j}\right|_{\mathbf{n}^*} = \left.\frac{\partial n_i}{\partial n_j} f_i(\mathbf{n})\right|_{\mathbf{n}^*} + n_i^* \left.\frac{\partial f_i(\mathbf{n})}{\partial n_j}\right|_{\mathbf{n}^*} = f_j(\mathbf{n}^*) + \left.\frac{\partial f_i(\mathbf{n})}{\partial n_j}\right|_{\mathbf{n}^*} n_i^*, \quad \text{(I.3)}$$

and then, by equation (I.2), we can simply write the community or Jacobian matrix $J_{ij}$ as:

$$J_{ij} = \left.\frac{\partial f_i(\mathbf{n})}{\partial n_j}\right|_{\mathbf{n}^*} n_i^*. \quad \text{(I.4)}$$

However, the problem with this method is that it can only establish **local** stability or instability. On the other hand, ecosystems in the real world are subject to large perturbations of the initial state, and continual disturbances on the system dynamics that may produce important departures from equilibrium. Since the equations of population biology are nonlinear, their solutions, which can be represented as an $S$-dimensional surface, can give rise to quite complicated ‘landscapes’. And therefore neighborhood stability analysis may give a misleading representation of the full global stability of the system.

If the dynamical equations are linear, local and global stability are identical. Unfortunately, we have seen in chapter 1 that while the linear approximation is very useful for approaching many problems in physics, it is rarely a sensible approach in population biology. However, many biologically interesting models, although non-linear, produce relatively simple landscapes, with one valley or hilltop whose sides slope ever upward or downward, respectively. In this case the local stability analysis correctly describes the global stability. Such circumstances are characterized by the existence of a *Lyapunov function* and constitute the basis of a powerful analytical method for establishing that an equilibrium is **globally** stable, i.e. stable relative to finite perturbations of the initial state. This is the so-called *direct* or *second* method of Lyapunov (LaSalle and Lefschetz 1961, Gurel and Lapidus 1968, Willems 1970, Strogatz 1994). There are many methods for constructing Lyapunov functions (Schultz 1965, Gurel and Lapidus 1968). However, unfortunately, there is no general way of knowing whether a Lyapunov function exists, let alone a straightforward procedure to construct it if it does exist.

In any event, for a given model it is possible to use computer simulations to investigate the behavior of the model for finite perturbations of its initial state. But computer simulations cannot guarantee that an equilibrium does indeed have a finite region of attraction. Certainly, this procedure becomes increasingly worse as the number of species in a given community increases.

In the next section of this appendix we will consider the local stability for two-dimensional systems. In the third and final section we will return to local and global stability, review the two methods outlined above, the one based on the eigenvalues of the Jacobian matrix and Lyapunov's method.

## A.2 Stability for two-dimensional systems

Stability theory addresses the stability of solutions of differential equations and of trajectories of dynamical systems under small perturbations of initial conditions. We discuss here the stability of a general autonomous ordinary differential bi-dimensional system of equations of the form

$$dx_1/dt = f_1(x_1, x_2),\ dx_2/dt = f_2(x_1, x_2), \tag{I.5}$$

where $f_1$ and $f_2$ are given functions or maps. This system can be written more compactly in vector notation as

$$d\mathbf{x}/dt = \mathbf{f}(\mathbf{x}), \tag{I.5$'$}$$

where bold denotes a column vector with two entries:

$$\mathbf{x} = \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}, \tag{I.6$a$}$$

$$\mathbf{f}(\mathbf{x}) = \begin{bmatrix} f_1(\mathbf{x}) \\ f_2(\mathbf{x}) \end{bmatrix}, \tag{I.6$b$}$$

Thus $\mathbf{x}$ represents a point in the phase plane, and $d\mathbf{x}/dt$ is the velocity vector at that point, which is given by the vector field or bi-dimensional map $\mathbf{f}(\mathbf{x})$. By flowing along the vector field, a phase point traces out a solution $\mathbf{x}(t)$, corresponding to a trajectory or *phase curve* winding through the phase plane (figure I1).

However, what guarantee do we have that the general nonlinear system $d\mathbf{x}/dt = \mathbf{f}(\mathbf{x})$ actually *has* solutions? Fortunately, it turns out that there is an existence and uniqueness theorem for $n$-dimensional systems:

*Existence and uniqueness theorem*

Consider the initial value problem $d\mathbf{x}/dt = \mathbf{f}(\mathbf{x})$, $\mathbf{x}(0) = \mathbf{x}_0$. Suppose that $\mathbf{f}$ is ***continuously differentiable***, i.e. $\mathbf{f}$ is continuous and all its partial derivatives $\partial f_i/\partial x_j$, $i, j = 1,\ldots,n$, are continuous for $\mathbf{x}$ in some open connected set $\mathcal{D}$ contained in $\mathbf{R}^n$.

Then for $\mathbf{x}_0$ in $\mathcal{D}$, the initial value problem has a solution $\mathbf{x}(t)$ on some time interval $(-\tau, \tau)$ about $t = 0$, and the solution is unique.

*Fixed or singular points*

Phase curves or phase trajectories of equation (A1.1) are solutions of

$$\frac{dx_1}{dx_2} = \frac{f_1(x_1, x_2)}{f_2(x_1, x_2)}. \tag{I.7}$$

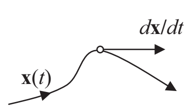


**Figure I1.** A trajectory or phase curve $\mathbf{x}(t)$ winding through the phase plane; the 'velocity' $d\mathbf{x}/dt$ is tangent to this curve.

We can imagine the entire phase plane as filled with such trajectories. In fact, through any point $(x_1, x_2)$ there is a unique curve except at *fixed points* $(x_1^*, x_2^*)$ where the vector field $\mathbf{f(x)}$ vanishes, i.e.

$$f_1(x_1^*, x_2^*) = f_2(x_1^*, x_2^*) = 0.$$

This is why fixed points are also called *singular points.*

It turns out that for systems of nonlinear equations in general it is impossible to find the trajectories analytically. Even when explicit formulas are available, they are often too complicated to provide much insight. However, something we can do is to determine the *qualitative* behavior of the solutions. That is, to find the system's phase portrait directly from the properties of the vector field $\mathbf{f(x)}$. To do this we will use the ***linearization*** technique developed earlier for one-dimensional systems, namely a Taylor expansion around fixed points. The hope of this *linear stability analysis* is that we can approximate the phase portrait near a fixed point by that of a corresponding linear system, so that we can classify fixed points of *nonlinear* systems. More rigorously speaking, there is a theorem about the local behavior of dynamical systems in the neighborhood of a certain type of equilibrium point which asserts that linearization is effective in predicting qualitative patterns of behavior.

*Linear stability analysis around fixed points, the linearization theorem of Hartman–Grobman*

Suppose the map $\mathbf{f}$ is ***smooth***, i.e. it is at least differentiable everywhere (hence continuous) has an equilibrium state $\mathbf{x}^*$: that is, $\mathbf{f}(\mathbf{x}^*) = 0$. Then, the ***Hartman–Grobman*** *theorem* or ***linearization theorem*** states that the behavior of a dynamical system in a domain near a ***hyperbolic equilibrium point*** (we will define in a moment this kind of equilibrium) is qualitatively the same as the behavior of its linearization near this equilibrium point. Therefore, when dealing with such dynamical systems one can use the simpler linearization of the system to analyze its behavior around equilibria.

Just for simplicity of expression let us make the change of coordinates $x = x_1 - x_1^*$, $y = x_2 - x_2^*$, that moves the singular point to the origin $x = 0$ and $y = 0$. Then (0,0) is a singular point of the transformed equation (I.7′):

$$\frac{dx}{dy} = \frac{f_1(x, y)}{f_2(x, y)}. \tag{I.7′}$$

If $f_1$ and $f_2$ are analytic functions near (0,0), by definition of an analytic function, we can expand $f_1$ and $f_2$ in a Taylor series and, retaining only the linear terms, we get

$$\frac{dx}{dy} = \frac{f_{1x}x + f_{1y}y}{f_{2x}x + f_{2y}y}, \tag{I.8}$$

where the $f_{ij}$ denote the partial derivative of the function $f_i$ ($i = 1$ or 2) with respect to the direction $j = x$ or $y$ evaluated at the origin, i.e. $f_{1x} = \frac{\partial f_1}{\partial x}|_{(0,0)}$, $f_{1y} = \frac{\partial f_1}{\partial y}|_{(0,0)}$, $f_{2x} = \frac{\partial f_2}{\partial x}|_{(0,0)}$, $f_{2y} = \frac{\partial f_2}{\partial y}|_{(0,0)}$. These four numbers define the ***Jacobian*** matrix $\mathbf{A}$:

$$\mathbf{A} = \begin{pmatrix} f_{1x} & f_{1y} \\ f_{2x} & f_{2y} \end{pmatrix} \equiv \begin{pmatrix} \dfrac{\partial f_1}{\partial x} & \dfrac{\partial f_1}{\partial y} \\ \dfrac{\partial f_2}{\partial x} & \dfrac{\partial f_2}{\partial y} \end{pmatrix}_{(0,0)} . \tag{I.9}$$

Therefore, equation (I.5′) is equivalent, to first order (i.e. linear approximation) to:

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\mathbf{x}. \tag{I.10}$$

Let $\lambda_1$ and $\lambda_2$ be the eigenvalues of $\mathbf{A}$; given by equating the determinant of $\mathrm{A} - \lambda\,\mathbf{I}$:

$$\begin{vmatrix} f_{1x} - \lambda & f_{1y} \\ f_{2x} & f_{2y} - \lambda \end{vmatrix} = 0, \tag{I.11}$$

i.e. $\lambda_1$ and $\lambda_2$ are the roots of the second order ***characteristic equation***:

$$\lambda^2 - (f_{1x} + f_{2y})\lambda + f_{1x}f_{2y} - f_{1y}f_{2x} = 0, \tag{I.12}$$

which can be re-written as:

$$\lambda^2 - \mathrm{tr}\mathbf{A}\lambda + \det\mathbf{A} = 0, \tag{I.13}$$

where ‘tr’ denotes the trace of matrix $\mathbf{A}$ (the sum of diagonal elements) and ‘det’ its determinant $|\mathbf{A}|$. Therefore, we get

$$\begin{aligned} \lambda_1 &= 1/2\left(\mathrm{tr}\mathbf{A} + \sqrt{\mathrm{tr}\mathbf{A}^2 - 4\det\mathbf{A}}\right), \\ \lambda_2 &= 1/2\left(\mathrm{tr}\mathbf{A} - \sqrt{\mathrm{tr}\mathbf{A}^2 - 4\det\mathbf{A}}\right). \end{aligned} \tag{I.14}$$

In general, $\lambda_1$ and $\lambda_2$ are complex numbers. An equilibrium $\mathbf{x}^*$ is hyperbolic if no eigenvalue of the linearization has real part equal to zero. That is, hyperbolic equilibrium implies that $\mathrm{Re}(\lambda_1) \neq 0$ and $\mathrm{Re}(\lambda_2) \neq 0$.

The typical situation is for the eigenvalues to be distinct: $\lambda_1 \neq \lambda_2$. In this case, a theorem of linear algebra states that the corresponding eigenvectors $\mathbf{v}_1$ and $\mathbf{v}_2$ of $\mathbf{A}$ are linearly independent, and hence span the entire plane. In particular, any initial condition $\mathbf{x}_0$ can be written as a linear combination of eigenvectors, say

$$\mathbf{x}_0 = c_1\mathbf{v}_1 + c_2\mathbf{v}_2, \tag{I.15}$$

where $c_1$ and $c_2$ are arbitrary constants and the eigenvector $\mathbf{v}_i$ associated with the eigenvalue $\lambda_i$ given by

$$\mathbf{v}_i = \left(1 + p_i^2\right)^{-1/2}\begin{bmatrix} 1 \\ p_i \end{bmatrix}, \quad p_i = \frac{\lambda_i - f_{1x}}{f_{1y}}, \quad f_{2x} \neq 0, \quad i = 1, 2. \tag{I.16}$$

This allows us to write down the general solutions of equation (I.10) simply as

$$\mathbf{x} = c_1\mathbf{v}_1 e^{\lambda_1 t} + c_2\mathbf{v}_2 e^{\lambda_2 t}. \tag{I.17}$$

This is a general solution because it is a linear combination of solutions to equation (A1.6), and hence is itself a solution. In addition, it satisfies the initial condition $\mathbf{x}(0) = \mathbf{x}_0$, and so by the existence and uniqueness theorem, it is the *only* solution.

If the eigenvalues are equal, i.e. equation (I.13) has a double root $\lambda_1 = \lambda_2 = \lambda$, the solutions are proportional to $(c_1 + c_2 t)\exp[\lambda t]$.

The mathematician Henri Poincaré distinguished four different singular points of differential equations. These are the ***node***, the ***saddle***, the ***focus*** and the ***center***. Figure I2 summarizes the possibilities in the so-called ***Poincaré diagram***, i.e. the (tr **A**, det **A**) parameter plane, which includes the parable $\Delta \equiv 1/4 \text{ tr } \mathbf{A}^2 - \det \mathbf{A} = 0$.

I. If det **A** < 0, then $\lambda_1$ and $\lambda_2$ are real and of opposite signs, regardless of the sign of tr **A**. Usually, solutions go to infinity as $t \to \infty$ so this case is considered to be unstable. Figure I2 shows the appearance of some trajectories near this kind of fixed point, denoted a **saddle point**. This type of behavior is found in the region below the horizontal axis of the (tr **A**, det **A**) parameter plane shown in the summary figure I2.

II. If det **A** > 0, then any of the following can happen:
   (A) det **A** < 1/4 tr $\mathbf{A}^2$ (i.e. below the parable): In this case $\lambda_1$ and $\lambda_2$ are real. We then have two possibilities:

   II(A).1. If tr **A** < 0: In this case $\lambda_1 < 0$ and $\lambda_2 < 0$. Solutions are both decreasing exponentials so that the *fixed point is stable*, denoted a **stable node** or **sink** (located in the Poincaré diagram between the horizontal axis and the parable, to the left-hand side of figure I2).

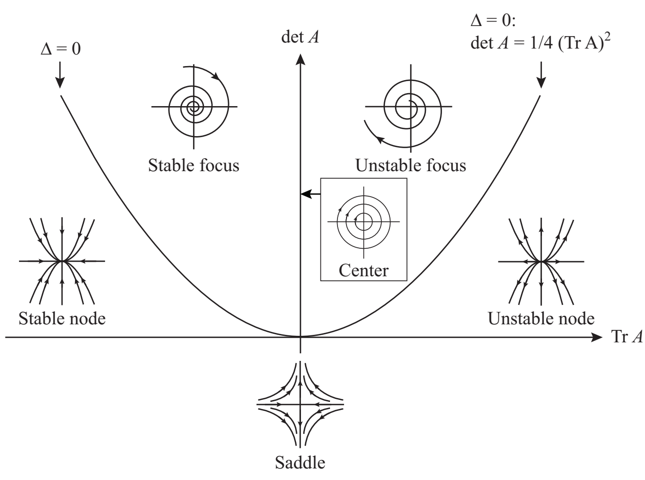


**Figure I2. Poincaré diagram.** Classification of phase portraits in the (tr **A**, det **A**)-plane. Author: Freesodas / Source: Gimp.

II(A).2. If tr $\mathbf{A} > 0$: In this case $\lambda_1 > 0$ and $\lambda_2 > 0$. Solutions are both increasing exponentials so that the *fixed point is unstable*, denoted an **unstable node** or **source** (between the horizontal axis and the parable, to the rhs of figure I2).

(B) det $\mathbf{A} > 1/4$ tr $\mathbf{A}^2$ (i.e. above the parable): In this case $\lambda_1$ and $\lambda_2$ are complex. We then have three possibilities:

II(B).1. If tr $\mathbf{A} < 0$: In this case $\mathrm{Re}(\lambda_1) < 0$ and $\mathrm{Re}(\lambda_2) < 0$. Solutions are oscillations with decreasing amplitude so that the *fixed point* is a **stable focus** or **spiral sink** (located in the Poincaré diagram between the vertical axis and the parable, to the lhs of figure I2).

II(B).2. If tr $\mathbf{A} > 0$: In this case $\mathrm{Re}(\lambda_1) > 0$ and $\mathrm{Re}(\lambda_2) > 0$. Solutions are oscillations with increasing amplitude so that the *fixed point* is an **unstable focus** or **spiral source** (located in the Poincaré diagram between the vertical axis and the parable, to the rhs of figure I2).

II(B).3. If tr $\mathbf{A} = 0$: In this case $\mathrm{Re}(\lambda_1) = \mathrm{Re}(\lambda_2) = 0$. Solutions are periodic, with constant amplitude, and thus the phase curves are ellipses. This corresponds to a **center**, but is a marginal case. Centers are not stable in the usual sense, they are *neutrally stable*; a small perturbation from one phase curve does not die out in the sense of returning to the original unperturbed curve. The perturbation simply gives another solution. This implies that, in general, nonlinear terms will either stabilize or destabilize the system. In the case of center singularities, determined by the linear approximation to $f_1(x, y)$ and $f_2(x, y)$, we must look at the higher-order (than linear) terms to determine whether or not it is really a spiral and hence whether it is stable or unstable.

*Summary*

- Fixed points are **stable** when **the real part of $\boldsymbol{\lambda_1}$ and $\boldsymbol{\lambda_2}$ are negative**.
- There are four types of fixed points:
  1. A **node** if $\lambda_1$ and $\lambda_2$ are real, non null, with the same sign; if both $\lambda_1$ and $\lambda_2$ are negative (positive) the node is **stable** (**unstable**).
  2. A **saddle point** if the signs of $\lambda_1$ and $\lambda_2$ are opposite.
  3. A **focus** when $\lambda_1$ and $\lambda_2$ are complex (with real part different from 0). Negative real parts for $\lambda_1$ and $\lambda_2$ imply a **stable focus**, whereas positive real parts for $\lambda_1$ and $\lambda_2$ mean an **unstable focus**.
  4. A **center** if $\lambda_1$ and $\lambda_2$ are purely imaginary the fixed point is. In this case we have to go beyond the linear stability analysis and look at the nonlinear terms to determine whether or not it is really a spiral and hence whether it is stable or unstable.

*Limit cycles and Kolmogorov's theorem for predator–prey systems*

An interesting question about trajectories that spiral outward from an unstable equilibrium is: do they spiral outward without bound until they intersect one of the axes and one of the species goes extinct? Or do they settle on a particular orbit which is itself stable? Such orbits are called stable **limit cycles**. A limit cycle is a closed trajectory such that neighboring trajectories are not closed; they spiral either toward (stable limit cycle) or away from the limit cycle (unstable limit cycle).

To elucidate the question of the fate of unstable spirals there are both negative theorems, which rule out closed orbit solutions in the phase plane, as well as the Poincaré–Bendixson theorem which establish that closed orbits exist under particular conditions. Before introducing these theorems, at the end of the next section, we will present a theorem by the Russian mathematician Andrei Kolmogorov for bi-dimensional predator–prey systems.

**Kolmogorov's theorem**

Given a bi-dimensional system like equation (I.5), if

$$\begin{aligned} f_1(x_1, x_2) &= x_1 f(x_1, x_2), \\ f_2(x_1, x_2) &= x_2 g(x_1, x_2), \end{aligned} \tag{I.18}$$

where $f(x_1, x_2)$ and $g(x_1, x_2)$ can be interpreted as the per capita growth rates for each species, provided that

**(i)** the functions $f$ and $g$ are continuous and differentiable in the domain $x_1 > 0$ and $x_2 > 0$

$$\begin{aligned}
&\textbf{(ii)} && \frac{\partial f}{\partial x_2} < 0 \\
&\textbf{(iii)} && \frac{\partial f}{\partial x_1} x_1 + \frac{\partial f}{d x_2} x_2 < 0 \\
&\textbf{(iv)} && \frac{\partial g}{\partial x_2} \leqslant 0 \\
&\textbf{(v)} && \frac{\partial g}{\partial x_1} x_1 + \frac{\partial g}{d x_2} x_2 > 0 \\
&\textbf{(vi)} && f(0, 0) > 0 \\
&\textbf{(vii)} && f(0, A) = 0 \\
&\textbf{(viii)} && f(B, 0) = 0 \\
&\textbf{(ix)} && f(C, 0) = 0 \\
&\textbf{(x)} && B > C
\end{aligned} \tag{I.19}$$

where $A$, $B$ and $C$ are three positive quantities, then this system has either a stable point of equilibrium or a stable limit cycle.

## A.3 Some general theorems[1]

We will introduce some valuable theorems that we will accept without proving them (for proofs of these theorems see Goh 1980).

*Local stability: the real parts of the eigenvalues of the Jacobian matrix must be negative*

Suppose the autonomous system (I.1) has a positive equilibrium at $\mathbf{n}^*$ and let $x_i = n_i - n_i^*$ for $i = 1, 2, \ldots, S$ denote a small departure of each species density from its equilibrium value. Performing a first order Taylor expansion around the equilibrium we get:

$$\begin{aligned} n_i f_i(\mathbf{n}) &= n_i^* \left( f_i(\mathbf{n}^*) + \sum_{j=1}^{S} \frac{\partial f_i(\mathbf{n})}{\partial n_j} \bigg|_{\mathbf{n}^*} x_j + O(x^2) \right) \\ &= n_i^* \left( 0 + \sum_{j=1}^{S} \frac{\partial f_i(\mathbf{n})}{\partial n_j} \bigg|_{\mathbf{n}^*} x_j + O(x^2) \right). \end{aligned} \tag{I.20}$$

Therefore, substituting equation (I.20) into (I.1) and using equation (I.4), the linearized dynamics is given by

$$\frac{dx_i}{dt} = \sum_{j=1}^{S} n_i^* J_{ij} x_j \qquad i = 1, \ldots, S. \tag{I.21}$$

It turns out that we have this valuable theorem for continuous time models:

**Theorem 1.** *The equilibrium* $\mathbf{n}^* = (n_1^*, n_2^*, \ldots, n_S^*)$ *of an autonomous continuum time system is locally stable if all the real parts of the eigenvalues of the Jacobian matrix* $J_{ij} \equiv \frac{\partial f_i(\mathbf{n})}{\partial n_j}\big|_{\mathbf{n}^*} n_i^*$ *are negative.*

Thus this theorem generalizes the two stability analysis for bi-dimensional systems of the previous section.

In the case of a Lotka–Volterra generalized linear model we have:

$$\frac{dn_i}{dt} = r_i n_i \left( 1 + \sum_{j=1}^{S} a_{ij} n_j \right) \qquad i = 1, \ldots, S. \tag{I.22}$$

And thus we have,

$$J_{ij} = r_i a_{ij} n_i^* \tag{I.23}$$

[1] This section is mainly based on chapters 1, 3 and 5 of the thorough study on stability by Goh (1980) and chapter 2 of May (1974).

The equilibrium $\mathbf{n}^*$ is locally stable if all the real parts of the eigenvalues of the matrix $[r_i a_{ij} n_i^*]$ are negative. Note that in general the stability properties of the matrix $[r_i a_{ij} n_i^*]$ are different from those of the matrix $\mathbf{A} = [a_{ij}]$.

For the discrete time description (I.1′), to first order, we have:

$$x_i(t+1) = \sum_{j=1}^{S} \frac{\partial G_i(\mathbf{n})}{\partial n_j}\bigg|_{\mathbf{n}^*} x_j. \tag{I.21′}$$

And, a theorem similar to theorem 1 but for discrete time models (Goh 1980) is:

**Theorem 1′.** *The equilibrium* $\mathbf{n}^* = (n_1^*, n_2^*, \ldots, n_S^*)$ *of a set of discrete difference equations is locally stable if the modulus of all the eigenvalues of the matrix* $\frac{\partial G_i(\mathbf{n})}{\partial n_j}|_{\mathbf{n}^*}$ *are less than one.*

*Global stability: Lyapunov functions*

There exists a method to determine whether a system is globally stable. It involves finding a function known as a *Lyapunov function*. The problem is that the existence of a Lyapunov function is often difficult to determine for multispecies models and, consequently, this approach has a limited utility. The discussion will be facilitated by considering physical systems analogous to the biological ones.

Consider an autonomous system of differential equations

$$dx_i/dt = f_i(\mathbf{x}) \tag{I.24}$$

with a fixed point at $\mathbf{x}^* = (x_1^*, x_2^*, \ldots, x_S^*)$.

Definition: A *Lyapunov function*, for this system is a continuously differentiable, real valued function $V(\mathbf{x})$ with the following properties:

i. $V(\mathbf{x}) > 0$ for all $\mathbf{x} \neq \mathbf{x}^*$, and $V(\mathbf{x}^*) = 0$. (We say that $V$ is *positive definite*.)

ii. $\frac{dV(x)}{dt} = \sum_{i=1}^{S} \frac{\partial V}{\partial x_i}\frac{dx_i}{dt} = \sum_{i=1}^{S} \frac{\partial V}{\partial x_i} f_i(\mathbf{x}) < 0$ for all $\mathbf{x} \neq \mathbf{x}^*$. (All trajectories flow 'downhill' toward $\mathbf{x}^*$.)

**Theorem 2.** *The equilibrium* $\mathbf{x}^*$ *of an autonomous continuum time system is locally asymptotically stable, i.e. for all initial conditions* $\mathbf{x}(t) \to \mathbf{x}^*$, *as* $t \to \infty$, *if there exists a Lyapunov function for* $\mathbf{x}^*$.

Intuitively, under conditions **i.** and **ii.**, all trajectories move monotonically down the graph of $V(\mathbf{x})$ toward $\mathbf{x}^*$ (figure I3).

For physical systems the direct method of Lyapunov generalizes the principle that a system, which continuously dissipates energy until it attains an equilibrium, is

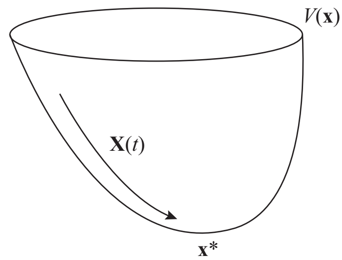


**Figure I3.** The solutions cannot get stuck anywhere else because if they did, $V$ would stop changing, but by assumption, $dV/dt < 0$ everywhere except at $\mathbf{x}^*$.

stable. If a physical system, for example a vibrating spring and mass, dissipates energy over time and the energy is never restored then eventually the system must reach some final resting state. This final state is called the *attractor*. However, finding a function that gives the precise energy of a physical system can be difficult, and for biological systems, the concept of energy may not be applicable. Lyapunov's realization was that stability can be proven without requiring knowledge of the true physical energy, provided a Lyapunov function can be found to satisfy the above constraints.

Goh (1977) has discussed a Lyapunov function that fits all Lotka–Volterra models:

$$V(\mathbf{n}) = \sum_{i=1}^{S} \mathrm{k}_i (n_i - n_i^* - n_i \ln(n_i/n_i^*)), \tag{I.25}$$

where the $k_i$ are constants. If the $k_i$ exist such that $dV/dt$ is always negative except at $\mathbf{n}^*$ (where it is zero) then the system is globally stable.

The problem is how to obtain the $k_i$ so that they satisfy condition $dV/dt < 0$. For simple examples this is easy, but for more complicated examples it is not.

*Ruling out closed orbits*

Closed orbits can be ruled out for the following systems[2]:

(A) ***Gradient systems***

That is, suppose the system can be written in the form $d\mathbf{x}/dt = -\nabla V$, for some continuously differentiable, single-valued scalar function $V(\mathbf{x})$ (this vector equality is written for each coordinate $i$ as $dx_i/dt = -\partial V/\partial x_i$). Such a system is called a *gradient* with *potential function V*.

(B) **Systems with a Lyapunov function**

If a Lyapunov function exists, then closed orbits are forbidden

[2] For proofs we refer the reader to section 7.2 of Strogatz (1994).

*Poincaré–Bendixson theorem*

The Poincaré–Bendixson theorem is the main tool which historically has been used to show that a dynamical system has a stable cycle limit.

> **Poincaré–Bendixson Theorem**
>
> Suppose that:
>
> (i) $R$ is a closed, bounded subset of the plane;
>
> (ii) $d\mathbf{x}/dt = \mathbf{f}(\mathbf{x})$ is a continuously differentiable vector field on an open set containing $R$;
>
> (iii) $R$ does not contain any fixed points;
>
> (iv) There exists a trajectory $\mathcal{C}$ that is 'confined' in $R$, this means that it starts in $R$ and stays in $R$ for all future time.
>
> Then either $\mathcal{C}$ is a closed orbit, or it spirals toward a closed orbit as $t \to \infty$. Thus, in either case, $R$ ***contains a closed orbit***.

For a proof of this theorem we refer the interested reader to Coddington and Levinson (1955) *or* Wiggins (1990).

## References

Coddington E A and Levinson N 1955 The Poincaré–Bendixson theory of two-dimensional autonomous systems *Theory of Ordinary Differential Equations* (New York: McGraw-Hill) pp 389–403

Goh B S 1977 Global stability in many species systems *Am. Nat.* **111** 135–43

Goh B-S 1980 *Management and Analysis of Biological Populations* (Amsterdam: Elsevier)

Gurel O and Lapidus L 1968 Stability via Liapunov's second method *Ind. Eng.Chem.* **60** 1–26

LaSalle J and Lefschetz S 1961 *Stability by Liapunov's Direct Method* (New York: AcademicPress)

May R M 1974 *Stability and Complexity in Model Ecosystems* (Princeton, NJ: Princeton University Press)

Schultz D G 1965 The generation of Liapunov functions *Advances in Control Systems* vol 2 ed. C T Leondes (New York: Academic)

Strogatz S H 1994 *Nonlinear dynamics and chaos. With Applications to Physics, Biology, Chemistry, and Engineering* (Reading, MA: Perseus)

Wiggins S 1990 *Introduction to Applied Nonlinear Dynamical Systems and Chaos* (New York: Springer)

Willems J L 1970 *Stability Theory of Dynamical Systems* (London: Nelson)

**IOP** Publishing

Ecological Modelling and Ecophysics

Agricultural and environmental applications

**Hugo Fort**

# Appendix II

## Fermi problems or back-of-the-envelope calculations

A **Fermi problem, Fermi question, or Fermi estimate** is an estimation problem based on heuristic methods. Named for the 20th century physicist Enrico Fermi, such problems typically involve making justified guesses about quantities that seem impossible to compute given limited available information.

Fermi was known for his ability to make good approximate calculations with little or no data. One well-documented example is his estimate of the yield of the atomic bomb detonated during the Trinity test, based on the distance traveled by pieces of paper dropped from his hand during the blast. Fermi's estimate of 10 kilotons of TNT was remarkably close to the now-accepted value of around 20 kilotons.

Let us consider a first Fermi problem:

'How much oil (in barrels) is consumed in the United States per year?' To answer this question we will split the problem into two simpler quantities to estimate:

First, let us estimate how much oil is used by cars every year.

Secondly, we will increase the estimate to account for non-automotive uses.

A typical solution might include the following assumptions and estimations:

1. There are approximately 330 000 000 people in the United States.
2. On average, each person owns a car, so let us say the number of cars $N_c \sim 3 \times 10^8$.
3. What about the number of gallons consumed per capita per day or year? Let us estimate this quantity in two different ways. (A) Thinking how frequently you refill the tank of your car at a gas station; e.g. every ten days. This implies an average consumption of 13 gallons every ten days or more roughly one gallon per day. (B) Using the annual average mileage of a car; maybe around 10 000 miles. A typical value for the miles per gallon (mpg) for a car is around 25. This gives 10 000/25 = 400 gallons per year or, once again, roughly one gallon per day.

doi:10.1088/978-0-7503-2432-8ch6

4. A rough and simple estimation of the fraction of oil used by cars is 1/2; the other half is used for other means of transportation (trucks, buses, trains, boats, planes, etc), for heating and cooling and for manufacturing plastics and chemicals, as well as many lubricants, waxes, tars, asphalts, pesticides and fertilizers.

From these assumptions:

$$\text{Oil used by cars per day} = (3 \times 10^8 \text{ cars}) \times (1 \text{ gallon per car per day})$$
$$= 3 \times 10^8 \text{ gallons d}^{-1}.$$

How many gallons does a barrel contain? The answer is 42. But suppose we do not know. We can estimate it using that a barrel costs around \$50 and the average US price of regular-grade gasoline is \$2.50. If we assume that half of the price of a gallon of gas (\$1.25) is the cost required to produce the oil, we get that a barrel contains roughly 50/1.25 = 40. Not so bad! Thus we have:

$$\text{Oil used by cars per day} = 3 \times 10^8 \text{ gallons d}^{-1}/40 \text{ gallon barrel}^{-1}$$
$$= 7.5 \times 10^6 \text{ barrels d}^{-1}$$

Therefore, we have a total consumption of oil of:

$$\text{Oil used in US per day} = 2 \times 7.5 \times 10^6 \text{ barrels d}^{-1} = 15 \text{ million barrels d}^{-1}$$

Or equivalently,

$$\text{Oil used in US per year} = 365 \times 15 \times 10^6 \text{ barrels d}^{-1} \approx 5 \times 10^9 \text{ barrels y}^{-1}$$

Let us perform a second estimation:

The world consumes around 100 millions of oil barrels per day. The US GDP represents between 15% (measured in purchasing power parity PPP) and 25% (measured in US \$) of the world GDP. Let us assume that the same proportionality holds true for the oil consumption. Therefore, we get 15–25 million barrels $d^{-1}$. If we take the midpoint we get 20 million barrels $d^{-1}$.

Notice the lower estimate is exactly the number we estimated before using a different procedure! But this is just a coincidence. Actually, overall, there were an estimated 272.48 million vehicles registered in 2017. The figures include passenger cars, motorcycles, trucks, buses, and other vehicles (Statista 2019a). So if we remove the number of trucks and buses it turns out we overestimated the number of cars by more than 10% (and probably more than 15%). However, our estimation of the fraction of the gasoline consumed by cars of 1/2 was quite accurate: in 2018, consumption of finished motor gasoline averaged about 9.33 million b/d (392 million gallons per day), which was equal to about 45% of total US petroleum consumption according to the US Energy Information Administration (EIA 2019a). Additionally, we also had luck when estimating the number of gallons in a barrel with an error of only 5%. Nevertheless, notice that had we performed this same estimation five years ago, when the price of the oil barrel was around \$100, we would have gotten a much worse estimate of 80 gallons per barrel!

The true value for 2018 was 20.5 million barrels of petroleum per day, or a total of about 7.5 billion barrels of petroleum per year (EIA 2019b). Thus, we underestimated the number of barrels consumed in the US by 25% according to our first estimation and by less than 3% according to our second estimation. Not so bad, remember that the goal of Fermi problems is to estimate quantities with scarce information within one order of magnitude from its actual value. Therefore, overall we can assume our guesses were not quite off the mark.

Another Fermi problem could be: 'How many shopping malls $S$ there are in the USA?'

The total number of customers $C$ is smaller but comparable with the population of the US, $N$, say $C = 2/3 \times N$, then we will estimate $S$ by dividing the total amount of money all the shopping malls receive from customers by the average net profits all the owners of stores of an average shopping mall make.

Let us call the average percentage of net profits of a retail store, $p$.

Now, owning a business means risking your money, dealing with employees, etc. Therefore, we assume that, on average, the owner makes more money than employees. This implies that the mean profits of a store > mean income ($i$); say $3 \times i$.

An average consumer spends, say a percentage $q$ of her/his income in shopping malls.

If we denote by $n$ the average number of stores in a shopping mall, thus we have

$$3 \times i \times S \times n = C \times i \times (q/100) \times (p/100).$$

So we see that $i$ cancels out because it multiplies in both sides of the equality, so we get:

$$S = 2/3 \times N \times q \times p/(3 \times n \times 10^4)$$

Now we have to put numerical values for the percentages $p$ and $q$, say: $p = 10\%$, $q = 20\%$ and for n, say, on average, $n = 20$ stores per shopping mall. Thus we finally get:

$$S = 2 \times 3.3 \times 10^8 \times 20 \times 10/(9 \times 20 \times 10^4) = 73\,333.$$

According to Statista (2019b) there are 116 000 shopping malls in the US.

According to the US Bureau of Labor Statistics (2020), an average consumer spends \$11 185 in 'other goods and services' from the \$67 241 average income after taxes (this number does not include other expenses like food away from home, etc). Therefore, we can estimate $q$ as 16.6%.

According to this NYU Stern database for more than 7000 US companies (Stern 2020) in many different industries, **the average profit margin is $p$ = 7.9% for all companies and 6.9% for more than 6000 companies excluding financials**.

## Additional Fermi problems

Try your hand at the following problems. Remember, you are not expected to get the 'right' answer, and you will not be rewarded for extra accuracy, but you do need to clearly show your reasoning at each step. After solving these problems by estimation, search the Web for the 'true' answer.

I. Estimate the total number of cattle in the world.
II. How much milk is produced in the US each year?
III. Estimate the total number of hairs on your head.
IV. How many commercial planes are flying simultaneously over the US?

## References

EIA 2019a https://www.eia.gov/energyexplained/oil-and-petroleum-products/use-of-oil.php

EIA 2019b https://www.eia.gov/tools/faqs/faq.php?id=33&t=6

Statista 2019a https://www.statista.com/statistics/183505/number-of-vehicles-in-the-united-states-since-1990/

Statista 2019b https://www.statista.com/statistics/208059/total-shopping-centers-in-the-us/

Stern 2020 http://pages.stern.nyu.edu/~adamodar/New_Home_Page/datafile/margin.html

US Bureau of Labor Statistics 2020 https://www.bls.gov/news.release/wkyeng.nr0.htm

# Glossary

| | |
|---|---|
| **Adiabaticity or quasistatic evolution** | A slow process in which all time derivatives are very small. |
| **Attractor** | In dynamical systems, an attractor is a set of numerical values toward which a system tends to evolve, for a wide variety of starting conditions of the system. System values that get close enough to the attractor values remain close even if slightly disturbed, in such a way that all trajectories not contained in that region will eventually wind up in the region. An attractor may be a point or a cycle that is an equilibrium and generates transients that return to the equilibrium state after perturbation. It may also be an attractive region that has no individual equilibrium points or cycles (a chaotic or strange attractor). |
| **Autonomous dynamical system** | A system of ordinary differential equations which does not explicitly depend on the independent variable. When the independent variable is time, they are also called time-invariant systems. |
| **Basin of attraction** | For each attractor, its basin of attraction is the set of initial conditions leading to long-time behavior that approaches that attractor. That is, the collection of points that converge on a particular attractor. |
| **Bifurcation** | A bifurcation occurs when a small smooth change made to the parameter values (the 'bifurcation' parameters) of a system causes a sudden 'qualitative' or topological change in its behavior. |
| **Bifurcation diagram** | A graph of the attractors of a system as a function of some parameter (the 'bifurcation' parameter). It shows the values visited or approached asymptotically (fixed points, periodic orbits, or chaotic attractors) of a system as a function of this bifurcation parameter in the system. |
| **Bifurcation, local** | A local bifurcation occurs when a parameter change causes the stability of an equilibrium (or fixed point) to change. In continuous systems, this corresponds to the real part of an |

doi:10.1088/978-0-7503-2432-8ch7

| | |
|---|---|
| | eigenvalue of an equilibrium passing through zero. In discrete systems (those described by maps rather than ODEs), this corresponds to a fixed point having an eigenvalue with modulus equal to one. In both cases, the equilibrium is **non-hyperbolic** (at least the real part of one eigenvalue becomes zero) at the bifurcation point. The topological changes in the phase portrait of the system can be confined to arbitrarily small neighborhoods of the bifurcating fixed points by moving the bifurcation parameter close to the bifurcation point (hence 'local'). By contrast, global bifurcations cannot be revealed by eigenvalue degeneracies. |
| **Bifurcation, normal form of** | In mathematics, the normal form of a dynamical system is a simplified form that can be useful in determining the system's behavior. Normal forms are often used for determining local bifurcations in a system. All systems exhibiting a certain type of bifurcation are said to be locally (around the equilibrium) topologically equivalent to the normal form of the bifurcation. |
| **Bifurcation point** | A point of structural instability in which a single equilibrium condition is split into two. |
| **Carrying capacity** | The maximum attainable size of a population, usually symbolized as $K$. |
| **Catastrophe or Imperfect bifurcation** | A catastrophe occurs when the stability of an equilibrium breaks down, causing the system to jump into another state. This jump could be truly catastrophic for the equilibrium of a bridge or a building or a species that extinguishes. Catastrophes can be also regarded as *imperfect bifurcations*, often described by the addition of an imperfection parameter to the **normal form of a bifurcation**. |
| **Competitive exclusion principle** | Sometimes referred to as Gause's law, is the proposition that two species competing for the same limiting resource cannot coexist at constant population values. When one species has even the slightest advantage over another, the one with the advantage will dominate in the long term. This result can be derived from the Lotka–Volterra competition equations: if interspecific competition between two species is sufficiently large, the equilibrium of both species coexisting is unstable. |
| **Density dependence** | The condition in which the rate at which a population increases or decreases is a function of its density (in contrast with density independence) |
| **Dynamical system** | A means of describing how one state develops into another state over the course of time in terms of a system of equations. These equations describe the time dependence of a point's position in its ambient (geometrical) space. *Dynamical systems theory* brings a qualitative and geometrical approach to the analysis of ordinary differential equations (ODEs), addressing the existence, stability, and global behavior of sets of solutions, rather than seeking exact or approximate expressions for individual solutions. |

**Equilibrium point** The value of a variable that does not change under the rules of a dynamical system. An equilibrium point may be stable (in which case it is commonly referred to as an **attractor**) or unstable (in which case it is commonly referred to as a **repeller**).

**Euler's constant** Approximately 2.7183, the base of natural logarithms, normally symbolized by a lowercase *e*.

**Facultative mutualism** Mutualism in which one species can survive without its mutualist but performs better with it.

**Ferromagnetism** The basic mechanism by which certain materials, such as iron and nickel, form permanent magnets. Microscopically the ferromagnetism is explained in terms of the electrons contained in the material. Specifically, one of the fundamental properties of an electron is that it has a magnetic dipole moment, i.e. it behaves itself as a tiny magnet. When these tiny magnetic dipoles are aligned in the same direction, their individual magnetic fields add together to create a measurable macroscopic magnetic field.

**Functional response** In consumer–resource (predator–prey) equations, the function that stipulates how the per capita consumption rate (or predation rate) changes with changes in resource density.

**Gause principle** See **Competitive exclusion principle.**

**Hamiltonian** The mathematical descriptor for the energy of a given interaction. The total Hamiltonian describes all energies of all the interactions that affect the system.

**Intraspecific competition** The competitive interaction among individuals in the same population.

**Intrinsic rate of natural increase** The growth of a population under the theoretical state of extremely low population density, usually symbolized as $r$.

**Isocline or Nullcline** In population dynamics, the term isocline refers to the set of population sizes at which the rate of change for one population in a pair of interacting populations is zero. More generally, for a dynamical system, the set of all points for which one of the variables does not change, so that the time derivative is equal to zero.

**Limit cycle** An oscillatory system that can be either stable (an oscillatory attractor) or unstable (an oscillatory repeller).

**Logistic equation** Sometimes called the Verhulst model or logistic growth curve, is a model of population growth first published by Pierre Verhulst (1845). The model is continuous in time, but a modification of the continuous equation to a discrete quadratic recurrence equation known as the logistic map is also widely used.

**Logistic population growth** Population growth that appears qualitatively exponential at low population density but approaches an asymptote as the population becomes larger; population growth that follows the logistic equation.

**Malthus equation** The simplest population equation describing an exponentially growing population, introduced by Thomas R Malthus in 1798.

**Mean-field approximation (MFA)** In physics and probability theory, the mean-field approximation consists in approximating a random (stochastic) model by a simpler model that results from averaging over degrees of freedom. Such models consider many individual components that interact with each other. The effect of all the other individuals on any given individual is approximated by a single averaged effect, thus reducing a **many-body problem** to a **one-body problem**.

**Metastability** In physics, metastability is a stable state of a dynamical system other than the system's state of least energy. In isolation the state of least energy is the only one the system will inhabit for an indefinite length of time, until more external energy is added to the system. That is, the system will spontaneously leave any other state (of higher energy) to eventually return (after a sequence of transitions) to the least energetic state. A ball resting in a hollow on a slope is a simple example of metastability. If the ball is only slightly pushed, it will settle back into its hollow, but a stronger push may start the ball rolling down the slope.

**Nullcline = Isocline = Zero growth line**

**Obligate mutualism** Mutualism in which one species is unable to survive without its mutualist.

**Ordinary differential equations (ODEs)** A differential equation containing one or more functions of one independent variable and the derivatives of those functions. The term *ordinary* is used in contrast with the term partial differential equation (PDE) which may be with respect to *more than* one independent variable.

**One-dimensional map** A function $f$ that projects a single variable $x_t$ through discrete time $t$, $x_{t+1} = f(x_t)$. For example, in the logistic map $f(x_t) = rx_t(1 - x_t)$.

**Partial differential equation (PDE)** A differential equation that contains several unknown variables and their partial derivatives (i.e. the derivative with respect to one of those variables, with the others held constant). PDEs are used to formulate problems involving functions of several variables, typically space coordinates and time. A special case is ordinary differential equations (ODEs), which deal with functions of a single variable and their derivatives.

**Population** A group of individual items. In the context of population ecology, a population is a group of individual living organisms.

**Repeller** A point or cycle that is theoretically an equilibrium but generates transients that deviate from the equilibrium position when perturbed.

**Separatrix** The boundary between two basins of attraction.

**Simulation** A numerical simulation is a calculation that is run on a computer following a program that implements a mathematical model for a physical system. Numerical simulations are required to study the behavior of systems whose

| | |
|---|---|
| | mathematical models are too complex to provide analytical solutions, as in most nonlinear systems. |
| **Strange attractor** | A chaotic attractor. A region of space that attracts all trajectories but contains no attractive points or cycles. |
| **Structural stability** | A higher-level stability concept in which the qualitative nature of a system is unchanged when the parameters of the system are varied. |
| **Structured models** | Models that do not assume that all individuals in the population are identical. E.g. models can be spatially-structured (spatial heterogeneous environment), age-structured or sex-structured. |
| **Vector field** | The set of vectors that determine the behavior of a dynamic system. |
| **Zero growth line = Nullcline = Isocline** | |