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Methods for Mathematical Modeling I

Intended for students of

First Year Master in Biomathematics (M1)

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May 1, 2025

General introduction

Mathematical modeling has become an essential component of research and studies in ecology. This book is intended for undergraduate and master's level students who wish to acquire mathematical modeling techniques in ecology and epidemiology. It introduces fundamental concepts of mathematical modeling, focusing on deterministic dynamic systems, particularly ordinary differential equations.

The book also presents a series of classical models in population dynamics and ecology. It aims to provide a rigorous yet accessible introduction to these methods, making them understandable not only for mathematicians but also for students from various scientific backgrounds, including life sciences, who may not have prior training in dynamic systems.

Numerous examples and exercises illustrate the techniques presented, allowing students to practice and apply them to real ecological problems.

We hope that students with a mathematical background will find clear explanations of qualitative analysis methods for dynamic systems—methods they may already be familiar with—along with numerous applications in ecology. Likewise, we hope that students with a biological background will find a comprehensive and accessible introduction to the main techniques used to study dynamic systems, as well as their implementation in classical ecological models such as the Lotka-Volterra model, Holling's model, and many others.

This book is a synthesis of the authors' teaching experience in mathematical modeling applied to ecology. While primarily intended for students, doctoral candidates, postdoctoral researchers, and academics looking to acquire or deepen their knowledge in this field will also find it useful. Many researchers in both public and private institutions study complex natural and social systems, and mathematical modeling has become an indispensable tool in modern research to understand the mechanisms governing these systems' dynamics.

Although several books cover similar topics, most of them are written in English. This book aims to make mathematical modeling methods in ecology more accessible to a wider audience. It brings together a broad range of classical mathematical models in ecology, some of which are traditionally scattered across different sources, while also introducing some original models. Students will find a comprehensive collection of commonly used models in ecology, while researchers will have a fundamental reference for constructing and analyzing mathematical models relevant to their work.

The book is organized into chapters that are either methodological or applied. The methodological chapters introduce techniques for analyzing mathematical models which includes the continuous-time models. The applied chapters use these techniques to study population and community dynamics. We provide an overview of population growth models and interaction models between two species (e.g., predator-prey, host-parasitoid, competition, mutualism). We also discuss models of multi-species interactions within trophic networks and structured population models incorporating age classes.

Contents

Chapter 1

Model for the dynamics of one population

Introduction

The study of population dynamics plays a fundamental role in understanding biological, ecological, and environmental systems. A key aspect of this analysis relies on mathematical modeling, particularly through differential equations, which provide a formal framework for describing the evolution of a population over time under various influences.

In this chapter, we focus on the dynamics of a single population using a first-order differential equation. We begin by analyzing equilibrium points and their local stability, which allows us to determine under what conditions a population remains constant or evolves. To deepen this study, we introduce phase portraits, which offer a graphical representation of the system's behavior.

A central element of our analysis is the study of the local stability of equilibrium points using the Taylor expansion. This mathematical tool allows us to approximate the behavior of a function around a given point and gain insights into the stability of the system. We also examine the particular case where the stability coefficient λ^* is zero, requiring a more in-depth analysis by considering higher-order terms in the Taylor expansion.

To illustrate these theoretical concepts, we present concrete examples highlighting the stability of equilibrium points. Furthermore, we introduce the notion of hyperbolic equilibria, a key concept in nonlinear dynamics, which helps classify equilibrium points based on their stability properties.

1.1 Study of a First-Order Differential Equation

Definition 1 (First-Order Differential Equation)**.** *Let t be a real variable and $x(t)$ a differentiable function of t with real values, where in our case, t represents time. A first-order differential equation has the general form:*

$$\frac{dx}{dt} = f(x, t). \tag{1.1}$$

If the function f depends explicitly on time, the equation (1.1) *is said to be non-autonomous. Conversely, if f does not explicitly depend on time, the equation is called autonomous:*

$$\frac{dx}{dt} = f(x). \tag{1.2}$$

We will limit our study to autonomous equations. Equation (1.2) is classified as a first-order equation because it involves only the first derivative of x. The equation is said to be *linear* if the function f is a first-degree polynomial in x. Otherwise, it is *nonlinear*.

A **solution** $x(t, x_o)$ of the differential equation is a function of time that satisfies the equation. It can be interpreted as describing the motion of a point whose position x changes over time. A particular solution depends on the initial condition x_o, i.e., the value of the variable at an initial time t_o:

$$x_o = x(t_o). \tag{1.3}$$

When the function $f(x)$ is continuously differentiable over an interval $I \subset \mathbb{R}$, the existence and uniqueness of the solution for any initial condition $x_o \in I$ are guaranteed. More precisely, we have the following theorem.

Théorèm 2 (Existence and Uniqueness). *Consider the differential equation given by* (1.2)*, where the function f is defined on an open interval $I \subset \mathbb{R}$. If f is continuously differentiable on I, then for any initial condition $x_o \in I$, there exists a positive real number T and a function x defined on $[-T, T] \times \{x_o\}$ such that $x(t, x_o)$ is a solution of the differential equation for all $t \in [-T, T]$. Moreover, the solution is unique: if y is also a solution of the differential equation, then for all $t \in [-T, T]$,*

$$x(t, x_o) = y(t, x_o). \tag{1.4}$$

Example: Solving a Linear Differential Equation

Example 3. *Solve the following differential equation:*

$$\frac{dx}{dt} = ax. \tag{1.5}$$

Solution*: This is a separable differential equation, meaning it can be rewritten as:*

$$\frac{dx}{x} = adt, \tag{1.6}$$

where the left-hand side involves only x and the right-hand side only t. The solution is obtained by integrating both sides:

$$\ln |x| - \ln |x_o| = a(t - t_o), \tag{1.7}$$

which simplifies to:

$$x(t, x_o) = x_o e^{a(t-t_o)}. \tag{1.8}$$

Assuming $x_o > 0$, the behavior of the solution depends on the sign of a: - If $a > 0$, the function grows exponentially over time. - If $a < 0$, the function decays exponentially. - If $a = 0$, the solution remains constant.

The differential of the function $f(x)$ represents the variation of this function corresponding to an infinitesimal change dx in the variable x. The differential is denoted by df and is defined by the following expression:

$$df = \frac{df}{dx} dx.$$

More precisely, we have the following definition.

Definition 4. *Let f be a function from $\mathbb{R}$ to $\mathbb{R}$. The differential of the function f is a function from $\mathbb{R}$ to $\mathbb{R}$ that associates to each x the value $\frac{df}{dx}(x)$. The notation dx represents the mapping that associates to each x the value 1, i.e., $dx(x) = 1$.*

For example, the differential of the function $f(x) = \sin^2(x)$ is given by:

$$df = 2\sin(x)\cos(x)dx.$$

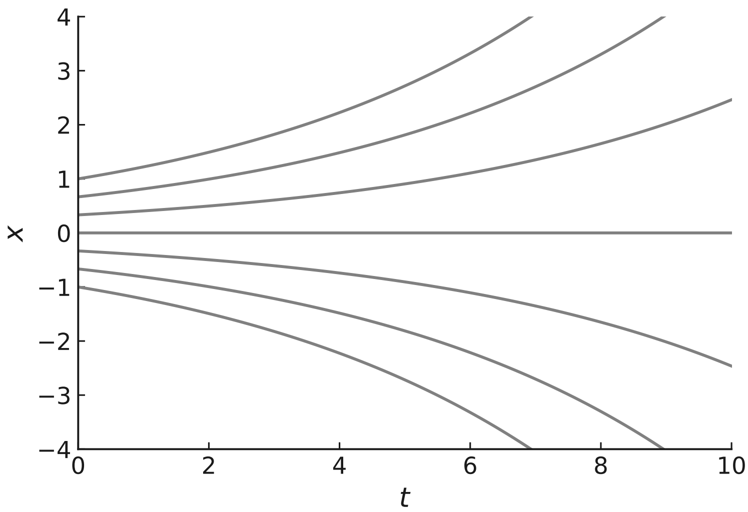

Figure 1.1: Graph of the solutions $x(t, x_0)$ for different initial values.

1.1.1 Equilibrium Points, Local Stability, and Phase Portraits

In general, solving the differential equation (1.2) explicitly is not always possible. Therefore, we perform a qualitative analysis of its solutions. This analysis begins with the search for equilibrium points (also called singularities, stationary points, fixed points, or simply equilibria) of the differential equation. At an equilibrium point, the velocity vanishes:

$$\frac{dx}{dt} = 0.$$

Equilibrium points, denoted as x^*, satisfy the equation:

$$f(x^*) = 0.$$

A differential equation can have a single equilibrium point, multiple equilibrium points, or none. When multiple equilibria exist, it is useful to index them as x_i^*, where $i \in [1, N]$ and N is the number of equilibrium points.

For example, the differential equation:

$$\frac{dx}{dt} = \sin(x)$$

has equilibrium points that satisfy $\sin(x) = 0$, leading to an infinite number of equilibria:

$$x_k^* = k\pi, \quad k \in \mathbb{Z}.$$

1.1.2 Local Stability of an Equilibrium Point

The next step is to determine whether an equilibrium point is locally stable. To do so, we consider a point $x(t)$ in the neighborhood of an equilibrium x^*. Let us define a new local variable:

$$u(t) = x(t) - x^*.$$

The variable $u(t)$ is equal to zero when $x(t) = x^*$. We now seek the differential equation governing $u(t)$ when $u(t)$ remains small, i.e., when $x(t)$ stays in the vicinity of x^*. Since x^* is a constant, we have:

$$\frac{du}{dt} = \frac{dx}{dt} = f(x).$$

As $x(t)$ remains close to the equilibrium x^*, we expand $f(x)$ in a first-order Taylor series around x^*:

$$\frac{du}{dt} = f(x^*) + \frac{df}{dx}(x^*)(x - x^*) + o(x - x^*).$$

Using the definition of equilibrium, $f(x^*) = 0$, we obtain:

$$\frac{du}{dt} = \lambda^* u + o(u),$$

where $\lambda^* = \frac{df}{dx}(x^*)$. Neglecting the higher-order term $o(u)$, the differential equation above admits the following solution:

$$u(t) = u(0)\exp(\lambda^* t).$$

The stability of the fixed point is determined by the sign of λ^*:

- If $\lambda^* < 0$, then $u(t)$ tends to 0 as $t \to +\infty$, implying that $x(t)$ converges to x^*. The equilibrium is said to be *stable*. Any solution starting in the vicinity of x^* returns to it.

- If $\lambda^* > 0$, then $u(t)$ tends to $\pm\infty$, depending on the sign of $u(0)$, meaning that $x(t)$ moves away from x^*. The equilibrium is *unstable*. Any nearby initial condition results in a trajectory that diverges from x^*.

- If $\lambda^* = 0$, the linearization does not provide information about the local dynamics. In this case, it is necessary to consider higher-order terms in the Taylor expansion of $f(x)$ near x^*.

Remark: The stability discussed here is *local*, meaning that the criterion applies only in the vicinity of the equilibrium x^*, since we have neglected terms that are small only in that neighborhood. Figure 1.3 presents the phase portraits, which represent the equilibrium point and the evolution of trajectories in its vicinity along the x-axis. The

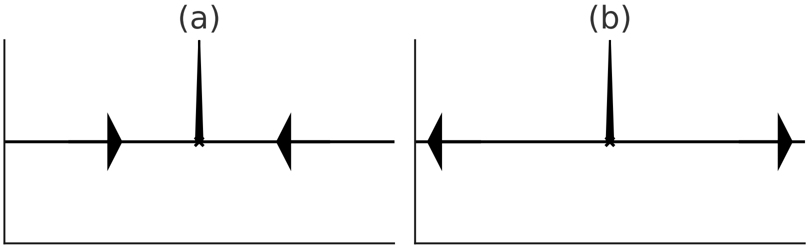

Figure 1.2: (a) Phase portrait of a stable equilibrium. (b) Phase portrait of an unstable equilibrium.

arrows indicate the sign of the derivative $\frac{dx}{dt} = f(x)$, pointing towards positive x if $x(t)$ increases with time and towards negative x if $x(t)$ decreases with time.

Consequently, the arrows are directed towards the equilibrium from both sides when it is stable, as shown in Figure 1.3 (a), meaning that any trajectory with an initial condition in the neighborhood of the equilibrium returns to it. On the contrary, they are directed away from the equilibrium if it is unstable, as illustrated in Figure 1.3 (b).

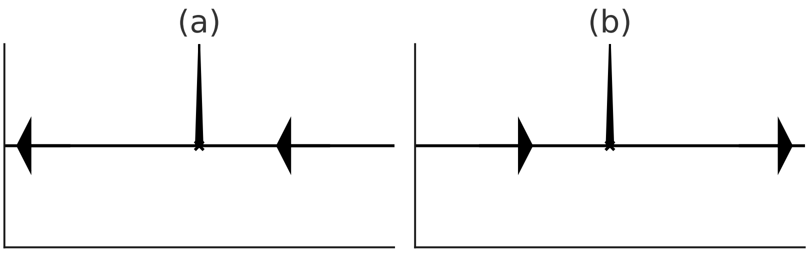

Figure 1.3: (a) Phase portrait of a positive shunt. (b) Phase portrait of a negative shunt.

1.1.3 Reminder on the Taylor Expansion of a Function $f(x)$ Around a Point $\bar{x}$

The Taylor expansion of a function $f(x)$ in the neighborhood of a point $\bar{x}$ is given by the following expression:

$$f(x) = f(\bar{x}) + \frac{df}{dx}(\bar{x})(x-\bar{x}) + \frac{1}{2!}\frac{d^2 f}{dx^2}(\bar{x})(x-\bar{x})^2 + \cdots + \frac{1}{n!}\frac{d^n f}{dx^n}(\bar{x})(x-\bar{x})^n + o((x-\bar{x})^n),$$

where $o((x-\bar{x})^n)$ is called the "little-o" notation of $(x-\bar{x})^n$, which represents a function that tends to 0 faster than $(x-\bar{x})^n$ as $x \to \bar{x}$.

Alternatively, we can write:

$$o((x-\bar{x})^n) = (x-\bar{x})^n \cdot \epsilon(x),$$

where $\epsilon(x)$ is a function that tends to 0 as $x \to \bar{x}$.

A *first-order approximation* consists of truncating the series from the second-degree term onward.

1.1.4 Case of $\lambda^* = 0$

The case where $\lambda^* = 0$ requires special treatment. In this scenario, the equilibrium point may be stable, unstable, or lead to two new types of phase portraits, illustrated in Figure 1.3. These are referred to as *positive shunt* and *negative shunt*, depending on whether the velocity is positive or negative on both sides of the equilibrium point. These two types of equilibria are also known as *semi-stable equilibria*, a terminology that extends to multiple-variable cases.

1.1.5 Examples

1) $\frac{dx}{dt} = f(x) = x^2$

This equation has a single equilibrium at $x = 0$. The derivative $\frac{df}{dx} = 2x$ is zero at equilibrium, so we have $\lambda^* = 0$. However, for all x, $\frac{dx}{dt} > 0$, meaning this corresponds to a "positive shunt".

2) $\frac{dx}{dt} = f(x) = -x^2$

Again, we have $\lambda^* = 0$, but here, for all x, $\frac{dx}{dt} < 0$, indicating a "negative shunt".

3) $\frac{dx}{dt} = f(x) = x^3$

Here, $\lambda^* = 0$, but the sign of $\frac{dx}{dt}$ changes when crossing the fixed point. In this case, the equilibrium is "unstable".

4) $\frac{dx}{dt} = f(x) = -x^3$

In this case, we still have $\lambda^* = 0$, but now the equilibrium is **stable**.

1.1.6 Higher-Order Terms in the Taylor Expansion

The four previous examples illustrate that when $\lambda^* = 0$, it becomes necessary to consider higher-order terms in the Taylor series expansion around the equilibrium point. When the first-order term vanishes, the second-order expansion is given by:

$$\frac{du}{dt} = \frac{1}{2}\frac{d^2 f}{dx^2}(x^*)(x - x^*)^2 + o((x - x^*)^2) = \frac{1}{2}\frac{d^2 f}{dx^2}(x^*)u^2 + o(u^2).$$

The nature of the equilibrium point is determined by the sign of the second derivative $\frac{d^2 f}{dx^2}(x^*)$: - If it is positive, the equilibrium corresponds to a **positive shunt**. - If it is negative, it corresponds to a **negative shunt**.

If the second-order term is also zero, we must consider the third-order term, leading to the expression:

$$\frac{du}{dt} = \frac{1}{3!}\frac{d^3 f}{dx^3}(x^*)u^3 + o(u^3).$$

In this case: - If the third derivative is positive, the point is **locally unstable**. - If it is negative, the point is **locally stable**.

More generally, by identifying the first nonzero derivative of order n, we can determine the local stability nature of the equilibrium.

1.1.7 Definition of Hyperbolic Equilibria

Definition 1.4: An equilibrium x^* of the differential equation

$$\frac{dx}{dt} = f(x)$$

is called **hyperbolic** if $\frac{df}{dx}(x^*) \neq 0$.

Hyperbolic equilibria have the particular property that the local behavior of the differential equation can be understood solely by analyzing the derivative $f'(x^*)$.

From a practical perspective, it is also useful to plot the graph of the function $f(x)$. The differential equation

$$\frac{dx}{dt} = f(x)$$

shows that equilibrium points correspond to the zeros of $f(x)$, and the sign of $f(x)$ determines whether the solution $x(t)$ increases ($f(x) > 0$) or decreases ($f(x) < 0$) over time. This approach provides both local and global insights into the system's dynamics.

1.1.8 Example: Stability of Equilibria

Exercise: Determine the equilibrium points of the differential equation and analyze their local stability:

$$\frac{dx}{dt} = x^3 - 4x^2 - 11x + 30 = f(x).$$

Solution: We rewrite the equation as:

$$\frac{dx}{dt} = (x-2)(x+3)(x-5).$$

This equation has three equilibrium points:

$$x_1^* = -3, \quad x_2^* = 2, \quad x_3^* = 5.$$

Computing the derivative:

$$\frac{df}{dx} = 3x^2 - 8x - 11.$$

Evaluating at the equilibria:

$$\lambda_1^* = 40, \quad \lambda_2^* = -15, \quad \lambda_3^* = 24.$$

Thus: - x_1^* and x_3^* are **unstable**. - x_2^* is **stable**.

Exercise: Analyze the equilibria and their stability for the differential equation:

$$\frac{dx}{dt} = \sin(x).$$

Solution: This equation has an infinite number of equilibrium points:

$$x_k^* = k\pi, \quad k \in \mathbb{Z}.$$

To determine their stability, we compute the first derivative:

$$\lambda_k^* = \frac{df}{dx}(x_k^*) = \cos(x_k^*).$$

$$\lambda_k^* = 1, \quad \text{if } k = 2p,$$

$$\lambda_k^* = -1, \quad \text{if } k = 2p + 1,$$

where p is an integer.

- The origin ($x = 0$) is **unstable**, surrounded by two stable points at $\pm\pi$. - This pattern continues, with an alternating sequence of stable and unstable points occurring at intervals of π.

The phase portrait is illustrated in Figure 1.5, while Figure 1.6 presents qualitative solution curves for different initial conditions. The arrows indicate the direction of variation (growth or decay) of $x(t)$ between equilibrium points.

Different differential equations can exhibit qualitatively equivalent dynamic behaviors. This motivates grouping equations into categories with similar phase portraits.

Definition 5. *Two ordinary differential equations are called* ***qualitatively equivalent*** *if they share the same phase portrait—i.e., the same number of equilibrium points, with identical stability properties, arranged in the same order.*

Exercise: Determine which of the following differential equations are qualitatively equivalent:

- $\frac{dx}{dt} = x^2$
- $\frac{dx}{dt} = x^2 - 9$
- $\frac{dx}{dt} = \cosh(x) - 1$
- $\frac{dx}{dt} = x(1 - x)$
- $\frac{dx}{dt} = (x - 1)(3 + x)$

Solution: By sketching the phase portraits, one can verify that:
- Systems (1) and (3) are **qualitatively equivalent**.
- Systems (2) and (5) are also **qualitatively equivalent**.

Chapter 2

Two interacting populations

Introduction

The study of dynamical systems modeling interactions between two populations plays a crucial role in mathematical biology, ecology, and various applied sciences. These models help describe and predict the evolution of species, competition between organisms, predator-prey relationships, and even interactions in economic and social systems.

This chapter focuses on the mathematical formulation and analysis of two interacting populations through differential equations. We begin with the study of first-order differential equations, followed by the linearization process near equilibrium points. A key tool in this analysis is the Taylor expansion, which allows us to approximate nonlinear systems and understand their local behavior.

We then explore linear systems of two ordinary differential equations and their solutions, classifying different cases based on the nature of eigenvalues. The typology of planar linear systems is introduced, considering cases such as distinct real eigenvalues, double real eigenvalues, and complex conjugate eigenvalues. These cases help in understanding the qualitative behavior of phase portraits, including stable and unstable equilibria, node types, spirals, and limit cycles.

Additionally, we study dynamical systems in continuous time, introducing concepts such as topological equivalence, Lyapunov functions for stability analysis, and the existence of limit cycles. The divergence criterion is also discussed as a tool for determining the presence or absence of periodic solutions.

Beyond planar systems, the chapter extends to non-planar systems and general linear systems in dimension n, culminating with the Routh-Hurwitz criteria for determining stability conditions. These results provide a strong foundation for analyzing more complex population dynamics and nonlinear interactions in multi-species systems.

This chapter thus establishes fundamental concepts and analytical methods essential for studying two-species interactions, serving as a foundation for more advanced models in population dynamics and ecological systems.

2.1 Study of a First-Order Differential Equation

The general form of a system of two autonomous ordinary differential equations is given by:

$$\begin{cases} \dot{x} = f(x, y), \\ \dot{y} = g(x, y), \end{cases} \tag{2.1}$$

where we use the simplified notation for the derivative of the variable x with respect to time, denoted by a dot above it, i.e., $\dot{x} = \frac{dx}{dt}$. The system is defined by the functions f and g, which are generally nonlinear functions of the variables x and y. One can think of a moving point in a plane whose coordinates depend on time, $(x(t), y(t))$. The velocity of the moving point is defined by the vector with components $(\dot{x} = f(x, y), \dot{y} = g(x, y))$. Consequently, equations (2.53) determine the components of the velocity vector at every point in the plane. Given an initial condition (x_0, y_0), which defines the position of the moving point at an initial reference time t_0, i.e., $x_0 = x(t_0)$ and $y_0 = y(t_0)$, the moving point will follow a trajectory in the plane.

The set of positions occupied successively over time, starting from the initial condition, forms a particular trajectory. The collection of all such trajectories constitutes the phase portrait.

The system (2.53) uniquely defines a velocity vector at each point in the plane. An important consequence is that two trajectories can never intersect at a point in the plane, except at an equilibrium. Indeed, if two trajectories intersected transversally, there would be two different velocities at the same point (x, y), which contradicts the uniqueness of the velocity at each point. This result is a consequence of the Cauchy theorem on the existence and uniqueness of solutions for an autonomous differential system with given initial conditions (x_0, y_0). It is stated as follows:

Théorèm 6. *Consider an open set $U \subset \mathbb{R}^2$ where the differential system* (2.53) *is defined, and where the functions f and g are differentiable with continuous derivatives. Suppose that the point (x_0, y_0) belongs to the open set U. Then, there exists a strictly positive real number T such that the system* (2.53) *with initial condition $(x(0), y(0)) = (x_0, y_0)$ admits a unique solution $(x(t), y(t))$ for all $t \in [-T, T]$.*

In other words, if a point in the phase space is not an equilibrium, its trajectory is a unique curve locally (and therefore globally). As a result, trajectories cannot cross in the phase space.

2.2 Linearization Near an Equilibrium Point

The approach for studying a system of two differential equations is partially the same as that used for a single equation. The first step consists of finding the equilibria and determining their local stability properties. An equilibrium point (x^*, y^*) of system (1.5) is a point where the velocity is zero. An equilibrium point is thus defined by the following relations:

$$f(x^*, y^*) = 0, \tag{2.2}$$

$$g(x^*, y^*) = 0. \tag{2.3}$$

A system of ordinary differential equations may have no equilibrium points, one equilibrium point, or multiple equilibrium points. In the latter case, they need to be indexed as (x_i^*, y_i^*), where $i \in [1, N]$ and N is the number of equilibrium points. To obtain information about the local stability of an equilibrium point, we linearize the system in the neighborhood of each equilibrium point. Let $(u(t), v(t))$ be the local coordinates near a given equilibrium point (x^*, y^*):

$$u(t) = x(t) - x^*, \tag{2.4}$$

$$v(t) = y(t) - y^*. \tag{2.5}$$

If the local variables $u(t)$ and $v(t)$ tend to 0, then the trajectory converges to the equilibrium (x^*, y^*). To linearize, as in the case of a single equation, we seek the system of equations governing the variables (u, v) by making a first-order approximation in the neighborhood of the equilibrium point:

$$\dot{u} = \dot{x} = f(x, y) = f(x^*, y^*) + \frac{\partial f}{\partial x}(x^*, y^*)(x - x^*) + \frac{\partial f}{\partial y}(x^*, y^*)(y - y^*) + \dots, \tag{2.6}$$

$$\dot{v} = \dot{y} = g(x, y) = g(x^*, y^*) + \frac{\partial g}{\partial x}(x^*, y^*)(x - x^*) + \frac{\partial g}{\partial y}(x^*, y^*)(y - y^*) + \dots. \tag{2.7}$$

Using the equilibrium point conditions, i.e., $f(x^*, y^*) = g(x^*, y^*) = 0$, and substituting the local coordinates into the equations, while neglecting higher-order terms in the Taylor expansion, we obtain the following linearized system:

$$\dot{u} = \frac{\partial f}{\partial x}(x^*, y^*)u + \frac{\partial f}{\partial y}(x^*, y^*)v, \tag{2.8}$$

$$\dot{v} = \frac{\partial g}{\partial x}(x^*, y^*)u + \frac{\partial g}{\partial y}(x^*, y^*)v. \tag{2.9}$$

This system can be rewritten in matrix form:

$$\begin{bmatrix} \dot{u} \\ \dot{v} \end{bmatrix} = \begin{bmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix}. \tag{2.10}$$

The previous matrix of partial derivatives, which we denote by A, is called the Jacobian matrix:

$$A = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}, \tag{2.11}$$

where a_{ij} is the (i, j) coefficient of the Jacobian matrix. The linear model is obtained by computing the Jacobian at the equilibrium point of the system:

$$\begin{bmatrix} \dot{u} \\ \dot{v} \end{bmatrix} = \begin{bmatrix} a_{11}^* & a_{12}^* \\ a_{21}^* & a_{22}^* \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix}, \tag{2.12}$$

where $a_{ij}^* = a_{ij}(x^*, y^*)$. The linear model (1.11) is also called the linear part of system (1.5) near an equilibrium. This model is simpler than the nonlinear system it originates from because it is linear. However, it is only a first-order approximation of system (1.5) and is valid only in an immediate neighborhood of an equilibrium point of this system.

2.2.1 Reminder on Taylor Expansions in Two Dimensions

Let $f(x,y)$ be a function of two variables. The Taylor expansion of $f(x,y)$ in the neighborhood of a point $(\bar{x},\bar{y})$ up to order n is given by:

$$f(x,y) = f(\bar{x},\bar{y}) + \frac{\partial f}{\partial x}(x-\bar{x}) + \frac{\partial f}{\partial y}(y-\bar{y}) + \frac{1}{2!}\left(\frac{\partial^2 f}{\partial x^2}(x-\bar{x})^2 + \frac{\partial^2 f}{\partial y^2}(y-\bar{y})^2\right) \tag{2.13}$$

$$+\frac{\partial^2 f}{\partial x \partial y}(x-\bar{x})(y-\bar{y}) + \cdots + \frac{1}{n!}\left(\frac{\partial f}{\partial x}(x-\bar{x}) + \frac{\partial f}{\partial y}(y-\bar{y})\right)^n + \ldots, \tag{2.14}$$

where we use the symbolic notation of power expansion. In this notation, the term of power $(p, n-p)$ corresponds to the nth derivative $\frac{\partial^n f}{\partial x^p \partial y^{n-p}}$. All derivatives are evaluated at $(\bar{x},\bar{y})$.

2.3 Linear System of Two Ordinary Differential Equations

In the previous section, we obtained a linear model by making a first-order approximation in the neighborhood of an equilibrium of the nonlinear system. It is now necessary to find the solutions of a linear system in two dimensions. The general form of a linear system of two ordinary differential equations is as follows:

$$\dot{x} = a_{11}x + a_{12}y, \tag{2.15}$$

$$\dot{y} = a_{21}x + a_{22}y, \tag{2.16}$$

or equivalently,

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}, \tag{2.17}$$

where $A = [a_{ij}]$ is a constant coefficient matrix. In the case of linearization around an equilibrium, the matrix A is the Jacobian matrix evaluated at the equilibrium.

First, it is easy to see that a system of two ordinary differential equations is equivalent to a second-order ordinary differential equation. Indeed, differentiating the first equation with respect to time gives:

$$\ddot{x} = a_{11}\dot{x} + a_{12}\dot{y} = a_{11}\dot{x} + a_{12}(a_{21}x + a_{22}y). \tag{2.18}$$

From the first equation of the linear system, we obtain:

$$y = \frac{1}{a_{12}}(\dot{x} - a_{11}x). \tag{2.19}$$

After substitution into the previous equation, we obtain a second-order linear equation for the variable x:

$$\ddot{x} - (a_{11} + a_{22})\dot{x} + (a_{11}a_{22} - a_{12}a_{21})x = 0, \tag{2.20}$$

which can be rewritten in terms of the trace ($\operatorname{tr} A = a_{11} + a_{22}$) and determinant ($\det A = a_{11}a_{22} - a_{12}a_{21}$) of the matrix A:

$$\ddot{x} - \operatorname{tr} A\dot{x} + \det A x = 0. \tag{2.21}$$

The inverse result is also valid, meaning that a second-order equation can be transformed into a system of two first-order differential equations. Given a second-order equation:

$$\ddot{x} + b\dot{x} + cx = 0, \tag{2.22}$$

this equation can be rewritten as a system of two first-order differential equations by setting $\dot{x} = y$:

$$\dot{x} = y, \tag{2.23}$$

$$\dot{y} = \ddot{x} = -by - cx. \tag{2.24}$$

It is often useful to switch between these forms. We will now use the Jordan forms of 2×2 matrices to find solutions to the linear system. We refer the reader to the linear algebra appendix for methods to transform a two-dimensional matrix into its real Jordan form.

2.4 Solutions of a Linear System in Dimension 2

Consider a linear system of two ordinary differential equations of the form:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}. \tag{2.25}$$

Let $A = (a_{ij})$ be the matrix of constant coefficients of the linear system. We seek the solution of this system for a given initial condition:

$$x(0) = x_0,$$
$$y(0) = y_0.$$

The method we will use involves several steps:

1. Perform a change of basis to transform the matrix into its Jordan form;

2. Solve the system in the new basis;

3. Transform back to the original basis.

In the linear algebra appendix, we see that there are different Jordan forms depending on the sign of the discriminant of the characteristic equation. We will distinguish these different cases.

2.4.1 Case of Two Distinct Real Eigenvalues

In the original basis, the system is written in the form (1). In this case, the discriminant of the characteristic equation associated with the matrix A is positive, meaning that this matrix has two distinct real eigenvalues λ_1 and λ_2.

Recall the formulas used to change from the original basis (x, y) to the Jordan basis (u, v):

$$\begin{pmatrix} x \\ y \end{pmatrix} = P \begin{pmatrix} u \\ v \end{pmatrix},$$

$$\begin{pmatrix} u \\ v \end{pmatrix} = P^{-1} \begin{pmatrix} x \\ y \end{pmatrix},$$

where P is the matrix used to transform the matrix A into its Jordan form. In this case, the matrix P has in its first column the eigenvector m_1 associated with the first eigenvalue λ_1, and in its second column the eigenvector m_2 associated with the second eigenvalue λ_2. Thus, we have:

$$J = P^{-1}AP = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}. \tag{2.26}$$

In the new basis, the system takes the following simple form:

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}, \tag{2.27}$$

which results in two decoupled equations:

$$\dot{u} = \lambda_1 u,$$
$$\dot{v} = \lambda_2 v.$$

The obvious solution to this system is:

$$u(t) = ge^{\lambda_1 t},$$
$$v(t) = de^{\lambda_2 t},$$

where g and d are integration constants. The solution in the original basis is obtained by transforming back:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = P \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} = \begin{pmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{pmatrix} \begin{pmatrix} ge^{\lambda_1 t} \\ de^{\lambda_2 t} \end{pmatrix}. \tag{2.28}$$

Expanding, we obtain:

$$x(t) = gm_{11}e^{\lambda_1 t} + dm_{12}e^{\lambda_2 t},$$
$$y(t) = gm_{21}e^{\lambda_1 t} + dm_{22}e^{\lambda_2 t}.$$

This can also be written as:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = g \begin{pmatrix} m_{11} \\ m_{21} \end{pmatrix} e^{\lambda_1 t} + d \begin{pmatrix} m_{12} \\ m_{22} \end{pmatrix} e^{\lambda_2 t}. \tag{2.29}$$

The constants g and d are determined by the initial conditions.

2.4.2 Case of a double real eigenvalue

With an appropriate change of basis, the matrix can be transformed into its Jordan form. In this new basis, the system is written as:

$$\begin{pmatrix} u' \\ v' \end{pmatrix} = \begin{pmatrix} \lambda_0 & 1 \\ 0 & \lambda_0 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}.$$

In this case, recall that the transformation matrix has its first column as the eigenvector m_0 associated with the double eigenvalue λ_0, and its second column is an independent vector m:

$$P = \begin{pmatrix} m_{10} & m_1 \\ m_{20} & m_2 \end{pmatrix}.$$

The second equation of the linear system is decoupled from the first:

$$v' = \lambda_0 v,$$

and can be easily solved:

$$v(t) = de^{\lambda_0 t},$$

where d is an integration constant. Substituting this solution into the first equation leads to a first-order differential equation with a forcing term:

$$u' = \lambda_0 u + v,$$

or equivalently:

$$u' - \lambda_0 u = de^{\lambda_0 t}.$$

The solution to this equation is:

$$u(t) = (dt + g)e^{\lambda_0 t},$$

where g is another integration constant. The solution of the original system is obtained by transforming back to the initial basis:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = P \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} = \begin{pmatrix} m_{10} & m_1 \\ m_{20} & m_2 \end{pmatrix} \begin{pmatrix} (dt + g)e^{\lambda_0 t} \\ de^{\lambda_0 t} \end{pmatrix}.$$

Expanding, we obtain:

$$x(t) = e^{\lambda_0 t}(gm_{10} + dm_1 + dm_{10}t),$$

$$y(t) = e^{\lambda_0 t}(gm_{20} + dm_2 + dm_{20}t).$$

The constants g and d are determined by the initial conditions.

2.4.3 Case of Two Complex Conjugate Eigenvalues

With an appropriate change of basis, the matrix A can be put into Jordan form. In this new basis, the system is written as:

$$\begin{pmatrix} u \\ v \end{pmatrix}' = \begin{pmatrix} a & -b \\ b & a \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}.$$

In this case, recall that the matrix A has two complex conjugate eigenvalues (the reader may refer to the appendix on complex numbers if necessary):

$$\lambda_1 = a + ib, \quad \lambda_2 = a - ib,$$

and that the transition matrix has in its first column the vector associated with the imaginary part and in its second column the vector corresponding to the real part of the conjugate eigenvectors:

$$P = \begin{pmatrix} b_1 & a_1 \\ b_2 & a_2 \end{pmatrix}.$$

The system of equations is thus written as:

$$\begin{cases} u' = au - bv, \\ v' = bu + av. \end{cases}$$

To solve this system, we perform a coordinate transformation. This can be done in two ways, theoretically equivalent but differing slightly in practical implementation. The first approach uses only real numbers but requires more calculations than the second, which relies on complex numbers.

Method 1: Polar Coordinates

The first method transforms the rectangular coordinates (u, v) into polar coordinates (r, θ), where:

$$r = \sqrt{u^2 + v^2}, \quad \tan\theta = \frac{v}{u},$$

and also:

$$u = r\cos\theta, \quad v = r\sin\theta.$$

Differentiating $r^2 = u^2 + v^2$ leads to:

$$rr' = uu' + vv' = u(au - bv) + v(bu + av) = a(u^2 + v^2) = ar^2.$$

Thus, the equation governing r is:

$$r' = ar,$$

with the solution:

$$r(t) = ge^{at},$$

where g is an integration constant.

Similarly, for θ:

$$\frac{d}{dt}(\tan\theta) = \frac{uv' - vu'}{u^2} = \frac{u(bu + av) - v(au - bv)}{u^2} = b\frac{(u^2 + v^2)}{u^2} = b.$$

So, we obtain:

$$\theta' = b,$$

with the solution:

$$\theta(t) = bt + d,$$

where d is another integration constant.

From these, the solutions in the Jordan base are:

$$u(t) = r(t)\cos\theta(t) = ge^{at}\cos(bt + d),$$

$$v(t) = r(t)\sin\theta(t) = ge^{at}\sin(bt + d).$$

Returning to the original base:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = P\begin{pmatrix} u(t) \\ v(t) \end{pmatrix} = ge^{at}\begin{pmatrix} b_1 & a_1 \\ b_2 & a_2 \end{pmatrix}\begin{pmatrix} \cos(bt + d) \\ \sin(bt + d) \end{pmatrix}.$$

Expanding:

$$x(t) = ge^{at}(b_1\cos(bt + d) + a_1\sin(bt + d)),$$
$$y(t) = ge^{at}(b_2\cos(bt + d) + a_2\sin(bt + d)).$$

The constants g and d are determined by the initial conditions:

$$r(0) = g, \quad \theta(0) = d.$$

Method 2: Using Complex Numbers
The second approach uses complex notation, defining:

$$z(t) = u(t) + iv(t).$$

Then,
$$z' = u' + iv' = a(u + iv) + b(-v + iu) = az + ibz = \lambda_1 z.$$

This is a separable differential equation whose general solution is:

$$z(t) = Ce^{\lambda_1 t}.$$

Expanding the exponential:

$$e^{\lambda_1 t} = e^{at}e^{ibt} = e^{at}(\cos(bt) + i\sin(bt)).$$

Thus, the real solutions are:

$$u(t) = e^{at}(u(0)\cos(bt) - v(0)\sin(bt)),$$

$$v(t) = e^{at}(u(0)\sin(bt) + v(0)\cos(bt)).$$

Finally, the solutions $x(t), y(t)$ in the original base are obtained by multiplying $(u(t), v(t))$ by the transition matrix P.

Exercise
Solve the following linear systems:

1. $\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} 5 & -1 \\ 6 & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix},$

2. $\begin{pmatrix} x \\ y \end{pmatrix}' = \frac{1}{2} \begin{pmatrix} 5 & -1 \\ 1 & 3 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix},$

3. $\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} 3 & 4 \\ -2 & -1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix},$

with the initial condition $x(0) = 1, y(0) = 0$.

Solution
These are systems whose matrices have been transformed into Jordan form in the exercises of the linear algebra appendix, to which we refer the reader.

1. Distinct Real Eigenvalues.
   The eigenvalues of the associated matrix are distinct real numbers: $\lambda_1 = 3$, $\lambda_2 = 2$.
   The matrix is diagonalizable using the following transition matrix:

   $$P = \begin{pmatrix} 1 & 1 \\ 2 & 3 \end{pmatrix}.$$

   In the Jordan basis, the system is written as:

$$\begin{pmatrix} u \\ v \end{pmatrix}' = \begin{pmatrix} 3 & 0 \\ 0 & 2 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix},$$

whose solutions are:

$$u(t) = ge^{3t}, \quad v(t) = de^{2t}.$$

Returning to the original basis:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = P \begin{pmatrix} u(t) \\ v(t) \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 2 & 3 \end{pmatrix} \begin{pmatrix} u(t) \\ v(t) \end{pmatrix},$$

yielding:

$$x(t) = ge^{3t} + de^{2t}, \quad y(t) = 2ge^{3t} + 3de^{2t}.$$

Solving for the constants using initial conditions:

$$1 = g + d, \quad 0 = 2g + 3d.$$

Solving the system gives: $g = 3, d = -2$.

2. Repeated Real Eigenvalues.
   The matrix has a repeated real eigenvalue: $\lambda_0 = 2$. The transition matrix is:

$$P_1 = \begin{pmatrix} 1 & 2 \\ 1 & 0 \end{pmatrix}.$$

In the Jordan basis, the system transforms to:

$$\begin{pmatrix} u \\ v \end{pmatrix}' = \begin{pmatrix} 2 & 1 \\ 0 & 2 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix},$$

with solutions:

$$u(t) = (dt + g)e^{2t}, \quad v(t) = de^{2t}.$$

Returning to the original basis:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = P_1 \begin{pmatrix} u(t) \\ v(t) \end{pmatrix},$$

gives:

$$x(t) = e^{2t}(dt + g + 2d), \quad y(t) = e^{2t}(dt + g).$$

Solving for constants using initial conditions:

$$1 = g + 2d, \quad 0 = g,$$

yields $g = 0, d = \frac{1}{2}$.

3. Complex Eigenvalues.
The matrix has complex eigenvalues: $\lambda_1 = 1 + 2i$, $\lambda_2 = 1 - 2i$. The transition matrix is:

$$P = \begin{pmatrix} 0 & 2 \\ 1 & -1 \end{pmatrix}.$$

In the Jordan basis, the system is transformed into polar coordinates:

$$\dot{r} = r, \quad \dot{u} = 2,$$

with solutions:

$$r(t) = ge^t, \quad u(t) = 2t + d.$$

The rectangular coordinates solutions are:

$$u(t) = ge^t \cos(2t + d), \quad v(t) = ge^t \sin(2t + d).$$

Returning to the original basis:

$$x(t) = 2ge^t \sin(2t + d), \quad y(t) = ge^t(\cos(2t + d) - \sin(2t + d)).$$

Using initial conditions:

$$2g \sin d = 1, \quad \tan d = 1,$$

yields:

$$g = \frac{\sqrt{2}}{2}, \quad d = \frac{\pi}{4}.$$

2.5 Typology of Planar Linear Systems

We restrict our study to the case where $\det A \neq 0$. In the previous section, we presented the solutions of a system of two coupled linear equations:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}, \tag{2.30}$$

where $A = (a_{ij})$ is a matrix with constant coefficients. We distinguish three cases based on the eigenvalues of this matrix:

1. The eigenvalues are real and distinct.

2. There is a double real eigenvalue.

3. The eigenvalues are complex conjugates.

It is common to represent these different types of solutions in the plane of the trace and determinant of the matrix $(\operatorname{tr} A, \det A)$. To distinguish the three cases, we return to the characteristic equation (A.2) seen in the linear algebra appendix:

$$\lambda^2 - (\operatorname{tr} A)\lambda + \det A = 0. \tag{2.31}$$

Recall that for a second-degree equation $ax^2+bx+c=0$, the sum of the roots is given by $-\frac{b}{a}$ and the product of the roots by $\frac{c}{a}$. Consequently, if λ_1 and λ_2 are the eigenvalues (roots of the characteristic equation), we have the following relations:

$$\operatorname{tr} A = \lambda_1 + \lambda_2, \tag{2.32}$$

$$\det A = \lambda_1 \lambda_2. \tag{2.33}$$

The three cases mentioned above depend on the sign of the discriminant:

$$D = (\operatorname{tr} A)^2 - 4 \det A. \tag{2.34}$$

First, case (2) corresponds to $D = 0$, or equivalently $\det A = \frac{1}{4}(\operatorname{tr} A)^2$, which determines a parabola in the $(\operatorname{tr} A, \det A)$ plane passing through the origin with its axis oriented upwards.

Case (1) corresponds to $D > 0$, meaning points in the $(\operatorname{tr} A, \det A)$ plane located below this parabola.

Finally, case (3) corresponds to $D < 0$, meaning points located above the parabola.

Now we will examine these three cases in more detail.

2.5.1 Case of Two Distinct Real Eigenvalues

Recall that in this case, the matrix A can be written in Jordan form as:

$$J = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}. \tag{2.35}$$

The solutions in the Jordan basis are given by:

$$u(t) = g \exp(\lambda_1 t),$$
$$v(t) = d \exp(\lambda_2 t),$$

and thus, the nature of the trajectories depends on the sign of the eigenvalues. Three cases can be distinguished:

- If $\lambda_1 > 0$ and $\lambda_2 > 0$, both eigenvalues are positive. This corresponds to an **unstable node** (or a extbfsource). As $t \to +\infty$, the solutions $u(t)$ and $v(t)$ tend to infinity. All trajectories move away from the equilibrium point $(0, 0)$, making it unstable. In the $(\operatorname{tr} A, \det A)$ plane, unstable nodes are located below the parabola in the upper half-plane where $\det A > 0$, and in the region where $\operatorname{tr} A > 0$, since both the sum and product of the eigenvalues are positive.

- If $\lambda_1 < 0$ and $\lambda_2 < 0$, both eigenvalues are negative. This corresponds to a extbfstable node (or a extbfsink). As $t \to +\infty$, the solutions $u(t)$ and $v(t)$ tend to 0. All trajectories move towards the equilibrium point $(0, 0)$, making it stable. In the $(\operatorname{tr} A, \det A)$ plane, stable nodes are located below the parabola in the upper half-plane where $\det A > 0$, and in the region where $\operatorname{tr} A < 0$, since the sum of the eigenvalues is negative while their product is positive.

- If λ_1 and λ_2 have opposite signs, this corresponds to a extbfsaddle point. As $t \to +\infty$, one solution tends to $\pm\infty$ while the other tends to 0. The equilibrium point $(0, 0)$ is unstable. In the $(\operatorname{tr} A, \det A)$ plane, saddle points are located in the lower half-plane where $\det A < 0$ (Figure 1.13), since the product of the eigenvalues is negative.

2.5.2 Case of a Double Real Eigenvalue

In this case, the matrix can be written in the form:

$$J = \begin{pmatrix} \lambda_0 & 1 \\ 0 & \lambda_0 \end{pmatrix}. \tag{2.36}$$

In the $(\operatorname{tr} A, \det A)$ plane, these points lie exactly on the parabola. Two cases can be distinguished:

- If $\lambda_0 > 0$, it corresponds to a degenerate unstable node, where $\operatorname{tr} A > 0$.

- If $\lambda_0 < 0$, it corresponds to a degenerate stable node, where $\operatorname{tr} A < 0$.

The general behavior of the trajectories is very similar to that of a stable or unstable node and is not presented here.

2.5.3 Case of Two Complex Conjugate Eigenvalues

In this case, the matrix can be written in the form:

$$J = \begin{pmatrix} a & -b \\ b & a \end{pmatrix}. \tag{2.37}$$

Recalling that the eigenvalues of the matrix A are:

$$\lambda_1 = a + ib, \quad \lambda_2 = a - ib, \tag{2.38}$$

we can express the system in Jordan's basis using polar coordinates:

$$\dot{r} = ar, \quad \dot{\theta} = b, \tag{2.39}$$

whose solutions are:

$$r(t) = g \exp(at), \quad \theta(t) = bt + d. \tag{2.40}$$

The trajectory results from the combination of two motions: a rotational movement around the equilibrium point with a constant angular velocity b, and an approach or departure from the equilibrium point following an exponential function of time with factor a. Three cases can be distinguished:

- If $a > 0$, it corresponds to an *unstable focus*. As $t \to +\infty$, the solutions $u(t)$ and $v(t)$ spiral outward from the equilibrium point $(0, 0)$, which is therefore unstable. In the $(\operatorname{tr} A, \det A)$ plane, unstable foci are located above the parabola in the region where $\operatorname{tr} A = 2a > 0$.

- If $a = 0$, the two eigenvalues are purely imaginary, corresponding to a *center*. All trajectories form closed circles around the equilibrium point $(0, 0)$. In the $(\operatorname{tr} A, \det A)$ plane, centers are located above the parabola on the positive semi-axis where $\operatorname{tr} A = 0$ with $\det A > 0$.

- If $a < 0$, it corresponds to a *stable focus*. The trajectories spiral inward towards the equilibrium point $(0, 0)$, which is stable. In the $(\operatorname{tr} A, \det A)$ plane, stable foci are located above the parabola in the region where $\operatorname{tr} A = 2a < 0$.

The return to the original basis corresponding to the solutions in (x, y) does not modify the general shape of the trajectories since it is a linear transformation.

We do not present the cases corresponding to $\det A = 0$, which lead to other possible cases where one or both eigenvalues are zero.

2.5.4 Asymptotic Stability, Neutral Stability, Structural Stability

Consider the system of two coupled ordinary differential equations:

$$\dot{x} = f(x, y), \quad \dot{y} = g(x, y). \tag{2.41}$$

Let (x^*, y^*) be an equilibrium point of this system. The linearization of the system near this equilibrium leads to the following linear system:

$$\dot{u} = \frac{\partial f}{\partial x}(x^*, y^*)u + \frac{\partial f}{\partial y}(x^*, y^*)v, \quad \dot{v} = \frac{\partial g}{\partial x}(x^*, y^*)u + \frac{\partial g}{\partial y}(x^*, y^*)v, \tag{2.42}$$

where $(u(t), v(t))$ are the local coordinates near the equilibrium point, with $u(t) = x(t) - x^*$ and $v(t) = y(t) - y^*$.

This system can be rewritten in matrix form as:

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = A \begin{pmatrix} u \\ v \end{pmatrix}, \tag{2.43}$$

where

$$A = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}, \tag{2.44}$$

is the Jacobian matrix computed at the equilibrium point.

From the previous study, we can summarize that the local stability conditions are determined by two conditions:

$$\det A > 0, \quad \operatorname{tr} A < 0. \tag{2.45}$$

Under these conditions, any trajectory starting from an initial condition in the vicinity of the equilibrium point will return to it (stable node or focus).

Definition 7 (Stability of an Equilibrium Point). *An equilibrium point (x^*, y^*) of a system of type (1.16) is said to be stable if for any neighborhood V of (x^*, y^*), there exists a neighborhood $U \subseteq V$ such that any trajectory entering U remains in V for all future times.*

If the equilibrium is a *center*, it is stable but not asymptotically stable. To distinguish between different types of stability, we define *asymptotic stability* when the trajectory tends to the equilibrium point as $t \rightarrow +\infty$. When an equilibrium is stable but not asymptotically stable, we speak of *neutral stability*, meaning that the trajectory remains in the neighborhood of the equilibrium point without tending toward it as $t \rightarrow +\infty$. A point is said to be *unstable* when it is not stable. Consequently, unstable foci and nodes, as well as saddle points, are unstable.

Structural Stability

An important notion concerns the structural stability of a system. Unlike the previous stability concepts that deal with equilibrium points, structural stability concerns the system as a whole. To clarify this, consider a small perturbation of a system exhibiting a center at the origin.

Recall that the matrix corresponding to a center has the following form:

$$A = \begin{pmatrix} 0 & -b \\ b & 0 \end{pmatrix}, \tag{2.46}$$

because it corresponds to the case where the eigenvalues are purely imaginary $\lambda_{1,2} = \pm ib$.

Consider a small perturbation of the center by a diagonal matrix B_ϵ:

$$B_\epsilon = \begin{pmatrix} \epsilon & 0 \\ 0 & \epsilon \end{pmatrix}, \tag{2.47}$$

where $\epsilon \ll 1$ is an arbitrarily small parameter. The perturbation of the center is given by adding the matrix B_ϵ to the matrix A:

$$A + B_\epsilon = \begin{pmatrix} \epsilon & -b \\ b & \epsilon \end{pmatrix}. \tag{2.48}$$

The eigenvalues of this matrix are complex conjugates $\lambda_{1,2} = \epsilon \pm ib$, which no longer correspond to a center but to a stable or unstable focus, depending on the sign of ϵ. Thus, even an arbitrarily small perturbation B_ϵ destroys the center and induces a focus. We say that a differential system admitting a center is *not structurally stable.*

Conversely, a sufficiently small perturbation of a focus preserves the focus. Planar linear systems that satisfy $detA \neq 0$ and $trA \neq 0$ are *structurally stable.* However, systems where $\det A = 0$ are not structurally stable. Indeed, since the trace and determinant of a matrix continuously depend on its coefficients, if a matrix has a zero determinant, a sufficiently small perturbation can make the determinant strictly positive or strictly negative. This implies that one can obtain a saddle point, a node, or a focus for the equilibrium at $(0, 0)$ in systems arbitrarily close to the initial system.

Definition 8 (Hyperbolic Equilibrium). *An equilibrium is said to be hyperbolic if the Jacobian matrix at that equilibrium has eigenvalues with nonzero real parts.*

This definition extends the notion of a hyperbolic equilibrium seen in the previous chapter and can be generalized to systems with more than two equations. We have the following result:

Théorèm 9. *Let a differential system be defined on an open set U by the system (1.16), with f and g differentiable and having continuous partial derivatives on U. Suppose that this system has only one equilibrium in U and that this equilibrium is hyperbolic. Then the system is structurally stable.*

When the linearized model is structurally unstable, that is, by virtue of the previous theorem, the origin is not a hyperbolic equilibrium, it is evidently necessary to take into account the nonlinear terms to understand the true dynamics in the vicinity of the equilibrium point.

Structural stability is a very important concept and generalizes to all dynamical systems. Roughly speaking, structural stability means that the dynamics are robust and preserved under sufficiently small perturbations.

2.5.5 Phase Portrait Analysis in Planar Systems

Consider a system of two coupled ordinary differential equations of the form (1.16) admitting equilibrium points (x_i^*, y_i^*) with $i \in [1, N]$, where N is the number of equilibria. The methods presented in the previous sections allow us to determine the local stability of each equilibrium point. To determine the behavior of trajectories in the (x, y) plane, also known as the phase portrait, it is useful to identify the zero isoclines.

Zero isoclines are the loci of points in the (x, y) plane where one of the components of the velocity vector is zero. In two-dimensional systems, there are two types of zero isoclines:

- Isoclines satisfying $\dot{x} = f(x, y) = 0$, called vertical isoclines. The horizontal component (i.e., along the x-axis) of the velocity is zero. When a trajectory crosses a vertical isocline, the direction of the velocity vector, which is tangent to the trajectory, is vertical.

- Isoclines satisfying $\dot{y} = g(x, y) = 0$, called horizontal isoclines. The vertical component (i.e., along the y-axis) of the velocity is zero. When a trajectory crosses a horizontal isocline, the direction of the velocity vector is horizontal.

Clearly, equilibrium points must nullify both components of the velocity vector and are thus located at the intersections of horizontal and vertical isoclines. In practice, when possible, it is very useful to plot the isoclines to identify equilibrium points at their intersections. We now illustrate the procedure using an example.

Example: Analysis of a Planar Dynamical System. Consider the system of two coupled nonlinear ordinary differential equations:

$$\dot{x} = x - xy^2 = f(x, y), \tag{2.49}$$

$$\dot{y} = y - yx^2 = g(x, y). \tag{2.50}$$

First, we determine the equilibrium points, which satisfy:

$$f(x, y) = x(1 - y^2) = 0,$$

$$g(x, y) = y(1 - x^2) = 0.$$

It is evident that this system admits five equilibrium points: the origin $(0, 0)$, and the points $(-1, -1)$, $(-1, 1)$, $(1, -1)$, and $(1, 1)$.

The isoclines $\dot{x} = 0$ satisfy the equation $x(1 - y^2) = 0$, defining three lines: $x = 0$ and $y = \pm 1$. The isoclines $\dot{y} = 0$ satisfy the equation $y(1 - x^2) = 0$, defining three lines: $y = 0$ and $x = \pm 1$.

Figure shows the plot of the isoclines as well as the equilibrium points, which are indeed located at the intersections of the isoclines of different nature.

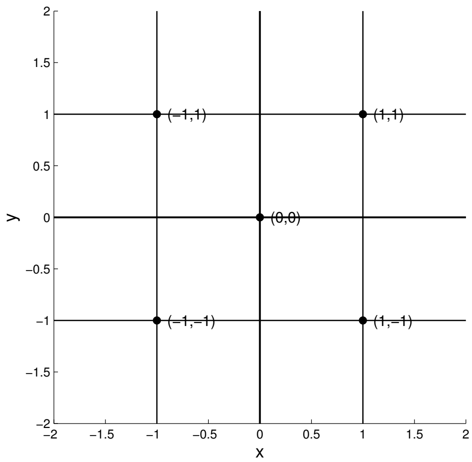

Figure 2.1: Zero isoclines of the system $\dot{x} = x - xy^2$, $\dot{y} = y - yx^2$. The equilibrium points are located at the intersections of the horizontal and vertical isoclines.

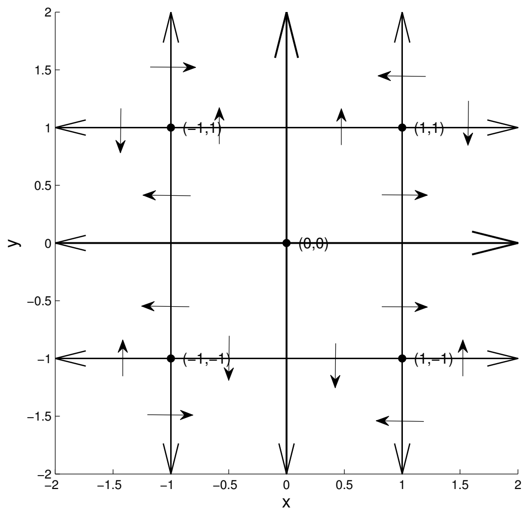

Figure 2.2: Velocity vector field for system $\dot{x} = x - xy^2$, $\dot{y} = y - yx^2$. The arrows indicate the direction and sense of the velocity vector in different regions of the plane.

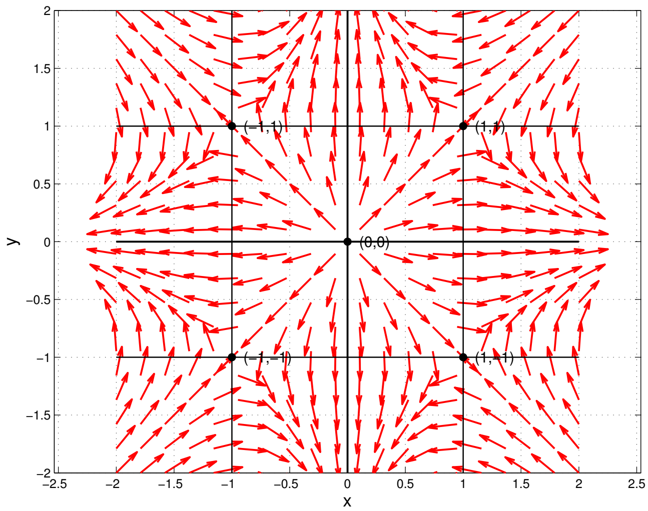

Figure 2.3: Phase portrait of system $\dot{x} = x - xy^2$, $\dot{y} = y - yx^2$. The local phase portrait near each equilibrium point corresponds to the prediction from linearization: saddle points at $(-1,-1)$, $(-1,1)$, $(1,-1)$, $(1,1)$, and an unstable node at the origin.

The next step is to linearize the system around each equilibrium point by computing the Jacobian matrix A:

$$A = \begin{bmatrix} 1 - y^2 & -2xy \\ -2xy & 1 - x^2 \end{bmatrix}.$$

To determine the local stability properties of the equilibria, we compute the Jacobian matrix at each equilibrium point.

At the origin, we obtain:

$$A(0,0) = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}.$$

This matrix is diagonal with a repeated positive eigenvalue $\lambda_0 = 1$. It corresponds to a degenerate unstable node, known as a star.

For the equilibrium points $(-1,-1)$ and $(1,1)$, we find:

$$A(-1,-1) = A(1,1) = \begin{bmatrix} 0 & -2 \\ -2 & 0 \end{bmatrix}.$$

Since $\operatorname{tr} A = 0$ and $\det A = -4$, these points correspond to saddle points ($\det A < 0$).

Similarly, for the remaining equilibrium points, we obtain:

$$A(-1,1) = A(1,-1) = \begin{bmatrix} 0 & 2 \\ 2 & 0 \end{bmatrix}. \tag{2.51}$$

We still have $\operatorname{tr} A = 0$ and $\det A = -4$, which again implies saddle points. The linearization has thus allowed us to show that the origin is an unstable node surrounded by four saddle points.

To sketch the trajectory behavior, it is common to analyze the direction and orientation of the velocity vector along an isocline. For example, the line $x = 0$ is a vertical isocline where $\dot{x} = 0$, meaning the velocity vector is purely vertical along this line. To determine its direction, we substitute $x = 0$ into the equation for the vertical component:

$$\dot{y} = y.$$

Since the sign of $\dot{y}$ matches that of y, the velocity vector points upward for $y > 0$ and downward for $y < 0$.

Similarly, for the horizontal isocline $y = 0$, we analyze the horizontal component:

$$\dot{x} = x.$$

Again, the sign of $\dot{x}$ matches that of x, so the velocity vector points rightward for $x > 0$ and leftward for $x < 0$.

Knowing the velocity direction along one isocline, we apply two key rules to deduce its behavior along other isoclines of the same type:

- *Continuity rule*: When two isoclines of the same nature intersect, the velocity vector at their intersection is common, and by continuity, it maintains the same direction on both isoclines. - *Equilibrium sign inversion rule*: The velocity vector reverses direction upon crossing an equilibrium point.

This last rule holds unless the determinant of the Jacobian matrix at the equilibrium is zero (i.e., $\det A = 0$), in which case a deeper analysis is required.

Applying these rules to our system allows us to determine the velocity vector direction across all isoclines. The zero isoclines divide the (x, y)-plane into several regions, and examining the general trend within each is also useful. The horizontal (resp. vertical) component of the velocity vector vanishes when crossing a vertical (resp. horizontal) zero isocline.

In our example, the application of these two rules allows us to determine the direction of the velocity vector along all the isoclines (see Figure 2.2). The zero isoclines divide the (x, y) plane into different compartments. It is also useful to examine the general trend within each of them. The horizontal (respectively vertical) component of the velocity vector cancels out when crossing a vertical (respectively horizontal) zero isocline. Figure 2.3 shows the direction of the velocity vectors at various points. The trajectories are tangent at each point to these directions.

Finally, it is possible to sketch the shape of the trajectories in the (x, y) plane while respecting the directions and sense of the velocity vector along the isoclines and within each compartment, taking into account the nature of the equilibrium points. Figure 2.3 presents the phase portrait for the given dynamical system. From this figure, we observe that as we approach an equilibrium point, the local phase portrait corresponds to the one predicted by linearization, that is, a saddle point for the four points $(-1, -1)$, $(-1, 1)$, $(1, -1)$, and $(1, 1)$, and an unstable node at the origin.

To conclude this section, we provide some definitions to characterize phase portraits and certain particular trajectories.

Definition 10. *Consider a solution $x(t)$ of system (1.16) such that $x(t)$ tends to an equilibrium x_1^* as $t \to -\infty$ and $x(t)$ tends to an equilibrium x_2^* as $t \to +\infty$. The trajectory associated with $x(t)$ is called a* ***heteroclinic trajectory****.*

Definition 11. *If $x_1^* = x_2^*$ in the previous definition, the trajectory is called a* ***homoclinic trajectory****.*

2.6 Study of Dynamical Systems in Continuous Time

The linearization of a system allows us to understand the behavior of trajectories in the vicinity of its equilibria. However, in some cases, the dynamics of the system and those of the linearized system do not correspond. Consider, for example, the following system:

$$\begin{aligned} \dot{x} &= x^2, \\ \dot{y} &= y. \end{aligned} \tag{2.52}$$

This system has a single equilibrium, the origin $(0, 0)$. The system consists of two decoupled equations: a positive shunt along the x-axis and an unstable point along the y-axis, leading to the phase portrait shown in Figure 2.4.

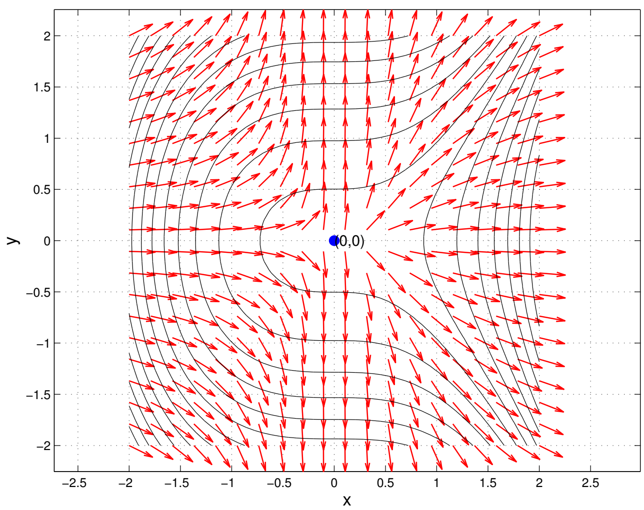

Figure 2.4: Phase portrait of the system $\dot{x} = x^2, \dot{y} = y$. The left part $(x < 0)$ corresponds to a saddle point, while the right part $(x > 0)$ corresponds to an unstable node.

2.6.1 Linearization Near the Origin

Linearization in the vicinity of the origin leads to the following system:

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}.$$

This is a case where the matrix of the linearized system has an eigenvalue equal to zero, with $\det A = 0$. The solution to this linear system is given by:

$$u(t) = g, \quad v(t) = de^t.$$

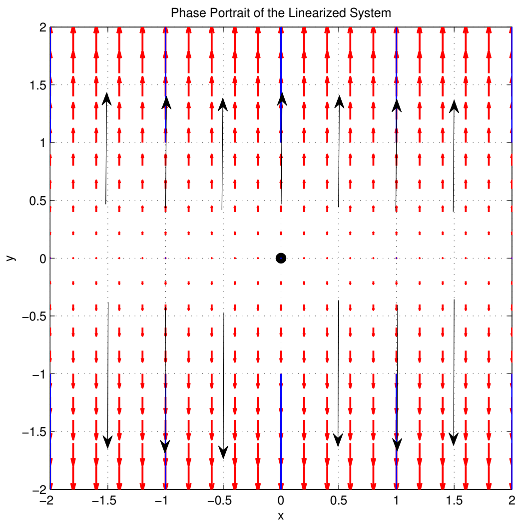

Figure 2.5: Phase portrait of the linearized system near the origin of the system $\dot{x} = x^2, \dot{y} = y$.

Figure 2.5 presents the phase portrait of the linearized system. A comparison between Figures 2.4 and 2.5 shows that the two phase portraits are different. As a consequence, the linearized system cannot be used to predict the dynamics of the nonlinear system, even in the vicinity of equilibrium. In this example, linearization fails. It is therefore important to understand under which conditions linearization is valid, which is the subject of the linearization theorem.

2.6.2 Definition and Theorem on Topological Equivalence

Definition 12 (Topological Equivalence)**.** *Let S_1 and S_2 be two differential systems defined on open sets $U \subset \mathbb{R}^2$ and $V \subset \mathbb{R}^2$, respectively. They (or their phase portraits) are said to be **topologically equivalent** if there exists a homeomorphism $H : U \to V$ such that the image of the phase portrait of S_1 under H is the phase portrait of S_2.*

This definition implies that the trajectories of the two vector fields resemble each other to the extent that one can be transformed into the other by a continuous transformation and vice versa.

Théorèm 13 (Linearization Theorem)**.** *Let a nonlinear dynamical system be defined on an open set $U \subset \mathbb{R}^2$ with a unique equilibrium at $0 \in U$. The phase portraits of the nonlinear system and its linearized system near the equilibrium are topologically equivalent if the equilibrium is hyperbolic.*

Thus, linearization near an equilibrium point is valid when the linearized system predicts a focus, a node, or a saddle point. However, it is insufficient to fully understand the dynamics of a nonlinear system when the linearized system has an eigenvalue with zero real part. In such cases, linearization does not allow for conclusions, and alternative methods must be used.

Moreover, the nature of fixed points obtained through linearization, even when valid, provides only local insights into the dynamics—i.e., within the immediate neighborhood of each equilibrium. To determine the global phase portrait, other methods must be employed, taking into account the nonlinear terms in the equations.

We now introduce additional tools to analyze system dynamics when linearization fails and to provide global insights into the dynamics of the nonlinear system.

2.6.3 Lyapunov Functions

A Lyapunov function is a useful tool for determining, for instance, the global stability of an equilibrium, not just local stability. Furthermore, a Lyapunov function can also be used to assess the stability of a non-hyperbolic equilibrium, where linearization is inconclusive. To begin, we define a **positive definite function**.

Definition 14 (Positive Definite Function)**.** *A function $V(x, y)$ is called **positive definite** (respectively, negative definite) if it is defined, differentiable, and continuously differentiable on an open set D containing the origin, and satisfies the following properties:*

- $V(0, 0) = 0$*;*
- $\forall (x, y) \in D \setminus \{(0, 0)\}, V(x, y) > 0$ *(respectively, $V(x, y) < 0$).*

For example, the function

$$V(x, y) = x^2 + y^2$$

is positive definite on $\mathbb{R}^2$, since it is zero at the origin and strictly positive elsewhere.

Consider a dynamical system of the form (1.16). We assume that the origin is an equilibrium point of the system, which implies:

$$f(0, 0) = g(0, 0) = 0.$$

This condition of having an equilibrium at the origin is not restrictive, as it is always possible to shift any equilibrium point (x^*, y^*) to the origin via the following change of variables:

$$u = x - x^*, \quad v = y - y^*.$$

As a result, we assume from now on that the equilibrium point is at the origin.

Now, let us compute the time derivative of the function $V(x, y)$:

$$\dot{V} = \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y} = \frac{\partial V}{\partial x} f(x, y) + \frac{\partial V}{\partial y} g(x, y).$$

This derivative can be rewritten as the dot product of two vectors: the gradient vector $\nabla V = \left(\frac{\partial V}{\partial x}, \frac{\partial V}{\partial y}\right)^T$ and the velocity vector $\mathbf{v} = (\dot{x}, \dot{y})^T$.

The gradient vector is always orthogonal to the level curves of $V(x, y) = k$ and points in the direction of the steepest ascent of the function $V(x, y)$. For example, in the case of the function:

$$V(x, y) = x^2 + y^2,$$

the level curves are circles of radius $\sqrt{k}$ centered at the origin. The gradient vector at any point in the plane is perpendicular to the corresponding circle and points outward (see Figure 2.6).

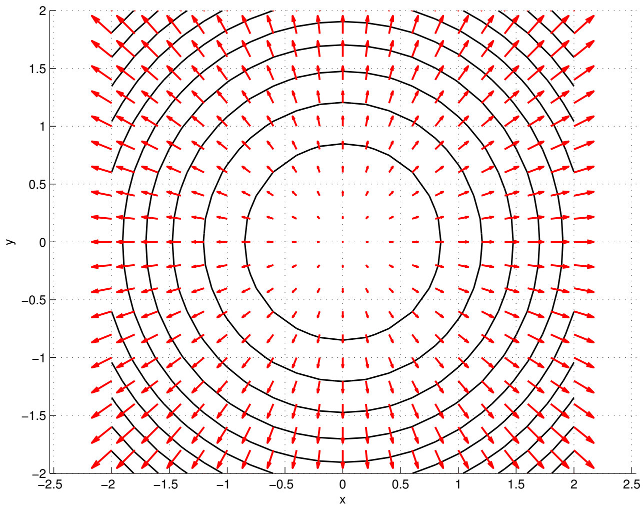

Figure 2.6: Direction and orientation of the gradient vector orthogonal to the level curves of $V(x, y) = x^2 + y^2$.

It is also important to note that if V is a positive definite function, then $(0, 0)$ is a minimum of V, and the level curves of V form closed curves near the origin. The velocity vector, on the other hand, is always tangent to the trajectory passing through a given point and points in the direction of motion as time progresses.

The dot product can also be rewritten as:

$$\dot{V} = \|\nabla V\| \cdot \|\mathbf{v}\| \cos\varphi,$$

where φ is the angle between the gradient vector and the velocity vector. The sign of $\dot{V}$ depends on $\cos\varphi$, leading to three possible cases:

1. $-\frac{\pi}{2} < \varphi < \frac{\pi}{2}$, in which case $\cos\varphi > 0$ and $\dot{V} > 0$. 2. $-\pi < \varphi < -\frac{\pi}{2}$ or $\frac{\pi}{2} < \varphi < \pi$, in which case $\cos\varphi < 0$ and $\dot{V} < 0$. 3. $\varphi = \pm\pi$, where $\cos\varphi = 0$ and $\dot{V} = 0$.

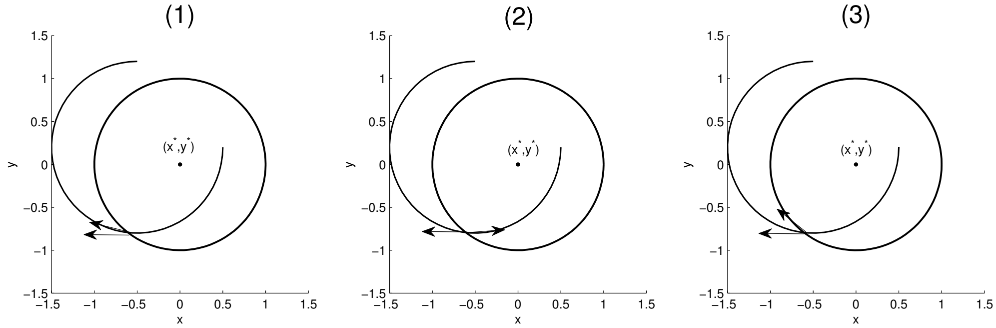

Figure 2.7: (1) The trajectory is outgoing. (2) The trajectory is incoming. (3) The trajectory is tangent to the level curve of the Lyapunov function and orthogonal to its gradient.

These three cases correspond to different situations illustrated in Figure 2.7.

- In case (1), the trajectory crosses the level curve from the inside to the outside, meaning it is **outgoing** relative to the corresponding level curve. - In case (2), the trajectory crosses the level curve from the outside to the inside, meaning it is **incoming**.
- In case (3), the trajectory is tangent to the level curve at that point.

Consequently, if in a compact domain D containing the origin, the sign of $\dot{V}$ is strictly negative everywhere, then trajectories always move inward toward the equilibrium, ultimately converging to it. This implies the asymptotic stability of the equilibrium.

On the other hand, if the sign of $\dot{V}$ is strictly positive in a compact domain containing the equilibrium point, then trajectories are outgoing everywhere, and we should expect the origin to be unstable.

The **Lyapunov stability theorem** provides the necessary conditions for determining the stability or instability of the equilibrium.

Théorèm 15 (Lyapunov Stability Theorem)**.** *Consider the dynamical system:*

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

which has the origin as a fixed point. Suppose there exists a real-valued function $V(x, y)$ defined in a neighborhood of the origin such that:

- *The partial derivatives $\frac{\partial V}{\partial x}$ and $\frac{\partial V}{\partial y}$ exist and are continuous;*
- *$V(x, y)$ is positive definite;*
- *$\dot{V}$ is negative definite, then the origin is an asymptotically stable equilibrium.*

*In this case, V is called a **strong Lyapunov function**.*

- *If $\dot{V}$ is positive definite, then the origin is an unstable equilibrium.*

There are cases where it is impossible to find a strong Lyapunov function, meaning that we only have $\dot{V} \leq 0$ in a domain containing the equilibrium. In such cases, there exist points in the domain where $\dot{V} = 0$. In this situation, V is called a ***weak Lyapunov function****, and we can conclude that the equilibrium is stable but not necessarily asymptotically stable.*

For a weak Lyapunov function, it is still possible to determine asymptotic stability in certain cases using a specialized theorem for weak functions. For more details, see [1].

Exercise 1

Consider the following dynamical system:

$$\dot{x} = -x^3, \quad \dot{y} = -y^3.$$

Determine the stability of the origin.

Solution

The origin is the unique equilibrium point. The Jacobian matrix is given by:

$$A = \begin{bmatrix} -3x^2 & 0 \\ 0 & -3y^2 \end{bmatrix},$$

which at the origin becomes:

$$A(0,0) = \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix}.$$

Thus, linearization provides no information about the stability of the origin.

Consider the following Lyapunov function:

$$V(x,y) = \frac{1}{2}(x^2 + y^2).$$

which is positive definite. Computing its derivative:

$$\dot{V} = \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y} = -(x^4 + y^4),$$

which is negative definite. Since this derivative is strictly negative for all points in the plane, we conclude that the origin is globally asymptotically stable. This means that, regardless of the initial condition in the plane, the trajectory tends to the origin as $t \to +\infty$.

Exercise 2

Study the following system:

$$\dot{x} = x - 3, \quad \dot{y} = 2y^3.$$

Solution.

The point $(3,0)$ is the unique equilibrium. The Jacobian matrix is:

$$A = \begin{bmatrix} 1 & 0 \\ 0 & 6y^2 \end{bmatrix},$$

which at the equilibrium becomes:

$$A(3,0) = \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}.$$

This matrix has a zero eigenvalue, which means that the equilibrium $(3, 0)$ is non-hyperbolic.

Consider the following Lyapunov function:

$$V(x, y) = \frac{1}{2}((x-3)^2 + y^2).$$

Computing its derivative:

$$\dot{V} = \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y} = (x-3)x + y \cdot 2y^3 = (x-3)^2 + 2y^4.$$

Since this derivative is positive for all points in the plane, we conclude that the equilibrium $(3, 0)$ is unstable.

Exercise 3

Consider the following dynamical system:

$$\dot{x} = -y + ax(x^2 + y^2), \quad \dot{y} = x + ay(x^2 + y^2).$$

Study the stability of the equilibrium point as a function of the sign of the real parameter a.

Solution

First, it is evident that the only equilibrium of this system is the origin. The Jacobian matrix is:

$$A = \begin{bmatrix} 3ax^2 + ay^2 & -1 + 2axy \\ 1 + 2axy & 3ay^2 + ax^2 \end{bmatrix},$$

which at the origin simplifies to:

$$A(0, 0) = \begin{bmatrix} 0 & -1 \\ 1 & 0 \end{bmatrix}.$$

This matrix has a zero trace and a positive determinant, which corresponds to a center. However, the linearization theorem cannot be applied in the case of a center.

To analyze stability, consider the Lyapunov function:

$$V(x, y) = \frac{1}{2}(x^2 + y^2),$$

which is positive definite. Computing its derivative:

$$\dot{V} = \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y} = a(x^2 + y^2)^2.$$

We distinguish three cases:

- If $a < 0$, then $\dot{V} < 0$, so the origin is asymptotically stable.
- If $a = 0$, then $\dot{V} = 0$, meaning the origin is a center (this case will be discussed further in the context of first integrals).
- If $a > 0$, then $\dot{V} > 0$, meaning the origin is unstable.

To further analyze the dynamics, we can switch to polar coordinates (r, θ), where we obtain:

$$\dot{r} = ar^3, \quad \dot{\theta} = 1.$$

Thus, it is clear that:

- When $a < 0$, trajectories spiral toward the origin, which is asymptotically stable.
- When $a = 0$, trajectories are circles centered at the origin, making it a stable but neutrally stable center.
- When $a > 0$, trajectories spiral outward from the origin, which is unstable.

This example illustrates that in all three cases, the linear system predicts centers, but this is only accurate in the case $a = 0$.

2.6.4 Limit Cycle

Definition 16. *A limit cycle is an isolated closed trajectory, at least on one side.*

A limit cycle is different from closed trajectories in a center, where there exist infinitely many closed trajectories. In the case of a center, it is impossible to isolate a single closed trajectory. For example, in the previous exercise where $a = 0$, the origin is a center. Any circle centered at the origin is a solution and thus constitutes a closed trajectory. In this case, it is impossible to isolate one.

Example.

Consider the following dynamical system:

$$\begin{cases} \dot{x} = y + x(1 - (x^2 + y^2)), \\ \dot{y} = -x + y(1 - (x^2 + y^2)). \end{cases} \tag{2.53}$$

The only equilibrium of this system is at the origin. The linear part of this system near the origin is given by:

$$A(0,0) = \begin{bmatrix} 1 & 1 \\ -1 & 1 \end{bmatrix}. \tag{2.54}$$

The characteristic equation is:

$$\lambda^2 - 2\lambda + 2 = 0, \tag{2.55}$$

with discriminant:

$$\Delta = -4. \tag{2.56}$$

The two eigenvalues are complex and conjugate:

$$\lambda_{1,2} = 1 \pm i. \tag{2.57}$$

Thus, the origin is an unstable focus since the real part of the eigenvalues is positive.

To understand the global dynamics, we transform the system into polar coordinates (r, θ):

$$\begin{cases} \dot{r} = r(1 - r^2), \\ \dot{\theta} = -1. \end{cases} \tag{2.58}$$

The solution of the second equation is:

$$\theta(t) = -t + \theta_0, \tag{2.59}$$

where θ_0 is an integration constant representing the initial angle at $t = 0$. The angle thus evolves at a constant angular velocity.

The first equation describes the radial dynamics. The sign of $\dot{r}$ depends on $1 - r^2$ since $r > 0$, leading to:

- If $r < 1$, then $\dot{r} > 0$.
- If $r = 1$, then $\dot{r} = 0$.
- If $r > 1$, then $\dot{r} < 0$.

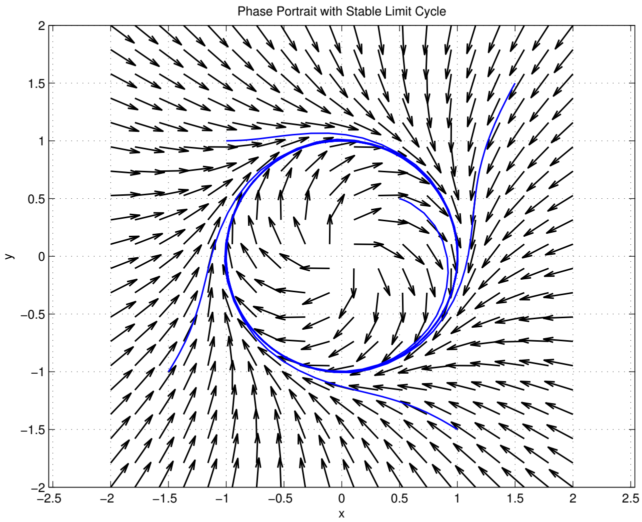

Figure 2.8: Phase portrait of the system $\dot{x} = y + x(1-(x^2+y^2))$, $\dot{y} = -x + y(1-(x^2+y^2))$, admitting a stable limit cycle.

Thus, the unit circle is a closed trajectory since for $r = 1$, we have $\dot{r} = 0$. Moreover, for $r < 1$, the trajectory spirals outward, while for $r > 1$, the trajectory spirals inward. This implies that any initial condition inside or outside the unit circle will eventually approach this closed trajectory, known as a limit cycle. Figure 2.8 illustrates the phase portrait of this system and the limit cycle C. Furthermore, for any initial condition (r_0, θ_0), every trajectory tends to the limit cycle as $t \to +\infty$. We say that the limit cycle is stable, and in this case, it is even globally stable.

A limit cycle is not always stable. Consider the following dynamical system:

$$\begin{cases} \dot{r} = r(1-r)(r-2), \\ \dot{\theta} = 1. \end{cases} \tag{2.60}$$

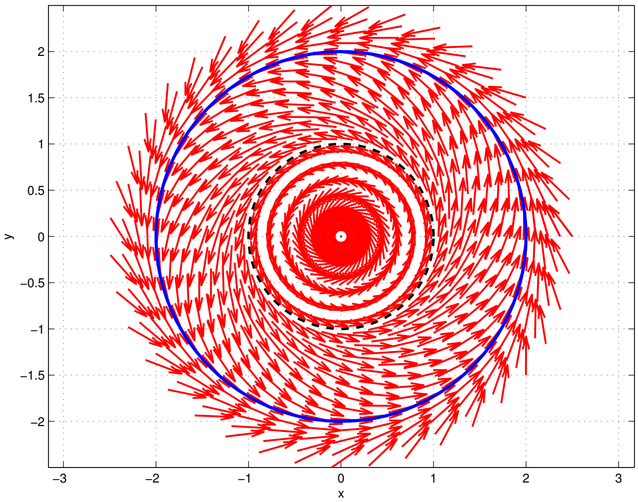

Figure 2.9: Phase portrait of the system with an unstable limit cycle C_1 and a stable limit cycle C_2.

The first equation has three equilibrium points: $r = 0$, $r = 1$, and $r = 2$. Analyzing the sign of $\dot{r}$, we find:

- If $r < 1$, then $\dot{r} < 0$.
- If $r = 1$, then $\dot{r} = 0$.
- If $1 < r < 2$, then $\dot{r} > 0$.
- If $r = 2$, then $\dot{r} = 0$.
- If $r > 2$, then $\dot{r} < 0$.

Therefore, there exist two limit cycles: C_1 (a unit circle) and C_2 (a circle of radius 2). The cycle C_1 is unstable, whereas C_2 is stable.

Another example is given by:

$$\begin{cases} \dot{r} = r(1 - r)^2, \\ \dot{\theta} = 1. \end{cases} \tag{2.61}$$

Here, $\dot{r}$ is always positive, implying the existence of a "semi-stable" limit cycle, which is attractive from the inside but repulsive from the outside.

To prove the existence of a limit cycle, one can use the Poincaré-Bendixson theorem. However, note that this theorem is only valid in two dimensions. To apply it, we first define a positively invariant domain.

Definition 17 (Positively Invariant Domain)**.** *Consider a dynamical system given by:*

$$\dot{x} = f(x, y), \tag{2.62}$$

$$\dot{y} = g(x, y), \tag{2.63}$$

where f and g are differentiable functions with continuous differentials on $\mathbb{R}^2$. A domain D in the plane is said to be positively invariant if, for any initial condition $(x_0, y_0) \in D$, the corresponding trajectory remains in D as $t \to +\infty$.

For example, consider the following system:

$$\dot{x} = x(1 - y), \tag{2.64}$$

$$\dot{y} = y(1 - x). \tag{2.65}$$

The axes $x = 0$ and $y = 0$ are respectively vertical and horizontal isoclines. Thus, no trajectory can cross these axes. The positive quadrant defined by the domain $D = \{(x, y) \mid x > 0, y > 0\}$ is therefore positively invariant, since any trajectory starting from an initial condition within D remains in D.

To apply the Poincaré-Bendixson theorem, we introduce the notion of an *attracting domain.*

Definition 18 (Attracting Domain of the Plane)**.** *An attracting domain is a bounded and compact region D of the plane such that any trajectory starting from the boundary ∂D enters the interior of D.*

A positively invariant set is not necessarily an attracting domain. For example, consider the system:

$$\dot{x} = y, \tag{2.66}$$

$$\dot{y} = -x. \tag{2.67}$$

The origin is the only equilibrium and is a center. All trajectories are circles centered at the origin. Let $D = \{(x, y) \mid r = \sqrt{x^2 + y^2} \leq 1\}$ be the domain defined by the disk of radius 1. This is a bounded and compact domain that is positively invariant because any trajectory within D remains in D, including for an initial condition on the boundary of D, which corresponds to the unit circle (a trajectory itself). However, the domain is not attracting, as the trajectory defined by the unit circle does not enter D.

The last notion we introduce before stating the theorem is the ω-limit set of a trajectory, which rigorously describes the long-term behavior of a trajectory.

Definition 19 (ω-Limit Set)**.** *Let p_0 be a point in the domain of definition of system (1.22). The ω-limit set of p_0 is defined as:*

$$\omega(p_0) = \bigcup_{t \geq 0} \{(x(s, p_0), y(s, p_0)) \mid s \geq t\}. \tag{2.68}$$

A point (x, y) belongs to $\omega(p_0)$ if there exists a sequence t_i, with $i \in \mathbb{N}$ and $t_i \to +\infty$, such that $(x(t_i, p_0), y(t_i, p_0))$ tends to (x, y) as $i \to +\infty$. Thus, the ω-limit set consists of all points that the trajectory of p_0 approaches infinitely often as time increases. The ω-limit set of a trajectory γ is defined as the union of all ω-limit sets of points on γ.

We can now state the following theorem.

Théorèm 20 (Poincaré-Bendixson Theorem)**.** *If D is a bounded attracting domain in the plane, then every trajectory in D has an ω-limit set that is:*

- *either an equilibrium point;*

- *or a periodic orbit;*
- *or a set consisting of the union of equilibrium points and regular orbits connecting them (heteroclinic or homoclinic).*

The theorem thus states that any trajectory in the plane "trapped" in an attracting set can only do one of two things: either tend toward a set containing at least one equilibrium, or tend toward a periodic orbit. To prove the existence of a periodic orbit, it suffices to find an attracting set and exclude the first possibility.

2.6.5 Divergence of a Vector Field and Negative Criteria for Limit Cycles

Definition 21 (Divergence of a Vector Field)**.** *Consider a vector field X defined by the differential system (1.22) in a domain D. The divergence of X at the point (x, y) is given by:*

$$\operatorname{div}(X)(x,y) = \frac{\partial f}{\partial x}(x,y) + \frac{\partial g}{\partial y}(x,y). \tag{2.69}$$

The divergence of a system at a given point measures how trajectories converge or diverge in the neighborhood of that point. More precisely, if we consider a small disk around a point, the divergence at that point indicates whether the area of the disk increases or decreases due to the motion induced by the differential system. If the divergence is negative, the disk contracts, whereas if the divergence is positive, the disk expands locally in the vicinity of the point due to the movement induced by the trajectories.

Proposition 22 (Bendixson's Negative Criterion)**.** *Consider a dynamical system of the form (1.22). Let D be a simply connected region, i.e., a region without holes. If the quantity $\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y}$ has a constant sign in D, then no limit cycle can be entirely contained in D.*

Proposition 23 (Dulac's Negative Criterion)**.** *Consider a dynamical system of the form (1.22). Let D be a simply connected region. Let $B(x, y)$ be an arbitrary strictly positive, continuous, and differentiable function in D. If the quantity*

$$\frac{\partial(Bf)}{\partial x} + \frac{\partial(Bg)}{\partial y} \tag{2.70}$$

has a constant sign in D, then no limit cycle can be entirely contained in D.

To better understand this criterion, note that multiplying the components of a vector field by a strictly positive function does not modify the trajectories but only changes the speed at which they are traversed.

Exercise Prove that a linear system of the following form cannot admit a limit cycle:

$$\dot{x} = ax + by, \tag{2.71}$$

$$\dot{y} = cx + dy, \tag{2.72}$$

where $a + d \neq 0$.

Solution We have:

$$\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} = a + d, \tag{2.73}$$

which is constant for every point in the plane. By applying Bendixson's negative criterion, no limit cycle can exist for a linear system.

Exercise Prove that the following dynamical system (called a competition system) does not admit a limit cycle entirely contained in the positive quadrant:

$$\dot{x} = x(1 - x - ay), \tag{2.74}$$

$$\dot{y} = y(1 - y - bx), \tag{2.75}$$

where a and b are strictly positive parameters.

Solution Consider the function $B(x, y) = \frac{1}{xy}$. We obtain:

$$Bf = \frac{1 - x - ay}{y}, \tag{2.76}$$

$$Bg = \frac{1 - y - bx}{x}. \tag{2.77}$$

Thus, we have:

$$\frac{\partial Bf}{\partial x} + \frac{\partial Bg}{\partial y} = -\frac{1}{x} - \frac{1}{y}. \tag{2.78}$$

This quantity is strictly negative for any point strictly inside the positive quadrant. By Dulac's criterion, we conclude that no limit cycle can exist entirely within the positive quadrant. Furthermore, since the positive quadrant is also positively invariant, no trajectory can cross the axes, ruling out the possibility of a partially contained limit cycle.

2.7 Non-Planar Systems

2.7.1 Linearization Near an Equilibrium

We now consider dynamical systems in dimensions higher than two. The general form of a system in dimension n is given by:

$$\dot{x}_i = f_i(x_1, x_2, \ldots, x_n), \tag{2.79}$$

where $i \in [1, n]$, with coordinates of a point denoted as $(x_1, x_2, \ldots, x_n)$, and the functions f_i depend on the state variables. An equilibrium point $(x_1^*, x_2^*, \ldots, x_n^*)$ is defined by the algebraic system:

$$f_i(x_1^*, x_2^*, \ldots, x_n^*) = 0, \quad \text{for } i \in [1, n], \tag{2.80}$$

which ensures that all components of the velocity vector vanish at this point.

To linearize this system near an equilibrium point, we introduce local variables:

$$u_i(t) = x_i(t) - x_i^*, \quad \text{for } i \in [1, n]. \tag{2.81}$$

A calculation similar to the planar case leads to the following linearized model:

$$\dot{u}_i = \sum_{j=1}^{n} \frac{\partial f_i}{\partial x_j} u_j, \tag{2.82}$$

where the partial derivatives are evaluated at the equilibrium point. As in the planar case, the $n \times n$ Jacobian matrix

$$A = \left[\frac{\partial f_i}{\partial x_j}\right], \quad i, j \in [1, n], \tag{2.83}$$

defines the linear system. In ecology, this matrix is often called the community matrix when the variables x_i represent population abundances.

The stability condition of the equilibrium point depends on the n eigenvalues λ_k of the Jacobian matrix:

$$(x_1^*, x_2^*, \ldots, x_n^*) \text{ is asymptotically stable} \iff \forall k, \Re(\lambda_k) < 0, \tag{2.84}$$

where $\Re(\lambda_k)$ denotes the real part of the eigenvalue λ_k. Asymptotic stability requires all eigenvalues of the linearized system matrix to have negative real parts.

As in previous sections, we can introduce the notion of a hyperbolic equilibrium.

Definition 24. *An equilibrium is said to be* ***hyperbolic*** *if all eigenvalues of the Jacobian matrix at equilibrium have a nonzero real part.*

This definition extends the result stated in two dimensions: the Jacobian matrix informs us about the nature of an equilibrium of a nonlinear system only if the equilibrium is hyperbolic.

2.7.2 Linear Systems in Dimension n

Consider a linear system in dimension n:

$$\dot{x}_i = \sum_{j=1}^{n} a_{ij} x_j, \tag{2.85}$$

where $i \in [1, n]$, and $A = [a_{ij}]$ is an $n \times n$ square matrix with constant coefficients. The solutions of this linear system depend on the eigenvalues of matrix A, which are the solutions of the characteristic equation:

$$\det(A - \lambda I) = 0, \tag{2.86}$$

which is a polynomial of degree n. Recall that a polynomial of degree n with real coefficients has at most n real roots, and if λ is a complex root, then its complex conjugate $\bar{\lambda}$ is also a root. Therefore, complex eigenvalues appear in conjugate pairs.

The Jordan forms used for studying planar systems generalize to any dimension. In dimension 3, with an appropriate change of basis, the matrix can be transformed into one of the following Jordan forms, depending on the eigenvalues.

1) If the matrix A is diagonalizable in $\mathbb{R}^3$, meaning it has only real eigenvalues and its eigenvectors form a basis of $\mathbb{R}^3$, we denote the eigenvalues as $\lambda_1 \leq \lambda_2 \leq \lambda_3$, and let P be the change of basis matrix:

$$J = P^{-1}AP = \begin{bmatrix} \lambda_1 & 0 & 0 \\ 0 & \lambda_2 & 0 \\ 0 & 0 & \lambda_3 \end{bmatrix}. \tag{2.87}$$

The change of basis matrix P is a 3×3 matrix whose columns contain the eigenvectors m_i corresponding to eigenvalues λ_i.

Solving the linear system follows the same approach as in the planar case by seeking the solution in the new basis, where the system decouples into three independent equations:

$$\dot{u}_1 = \lambda_1 u_1, \tag{2.88}$$
$$\dot{u}_2 = \lambda_2 u_2, \tag{2.89}$$
$$\dot{u}_3 = \lambda_3 u_3. \tag{2.90}$$

The solutions are straightforward:

$$u_i(t) = g_i \exp(\lambda_i t),$$

where g_i are integration constants.

As in the planar case, the solution in terms of (x_1, x_2, x_3) is obtained by transforming back to the original basis using the transition matrix P:

$$\begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} = P \begin{bmatrix} u_1 \\ u_2 \\ u_3 \end{bmatrix}.$$

2.8 Routh-Hurwitz Criteria

We previously saw that the stability condition of an equilibrium point requires verifying that all eigenvalues of the Jacobian matrix have negative real parts. In practice, computing the eigenvalues of the linearized system's matrix is not always straightforward. However, there exist criteria that allow us to conclude the local stability of an equilibrium point without explicitly computing the eigenvalues.

Consider the following linear system of dimension n:

$$\dot{x}_i = \sum_{j=1}^{n} a_{ij} x_j,$$

for $i \in [1, n]$, where $A = [a_{ij}]$ is an $n \times n$ square matrix with constant coefficients. We assume that $\det A \neq 0$, which notably implies that the origin is the unique equilibrium. The matrix A has n eigenvalues, which are solutions of the characteristic equation:

$$\det(A - \lambda I) = 0,$$

which is a polynomial of degree n, written as:

$$\lambda^n + a_1 \lambda^{n-1} + a_2 \lambda^{n-2} + \cdots + a_{n-1}\lambda + a_n = 0.$$

Consider the following n determinants:

$$H_1 = a_1,$$

$$H_2 = \begin{vmatrix} a_1 & a_3 \\ 1 & a_2 \end{vmatrix},$$

$$H_3 = \begin{vmatrix} a_1 & a_3 & a_5 \\ 1 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{vmatrix},$$

$$H_k = \begin{vmatrix} a_1 & a_3 & a_5 & \dots \\ 1 & a_2 & a_4 & \dots \\ 0 & a_1 & a_3 & \dots \\ 0 & 1 & a_2 & \dots \\ \vdots & \vdots & \vdots & \ddots \\ 0 & 0 & \dots & a_k \end{vmatrix},$$

for $k \in [1, n]$. In the case of dimension n, all a_j with $j > n$ are taken as zero. We then have the following result:

$$\text{The equilibrium is asymptotically stable} \iff \forall k \in [1, n], \quad H_k > 0.$$

Thus, we must verify that all n determinants H_k are strictly positive. These are necessary and sufficient conditions for local asymptotic stability, meaning that all eigenvalues of the Jacobian matrix computed at the equilibrium have negative real parts.

In the case of dimension two, the characteristic equation is:

$$\lambda^2 - \mathrm{tr}A\lambda + \det A = 0.$$

We have $a_1 = -\mathrm{tr}A$, $a_2 = \det A$, and $a_3 = 0$. The Routh-Hurwitz criteria then become:

$$H_1 = a_1 = -\mathrm{tr}A > 0 \iff \mathrm{tr}A < 0,$$

$$H_2 = a_1 a_2 - a_3 = -\mathrm{tr}A \det A > 0 \iff \det A > 0.$$

These conditions are precisely those given in the planar case.

In dimension three, the characteristic equation is:

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0,$$

and the stability conditions obtained by applying the Routh-Hurwitz criteria are:

$$a_1 > 0, \quad a_1 a_2 - a_3 > 0, \quad a_3 > 0.$$

In dimension four, the characteristic equation is:

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0,$$

and the stability conditions are:

$$a_1 > 0, \quad a_1 a_2 - a_3 > 0, \quad a_1 a_2 a_3 - (a_1)^2 a_4 - (a_3)^2 > 0, \quad a_4 > 0.$$

Sometimes, verifying these criteria is easier than explicitly computing the eigenvalues, as we will see in application examples.

Chapter 3

Models in community

Introduction

Understanding the dynamics of populations within a community is essential for studying ecological and biological interactions. Mathematical models provide powerful tools to describe and analyze these dynamics, allowing us to predict population behavior under different conditions and to explore the effects of interactions among species.

In this chapter, we examine various models that describe population dynamics within a community. We begin with single-species models, including the linear growth model, which represents unrestricted population increase, and the logistic growth model, which incorporates environmental carrying capacity to reflect resource limitations. Additionally, we introduce the growth model with the Allee effect, which accounts for the impact of population density on individual survival and reproduction.

Following the study of single-species dynamics, we explore interactions between populations through the classical Lotka-Volterra model. This model describes predator-prey relationships and competitive interactions, providing fundamental insights into how species coexist or compete for resources. We also consider an extension of the Lotka-Volterra model that includes logistic growth, offering a more realistic representation of population constraints.

By analyzing these models, we aim to build a comprehensive understanding of how populations evolve within a community, how interactions influence stability and coexistence, and what conditions lead to equilibrium or fluctuations in population sizes. These models serve as a foundation for more complex ecological and evolutionary studies.

3.1 Single Population Dynamics Model

3.1.1 Linear Growth Model

Many models of single population dynamics have been developed. This section provides a review of the most classical models. In the case of an isolated population, the state variable is the population size, i.e., the number of individuals $x(t)$ at time t. Sometimes, the variable used is the density of individuals, representing the number of individuals per unit area. The general form of the population growth law is:

$$\frac{dx}{dt} = f(x),$$

with the initial condition $x(t_o) = x_o$.

The simplest case is the linear model. Let n be the birth rate per unit time per individual. Similarly, let m be the mortality rate. Assuming that birth and mortality rates are constant, this leads to the following linear model:

$$\frac{dx}{dt} = nx - mx = rx, \tag{3.1}$$

where $r = n - m$ is the population growth rate.

The solution to this differential equation, as obtained in the first exercise of this book, is:

$$x(t) = x_0 \exp(rt).$$

The sign of r determines whether the population is growing ($r > 0$) or declining ($r < 0$). The case $r = 0$ corresponds to a population whose size remains constant and equal to its initial value.

Exercise Calculate the average lifespan $\bar{T}$ of an individual in a population following a linear growth law with rate $-\lambda$.

Solution: Let x_0 be the number of individuals at the initial time $t = 0$. The number of individuals still alive at time t is:

$$x(t) = x_0 \exp(-\lambda t).$$

The number of individuals disappearing between times t and $t + dt$, i.e., those having had a lifespan equal to t, is:

$$dx = x(t) - x(t + dt) = -\frac{dx}{dt} dt,$$

which gives:

$$dx = \lambda x_0 \exp(-\lambda t) dt.$$

To compute the mean lifespan, we consider a single individual ($x_0 = 1$) and integrate over all possible times, weighting by t the proportions of individuals with a lifespan of t. The mean lifespan $\bar{T}$ is then given by:

$$\bar{T} = \lambda \int_0^\infty t \exp(-\lambda t) dt.$$

Using integration by parts, we obtain:

$$\bar{T} = \frac{1}{\lambda}.$$

3.1.2 Logistic Growth Model

A more realistic assumption is to consider that the birth rate is not constant but decreases with population size. Indeed, as the number of individuals in a population increases, resources become limited, which can lead to a decrease in the birth rate. In the simplest case, the birth rate is chosen as a linearly decreasing function of the population size:

$$n(x) = a - bx,$$

where a and b are positive constants.

Similarly, it is reasonable to assume that the mortality rate, unlike the birth rate, increases with population size. For example:

$$m(x) = g + dx,$$

where g and d are also positive constants.

Substituting the population-dependent birth and mortality rates into the previous equation (3.1) leads to the following growth equation:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) = f(x),$$

where $r = a - g$ is the intrinsic growth rate of the population. We assume that $a > g$, meaning the intrinsic growth rate r is positive.

K is called the carrying capacity of the environment and is given by:

$$K = \frac{a-g}{b+d},$$

which is positive as long as $r > 0$.

This differential equation is called the *logistic equation*. It has two equilibrium points: the origin and K. To determine their stability, we compute the derivative of the function $f(x)$:

$$\frac{df}{dx} = r - 2r\frac{x}{K}.$$

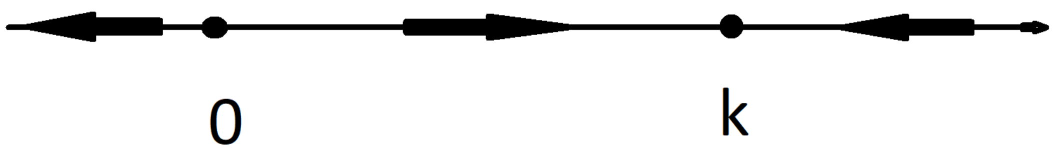

Figure 3.1: Phase portrait of the logistic equation.

The value of this derivative at the origin is r, and at K, it is $-r$. Consequently, the origin is unstable, while K is a stable equilibrium. For any positive initial condition, we have:

$$\lim_{t \to \infty} x(t) = K.$$

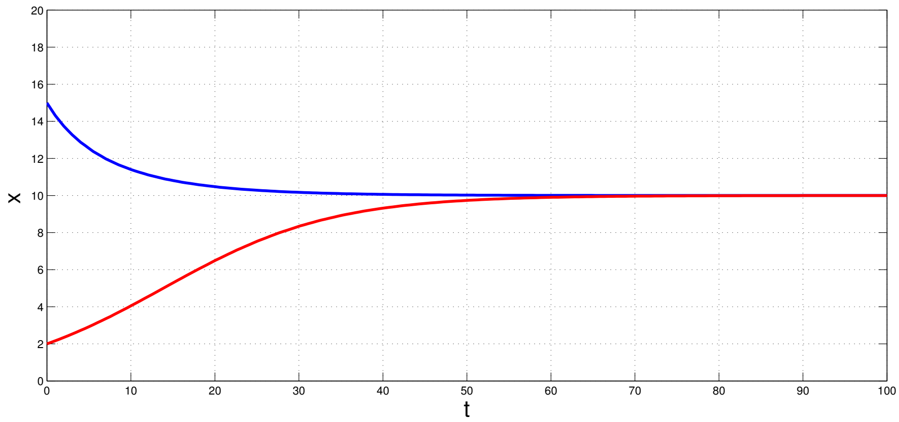

Figure 3.2: Asymptotic behavior of the logistic equation for r = 0.1 et K = 10.

Figure 3.1 shows the **phase portrait**, while Figure 3.2 presents the numerical simulation of the population dynamics obtained by numerically integrating the differential equation using the **Runge-Kutta method**. The carrying capacity corresponds to the stable equilibrium of the equation and thus represents the **long-term population size** that can be sustained in an environment with limited resources.

3.1.3 Growth Model with the Allee Effect

Consider the following differential equation:

$$\frac{dx}{dt} = rx(x-M)(K-x) = f(x), \tag{3.2}$$

where $0 < M < K$.

This equation has three equilibrium points: the origin, M, and K. The derivative of the function $f(x)$ is given by:

$$\frac{df}{dx} = r\left(-3x^2 + 2(M+K)x - MK\right).$$

At the origin, this derivative takes the value $-rMK < 0$. At M, it is $rM(K-M) > 0$, and at K, it is $rK(M-K) < 0$. Consequently, the origin and K are stable, while the intermediate equilibrium M is unstable. Figure 3.3 shows the corresponding *phase portrait*.

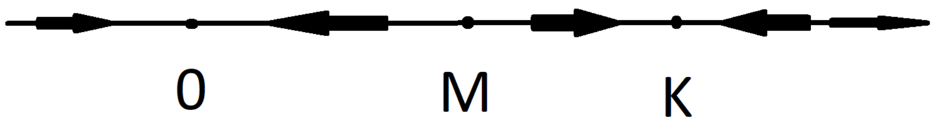

Figure 3.3: Phase portrait of the Allee effect. The origin and K are stable, while the intermediate equilibrium M is unstable.

Figure 3.4 presents the time series solutions of equation (3.2). A *threshold effect* is observed: For an initial condition $0 < x_0 < M$, the population declines and goes extinct. However, if the initial condition exceeds this threshold, $x_0 > M$, the population grows towards the carrying capacity K.

This phenomenon is known in population dynamics as the *Allee effect*. It describes populations that are only viable if their size exceeds a critical threshold.

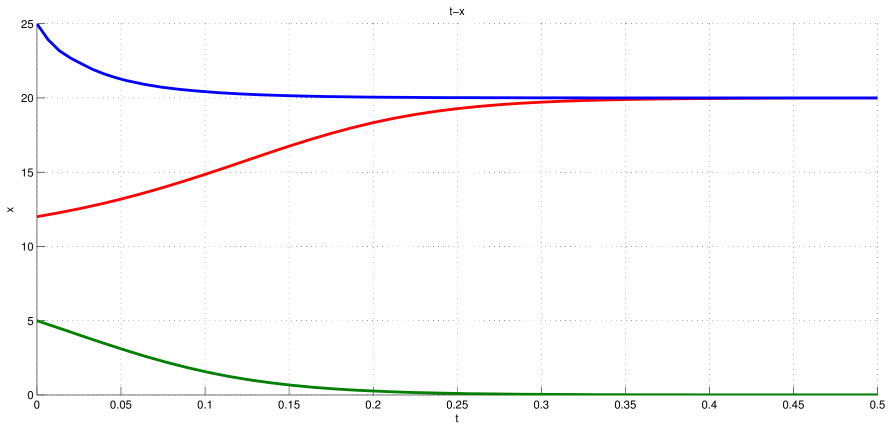

Figure 3.4: Time series of the population growth equation with the *Allee effect*, obtained for $r = 0.1$, $M = 10$, and $K = 20$.

Exercise Study the growth law of a population where the growth rate is assumed to be proportional to the population density:

$$\frac{dx}{dt} = ax^2.$$

In this case, we assume that the growth rate is proportional to the *encounter rate between individuals*, which corresponds, for instance, to sexual reproduction. Show that the population density tends to infinity in a finite time.

Solution: Let $x(0)$ be the initial condition. By separating variables, we obtain:

$$\frac{dx}{x^2} = adt.$$

After integration:

$$\frac{1}{x(0)} - \frac{1}{x(t)} = at,$$

which gives:

$$x(t) = \frac{x(0)}{1 - ax(0)t}.$$

Thus, the population tends to infinity in finite time T_∞:

$$T_\infty = \frac{1}{ax(0)}.$$

Exercise Study the growth law of a population where the growth rate is proportional to the population density but includes a constant mortality rate m, following the equation:

$$\frac{dx}{dt} = ax^2 - mx.$$

Find the equilibrium points and determine their local stability. Sketch the solution behavior.

Exercise Consider the following population growth model:

$$\frac{dx}{dt} = \frac{ax}{N + x} - mx.$$

Find the equilibrium points and determine their local stability.

Solution: The equilibrium points are 0 and $x^* = \frac{a-mN}{m}$. If $a > mN$, the origin is unstable, and the equilibrium x^* is positive and stable, meaning the population tends to a steady state. Conversely, if $a < mN$, the origin is stable, and x^* is negative, implying that the population goes extinct.

3.2 Lotka-Volterra Model

This model assumes that in the absence of predators, the growth of prey is unlimited, i.e.,

$$f(x) = rx, \tag{3.3}$$

whose solution is given by

$$x(t) = x(0)\exp(rt), \tag{3.4}$$

where $r > 0$ is the growth rate of the prey.

The model also assumes a natural mortality rate for the predator, meaning it cannot survive without prey:

$$g(y) = -my, \tag{3.5}$$

whose solution is given by

$$y(t) = y(0)\exp(-mt), \tag{3.6}$$

where $m > 0$ represents the natural mortality rate of the predator. Thus, in the absence of predators, the prey population would grow uncontrollably, and their numbers would only be regulated by the presence of predators. Conversely, without prey, predators would disappear. The interaction between the two populations through predation can have stabilizing effects on the overall dynamics of the system.

In this model, it is also assumed that the interaction term follows the classical Lotka-Volterra type I form described earlier. Under these assumptions, the Lotka-Volterra model is written as:

$$\dot{x} = rx - axy, \tag{3.7}$$

$$\dot{y} = -my + eaxy. \tag{3.8}$$

By factoring, we can rewrite it as:

$$\dot{x} = x(r - ay), \tag{3.9}$$

$$\dot{y} = y(-m + bx), \tag{3.10}$$

where we define $b = ea$. The ability to factor out x in the first equation and y in the second is important because it implies that the axes are zero isoclines of the system. Consequently, no trajectory can cross either the x-axis or the y-axis. This ensures that any trajectory originating in the positive quadrant remains within this quadrant for all $t > 0$. This property, known as positive invariance, is crucial since the variables $x(t)$ and $y(t)$ represent population sizes and must remain non-negative for all $t > 0$. The model guarantees that if the initial conditions are positive, i.e., $x(0) > 0$ and $y(0) > 0$, then the populations remain positive indefinitely and never become negative, which would be biologically meaningless.

The zero isoclines are given by:

$$\dot{x} = 0 \Rightarrow x = 0 \text{ or } y = \frac{r}{a}, \tag{3.11}$$

$$\dot{y} = 0 \Rightarrow y = 0 \text{ or } x = \frac{m}{b}. \tag{3.12}$$

It is easy to see that on the $x = 0$ axis, for $y > 0$, we have $\dot{y} = -my < 0$, meaning the vertical velocity component is negative. Similarly, on the $y = 0$ axis, for $x > 0$, we have $\dot{x} = rx > 0$, meaning the horizontal velocity component is positive.

Applying continuity rules for the velocity vector direction at intersections of isoclines of the same nature and applying direction changes at intersections of different types of isoclines, we can determine the velocity vector's direction throughout the phase space.

Finally, Figure 3.5 shows the velocity vector field, specifically the direction of velocity vectors in the (x, y) plane. The trajectories are tangent to these vectors at every point.

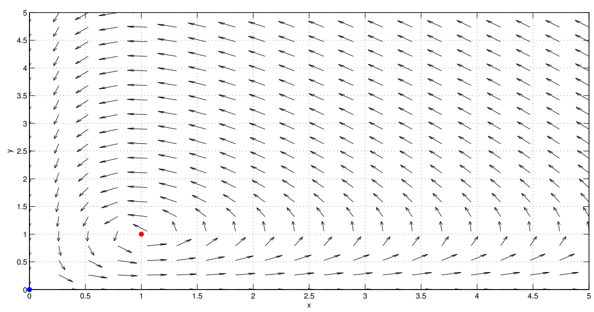

Figure 3.5: Velocity vector field in the (x, y) plane.

3.2.1 Lotka-Volterra Model with Logistic Growth

We have seen that the Lotka-Volterra model predicts centers, which are structurally unstable. This means that the periodic solutions obtained for the prey and predator populations are generally not preserved under small perturbations of the model. For this reason, the model is not entirely satisfactory. Furthermore, in the absence of predators, prey growth is unlimited, which is unrealistic. Instead, we should consider that in the absence of predators, the prey population reaches an equilibrium that depends on the available resources in the environment.

Consequently, a modification of the model consists of choosing a logistic growth law for the prey population, leading to the following model:

$$\begin{cases} \dot{x} = rx\left(1 - \frac{x}{K}\right) - axy, \\ \dot{y} = -my + bxy, \end{cases} \tag{3.13}$$

where $K > 0$ is the carrying capacity of the environment. Again, the model can be rewritten by factoring variables x and y in each equation:

$$\begin{cases} \dot{x} = x\left(r\left(1 - \frac{x}{K}\right) - ay\right), \\ \dot{y} = y(-m + bx). \end{cases} \tag{3.14}$$

This implies that, as in the previous case, the positive quadrant is positively invariant. The zero isoclines are given by:

$$\dot{x} = 0 \Rightarrow y = \frac{r}{a}\left(1 - \frac{x}{K}\right) \text{ or } x = 0, \tag{3.15}$$

$$\dot{y} = 0 \Rightarrow x = \frac{m}{b} \text{ or } y = 0. \tag{3.16}$$

The direction of velocity vectors on the isoclines is straightforward to determine: in the absence of predators ($y = 0$), the prey population increases until it reaches the carrying capacity K, and in the absence of prey ($x = 0$), the predator population declines.

As a result, two cases arise, where possible equilibria are at the intersections of horizontal and vertical isoclines:

1. If $\frac{m}{b} < K$, there are three equilibrium points: $(0, 0)$, $(K, 0)$, and $(x^* = \frac{m}{b}, y^* = \frac{r}{a}(1 - \frac{bK}{m}))$, where the last equilibrium is in the positive quadrant. 2. If $\frac{m}{b} > K$, there are only two equilibrium points: $(0, 0)$ and $(K, 0)$. A third equilibrium exists but has a negative component, which has no biological meaning and is disregarded.

To analyze the stability of the equilibria, we compute the Jacobian matrix of the system:

$$A = \begin{bmatrix} r - \frac{2rx}{K} - ay & -ax \\ by & -m + bx \end{bmatrix}. \tag{3.17}$$

Evaluating at the origin $(0, 0)$:

$$A(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix}, \tag{3.18}$$

which corresponds to an unstable saddle point.

For the point $(K, 0)$, the Jacobian is:

$$A(K,0) = \begin{bmatrix} -r & -aK \\ 0 & -m + bK \end{bmatrix}, \tag{3.19}$$

with eigenvalues:

$$\lambda_1 = -r < 0, \quad \lambda_2 = -m + bK. \tag{3.20}$$

Depending on parameter values:

1. If $\frac{m}{b} < K$, then $\lambda_2 > 0$, so $(K, 0)$ is an unstable saddle point. 2. If $\frac{m}{b} > K$, then $\lambda_2 < 0$, so $(K, 0)$ is a stable node.

For the equilibrium (x^*, y^*), the Jacobian simplifies as follows:

$$A(x^*, y^*) = \begin{bmatrix} -\frac{rx^*}{K} & -ax^* \\ by^* & 0 \end{bmatrix}. \tag{3.21}$$

From this, we obtain:

$$\text{tr } A = -\frac{rx^*}{K}, \quad \det A = abx^*y^*. \tag{3.22}$$

Since $x^* > 0$ and $y^* > 0$, we conclude:

$$\text{tr } A < 0, \quad \det A > 0. \tag{3.23}$$

which ensures the stability of the equilibrium (x^*, y^*).

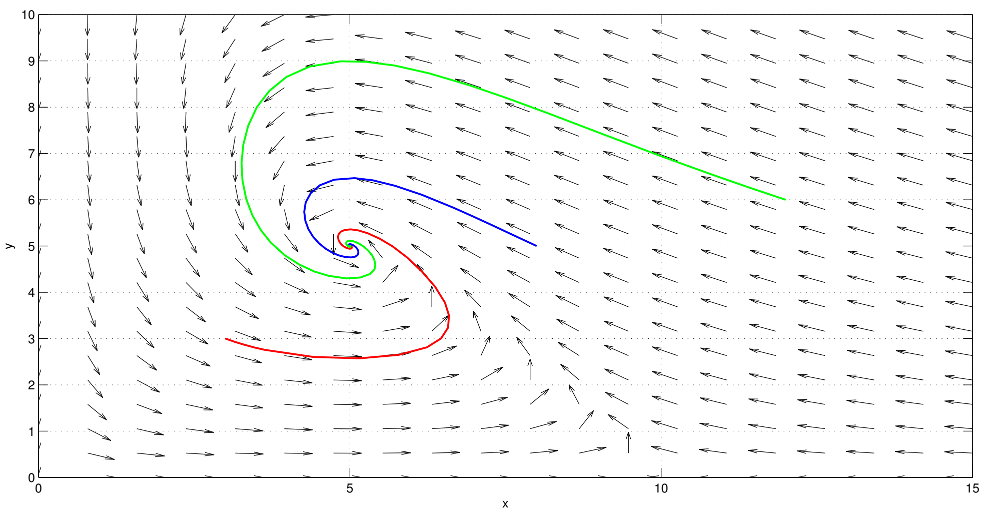

Figure 3.6: Phase portrait of the Lotka-Volterra model with logistic growth of prey. Case where prey and predator coexist, $r = 0.1$, $K = 10$, $a = 0.1$, $m = 0.2$, $b = 0.05$.

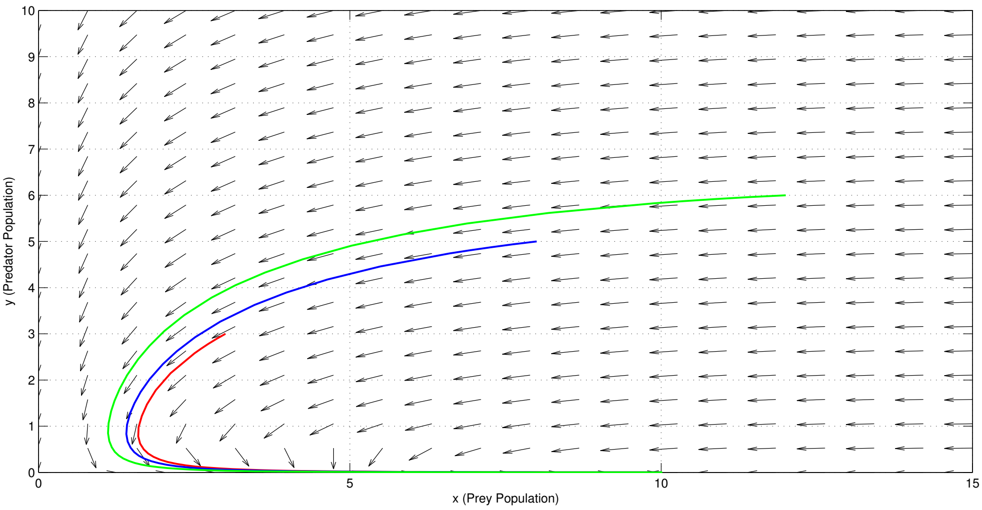

Figure 3.7: Phase portrait of the Lotka-Volterra model with logistic growth of prey. Predator extinction case: $r = 0.1$, $K = 10$, $a = 0.1$, $m = 0.2$, $b = 0.01$.

Figures 3.6 and 3.7 illustrate the phase portraits obtained through numerical simulations:
- When $\frac{m}{b} < K$, both prey and predators coexist with constant population levels (x^*, y^*).
- When $\frac{m}{b} > K$, predators become extinct, and the prey population approaches its carrying capacity K.

Introducing logistic growth for the prey instead of exponential growth significantly affects predator-prey dynamics by allowing the possibility of predator extinction.

Chapter 4

Other examples of biological models.

Introduction

Mathematical modeling plays a crucial role in understanding complex biological interactions. By formulating differential equations that describe population dynamics, researchers can analyze various ecological and biological processes, predict long-term behavior, and explore the effects of different interaction mechanisms.

In this chapter, we present several important biological models that extend beyond simple population dynamics to incorporate more realistic interaction functions. We begin with the predator-prey model using the Holling-type interaction functional, which accounts for different predator response mechanisms to prey density. This formulation improves upon the classical Lotka-Volterra model by introducing saturation effects in predation rates.

Next, we introduce the Beddington-DeAngelis interaction functional, which provides a more generalized framework for predator-prey dynamics by considering mutual interference among predators. This model helps in understanding scenarios where predator efficiency is affected by the density of both prey and predators.

We then explore the mutualism model, which describes cooperative interactions between species where both populations benefit. This type of interaction is commonly observed in nature, such as in pollination networks or symbiotic relationships.

Finally, we analyze the three-species trophic chain model, which extends predator-prey dynamics to multiple levels of interactions, representing hierarchical food chains. This model allows for the study of cascading effects and stability conditions in ecosystems with multiple interacting species.

Through these models, we aim to provide a deeper understanding of how species interact in natural environments and how mathematical frameworks can be used to capture the complexity of biological systems.

4.1 Predator-Prey Model with Holling Type Interaction Functional

The fairly general, say standard or generic, form of a predator-prey model is as follows:

$$\begin{cases} \dot{x} = f(x) - h(x,y), \\ \dot{y} = g(y) + eh(x,y), \end{cases} \tag{4.1}$$

where the negative sign in front of the function $h(x, y)$ indicates that the interaction with predators has a negative effect on the growth of the prey. The parameter $e > 0$ is the rate of conversion of prey biomass into predator biomass. It is common to consider the number of prey killed by a single predator per unit time, which is also called the response function of the predator-prey model. In the above model, the response function $F(x, y)$ is given by:

$$F(x, y) = \frac{h(x, y)}{y}. \tag{4.2}$$

In the particular case of the Lotka-Volterra model, the function $h(x, y) = axy$, and therefore:

$$F(x, y) = ax. \tag{4.3}$$

However, it is evident that this response function is unrealistic. Indeed, F is proportional to x, meaning that the number of prey ingested by a single predator can be very large if x is large. One should rather expect a limitation on the number of prey killed and ingested by a predator even if the prey density is high. The physiological absorption capacities of a predator are limited, and even if a large number of prey is available, a predator will not be able to consume more than a certain limit. It is therefore more realistic to conceive a response function that exhibits a saturation effect with prey density.

A response function that levels off at high prey densities is called a type II response function, in contrast to the Lotka-Volterra response function, known as type I. The type II function, called the Holling response function, is given by:

$$F(x, y) = \frac{ax}{x + D}, \tag{4.4}$$

where D is a positive constant (see Figure 4.1).

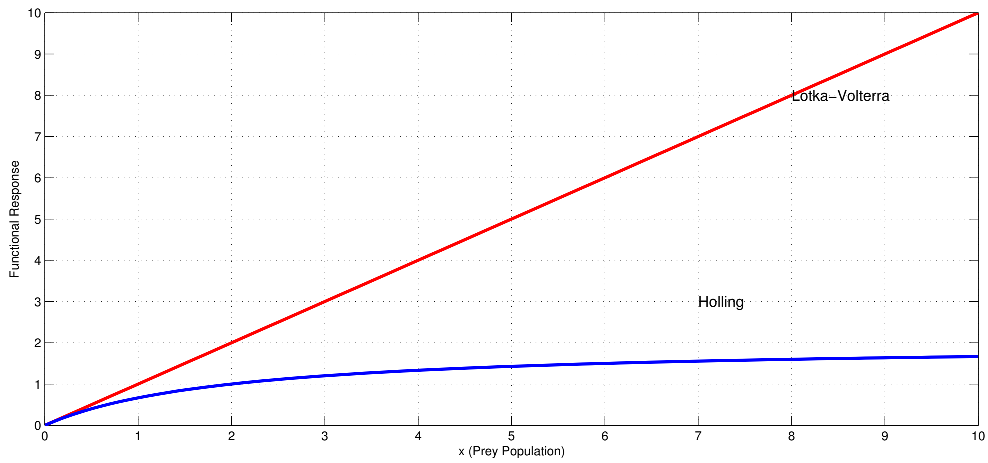

Figure 4.1: Lotka-Volterra and Holling response functions, the latter exhibiting a saturation effect.

With such a response function, and retaining the assumptions of the previously studied model, we obtain the following Holling predator-prey model:

$$\begin{cases} \dot{x} = rx\left(1 - \frac{x}{K}\right) - \frac{axy}{x+D}, \\ \dot{y} = -my + \frac{bxy}{x+D}, \end{cases} \tag{4.5}$$

where we define $b = ea$. The positive quadrant remains positively invariant. To find the equilibria of the Holling model, we seek the zero isoclines:

$$\dot{x} = 0 \Rightarrow y = \frac{r}{a}\left(1 - \frac{x}{K}\right)(x + D), \quad \text{or} \quad x = 0, \tag{4.6}$$

$$\dot{y} = 0 \Rightarrow x = \frac{mD}{b - m}, \quad \text{or} \quad y = 0. \tag{4.7}$$

Assuming $b > m$, the two axes are again isoclines. The following vertical isocline:

$$y = \frac{r}{a}\left(1 - \frac{x}{K}\right)(x + D), \tag{4.8}$$

is a downward-opening parabola intersecting the x-axis at two points $(K, 0)$ and $(-D, 0)$, the latter having no biological meaning. The vertex of this parabola is located at:

$$\hat{x} = \frac{K - D}{2}. \tag{4.9}$$

We make the realistic assumption that $K > D$.

Two cases are possible:

1) If $\frac{mD}{b-m} < K$, there are three biologically relevant equilibrium points: $(0, 0)$, $(K, 0)$, and (x^*, y^*), where the latter lies in the positive quadrant.

2) If $\frac{mD}{b-m} > K$, there are only two equilibria: $(0, 0)$ and $(K, 0)$.

To analyze the stability of these equilibria, we compute the Jacobian matrix:

$$A = \begin{bmatrix} r - \frac{2rx}{K} - \frac{aDy}{(x+D)^2} & -\frac{ax}{x+D} \\ \frac{bDy}{(x+D)^2} & -m + \frac{bx}{x+D} \end{bmatrix}. \tag{4.10}$$

For the equilibrium at the origin:

$$A(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix}, \tag{4.11}$$

which is a saddle point.

For the predator-free equilibrium:

$$A(K, 0) = \begin{bmatrix} -r - \frac{aK}{K+D} & 0 \\ 0 & -m + \frac{bK}{K+D} \end{bmatrix}, \tag{4.12}$$

with eigenvalues $\lambda_1 = -r < 0$ and $\lambda_2 = -m + \frac{bK}{K+D}$. Depending on whether $\frac{mD}{b-m} < K$ or $\frac{mD}{b-m} > K$, the equilibrium can be a saddle point or a stable node.

Finally, for the non-trivial equilibrium (x^*, y^*), we simplify the Jacobian and analyze its determinant and trace:

$$\det A = \frac{abDx^*y^*}{(x^* + D)^3} > 0, \tag{4.13}$$

ensuring stability when:

$$\operatorname{tr} A < 0 \iff x^* > \frac{K - D}{2}. \tag{4.14}$$

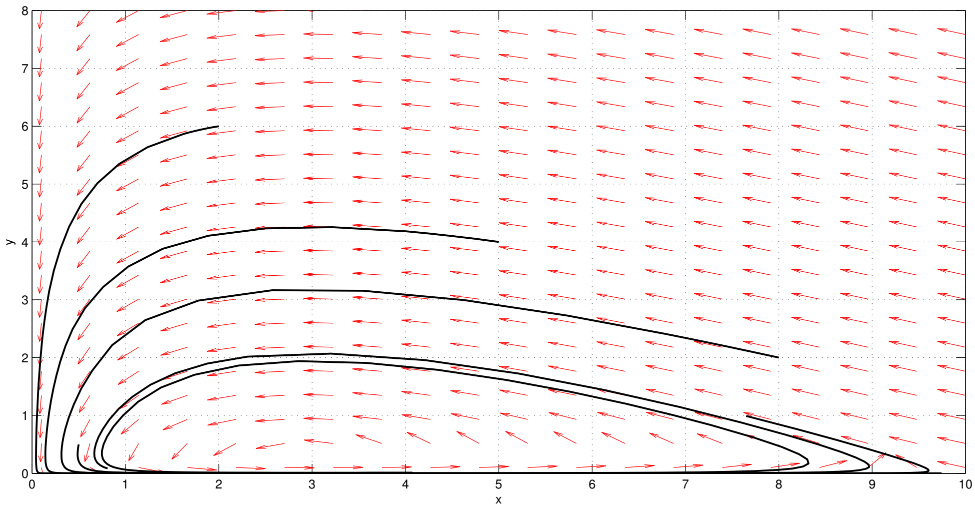

Figure 4.2: Limit cycle case. r = 0.1, K = 10, D = 3, a = b = 1, m = 1/2. The inner trajectory from A and the outer trajectory from B spiral toward the limit cycle.

If $x^* > \hat{x}$, the equilibrium is stable; otherwise, it is unstable, leading to a stable limit cycle via the Poincaré-Bendixson theorem. This system exhibits a Hopf bifurcation when the trace of A changes sign.

4.2 Predator-Prey Model with Beddington-DeAngelis Interaction Functional

In the case of Beddington's model, the response function is written as:

$$F(x, y) = \frac{ax}{1 + bx + cy}, \tag{4.15}$$

where a, b, and c are positive constants. This response function assumes an influence of predator density on the number of prey captured per predator per unit time. This is a negative effect because the response function is a decreasing function of predator density. Using this response function and assuming a linear growth of prey in the absence of predators and natural mortality of predators in the absence of prey, Beddington's predator-prey model is written as:

$$\dot{x} = rx - \frac{axy}{1 + bx + cy}, \tag{4.16}$$

$$\dot{y} = -my + \frac{eaxy}{1 + bx + cy}, \tag{4.17}$$

where r is the growth rate of prey and m is the mortality rate of predators.

The vertical zero isoclines are given by:

$$\dot{x} = 0 \Rightarrow y = \frac{r}{a - rc}(1 + bx) \quad \text{or} \quad x = 0. \tag{4.18}$$

The first equation corresponds to a line intersecting the axes at $(-\frac{1}{b}, 0)$ and $(0, \frac{r}{a-rc})$.

The horizontal zero isoclines are given by the equations:

$$\dot{y} = 0 \Rightarrow y = \frac{1}{mc}((ea - mb)x - m) \quad \text{or} \quad y = 0. \tag{4.19}$$

The first equation is again a line intersecting the axes at $\left(\frac{m}{ea-mb}, 0\right)$ and $\left(0, -\frac{1}{c}\right)$.

The case we will study corresponds to the existence of a non-trivial equilibrium (x^*, y^*) in the positive quadrant. The conditions on the parameters are as follows:

$$a > rc \quad \text{and} \quad \frac{ea}{mc} > \frac{rb}{a - rc} + \frac{b}{c}. \tag{4.20}$$

The second of these inequalities imposes a greater slope on the horizontal isocline than that of the vertical isocline.

It is trivial to verify that the origin is a saddle point since the Jacobian matrix at the origin is given by:

$$A(0,0) = \begin{bmatrix} r & 0 \\ 0 & -m \end{bmatrix}. \tag{4.21}$$

Regarding the point (x^*, y^*), after some calculations, we obtain:

$$A(x^*, y^*) = \frac{1}{(1 + bx^* + cy^*)^2} \begin{bmatrix} aby^*x^* & -ax^*(1 + bx^*) \\ eay^*(1 + cy^*) & -eacy^*x^* \end{bmatrix}. \tag{4.22}$$

Its determinant is strictly positive, and the trace can change sign:

$$\mathrm{tr}A(x^*, y^*) = \frac{ay^*x^*(b - ec)}{(1 + bx^* + cy^*)^2}. \tag{4.23}$$

Thus, we have: 1) If $b > ec$, the trace is positive, and the equilibrium is unstable. 2) If $b < ec$, the trace is negative, and the point is stable. 3) If $b = ec$, the trace is zero, and the linearized system corresponds to a center.

As a result, in Beddington's model, the determinant is positive, and the trace can change sign when b crosses the value ec. This is again a Hopf bifurcation. However, in this case, it is a degenerate Hopf bifurcation, meaning that no limit cycle appears, and centers are preserved at the bifurcation.

To demonstrate the existence of centers at the bifurcation when $b = ec$, it is possible to construct a first integral $H(x, y)$, which has an extremum at the equilibrium point (x^*, y^*). This first integral is given by the following expression:

$$H(x, y) = eax - m\ln(x) + ay - r\ln(y) - bx - cy + \ln(bx + cy), \tag{4.24}$$

up to a constant.

4.3 Mutualism Model

The classical model of mutualism is written as:

$$\begin{cases} \dot{x} = r_1 x \left(1 - \frac{x}{K_1} + a\frac{y}{K_1}\right), \\ \dot{y} = r_2 y \left(1 - \frac{y}{K_2} + b\frac{x}{K_2}\right), \end{cases} \tag{4.25}$$

where the signs of the coefficients a and b are positive compared to the previous competition model, where they were negative. Each population has a positive effect on the growth of the other, which characterizes mutualism or symbiosis. Symbiosis is generally stronger than mutualism, in the sense that the two symbiotic populations cannot exist independently, meaning one cannot survive without the other. However, in the case of mutualism, each isolated population is viable. The presented model is thus a mutualism model because in the absence of one of the two populations, the other follows a logistic-type equation and tends toward its carrying capacity.

As with the competition model, it is common to perform the following variable change:

$$u = \frac{x}{K_1}, \quad v = \frac{y}{K_2}, \quad t = r_1 t. \tag{4.26}$$

The system then becomes:

$$\frac{du}{dt} = u(1 - u + av), \quad \frac{dv}{dt} = rv(1 - v + bu). \tag{4.27}$$

The new parameters are expressed in terms of the old ones in the same way as in the competition model. The vertical null isoclines are:

$$\frac{du}{dt} = 0 \Rightarrow u = 0 \text{ or } v = \frac{1}{a}(u - 1), \tag{4.28}$$

and the horizontal null isoclines are:

$$\frac{dv}{dt} = 0 \Rightarrow v = 0 \text{ or } v = (1 + bu). \tag{4.29}$$

Depending on the parameter values, two cases are possible: - If $ab < 1$, the equilibrium point (u^*, v^*) is stable and located in the positive quadrant:

$$u^* = \frac{1 + a}{1 - ab}, \quad v^* = \frac{1 + b}{1 - ab}. \tag{4.30}$$

- If $ab > 1$, (u^*, v^*) is unstable, and the system exhibits unlimited population growth.

The linearized system around equilibrium is given by the Jacobian matrix:

$$A = \begin{bmatrix} 1 - 2u + av & au \\ rbv & r(1 - 2v + bu) \end{bmatrix}. \tag{4.31}$$

For (u^*, v^*), the matrix simplifies to:

$$A(u^*, v^*) = \begin{bmatrix} -u^* & au^* \\ rbv^* & -rv^* \end{bmatrix}. \tag{4.32}$$

The trace is negative for $ab < 1$, ensuring stability. The determinant is given by:

$$\det(A) = r(1 - ab)u^* v^*, \tag{4.33}$$

which determines the stability conditions: - If $ab < 1$, then $\det(A) > 0$, and (u^*, v^*) is globally asymptotically stable. - If $ab > 1$, then $\det(A) < 0$, making (u^*, v^*) a saddle point, leading to uncontrolled growth.

This result suggests that in the case of strong mutualism ($ab > 1$), populations grow indefinitely, which is unrealistic in a limited environment. A more refined model would include additional constraints.

4.4 Three-Species Trophic Chain Model

We study a system of more than two interacting populations or species. The simplest case is that of a prey, a predator, and a super-predator that feeds on the predator. This is known as a three-level trophic chain. A simple model describing this system is based on the Lotka-Volterra equations with Type I functional responses. The system of differential equations governing the dynamics is:

$$\begin{cases} \dot{x} = x(r - ay), \\ \dot{y} = y(-m + bx - cz), \\ \dot{z} = sz(1 - Kz) + dyz, \end{cases} \tag{4.34}$$

where:

- $x(t)$ represents the density of the prey,
- $y(t)$ represents the density of the predator,
- $z(t)$ represents the density of the super-predator.

The parameters $r, a, m, b, c, d, s,$ and K are all positive and describe interaction rates, growth rates, and carrying capacity.

Variable Transformations.
To simplify the model, we introduce the new variables:

$$u = x, \quad v = y, \quad w = \frac{z}{K}, \tag{4.35}$$

and perform a time rescaling:

$$t = st. \tag{4.36}$$

This transforms the system into:

$$\begin{cases} \frac{du}{dt} = u(r - av), \\ \frac{dv}{dt} = v(-m + bu - gw), \\ \frac{dw}{dt} = w(1 - w) + dvw, \end{cases} \tag{4.37}$$

with the transformed parameters:

$$r = \frac{r}{s}, \quad a = \frac{a}{s}, \quad m = \frac{m}{s}, \quad b = \frac{b}{s}, \quad g = \frac{cK}{s}, \quad d = \frac{d}{s}. \tag{4.38}$$

Equilibrium Points.
Setting the right-hand sides of the equations to zero, we find the equilibrium conditions:

$$u(r - av) = 0, \quad v(-m + bu - gw) = 0, \quad w(1 - w + dv) = 0. \tag{4.39}$$

The trivial equilibrium is $(0, 0, 0)$. A unique non-trivial equilibrium (u^*, v^*, w^*) exists in the positive quadrant, given by:

$$u^* = \frac{m}{b} + \frac{g}{b}\left(1 + \frac{dr}{a}\right), \quad v^* = \frac{ar}{a}, \quad w^* = 1 + \frac{dr}{a}. \tag{4.40}$$

Since all parameters are positive, this equilibrium always belongs to the positive quadrant.

Stability Analysis.

The Jacobian matrix at equilibrium is computed as:

$$A^* = \begin{bmatrix} 0 & -au^* & 0 \\ bv^* & 0 & -gv^* \\ 0 & dw^* & -w^* \end{bmatrix}. \tag{4.41}$$

The characteristic equation is:

$$\lambda^3 + w^*\lambda^2 + (abu^*v^* + adv^*w^*)\lambda + abu^*v^*w^* = 0. \tag{4.42}$$

Using Routh-Hurwitz criteria, the necessary conditions for stability are:

$$H_1 = a_1 > 0, \quad H_2 = a_1a_2 - a_3 > 0, \quad H_3 = a_3 > 0. \tag{4.43}$$

where:

$$a_1 = w^*, \quad a_2 = abu^*v^* + adv^*w^*, \quad a_3 = abu^*v^*w^*. \tag{4.44}$$

Since all conditions are met, the non-trivial equilibrium is locally asymptotically stable.

We have analyzed a three-species trophic model with Lotka-Volterra dynamics. Stability was determined using Routh-Hurwitz criteria, showing that the equilibrium is locally stable. This approach simplifies eigenvalue computation and provides insight into the system's behavior.

Conclusion

In this book, we have explored a wide range of mathematical models that describe the dynamics of biological populations. Starting with the fundamental principles of single-population models, we progressively extended our study to systems involving multiple interacting populations, as well as more complex ecological and epidemiological models.

The first chapter introduced the basic concepts of dynamical systems through the study of a single population, including equilibrium points, stability analysis, and phase portraits. We then examined two-species interactions in the second chapter, where we analyzed various types of equilibrium behaviors using tools such as linearization, eigenvalue analysis, and phase portrait classifications. Special attention was given to the Routh-Hurwitz criteria, Lyapunov functions, and limit cycles, which are crucial for understanding long-term system behavior.

In the third chapter, we expanded our discussion to community models, including classical frameworks such as logistic growth, the Allee effect, and the Lotka-Volterra equations. Finally, in the last chapter, we introduced more sophisticated models, such as predator-prey systems with different functional responses, mutualistic interactions, and trophic chain models, demonstrating how mathematical approaches can be used to capture the complexities of real-world ecological and biological systems.

Throughout this book, we emphasized both analytical and qualitative methods to understand dynamical systems. The tools and techniques presented serve as a foundation for further studies in biomathematics, mathematical ecology, and epidemiology.

This book is designed as a resource for **First-Year Master's students in Biomathematics (M1)**, providing them with essential theoretical and computational tools to model and analyze biological phenomena. We hope that this work serves as a stepping stone for more advanced studies and inspires future research in the fascinating field of biomathematics.

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