Chapter 2

Mathematical Foundations: Dynamical Systems

2.1 Introduction to dynamical systems

Any system that varies as a function of time may be termed a dynamical system; the study of dynamical systems has a long history, spanning many fields. The description of a dynamical system begins with the definition of a set of variables that define the *space* through which the system may evolve. These variables are quantitative descriptions of the system; in a biological context they may be values such as the populations of several species (rabbits, wolves, mice, *etc.*) or the concentrations of some defined set of biochemical molecules. We often think of these as coordinates in a Cartesian space (*e.g.* (x, y) in two-dimensions or (x, y, z) in three). The *state* of the systems is described by the values of each of the variables, that is, its *position* in the Cartesian space.

The second component in the description of a dynamical system is the definition of an *evolution rule*, which determines how the state of the system changes over time. In general, this rule is deterministic — meaning that if you know the state of the system at any time, t, then you can predict the state at any future time, $t+\Delta t$.[1] Note that this level of determinism only holds if the state of the system is known exactly, as we will discuss later, in some cases, small changes at one time can lead to dramatic differences later on.

A good example of a dynamical system is the motion of a ball on a three-dimensional surface. If a ball is placed in different positions on the surface, it will move along a predictable path, governed by the slope of the surface. How is this written mathematically? We use Newton's Laws of motion. First, we note that the ball will accelerate in a given direction dependent on the steepness in that direction, because the ball experiences a force related to the steepness of the slope; we may refer to the forces in the x and y directions as F_x and F_y. Given these forces, the acceleration in each direction is given by the relationship $F = ma$, where m is the mass of the ball. Thus:

$$a_x = \frac{F_x}{m} \qquad a_y = \frac{F_y}{m} \tag{2.1}$$

[1] Systems that are fundamentally non-deterministic are known as "stochastic dynamical systems", and must be described in a different manner. These systems also play an important role in some areas of biology.

gives the acceleration in the x and y directions, respectively. Since acceleration is the derivative of velocity with respect to time ($a = \frac{dv}{dt}$) and velocity is the derivative of position with respect to time ($v = \frac{r}{t}$), we get the result that:

$$\frac{d^2x}{dt^2} = \frac{F_x}{m} \qquad \frac{d^2y}{dt^2} = \frac{F_y}{m} \tag{2.2}$$

This is a *second-order* system of differential equations — if we know the position of the ball at a given time, $(x(t), y(t))$, then we can determine the force on the ball, and thus it's acceleration. In order to predict the path of the ball, however, we also need to know it's velocity. A ball that is placed carefully at a point and released does not follow the same path of a ball that rolls through the same point — the ball has *momentum*.[2]

Many biological systems, on the other hand, are described by *first-order* differential equations. That is, the rate of change of a variable (*i.e.* the velocity), depends only the the values of the variables, and not on the previous velocity. We can write this as:

$$\frac{dx}{dt} = f(x, y) \qquad \frac{dy}{dt} = g(x, y) \tag{2.3}$$

where $f(x, y)$ and $g(x, y)$ are functions that will be defined in each system. There is no momentum in a first-order system; the system will evolve in an identical manner if the system is carefully arranged at a particular state, or if the system "rolls" through that same state. As a result, we often describe first-order dynamical systems as a velocity field. This is a map in which each point in the space is described by a vector that gives the velocity associated with that point; the velocity vector will have a directionality (indicating the path the system will take as it evolves in time) and a magnitude (indicating how quickly the system will evolve). Given such a map, it is easy to determine the path (or *trajectory*) that the system will take from any given point — it is simply a matter of following the vectors of the velocity field.

2.2 Linear dynamical systems

So far we have discussed the general concept of dynamical systems, as governed by a set of evolution rules. When these rules are *linear* equations, we say that the system is a linear dynamical system. Linear systems have many properties with make them particularly easy to study. First, let's be clear on what we mean by linear evolution rules. Briefly, the evolution rules must be of the form:

$$\frac{dx_i}{dt} = \sum_{j=1}^{n} a_{ij} x_j \tag{2.4}$$

where x_i describes the "i^{th}" variable (of n total), and a_{ij} is a constant associated with both equation i and variable j. For example, a linear system of two variables is:

$$\frac{dx}{dt} = ax + by \qquad \frac{dy}{dt} = cx + dy \tag{2.5}$$

[2]We thus say that the *phase space* of physical systems includes both the position and the momentum; both properties are required to describe the system's state.

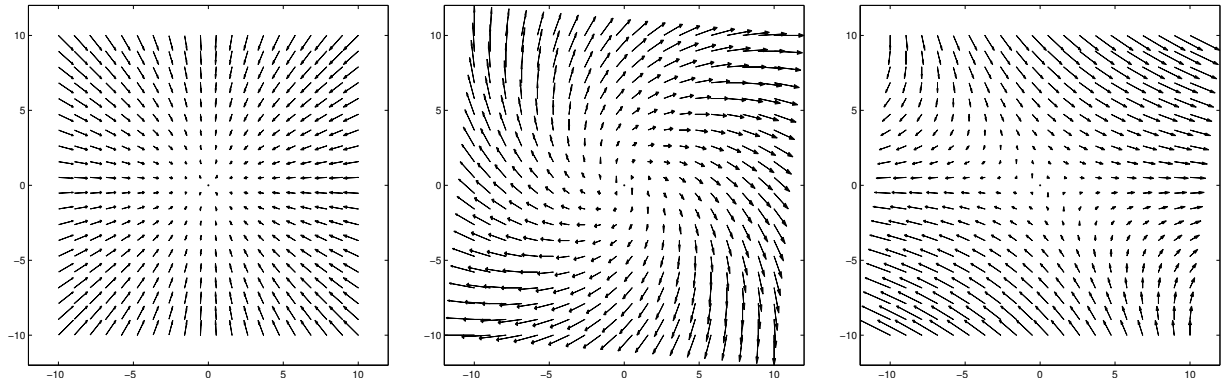


Figure 2.1: The velocity fields of three linear systems. (a) Equation 2.7: $\frac{dx}{dt} = -x$, $\frac{dy}{dt} = -y$; (b) Equation 2.8: $\frac{dx}{dt} = x + y$, $\frac{dy}{dt} = -x + y$; (c) Equation 2.9: $\frac{dx}{dt} = x + y$, $\frac{dy}{dt} = -y$.

and a linear system of three variables is:

$$\frac{dx}{dt} = a_1x + b_1y + c_1z \qquad \frac{dy}{dt} = a_2x + b_2y + c_2z \qquad \frac{dz}{dt} = a_3x + b_3y + c_3z \tag{2.6}$$

All linear systems obey the following rules:

- At the origin ($x_1 = x_2 = \cdots = x_n = 0$), all the velocities are also zero; a system at the origin will never move.
- If the velocities at point $\vec{x}_1$ (we use vector notation to denote the set of all variables), are $\vec{v}_1$, then the velocities at point $c\vec{x}_1$ (c is a constant) are $c\vec{v}_1$; if all variables are scaled by a constant, then the velocities in each direction are scaled by the same amount.
- If the velocities at two points, $\vec{x}_1$ and $\vec{x}_2$, are $\vec{v}_1$ and $\vec{v}_2$, then the velocity at the point described by the vector sum, $(\vec{x}_1 + \vec{x}_2)$ is $\vec{v}_1 + \vec{v}_2$.

The last two points are often combined in a rule called *linear superposition*:

- If the velocities at two points, $\vec{x}_1$ and $\vec{x}_2$, are $\vec{v}_1$ and $\vec{v}_2$, then the velocity at the point $a\vec{x}_1 + b\vec{x}_2$ (where a and b are constants) is $a\vec{v}_1 + b\vec{v}_2$.

2.2.1 Examples of linear dynamical systems and their velocity fields.

First, take the system:

$$\frac{dx}{dt} = -x \qquad \frac{dy}{dt} = -y \tag{2.7}$$

In this case, the velocity vector at every point in space is oriented directly towards the origin (see Figure 2.1a). Thus, all trajectories will lead in a straight line to the origin, and then stay there.

Now, consider a second system:

$$\frac{dx}{dt} = x + y \qquad \frac{dy}{dt} = -x + y \tag{2.8}$$

Along the x-axis ($y = 0$), the velocity is given by $(x, -x)$ — the vectors are pointed downwards and to the right for positive x, and upwards and to the left for negative x. Along the y-axis ($x = 0$), the velocities are (y, y) — the vectors are oriented upwards and to the right for positive y and downwards and to the left for negative y. Along the line of $y = x$, the velocity in the y direction is zero, and the velocity is x is $2x$ — the velocity vectors are horizontal lines, to the right when $x > 0$ (first quadrant) and to the left when $x < 0$ (third quadrant). Similarly, along the line of $y = -x$, the velocity in the x direction is zero, and that in the y direction is $-2x$ — the velocity vectors are vertical lines, oriented down when $x > 0$ (fourth quadrant) and up when $x < 0$ (second quadrant). Thus, from *any point* other than the origin, the system will evolve by moving away from the origin in clockwise spiral; this system is shown in Figure 2.1b.

This example highlights an important point — *linear dynamical systems can have interesting, non-trivial dynamic behaviors.* A linear dynamic system does **not** mean that all trajectories are straight lines. Conversely, very simple dynamic systems may be non-linear; for example, the uniform velocity field (the velocity of the system is the same at every point in space) is a non-linear system, as the velocity at the origin is non-zero.

Now let's take a third case:

$$\frac{dx}{dt} = x + y \qquad \frac{dy}{dt} = -y \tag{2.9}$$

Along the x-axis, the velocity is given by $(x, 0)$ — the vectors are horizontal lines pointed away from the origin. Along the y-axis, the velocity is $(y, -y)$ — for positive y, the vectors point down and to the right, and for negative y, they point up and to the left. Along the line $y = -x$, the x velocity is zero, and the y velocity is x (or $-y$) — the velocity vectors are vertical lines, pointed downwards in the second quadrant ($x < 0$, $y > 0$) and upwards in the fourth quadrant ($x > 0$, $y < 0$). Now, something interesting happens when we consider the line $y = -2x$. Along this line, the x velocity is $x - 2x = -x$ and the y velocity is $-(-2x) = 2x$. If we consider the slope of the velocity vector:

$$\frac{dy/dt}{dx/dt} = \frac{v_y}{v_x} = \frac{2x}{-x} = -2 \tag{2.10}$$

we find that the velocity vector has the same slope as the line we began on, (-2). Thus, any point on this line will follow a trajectory along the same line! Considering the signs, we note that in the second quadrant (negative x, positive y), the x velocity is positive and the y velocity is negative, so the trajectory moves towards the origin. In the fourth quadrant (positive x, negative y), the sign of the velocities is reversed (x velocity is negative, and y velocity is positive), so again, the trajectories lead to the origin. Following the velocity field (Figure 2.1c) give different types of trajectory for different starting points:

- For all points above the x-axis and to the right of $y = -2x$, the trajectory will curve down and to the right, approaching the x-axis asymptotically (and continuing away

from the origin); for all points below the x-axis and to the left of $y = -2x$, the behaviors are symmetric to this — they curve up and to the left, asymptotically approaching the x-axis.

- For all points below the x-axis and to the right of $y = -2x$, the trajectories again move asymptotically towards to the positive x-axis (away from the origin), but the curves do not move strictly to the right. Rather, for all points below (or left of) the $y = x$ line, they will move to the left (and up), and then switch directions to the right (and up). Again, the trajectories in the symmetry-related region behave symmetrically.

- Points lying precisely on the x-axis move along this line, away from the origin.

- Points lying on the $y = -2x$ line also move along this line, but *towards* the origin, at which point the system does not evolve further.

2.3 Qualitative description of dynamical systems

In these three examples, we have seen three distinct types of behavior. In the first two cases, all trajectories were qualitatively the same: moving either only towards, or only away from, the origin, and always in the same pattern (in the examples, as a straight line or as a clockwise spiral). The only noticeable point in these systems is the origin, which defines the center about with all trajectories are oriented. However, in the last example, there was seen to be greater diversity in the paths; not only was the origin a key point, but the lines of $y = 0$ (the x-axis) and $y = -2x$ play an important role.

2.3.1 Stationary points and manifolds

These observations motivate the definition of several terms that are frequently used in describing dynamical systems:

- A **stationary point** is any location where the velocity field is equal to zero; any system beginning at a stationary point will not evolve with time. In linear systems, the origin is always a stationary point; there also may be lines through the origin for which all points on the line are stationary points.

- A **stable** or **attracting stationary point** (also termed an **attractor**), is a stationary point for which all the velocity lines around it point *towards* the point. If a system starts out anywhere *nearby* a stable stationary point, the system will evolve towards the point, and then stay there.

- An **unstable** or **repelling stationary point** (also termed a **repellor**) is a stationary point for which all the velocity lines around it point *away* from the point. If a system starts out anywhere nearby an unstable stationary point (but not precisely on it), the system will move away from the point over time. In linear systems, this means that at least one variable will tend towards infinity.

- An **attracting manifold** is a line for which all velocity lines point *towards it* in all directions except one (the direction of the line itself); the velocity vectors point along the line in this direction. When a system starts out near an attracting manifold, it moves both towards and along the line.

- A **repelling manifold** is a line for which all velocity lines point *away* from the line, except in the direction of the line itself; again the velocity vectors point along the line in this direction. When a system starts out near a repelling manifold, it tends to move away from the line, but with a component of the motion parallel to the line.

- A **saddle point** is a stationary point which has characteristics of both an attractor and a repellor — velocity lines are oriented towards the point in some directions, but away from the point in others. Saddle points typically lie at the intersection of an attracting and a repelling manifold.

- A **null cline** is a line along which the velocity in *one direction* is zero; the velocity in other directions need not be. We speak of the x null cline when $\frac{dx}{dt} = 0$, the y null cline when $\frac{dy}{dt} = 0$, and so on.

In analogy to the motion of a ball on a three-dimensional surface, a stable stationary point can be compared to the bottom of a mountain bowl, and an unstable stationary point to the top of a mountain peaks. In both cases, a ball placed perfectly at the point will not move, but a ball placed *near* the bottom of the bowl will move towards that point, while a ball placed near the peak will move away. An attracting manifold is similar to a long narrow valley that slopes downwards in one direction, and a repelling manifold is similar to a mountain ridge. Finally, a saddle point is like a mountain pass — a valley that passes between a ridge.

Just as understanding the topology of a three-dimensional physical surface is enough to qualitatively describe the behavior of a dropped ball, so can the location and types of stationary points and manifolds be used to give a qualitative idea of the behavior of general dynamical systems.

2.3.2 Qualitative description of dynamics between null clines

How can we characterize a dynamical system? To answer this question, we must first think carefully about what exactly we wish to know. Do we wish to know the exact trajectory that will be followed from a particular starting point, or do we only wish to know the ultimate destination of the system (if such can be defined)? Do we want how long it takes for the system to evolve along a path, or is the path followed an adequate solution? Do we wish to make quantitative predictions, or to gain a qualitative intuition? Under different circumstances, we may choose any of these, and different methods of analysis are applicable in each case.

One of the key things we may want to know is the location of stationary points; additionally, we are often interested in the behavior of the system as it evolves from a non-stationary starting point. For systems of two or three variables, we can learn a lot about these dynamics by a simple graphical analysis. First, consider the set of null clines for a system; recall that

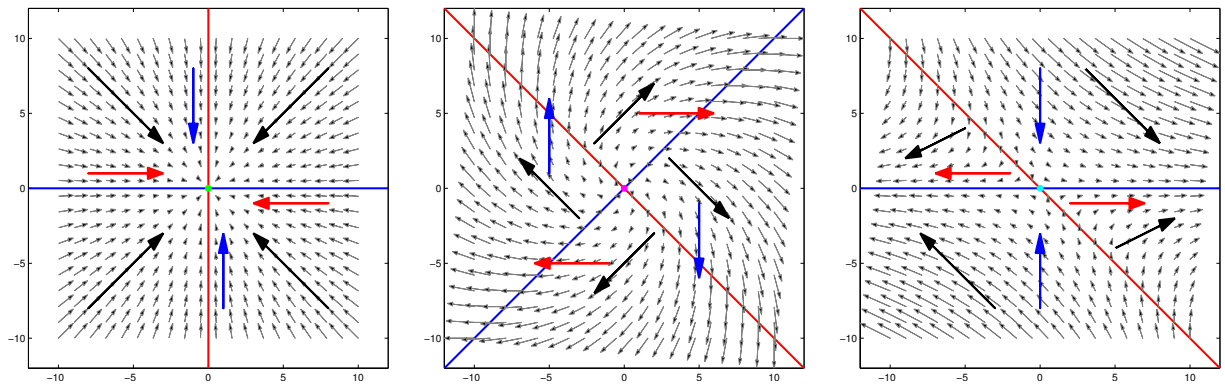


Figure 2.2: The velocity fields of three linear systems, characterized by null clines. Red lines indicate null clines for $\frac{dy}{dt}$, and red arrows the direction of motion; blue lines and arrows are the same for $\frac{dx}{dt}$. Black arrows indicate direction of motion in each region. (a) Equation 2.7: $\frac{dx}{dt} = -x$, $\frac{dy}{dt} = -y$ has a stable stationary point; (b) Equation 2.8: $\frac{dx}{dt} = x + y$, $\frac{dy}{dt} = -x + y$ has an oscillatorally unstable stationary point; (c) Equation 2.9: $\frac{dx}{dt} = x + y$, $\frac{dy}{dt} = -y$ has a saddle point.

a null cline is a line (in 2-D) or a plane (in 3-D) for which rate of change of a single variable is zero. That is, the null cline represents the roots of one of the equations in the system. If each equation is equal to zero along its null clines, then it should be obvious that the intersection of null clines for each of the variables in the system will be a stationary point; all equations at this point will simultaneously be zero.

Now, consider how the rate of change of a given variable will change as we move from one side of its null cline to another. Since the rate of change is zero at the null cline, either the rate of change will switch sign (from positive to negative, or vice versa) or it will briefly touch zero and then return to a small value of the same sign. More importantly, though, the *only* time that the rate of change of a variable can change sign, is when it crosses a null cline — the only way the function can move from a positive to a negative value (or the reverse) is to pass through zero.[3] This allows to use a very simple approach to characterize the dynamics of a system:

1. Plot the null clines for each variable in the system; be sure to keep track of which variable each null cline corresponds to.

2. Characterize the *sign* of each variable's rate of change on either side of its null clines.

3. Break the entire space of the system into regions bordered by the null clines, then assign an overall direction of motion based on the signs of the velocities of each variable.

Knowing the general direction of motion of the system in each region will give a qualitative idea of how the system will evolve from an arbitrary starting point. This analysis also allows us to characterize the stationary points. Recall that a stationary point corresponds to an

[3]This is a consequence of the Mean-Value Theorem, which strictly applies only to continuous functions. Thus, if one of the update rules is not continuous in the domain of interest, this rule fails.

intersection of the null clines of each variable; this means that several of the regions discussed above will touch at this point. Considering the general direction of motion in each of these regions can be used to characterize the stationary point as follows:

- If the general direction of motion of all regions around the point is oriented towards it, the point is an *attractor*.
- If the general direction of motion of all regions around the point is oriented away from it, the point is a *repellor*.
- If the direction of motion is away from the point in some bordering regions, and towards it in others, then the point is a *saddle point*.
- If the direction of motion in the each region around the point is neither towards nor away from the point, but rather seems to form a unidirectional circle around it, then the point is *oscillatory*. This type of stationary point may either be stable, unstable, or neither, but this degree of characterization requires more detailed analysis.

2.4 Non-linear dynamical systems

Any system that does not obey the rules of linear superposition is grouped under the general category of non-linear dynamical systems. The origin of the non-linearities can come from a number of sources. For example, in the Lotka–Volterra model of predator-prey dynamics, we have:

$$\frac{dN_{prey}}{dt} = N_{prey}(A - BN_{predator}) \qquad \frac{dN_{predator}}{dt} = N_{predator}(CN_{prey} - D) \tag{2.11}$$

which is of the form:

$$\frac{dx}{dt} = ax - bxy \qquad \frac{dy}{dt} = cxy - dy \tag{2.12}$$

Here we have terms involving the product of x and y: non-linear cross-terms that combine contributions from multiple species.

In the description of enzyme kinetics, the rate of an enzyme-catalyzed reaction is often described by the Michaelis–Menten equation:

$$v = \frac{V_{\max} S}{K_M + S} \tag{2.13}$$

or the Hill equation:

$$v = \frac{V_{\max} S^h}{K_{1/2}^h + S^h} \tag{2.14}$$

where S is the concentration of the substrate of the reaction, and the other terms are constants. These are equations of a single variable, but with fundamentally non-linear behaviors. In particular, there is a maximal capacity, $V_{\max}$, which describes the highest possible rate, reached in the limit of large substrate concentrations. This can result in any system where there is some environmental limiting capacity (such as the availability of enzyme). In the

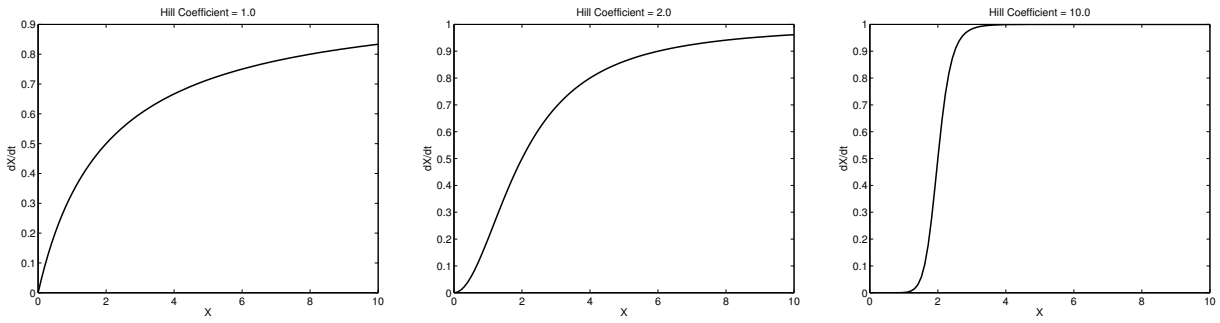


Figure 2.3: The behavior of the Michaelis–Menten and Hill equations. (a) Michaelis–Menten ($h = 1.0$); (b) Hill equation with $h = 2.0$; (c) Hill equation with $h = 10.0$.

case of the Hill equation (with the Hill coefficient, h, greater than 1), there is additionally a lag-phase, where the rate at low substrate concentrations is particularly slow. This behavior can result when there is cooperativity in the system — the presence of substrate promotes the reaction. Greater cooperativity would be described by a larger Hill coefficient.

An example non-linear system

Non-linear systems can be understood through the description of the stationary points and manifolds, just as was done for linear systems. However, while linear systems have a single stationary point at the origin (in some cases extending along lines through the origin), non-linear systems often have multiple stationary points.

Consider a system with three stationary points located along the $y = x$ line — an attractive stationary point at the origin and another somewhere along $y = x$ in the first quadrant, with a saddle point located in between the two. Further more, consider the line of $y = x$ to be an attractive manifold, and the saddle point to lie at the intersection of a repelling manifold that is perpendicular to $y = x$. The dynamics of this system are such that all points lying below (and to the left) of the repelling manifold give rise to trajectories that lead to the origin, and remain there; none of these trajectories cross the attractive manifold of $y = x$. All points above (and to the right) of the repelling manifold give rise to trajectories that lead to the second (non-zero) stable stationary point, and again, none cross $y = x$. The only points that do not yield trajectories that lead to one of the two attractors are those lying precisely on the repelling manifold; trajectories along the manifold lead to the saddle point. A system like this is said to have a **bifurcation** — there are (generally) two possible behaviors of the system, and there is a clear dividing line between the two. We also say that such a system is **bi-stable**, because there are two distinct stable stationary points.

How might one get such a system? Consider two populations (of organisms, or of biomolecules, for example), in which:

1. Both populations grow in a Hill-like fashion, dependent on the *other* species.

2. Both populations decay linearly, dependent on themselves.

That is:

$$\frac{dx}{dt} = \frac{Vy^2}{K^2 + y^2} - Cx \qquad \frac{dy}{dt} = \frac{Vx^2}{K^2 + x^2} - Cy \tag{2.15}$$

We may expect a few regimes of behavior:

- At *low x and y*, the linear decay term will dominate, due to the lag in the Hill equation (*c.f.* $x > x^2$ if $x < 1$); the system will **decay towards zero**.
- At *moderate x and y*, the Hill-based growth term will dominate (*c.f.* $x < x^2$ if $x > 1$); the system will **grow towards the non-zero attractor**.
- At *high x and y*, the growth is limited to V, and thus the linear decay term once again dominates; the system will **decay towards the non-zero attractor**.

Along the $y = x$ line, the two rates of change will be identical, and will be a function of a single variable:

$$\frac{dx}{dt} = \frac{Vy^2}{K^2 + y^2} - Cx \qquad \frac{dy}{dt} = \frac{Vx^2}{K^2 + x^2} - Cy \tag{2.16}$$

$$\frac{dy}{dt} = \frac{dx}{dt} = \frac{Vx^2}{K^2 + x^2} - Cx \tag{2.17}$$

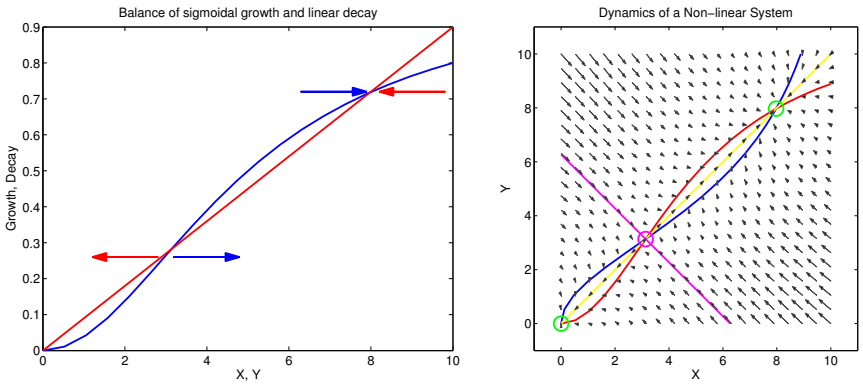
Plotting the two terms in this equation, $\frac{Vx^2}{K^2+x^2}$ and Cx, we see that the two curves intersect at several points. Initially, the linear term is above the Hill equation curve, representing dominance of the decay term, and evolution to lower x. After the first non-zero intersection of the curves, the Hill equation becomes larger than the linear term. Thus, to the right of this point, the system will evolve to larger x; the system moves away from the point in both directions. This is the location of the saddle point (the attractive direction is perpendicular to $y = x$). Finally, the curves intersect again, with the liner term again dominating; to the right of this point the system will evolve towards lower x. Since to the left of this point, x will increase, the system will stabilize at this point — the non-zero stable stationary point. Of course, the curves also intersect at the origin, the first stationary point.

Also note the null clines, obtained when either $\frac{dx}{dt}$ or $\frac{dy}{dt}$ are zero, are given by:

$$x = \frac{Vy^2}{C(K^2 + y^2)} \qquad y = \frac{Vx^2}{C(K^2 + x^2)} \tag{2.18}$$

These are simply curves of exactly the same form as the Hill-equation, with V scaled by C.

We can understand this system with a velocity field plot, as above, and by considering the exact details of the differential equations that describe the system. However, sometimes it is useful to be able to describe in qualitative terms how the various components of the system interact. One way of doing this is with schematic diagrams. A diagram that simply expresses whether each component tends to increase, decrease, or have no effect upon each other component is reminiscent of the schematics of biochemical pathways that are seen in most texts, and of similar diagrams that describe ecological dependencies. Thus, they represent a useful means of explaining, at some level, the details of a mathematical model, to an experimental biologist with significant mathematical training.



(a) **(b)**

Figure 2.4: A symmetric non-linear system with Hill-like growth and linear decay. (a) Balance of growth and decay terms in one dimension. The decay curve (red) dominates at low and high values, while the growth term (blue) dominates in between. As a result two of the intersecting points (the origin and the largest) are sable, and the middle one is unstable. (b) The non-linear velocity field. The x null cline (blue line) and y null cline (red line) intersect at two stable points (green circles) and one saddle point (magenta circle). There are also two manifolds: an attractive manifold (yellow line) along $y = x$, and a repelling manifold along $y = -x + b$, where $b = 6.2684$.

In this system, we have **feedback**, which is seen as a loop in the interaction diagram. Because both interactions are positive, we say we have a **positive feedback** loop. These interactions tend to lead to enhancement of a variable (consider how positive feedback in a microphone–amplifier system leads to enhancement of even minor noise from the mic). In this case, however, the maximal response is limited both by the Hill-like behavior of the positive response and the negative decay term.

We can also have **negative feedback**, where the increase of a component ultimately suppresses itself. For example, in Lotka–Volterra model we have a negative feedback loop, since prey enhance the predator population, but predators reduce the prey population. Negative feedback loops can lead to oscillations in a system:

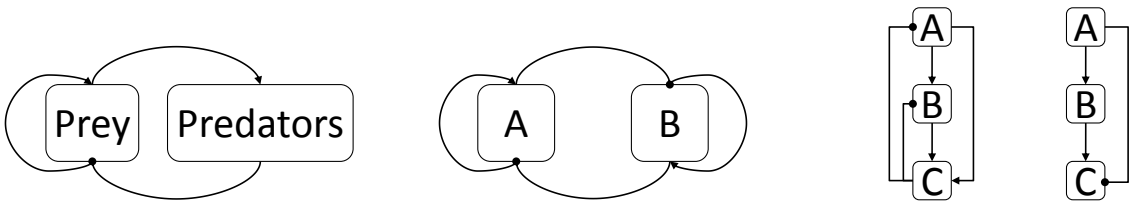
1. Prey grow to a large population when the predator population is low.

2. Predators grow to a large population in response, and ultimately decimate the prey population.

3. With few prey, the predator population again falls to a low value; the system now appears just like (1), and thus the cycle repeats.

When both interactions are suppressive, we have **double negative feedback** — for example, A activates itself and deactivates B, while B activates itself and deactivates B. Examples of this type of interaction are common in the networks of interactions that control gene expression. How does this system behave?

- If there is no A or B, nothing happens.



(a) **(b)** **(c)**

Figure 2.5: Examples of networks with feedback. (a) Negative feedback in the Lotka–Volterra model; (b) Double negative feedback; (c) Positive and negative feed-forward (the positive feed-forward model on the left also contains negative feedback).

- If there is some A, but no B, A grows (to a maximum, if there is a limiting capacity).
- Similarly, if there is some B, but not A, B grows (perhaps to a maximum).
- If there is a little B, but more A, then B is repressed by A and decays to 0, while A remains high.
- If there is a little A, but more B, the reverse is true — A is repressed to 0, and B remains elevated.

Thus, we see that we have two attractors — one at high A and low B, and another at high B and low A. Just as in the first example, we have a bistable system. However, rather than the two stable points being both low or both high, only one component can be high at a time. It is not surprising that this system give bistability as well, since a double negative feedback loop acts as positive feedback in many ways — suppressing the suppressor leads to activation.

So far we have focused on two component systems, but when we have three of more components, additional sorts of interactions can arise. For example, we may have **feed-forward** systems, where one component interacts with another both directly and through an intermediate. For example, there is a positive feed-forward loop in the dynamics of a food web of whales, salmon and herring: salmon eat herring, and whales eat salmon, but whales will also eat herring (there is also negative feedback in this system, as in any predator–prey relationship). We also can have negative feed-forward, as in a gene regulatory network where gene A activates gene B which in turn activates gene C, but where A also deactivates C. Such interactions introduce delays into the system — as A increases, C does not increase immediately, but remains low until there enough B has accumulated to activate it (and overcome its suppression by A).

2.5 Quantitative description of dynamical systems

2.5.1 Identification of stationary points

One of the fundamental properties of any dynamical system is the location and characteristics of stationary points. The reason for this is quite simple — key aspects of the dynamics of a system can be understood by these alone. For example, attracting stationary points correspond to locations where the system will reside in equilibrium, locations that the system will evolve to — from at least some starting points — given adequate time. Conversely, repelling stationary points correspond to locations that will be avoided by essentially all trajectories.

Stationary points correspond to the roots of the system; that is, points where all of the differential equations in the system are simultaneously equal to zero. For simple systems of two or three variables, these can often be solved by a little pencil work and knowledge of algebra — one expression can be manipulated to give the value of one variable in terms of the others, followed by substitution into a second equation, and so forth. In later sections, we will discuss several models that can be treated in this manner. Additionally, the graphical methods involving null-clines (discussed above) can also give the location of the stationary points.

2.5.2 Newton's Method for finding roots

In other cases, the system can be too complex to solve for the roots analytically, or have too many dimensions to be ammenable to graphical analysis; when this situation arises, numerical root finding techniques, such as Newton's method, come into play. Newton's method is an iterative algorithm, where we begin with a guess of where a root may lie, and repeated improve that guess in a systematic manner. It works by taking a *linearization* of a function about a particular point — that is, describing the function by the tangent to the function at that point. For a function of a single variable, linearized about the point x_o, this corresponds to:

$$\tilde{f}(x) = f'(x_o)x + (f(x_o) - f'(x_o)x_o) \tag{2.19}$$

where the first term gives the slope equal to the first derivative, and the second term sets the intercept such that $\tilde{f}(x_o) = f(x_o)$. Often this is written in terms of $x = x_o + \Delta x$ (a perturbation of Δx from the point x_o):

$$\begin{aligned} \tilde{f}(x + \Delta x) &= f'(x_o)(x_o + \Delta x) + (f(x_o) - f'(x_o)x_o) \\ &= f'(x_o)x_o + f'(x_o)\Delta x + f(x_o) - f'(x_o)x_o) \\ &= f(x_o) + f'(x_o)\Delta x \end{aligned} \tag{2.20}$$

Each iteration of Newton's method involves solving for the root of this linearized form; as a linear equation, there is a single root that is simple to find:

$$f'(x_o)x + (f(x_o) - f'(x_o)x_o) = 0 \rightarrow x = \frac{f'(x_o)x_o - f(x_o)}{f'(x_o)} = x_o - \frac{f(x_o)}{f'(x_o)} \tag{2.21}$$

Thus, we see that the root of the linearized form is given by subtracting the ratio of the value of the function and its derivative (at x_o) from x_o. This value should be closer to the true

root than the initial guess, but still not perfect. To find the root to arbitrary accuracy, we may use the root of the linearized equation a new guess, repeating until our answer doesn't change significantly. Thus, we may summarize the approach as:

1. Begin with a guess of a root, x_o.
2. Solve for the linearized root, $x_1 = x_o - \frac{f(x_o)}{f'(x_o)}$.
3. Repeat, solving for $x_{i+1} = x_i - \frac{f(x_i)}{f'(x_i)}$.
4. Stop when either the value of the function is within some small value (ϵ) of zero, $f(xi+1) < \epsilon$, or when the difference between incremental values of x_i is similarly small ($|x_{i+1} - x_i i| < \epsilon$).

For *systems* of equations, Newton's method can be generalized, using the linearization of:

$$\tilde{F}(\vec{x}_o + \Delta\vec{x}) = F(\vec{x}_o) + \mathbf{J}(\vec{x}_o)\Delta\vec{x} \tag{2.22}$$

where $F(\vec{x})$ is the vector function describing the full system, and $\mathbf{J}(\vec{x})$ is the Jacobian matrix of the system of equations. *Note: This involves an understanding of linear algebra which may exceed the background of some students; this material is thus optional.* In a similar manner, we can solve for the root of the linearized system:

$$F(\vec{x}_o) + \mathbf{J}(\vec{x}_o)\Delta\vec{x} = 0 \quad \rightarrow \quad \Delta\vec{x} = -\mathbf{J}^{-1}(\vec{x}_o)F(\vec{x}_o) \tag{2.23}$$

which leads to the iterative update rule for Newton's method:

$$\vec{x}_{i+1} = \vec{x}_i - \mathbf{J}^{-1}(\vec{x}_i)F(\vec{x}_i) \tag{2.24}$$

It is important to note that this update requires the *inverse* of the Jacobian matrix at point $\vec{x}_i$, thus, this method is poorly defined if the matrix is singular.

2.5.3 Time evolution of a dynamic system

The methods described above can give a qualitative ides of the dynamics of a system, but in many cases we want a more quantitative description — precisely how does each variable change over time. To consider how we might do this, we will begin with a single variable system, with the velocity of that variable described by some arbitrary, continuous function of time:

$$\frac{dx}{dt} = f(t) \tag{2.25}$$

Now, if we know that at time $t = 0$ the value of x is x_o, then the value of x at an arbitrary time is given by:

$$x(\tau) = x_o + \int_{t=0}^{\tau} f(t)dt \tag{2.26}$$

We have to solve a definite integral, which we may do either analytically or by a numerical method. This is very straight forward, but the equations we have are somewhat different, as

the rate of change is not a function of *time* by rather a function of the variable itself, which is an *implicit* function of time, $x(t)$, and so we have:

$$\frac{dx}{dt} = f(x(t)) \qquad x(\tau) = x_o + \int_{t=0}^{\tau} f(x(t))dt \tag{2.27}$$

However, the function $x(t)$ is precisely what we are trying to find, and so it is impossible to evaluate this integral directly! To solve this problem, consider the value of x a short time interval ($\Delta\tau$) after an arbitrary time, τ. We have:

$$\begin{aligned} x(\tau+\Delta\tau) &= x_o + \int_{t=0}^{\tau+\Delta\tau} f(x(t))dt \\ &= x_o + \int_{t=0}^{\tau} f(x(t))dt + \int_{t=\tau}^{\Delta\tau} f(x(t))dt \\ &= x(\tau) + \int_{t=\tau}^{\tau+\Delta\tau} f(x(t))dt \end{aligned} \tag{2.28}$$

This is very similar to the result of Equation 2.27, but with a very important difference; the integral here is over a very small domain of time (from τ to $\Delta\tau$). As we are only considering a very small domain, we may be able to make approximations that will allow us to compute this integral without knowing $x(t)$ explicitly.

One frequently used approximation to describe the behavior of a function near a particular point is the Taylor series:

$$f(x) = f(x_o) + f'(x_o)|x - x_o| + \frac{1}{2}f''(x_o)|x - x_o|^2 + \cdots + \frac{1}{i!}f^i(x_o)|x - x_o|^i + \cdots \tag{2.29}$$

When the infinite series is considered, this expansion is exact for x in the immediate neighborhood of x_o; for many functions, in fact, the expansion is exact over the entire domain. However, most applications of the Taylor series involve approximations involving only a few of the first terms. Note that if x is close to x_o, then $|x - x_o|^n$ is an exponentially decreasing function of n. As a result, only the lowest order terms will be significant, and higher order terms may be dropped with little loss of accuracy. The zeroth order approximation is that the function is constant over the region of interest:

$$\tilde{f}_0(x) = f(x_o) \tag{2.30}$$

and the first order approximation is:

$$\tilde{f}_1(x) = f(x_o) + f'(x_o)|x - x_o| \tag{2.31}$$

If we apply the zeroth order approximation to the result in Equation 2.28, we get:

$$\begin{aligned} x(\tau+\Delta\tau) &\approx x(\tau) + \int_{t=\tau}^{\tau+\Delta\tau} \tilde{f}_0(x(\tau))dt \\ &\approx x(\tau) + \int_{t=\tau}^{\tau+\Delta\tau} f(x(\tau))dt \\ &\approx x(\tau) + f(x(\tau))t|_{t=\tau}^{\tau+\Delta\tau} \\ &\approx x(\tau) + f(x(\tau))\Delta\tau \end{aligned} \tag{2.32}$$

If we apply thus update rule iteratively, beginning with the initial state $x(0)$, we can obtain first $x(\Delta\tau)$, then $x(2\Delta\tau)$, $x(3\Delta\tau)$, and so on. If we choose a suitably low value of $\Delta\tau$, then the resulting trajectory will be a close approximation to the "true" trajectory. This application of the zeroth order Taylor series expansion of the velocity function is known as the **Forward Euler** method. Forward Euler is conceptually the most simple method, but also is rather inaccurate, unless very small steps in time are taken; other methods allow for larger time steps, but the details of these are beyond the scope of the class.