Part I

Classical population and community ecology

Chapter 1

From growth equations for a single species to Lotka–Volterra equations for two interacting species

'The importance of the method is this: if we know certain variables, mostly desired by ecologists and in some cases already determined by them, we can predict certain results which would not normally be predictable or even expected by ecologists. The stage of verification of these mathematical predictions has hardly begun; but their importance cannot be under-estimated, and we look forward to seeing the further volumes of Lotka's studies.'

Charles Elton 1935 review of A J Lotka's *Théorie analytique des associations biologiques*.

Summary

We start this chapter in section 1.1 with the simplest growth equation for a single isolated population, the Malthus equation. The problem with this equation is that it assumes a constant per capita growth rate, leading to exponential growth. Then we will show that if we assume resource limitation, which means replacing the constant per capita growth rate by a **density dependent** per-capita growth rate, the resulting **logistic equation**, saturates the population to an equilibrium value called the **carrying capacity**.

Before we move to two interacting species, in section 1.2, we consider general models for single species populations and show how to analyze the **local equilibrium stability**, both algebraically and geometrically.

In section 1.3 we present the Lotka–Volterra equations for a predator and its prey. We first consider the original Lotka–Volterra predator–prey model.

We introduce the useful concept of **phase plane** for representing the dynamical behavior of a two-species system as a trajectory followed by a point representing the system in this plane. We show that this model gives rise to periodic oscillations in the abundances of predator and prey populations, resembling the empirically observed behavior. However, the model is unrealistic and it has conceptual problems, mainly its **structural instability**. Namely, oscillations of predator and prey abundances correspond to closed trajectories in the phase plane and any small perturbation could make the system jump onto another orbit which can be quite different from the original one. We next show that the Lotka–Volterra model can be modified in simple ways to make it more biologically realistic. These modifications, consisting in making the prey populations density-dependent (e.g. logistically) and making the predator death rate depend inversely on prey density, cure the problem of the structural instability: the modified predator–prey equations give rise to robust periodic orbits, termed stable **limit cycle** oscillations.

In section 1.4, we introduce the Lotka–Volterra competition equations for a pair of species and analyze the possible equilibria: competitive exclusion of one species or species coexistence. We also show how this descriptive or phenomenological model (i.e. without specifying either the limiting resources the two species are competing for or the mechanism of competition) can be transformed into a mechanistic model by expressing the competition coefficients and carrying capacities in terms of rates of utilization and renewal of resources.

Finally, in section 1.5, we discuss a system formed by a pair of species engaged in a mutualistic relationship. Two types of mutualism between two species, obligate and facultative, are introduced as well as the corresponding Lotka–Volterra equations. We conclude by analyzing the possible equilibria.

1.1 From the Malthus to the logistic equation of growth for a single species

1.1.1 Exponential growth

Describing how a population of a given species changes with time has a long history. For example, the Italian mathematician Leonardo of Pisa (1175–1250), better known as Fibonacci, in his book *Liber Abaci* (1202) posed this problem involving the growth of a population of rabbits:

A certain man had one pair of rabbits together in a certain enclosed place. How many pairs of rabbits can be created from the pair in one year if we suppose that each month each pair begets a new pair, which on the second month on becomes productive?

Fibonacci used a simple mathematical model based on idealized assumptions to solve this problem (see exercise 1.1).

Here we will devote some space to explain step by step the population dynamics approach as well as analyzing its implicit underlying assumptions. So imagine a population of a given species, rabbits if you like, in a given area. This population changes in a given period due to births, deaths, immigration and emigration that occur in this period. We can express this as a population balance (inputs minus outputs) relationship:

change in the population = births − deaths + immigration − emigration, (1.1)

Let us assume the simplest situation without migration in which the above relation simplifies to:

change in the population = births − deaths,   (isolated population)   (1.2)

and see how we can traduce the above conceptual relationship into a mathematical equation.

Let N_t be the population density (number of individuals in a specific area) of the species at time t. Hence, the left-hand side of equation (1.2) can be written as a **difference equation**

$$N_{t+1} - N_t = B_t - D_t. \tag{1.3}$$

where B_t and D_t denote, respectively, the number of births and deaths that occurred during the interval from t and $t + 1$. This interval between consecutive integer time values may denote, depending on the problem and the species involved, from minutes (in the case of bacteria or protozoa) to years (in the case of say humans).

Suppose now that the population N is a large number and we are interested in changes of this population for an arbitrary small interval of time Δt. In particular, if we take Δt infinitesimally small, equation (1.3) can be rewritten in terms of instantaneous rates of births and deaths, b_t and d_t (measured as individuals per unit of time), as

$$\frac{N_{t+\Delta t} - N_t}{\Delta t} = \frac{B_t}{\Delta t} - \frac{D_t}{\Delta t} = b_t - d_t. \tag{1.3$'$}$$

Actually, N_t and $N_{t+\Delta t}$ are discrete variables so they cannot differ in less than one individual, and if Δt is taken small enough, they will be equal and equation (1.3$'$) breaks down. The 'trick' is to promote the discrete (integer number) population variable N_t to a continuous (real number) $N(t)$ (to emphasize we are using continuous variables, t appears between parentheses rather than as a sub-index). The left-hand side of equation (1.3$'$) defines the derivative of N with respect to time:

$$\lim_{\Delta t \to 0} \frac{N_{t+\Delta t} - N_t}{\Delta t} = \frac{dN}{dt}$$

—which sometimes is also denoted as $\dot{N}$—, so that equation (1.3$'$) becomes a **differential equation**:

$$\frac{dN}{dt} = b(t) - d(t). \tag{1.3$''$}$$

So, what should we use, a continuous or discrete time description? From a biological point of view, if births occur continuously with overlapping generations in relatively seasonal environments, continuous time is a sound choice. However, for many species births occur in regular time-intervals so they have no overlap whatsoever between successive generations and therefore population growth is

better-suited for a discrete-time description. For primitive organisms such discrete steps can be quite short in which case a continuous time model may be a reasonable approximation. In fact, the step lengths can vary widely from species to species.

Biological considerations aside, the advantage of using differential equations is that qualitative insight is usually gained from simple model problems that may be solved using analytical methods. That is, as we shall see in a moment, calculus often helps in uncovering functional relationships between the relevant problem variables. However, most problems of interest lead to differential equations that cannot be solved easily using analytic techniques. In such cases numerical methods allow us to use the power of a computer to obtain quantitative insight. Since a computer is limited to finite combinations of the four arithmetic operations, $+$, $-$, $\times\_$, $\div\_$, and logical operations, numerical methods require discrete time for running such computations. Therefore, hereafter in Part I, we will resort to the continuous time description and to equation (1.3′) as the starting point to introduce the formalism of population dynamics. On the other hand, for most practical applications, it seems more natural to build the model as a *discrete* difference equation from the start, without going through the doubly approximative process of first, during the modelling stage, finding a differential equation to approximate a basically discrete situation, and then, for numerical computing purposes, approximating that differential equation by a difference scheme (for an interesting discussion see van der Vaart 1973). Thus, in the companion practical application chapters, involving more advanced models that need to be approached by numerical solution techniques, we will use the discrete time representation[1].

The birth and death rates, $b(t)$ and $d(t)$, in equation (1.3′) are still unspecified functions of the time t. Obviously, both rates depend on population size; the larger $N(t)$ the larger the number of births and deaths per unit of time. The simplest assumption we can make is that both rates are proportional to $N(t)$:

$$b(t) = bN(t), \tag{1.4a}$$

$$d(t) = dN(t), \tag{1.4b}$$

where b and d[2] are **constant** per-capita rates, measured, respectively, as births and deaths per individuals per unit of time. Therefore the equation (1.3′) becomes

$$\frac{dN}{dt} = (b - d)N(t). \tag{1.5}$$

It is customary to group $(b - d)$ into a net constant per-capita growth rate r and write equation (1.5) as (Malthus 1798):

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[1] A note of caution is in order here. As was shown by Robert May (1976), some of the simplest nonlinear difference equations can exhibit a wide spectrum of dynamical behavior. From stable equilibrium points, to stable cyclic oscillations between two population points, four points, eight points, etc, through to a chaotic regime in which (depending on the initial population value) cycles of any period, or even totally aperiodic but bounded population fluctuations, can occur.

[2] Warning: dN in equation (1.4b) is NOT the same as the numerator of the temporal derivative dN/dt!

$$\boxed{\frac{dN}{dt} = r\, N.} \tag{1.6}$$

(where we have omitted the temporal dependence of N for compactness of notation.)

We know from calculus that the solution of this equation is

$$N(t) = N_0 e^{rt}, \tag{1.7}$$

where $N_0 = N(0)$ is the initial population. Thus if $r > 0$ (i.e. $b > d$) the population grows exponentially while if $r > 0$ (i.e. $b < d$) it dies out. The graph of this exponential function (figure 1.1) shows the behavior of the population over time.

The differential equation (1.6), due to Malthus in 1798, is fairly unrealistic. It says that the rate of change in population size over time (dN/dt) increases by a proportional rate of growth (r) multiplied by the current population size (N). This is an example of a density-independent biological force, because it depends only on the population N, not on external forces such as crowding or food supply. We already mentioned some of the simplifications leading to equation (1.6). In addition, there are several underlying implicit assumptions and it is worth making them explicit because it is important for modellers to be aware of the approximations behind the models they use so that they understand how these models can fail. Box 1.1 summarizes the assumptions behind equation (1.6) as well as the corresponding mathematical implications.

In principle, all the above assumptions would be only justified for an isolated, well mixed in a homogeneous habitat, sexless *parthenogenetic* (i.e. exhibiting asexual reproduction) population in which individuals are immediately reproductive when they are born, with no resource limitation and completely controlled conditions (no stochasticity). A growing population of bacteria or protozoa most closely approximates this situation for a while (until it faces resource limitations).

Unrealistic as it is, equation (1.6) is the foundation for all of the population models that we will discuss in this book. In particular, the mean-field approximation IV together with the approximations V and VI of a dynamical autonomous system is common to all population ecology, the subject of part I. As we will see in the
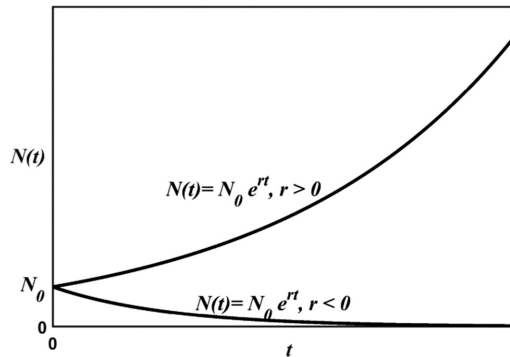

Figure 1.1. Exponential growth ($r > 0$) and decay ($r < 0$).

Box 1.1. Assumptions behind Malthus equation (1.6).

	Assumption	Mathematical implication
I	**Continuous overlap of generations.**	Use of differential equations.
II	**Geographical isolation.**	No migration rates in the differential equation.
III	**Interactions with individuals of other species are negligible.**	The rates $b(t)$ and $d(t)$ do not depend on other species neither through parameters (exercise 1.4) nor through population variables (sections 1.3 and 1.4).
IV	***Mean-field approximation*** (MFA): the spatial nature of interactions is ignored; only changes in mean quantities, such as global densities, are tracked. The MFA in fact implies two approximations (Morozov and Poggiale 2012): **IVa** The approximation of ***well mixed population***, i.e. the individuals in the habitat are well mixed and the probability of interaction of a randomly taken individual with any other individual does not depend on the individual chosen. **IVb** The environment is considered to be **homogeneous** (e.g. no sharp gradients of resource distribution).	$N(t)$, $b(t)$ and $d(t)$ do not depend on space coordinates. No spatial derivatives in the differential equation.
V	***Dynamical system***. There is a branch of mathematics developed specifically to deal with dynamics: *dynamical systems theory*.	No higher time derivatives than the first appear in the differential equation[3].
VI	***Autonomous system.***	The rates $b(t)$ and $d(t)$ do not *explicitly* depend on t, their dependence is only *implicit* through $N(t)$ i.e. they are functions of $N(t)$.
VII	**Non interacting individuals.** Equivalent to assume that resources for growth and repro-duction are unlimited (see next subsection).	$b(t) = \ell N(t)$, $d(t) = \partial N(t)$, ℓ, ∂ constants
VIII	**No age or size structure.**	There are no differences in the per-capita rates ℓ and ∂ among individuals due to age or body size.
IX	**Deterministic.** The population is determined solely by N_0 and r: If we started over with the same set of conditions, the population would grow to precisely the same size.	No noise or stochastic term in the differential equation.

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[3] Notice however that many higher-order differential equations can be written as first order systems of differential equations by the introduction of derivatives as new dependent variables (see exercise 1.12).

Application chapters, very simple models based on most of the above assumptions still produce reliable results for more complex species under much less restrictive conditions.

1.1.2 Resource limitation, density dependent per-capita growth rate and logistic growth

In deriving equation (1.6) we unrealistically assumed that per-capita rates ℓ and d were constant, independent of the population density (assumption VII in box 1.1), and thus the same happens for $r = \ell - d$. However, when resources (nutrients, water, space, etc) are limited, if crowding is increased, we expect the per capita birth rate to decrease and the per capita death rate to increase because fewer resources are available for organisms to use for reproduction and survival, respectively. Hence, these per-capita rates should really be a function of the population density of the species, so that, as population density increases to sufficiently high levels, the death rate rises and the birth rate falls, bringing about a fall in r toward zero and below, into negative values. In other words, more realistic per-capita rates ℓ and d exhibit *density dependence*. The simplest formula for a decreasing net growth rate $r(N)$ is a linear one—straight line with a proportionality constant c—as shown in figure 1.2:

$$r(N) \equiv r - cN = r - cN = r\left(1 - \frac{N}{r/c}\right). \tag{1.8}$$

If we define $\mathcal{K} \equiv r/c$ and replace r in equation (1.6) by (1.8), we re-obtain the logistic equation of Pearl and Reed (1920):
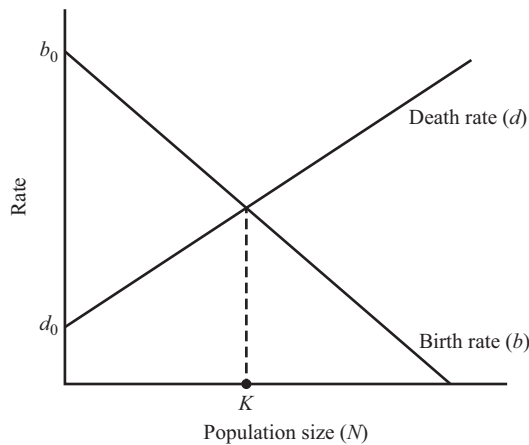

Figure 1.2. Linear density-dependent birth and death rates for the logistic model illustrating how the per capita rates of birth and death change as a function of crowding. The population reaches a stable equilibrium $(N = \mathcal{K})$ at the intersection of the curves, where birth and death rates are equal.

$$\boxed{\frac{dN}{dt} = r\,N\!\left(1 - \frac{N}{\mathcal{K}}\right).}$$ (1.9)

The logistic equation which was originally described as a model for human population growth by Pierre-Francois Verhulst (1838), is a simple descriptive model of how competition limits the growth of populations. The model assumes that a maximum sustainable population density, the carrying capacity $\mathcal{K}$, exists where $dN/dt = 0$. The per capita population growth rate $(1/N)(dN/dt)$ is at its maximum value of r when N is close to zero, then declines linearly to zero when N reaches $\mathcal{K}$. If N exceeds $\mathcal{K}$, the per capita growth rate becomes negative.

The logistic model is the simplest nonlinear differential equation (box 1.2). Most nonlinear differential equations cannot be explicitly solved, that is, there are no methods to integrate them to obtain an explicit equation for $N(t)$ in terms of initial conditions, $N(0)$, and the parameters—or else the explicit, time-dependent solutions are too unwieldy to be of much help. Fortunately, the logistic equation has an explicit simple solution. Let us integrate this equation to review, at least once, how differential equations are solved analytically by the *separation of variables* method. So the first step is to separate the terms in N on the lhs and those in t on the rhs:

$$\frac{dN}{N(1 - N/\mathcal{K})} = r\,dt$$

Then integrate the lhs from $N(0)$ to $N(T)$ and the rhs from $t = 0$ to $t = T$:

$$\int_{N(0)}^{N(T)} \frac{dN}{N(1 - N/\mathcal{K})} = \int_0^T r\,dt$$

Box 1.2. Logistic model assumptions.

Because the logistic model is derived from the Malthus model it shares all its assumptions except # VII of box 1.1, i.e. we have seen that resources are limited in the logistic model, which implies a density dependent per capita growth rate. So assumption VII is replaced by two additional assumptions:

VIIa *Constant carrying capacity*. In order to achieve the S-shaped logistic growth curve, we must assume that $\mathcal{K}$ is a constant: resource availability does not vary through time. In the companion Application chapter, we will relax this assumption, and consider a periodically forced carrying capacity.

VIIb *Linear density dependence*. Each individual added to the population causes an incremental decrease in the per capita rate of population growth. This is illustrated in figure 1.2 which shows the per capita population growth rate $(1/N)(dN/dt)$ as a function of population density.

The integral of the rhs is the simplest one and we immediately get $\imath t$. To integrate the lhs we will use the identity:

$$\frac{1}{N(1 - N/\mathcal{K})} = \frac{1}{N} + \frac{1}{1 - N/\mathcal{K}},$$

and then we integrate each part separately:

$$\int_{N(0)}^{N(T)} \frac{dN}{N(1 - N/\mathcal{K})} = \int_{N(0)}^{N(T)} \frac{dN}{N} + \int_{N(0)}^{N(T)} \frac{dN}{1 - N/\mathcal{K}}.$$

Recall that the integral of $1/N$ is $\ln N$ and the integral of the second term on the lhs can be obtained, by making a change of variable $N' = 1 - N/\mathcal{K}$, as $-\ln(1 - N/\mathcal{K})$.[4] To find definite integrals we have to evaluate at the upper and lower bounds and subtract the expression for the lower bound from that of the upper. Therefore, we get:

$$\ln(N(t)) - \ln(N(0)) - \ln(1 - N(t)/\mathcal{K}) + \ln(1 - N(0)/K) = \imath t.$$

Finally, after some algebraic manipulation we get:

$$N(t) = \frac{\mathcal{K}}{1 + \left(\dfrac{\mathcal{K}}{N(0)} - 1\right)e^{-\imath t}}. \tag{1.10}$$

We can easily check that equation (1.10) produces for $T = 0$, $N(0)$ and for very large times the asymptotic value $N(\infty) = \mathcal{K}$.

Of particular importance for models like the logistic equation is the question of whether the model has an equilibrium, that is, whether there is a value N^* of N such that $dN/dt = 0$, and if the equilibrium is stable or not. The right-hand side becomes 0 either for the trivial case where $N = 0$ or, as we just have seen, for $N = \mathcal{K}$. So we have two equilibria: $N^* = 0$, i.e. the population is extinct, and $N^* = \mathcal{K}$, i.e. the population density reaches its maximum sustainable value or carrying capacity. We will see in the next section different methods to find out whether an equilibrium is stable or unstable.

1.2 General models for single species populations and analysis of local equilibrium stability

1.2.1 General model and Taylor expansion

Both the Malthus equation (1.6) and the logistic equation (1.9) are examples in which the growth rate depends on population density. We can generalize them and write a general growth equation for a single population as

$$\frac{dN}{dt} = f(N), \tag{1.11}$$

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[4] Or, you can also obtain it from a table of integrals.

where $f(N)$ is a general function of the population density N. Notice that for equations (1.6) and (1.9) the function/is the polynomial

$$f(N) = a_o + a_1N + a_2N^2,$$

where $a_0 = 0$; for equation (1.6) $a_1 = \imath$ and $a_2 = 0$; for equation (1.9) $a_1 = \imath$ and $a_2 = -\imath/\mathcal{K}$, i.e.

$$\begin{cases} \text{Malthus model: } f(N) = \imath N & (1.12a) \\ \text{Logistic model: } f(N) = \imath N(1 - N/\mathcal{K}) = \imath N - (\imath/\mathcal{K})N^2 & (1.12b) \end{cases}$$

More generally, if the function f is sufficiently smooth or 'well behaved', it is possible to write f as a Taylor infinite power series around a fixed value of N, $N = N^*$:

$$f(N) = \sum_{n=0}^{\infty} f^{(n)}(N^*)\frac{(N - N^*)^n}{n!} = f(N^*) + f'(N^*)\frac{(N - N^*)}{1!}$$
$$+ f''(N^*)\frac{(N - N^*)^2}{2!} + f'''(N^*)\frac{(N - N^*)^3}{3!} + \cdots, \tag{1.13}$$

where $n!$ denotes the factorial of n and $f^{(n)}(N^*)$ denotes the nth derivative of f evaluated at the point N^*, i.e. $f^{(0)} = f, f^{(1)} = f' = df/dN, f^{(2)} = f'' = d^2f/dN^2$ and so on. Substituting equation (1.13) into (1.11) we get the general (infinite) series expression for the growth of a single population:

$$\frac{dN}{dt} = f(N^*) + f'(N^*)\frac{(N - N^*)}{1!} + f''(N^*)\frac{(N - N^*)^2}{2!}$$
$$+ f'''(N^*)\frac{(N - N^*)^3}{3!} + \cdots, \tag{1.14}$$

Remark. Thus any growth function may be written as a (possibly infinite) polynomial

$$f(N) = \sum_{n=0}^{\infty} a_n N^n = a_0 + a_1N + a_2N^2 + a_3N^3 + \cdots. \tag{1.15}$$

1.2.2 Algebraic and geometric analysis of local equilibrium stability

We have seen that the equilibrium points N^* satisfy

$$f(N^*) = 0, \tag{1.16}$$

so that $dN/dt = 0$ when evaluated at these N^*. Thus, to find the equilibrium points we have to solve for all N^* that satisfy equation (1.16).

To perform the algebraic stability analysis of an equilibrium point N^* we consider a perturbation or departure x from the equilibrium value N^*,

$$x(t) = N(t) - N^*, \tag{1.17}$$

which we initially assume is much smaller than 1 ($x(0) << 1$)[5]. Substituting equations (1.15) and (1.17) into equation (1.14) we get:

$$\frac{dx}{dt} = f'(N^*)x + f''(N^*)\frac{x^2}{2} + f'''(N^*)\frac{x^3}{6} + \cdots,$$

and neglecting terms of order x^2 and higher, we obtain an approximate *linear* differential equation for the perturbation $x(t)$:

$$\frac{dx}{dt} \approx f'(N^*)x. \tag{1.18}$$

Since $f'(N^*)$ is equal to constant a 1, we know that the solution of equation (1.18) is given by an exponential:

$$x(t) = x(0)e^{at}. \tag{1.19}$$

Therefore, if $a < 0$ this perturbation dies away exponentially, whereas for $a > 0$ the disturbance grows unbendingly (the special case $a = 0$ corresponds to neutral stability). In summary, this neighborhood stability analysis gives the equilibrium point at N^* as

$$\begin{cases} \textbf{stable} \text{ if } a = f'(N^*) < 0 \\ \textbf{unstable} \text{ if } a = f'(N^*) > 0 \end{cases}.$$

More formally, we say that if and only if $f'(N^*) < 0$ the equilibrium is **locally stable**. This means, starting at the equilibrium value of N, N^*, if the population changes slightly in size, will it tend to return to its equilibrium value. **Global stability** is a more general property that implies that a system will return to the equilibrium point *from any initial population value*. We will illustrate the difference between local and global stability by considering the Malthus and logistic models.

Let us start by considering the simplest Malthus model. According to equation (1.12a) there is only one equilibrium solution to this model, $N^* = 0$. To determine the stability of this equilibrium, we take the derivative of $f(N) = rN$ with respect to N:

$$f'(N) = r \text{ for all } N. \quad \text{(Malthus equation)} \tag{1.20}$$

That is, it is a constant—the parameter r. Therefore, 0 is an unstable equilibrium point when $r > 0$ and a stable equilibrium when $r < 0$. Furthermore, *any perturbation of any size x away from* $N^* = 0$ will decrease to 0 if $l < d(r < 0)$ or increase unbounded and diverge to infinity if $l > d(r > 0)$ (figure 3.1). This is because the differential equation is a linear equation and N has disappeared after we took the derivative with respect to it. Linear models are therefore *globally stable* or *globally unstable*. That is, if the model is globally stable, $N(t)$ will converge to the single equilibrium point N^* from any starting value of N. If the model is globally unstable, $N(t)$ will be repelled away from the single unstable equilibrium point N^* for any value of N.

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[5] Remember that we are assuming that N is a continuous variable so that x can be as small as we want.

In the case of the logistic equation, by equation (1.12b),

$$f'(N) = r(1 - 2N/K). \quad \text{(logistic equation)} \quad (1.21)$$

Hence, inserting the two equilibria: $N^* = 0$ and $N^* = \mathcal{K}$, we have

$$\begin{cases} f'(0) &= r(1 - 2 \times 0) = r > 0, & (1.22a) \\ f'(\mathcal{K}) &= r(1 - 2 \times 1) = -r < 0. & (1.22b) \end{cases}$$

Therefore,

$$\begin{cases} N^* &= 0 \text{ is an } \textbf{unstable equilibrium} \\ N^* &= \mathcal{K} \text{ is a } \textbf{stable equilibrium} \end{cases}$$

In the logistic model, unlike the Malthus linear model, the equilibria are locally stable. The simplest way to see this is by using the geometric analysis (see below).

For the geometric stability analysis, we graph $f(N)$ against N, thus showing how the rate of change of the population varies with population density, N. In the case of the logistic equation[6], since its rhs is a quadratic expression, the graph is simply a parabola that crosses the N-axis at the two equilibrium points, 0 and $\mathcal{K}$, where $f(N) = dN/dt = 0$ as shown in figure 1.3. We now place arrows in this figure to the right or left to each side of each equilibrium point in the direction of population change specified by the sign of the derivative. Notice that arrows point away from $N^* = 0$ on either side but they both point towards $N^* = \mathcal{K}$ from either side. This means that by introducing or removing at least one individual (e.g. by emigration or immigration) in the vicinity of $\mathcal{K}$ will always result in the population returning to $\mathcal{K}$. Doing the same around 0 will always result in the population moving away from 0, so long as $r > 0$ (a point to which we shall return shortly). Therefore, $N^* = \mathcal{K}$ is a
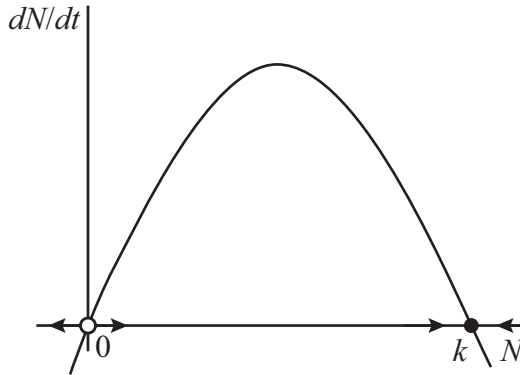

Figure 1.3. The inverted parabola of the logistic equation and its two equilibria: $N^* = 0$ (unstable) and $N^* = \mathcal{K}$ (stable).

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[6] We will discuss only the case of the logistic equation because it includes the simplest case of Malthus equation.

stable equilibrium point while $N^* = 0$ is an unstable equilibrium point, in complete agreement with the algebraic stability analysis. For the Malthus equation, instead of an inverted parabola, we have a straight line by the origin and therefore only one intersection point, $N^* = 0$, which is an unstable equilibrium.

Notice that, when $r > 0$, $N^*=\mathcal{K}$ is stable only for $N > 0$: if we start from a $N < 0$,[7] figure 1.3 shows that the trajectory will be repelled towards the left and will never reach $N^*=\mathcal{K}$. Likewise, if we start from $N > \mathcal{K}$ the trajectory will move towards the left (towards $\mathcal{K}$) rather than be repelled towards the right by $N^* = 0$. Therefore, $N^*=\mathcal{K}$ is locally stable rather than globally stable and $N^* = 0$ is locally unstable rather than globally unstable.

Remarks.

  (i) The algebraic stability analysis, through equation (1.19), tell us that r controls *quantitatively* the fate of perturbations near equilibria for the Malthus and logistic equations: they grow unboundedly as $\exp(rt)$ near $N^* = 0$ for both equations and they die out as $\exp(-rt)$ near $N^*=\mathcal{K}$ for the logistic model. On the other hand, the geometric analysis only provides *qualitative information*: it tell us whether the equilibria are stable or unstable.

 (ii) In the logistic model, unlike the Malthus linear model, the equilibria are locally stable. The reason is because nonlinear models, which typically have powers of N, can have several equilibrium solutions. Because these models are in powers of N, taking the derivative with respect to N and evaluating it at an equilibrium point results in an expression for the eigenvalue which is itself a function of N^*. For nonlinear models, the sign of f' and the stability of the equilibrium point will depend on which equilibrium point they are evaluated at. In general, unlike globally stable or unstable linear models, nonlinear models are typically stable or unstable only within certain local values of N in the neighborhood of a particular N^*.

1.3 The Lotka–Volterra predator–prey equations

1.3.1 A general dynamical system for predator–prey

A general dynamical system for modelling predator–prey involves two species. One of them (the predators) feeds on the other species (the prey), which in turn feeds on some third food resource available around, i.e. the model assumes *implicitly* a third trophic level below the prey. The population densities of prey and predator at a reference time t are denoted by $N(t)$ and $P(t)$, respectively, and obey two autonomous differential equations:

$$\dot{N} = Nf(N, P) \qquad (1.23a)$$

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[7] Of course, from a mathematical point of view, a negative population density does not make sense. But the global stability is a mathematical concept.

$$\dot{P} = Pg(N, P), \tag{1.23b}$$

i.e. the time t does not appear explicitly in the functions $f(N,P)$ and $g(N,P)$ which denote the respective per capita growth rates of the two species. It is assumed that these functions are *continuously differentiable* and that $df(N,P)/dP < 0$ and $dg(N,P)/dN > 0$, that is, the prey abundance is negatively affected by the predator abundance and vice versa, the predator abundance is positively affected by the prey abundance. A standard example is a population of Canadian lynxes and snowshoe hares. However, depending on their specific settings of applications, predator–prey models can take the forms of resource–consumer, plant–herbivore, parasite–host, etc.

1.3.2 A first model for predator–prey: the original Lotka–Volterra predator–prey model

In 1926, the Italian mathematician Vito Volterra proposed a differential equation model to explain the observed simultaneous increase in predator fish and decrease in prey fish in the Adriatic Sea during World War I (when fishing was largely suspended). At the same time in the United States, the equations studied by Volterra were derived independently by Alfred Lotka (1925) to describe a hypothetical chemical reaction in which the chemical concentrations oscillate. The Lotka–Volterra model is the simplest model of predator–prey interactions. It is based on linear per capita growth rates, written as

$$f(N, P) = r - cP \tag{1.24a}$$

$$g(N, P) = aN - d, \tag{1.24b}$$

where the parameter r denotes, as usual, the growth rate of the prey species in the absence of interaction with the predator species (a positive quantity), the parameter c is a consumption rate of prey by predators that measures per-capita loss of prey due to predators, the parameter a denotes the net rate per capita of growth of the predator population in response to the size of the prey population, and the parameter d is the per-capita loss (by death or emigration) rate of predators in the absence of interaction with prey. Substituting the equations (1.24) into (1.23) we get:

$$\dot{N} = rN - cNP \tag{1.25a}$$

$$\dot{P} = aNP - dP. \tag{1.25b}$$

Let us interpret what these equations are telling us. The idea of the first equation is that in the absence of predators ($P = 0$), the prey would grow in a Malthusian way at a constant rate r, but decreases linearly as a function of the density P of the predators. Similarly, in the absence of prey ($N = 0$), the density of predators would decrease but the rate increases proportional to the density of the prey. A necessary condition for predation to occur is that an individual predator and an individual prey physically meet. The product of the two densities, NP, represents the

expectation that an individual predator will meet an individual prey (assuming random movement of the two through a homogeneous landscape). It is equivalent to the chemistry **law of mass action**, which states that the rate of molecular collisions of two chemical species in a dilute gas is proportional to the product of the two concentrations of the reactants. Hence the parameter ϵ can be interpreted as the probability that, upon meeting a prey, the predator will successfully kill it. The total prey kill is therefore ϵNP. Since not all the biomass of a killed individual is transformed into predator biomass, so the growth of the predator is itself proportional to the total prey harvest, or $\beta \epsilon NP$, where β represents the conversion efficiency of prey biomass into predator biomass. Thus we can write $a = \beta \epsilon$ and the NP term can be thought of as representing the conversion of energy from one species to another: ϵNP is taken from the prey and aNP accrues to the predators. This first predator–prey model inherits all the nine assumptions of the Malthus equation (box 1.1). Three additional assumptions are listed in box 1.3.

We shall see that this model has serious drawbacks. Nevertheless, it has been of considerable value in posing relevant questions and as a starting point for more realistic models that we will briefly review in the next subsection. But before doing this we are going to analyze the solution of the Lotka–Volterra predator–prey model and compare it against empirical data.

As a first step in analyzing the Lotka–Volterra model it is convenient, for simplicity, to nondimensionalize the system by introducing a change of variables:

$$\tau = \imath t, \; x(\tau) = \frac{aN(t)}{d}, \; y(\tau) = \frac{\epsilon P(t)}{\imath}, \; \alpha = d/\imath, \tag{1.26}$$

so that the Lotka–Volterra equations (1.25) can be rewritten as:

$$\frac{dx}{d\tau} = x(1 - y), \tag{1.27a}$$

$$\frac{dy}{d\tau} = \alpha y(x - 1). \tag{1.27b}$$

The system of differential equations (1.27) has two immediate advantages over that of (1.25). First, it involves just a single parameter α. It is much easier to explore how the solutions of these equations change when we move in this single-dimensional 'space of parameters' than in the original four-dimensional one (exercises 1.7 and 1.8

Box 1.3. Additional assumptions of the original Lotka–Volterra predator–prey model.

X The effect of the predation is to reduce the prey's per capita growth rate by a term proportional to the prey and predator populations; this is the $-\epsilon N P$ term.

XI In the absence of any prey for sustenance the predator population would experiment an exponential decay, that is, the $-dP$ term in (1.25b).

XII The *functional response*, or per capita consumption rate of prey per predator, increases linearly with prey abundance as ϵN.

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illustrate this point clearly). Second, the two equilibrium states now become very simple, either

$$\begin{cases} x^* = 0 = y^* & \text{or} \quad (0, 0), & (1.28a) \\ x^* = 1 = y^* & \text{or} \quad (1, 1). & (1.28b) \end{cases}$$

In spite of its simplicity, the system of differential equations cannot be solved analytically. However, we will first show that we can get useful qualitative insights using calculus. Next, to obtain the model quantitative predictions we will solve these equations numerically. Therefore, dividing equation (1.27b) by equation (1.27a) we get:

$$\frac{dy}{dx} = \alpha \frac{y(x-1)}{x(1-y)}, \tag{1.29}$$

We can separate variables and express (1.29) as

$$\frac{dy}{y} - dy = \alpha\left(dx - \frac{dx}{x}\right), \tag{1.29'}$$

so that we can integrate exactly the lhs and the rhs of (1.29′) to get:

$$\ln y - y = H = \alpha(x - \ln x),$$

where H is an undetermined constant. Or equivalently

$$ax + y - \ln x^a y = H. \tag{1.30}$$

To visualize the meaning of equation (1.30), a useful representation is provided by the *phase plane*; a coordinate plane with axes x and y (see box 1.4).

   The direction field or phase portrait corresponding to equation (1.27) is plotted in figure 1.4. There are two singular points at which both the numerator and denominator of equation (1.29) become 0: at $x = y = 0$ and $x = y = 1$ (i.e. the two equilibrium states). We have also drawn the predator and prey **zero-growth isoclines** or **nullclines**, along these zero growth lines population densities do not change. We can see from equation (1.27a) that the prey zero growth isoclines are given by $x = 0$ and $y = 1$. likewise, the predator zero growth isoclines are given by $x = 1$ and $y = 0$. Obviously, equilibria occur at the intersections of the predator and prey zero-growth isoclines. If predator and prey numbers are both low, i.e. the particle representing the system is in quadrant $[x < 1, y < 1]$, predator numbers decrease while prey numbers increase (the arrows point towards the right and downward directions). If prey numbers are high but predator numbers are low, i.e. the particle is in quadrant $(x > 1, y < 1)$, both predators and prey increase (the arrows point towards the right and upward). As predator numbers increase so that we move to quadrant $[x > 1, y > 1]$, prey now begin to decrease (the arrows point towards the left and upward directions). Finally, in quadrant $[x < 1, y > 1]$, when predator numbers are high but prey numbers are low, both predators and prey decrease (the arrows point towards the left and downward directions).

Box 1.4. Phase plane.

For analyzing the dynamics of pairs of interacting populations, governed by coupled pairs of differential equations, a useful visual representation is provided by the *phase plane*; a coordinate plane with axes being the values of the two state variables, say (x, y), or (q, p) etc (any pair of variables). In this plane, the evolution of a dynamical system governed by a couple of differential equations of the form $dx/dt = f(x,y)$ and $dy/dt = g(x,y)$ can be visualized as a the 'flow' of a 'particle' with coordinates $x(t)$ and $y(t)$.

Let us provide some definitions.

- *Phase curves or phase trajectories* of this system in the x–y phase plane are a family of curves solutions of

$$\frac{dy}{dx} = \frac{f(x,\ y)}{g(x,\ y)}.$$

- *Phase portrait*: two-dimensional vector field whose vectors have components (dx/dt, dy/dt). Each point in phase space has one phase trajectory going through it and therefore can be associated with only one vector. This is a consequence of the fact that continuously differentiable equations such as equations (1.23) have unique solutions at each point, a unique solution guaranteeing one and only one vector at each point.

- Through any point $(x_0,\ y_0)$ there is a unique curve except at *singular* or *fixed points* (x_s, y_s) where

$$f(x_s,\ y_s) = g(x_s,\ y_s) = 0.$$

Therefore, a particular path taken along a flow line (i.e. a path always tangent to the vectors of the phase portrait) is a phase trajectory. The flows in the vector field indicate the time-evolution that the pair of differential equations describes. With enough of these arrows in place the system evolution over a region of the plane phase can be visualized as the flow of a particle representing the state of the system.

In this way, phase planes are useful in visualizing the behavior of dynamical systems; phase trajectories can 'spiral in' towards zero, 'spiral out' towards infinity, or reach neutrally stable situations called centers where the path traced out can be either circular, elliptical, or any other closed curve (see appendix I). This is useful in determining if the dynamics are stable or not.

We can get additional qualitative information by applying a useful modelling tip we mentioned in the previous chapter, namely constructing linear approximations. Hence we will linearize equations (1.27a) and (1.27b) about each one of the two equilibrium points: (0, 0) and (1, 1). Near (0, 0), we may neglect the nonlinear terms and consider

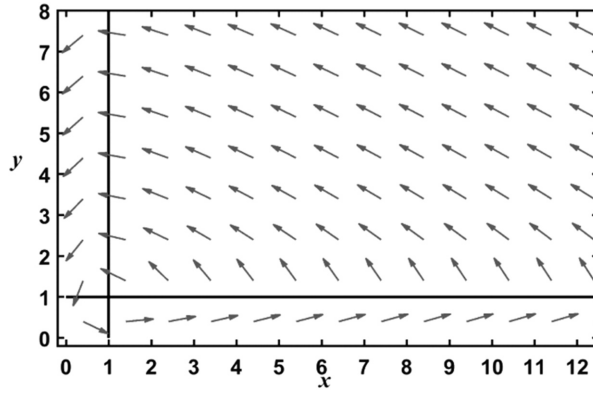$$\frac{dx}{d\tau} \approx x, \tag{1.31a}$$

Figure 1.4. Phase portrait for the Lotka–Volterra predator–prey equation (1.27) with nullclines for prey and predator.

$$\frac{dy}{d\tau} \approx -\alpha y. \tag{1.31b}$$

Thus, the prey increase exponentially fast close to the origin, while the predators decrease, corresponding to the horizontal arrows at the bottom of figure 1.4. The equilibrium at the origin has one stable direction (y) and one unstable direction (x) and, as such, is referred to as a *saddle point* (see appendix I).

Near the nontrivial equilibrium (1,1), we introduce new variables u and v that measure the distance from (1, 1),

$$u = x - 1, \, v = y. \tag{1.32}$$

Therefore, equations (1.27a) and (1.27b) become

$$\frac{du}{d\tau} = v(1 + u), \tag{1.33a}$$

$$\frac{dv}{d\tau} = \alpha u(1 + v). \tag{1.33b}$$

Since u and v are small close to equilibrium (1,1), we again can linearize equations (1.33) and obtain:

$$\frac{du}{d\tau} \approx -v, \tag{1.34a}$$

$$\frac{dv}{d\tau} \approx \alpha u. \tag{1.34b}$$

Deriving both equations with respect to t we can get a second order differential equation for u:

$$\frac{d^2u}{d\tau^2} + \alpha u = 0 \tag{1.35}$$

For this linear, constant-coefficient equation, we may try an exponential solution of the form

$$u(t) = ce^{\lambda\tau}. \tag{1.36}$$

We thus obtain a characteristic equation,

$$\lambda^2 + \alpha = 0, \tag{1.37}$$

that has two purely imaginary roots,

$$\lambda = \pm i\sqrt{\alpha}. \tag{1.38}$$

And, substituting into equation (1.36) we get for the small departure $u(t)$ around $x = 1$:

$$u(t) = ce^{\sqrt{\alpha\tau}} = c\,\cos\,\sqrt{\alpha\tau} + ic\,\sin\,\sqrt{\alpha\tau}. \tag{1.39}$$

That is, the linearized system has sinusoidal solutions in τ, which have period $2\pi/\sqrt{\alpha}$. Let us see what this means in terms of ecological parameters like intrinsic growth and death rates. From equation (1.26), this period is $T = 2\pi\sqrt{\imath/d}$; that is, it increases with the ratio of the linear growth rate, $\imath$, of the prey to the death rate, d, of the predators. Hence, either an increase in the growth rate of the prey or a decrease of the predator death rate will increase the period. We can see that this makes sense. in the limit in which $\imath/d$ tends to infinity, then $\alpha = d/\imath$ tends to 0, so equation (1.27b) can be approximated as $dy/dt \approx 0$, this implies that y can be replaced by a constant value, and therefore equation (1.27a) would become a Malthusian equation, with infinite period (i.e. non periodic).

Unfortunately, we cannot conclude that the fully nonlinear system has these same simple periodic solutions. Purely imaginary roots, like equation (1.38), imply that the linearized system is on the knife-edge between instability and asymptotic stability and on the edge between oscillatory solutions that increase in amplitude and those that decrease in amplitude (see appendix I). For the fully nonlinear system, the nonlinear terms that we have neglected are now critical, since they may tip the nonlinear system one way or another with regard to stability. Three qualitatively different types of phase trajectories that would be, in principle, consistent both with the information from the linearized system and the direction field are shown in figure 1.5. All these three types of phase
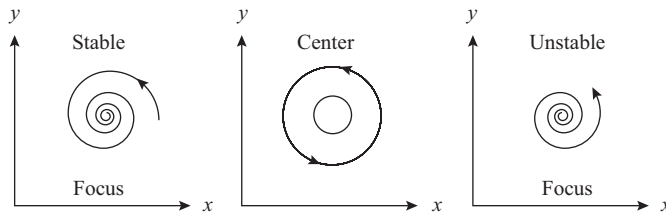

Figure 1.5. Possible scenarios for the equilibrium point (1,1).

trajectories are tangent to the arrows representing the direction field which rotate as we move through the plane. To elucidate which of these scenarios is the correct one we will use equation (1.30) obeyed by the family of phase trajectories, with one phase trajectory for each value of H. Firstly, it can be shown that the minimum possible value for H is $H_{min} = 1 + \alpha$ and it occurs at the singular point $x = y = 1$ (exercise 1.5). Secondly, equation (1.30) can be solved graphically (exercise 1.6) and we conclude that the nontrivial equilibrium is a *center* surrounded by a family of periodic orbits, and not a stable or unstable focus (aka spiral). This is also termed *neutral stability*.

Hence, we have seen that although the Lotka–Volterra predator–prey equations cannot be solved analytically, a lot of enlightening qualitative information can be obtained using analytical calculations. In general, before embarking on solving a problem by numerical methods it is advisable trying to approach it by analytical calculations which are more efficient to understand the fundamentals, easier to visualize and also serve for verification purposes (numerical calculations are more prone to errors).

Now we will integrate numerically the system of differential equations (1.27) (exercise 1.7) and draw the phase trajectories. For a given $H > 1 + \alpha$, the trajectories (1.30) in the phase plane are closed as illustrated in figure 1.6. The larger the H the larger is the area enclosed by the phase trajectory. The initial conditions, $x(0)$ and $y(0)$, determine the constant H in equation (1.30) and hence the phase trajectory in figure 1.6.

A closed trajectory in the x-y plane implies periodic solutions in τ for x and y. Typical periodic solutions $x(\tau)$ and $y(\tau)$ are shown in figure 1.7. From equations (1.27) we can see immediately that x has a turning point when $y = 1$ and y has one when $x = 1$.

How do the oscillatory solutions compare with predator–prey abundances observed in nature? It turns out that there is a classical set of data on a pair of interacting
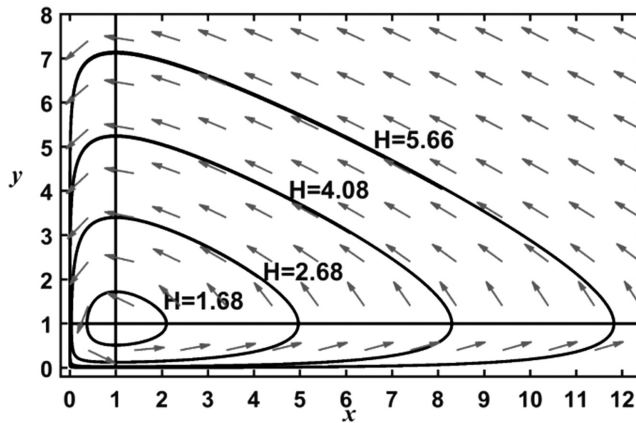

Figure 1.6. Phase portrait for the Lotka–Volterra predator–prey equations (1.27), nullclines for prey ($x = 0$, $y = 1$) and predator ($x = 1$, $y = 0$) and four orbits surrounding (1,1) for different values of H.
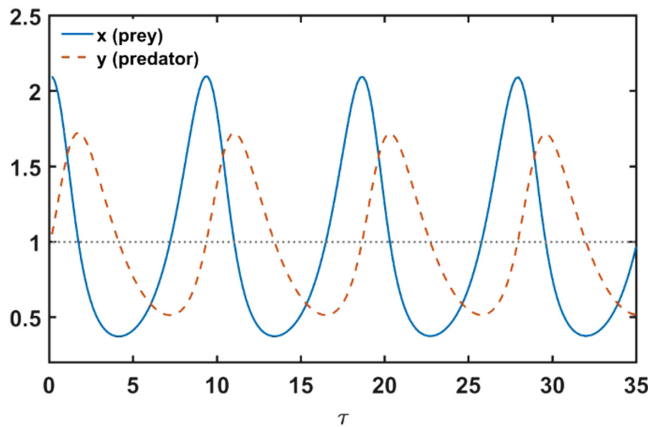
Figure 1.7. Predator–prey cycles corresponding to the closed orbit with $H = 1.68$ of figure 1.6.
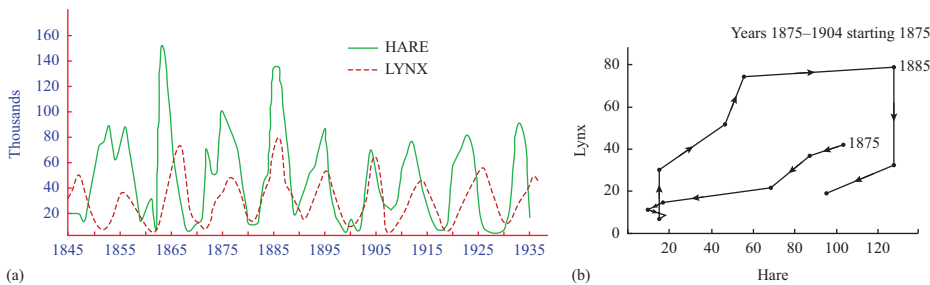

Figure 1.8. (a) Fluctuations in the number of pelts sold by the Hudson Bay Company. (Redrawn from Odum 1953.) (b) Phase plane plot of the data represented in (a) from 1875 to 1904. (After Gilpin 1973.)

populations that come close: the Canadian lynx and snowshoe hare pelt-trading records of the Hudson Bay Company over almost a century. Figure 1.8 (adapted from Odum 1953) shows a plot of that data. We can see they look similar to figures 1.6 and 1.7. However, we shall see in a moment that there is an important difference.

Let us conclude this subsection with a criticism on this first predator–prey model.

A major inadequacy of the Lotka–Volterra model is clear from figure 1.6 which shows that all phase trajectories pass close to the x and y axes. Suppose, for example, $x(0)$ and $y(0)$ are such that x and y for $\tau > 0$ are on the phase trajectory defined by a given value of H (e.g. $H = 4.08$). Then, when the system is 'traveling' along the horizontal or vertical segment of an orbit, any small perturbation could make it jump onto another orbit which does not lie *everywhere* close to the original one. Thus no single orbit is stable in the sense that the system converges to it after perturbations in either direction: perturb the system away from any cycle (for example by harvesting or stocking) and the system will automatically move to another cycle with different amplitude and period. Such a set of equations are called

structurally unstable[8]. Structural instability is a consequence of the fact that the equilibrium is a center, i.e. of neutral stability.

Another inconsistency of this simple model is that figure 1.8(a) shows reasonable periodic fluctuations and figure 1.8(c) a more or less closed curve in the phase plane as we now expect from a time-periodic behavior in the variables. Nevertheless, if we examine the results given in figure 1.8 a little more carefully we note that: first, the *direction* of the time arrows in figure 1.8(b) is clockwise in contrast to that in figure 1.6. This is reflected in the time curves in figure 1.8(a) where the lynx oscillation precedes the hare's. The opposite is the case in the predator–prey situation illustrated in figure 1.7. We have a severe interpretation problem; figure 3.3 would imply that the hares are eating the lynx! Different ways to solve this nonsense were proposed by Gilpin (1973): for example the hares could kill the lynx if they carried a disease which they passed on to the lynx. Or, a more probable candidate is *Homo sapiens*, i.e. the Canadian fur trappers. That is, trappers might sit out poor years and return to the trap lines only when the hare again became abundant. Since lynx were more profitable to trap than hare they could turn a disproportionately large share of their efforts toward catching the more profitable lynx.

1.3.3 Realistic predator–prey models: logistic growth of prey and Holling predator functional responses

The original Lotka–Volterra predator–prey model, unrealistic though it is, suggests that simple predator–prey interactions can give rise to oscillations of the abundances, i.e. to periodic orbits in the phase space. This oscillatory behavior is expected since if the prey population increases, it promotes growth of its predator. Since more predators consume more prey, the prey population starts to decline. With less available food the predator population, in turn, declines and when it is low enough, this allows the prey population to recover and the whole cycle starts over again. We have seen that the problem with these periodic orbits is that they are unstable.

The Lotka–Volterra model can be modified in simple ways to make it more biologically realistic. Reasonable modifications include making the prey populations density-dependent (e.g. logistically), and making the predator death rate depend inversely on prey density. Remarkably, these changes, inspired by biological arguments, solve the problem of the structural instability: the modified predator–prey equations give rise to robust periodic orbits, termed stable *limit cycle* oscillations. Here we will briefly present this modified model version. A very pedagogical treatment discussing by stages the buildup of such a more realistic and well behaved model is provided in chapter 8 of the book by Pastor (2008).

We have seen that one of the unrealistic assumptions in the Lotka–Volterra predator–prey equations (1.25a) and (1.25b), is that the prey growth is unbounded in

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[8] Note that structural instability is different as a change in stability due to a ***bifurcation*** when a parameter passes through a critical value. In a bifurcation, the stability of an equilibrium of the model changes because of a change in the value of a parameter, but the form of the equations remains unchanged. In a structurally unstable equation, either slight modifications of the initial conditions or of the form of the model equations alter the stability.

the absence of predation. We already know that a more realistic growth rate is provided by the logistic function. So, for example, a more realistic prey population equation might take the form

$$\frac{dN}{dt} = r\, N\left(1 - \frac{N}{\mathcal{K}}\right) - NPR(N). \tag{1.40a}$$

where $R(N)$ is the predator's functional response. C S Holling (1959) proposed three different functional response types:

$$\begin{cases} R(N) = c & \text{(1.41a)} \\ R(N) = \dfrac{c}{N + h} & \text{(1.41b)} \\ R(N) = \dfrac{cN}{N^2 + h^2} & \text{(1.41c)} \end{cases}$$

which are called, respectively, Holling's type I, II, and III (see figure 1.9). The constant c is the maximum per capita *consumption rate* and the parameter h is the *half-saturation constant* or the value of N which gives half the per capita consumption rate $c/2$.

Type I functional response is used in the Lotka–Volterra predator–prey model. It corresponds to a linear increase in intake rate with food density and assumes that the time needed by the consumer to process a food item is negligible, or that consuming food does not interfere with searching for food.

On the other hand, type II and III functional responses, are characterized by a decelerating intake rate, which follows from the assumption that the consumer is limited by its capacity to process food. Type II functional response describes the observed behavior of insects and parasitoids, as well as modelling microbial growth rates in a limiting nutrient environment, which is known as the Monod equation (Monod 1949). This functional response is also termed the Michaelis–Menten (1913) equation in the context of enzymatic reactions. Type III functional response is similar to type II in that at high levels of prey density, saturation occurs. But it has an inflection point when concavity changes. So, first at low prey density the rate of prey capture accelerates, and then it decreases with increasing prey density. This
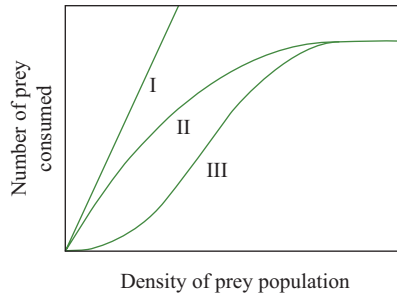

Figure 1.9. Holling type I, II and III response functions.

'sigmoidal' behavior has been attributed (Real 1977) to the existence of 'learning behavior' in the predator population. That is, predators learn more specialized techniques for hunting or focusing their search in particular places within the environment. Type III works well in general for vertebrates. For example, Holling (1959) identified this mechanism in deer mice feeding on sawflies. At low numbers of sawfly cocoons per acre, deer mice especially experienced exponential growth in terms of the number of cocoons consumed per individual as the density of cocoons increased, until a saturation point was reached.

The equation for predator dynamics can take different forms. For example,

$$\frac{dP}{dt} = \beta P R(N) - \alpha P, \tag{1.40b}$$

where β, as before, represents the conversion efficiency of prey biomass into predator biomass.

However, there are several other possible choices for the predator equation. For example, in the so-called Holling–Tanner model (Tanner 1975) the predator equations are:

$$\frac{dN}{dt} = r N\left(1 - \frac{N}{\mathcal{K}}\right) - \frac{cN}{N + h}P \tag{1.40a'}$$

$$\frac{dP}{dt} = sP\left(1 - \eta\frac{P}{N}\right). \tag{1.40b'}$$

It turns out that the above modified Lotka–Volterra predator–prey equations with functional responses of Holling type II or III exhibit stable ***limit cycle*** oscillations (see exercises 1.10 and 1.11). A limit cycle solution is a closed trajectory in the predator–prey space which is not a member of a continuous family of closed trajectories such as the solutions of the original Lotka–Volterra predator–prey depicted in figure 1.6. Rather, it is an isolated periodic orbit (the thick closed curve shown in figure 1.10), such that any small perturbation from this trajectory decays to zero. This limit cycle persists for a range of parameter values. And, its name is because it also attracts orbits that occur at nearby initial conditions, as shown in figure 1.10 for the Holling–Tanner model. For two different initial conditions, one inside and the other outside the limit cycle, the phase trajectories spiral into it (see exercise 1.11). In the application chapter companion to this chapter we will consider a modified Lotka–Volterra predator–prey model with a variable carrying capacity and a Holling type III consumption to model extensive livestock farming.

1.4 The Lotka–Volterra competition equations for a pair of species

1.4.1 A descriptive or phenomenological model

Lotka (1925) and Volterra (1926) independently proposed the simplest dynamical system for modelling two-species competition using extensions of the logistic equation. The Lotka–Volterra competition model is an *interference* competition
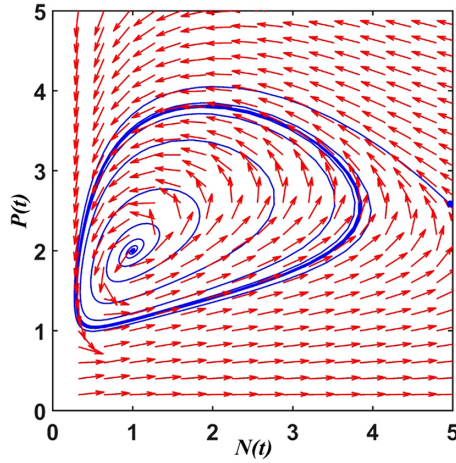
Figure 1.10. Limit cycle for the Holling–Tanner model, i.e. $dP/dt = sN(1 - \eta p/N)$ for the predator and with parameters given by $r = 1$, $\mathcal{K} = 7$, $c = 6/7$, $k = 1$, $s = 0.2$, $\eta = 0.5$.

model: two species are assumed to diminish each other's per capita growth rate by direct interference. But the model does not specify either the limiting resource(s) the two species are competing for (nutrients, light, shelter, nesting sites, whatever), or the mechanism of competition. Thus it is a *descriptive* or **phenomenological** model of competition rather than a *mechanistic* model.

We begin by assuming that two species, with populations densities N_1 and N_2, each grow logistically in the absence of the other. Each species has a per capita growth rate that decreases linearly with population size,

$$\frac{dN_1(t)}{dt} = r_1 N_1(t)\left(1 - \frac{N_1(t) + \alpha_{12}N_2(t)}{\mathcal{K}_1}\right), \tag{1.42a}$$

$$\frac{dN_2(t)}{dt} = r_2 N_2(t)\left(1 - \frac{N_2(t) + \alpha_{21}N_1(t)}{\mathcal{K}_2}\right), \tag{1.42b}$$

where the competition coefficients α_{ij} are positive parameters measuring the per capita effect of species j on the abundance of species i; all other parameters are as before, except that subscripts indicate the particular species referred to.

1.4.2 Stable equilibrium: competitive exclusion or species coexistence?

To understand the dynamics and equilibria of this model, let us start by finding the nullclines. Both the nullclines and the equilibrium solutions are found by setting either the $r_i N_i$ terms or the $[1 - (N_i - \alpha_{ij}N_j)/\mathcal{K}_i]$ terms equal 0. The nullclines for N_1 are:

$$N_1 = 0 \tag{1.43a}$$

and

$$N_1 = \mathcal{K}_1 - \alpha_{12}N_2 \qquad (1.43b)$$

Likewise, the nullclines for N_2 are:

$$N_2 = 0 \qquad (1.43c)$$

and

$$N_2 = \mathcal{K}_2 - \alpha_{21}N_1 \qquad (1.43d)$$

As with predator–prey models, the N_1 and N_2 axes are the 'extinction' nullclines for the other species. The N_1 nullcline (1.43b) intersects the N_1-axis at $\mathcal{K}_1$ and intersects the N_2-axis at $\mathcal{K}_1/\alpha_{12}$. Similarly, the N_2 nullcline (1.43d) intersects the N_1-axis at $\mathcal{K}_2/\alpha_{21}$ and the N_2-axis at $\mathcal{K}_2$. One of these nullclines may lie entirely above the other (figures 1.11(a) and (b)), and it is reasonable to expect that the first will always outcompete the other and drive the other to extinction. Alternatively, these two zero-growth isoclines may cross. Thus, there are four cases, depending on the relative positions of the horizontal and vertical intercepts of these two nullclines in the first quadrant (remember population densities must be positive). Each of the four cases corresponds to a qualitatively different phase portrait and is depicted in a separate panel in figure 1.11. Let us consider each phase portrait in turn, the corresponding equilibria and their stability (in exercise 1.13 we check the qualitative results obtained by this graphical analysis by solving numerically equations (1.42)):

I. If each intercept of the nullcline (1.43d), $N_1 = \mathcal{K}_2/\alpha_{21}$ and $N_2 = \mathcal{K}_2$, is greater than the corresponding intercept of that for (1.43b), $N_1 = \mathcal{K}_1$ and $N_2 = \mathcal{K}_1/\alpha_{12}$, (figure 1.11(a)) i.e. $\mathcal{K}_2/\alpha_{21} > \mathcal{K}_1$ and $\mathcal{K}_2 > \mathcal{K}_1/\alpha_{12}$, which implies that

$$\alpha_{12} > \mathcal{K}_1/\mathcal{K}_2, \ a_{21} < \mathcal{K}_2/\mathcal{K}_1 \qquad (1.44a)$$

N_2 excludes N_1. Indeed, if species 2 has a relatively large negative effect on species 1 and species 1 has a relatively small negative effect on species 2, an expected outcome is that species 1 will go extinct while species 2 will approach its carrying capacity $\mathcal{K}_2$. Therefore, it appears that $N_1^* = 0$, $N_2^* = \mathcal{K}_2$ or $(0, K_2)$, indicated as a black circle in figure 1.11(a), is a stable equilibrium point under conditions (1.44a). Likewise, $N_1^* = 0, N_2^* = 0$ or $(0, 0)$, indicated as a white circle, appears as an unstable equilibrium point.

II. If each intercept of the nullcline (1.43b), $N_1 = \mathcal{K}_1$ and $N_2 = \mathcal{K}_1/\alpha_{12}$, is greater than the corresponding intercept of that for (1.43d), $N_1 = \mathcal{K}_2/\alpha_{21}$ and $N_2 = \mathcal{K}_2$, (figure 1.11(b)), i.e. $\mathcal{K}_1 > \mathcal{K}_2/\alpha_{21}$ and $\mathcal{K}_1/\alpha_{12} > \mathcal{K}_2$, which implies that

$$\alpha_{12} > \mathcal{K}_1/\mathcal{K}_2, \ a_{21} < \mathcal{K}_2/\mathcal{K}_1 \qquad (1.44b)$$

N_1 excludes N_2. That is, species 2 will go extinct while species 1 will approach its carrying capacity $\mathcal{K}_1$. Therefore, it appears that $N_1^* = \mathcal{K}_1$, $N_2^* = 0$ is a stable equilibrium point, indicated as a black circle in figure 1.11(b), is a stable equilibrium point under conditions (1.44b).
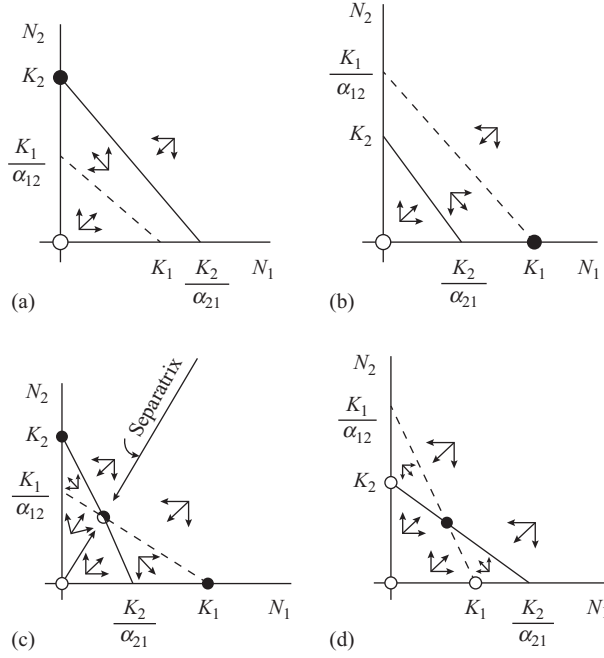
Figure 1.11. Schematic representation of the four possible phase portraits for the competition Lotka–Volterra equations (1.42) depicting vector fields at the different regions delimited by the nullclines of (dashed line for species 1 and filled line for species 2). Stable equilibria are denoted by filled black circles, unstable equilibria by empty circles and saddle points by half filled circles. (a) and (b) When one nullcline lies completely above the other in the first quadrant, the equilibria are stable monocultures. (c) Strong competition results in stable monocultures of either species. (d) Weak competition results in stable coexistence. Adapted from Pastor 2008, with permission from John Wiley & Sons.

Again, $N_1^* = 0$, $N_2^* = 0$ or $(0, 0)$, indicated as a white circle, appears as an unstable equilibrium point. Notice that the reversing of inequalities implies a reversing of the competitive outcome.

III. If the two nullclines cross in such a way that $\mathcal{K}_1 > \mathcal{K}_2/\alpha_{21}$ and $\mathcal{K}_2 > \mathcal{K}_1/\alpha_{12}$, which implies that

$$\alpha_{12} > \mathcal{K}_1/\mathcal{K}_2, \ a_{21} < \mathcal{K}_2/\mathcal{K}_1 \tag{1.44c}$$

i.e. both species are **strong competitors** against the other, then an examination of the vector field of figure 1.11(c) shows that either species can displace the other to extinction, depending on the initial conditions. That is, the two equilibria $(\mathcal{K}_1, 0)$ and $(0, \mathcal{K}_2)$, corresponding to the exclusion of one or the other species, are now both stable nodes (figure 1.11(c)). It is apparent that the species which is initially most abundant will always displace the other. The intersection of the nullclines is therefore a saddle-node: it will be approached only if the system initially lies on the line dividing the two regions of local stability of $(\mathcal{K}_1, 0)$ and $(0, \mathcal{K}_2)$. This line is called a *separatrix* (see Glossary) since it separates the two regions. Except for perturbations exactly on the separatrix, any perturbation away from the

coexistence equilibrium will be attracted to the nearest monoculture equilibrium.

IV. Finally, if both species are **weak competitors** as defined by inequalities

$$\alpha_{12} > \mathcal{K}_1/\mathcal{K}_2, \ a_{21} < \mathcal{K}_2/\mathcal{K}_1, \tag{1.44d}$$

the vector field of figure 1.11(d) now shows that once trajectories arrive in the triangular regions between the two nullclines, the vectors point to the coexistence equilibrium, which appears to be stable to perturbations away from it in any direction. In other words, the equilibria $(\mathcal{K}_1, 0)$ and $(0, \ \mathcal{K}_2)$ are now unstable saddle points and trajectories are drawn towards a stable node in the interior of the first quadrant at $\left(\frac{\mathcal{K}_1 - \alpha_{12}\mathcal{K}_2}{1 - \alpha_{12}\alpha_{21}}, \ \frac{\mathcal{K}_2 - \alpha_{21}\mathcal{K}_1}{1 - \alpha_{12}\alpha_{21}} \right)$. Thus the four possible equilibria are:

$$N_1^* = N_2^* = 0 \tag{1.45a}$$

$$N_1^* = \mathcal{K}_1, \ N_2^* = 0 \tag{1.45b}$$

$$N_1^* = 0, \ N_2^* = \mathcal{K}_2 \tag{1.45c}$$

$$N_1^* = \frac{\mathcal{K}_1 - \alpha_{12}\mathcal{K}_2}{1 - \alpha_{12}\alpha_{21}}, \ N_2^* = \frac{\mathcal{K}_2 - \alpha_{21}\mathcal{K}_1}{1 - \alpha_{12}\alpha_{21}} \tag{1.45d}$$

The above four possible competitive situations, defined by the relative positions of the nullclines, are summarized in table 1.1.

It is enlightening to nondimensionalize the Lotka–Volterra competition model by writing, using *relative yields* $y_i = N_i/\mathcal{K}_i$ (the species yield in mixture normalized by its yield in monoculture), as

Table 1.1. Summary of effects of relative competitive ability on the outcome of competition between two species, equilibria and their stability.

	Effect of species 2 on species 1	
Effect of species 1 on species 2	Weak: $\alpha_{12} < K_1/K_2$	Strong: $\alpha_{12} > K_1/K_2$
Weak: $\alpha_{21} < K_2/K_1$	**Coexistence** equilibrium at $\left(\frac{\mathcal{K}_1 - \alpha_{12}\mathcal{K}_2}{1 - \alpha_{12}\alpha_{21}}, \ \frac{\mathcal{K}_2 - \alpha_{21}\mathcal{K}_1}{1 - \alpha_{12}\alpha_{21}} \right)$	**Species 2 always displaces species 1**, equilibrium at $(0, K_2)$
Strong: $\alpha_{21} > K_2/K_1$	**Species 1 always displaces species 2**, equilibrium at $(K_1, 0)$	**Winner depends on initial conditions**, if $N_1(0) > N_2(0)$, equilibrium at $(K_1, 0)$ if $N_1(0) < N_2(0)$, equilibrium at $(0, K_2)$

$$\frac{dy_1(\tau)}{d\tau} = y_1(\tau)(1 - y_1(\tau) + a_{12}y_2(\tau)), \tag{1.46a}$$

$$\frac{dy_2(\tau)}{d\tau} = \rho y_2(\tau)(1 - y_1(\tau) + a_{12}y_2(\tau)), \tag{1.46b}$$

where $\tau = \tau_1 t$, $\rho = \tau_1/\tau_2$, and the a_{ij} denote the interspecific interaction coefficients in terms of these relative yields, defined as $a_{ij} = \alpha_{ij} \, \mathcal{K}_j/\mathcal{K}_i$ (see exercise 1.14).

Notice that in terms of these new interspecific interaction coefficients the condition separating weak from strong competition of species j over species i becomes $a_{ij} = 1$, i.e.

$$\text{if} \begin{cases} a_{ij} & < \quad 1 \text{ weak competition of species } j \text{ over species } i \\ a_{ij} & > \quad 1 \text{ strong competition of species } j \text{ over species } i \end{cases}$$

Since the intraspecific competition term is taken $= 1$ (to recover the logistic equation) we can conclude form table 1.1 that whenever at least one of the two interspecific effects is strong, i.e. stronger than intraspecific competition, we end up with competitive exclusion of one species. Only in case IV, where **both interspecific effects were weak relative to intraspecific effects**, **did the two competing species coexist**. This forms the basis for *Gause's Principle* (Gause 1934) aka the *Principle of Competitive Exclusion* (Hardin 1960). This principle states that, two species competing for the same *ecological niche* cannot coexist. This leads either to the extinction of the weaker competitor or to an evolutionary or behavioral shift toward a different ecological niche. Thus it begs the question: just how similar can the two niches be in order that the two species manage to coexist? We will revisit this question in the second part of this book when dealing with *niche theory*.

1.4.3 Transforming the competition model into a mechanistic model

As we said, the Lotka–Volterra competition equations are a phenomenological approach for the population dynamics of competition since they describe the process of competition by the rather abstract parameters of competition coefficients and carrying capacity. Therefore, these equations have limited ability to explore how the outcomes of competition might change in environments that differ in, for example, the availability of different resources or among species that differ in the use of these resources.

The descriptive Lotka–Volterra model can be transformed into a mechanistic model by explicitly introducing resources as population variables which are consumed or utilized by the two species whose competition we want to model. That is, we explicitly model the dynamics of the resources for which competition occurs and allow species to interact solely through their consumption of shared resources by using the Lotka–Volterra predator–prey equations. In this way we can express the competition coefficients and carrying capacities in terms of rates of utilization and renewal of resources. Hence, imagine two populations N_1 and N_2

(say of herbivores) consuming one resource R (e.g. grass); we can begin by writing the resource equation:

$$\frac{dR}{dt} = r R\left(1 - \frac{R}{k} - c_1 N_1 - c_2 N_2\right), \tag{1.47a}$$

where k is the carrying capacity of the resource and all the other parameters are defined as for equation (1.25a): r denotes, as usual, the growth rate of the prey species in the absence of interaction with the predator species, the parameter $c_i = r \cdot c_i$ is a per-capita consumption rate of resource by species i. Now we can write the corresponding dynamical equations for N_1 and N_2 as if they were predators governed by equation (1.25b):

$$\frac{dN_1}{dt} = N_1(a_1 R - d_1), \tag{1.47b}$$

$$\frac{dN_2}{dt} = N_2(a_2 R - d_2). \tag{1.47c}$$

Hence, in essence, the model describes a simple food web. We now assume that the dynamics of the resource is much more rapid compared to that of the consumer, such that we can set the derivative of equation (1.47a) equal to zero, solve for the equilibrium value of R:

$$R^* = (1 - c_1 N_1 - c_2 N_2)k, \tag{1.48}$$

and approximate the consumer dynamics at any particular value of N_1 and N_2 by simply substituting R^* in place of R in equations (1.47b) and (1.47c). Thus we obtain

$$\frac{dN_1}{dt} = N_1(a_1 k - d_1 - a_1 c_1 k N_1 - a_1 c_2 k N_2), \tag{1.49a}$$

$$\frac{dN_2}{dt} = N_2(a_2 k - d_2 - a_2 c_1 k N_1 - a_2 c_2 k N_2). \tag{1.49b}$$

By rearranging we can write equations (1.49a) and (1.49b) as:

$$\frac{dN_1}{dt} = (a_1 k - d_1)N_1\left(1 - \frac{a_1 c_1 k}{a_1 k - d_1}N_1 - \frac{a_1 c_2 k}{a_1 k - d_1}N_2\right), \tag{1.50a}$$

$$\frac{dN_2}{dt} = (a_2 k - d_2)N_2\left(1 - \frac{a_1 c_1 k}{a_2 k - d_2}N_1 - \frac{a_1 c_2 k}{a_2 k - d_2}N_2\right). \tag{1.50b}$$

Hence, identifying coefficients with equations (1.42a) and (1.42b) we can express parameters r_i and $\mathcal{K}_i$ in terms of the mechanistic parameters a_i, c_i, d_i and k as :

$$r_i = a_i k - d_i, \tag{1.51a}$$

$$\mathcal{K}_i = \frac{a_i k - d_i}{a_i \ell_i k} \qquad (1.51b)$$

$$\alpha_{ij} = \frac{\ell_j}{\ell_i}. \qquad (1.51c)$$

Notice that:

(a) As expected, equation (1.51a) tells us that the net growth rate of a species, r_i, grows with its predation rate, a_i, and with the carrying capacity of the resource, k (and of course decreases with its death rate).

(b) There is a proportionality relationship between the net growth rate of a species, r_i, and its carrying capacity, $\mathcal{K}_i$, since the numerator of equation (1.51b) is r_i. Equation (1.51b) also tells us that, when the death rate of a species, d_i, is negligible with respect to the product $a_i k$, its carrying capacity, $\mathcal{K}_i$, is inversely proportional to its per-capita consumption rate of resource, ℓ_i.

(c) The competition coefficients α_{ij}s represent the use of resources by the competing species j relative to the use of resources by the species whose dynamics are being considered i. It is important to emphasize that they do *not* represent the absolute intensity of competition but are rather a ratio of the intensity of interspecific to intraspecific competition.

Remark. Equations (1.47) dealt with a single resource. However, interspecific competition is almost never for a single resource. Indeed, by virtue of the principle of Competitive Exclusion, most ecologists think that two species competing for a single resource cannot persist together forever. MacArthur (1972) proposed a mechanistic model of two species consuming two distinct resources, in terms of predator–prey equations, that overcomes this problem. Results become algebraically more cumbersome.

1.5 The Lotka–Volterra equations for two mutualist species

To complete the description of elementary interactions between species in this section we consider mutualisms, i.e. reciprocally positive interactions between species. Other kinds of beneficial associations of at least one species, like commensalism (0/+ interaction), can be considered as a limiting case of mutualism (likewise, the amensalism −/0 interaction can be thought as a limiting case of prey–predator interaction).

Mutualisms are ubiquitous in nature. Prominent examples include most vascular plants engaged in mutualistic interactions with mycorrhizal fungi, the association of *Rhizobium* bacteria with leguminous plants, and the diverse community of bacteria in all mammalian guts.

There are two broad types of mutualism, ***facultative*** and ***obligate***. Facultative mutualists can live independently of each other, the mutualism is non-essential but

the growth of each species is enhanced in the presence of each other. Examples of facultative mutualism are the fish-cleaning mutualism, one fish (the cleaner) removes and eats parasites from the surface of the other (the client) or seed dispersal mutualism, such as the association between the Clark's nutcracker and whitebark pine. Obligate mutualism is essential for both parties, the two partners cannot survive without each other. Ruminants and the bacteria in their digestive tracts that actually digest the cellulose in the animal's food, is an example of obligate mutualists.

A candidate for a mutualism model results from inverting the sign of the interspecific competition coefficients of the Lotka–Volterra competition equations (1.42), from negative to positive. That is:

$$\frac{dN_1(t)}{dt} = r_1 N_1(t)\left(\frac{\mathcal{K}_1 - N_1(t) + \alpha_{12}N_2(t)}{\mathcal{K}_1}\right), \; (\alpha_{12} > 0) \qquad (1.52a)$$

$$\frac{dN_2(t)}{dt} = r_2 N_2(t)\left(\frac{\mathcal{K}_2 - N_2(t) + \alpha_{21}N_1(t)}{\mathcal{K}_2}\right), \; (\alpha_{21} > 0). \qquad (1.52b)$$

We will see in a moment that equations (1.52), with all their quantities **positive**, serve to describe mutualism between two facultative species.

Proceeding in a completely similar way as we did for the competition model, let us calculate the nullclines. The nullclines for N_1 are:

$$N_1 = 0 \qquad (1.53a)$$

and $N_1 = \mathcal{K}_1 + \alpha_{12}N_2$, or equivalently

$$N_2 = (1/a_{12})N_1 - \mathcal{K}_1/a_{12}. \qquad (1.53b)$$

Similarly, the nullclines for N_2 are:

$$N_2 = 0 \qquad (1.53c)$$

$$N_2 = \alpha_{21}N_1 + \mathcal{K}_2. \qquad (1.53d)$$

These are identical to the nullclines of the competition equations, except that they have a positive slope (figure 1.12). Notice first that equations (1.53b) and (1.53d) imply that increasing the density of species j, the mutualist of species i, supports an increase in N_i *above* its carrying capacity (defined as its equilibrium density when alone). And, second that if species j disappears each species converges to its carrying capacity. Therefore, according to our definition, equations (1.52) describe a facultative mutualism (species do not collapse when the mutualist species disappears).

The equilibria are obtained as usual by intersecting the nullclines and are:

$$N_1^* = N_2^* = 0 \qquad (1.54a)$$

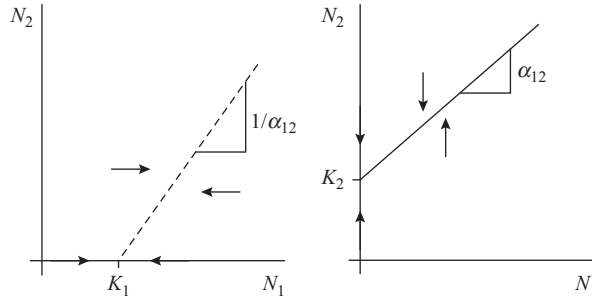$$N_1^* = \mathcal{K}_1, \; N_2^* = 0 \qquad (1.54b)$$

Figure 1.12. Nullclines of the Lotka–Volterra mutualism model equations (1.52) and a schematic representation of the vector field. Left: nullclines for N_1, horizontal axis and dashed line, with slope $1/\alpha_{12}$. Right: nullclines for N_2, vertical axis and filled line with their slope α_{21}. Adapted from Pastor 2008, with permission from John Wiley & Sons.

$$N_1^* = 0, \; N_2^* = \mathcal{K}_2 \tag{1.54c}$$

$$N_1^* = \frac{\mathcal{K}_1 + \alpha_{12}\mathcal{K}_2}{1 - \alpha_{12}\alpha_{21}}, \; N_2^* = \frac{\mathcal{K}_2 + \alpha_{21}\mathcal{K}_1}{1 - \alpha_{12}\alpha_{21}} \tag{1.54d}$$

Notice they become identical to the equilibria of the competition model, (equations (1.45)), by replacing α_{ij} by $-\alpha_{ij}$ in the coexistence equilibrium (equation (1.54d)).

In the same way as we defined weak and strong competition, let us now define weak and strong mutualism as:

$$\begin{cases} \alpha_{12}\alpha_{21} < 1 : \text{ weak mutualism} \\ \alpha_{12}\alpha_{21} > 1 : \text{ strong mutualism} \end{cases}$$

Since all parameters, the carrying capacities and the interaction coefficients, are positive, it is straightforward to show analytically that the coexistence equilibrium (1.54d) is only possible for weak mutualism. (The strong mutualism condition implies that the equilibrium densities would be negative!) The same can be shown geometrically. The weak mutualism condition implies that the slope of the nullcline (1.53b) for N_1, equal to $1/\alpha_{12}$, is always larger than the slope of the nullcline (1.53d) for N_2, equal to $1/\alpha_{21}$. Consequently, both nullclines will intersect in the first quadrant (figure 1.13(a)). Furthermore, the vector field tells us that for weak mutualism this coexistence equilibrium is stable. Remember that the same happened for two competing species: the coexistence equilibrium was stable only for weak competition. The difference is that populations are larger, rather than smaller, than their respective carrying capacities (figure 1.13(a)). In contrast, the strong mutualism condition implies that the slope of the nullcline (1.53b) for N_1 is always smaller than the slope of the nullcline (1.53d) for N_2 and thus both nullclines will not intersect in the first quadrant (figure 1.13(b)). Rather, under strong mutualism, the vector field indicates that both populations increase indefinitely (figure 1.13(b)).
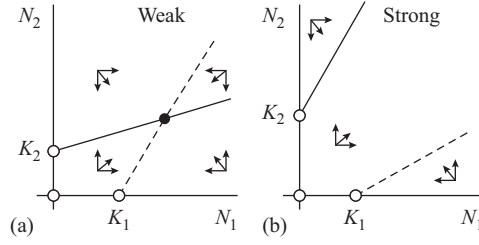
Figure 1.13. Nullclines, equilibria with their stability (a stable equilibrium is denoted by a filled black circle and an unstable one by an open white circle) and a schematic representation of the vector field for **facultative mutualism**. (a) Weak mutualism. (b) Strong mutualism. Adapted from Pastor 2008, with permission from John Wiley & Sons.
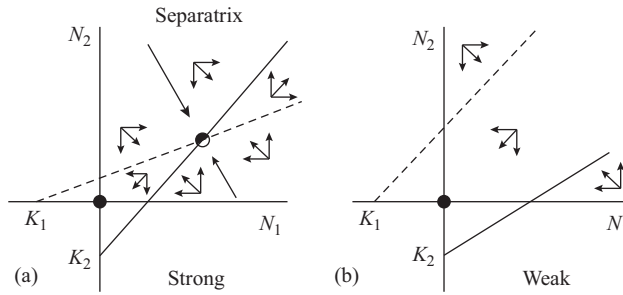

Figure 1.14. Nullclines, equilibria with their stability (stable equilibria denoted by a filled black circle and an unstable one by an open white circle) and a schematic representation of the vector field for **obligate mutualism**. (a) Strong mutualism. (b) Weak mutualism. Adapted from Pastor 2008, with permission from John Wiley & Sons.

In other words, for coexistence to be possible, the equilibrium solution must lie in the first quadrant. And, this is only possible for facultative mutualism if $\alpha_{12}\alpha_{21} < 1$, which is weak mutualism. This means that the positive feedback between the two species is not strong enough to result in destabilizing positive feedback. On the other hand, in the case of strong mutualism $\alpha_{12}\alpha_{21} > 1$ the nullclines in the first quadrant diverge from each other and the coexistence equilibrium is in the third quadrant (both N_1^* and N_2^* are negative). So, we conclude that **for two facultative mutualists to coexist, mutualism must be weak**.

What about equations describing obligate mutualism? Indeed, figure 1.13(b) gives us a clue about how to modify equations (1.52) to obtain a coexistence equilibrium for obligate mutualism. Notice that if we move the nullcline of species 1 parallel to itself toward the left until the intersection point with the horizontal axis becomes $-\mathcal{K}_1$ and the nullcline of species 2 parallel to itself downward until the intersection point with the vertical axis becomes $-\mathcal{K}_2$, the two nullclines would intersect in the first quadrant (figure 1.14(a)). This is equivalent to making the two carrying capacities negative. Obviously one cannot have a negative carrying capacity. But a negative carrying capacity in the equations can be interpreted simply as requiring that there is a minimal number of individuals of the mutualist partner that can

actually initiate the mutualism process and result in increasing population numbers. Replacing $\mathcal{K}_1$ and $\mathcal{K}_2$ by $-\mathcal{K}_1$ and $-\mathcal{K}_2$ equations (1.52) transform into:

$$\frac{dN_i(t)}{dt} = \varkappa_i N_i(t)\left(\frac{-\mathcal{K}_i - N_i(t) + \alpha_{ij}N_j(t)}{-\mathcal{K}_i}\right)$$

$$= -\varkappa_i N_i(t)\left(\frac{-\mathcal{K}_i - N_i(t) + \alpha_{ij}N_j(t)}{\mathcal{K}_i}\right).$$

We are almost done. As we just mentioned, we want that species i grows if the density of its mutualist species j is large enough. The above equation would describe this provided $\varkappa_i$ is also negative (this is because the minus sign in front of $\varkappa_i$ and the fact that the bracketed factor is positive for large values of N_j). Thus, in the same way that facultative mutualism has parameters $\varkappa_1 > 0$, $\varkappa_2 > 0$, $\mathcal{K}_1 > 0$, $\mathcal{K}_2 > 0$, let us define obligate mutualism as having parameters $\varkappa_1' < 0$, $\varkappa_2' < 0$, $\mathcal{K}_1' < 0$, $\mathcal{K}_2' < 0$. Therefore the equations for obligate mutualism can be written as:

$$\frac{dN_1(t)}{dt} = \varkappa'_1 N_1(t)\left(\frac{\mathcal{K}_1' - N_1(t) + \alpha_{12}N_2(t)}{\mathcal{K}_1'}\right), \; (\alpha_{12} > 0, \, \varkappa'_1 < 0, \, \mathcal{K}_1' < 0) \quad (1.55a)$$

$$\frac{dN_2(t)}{dt} = \varkappa'_2 N_2(t)\left(\frac{\mathcal{K}_2' - N_2(t) + \alpha_{21}N_1(t)}{\mathcal{K}_2'}\right), \; (\alpha_{21} > 0, \, \varkappa'_2 < 0, \, \mathcal{K}_2' < 0). \quad (1.55b)$$

They have precisely the same form as the original mutualism equations, with the intrinsic rates of increase and with the carrying capacities both negative (we use the primes for stressing this). And, since the quotient $\varkappa_i'/\mathcal{K}_i'$ is positive, they tell us that in the obligate case, the mutualism coefficients must be large enough to make the growth of each species positive in **the presence of** the other species, but each species on its own will not have positive equilibria.

Could two obligate mutualists coexist? As we have observed, for a strong obligate mutualism the nullclines intersect at one point in the first quadrant. But, is this coexistence equilibrium stable? The vector field for the strong facultative mutualism indicates that the coexistence equilibrium is a semistable saddle-point (figure 1.14(a)). In turn, the weak obligate mutualism has an equilibrium solution in the third quadrant because its nullclines diverge in the first quadrant.

We can verify analytically the stability of the coexistence equilibrium both for two weak facultative mutualists and for two strong obligate mutualists (exercise 1.15) by examining the stability of the Jacobian matrix evaluated at each of these coexistence points (see appendix I).

So far we have discussed symmetrical relationships, i.e. either facultative–facultative or obligate–obligate mutualisms. What about asymmetrical facultative–obligate associations? For example, if N_1 is the facultative species

Table 1.2. Summary of the possibility and stability of coexistence for different mutualistic associations, both weak and strong, and either symmetrical or not.

Intensity	Species 1	Species 2	
		Facultative	Obligate
Weak	Facultative	**Stable node**	**Stable node if**
$\alpha_{12}\alpha_{21} < 1$			$\mathcal{K}_1 > -\alpha_{12}\mathcal{K}_2', \; \alpha_{12}\mathcal{K}_1 > -\mathcal{K}_2'$
	Obligate	**Stable node if**	**Impossible**
		$\alpha_{12}\mathcal{K}_2 > -\mathcal{K}_1', \; \mathcal{K}_2 > -\alpha_{12}\mathcal{K}_1'$	
Strong	Facultative	**Impossible**	**Unstable**
$\alpha_{12}\alpha_{21} > 1$	Obligate	**Unstable**	**Saddle node**

($\imath_1 > 0$, $\mathcal{K}_1 > 0$) and N_2 the obligate species ($\imath_2' < 0$, $\mathcal{K}_2' < 0$) the coexistence equilibrium becomes:

$$N_1^* = \frac{\mathcal{K}_1 + \alpha_{12}\mathcal{K}_2'}{1 - \alpha_{12}\alpha_{21}}, \; N_2^* = \frac{\mathcal{K}_2' + \alpha_{21}\mathcal{K}_1}{1 - \alpha_{12}\alpha_{21}}. \tag{1.56}$$

For weak mutualism the denominator of equation (1.56) is positive and therefore a coexistence equilibrium exists in the first quadrant provided both numerators are also positive, i.e. $\mathcal{K}_1 > -\alpha_{12}\mathcal{K}_2'$, $\alpha_{12}\mathcal{K}_1 > -\mathcal{K}_2'$. The stability of non symmetrical cases can be easily derived by an analysis similar to the one we performed for the symmetrical cases[9]. The outcome for all cases of mutualism, both symmetrical and asymmetrical, are summarized in table 1.2.

Exercises

Exercise 1.1

Fibonacci numbers and the Golden Ratio

(A) A certain man had one pair of rabbits together in a certain enclosed place. How many pairs of rabbits can be created from the pair in one year if we suppose that each month each pair begets a new pair, which on the second month on becomes productive?

(B) Show that if we call F_n the number of rabbits at month n, the following relation holds: $F_{n+2} = F_{n+1} + F_n$, for $n = 0, 1, 2, \ldots$.

(C) To solve the above recurrence equation try $F_n = \lambda^n$, where λ is a constant you have to compute.

(D) Plot F_n, versus n.

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[9] We refer the reader interested in these non symmetrical mutualistic associations to Vandermeer and Boucher (1978) or Pastor (2008).

Exercise 1.2

Obtaining the logistic parameters by least square regression method.

Using the least square regression method obtain from the data below (Gause 1932) the carrying capacity $\mathcal{K}$, and the growth rate r as well as the initial volume V_0.

Time (h)	Yeast vol (ml)
6	0.37
7.5	1.63
15	6.2
16	8.87
24	10.66
29	12.5
31.5	12.6
33	12.9
40	13.27
44	12.77
48	12.87
51.5	12.9

Exercise 1.3

(from Hale and McCarthy 2005).

Let us consider the population of white-tailed deer in the state of Kentucky. The Kentucky Department of Fish and Wildlife Resources (KDFWR) sets guidelines for hunting and fishing in the state, and it reported an estimate of 900 000 deer prior to the hunting season of 2004. Johnson (2003) notes: 'A deer population that has plenty to eat and is not hunted by humans or other predators will double every three years.' This corresponds to a rate of increase $r = \ln(2)/3 = 0.2311$. (This assumes—with plentiful food supply and no predation—that the population grows exponentially, which is reasonable, at least in the short term.) The KDFWR also reports deer densities for 32 counties in Kentucky, the average of which is approximately 27 deer per square mile. Suppose this is the deer density for the whole state (39 732 square miles). The carrying capacity $\mathcal{K}$ is 39 732 sq. mi. × 27 deer/sq. mi. or 1 072 764 deer.

Investigate if the above data are consistent with the logistic growth model.

Exercise 1.4

Consumption by fixed quota for a population with logistic growth.

Consider the logistic model with fixed consumption per share:

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{\mathcal{K}}\right) - C,$$

(A) Calculate the equilibria and analyze their stability using pencil and paper.
(B) Write a script (in MATLAB, Fortran, R, etc) to solve this differential equation (for example using the Runge–Kutta second order method) and compute $X/\mathcal{K}$ for $\tau = 1$ and $C = \mathcal{K}/2$, $C = \mathcal{K}/4$ and $C = \mathcal{K}/8$ with the initial condition $X(0) = \mathcal{K}/2$, and $X(0) = 2\mathcal{K}$.
(C) Solve the equation using some ODE integrator package.

Exercise 1.5

Calculation of $H_{\min}$ for Lotka–Volterra predator–prey phase trajectories.

Equation (1.30) is obeyed by the family of phase trajectories generated by the Lotka–Volterra predator–prey equations (1.27a) and (1.27b), with one phase trajectory for each value of H. Show that the minimum possible value for H is $H_{\min} = 1 + \alpha$ and it occurs at the singular point $x = y = 1$.

Exercise 1.6

Graphical solution of equation (1.30) for the phase trajectories to conclude the singular point is a center.

We can solve equation (1.30) graphically by considering the two functions

$$z_1 = ye^{-y} \text{ and } z_2 = \frac{e^{-\alpha x}}{x^\alpha}$$

(A) Plot z_1 versus y and z_2 versus x.
(B) Verify that for a given value of x, there are either two, one, or zero values of y such that $z_1(y) = z_2(x)$ and vice versa, for a given value of y, there are either two, one, or zero values of x such that $z_1(y) = z_2(x)$. The only one of the three scenarios depicted in figure 1.5 that has no more than two points of intersection between each orbit and each vertical line is the center scenario. We conclude that the nontrivial equilibrium is a center surrounded by a family of periodic orbits, and not a stable or unstable focus.

Exercise 1.7

Numerical solution of the dimensional Lotka–Volterra predator–prey.

A couple of hints to explore numerically the Lotka–Volterra predator–prey dimensional model:

1. There are four parameters to choose a, b, c, d. The linear coefficients for the prey and the predator, a and d, respectively, should be chosen between 1 and 10 and $a < d$ (try different values and see which one convinces you most).
2. You can use some ODE solver package, for example the MATLAB ODE functions.

Exercise 1.8

Numerical solution of the Lotka–Volterra predator–prey non dimensional model.

By a change of variables $x = (c/d)N$ and $y = (b/a)P$, the Lotka–Volterra predator–prey equations can be rewritten in terms of a single parameter $\alpha = d/a$.

(A) Solve this system of equations for different initial conditions. (You can use some ODE solver package or write your own script implementing Runge–Kutta method.)

(B) Graph the vector diagram (the vector field at each point has by components dx/dt and dy/dt) in the phase plane x–y.

Exercise 1.9

Lynx and hares.

Assume initial populations of 100 lynx and 5000 hares and you want to predict what will happen to them in the next 10 years. Write a program in MATLAB to solve the corresponding Lotka–Volterra differential equations.

Exercise 1.10

Realistic Lotka–Volterra predator–prey model.

(a) Show that a simple inclusion of density-dependence in the prey population replacing the prey equation by $\frac{dN}{dt} = r N(1 - \frac{N}{\mathcal{K}}) - cNP$ is enough to shift the behavior of the model from neutral stability to local stability about the equilibrium point.

(b) Now modify both equations by

$$\frac{dN}{dt} = r N\left(1 - \frac{N}{\mathcal{K}}\right) - c\frac{N^2}{N^2 + k^2}P$$

$$\frac{dP}{dt} = \beta c\frac{N}{N^2 + k^2}P - dP$$

Solve this system of equations for $r = 0.02$, $c = 6.2 \times 10^{-4}$, $k = 2.3$ and $\beta = 81$ (in some appropriate system of units) and show that there appear stable *limit cycle* oscillations.

Exercise 1.11

Holling–Tanner model.

Solve the Holling–Tanner model (Tanner 1975)

$$\frac{dN}{dt} = r N\left(1 - \frac{N}{\mathcal{K}}\right) - \frac{cN}{N + k}P$$

$$\frac{dP}{dt} = sP\left(1 - \eta\frac{P}{N}\right).$$

with parameters given by $r = 1$, $\mathcal{K} = 7$, $c = 6/7$, $k = 1$, $s = 0.2$, $\eta = 0.5$ and reproduce the figure 1.10.

Exercise 1.12

From one second order differential equation to two first order differential equations.

The equation governing the dynamics of a mass m attached to a linear spring of constant k is the second order equation $md^2x/dt^2 = -kx$ for small displacements x with respect to the equilibrium position (when the spring is neither compressed nor stretched). Introducing the new variable $y = dx/dt$ write the two-dimensional system of first order equations for the variables x and y.

Exercise 1.13

Lotka–Volterra competition (LVC) model for two species

The Lotka–Volterra model for competition between 2 species is given by equation (1.42).

   (A) Check that this system has the four equilibria of equations (1.45a)–(1.45d).
   (B) Write a script in MATLAB or Fortran or R, etc, to solve the system of two LVC equations.
   (C) Graph for $\mathcal{K}_1 = \mathcal{K}_2 = 10$, $\alpha_{12} = \alpha_{21} = 0.5$ the trajectories of the system in the phase plane X_1–X_2 starting from different initial conditions along with the velocity field.
   (D) Repeat (C) for $\mathcal{K}_1 = \mathcal{K}_2 = 10$, $\alpha_{12} = \alpha_{21} = 2$. What difference do you find with respect to (C) and how do you explain it?

Exercise 1.14

Non dimensional Lotka–Volterra competition (LVC) model for two species

Check that the LVC system can be re-written in terms of non dimensional variables as:

$$\frac{dy_1(\tau)}{d\tau} = y_1(\tau)(1 - y_1(\tau) + a_{12}y_2(\tau)), \qquad (1.57a)$$

$$\frac{dy_2(\tau)}{d\tau} = \rho y_2(\tau)(1 - y_1(\tau) + a_{12}y_2(\tau)), \qquad (1.57b)$$

where $y_i = N_i/\mathcal{K}_i$, $\tau = \tau_1 t$, $\rho = \tau_1/\tau_2$, and the a_{ij} denote the interspecific interaction coefficients in terms of these relative yields, defined as $a_{ij} = \alpha_{ij} \mathcal{K}_j/\mathcal{K}_i$.

Exercise 1.15

Stability of the coexistence equilibria for two mutualist species.
   (A) Evaluate the Jacobian matrix at the coexistence equilibrium of two mutualist species $\mathbf{J}_{\text{coex}}$.
   (B) The sign of the trace $\text{tr}(\mathbf{J}_{\text{coex}})$ and of the determinant $\det(\mathbf{J}_{\text{coex}})$ of this matrix allow to determine the stability of the equilibrium (see appendix I): for stability, the trace must be negative and the determinant positive. Compute $\text{tr}(\mathbf{J}_{\text{coex}})$ and $\det(\mathbf{J}_{\text{coex}})$.

(C) Show that for the weak facultative–facultative mutualism the coexistence equilibrium is a stable node and that for the strong obligate–obligate mutualism the coexistence equilibrium is a semistable saddle-node.

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