

## Linear models in social processes: the case of two interacting populations

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### Introduction

After having presented, in the paragraphs above, several versions of one of the simplest and most important models in mathematical physics, the model of the oscillator, which has served as a basis for developments and extensions into other sectors, we will now look at another example of modelling that has become a classic theme in social science: the case of a system of two interacting populations.

A number of different theories have been adopted in the approach to this subject which have given rise to a numerous family of models. In general these are models that are essentially of theoretical interest: they do not represent anything more than an initial attempt to model extremely complex phenomena such as social ones (in this context, naturally, the term social is intended in a broad sense, referring to any group of individuals, identifiable according to certain parameters, that interact with another group of individuals).

The simplest hypothesis on which a model can be formed is that in which the two populations interact with each other in a manner that can be expressed in a purely linear form; this hypothesis, however, is unrealistic, as we have already pointed out several times for other types of linear models. The linear model of two populations interacting with each other that we will illustrate in this part of the book, constitutes a very schematic example of how an extremely simplified mathematical model can be constructed to describe phenomenologies that belong to sciences that, at least in the past, have been little mathematized, and of how mathematical techniques developed in certain contexts (differential equations in mathematical physics) can be usefully transferred to other environments.

In the picture that we will be illustrating, we will not enter into the mathematical details; for a more in-depth exploration of the technical

aspects, we recommend the reader consult specific literature on the topic of differential equations and dynamics systems, such as for example Zeldovich and Myřkis (1976); Elsgolts (1977); Jordan and Smith (1977); Bender and Orszag (1978); Arnold (1983, 1992); Beltrami (1987); Anosov and Arnold (1988); Perko (1991); Moon (1992); Epstein (1997); Bellomo and Preziosi (1995); Hannon and Ruth (1997ab); Riganti (2000).

### The linear model of two interacting populations

Let us consider two populations  $P_1$  and  $P_2$  evolving over time; the number of members of  $P_1$  and  $P_2$  are respectively  $n_1(t)$  and  $n_2(t)$ . The two populations interact with each other in a linear manner, that is to say in such a way that the instantaneous speeds of change of  $n_1(t)$  and  $n_2(t)$ , i.e. their first derivatives with respect to time,  $\dot{n}_1(t)$  and  $\dot{n}_2(t)$ , are directly proportional to a linear combination of the same values of  $n_1(t)$  and  $n_2(t)$ . For the sake of clarity, imagine the case of two populations that collaborate for their reciprocal development in the presence of unlimited natural resources. We can therefore deduce that the higher the number of individuals in each population the faster the growth of said population.

Let us now assume that the speed of growth of population  $P_1$ , indicated by  $\dot{n}_1(t)$ , is proportional to the number of individuals  $n_1$  of the same population, through coefficient  $k_{11}$ , and also to the number of individuals  $n_2$  of the other population, through coefficient  $k_{12}$ . In other words, we assume that the speed of growth of  $P_1$  is given by a linear combination of the numbers of individuals of  $P_1$  and  $P_2$ . The same is valid for  $P_2$ . In formulae, this translates into the following system of first order homogeneous linear differential equations with constant coefficients:

$$\begin{cases} \dot{n}_1(t) = k_{11}n_1(t) + k_{12}n_2(t) \\ \dot{n}_2(t) = k_{21}n_1(t) + k_{22}n_2(t) \end{cases} \quad (11.1)$$

The (real) values of the coefficients  $k_{ij}$  of the linear combination in the second member determine the contribution that *each* of the two populations, individually, makes to the speed of growth of *each* population. The values of coefficients  $k_{ij}$ , therefore, express the reciprocal relationship between the growth (or decline) of the two populations.

Depending on the sign of each of the coefficients  $k_{ij}$ , we have a constructive action if  $k_{ij} > 0$ , or destructive action if  $k_{ij} < 0$ . More specifically,  $k_{12}$ , in the first of the equations (11.1), and  $k_{21}$ , in the second of the equations (11.1), relate the speed of growth of a population to the number of indi-

viduals in the other. For example, a positive value of  $k_{12}$  indicates the positive contribution by  $P_2$  to the speed of growth of  $P_1$ , in the sense that the higher the number of individuals in  $P_2$ , the faster population  $P_1$  grows. Coefficients  $k_{12}$  and  $k_{21}$ , taken separately, therefore represent the effect of the cooperation (if both are positive) or of the competition (if both are negative), on  $P_1$  by  $P_2$  and on  $P_2$  by  $P_1$  respectively, or of the parasitism of a population on another (if  $k_{12}$  and  $k_{21}$  have opposite signs).

The coefficient  $k_{11}$  in the first of the equations (11.1) and the coefficient  $k_{22}$  in the second of the equations (11.1) indicate the effect of the number of individuals on the speed of growth of the population to which they belong. Therefore, if  $k_{11} > 0$ , population  $P_1$  sustains itself and grows exponentially (à la Malthus), for example following an increasing amount of reproductive activity of the number of individuals  $n_1$  of population  $P_1$ ; if on the other hand  $k_{11} < 0$ , the speed of growth of  $P_1$  decreases in proportion to the growth of the number of individuals  $n_1$  in population  $P_1$ , for example due to the effect of internal competition within population  $P_1$ , caused by a lack of food resources (overpopulation crises).

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### Some qualitative aspects of linear model dynamics

Without resorting to the actual integration of (11.1) (so-called quadrature), we can often form a qualitative picture of the dynamics of a system by examining the state of equilibrium of the dynamics. The understanding of the behaviour of the system in relation to states of this nature, once identified, can actually enable us to predict the general behaviour of the system in any other condition: in actual fact the system evolves by following trajectories that distance themselves from the (stationary) states of unstable equilibrium and come closer to the (stationary) states of stable equilibrium. It is as if we were studying the dynamics of a ball that is rolling on ground that has rises and depressions; more than the slopes between them, where the dynamics are obvious and easy to describe, we would be interested, in order to have a clear picture of the general dynamics, in identifying the peaks of the rises, as points of unstable equilibrium (repellers) and the bottoms of the depressions, as points of stable equilibrium (attractors).

Using the metaphor of the pendulum again, a subject that has been discussed at some length in the previous paragraphs, a point of stable equilibrium is that occupied by the pendulum in a vertical position under the pivot, while at a point of unstable equilibrium the pendulum occupies a vertical position above the pivot.

The states of equilibrium, whether stable or unstable, are therefore the fundamental references of the system's dynamics. This justifies the interest taken in their identification and in the study of the system's dynamics in the neighbourhood of the equilibrium points.

Establishing the states of equilibrium of the system of equations (11.1) is not difficult. Based on the definition of derivative, they are those in which the first derivatives  $\dot{n}_1$  and  $\dot{n}_2$  are both equal to zero (for the sake of simplicity, from now on we will not indicate the dependence of  $n_1$  and  $n_2$  on time):

$$\begin{cases} 0 = k_{11}n_1 + k_{12}n_2 \\ 0 = k_{21}n_1 + k_{22}n_2 \end{cases} \quad (11.1')$$

Excluding the trivial case in which all the  $k_{ij}$  are null, the *only* solution of the system is given by  $n_1 = n_2 = 0$ , which thus identifies the *only* point of equilibrium of the linear model (11.1); this is the situation in which the populations are 'empty', i.e. they contain no individuals. The question that we now ask ourselves is: how do the dynamics of the two populations behave with respect to the point of coordinates  $n_1 = n_2 = 0$ ? Do the evolutions of  $P_1$  and  $P_2$ , tend towards extinction (point of stable equilibrium, attractor point) or towards unlimited growth (point of unstable equilibrium, repeller point)? We observe that, as  $n_1 = n_2 = 0$ , the *only* state of equilibrium of the linear model, we cannot have the extinction of only one of the populations: in fact if we assume that  $n_1 = 0$  and  $\dot{n}_1 = 0$ , we see that equation (11.1) gives  $n_2 = 0$  and  $\dot{n}_2 = 0$ .

Before discussing the solution of system (11.1), we need to make another observation: we are attempting to find a link between the numbers  $n_1$  and  $n_2$  of the individuals of  $P_1$  and  $P_2$ , starting from (11.1), by eliminating time from it; the function that we obtain will be the orbit of the system of the two populations in the phase space. Eliminating time from the two derivatives in equations (11.1), we obtain, after several steps:

$$\frac{dn_2}{dn_1} = \frac{k_{21}n_1 + k_{22}n_2}{k_{11}n_1 + k_{12}n_2} \quad (11.2)$$

Equation (11.2) illustrates, point by point, the position of the straight line tangent to the curve, and therefore the direction of the system's orbit.<sup>38</sup> Equation (11.2), in other words, shows what the *instantaneous* variation of

<sup>38</sup> To be thorough, together with (11.2) we should also consider the inverse, i.e. the derivative of  $n_1$  with respect to  $n_2$ :

the number of individuals of  $P_2$  is with respect to that of the number of individuals of  $P_1$ , whereas in (11.1) the instantaneous variations of the number of individuals of  $P_1$  and  $P_2$  with respect to time, were considered separately.

Equation (11.2) can be calculated only if  $n_1 \neq 0$  and  $n_2 \neq 0$ . The point of coordinates  $n_1 = 0$  and  $n_2 = 0$ , in which the derivative (11.2) does not exist, is called the *singular point*. But  $n_1 = n_2 = 0$  are also the only values that make both the derivatives of (11.1) equal to zero, which leads us to identify the states of equilibrium of model (11.1) with its singular points (this happens for any system, not just linear ones), and, in practice, to turn our attention to the study of solutions of the system of equations (11.1) in the neighbourhood of the only singular point.<sup>39</sup> We can claim, using a paragon that is slightly forced, but serves to clarify the situation, that the singular points of an equation are a bit like the points of support that hold a suspended chain: they determine the general form of the chain (the orbit in the phase space); what we are particularly interested in is studying the location of the supporting points, because they determine the form that the chain takes when suspended between one point and another.

In the discussion that follows in this chapter, we will turn our attention towards the study of the solutions of the system of equations (11.1) in a neighbourhood of the only singular point. We would like to state now that variables  $n_1$  and  $n_2$  should be understood in a general sense, not limiting ourselves to attributing only the meaning of the number of individuals of a populations in its strictest sense to them, but assuming that they can also have negative values.

$$\frac{dn_1}{dn_2} = \frac{k_{11}n_1 + k_{12}n_2}{k_{21}n_1 + k_{22}n_2} \quad (11.2')$$

The existence of (11.2) alone, in fact, is not sufficient, for example, to describe closed orbits, in which there are at least two points in which the curve has a vertical tangent. The existence of (11.2'), together with (11.2), guarantees that all points of the curve can be described using a formula that links  $n_1$  to  $n_2$ , and that the curve is continuous and has a unique tangent at any point.

<sup>39</sup> To be precise, we note that at the singular points of a differential equation, the conditions set by the well-know theorem of the existence and uniqueness of the solutions of a differential equation are not satisfied, conditions that, furthermore, are sufficient but not necessary. Therefore, it *could* occur, as we will see in the discussion that follows in this chapter, that more than one (from two to infinity) trajectory of the system's dynamics passes through the singular points. This means, for example, that the system evolves towards the same final state of stable equilibrium, starting from any point on the phase plane, following different orbits, as happens with a damped pendulum that tends to stop, regardless of the initial oscillation amplitude.

### The solutions of the linear model

A discussion, even if not complete nor rigorous, of the solutions of system (11.1) is useful because it enables us to highlight general characteristics and elements that can help us better understand certain aspects of the dynamics generated by more elaborate models. Some aspects of our discussion can be generalized, without making too many changes, to linear models with more than two interacting populations, and also, at least in part, and more or less along the same lines, to nonlinear models (which is actually much more interesting).

The theory of differential equations shows that the solutions of the system of linear equations (11.1) are made up of linear combinations of exponentials such as:

$$\begin{cases} n_1 = \alpha_1 e^{\beta_1 t} + \alpha_2 e^{\beta_2 t} \\ n_2 = \alpha_3 e^{\beta_1 t} + \alpha_4 e^{\beta_2 t} \end{cases} \quad (11.3)$$

In order to understand the evolutive dynamics of the two populations, the values of  $\beta_1$  and  $\beta_2$  are particularly important, because they determine the *nature* of the singular point: specifically its stability or instability characteristics. In fact, depending on whether the exponentials are real and increasing or real and decreasing or complex, we have, as we will see, a situation in which  $P_1$  and  $P_2$  distance themselves from a condition of equilibrium (instability) or tend towards a state of asymptotic equilibrium (stability) or make periodic oscillations.

The values of the coefficients  $\alpha$  of (11.3) depend on the two integration constants and are less important than the values of  $\beta_1$  and  $\beta_2$ . For now we will limit ourselves to observing that it can be demonstrated how, in reality, to define the dynamics of a system in the neighbourhood of the singular point we do not need to establish four independent coefficients  $\alpha$ , because it is sufficient to determine the ratios  $\alpha_1/\alpha_3$  and  $\alpha_2/\alpha_4$ , once  $\beta_1$  and  $\beta_2$  have been established, and therefore the nature of the singular point has been established.

The theory of differential equations shows that coefficients  $\beta_1$  and  $\beta_2$  can be found by solving a simple second degree algebraic equation, called the characteristic equation of (11.1), that can be written using the coefficients of the same (11.1):

$$\beta^2 - (k_{11} + k_{22})\beta + (k_{11}k_{22} - k_{12}k_{21}) = 0 \quad (11.4)$$

Now we need to examine the different cases that the signs of the coefficients  $k_{ij}$  of (11.1) give rise to. Depending on the signs of the  $k_{ij}$ ,  $\beta_1$  and  $\beta_2$  can be real or otherwise. If they are real we can identify the cases in which  $\beta_1$  and  $\beta_2$  are negative (Case 1A), positive (Case 1B) or one positive and one negative (Case 1C). If  $\beta_1$  and  $\beta_2$  are not real, two possible cases can be identified: either  $\beta_1$  and  $\beta_2$  are imaginary conjugates ( $\text{Re } \beta_1 = \text{Re } \beta_2 = 0, \text{Im } \beta_1 = -\text{Im } \beta_2$ ) (Case 2A), or  $\beta_1$  has a real part common to  $\beta_2$ , i.e.  $\beta_1$  and  $\beta_2$  are complex conjugates ( $\text{Re } \beta_1 = \text{Re } \beta_2 \neq 0, \text{Im } \beta_1 = -\text{Im } \beta_2$ ) (Case 2B).

Firstly, however, we would like to state three properties of the second degree equations to which we will be referring in the discussion that follows; we will refer to these properties indicating them as Point 1, Point 2 and Point 3 respectively:<sup>40</sup>

*Point 1.* The coefficient of (11.4), indicated by  $-(k_{11} + k_{22})$ , is equal to the sum of the roots  $\beta_1$  and  $\beta_2$  the sign of whose real component has been changed (obviously this does not mean that the roots of the equation are necessarily  $k_{11}$  and  $k_{22}$ ).

*Point 2.* The term  $(k_{11}k_{22} - k_{12}k_{21})$  is the product of the roots  $\beta_1$  and  $\beta_2$ .

*Point 3.* The characteristic equation (11.4) has real roots  $\beta_1$  and  $\beta_2$  only if the discriminant of the coefficients, that is indicated by  $\Delta$ , is positive or nil, i.e. if it is:

$$\begin{aligned}\Delta &= (k_{11} + k_{22})^2 - 4(k_{11}k_{22} - k_{12}k_{21}) \\ &= (k_{11} - k_{22})^2 + 4k_{12}k_{21} \geq 0\end{aligned}\tag{11.5}$$

*Real roots of the characteristic equation: both populations grow or both extinguish themselves*

*Case 1A* Real negative roots:  $\beta_1 < 0, \beta_2 < 0$ .

<sup>40</sup> In basic algebra it can be demonstrated that in the second order equation (in which  $a \neq 0$ ):

$$ax^2 + bx + c = 0$$

there are the following relations between coefficients  $a, b, c$  (real or complex) and roots  $x_1$  and  $x_2$  (real or complex):

$$(-x_1) + (-x_2) = b/a \text{ and } (-x_1) \times (-x_2) = c/a$$

The characteristic equation (11.4) has real and negative roots (for Point 1) if: (1)  $k_{11}$  and  $k_{22}$  are both negative or (2) only one is, but, in absolute value, it is higher than the other; at the same time, in both cases the following must be true:  $k_{11}k_{22} - k_{12}k_{21} > 0$  (for Point 2).

Let us interpret these conditions.

In case (1),  $k_{11}$  and  $k_{22}$  both negative means that there is internal competition within each of the two populations for the exploitation of the (limited) resources: as we can see from (11.1), in fact, an increase in population  $P_1$  impacts the speed of growth of both  $P_1$  and  $P_2$  which decreases, because the derivatives  $\dot{n}_1$  and  $\dot{n}_2$ , in this case, are both negative.

In case (2), on the other hand, we have real negative roots if there is a level of competition within only one population that is so high that it compensates for any (small) self-sustainment capacity of the other population. Let us suppose, for the sake of clarity, that there is internal competition within  $P_1$ , and therefore that  $k_{11} < 0$ , while  $P_2$ , on the other hand is self-sustaining:  $k_{22} > 0$ . As long as  $k_{11}k_{22} - k_{12}k_{21} > 0$  (Point 2), the term  $-k_{12}k_{21}$  must now be positive, in order to compensate for the product  $k_{11}k_{22}$  which is negative:  $k_{12}$  and  $k_{21}$  therefore must have opposite signs. This means that one of the two populations benefits from the growth of the other, but at the same time, damages its growth.

In this case (2) we not only have  $k_{11}$  and  $k_{22}$  that indicate internal competition within a population and self-sustainment of the other, but also the interaction between  $P_1$  and  $P_2$  and that between  $P_2$  and  $P_1$ , considered globally in the product  $k_{12}k_{21}$ , represents a relationship that we can call parasitic, for example of  $P_1$  with respect to  $P_2$ . In other words, we find ourselves in a situation in which the dominant characteristic of the system is the internal competition, which, even if present in only one population, is large enough to inevitably lead *both* populations towards extinction. On the other hand, as we have already observed, in a linear system, either both populations grow or both populations extinguish themselves; there is no possibility that just one population survives over the other which completely extinguishes itself.

An example will clarify which type of system can give real negative roots. If we give the following values to the coefficients of (11.1):

$$\begin{aligned} k_{11} &= -10 \text{ (high internal competition in } P_1) \\ k_{12} &= +3 \text{ (moderate gain by } P_1 \text{ due to cooperation with } P_2) \\ k_{21} &= +2 \text{ (moderate gain by } P_2 \text{ due to cooperation with } P_1) \\ k_{22} &= -5 \text{ (high internal competition in } P_2) \end{aligned}$$



system (11.1) thus becomes:

$$\begin{cases} \dot{n}_1 = -10n_1 + 3n_2 \\ \dot{n}_2 = 2n_1 - 5n_2 \end{cases}$$

for which the characteristic equation (11.4) is:

$$\beta^2 + 15\beta + 44 = 0$$

A simple calculation shows that, in this example, the characteristic equation has the following roots:

$$\beta_1 = -4 \text{ and } \beta_2 = -11$$

The high values of the internal competition indicated by the values of  $k_{11}$  and  $k_{22}$  in this example are such that they globally exceed the benefits of the cooperation given by the positive coefficients  $k_{12}$  and  $k_{21}$ , and therefore the populations tend to extinguish themselves.

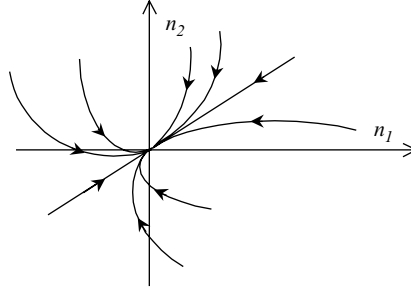
The fact that the evolution of the system leads inevitably to the extinction of both populations, regardless of their initial values, is reflected in the fact that exponents  $\beta_1$  and  $\beta_2$ , in this Case 1A, are both negative and give rise to solutions (11.3) that are linear combinations of exponentials that both decrease over time. This is a condition of asymptotically stable equilibrium, in which the origin of the axes acts as an attractor point, and is known as a *stable nodal point* (Figure 11.1).

In general, it can be demonstrated that the values of  $\beta_1$  and  $\beta_2$  determine the speed of convergence of the orbits towards the singular point, while the ratios  $\alpha_1/\alpha_3$  and  $\alpha_2/\alpha_4$  [equal to the two arbitrary constants of integration of the system (11.1)] determine the direction the orbits take to reach the stable nodal point, i.e. the inclination of the straight line in Figure 11.1 tangent to all the orbits at the singular point.

*Case 1B* Real negative roots:  $\beta_1 > 0, \beta_2 > 0$ .

The characteristic equation (11.4) has real and positive roots if the following conditions are satisfied:  $k_{11} > 0, k_{22} > 0$  (for Point 1) and, at the same time,  $k_{11}k_{22} - k_{12}k_{21} > 0$  (for Point 2).

Still with reference to (11.1), the conditions imposed by Point 1 tell us that each population, individually, grows indefinitely, as long as there are unlimited resources. The condition imposed by Point 2 tells us that the self-sustainment of both populations, considered globally in the product  $k_{11}k_{22}$ , is



**Figure 11.1** Dynamics of  $n_1$  and  $n_2$  in Case 1A: extinction of the populations, asymptotically stable equilibrium; the singular point is called a *stable nodal point*.

sufficient to compensate for any effect generated by the interaction of each population with the other, the combined value of which is represented by the product  $k_{12}k_{21}$ , regardless of the specific type of interaction between the populations. The product  $k_{11}k_{22}$  is positive like in Case 1A, but, and this is the only difference between the two cases,  $k_{11}$  and  $k_{22}$  are now both positive.

A numerical example will clarify the situation that occurs in this case. If, for example, we give the following values to the coefficients:

$$\begin{aligned} k_{11} &= +10 \text{ (high level of self-sustainment of } P_1) \\ k_{12} &= +3 \text{ (moderate gain by } P_1 \text{ due to cooperation with } P_2) \\ k_{21} &= +2 \text{ (moderate gain by } P_2 \text{ due to cooperation with } P_1) \\ k_{22} &= +5 \text{ (high level of self-sustainment of } P_2). \end{aligned}$$

system (11.1) thus becomes:

$$\begin{cases} \dot{n}_1 = 10n_1 + 3n_2 \\ \dot{n}_2 = 2n_1 + 5n_2 \end{cases}$$

for which the characteristic equation (11.4) is:

$$\beta^2 - 15\beta + 44 = 0$$

which has the following roots:

$$\beta_1 = +4 \text{ and } \beta_2 = +11$$

With all four coefficients  $k_{ij}$  positive, it is evident that the evolution can only be growth, as no term acts as a restraint to growth. Observe, however,

that in this Case 1B, growth is given above all by the self-sustainment of the two populations individually and not by their cooperation (the product of the terms of the self-sustainment is greater than the product of the terms of their interaction:  $10 \times 5 > 3 \times 2$ ). The case of growth driven mainly by cooperation, that occurs only if  $k_{11}k_{22} - k_{12}k_{21} < 0$ , is illustrated in Case 1C which follows.

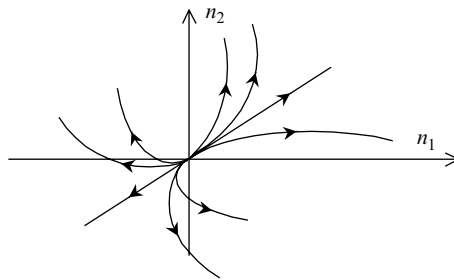
In a situation of this nature, in which all of the elements contribute to the growth of the populations, (11.3) gives  $P_1$  and  $P_2$ , which, regardless of their initial values, both tend to increase over time. This is a condition of unstable equilibrium, in which the origin of the axes acts as a repeller point, and is known as an *unstable nodal point* (Figure 11.2).

Note how the dynamics in Case 1B envisage orbits of the same form as those obtained in Case 1A, with the only difference that now the system is not directed *towards* the singular point, but distances itself *from* the singular point. Here again, the ratios  $\alpha_1/\alpha_3$  and  $\alpha_2/\alpha_4$  determine the direction the orbits take from the unstable nodal point.

**Case 1C** Real roots of opposite signs:  $\beta_1 < 0 < \beta_2$ .

The characteristic equation (11.4) has real roots of opposite signs only if the product of the roots is negative, i.e.  $k_{11}k_{22} - k_{12}k_{21} < 0$  (for Point 2). This occurs only if the product  $k_{12}k_{21}$ , which represents the combined effect of the interaction between  $P_1$  and  $P_2$ , is positive and is greater than the product  $k_{11}k_{22}$ , which represents the combined effect of the self-sustainment or of the internal competition of both  $P_1$  and  $P_2$ .

A situation of this type may arise if there is a very high level of cooperation between the two populations, in which each of them benefits considerably from its interaction with the other ( $k_{12} > 0$ ,  $k_{21} > 0$ ), so much so



**Figure 11.2** Dynamics of  $n_1$  and  $n_2$  in Case 1B: unlimited growth of the populations, unstable equilibrium; the singular point is called an *unstable nodal point*.

that the cooperation becomes the dominant element at the origin of the system's dynamics. The benefit brought by cooperation, in this case, is such that it exceeds the contribution to a population's speed of growth generated by the number of individuals in the same, regardless of its type and regardless of the fact that this contribution is positive (if  $k_{11} > 0$  and  $k_{22} > 0$ , self-sustainment of the two populations), negative (if  $k_{11} < 0$  and  $k_{22} < 0$ , internal competition within the two populations), or nil.<sup>41</sup>

An example of a linear system that gives rise to a situation of this nature is obtained with the following values of the coefficients:

$$\begin{aligned} k_{11} &= +5 \text{ (moderate level of self-sustainment of } P_1) \\ k_{12} &= +9 \text{ (high gain by } P_1 \text{ due to cooperation with } P_2) \\ k_{21} &= +6 \text{ (moderate gain by } P_2 \text{ due to cooperation with } P_1) \\ k_{22} &= +2 \text{ (low level of self-sustainment of } P_2). \end{aligned}$$

The system thus becomes:

$$\begin{cases} \dot{n}_1 = 5n_1 + 9n_2 \\ \dot{n}_2 = 6n_1 + 2n_2 \end{cases}$$

for which the characteristic equation (11.4) is:

$$\beta^2 - 7\beta - 44 = 0$$

which has the following roots:

$$\beta_1 = -4 \text{ and } \beta_2 = +11$$

In the above example, the roots are real, because the effect of the interaction between the two populations  $P_1$  and  $P_2$  is positive ( $9 \times 6 > 0$ ), but the most important aspect is that the given effect of the interaction between  $P_1$  and  $P_2$  exceeds the effect of the self-sustainment of the two populations ( $9 \times 6 > 5 \times 2$ ), i.e. the overall effect of the cooperation is greater than the overall effect of the self-sustainment. This latter aspect is what really

<sup>41</sup> From an algebraic point of view, if we want to be thorough, the situation illustrated in the text is not the only one that can give two real values with opposite signs for  $\beta_1$  and  $\beta_2$ . For example, the same result could be achieved by changing the signs of all four  $k$  coefficients with respect to those described in the text. We have limited ourselves to describing the situation indicated, because its interpretation is the most immediate in the terms that we have established, i.e. the application of the model to population dynamics, and we will ignore the other situations whose interpretation is less immediate, and whose significance is almost exclusively mathematical.

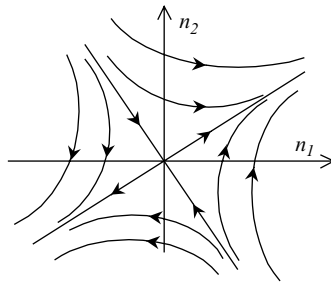
distinguishes Case 1C with respect to Case 1B: both cases involve the growth of the two populations, but in Case 1B this is the result of self-sustainment, while in Case 1C, the cooperation between the two populations is what ‘drives’ the growth of both.

In Case 1C, the solutions (11.3) of the linear model (11.1) are a linear combination of one increasing exponential and one decreasing exponential. The singular point at the origin of the axes is now an unstable point, but is a different type from that of Case 1B; it is called a *saddle point* (Figure 11.3).

It can be demonstrated that there is *one* direction, namely one *straight line*, along which the saddle point acts as if it were an attractor, and *another straight line* along which the instability, i.e. the ‘force’ with which the saddle point repels the system, is greatest. The two straight lines [two singular integrals of system (11.1)], are illustrated in Figure 11.3, and their equations are respectively:

$$n_2 = \frac{\alpha_1}{\alpha_3} n_1 \quad \text{and} \quad n_2 = \frac{\alpha_2}{\alpha_4} n_1$$

The first straight line indicates the *only* direction in which the linear system evolves over time following an orbit that brings it *towards* the saddle point, which is seen by the system (and only in this case) as a point of stable equilibrium and not as a repeller point. In all other directions, the saddle point is a point of unstable equilibrium. In particular, in the direction indicated by the second straight line, the ‘force’ with which the saddle point repels the orbit, and consequently the speed with which the system travels along the same orbit, is greater with respect to all other directions (see Figure 11.3). This second straight line is of particular interest to us because it is an asymptote for the system’s orbits. In a certain sense, we can say that this straight line ‘attracts’ all of the system’s orbits, which, after a



**Figure 11.3** Dynamics of  $n_1$  and  $n_2$  in Case 1C: unstable equilibrium; the singular point is called a *saddle point*.

sufficient period of time, end up as being approximated by this same straight line. The first straight line, on the other hand, the one that leads towards the saddle point, also an asymptote for the orbits, from a geometrical standpoint, acts in the opposite way to the second straight line in terms of dynamics: it repels the orbits that arrive in its direction, as shown in Figure 11.3. Both an unstable nodal point and a saddle point (with the exception of one direction), therefore, ‘repel’, so to speak, the orbits, but one saddle point differs from an unstable nodal point due to the fact that the effect of the repulsion that it exercises on them varies according to the direction, i.e. according to the orbit that follows the dynamics of the system.

In summary, the values of the ratios  $\alpha_1/\alpha_3$  and  $\alpha_2/\alpha_4$  determine the two asymptotes, while the values of  $\beta_1$  and  $\beta_2$  (one positive, the other negative) determine the specific curve that these two asymptotes have.<sup>42</sup>

Lastly, it can be shown that the straight line that drives the orbits away from the saddle point is more inclined towards axis  $n_1$  or axis  $n_2$ , the higher the value of the self-sustainment, respectively, of  $P_1$  or  $P_2$  (i.e. the larger  $k_{11}$  is with respect to  $k_{22}$ , or respectively, the larger  $k_{22}$  is with respect to  $k_{11}$ ). This restates the fact that the population that has the highest level of self-sustainment determines the general dynamics of the system, drawing, so to speak, the growth of the other population into its dynamics, which, over time, ends up growing at a speed that is directly proportional to that of the ‘stronger’ population in terms of self-sustainment. In a certain sense, therefore, it is as if the growth of the population of the two that has the higher self-sustainment coefficient ‘draws’ the growth of the other.

We will now examine Cases 2A and 2B whose characteristic equation (11.4) has roots  $\beta_1$  and  $\beta_2$ , which are not real.

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### **Complex conjugate roots of the characteristic equation: the values of the two populations fluctuate**

*Case 2A* Imaginary conjugate roots  $\beta_1$  and  $\beta_2$ :  $\text{Re}\beta_1 = \text{Re}\beta_2 = 0$ .

The characteristic equation (11.4) has imaginary conjugate roots if two conditions are satisfied simultaneously. The first condition is that the dis-

<sup>42</sup> The understanding in mathematical terms of this unique case of stability is simple: if we assume that  $\alpha_2 = \alpha_4 = 0$ , in (11.3) only two negative exponentials remain (remember that  $\beta_1$  is the negative root and  $\beta_2$  is the positive one). In the same way, by assuming  $\alpha_1 = \alpha_3 = 0$ , we have the condition of maximum instability of the singular point, because only the positive exponentials remain. The two straight lines are asymptotes common to all of the orbits characterized by the same values for ratios  $\alpha_1/\alpha_3$  and  $\alpha_2/\alpha_4$ .

criminant  $\Delta$  of the characteristic equation (11.4) is negative; in this case, instead of (11.5) of Point 3, we have:

$$\Delta = (k_{11} - k_{22})^2 + 4k_{12}k_{21} < 0 \quad (11.6)$$

Equation (11.6) dictates that  $4k_{12}k_{21}$  is negative and that  $(k_{11} - k_{22})^2$ , which is positive because it is a square, is not large enough to give a positive result if summed to  $4k_{12}k_{21}$ . This implies that  $k_{12}$  and  $k_{21}$  must have opposite signs, and thus that the interaction between  $P_1$  and  $P_2$  is advantageous to only one of the populations and not to the other.

The second condition that must be satisfied is that the sum of the roots  $\beta_1$  and  $\beta_2$  is nil, which, for Point 1, can occur in two cases: (1)  $k_{11} = k_{22} = 0$ , i.e. the two populations are not characterized by self-sustainment nor by internal competition; or (2)  $k_{11} = -k_{22}$ , i.e. the intensity, so to speak, of the effect of the self-sustainment of a population is equal and opposite to that of the effect of the internal competition of the other population.

To clarify, let us suppose, for example, that  $P_2$  is the population that benefits from its interaction with  $P_1$  ( $k_{21} > 0$ ), while, on the contrary,  $P_1$  is the population that is damaged by its interaction with  $P_2$  ( $k_{12} < 0$ ), to the extent that product  $k_{12}k_{21}$  is negative, and that  $P_2$  is the population characterized by internal competition ( $k_{22} < 0$ ), while  $P_1$  is self-sustaining ( $k_{11} > 0$ ).<sup>43</sup> The situation that the values of the coefficients generate is that typical of a relationship that, in biology, is defined as predation of population  $P_2$  over  $P_1$ , or also as parasitism of  $P_2$  towards  $P_1$ .

It is clear that in a prey–predator relationship, the extinction of the prey population  $P_1$  due to an excess of predation, would also lead to the extinction of the predator population  $P_2$ , as the growth of the number of predators depends, to a large extent, on coefficient  $k_{21}$ , namely on the number of available prey. The prey, for their part, would tend to multiply in an unlimited manner, in the absence of internal competition, if the predators did not intervene and reduce their numbers. A dynamic is thus established, according to which the number of prey decreases due to the action of the predators ( $k_{12} < 0$ ), but when such reduction becomes excessive, even the predators suffer due to the limited amount of food resources, which creates internal competition within the population and hinders its growth ( $k_{22} < 0$ ). A restricted number of predators, however, would leave the prey free to multiply, as the latter do not have any internal competition

<sup>43</sup> Our observations in note 41 on p. 82 are also valid in this case; as well as the situation that we have described here, whose interpretation is the most immediate, there are other configurations of the coefficients  $k$  that can give imaginary conjugate roots  $\beta_1$  and  $\beta_2$  but which are of less interest in this context.