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STATISTICAL

Stochastic Approach to Population Dynamics

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Abstract
We analyze a stochastic approach to population dynamics in which the number of individuals in each class is treated as a stochastic variable. The description of the dynamics is based on the Fokker-Planck equation from which we show that the time evolution of the average number of individuals are identified as the differential equations of the deterministic approach. We also show by calculating the time correlation function that the stochastic fluctuations as well as the stochastic oscillations in the number of individuals are proportional to the square root of the whole size of the population. We have applied the present approach to predator-prey or food chain models with three and four biological species and shown that both models display stochastic oscillations depending on the constant rates. The stochastic approach predicts extinction of species by the stochastic fluctuations in populations with small number of individuals.

Keywords Population dynamics · Stochastic dynamics · Stochastic oscillations

1 Introduction

Population dynamics is concerned with the time behavior in the number of individuals of a community that distinguish among themselves by belonging to different classes. In population biology the classes are the biological species. In the spreading of an infectious disease among humans, the classes are the conditions of a person with respect to the disease. In demography, the classes are identified with the age groups of persons. As a result of the action between individuals, or due to an external action involving one individual, or spontaneously, they may change classes, and the number of individual in each class may vary in time.

The theoretical studies of population dynamics [1–15] are divided into the deterministic and the stochastic approaches. The deterministic approach employs the ordinary differential equations of the first order in time. The variables are the number of individuals of each class and for each class there correspond an ordinary differential equation. These equations can be understood as analogous to the rate equations of the chemical kinetics. The individuals correspond to the molecules, the classes corresponds to the chemical species, and the processes leading to the change of classes correspond to the chemical reactions.

The deterministic approach describes successfully the time evolution of populations as long as we understand their predictions as the averages in the number of individuals of each class. This approach however does not describe the random fluctuations occurring in the number of individuals of a real population. In this sense a more adequate approach is to treat the number of individuals of a certain class as stochastic variables. Stochastic approaches of this type were developed in the context of epidemic spreading by Bartlett [16, 17] and by Bailey [18, 19].

Here, we present the stochastic approach to population dynamics which is a development of the stochastic approach to epidemic spreading presented previously by the authors [20], but which is further extended to show results specific of population dynamics. The point of depart is the master equation [21] that governs the probability distribution associated to the numbers of individuals. The master equation is then transformed into a Fokker-Planck equation which in turn can be solved.

From the solution of the Fokker-Planck equation we show that the equations for the average in the number of individuals are identified as the ordinary differential equations of the deterministic approach. The amplitude of the fluctuations in the number of individuals are shown to be proportional to the square root of the total number of individuals.

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The stochastic oscillation in the number of individuals are also shown to be proportional to the square root of the total number of individuals. One important consequence of the stochastic fluctuation is the extinction of species with a small population. If the number of individuals of a species is small, the fluctuations will be relatively great and may result in the vanishing in the number of individuals of this species.

Other stochastic approaches to population dynamics have been developed which are appropriate to describe the spatial structure of populations [22]. In these spatial stochastic models, a stochastic variable is assigned to each individual which lives in a site a lattice. The possible values of the stochastic variables are those associated to each one of the classes of individuals. We may thus say that a certain population model can be presented in three versions which correspond to the deterministic approach, the ordinary stochastic approach, which is the object of the present study, and the spatial stochastic approach.

2 Logistic Curve

2.1 Verhulst

The rapid growth of the human population in the eighteenth century lead Malthus in 1798 to the observation that the population, left by itself, would increase in a geometric ratio, which was a concern as the means of subsistence increased only in the arithmetic ratio [23]. The geometric increase of population was not completely new and was known by Euler but it was Malthus who gave it publicity [13]. In a treatise of 1748 [24], Euler exemplified the geometric progression by the population growth of a province. If initially the population is n, then in m years it will be $n(1+a)^m$ where $a = 1/30$. Euler chose $n = 100000$ and $m = 100$ years, and found 2654874.

The geometric increase of the population was reasserted by Quetelet in his studies on social physics of 1835 [25]. He observed with Malthus that the geometric increase of the population occurs if there are no obstacles to its development such as the shortage of means of subsistence. He then proposed that the resistance to the development is proportional to the square of the rate at which the population tends to grow. However, Quetelet took almost no advantage of these hypotheses and did not express them on analytical form [26].

In 1838, Verhulst used differential calculus to express the Malthus law as the equation $dp/dt = mp$, where p is the population, and argued that the population growth should in fact be retarded in view of a resistance to an infinite development of the population [27]. To describe the delay in the rate of the population growth, he subtracted from mp a function of p which he chose to be proportional to p squared, and wrote the differential equation for p as

$$\frac{dp}{dt} = mp - np^2. \tag{1}$$

This equation was solved by Verhulst and the solution is

$$p = \frac{mp_0}{np_0 + (m - np_0)e^{-mt}}, \tag{2}$$

where p_0 is the value of p at $t = 0$. The function $p(t)$, given by (2), has a sigmoid shape and was named logistic (*logistique*) curve by Verhulst in 1845 [28].

The French *logistique* has two meanings coming from the two etymological origins of the word. One of them is related to reasoning or calculus and its origin is the Greek *logos*. The other meaning has to do with the handling of an operation and comes from the same root as the French *logement*, which means lodging. It seems that Verhulst had in mind the first meaning of *logistique*.

2.2 Deschamps

The differential Eq. (1) and the logistic curve (2) also appeared independently in contexts of population growth other than human. They were independently proposed by Deschamps in a paper of 1902 [29] where he used differential calculus to describe the time evolution of cellular multiplication. If the nutrient is constant the increase in the quantity s of cellular substance is $ds = ksdt$ where k is the nutrient coefficient. If the nutrients are not renewed, Deschamps proposes the form $ds = kmsdt$, where m is the existing amount of nutrients. He then assumes that the decrease in the nutrients is proportional to the increase in the cellular substance, writing $kdm = -k'ds$.

The integration of this equation gives $km = c - k's$, where $c = km_0 + k's_0$, which replaced in $ds = ksdt$ gives

$$\frac{ds}{dt} = s(c - k's). \tag{3}$$

The integration of this equation is

$$s = \frac{cs_0e^{ct}}{km_0 + k's_0e^{ct}}, \tag{4}$$

which gives s as a function of time. This function is the same as that found by Verhulst.

2.3 Robertson

In 1908, Robertson proposed to apply the concepts of autocatalysis to describe the growth of an organism [30]. Based on the ideas developed by Loeb, he considered that the mass of nuclear material increases from the nuclear mass already formed, and that the nucleus itself acts as a catalyst in the synthesis of nuclei. Considering that the growth process as an autocatalytic reaction, Robertson wrote the equation for the time evolution of the amount of material x as

$$\frac{dx}{dt} = k_1x(a-x) - k_2x^2, \tag{5}$$

where k_1, k_2 and b are constants. The firs term on the right-hand side represents the rate of the autocatalytic reaction and the second term the rate of its reverse.

By a change of the constants, the rate equation can be written as

$$\frac{dx}{dt} = kx(A-x), \tag{6}$$

that is, the rate of the transformation is proportional the present amount of material and to the material that has already been transformed.

The integration of Eq. (6) gives

$$\ln\frac{x}{A-x} = Akt + C, \tag{7}$$

where C is a constant of integration. We see that this equation is equivalent to

$$x = \frac{A}{1+e^{-Akt-C}}, \tag{8}$$

which is the same as that found by Verhulst.

Robertson applied his equation to the growth of several types of individuals, which include white rat, man, frog, and *Cucurbita pepo* as well as various parts of the body.

2.4 McKendrick and Pai

The differential Eq. (1) was also proposed independently by McKendrick and Pai in 1911 in a paper concerning the multiplication of micro-organisms [31]. To reach the differential equation for the number y of micro-organisms they argued as follows. If the nutrients are unlimited, the micro-organisms growths in a geometric progression, which is represented by the equation $dy/dt = by$, which means that the rate of multiplication is proportional to y. If the nutrients are limited as occurring in a test-tube, the rate of multiplication decreases in time and the growth is no longer geometric. This is so because the amount of nutrients decreases in time as the number micro-organisms increases. McKendrick and Pai assumes that this decrease is proportional to $a - y$ and that the rate is also proportional to the decrease in the nutrients. The resulting equation from these reasoning is

$$\frac{dy}{dt} = by(a-y). \tag{9}$$

The integration of Eq. (9) gives

$$y = \frac{ay_0}{y_0 + (a-y_0)e^{-abt}}, \tag{10}$$

where y_0 is the initial number of micro-organisms, which is the same as that found by Verhulst.

2.5 Ross

In the second edition of his book on the prevention of malaria published in 1911 [32], Ross advanced the analytical study of the spreading of a infectious disease through first order differential equations. He argues that the increase in the number z of individuals affected by an infection disease in a population of p individuals is $h(p-z)$, the proportion of the unaffected which become affected per unit time. He also considered that the decrease in z is rz where r is the proportion of the affected that recover from the disease. These assumptions allowed him to write the equation

$$\frac{dz}{dt} = h(p-z) - rz. \tag{11}$$

Ross treats the more general case where the number of individuals may increase or decrease by birth, death, immigration and emigration. Here we are not considering these demographic processes, so that the population p remains constant in time.

Ross then argues that h is proportional to the number of infected individuals and writes $h = cz$ where c is a constant which he called infection rate [33]. The above equation becomes

$$\frac{dz}{dt} = cz(p-z) - rz. \tag{12}$$

The solution of this equation was obtained by Ross and is [33]

$$z = \frac{z_0a}{z_0c + (a-cz_0)e^{-at}}, \tag{13}$$

where $a = cp - r$, and x_0 is the initial fraction of infected individuals. This is again the same curve found by Verhulst.

2.6 Pearl and Reed

The Verhulst curve of human growth (2) was independently proposed by Pearl and Reed in 1920 [34] in their study of human population growth. They considered a population growing in an area of fixed limit and required that the curve be monotonic and approaching asymptotic values. Denoting by y the population and x the time, they wrote

$$y = \frac{be^{ax}}{1+ce^{ax}}, \tag{14}$$

where a, b, and c are positive constants. From (14), they obtained the rate of increase in the population,

$$\frac{dy}{dt} = \frac{ay}{b}(b - cy), \tag{15}$$

and pointed out that in this form the equation is the same a that describing an autocatalytic chemical reaction, referring to the paper of Robertson [30]. Later on Pearl recognized that the curve they found was the same as that introduced by Verhulst [35, 36].

2.7 Chemical Kinetics

The characterization of the processes involved in the growth of an organism as a chemical reaction or analogous to a chemical reaction allowed Robertson to use the theory of chemical kinetics to set up the rate Eq. (7). The rate equations describing the time evolution of chemical reactions was proposed by Guldberberg and Waage when they advanced the law of mass action in 1865 [37].

Let us suppose that a molecules of substance A and b molecules of substance B are transformed into c molecules of substance C and d molecules of substance D. According to the law of mass action the rate of the reaction is proportional to $A^a B^b$ where A and B are the concentrations of A and B, and the rate of the reverse reaction is proportional to $C^c D^d$ where C and D are the concentrations of C and D. The velocity dx/dt in which one of the substance increases is given by

$$\frac{dx}{dt} = kA^a B^b - k' C^c D^d, \tag{16}$$

where k and k' are constants.

Rate equation based on the law of mass action was used by Ostwald in 1883 in his studies on chemical dynamics of catalytic reactions [38]. He analyzed the decomposition of acetamide for which he writes the following rate equation

$$\frac{dx}{dt} = ka(b - x), \tag{17}$$

where k is a constant, a is the amount of acid, which remains unchanged, and $b - x$ is the amount of ester. Ostwald argued that in the case of weaker acids, the reaction releases a steadily amount of acid which in turn has also a decomposing effect. This effect is taken into account by adding a term to ka proportional to x. The rate equation becomes

$$\frac{dx}{dt} = (ka + \gamma x)(b - x). \tag{18}$$

The solution of the above equation is

$$(\gamma b + ka)t = \ln \frac{b(ka + \gamma x)}{ka(b - x)}. \tag{19}$$

The quantity x as a function of t has a sigmoid shape and it becomes identical with the logistic curve by a linear change of variable.

3 Lotka-Volterra Model

3.1 Lotka

In his book on physical biology of 1925, Lotka proposed that a system containing several biological species, evolves in time like a chemical system containing several chemical species [39, 40]. The components are under specific conditions such as that of area, topology, and climate. Accordingly, the growth in time of the mass X_i of the component i is given by

$$\frac{dX_i}{dt} = F_i, \tag{20}$$

where F_i is a function the components and depend parametrically on the specific conditions. Lotka calls (20) the fundamental equation of the kinetics of evolution.

The first example given by Lotka is a system of a single variable which describes the population growth, given by

$$\frac{dX}{dt} = aX + bX^2, \tag{21}$$

whose solution is

$$X = \frac{a/b}{ce^{-at} - 1}, \tag{22}$$

where c is a constant. Lotka states that this formula was applied by Pearl and Reed to the population growth. He then refers to the paper of Pearl and Reed of 1920 [34] as well as to the paper of Verhulst of 1845 [28].

Lotka treats a significant problem of the time evolution of two species in conflict. One of them is a parasite species and the other is the host species. The problem is treated by the method of kinetics. Let N_1 and N_2 be the numbers of host and parasite populations, respectively. The birth rate of a host is proportional to N_1. The birth of a parasite occurs by the laying of an egg in a host and the killing of the host. Thus the rate of the birthrate of a parasite and the deathrate of a host are proportional to $N_1 N_2$. Lastly, the deathrate of a parasite is proportional to N_2. From these results, Lotka writes the rate equations in the form

$$\frac{dN_1}{dt} = rN_1 - kN_1 N_2, \tag{23}$$

$$\frac{dN_2}{dt} = KN_1 N_2 - sN_2. \tag{24}$$

The model described by these equations were introduced by Lotka in 1920 concerning the oscillations in organic system [41, 42]. He had previously used chemical kinetics to described oscillations in chemical systems but the oscillations were found to be damped [43].

Dividing the Eq. (23) by the Eq. (24), Lotka obtains the equation [42]

$$\frac{dN_1}{dN_2} = \frac{N_1(r - kN_2)}{N_2(KN_1 - s)}, \tag{25}$$

which he integrates to obtain [42]

$$KN_1 - s\ln N_1 = r\ln N_2 - kN_2 + C. \tag{26}$$

By assigning different values to the constant of integration C, a family of closed curves are obtained.

Lotka remarks that the same rate Eqs.(23) and (24) are valid for a system of two species in which one species feeds on another species which in turn feeds on source of large scale so that the source may be considered constant.

3.2 Volterra

In a paper published in 1926, [44, 45] Volterra studied the variations on the number of individuals in animal species living together and arrived independently at the same equations found by Lotka. Later on his ideas on this subject were presented in his book published in 1931 [46]. He considers the case of two species one of which feeds on the other. Denoting by N_1 and N_2 the number of individuals of each species, Volterra writes the time variation of these numbers in the form

$$\frac{dN_1}{dt} = \beta_1 N_1 - \gamma_1 N_1 N_2, \tag{27}$$

$$\frac{dN_2}{dt} = -\beta_2 N_2 + \gamma_2 N_1 N_2. \tag{28}$$

The first term of (27) represents the increase of the first species by birth, and the first of (28) represents the decrease of the second species by death caused by lack of food. Considering that the second species feeds on the first, the first decreases by a term proportional to N_1 and N_2, which is represented by the last term of (27). Analogously, the second species increases by a similar term, which is represented by the last term of (28).

Multiplying (27) by γ_2 and (28) by γ_1 and summing up the two results one finds

$$\gamma_2\frac{dN_1}{dt} + \gamma_1\frac{dN_2}{dt} = \gamma_2\beta_1 N_1 - \gamma_1\beta_2 N_2. \tag{29}$$

Now if we multiply (27) by β_2/N_1 and (28) by β_1/N_2 one finds

$$\beta_2\frac{d\ln N_1}{dt} + \beta_1\frac{d\ln N_2}{dt} = \beta_1\gamma_2 N_1 - \beta_2\gamma_1 N_2. \tag{30}$$

Subtracting these two equations and integrating in time Volterra reached the result

$$\gamma_2 N_1 + \gamma_1 N_2 = \beta_2 \ln N_1 + \beta_1 \ln N_2 + C, \tag{31}$$

where C is a constant of integration.

3.3 Oscillations

The closed curves given by (31) or by (26) show us that N_1 and N_2 oscillates in time and that they are out of phase. Thus the Lotka-Volterra model predicts oscillations. When the perimeter of a closed curve is small it reduces to an ellipse. The ellipses in the plane N_1, N_2 have a common center A_1, A_2 given by $A_1 = \beta_2/\gamma_2$ and $A_2 = \beta_1/\gamma_1$. Defining the variables x and y by $N_1 = A_1 + x$ and $N_2 = A_2 + y$, the rate equations become

$$\frac{dx}{dt} = -\gamma_1 A_1 y, \tag{32}$$

$$\frac{dy}{dt} = \gamma_2 A_2 x, \tag{33}$$

where we have retained only the terms linear in x and y. The solution of these equations is an ellipse described by $x = x_0 \cos\omega t$ and $y = y_0 \sin\Omega t$ where $\omega = \sqrt{\beta_1\beta_2}$, and ratio of the semi-axes y_0 and x_0 is

$$\frac{y_0}{x_0} = \frac{\gamma_2}{\gamma_1}\sqrt{\frac{\beta_1}{\beta_2}}. \tag{34}$$

The period of oscillation is thus

$$T = \frac{2\pi}{\sqrt{\beta_1\,\beta_2}}. \tag{35}$$

The results above were derived by Volterra [44] and also by Lotka [39].

The analysis above shows that the Lotka-Volterra model displays oscillations whose amplitude is determined by the initial conditions and not by the parameters of the model [47]. That is, if the oscillations are perturbed, they acquire a new amplitude, a feature that is not expected to be found in real oscillations.

4 Deterministic Approach

The approach to population dynamics represented by the first order differential equations are called deterministic approach. These equations can be constructed by considering that the several processes involved in a population dynamics are analogous to the chemical reactions. The equations are then obtained by using the Guldberg-Waage law of mass action, which is considered a fundamental concept in theoretical epidemiology [5]. We have seen above that Robertson used this procedure to reach the rate Eq. (5). The rate equations developed by Kermack and McKendrick in 1927 for the spreading of an epidemic were also based on the law of mass action [48].

Let us consider a system consisting of a collection of individuals belonging to several classes or species that interact among themselves and transform in one another by one or more processes or reactions. We suppose that the individuals live in a certain space and as dynamic variables we consider the numbers of individuals of each class. Due to the processes occurring in the system, the number of individuals of each class will change in time. The equation that gives the time evolution of the number of individuals of a certain class per unit area x is assumed to be given by

$$\frac{dx}{dt} = \nu_1 r_1 + \nu_2 r_2 + \dots, \tag{36}$$

where r_i is the rate of the process i and ν_i is the change in the number of individuals by this process. The rates r_i are constructed according to the Guldberg-Waage law of mass action.

4.1 One Class of Individuals

The simplest processes that we may conceive are the creation and annihilation of and individual, which are represented by

$$O \to A, \quad A \to O, \tag{37}$$

respectively. The first process is the creation of an individual of class A and occurs with rate $k_1 a$ where k_1 is a constant and a is the density of O, considered constant. The second process is the annihilation of an individual of class A and occurs with rate $k_2 x$, where k_2 is a constant and x is the density of the individuals of class A. Taking into account that just one individual of type A is created and just one individual of type A is annihilated by these processes, the rate equation for x reads

$$\frac{dx}{dt} = k_1 a - k_2 x. \tag{38}$$

The two processes represented by (37) may also be used to describe the processes of migration. The first process O→A may represent the immigration of an individual A and the second process A→O may represent the emigration of an individual A.

The process of creation of an individual of type A by reproduction is represented by

$$\mathrm{O} + \mathrm{A} \to 2\mathrm{A}, \tag{39}$$

which is understood as an autocatalytic reaction. The rate equation for this process is

$$\frac{dx}{dt} = k_3 a x, \tag{40}$$

where k_3 is a constant and a is the density of O, considered constant. The solution of this equation gives an exponential growth, which is distinct from the arithmetic growth given by the creation process O→A.

The annihilation process

$$2\mathrm{A} \to \mathrm{O} + \mathrm{A}, \tag{41}$$

is the reverse of the creation by reproduction and occurs with rate $k_4 x^2$, where k_4 is a constant. The Verhulst equation for the population growth can be obtained by considering the two processes (39) and (41), which lead us to the rate equation

$$\frac{dx}{dt} = k_3 x - k_4 x^2. \tag{42}$$

4.2 Two Classes of Individuals

Let us consider now two types of individuals A and B and suppose that B is created from A by the autocatalytic process

$$\mathrm{A} + \mathrm{B} \to 2\mathrm{B}. \tag{43}$$

Denoting by x and y the density of A and B, respectively, the rate equations are

$$\frac{dx}{dt} = -k_1 xy, \tag{44}$$

$$\frac{dy}{dt} = k_1 xy. \tag{45}$$

From these equations it follows that $x + y$ is constant. Denoting this constant by a then $x = a - y$, which replaced in the second equation gives

$$\frac{dy}{dt} = k_1 y(a - y). \tag{46}$$

Suppose that B is created from A by the autocatalytic process (43), and that A disappears by the reverse process

$$2\mathrm{B} \rightarrow \mathrm{A} + \mathrm{B}. \tag{47}$$

In this case, the rate equations are

$$\frac{dx}{dt} = -k_1xy + k_2y^2, \tag{48}$$

$$\frac{dy}{dt} = k_1xy - k_2y^2, \tag{49}$$

where k_1 and k_2 are constants. Again $x + y$ is constant which allows us to replaced $x = a - y$ in the second equation to get

$$\frac{dy}{dt} = k_1y(a - y) - k_2y^2, \tag{50}$$

which is the Eq. (5) advanced by Robertson.

If B is created from A by the autocatalytic process (43) but B disappears through the spontaneous process

$$\mathrm{B} \rightarrow \mathrm{A}, \tag{51}$$

then the rate equations are

$$\frac{dx}{dt} = k_2y - k_1xy, \tag{52}$$

$$\frac{dy}{dt} = -k_2y + k_1xy. \tag{53}$$

Once more, the sum $x + y$ is a constant, which allows us to write $x = a - y$, and the second equation becomes

$$\frac{dy}{dt} = k_1y(a - y) - k_2y \tag{54}$$

which is the Eq. (12) advanced by Ross.

The two processes (43) and (51) can be interpreted as describing the spreading of and infectious disease on a population. The individuals of class B are the infected and those of class A are the susceptible. The autocatalytic process (43) represents the infection of A by B and the spontaneous process (51) represents the recovery of B which becomes A. For that reason this model is called susceptible-infected-susceptible (SIS) model.

In the stationary states the density of infected is

$$y = \frac{k_1a - k_2}{k_1}, \tag{55}$$

as long as $k_1a > k_2$. If $k_1a \leq k_2$, the density of infected vanishes. Thus as we increase the infection rate k_1, there is a change of behavior from a state with a population without infection to a state with a infected population.

The Lotka-Volterra model is understood as consisting of tree processes. One is the creation of individuals of type A by reproduction, represented by the process $\mathrm{O} + \mathrm{A} \rightarrow 2\mathrm{A}$, occurring with rate k_1ax. Another is the catalytic creation of individuals of type B and the simultaneous annihilation of A, represented by $\mathrm{A} + \mathrm{B} \rightarrow 2\mathrm{B}$, occurring with rate k_2xy. The third process is the spontaneous annihilation of B, represented by the process $\mathrm{B} \rightarrow \mathrm{O}$, occurring with rate k_2y. The rate equations are

$$\frac{dx}{dt} = k_1ax - k_2xy, \tag{56}$$

$$\frac{dy}{dt} = k_2xy - k_3y, \tag{57}$$

These equations are the same Eqs. (23) and (24) introduced by Lotka and Eqs. (27) and (28) introduced by Volterra.

4.3 Three Classes of Individuals

We consider now a population consisting of three classes of individuals A, B, and C, whose densities are denoted by x, y, and z, respectively. Several models can be devised. We consider first the processes leading to the model introduced by Kermack and McKendrick [48], consisting of two processes. The first is the autocatalytic creation of B from A, represented by (43) occurring with rate k_1xy. The second is the spontaneous transformation of B in to C, represented by

$$\mathrm{B} \rightarrow \mathrm{C}, \tag{58}$$

occurring with rate k_2y. The class A represent the susceptible individuals, the class B represents the infected individuals, and class C represents the recovered individuals. The model is also known as the susceptible-infected-recovered (SIR) model.

The rate equations are

$$\frac{dx}{dt} = -k_1xy, \tag{59}$$

$$\frac{dy}{dt} = k_1xy - k_2y, \tag{60}$$

$$\frac{dz}{dt} = k_2y. \tag{61}$$

From these equations we see that the sum $x + y + z = a$ is constant and we may consider only the first two equations, as z can be obtained from $z = a - x - y$. The first two equations are the equations of the model introduced by Kermack and McKendrick in 1927 [48].

Dividing the Eq. (60) by (59), we find

$$\frac{dy}{dx} = -1 + \frac{k_2}{k_1x}, \tag{62}$$

whose solution is

$$y = a - x + \frac{k_2}{k_1} \ln \frac{x}{a}, \tag{63}$$

where the constant of integration was obtained in such a way that when $x = a$ then $y = 0$. In Fig. 1 we show y as a function of x.

To obtain the value of x for large times, we must keep in mind that in this regime the infected disappear, $y = 0$, which replaced in (63) gives an equation for the stationary values of x,

$$a - x + \frac{k_2}{k_1} \ln \frac{x}{a} = 0. \tag{64}$$

When $k_1 \leq k_2/a$, the only solution is $x = a$, and the disease does not spread because the density of susceptible does not change. When $k_1 > k_2/a$, the value of stationary value of x is smaller than a, which means that the disease has spread.

In the SIR model just analyzed, the infected individuals becomes recovered and remains forever in this situation which means that they have acquired a permanent immunization. Now we suppose that they may lose immunization and become susceptible again. This process describing this situation is represented by

$$\text{C} \rightarrow \text{A}, \tag{65}$$

which occurs with rate $k_3 z$. The addition of this process turns the previous model into the susceptible-infected-recovered-susceptible (SIRS) model. The rate equations are

$$\frac{dx}{dt} = -k_1 xy + k_3 z, \tag{66}$$

$$\frac{dy}{dt} = k_1 xy - k_2 y, \tag{67}$$

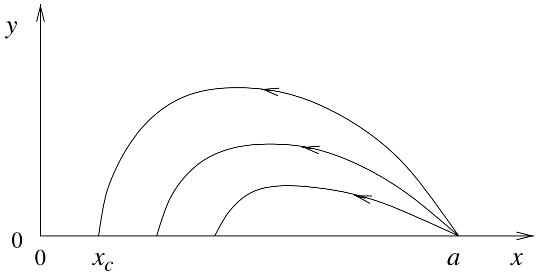

Fig. 1 SIR model. Density of infected y as a function of denstity of susceptible x for several values of $k_1 > k_2/a$, according to Eq. (63). At the initial time $x = a$ and $y = 0$. As time evolves, x and y change and eventually reaches the final value $x = x_c$ and $y = 0$. If $k_1 \leq k_2/a$ then x and y remain unchanged

$$\frac{dz}{dt} = k_2 y - k_3 z. \tag{68}$$

Again the sum $x + y + z = a$ is a constant and we may obtain z from $z = a - x - y$.

The stationary solution is either $x = 1$, $y = 0$, which is the state without spreading of disease, or

$$x = \frac{k_2}{k_1}, \quad y = \frac{(k_1 a - k_2)k_3}{(k_3 + k_2)k_1}, \tag{69}$$

which corresponds to the spread of the disease. This last solution occurs when $k_1 a > k_2$. Therefore, when k_1 increases, the disease becomes to spread at $k_1 a = k_2$.

Next we analyze a predator-prey model, similar to the Lotka-Volterra model, which was considered by Satulovsky and Tomé [49]. The individual of type A is a prey, B is a predator, and C is the food of A. It consists of three processes. One is the creation of an individual of type A by reproduction and simultaneous annihilation of an individual of type C, represented by the process C + A → 2A, occurring with rate $k_1 zx$. Another is the catalytic creation of individuals of type B and the simultaneous annihilation of A, represented by A + B → 2B, occurring with rate $k_2 xy$. The third process is the spontaneous annihilation of B and simultaneous creation of C, represented by the process B → C, occurring with rate $k_2 y$. The rate equations are

$$\frac{dx}{dt} = k_1 zx - k_2 xy, \tag{70}$$

$$\frac{dy}{dt} = k_2 xy - k_3 y, \tag{71}$$

$$\frac{dz}{dt} = k_3 y - k_1 zx. \tag{72}$$

From these equations it follows that the sum $x + y + z = a$ is constant.

One stationary solution of these equation is $x = a$, $y = 0$, which occurs when $k_2 \leq k_3/a$, and corresponds to a state deprived of predator. Another is

$$x = \frac{k_3}{k_2}, \quad y = \frac{(k_2 a - k_3)k_1}{(k_1 + k_2)k_2}, \tag{73}$$

which occurs when $k_2 > k_3/a$, and corresponds to a state in which prey and predator coexist. We remark that the Eqs. (70–72) predict no oscillation in contrast with the Lotka-Volterra Eqs. (56) and (57). However, we shall see that the oscillations will in fact occur if we consider the stochastic version of the prey-predator model.

5 Stochastic Approach

Let us denote by n_i the number of individuals of class i, and by n the vector with components $n_1, n_2, \ldots$, and we assume that the maximum number of individuals is N. There are several processes occurring in the system. When a process occurs the individuals change classes. We denote by ν_i^r the change in the number of individuals of class i due to the process r, and define ν^r as the vector with components $n_1^r, n_2^r, \ldots$. The time variation of the probability $P(n)$ is governed by the master equation

$$\frac{d}{dt}P(n) = \sum_r \{W_r(n-\nu^r)\,P(n-\nu^r) - W_r(n)\,P(n)\}, \tag{74}$$

where $W_r(n)$ is the transition rate of the process r.

We define the concentrations $x_i = n_i/N$ and change variables from n_i to x_i. The master equation becomes

$$\frac{\partial}{\partial t}\rho(x) = N\sum_r \{w_r(x^r)\,\rho(x^r) - w_r(x)\rho(x)\}. \tag{75}$$

where $w_r = W_r/N$ and $x^r = x - \nu^r/N$.

Next we expand the expression between brackets in powers of $1/N$. Up to $1/N^2$ we find

$$\frac{\partial\rho}{\partial t} = -\sum_i \frac{\partial f_i\rho}{\partial x_i} + \frac{\varepsilon}{2}\sum_{ij}\frac{\partial^2 g_{ij}\,\rho}{\partial x_i\partial x_j}, \tag{76}$$

where

$$f_i = \sum_r \nu_i^r\, w_r, \qquad g_{ij} = \sum_r \nu_i^r\,\nu_j^r\, w_r, \tag{77}$$

and $\varepsilon = 1/N$. The Eq. (76) is a Fokker-Planck equation, and the variables x_i are now continuous variables.

We remark that the Fokker-Planck (76) can be understood as coming from a stochastic Langevin equation. If we discretize the time t in interval of time τ, the Langevin equation equations can be written as

$$\Delta x_i = \tau f_i + \sqrt{\varepsilon\tau}\,\xi_i \tag{78}$$

where ξ_i are random variables with zero mean and covariance equal to g_{ij}. From this equation it becomes clear that the stochastic fluctuation in density is proportional to $1/\sqrt{N}$ and as a consequence the stochastic fluctuation in the number of individuals is proportional to $\sqrt{N}$.

To solve the Fokker-Planck equation we assume that a variable x_i takes values that are near its average which we denote by $\bar{x}_i$. That is, as time evolves, the trajectory $x(t)$ is near the trajectory $\bar{x}(t)$, the deviation being of the order $\sqrt{\varepsilon}$. In accordance with this assumption, we expand $f_i(x)$ to find

$$f_i = \bar{f}_i + \sum_j \bar{f}_{ij}\,(x_j - \bar{x}_j), \tag{79}$$

where $\bar{f}_i = f_i(\bar{x})$, and $\bar{f}_{ij} = f_{ij}(\bar{x})$, with $f_{ij} = \partial f_i/\partial x_j$. Replacing this result into the Fokker-Planck and using the notation $\bar{g}_{ij} = g_{ij}(\bar{x})$, it becomes

$$\begin{aligned}\frac{\partial\rho}{\partial t} &= -\sum_i \frac{\partial}{\partial x_i}(\bar{f}_i + \sum_j \bar{f}_{ij}(x_j - \bar{x}_j))\rho \\ &\quad + \frac{\varepsilon}{2}\sum_{ij}\bar{g}_{ij}\frac{\partial^2\rho}{\partial x_i\partial x_j}.\end{aligned} \tag{80}$$

It is straightforward to show that the solution of the Fokker-Planck (80) is the multivariate Gaussian

$$\rho = \frac{1}{Z}\exp\{-\frac{1}{2\varepsilon}\sum_{ij} b_{ij}(x_i - a_i)(x_j - a_j)\}, \tag{81}$$

where a_i and b_{ij} depend on time, and a_i is the average of x_i, that is $a_i = \bar{x}_i$. The time evolution of the average $\bar{x}_i$ is given by the equation

$$\frac{d}{dt}\bar{x}_i = \bar{f}_i, \tag{82}$$

which is obtained from the Fokker-Planck Eq. (80) by multiplying it by x_i and integrating in x, and performing integrations by parts. The Eq. (82) is the same equation given by the deterministic approach. To see this it suffices to replace x_i appearing in the deterministic equations by the average $\bar{x}_i$ of the present stochastic approach. In other words, we may say that the number of individuals of the deterministic approach should be understood as the average number of individuals.

As to the parameter b_{ij} appearing in (81), we say that the square matrix with elements b_{ij}/ε is the inverse of the covariant matrix. The elements of the covariant matrix are χ_{ij} defined by $\chi_{ij} = \langle x_i x_j\rangle - \langle x_i\rangle\langle x_j\rangle$. To determine the time evolution of the covariances χ_{ij} we first determine the time evolution of the average $\langle x_i x_j\rangle$, which is

$$\frac{d}{dt}\langle x_i x_j\rangle = \bar{x}_i\bar{f}_j + \bar{x}_j\bar{f}_i + \sum_k(\bar{f}_{jk}\chi_{ik} + \bar{f}_{ik}\chi_{jk}) + \varepsilon\bar{g}_{ij}. \tag{83}$$

Using the Eq. (82), we find

$$\frac{d}{dt}\chi_{ij} = \sum_k(\bar{f}_{jk}\chi_{ik} + \bar{f}_{ik}\chi_{jk}) + \varepsilon\bar{g}_{ij}. \tag{84}$$

Once $\bar{x}$ is found as a function of t, we may replace it in Eq. (84) to determine χ_{ij}.

Writting $\bar{f}_{ij} = f_{ij}^0 + f_{ij}^1$ as a sum of two parts, and defining the first part through

$$\sum_k f^0_{ik}\chi_{jk} = \sum_k f^0_{jk}\chi_{ik} = -\frac{\varepsilon}{2}\bar{g}_{ij}, \tag{85}$$

then in the stationary state the second part fulfills the following equation,

$$\sum_k (f^1_{jk}\chi_{ik} + f^1_{ik}\chi_{jk}) = 0. \tag{86}$$

6 Stochastic Oscillations

If we apply the stochastic approach just presented to the predator-prey model, the equations for the time evolution of the averages $\bar{x}_i$ will be identified as the rate Eqs. (70–72). From these equations one finds that after a transient, the averages $\bar{x}_i$ become constant in time and no oscillations in $\bar{x}_i$ is found. However, this does not mean necessarily that there is no oscillations in $x_i(t)$. Considering that $x_i(t)$ is a stochastic variable, the oscillations, if they exist, will be intertwined with the random fluctuations. Thus we are faced with the problem of distinguishing *pure stochastic fluctuations* from *stochastic oscillations*.

The distinction between the two behaviors can be accomplished by determining the time correlation function $C_{ij}(t)$ between the variable $x_i(t)$ at time t and the variable $x_j(0)$ at time zero, where we are here setting the origin of time inside the stationary regime where $\bar{x}_i$ is independent of time. In the case of pure stochastic fluctuations, the time correlation is characterized by a pure damped decay, given by

$$C_{ij} = A\, e^{-\gamma t}. \tag{87}$$

In the case of stochastic oscillations, it is characterized by a oscillatory damped decay, given by

$$C_{ij} = B\, e^{-\alpha t}\cos\omega t, \tag{88}$$

where ω is the frequency of oscillations. The time behavior of $x_i(t)$ whose time correlation is expressed by (88) is known as phase-forgetting quasi-cycles [3].

Next we will see how the two behaviors emerge from the present approach. To this end we have to define first the time correlation. We start by using the notation $K(x, t; y)$ for the expression on the right-hand side of Eq. (81), where $a_i(t)$ is such that $a_i(0) = y_i$. The time correlation is defined by

$$C_{ij}(t) = \int x_i\, K(x,t;y) y_j\, \rho_o(y)\, dxdy - x^\circ_i\, x^\circ_j, \tag{89}$$

where $\rho_o(y)$ is the probability distribution at $t = 0$ and x°_i is the average of x_i at $t = 0$. When $t \to 0$, $b(t) \to 0$ and $K(x, t; y)$ becomes a multivariate delta function. Therefore, we find

$$C_{ij}(0) = \int y_i y_j \rho_o(y) dy - x^\circ_i x^\circ_j = \chi^\circ_{ij}, \tag{90}$$

that is, the correlation at time zero becomes the covariance at time zero, denoted by χ°_{ij}.

If we integrate (89) in x, we find

$$C_{ij}(t) = \int a_i(y,t) y_j \rho_\circ(y) dy - x^\circ_i x^\circ_j, \tag{91}$$

where we are using the notation $a_i(y, t)$ to recall that a_i is such that when $t \to 0$ it becomes y_i. To determine a_i, we bear in mind that it is the solution of Eq. (82), that is,

$$\frac{da_i}{dt} = f_i(a). \tag{92}$$

Therefore to find $a_i(y, t)$, it suffices to solve this equation with the initial condition that a_i equals y_i.

An explicit solution of the Eq. (92) can be obtained for large values of t. In the limit $t \to \infty$, a_i approaches the asymptotic value which we are denoting by x°_i. Thus for large times, a_i will not differ much from x°_i. These considerations allow us to expand $f_i(a)$ and conserve the linear terms in $a_i - x^\circ_i = \xi_i$. The Eq. (92) becomes

$$\frac{d\xi_i}{dt} = \sum_j f^\circ_{ij}\xi_j, \tag{93}$$

where $f^\circ_{ij} = f_{ij}(x^\circ)$.

The solution of this linear equation is of the form

$$\xi_i = \sum_j A_j e^{\lambda_j t}, \tag{94}$$

where λ_j are the eigenvalues of the matrix whose elements are f°_{ij}, and A_j are constants. The sum on the right-hand side of this equation is dominated by the term corresponding to the eigenvalue with the largest real part, which we denote by λ. If λ has an imaginary part then λ^* is also a dominant eigenvalue so that

$$\xi_i = B_i e^{\lambda t} + B^*_i e^{\lambda^* t}, \tag{95}$$

where B_i is a constant. By an appropriate shift of the origin of time, we may choose B_i to be real, in which case we write

$$\xi_i = B_i(e^{\lambda t} + e^{\lambda^* t}). \tag{96}$$

Taking into account that a_i at $t = 0$ should be equal to y, it follows that ξ_i at $t = 0$ must be equal to $y_i - x^\circ_i$, and we conclude that $B_i = (y_i - x^\circ_i)/2$.

Replacing $a_i = x^\circ_i + \xi_i$ in the expression (91) for the correlation function we find

$$C_{ij}(t) = \int \xi_i(t)\xi_j(0)\rho_\circ(y)dy, \tag{97}$$

from which we reach the desired expression for the time correlation,

$$C_{ij}(t) = \frac{1}{2}(e^{\lambda t} + e^{\lambda^* t})\chi_{ij}^\circ. \tag{98}$$

If $\lambda = -\gamma$ is real, we obtain

$$C_{ij}(t) = \chi_{ij}^\circ e^{-\gamma t}, \tag{99}$$

which is identified with (87). If $\lambda = -\alpha + i\omega$ is complex, we obtain

$$C_{ij}(t) = \chi_{ij}^\circ e^{-\alpha t} \cos \omega t \tag{100}$$

which is identified with (88).

From these results we see that the asymptotic behavior of the time correlation function is the same asymptotic behavior of a_i, solution of (92). Since a_i obeys the same equation as $\bar{x}_i$, we may say that the $C_{ij}(t)$ and $\bar{x}_i$ have the same asymptotic time behavior. Thus if the rate equations predicts an oscillatory damped solution so will the correlation function and $x_i(t)$ will display stochastic oscillations, or phase-forgetting quasi-cycles.

We remark that C_{ij} is of the order ε because χ_{ij} is of the order ε. This means to say that the amplitude of the stochastic oscillations are of the order $\sqrt{\varepsilon}$ and not of the order ε as expected for synchronous oscillations.

7 Predator-prey Model

7.1 Three Species

We consider here the stochastic predator-prey model. This model consists of three biological species of and three processes, which are

$$\mathrm{C} + \mathrm{A} \to 2\mathrm{A}, \qquad \mathrm{A} + \mathrm{B} \to 2\mathrm{B}, \qquad \mathrm{B} \to \mathrm{C}. \tag{101}$$

The individuals of species A, B, and C are the prey, the predator, and the food of the prey. In the first process, a prey is created catalytically; in the second, a predator is created catalytically; and in the third, a predator disappears spontaneously.

Denoting by x_1, x_2, and x_3 the concentrations of A, B, and C, then the rate of the reactions are

$$w_1 = k_1 x_3 x_1, \qquad w_2 = k_2 x_1 x_2, \qquad w_3 = k_3 x_2, \tag{102}$$

and the functions f_i are

$$f_1 = k_1 x_3 x_1 - k_2 x_1 x_2, \tag{103}$$

$$f_2 = k_2 x_1 x_2 - k_3 x_2, \tag{104}$$

$$f_3 = k_3 x_2 - k_1 x_3 x_1. \tag{105}$$

The time evolution of x_i is given by $dx_i/dt = f_i$, and we are dropping the bar over x_i. Taking into account that $f_1 + f_2 + f_3 = 0$ it follows that $x_1 + x_2 + x_3$ is a constant which we choose to be equal to unity. In the stationary state $f_i = 0$ and the stationary values of x_1, x_2, and x_3 are, respectively

$$x_1 = \frac{k_3}{k_2}, \qquad x_2 = \frac{(k_2 - k_3)k_1}{(k_1 + k_2)k_2}, \qquad x_3 = \frac{(k_2 - k_3)}{(k_1 + k_2)}. \tag{106}$$

This solution may occur whenever $k_2 > k_3$.

There is also a trivial solution, $x_1 = 1$, $x_2 = 0$, and $x_3 = 0$ which exists for any values of the rate constants. However, when $k_2 > k_3$ it becomes unstable against a perturbation in x_2 and x_3 and the nontrivial solution given by (106) emerges. The change of behavior, observed when one increases k_2, is understood as a phase transition from an inactive state to an active state. The inactive state, corresponding to the trivial solution, is characterized by the absence of predator. The active state, corresponding to the nontrivial solution (106), is characterized by the coexistence of prey and predator. These two behaviors corresponds to two regions as shown in Fig. 2.

Next we determine the eigenvalues of the matrix whose elements are $f_{ij} = \partial f_i / \partial x_x$, which is

$$\begin{pmatrix} k_1 x_3 - k_2 x_2 & -k_2 x_1 & k_1 x_1 \\ k_2 x_2 & k_2 x_1 - k_3 & 0 \\ -k_1 x_3 & k_3 & -k_1 x_1 \end{pmatrix} \tag{107}$$

For the trivial solution $x_1 = 1$ and $x_2 = x_3 = 0$, one eigenvalue is $k_2 - k_3$ and the other two are zero or negative.

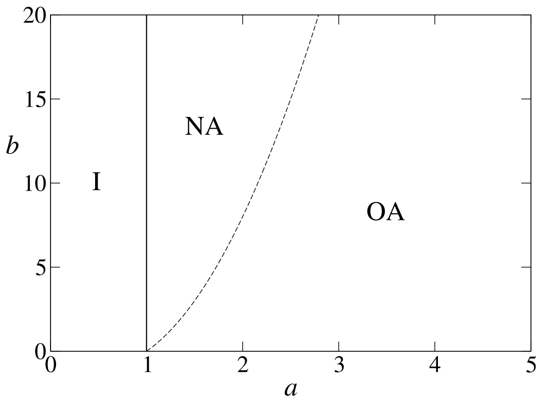

Fig. 2 Behavior of the predator-prey model in the plane $a = k_2/k_3$ and $b = k_1/k_3$. The regions are inactive (I), oscillatory active (OA), and nonoscillatory acitve (NA). The line between NA and OA is given by Eq. (114) or by $b = 4a(a - 1)$

Therefore, this solution becomes unstable when $k_2 > k_3$, as said above.

For the non trivial solution (106), which may exist whenever $k_2 > k_3$, this matrix becomes

$$\begin{pmatrix} 0 & -r & q \\ p & 0 & 0 \\ -p & r & -q \end{pmatrix} \tag{108}$$

where

$$p = \frac{k_1(k_2 - k_3)}{k_1 + k_2}, \quad q = \frac{k_1 k_3}{k_2}, \quad r = k_3, \tag{109}$$

and the eigenvalues other than zero are solutions of

$$\lambda^2 + q\lambda + p(q + r) = 0. \tag{110}$$

If the two eigenvalues are real then they are negative and the no trivial solution is stable. If they are complex then their real part are equal and negative and the solution is stable. Let us determine the line that separates the real and complex eigenvalues. Writing $\lambda = -\alpha + i\omega$ then

$$\alpha = \frac{k_1 k_3}{2k_2}, \tag{111}$$

$$\omega = \frac{\sqrt{k_1 k_3}}{k_2}\sqrt{4k_2(k_2 - k_3) - k_1 k_3}, \tag{112}$$

valid as long as

$$4k_2(k_2 - k_3) > k_1 k_3. \tag{113}$$

When the condition (113) is not fulfilled, then λ will be real. Thus the line that separated the real eigenvalue, which corresponds to pure stochastic fluctuations, from the complex eigenvalue, which corresponds to stochastic oscillations, is given by

$$4k_2(k_2 - k_3) = k_1 k_3. \tag{114}$$

In Fig. 2 we show the three regimes of the model in the space $q = k_1/k_3$ versus $p = k_2/k_3$. One regime corresponds to a state of inactivity, characterized by the absence of predator. The other two are characterized by the coexistence of the species, one of them displaying stochastic oscillations and the other only pure stochastic fluctuations. The line that separates these two behavior occurs is given by (114).

We have simulated the model by using a population of 1000 individuals and the transition rates w_i defined by Eq. (102). In Fig. 3 we show the result for the case of $k_2/k_3 = 2$ and $k_1/k_3 = 5$. According to the diagram of Fig. 2, for these values of the constant rates the three species coexist and fluctuates around their averages.

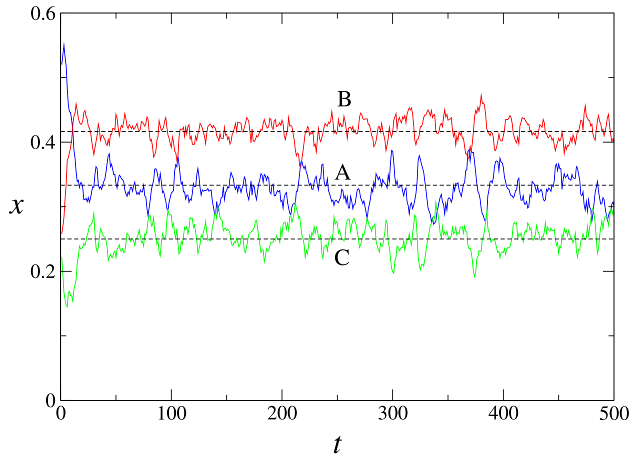

Fig. 3 Density of species **A**, **B**, and **C** for the predator-prey model with three species as a function of time for $a = k_2/k_3 = 3$ and $b = k_1/k_3 = 5$ and a population of 1000 individuals. The horizontal straight lines are the density averages of each species

7.2 Four Species

We consider here the stochastic predator-prey model with four biological species and four processes, which are

$$\mathrm{C} + \mathrm{A} \rightarrow 2\mathrm{A}, \qquad \mathrm{A} + \mathrm{B} \rightarrow 2\mathrm{B}, \quad \mathrm{B} \rightarrow \mathrm{C}, \tag{115}$$

$$\mathrm{B} + \mathrm{D} \rightarrow 2\mathrm{D}, \quad \mathrm{D} \rightarrow \mathrm{C}. \tag{116}$$

An individual A is a prey, B is a predator of A, D is the predator of B, and C is the food of prey. In the first process, a prey is created catalytically; in the second, a predator B is created catalytically; in the third, a predator B disappears spontaneously; in the fourth, a predator D is created catalytically; and in the fourth, a predator D disappears spontaneously.

Denoting by x_1, x_2, x_3, and x_4 the concentrations of A, B, C, and D, we find

$$f_1 = k_1 x_1 x_3 - k_2 x_1 x_2, \tag{117}$$

$$f_2 = k_2 x_1 x_2 - k_3 x_2 - k_2 x_2 x_4, \tag{118}$$

$$f_3 = k_3 x_2 - k_1 x_1 x_3 + k_3 x_4, \tag{119}$$

$$f_4 = k_2 x_2 x_4 - k_3 x_4. \tag{120}$$

where we are considering that the rate constants of the forth and the second are equal and that the rate constants of the fifth and the third are equal. The time evolution of x_i is given by $dx_i/dt = f_i$, and we are dropping the bar over x_i.

The trivial stationary solution is $x_1 = 1$ and $x_2 = x_3 = x_4 = 0$ and corresponds to the absence of the two predators B and D. It exists for any values of the rate constants but it becomes unstable against perturbation in x_2, x_3, and x_4 when $k_2 > k_3$.

A second solution corresponds to the case where $x_4 = 0$ and

$$x_1 = \frac{k_3}{k_2}, \quad x_2 = \frac{(k_2 - k_3)k_1}{(k_1 + k_2)k_2}, \quad x_3 = \frac{k_2 - k_3}{k_1 + k_2}, \tag{121}$$

and corresponds to the absence of the predator D. This solution exists if $k_2 > k_3$ but becomes unstable against perturbation in x_4 when $k_1k_2 < 2k_1k_3 + k_2k_3$.

A third solution corresponds to the case where x_i are all nonzero and are given by

$$x_1 = \frac{k_1 - k_3}{2k_1}, \quad x_2 = \frac{k_3}{k_2}, \quad x_3 = \frac{k_3}{k_1}, \tag{122}$$

$$x_4 = \frac{k_1k_2 - 2k_1k_3 - k_2k_3}{2k_1k_2}. \tag{123}$$

This solution exists whenever $k_1k_2 > 2k_1k_3 + k_2k_3$.

The three solutions correspond to three behaviors as illustrated in Fig. 4. The line separating the first behavior from the second is given by $k_2 = k_3$ whereas that separating the second from the third is

$$k_1k_2 = 2k_1k_3 + k_2k_3. \tag{124}$$

Next we determine the eigenvalues of the matrix whose elements are $f_{ij} = \partial f_i/\partial x_x$, which is

$$\begin{pmatrix} k_1x_3 - k_2x_2 & -k_2x_1 & k_1x_1 & 0 \\ k_2x_2 & k_2x_1 - k_3 - k_2x_4 & 0 & -k_2x_2 \\ -k_1x_3 & k_3 & -k_1x_1 & k_3 \\ 0 & k_2x_4 & 0 & k_2x_2 - k_3 \end{pmatrix} \tag{125}$$

For the trivial solution, one eigenvalue is $k_2 - k_3$ and the others are zero of negative. Therefore, this solution becomes unstable when $k_2 > k_3$, as said above.

For the second solution (121), one eigenvalue is

$$\frac{k_1k_2 - 2k_1k_3 - k_2k_3}{k_1 + k_2}, \tag{126}$$

the other is zero and the other two are given by (110). Thus this solution becomes unstable when the expression (126) becomes positive. The vanishing of this expression gives the line that separates the second solution from the third, which is the Eq. (124).

Whenever the expression (126) is negative, $x_4 = 0$ and the model of fours states reduces to the model with three states. Thus for the second solution the line that separates the regime of pure stochastic fluctuations from the stochastic oscillations is given by (114), that is, by

$$4k_2(k_2 - k_3) = k_1k_3. \tag{127}$$

as shown in Fig. 4.

For the third solution, the above matrix reduces to

$$\begin{pmatrix} 0 & -s & q & 0 \\ r & 0 & 0 & -r \\ -r & r & -q & r \\ 0 & p & 0 & 0 \end{pmatrix} \tag{128}$$

$$q = \frac{k_1 - k_3}{2}, \qquad r = k_3, \quad s = \frac{k_2(k_1 - k_3)}{2k_1}, \tag{129}$$

$p = s - r$, and the nonzero eigenvalues λ are given by

$$\lambda^3 + q\lambda^2 + r(2p + q + r)\lambda + 2pqr = 0. \tag{130}$$

Since the dominant eigenvalue is of the type $\lambda = -\alpha + i\omega$, we replace it in (130). After the replacement, the real and imaginary parts result in two coupled equations in α and ω. The border of the region of stochastic oscillations is obtained by taking the limit $\omega \to 0$ in these two equations. Performing this limit we find

$$\alpha^3 - q\alpha^2 + r(2p + q + r)\alpha - 2pqr = 0, \tag{131}$$

$$3\alpha^2 + 2q\alpha + r(2p + q + r) = 0. \tag{132}$$

The elimination of α from these two equations give a relation involving k_1, k_2, and k_3, which is the line separating the regions of stochastic oscillations from that of pure stochastic fluctuations. We have solved these two equations numerically and the result is shown in Fig. 4.

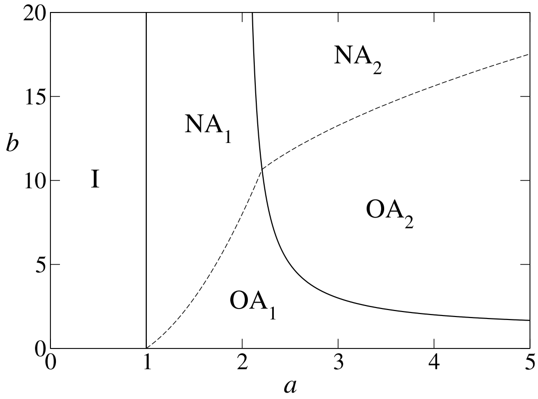

Fig. 4 Behavior of the predator-prey model with four species in the plane $a = k_2/k_3$ and $b = k_1/k_3$. The regions are inactive (I), oscillatory active with one predator (OA$_1$), nonoscillatory active with one predator (NA$_1$), oscillatory active with two predators (OA$_2$), nonoscillatory active with two predator (NA$_2$). The solid line that separates the regions with one and two predators is given by (124) or by $b = a/(a - 2)$

8 Extinction

The diagram of Fig. 4 shows that when $a = k_2/k_3 = 3$ and $b = k_1/k_3 = 5$, the four species coexist, which means that the densities of the four species are nonzero as shown in Fig. 5. Let us suppose that the predation constant rate k_2 decreases to a value such that $a = 2$ while b remains constant. According to the diagram of Fig. 4, only the three species, A, B, and C, coexist. The species D has disappeared, that is the species D has gone extinct.

The extinction of D occurred as a consequence of the decrease in predation represented by the rate constant k_2. This type of extinction is also predicted by the deterministic approach and is called natural extinction. However, there is another type of extinction which is predicted by the stochastic approach but not by the deterministic approach. This is the *extinction by fluctuation*. If the number of individuals of a certain species is small, the fluctuations will be relatively great and may result in the vanishing in the number of individuals of this species, as illustrated in Fig. 6. In this example, the species D becomes extinct and as a result the predator-prey model with four species reduces to the predator prey model with three species.

It is worth mentioning that the extinction of a a certain species by fluctuation can be reverted if a few individuals are introduced into the ecosystem. This is so because the state with a nonzero population of this species is stable. However, this procedure does not work when a natural extinction occurs because in this case the state with a nonzero population of this species is unstable.

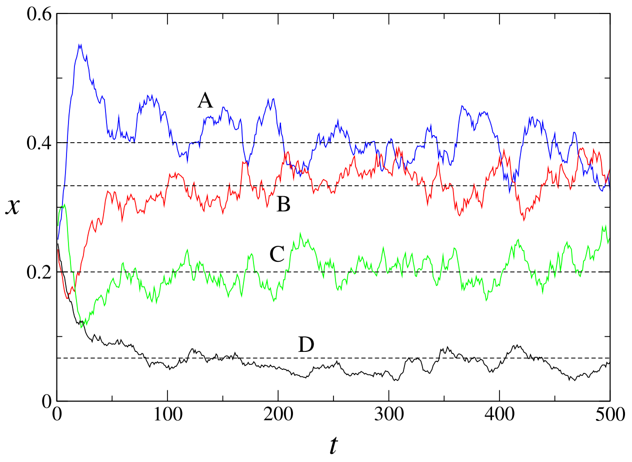

Fig. 5 Density of species **A**, **B**, **C**, and **D** for the predator-prey model with four species as a function of time for $a = k_2/k_3 = 3$ and $b = k_1/k_3 = 5$ and a population of 1000 individuals. The horizontal straight lines are the density averages of each species

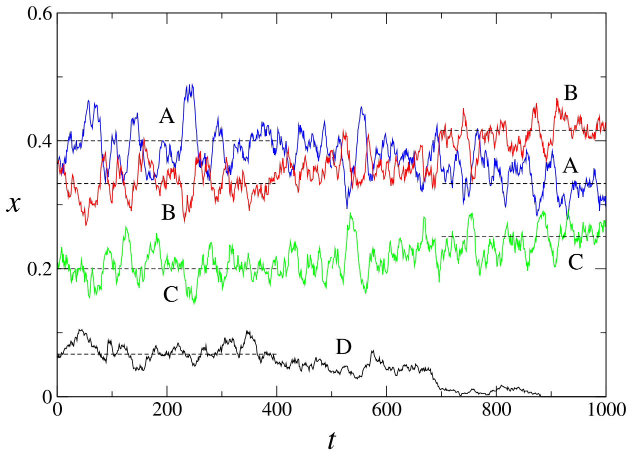

Fig. 6 Density of species **A**–**D** for the predator-prey model with four species as a function of time for $a = k_2/k_3 = 3$ and $b = k_1/k_3 = 5$ and a population of 1000 individuals. The extinction of species D by stochastic fluctuation occurs when the density of this species vanishes.The four horizontal straight lines at the left are the density averages of each species before extinction. The three horizontal lines at the right are the density averages of the remaining species after the extinction of species D

9 Conclusion

We have presented a stochastic approach to population dynamics where the number of individuals of each class is treated as stochastic variables. After setting up a master equation we performed an expansion in $1/N$ from which we have obtained a Fokker-Planck equation. The description of population dynamics based on this equation allowed us to draw the following conclusions. The equations that give the time evolution of the average number of individuals are identified with the rate equations of the deterministic approach. The stochastic fluctuation in the number of individuals is proportional to $\sqrt{N}$. The possible oscillations in the number of individuals are stochastic oscillations whose amplitude is proportional to $\sqrt{N}$.

The stochastic oscillations were characterized by determining the time correlation between the number of individuals. The stochastic oscillations are characterized by an oscillatory damped decay of the time correlation function. In this case the number of individuals of a given class displays a stochastic oscillation in time. When the time behavior of the correlation is a pure damped decay, there is no oscillation and only pure stochastic fluctuations. In this case the number of individuals of a given class displays pure stochastic fluctuations.

We have applied the present approach to some population models to the predator-prey model with three and four biological species. One of them is defined by three processes in a cycle, with two catalytic processes and one spontaneous process. The other is also cyclic and has three catalytic process and two spontaneous processes. Both models presents a regime were the individuals of distinct species coexist. This regime may display a stochastic oscillation depending on the constant rates.

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Declarations

Conflict of Interest No conflicts of interests or competing interests are related to the present work.

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