# Dynamics and thermodynamics of delayed population growth

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The dynamic and thermodynamic properties of delayed nonlinear reaction-diffusion equations describing population growth with memory are analyzed. In the dynamic study we first apply the speed selection mechanisms for wave fronts connecting two steady states obtaining, on one hand, a decrease in the lower bound speed, and also an upper bound velocity; we also calculate an exact wave front solution. In the thermodynamic study, we show an agreement between the stochastic description and extended irreversible thermodynamics in the presence of a source of particles. [S1063-651X(97)10205-7]

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## I. INTRODUCTION

Reaction-diffusion models have been used to describe different phenomena in fluid dynamics, dendritic growth, population growth, pulse propagation in nerves, and other biological phenomena. The ensuing equations are derived from the classical diffusion equation taking into account a source term of particles; the most commonly one used in the study of population growth is the Fisher equation, in which the source term is logistic [1–4]. Some authors have generalized this study by introducing diffusion coefficients depending on the number density [2,3], so that the problem becomes highly nonlinear. However, no memory is considered in the latter models.

In the present paper we generalize the previous reaction-diffusion models in biological populations by including memory effects. It is well known that an animal's motion during a small time period has a tendency to proceed in the same direction as it did in the immediate period before [5]. This memory has as an immediate consequence the delay in the appearance of the population flux, a delay that has not been considered in previous models to our knowledge. Let us notice, on the other hand, that delayed transport equations have been widely used to solve diffusion problems, hyperbolic heat conduction, and viscous transport processes [6]. These kinds of transport equations show an important feature: the propagation speed of the perturbations is finite, that is, these equations are causal.

In Sec. II the new equation is derived from three different methods: from the theory of stochastic processes, phenomenologically, and from the extended irreversible thermodynamics (EIT) framework [6].

In Sec. III we study the main dynamical features of the delayed reaction-diffusion equations. Firstly, we revise the recent problem of the speed selection mechanisms by applying to our model the classical linearization method and the recent method proposed by Benguria and Depassier [4]. Secondly, we find an exact solution for stable heteroclinic wave fronts connecting homogeneous steady states for the particular case of a generalized logistic source term.

We compare in Sec. IV the thermodynamic functions obtained at the stochastic level of the description and the ones supplied by EIT, and end the paper with some underlying conclusions.

## II. DELAYED NONLINEAR DIFFUSION EQUATIONS

In this section we provide some different frameworks for delayed reaction-diffusion equations in order to describe more realistic diffusive (for instance, migration animal) and generating particle (for instance, sexual reproduction) processes in an unbounded one-dimensional space. First of all, we find the evolution equation from the correlated or persistent random walk with a nonlinear population source. The second one is a phenomenological derivation, where the key is a delay of time $\tau$ for the population flow after imposing the population gradient. Finally, we obtain the delayed equation in the framework of extended irreversible thermodynamics.

### A. Correlated random walk

When memory effects are taken into account, successive movements of the dispersive particles are not mutually independent, so there is a correlation between successive steps. This model was developed initially by Goldstein [8] in 1951 starting from a pioneering work by Taylor in 1921 [9]. Following this approach we now show how to construct a difference equation and its limiting partial hyperbolic differential equation, which characterize the correlated random walk described. Let us assume that at initial time $t=0$ many particles (animals, viruses, bacterias, etc.) are at $x=0$. Let $n(x,t)$ be the fraction of particles that at time $t$ are at position $x$. Denoting by $n_+(x,t)$ and $n_-(x,t)$ the fraction of particles that are arriving from the left and from the right, respectively, then

$$n(x,t)=n_+(x,t)+n_-(x,t). \tag{1}$$

Thus $n_+(x,t)$ and $n_-(x,t)$ characterize right and left moving particles, respectively. Also let $p$ be the probability of jumping in the same direction as the previous jump, that is, the probability that the particle persists in its direction after completing a step, whereas $q=1-p$ denotes the probability for jumping in the opposite direction. Note that in a classical random walk, the probability of jumping to the right or to the left is 1/2, so there is no correlation between the speed direction at successive jumps. With steps of length $\delta$ occurring in time intervals of length $T$, we immediately obtain

 

$$n_+(x,t+T)=pn_+(x-\delta,t)+qn_-(x-\delta,t),$$

$$n_-(x,t+T)=pn_-(x+\delta,t)+qn_+(x+\delta,t). \quad (2)$$

Define now $\gamma=p-q$, the correlation coefficient between two successive steps. In the limit $T\to 0$, $\delta\to 0$, keeping the ratio $\delta/T\to v$ (the finite velocity of the particle), the correlation coefficient $\gamma\to 1$, and the probability of persistence $p$ tends to unity, whereas the probability $q$ of reversal should tend to zero. This means that we should have for small $T$, $p=1-\lambda T+O(T^2)$ and $q=\lambda T+O(T^2)$ where $\lambda$ is the rate of the reversal of direction. Introducing Taylor expansions for $n_+$ and $n_-$ up to the first order in $T$ and $\delta$ and taking into account the expansion of $p$ and $q$ on $T$ we find from the first equation of (2) that

$$\frac{\partial n_+}{\partial t}+v\frac{\partial n_+}{\partial x}=-m, \quad (3)$$

where $m=\lambda(n_+-n_-)$ is the rate of creation or loss of particles. From the second equation of (2) we find analogously

$$\frac{\partial n_-}{\partial t}-v\frac{\partial n_-}{\partial x}=m. \quad (4)$$

By adding Eqs. (3) and (4) one obtains the particle conservation equation

$$\frac{\partial n}{\partial t}+\frac{\partial J}{\partial x}=0, \quad (5)$$

taking into account Eq. (1), and subtracting Eqs. (3) and (4) one finds for the particle flux defined as $J(x,t)=v(n_+-n_-)$, the following equation

$$\tau\frac{\partial J}{\partial t}+J=-D\frac{\partial n}{\partial x}, \quad (6)$$

which adopts a Maxwell-Cattaneo form where $\tau=1/2\lambda$ is the relaxation time and $D=v^2\tau$ the diffusion coefficient.

If we consider that there exists a source of particles $F(n)>0$ the conservation equation (5) has $F(n)$ in its right-hand side instead of 0. Combining this equation together with Eq. (6) we find the nonlinear reaction-diffusion equation

$$\tau\frac{\partial^2 n}{\partial t^2}+\frac{\partial n}{\partial t}=D\frac{\partial^2 n}{\partial x^2}+F(n)+\tau\frac{\partial F(n)}{\partial t}, \quad (7)$$

which is the central one in the present paper and will be analyzed in the next section. This equation, without source terms, has been widely studied analytically with different boundary conditions in a one-dimensional medium [10,11].

### B. Phenomenological derivation

In this section we derive the transport equation (7) but from a macroscopic point of view. The balance equation for the fraction of particles $n$ in an one-dimensional problem is

$$\frac{\partial n}{\partial t}=-\frac{\partial J}{\partial x}+F(n), \quad (8)$$

where $F(n)$ is the generating particle source function. The particle flux $J(x,t)$ must take into account the relaxational effect due to the delay of the particles in adopting one definite direction to propagate. Therefore, memory in the correlation between steps may be understood macroscopically as a delay in the flux of particles for a given concentration gradient. Then, from the classical transport Fick's law,

$$J(x,t+\tau)=-D\frac{\partial n(x,t)}{\partial x}, \quad (9)$$

with $\tau$ a characteristic time. Note that expanding $J$ up to the first order in $\tau$, one has

$$\tau\frac{\partial J(x,t)}{\partial t}+J(x,t)=-D\frac{\partial n(x,t)}{\partial x}. \quad (10)$$

Combining Eqs. (8) and (9) we find the transport equation

$$\frac{\partial n(x,t+\tau)}{\partial t}=D\frac{\partial^2 n(x,t)}{\partial x^2}+F[n(x,t+\tau)]. \quad (11)$$

Expanding in Taylor series the functions $n(x,t+\tau)$ and $F(x,t+\tau)$ up to the first order in $\tau$ we recover Eq. (7), the telegrapher equation. The physical difference between this equation and the classical diffusion equation (we refer to the diffusion process without delay as classical) is that the first one has a finite velocity of dispersion $v_p$ whereas the classical one does not ($v_p$ must not be confused with the velocity of a wave front of a diffusing population $v_f$, which we treat later). In the limit $t\gg\tau$ both equations give similar behavior [11], but in the high-frequency limit ($\tau\omega\gg 1$) the telegrapher's equation gives a finite velocity of dispersion $v_p=\sqrt{D/\tau}$ while the classical Fick's law diverges in this limit. Since no organism can spread or propagate with an infinite speed, the telegrapher's equation is more realistic than the classical diffusion equation when applied to animal dispersal problems.

However, as we show in turn, the finite velocity is not maintained if we consider the exact expression given in Eq. (11) instead of its first order approximation (7). Transforming in the Fourier space $(\omega,k)$ we find for Eq. (11) the following dispersion relation:

$$k^2D=\omega e^{i\omega\tau}. \quad (12)$$

The phase velocity or the velocity of dispersion is

$$v_p=\frac{\omega}{\mathrm{Re}(k)}=\sqrt{\frac{2D\omega}{1+\cos\omega\tau}}. \quad (13)$$

This velocity diverges when $\omega\tau=\pm(2n+1)\pi$ for $n=0,1,2,\ldots$. For $\omega\tau=\pm 2n\pi$, $v_p=v_p^{\mathrm{clas}}/\sqrt{2}$ and for $\omega\tau=\pm(2n+1)\pi/2$ both velocities coincide. The attenuation distance reads

$$d=\frac{1}{\mathrm{Im}(k)}=\frac{\sqrt{D/\omega}}{\sin(\omega\tau/2)},$$

which diverges for $\omega\tau=\pm 2n\pi$. Surprisingly, the exact delayed equation gives a divergent behavior but not its first truncated equation.

This problem, however, does not occur when one deduces the transport equation in the framework of extended irreversible thermodynamics.

### C. Extended irreversible thermodynamics

In EIT one assumes that the entropy density depends on the classical variables and also the dissipative fluxes [6]; in this case $s=s(n,J)$, with $n$ the number density of particles and $J$ the particle flux. In differential form the entropy is written as

$$ds=\left(\frac{\partial s}{\partial n}\right)dn+\left(\frac{\partial s}{\partial J}\right)dJ, \tag{14}$$

where

$$\left(\frac{\partial s}{\partial n}\right)_J=-T^{-1}\mu, \quad \left(\frac{\partial s}{\partial J}\right)_n=-\frac{T^{-1}\alpha J}{n}, \tag{15}$$

$\mu$ being the chemical potential per particle and $\alpha$ a scalar function not depending on $J$ at the lowest order of approximation. The generalized Gibbs equation up to the second order in $J$ is then given by

$$ds=ds_{\rm eq}-T^{-1}\frac{\alpha}{n}JdJ \tag{16}$$

and integrating, one has for the generalized entropy

$$s=s_{\rm eq}-\frac{\alpha}{2Tn}J^2. \tag{17}$$

Combining Eqs. (14) and (15) with the particle balance equation

$$\frac{\partial n}{\partial t}+\frac{\partial J}{\partial x}=F(n)$$

and the balance equation for the entropy, $\dot{s}+\nabla J^s=\sigma_{\rm syst}$, we find for the entropy production of the system of particles (with $J^s=-\mu J/T$ as usual)

$$\sigma_{\rm syst}=-\frac{J}{T}\left[\nabla\mu+\frac{\alpha}{n}\frac{\partial J}{\partial t}\right]-\frac{\mu F}{T}. \tag{18}$$

Let us now notice that the physical volume element contains two subsystems; on one hand, the particles—which are the center of our attention—and on the other, the medium generating new particles. What must be positive definite according to the second law of thermodynamics is the total entropy production, namely, $\sigma_T=\sigma_{\rm syst}+\sigma_{\rm gen}$, i.e., the sum of the entropy productions of both subsystems (and not each term separately). Thus we have

$$\sigma_T=-\frac{J}{T}\left[\nabla\mu+\frac{\alpha}{n}\frac{\partial J}{\partial t}\right]-\frac{\mu F}{T}+\sigma_{\rm gen}\geqslant 0. \tag{19}$$

Expression (19) shows two contributions, one for each irreversible process present. The first term is related to diffusion, and the last two terms in the right-hand side are associated to the creation of particles; as usual in irreversible thermodynamics, each one must be positive definite

$$\sigma_{\rm dif}=-\frac{J}{T}\left[\nabla\mu+\frac{\alpha}{n}\frac{\partial J}{\partial t}\right]\geqslant 0, \quad \sigma_{\rm gen}-\frac{\mu F(n)}{T}\geqslant 0. \tag{20}$$

The first inequality in Eq. (20) requires the term inside brackets to depend on the flux $J$ in order to be positive definite. In the simplest case, this relation is linear,

$$-\left[\nabla\mu+\frac{\alpha}{n}\frac{\partial J}{\partial t}\right]=LJ, \tag{21}$$

with $L$ a positive scalar quantity.

Defining the positive parameters $\tau\equiv\alpha/nL$ and $D\equiv(\partial\mu/\partial n)/L$ as the relaxation time and the diffusion coefficient, we find for a one-dimensional environment at rest

$$\tau\frac{\partial J}{\partial t}+J=-D\frac{\partial n}{\partial x}, \tag{22}$$

as in Eqs. (6) and (10).

## III. TRAVELING WAVE SOLUTIONS

In this section we are interested in finding traveling wave solutions for our model. The motivation comes from the widespread existence of wave phenomena in biology as well as the vast mathematical literature on aspects of the wave behavior where diffusion plays a crucial role.

In contrast to simple diffusion processes, when reaction kinetics and diffusion are coupled there exist traveling waves of the particle density. As is usual in the literature, a traveling wave is taken to be a wave that travels without change of the shape and with a constant speed of propagation, which we denote by $v_f$. We treat in this section the same selection mechanisms for these wave fronts, and also find and exact solution for the wave front in a particular case.

Let us find the equation governing the wave front. We start from the nonlinear reaction-diffusion equation (7) derived in three different ways in the previous sections. The source term is often written as $F(n)=kf(n)$, where $k>0$ and $f(n)$ is usually a nonlinear polynomial. In the logistic case, for instance, $F(n)=kn(1-n)$. Our main objective is to find heteroclinic solutions $n(x,t)=n(x-v_ft)=N(z)$ connecting two steady states, $z=x-v_ft$ being the wave variable; then $n(x,t)$ is a traveling wave moving at constant speed in the positive $x$ direction. For further purposes it is convenient to rescale Eq. (7) as follows:

$$t^*=kt, \quad x^*=x\sqrt{k/D}. \tag{23}$$

So, the front velocity may be written as $v_f=c\sqrt{kD}$, thus $c$ is the dimensionless front wave speed. Defining the dimensionless group $a\equiv k\tau$, Eq. (7) becomes, omitting the asterisks for notational simplicity,

$$a\frac{\partial^2 n}{\partial t^2}+\frac{\partial n}{\partial t}=\frac{\partial^2 n}{\partial x^2}+f(n)+a\frac{\partial f(n)}{\partial t}. \tag{24}$$

Then, the steady spatially homogeneous states, $N^*=$const, satisfy $f(N^*)=0$ ($N^*\geqslant 0$ since $n<0$ has no physical mean-

ing). Due to the fact that Eq. (24) is invariant under the change $x \to -x$, the front speed may be positive or negative. To be specific we shall assume the positive values. Substituting the traveling wave form with $z^* = x^* - ct^*$ and omitting the asterisk in $z$, $N(z)$ satisfies

$$(1-ac^2)N_{zz} + c[1-af'(N)]N_z + f(N) = 0, \qquad (25)$$

where $' = d/dN$; in the limit $a \to 0$ one recovers the classical equation [1,4]. As is usual in this context, this equation may be written in the form of a damped oscillator

$$\frac{dE(z)}{dz} = -c[1-af'(N)]N_z^2 \qquad (26)$$

for $f' < 1/a$, where $E(z) = \frac{1}{2}(1-ac^2)N_z^2 + V(N)$ and $V(N) = \int f(N)dN$. The kinetic energy term is lower than in the classical case but the dissipative term is also lower if $f' > 0$ or, on the contrary, higher if $f' < 0$.

### A. Speed selection mechanisms for fronts

In this subsection we study two main mechanisms of speed selection for the velocity of propagation of front solutions connecting two homogeneous regions, let, say, $n = 0$ and $n = M$. It is observed both numerically and experimentally that, despite the fact that the system can typically accommodate families of fronts, the global nonlinear dynamics rapidly selects a unique solution. The physically relevant question is at what speed does the front move towards the unstable region. This speed will be referred to as selected speed. [The asymptotic speed will be the lowest speed for which Eq. (24) has a front joining both states.] The oldest studied mechanism was supplied by Kolmogorov *et al.* [12], who obtained the limit front speed from stability considerations on the linearized equation. Since this work, the attention has been focused in applying more restrictive mechanisms of selection and giving lower bounds to that obtained by linearizing. We subsequently apply to our Eq. (24) the linearized method and another one recently proposed by Benguria and Depassier based in a variational analysis [4].

#### *1. Linearization method*

In this subsection we apply the linearization method proposed by Kolmogorov *et al.* [12]. This method takes advantage of the fact that the front profile $N(z)$ can be represented in a phase space $(N, N_z)$ as a trajectory joining the homogenous steady states $N^* = 0$ and $N^* = M$. The trajectory leaves from the unstable solution and finishes in the stable one; the stability analysis is performed around this stable point.

*$ac^2 \neq 1$.* We rewrite Eq. (25) as the dynamical system

$$N_z = y, \quad y_z = \frac{c(1-af')}{ac^2-1}y + \frac{f}{ac^2-1}. \qquad (27)$$

The fixed points are the roots of $f(N)$, namely, $N^*$. To analyze the stability of these fixed points in the phase space $(N, N_z)$ we must construct the Jacobian matrix of the system. The eigenvalues of this matrix are given by

$$\lambda_{\pm} = \frac{c[1-af'(N^*)]}{2(ac^2-1)} \pm \frac{1}{2(ac^2-1)} \times \sqrt{c^2[1-af'(N^*)]^2 + 4f'(N^*)(ac^2-1)}. \qquad (28)$$

The solutions for $N$ have to be positive in order to be physically meaningful, therefore the stable root $N^*$ must be a stable node. Consequently, the radicand in Eq. (28) must be positive for the eigenvalues to be real numbers. Then one has

$$c \geq \frac{2\sqrt{f'(N^*)}}{1+af'(N^*)} \equiv c_L, \qquad (29)$$

thus we find a lower limit for the possible wave speeds. Note that inequality (29) only makes sense for solutions $f'(N^*) \geq 0$, so that this is a necessary condition for stability. Furthermore, for $\lambda_{\pm}$ to be negative as required by stability, it is necessary that $ac^2 < 1$ and $f'(N^*) < 1/a$. Notice that inequality $ac^2 < 1$ provides an upper bound for $c$, namely $\tilde{c} \equiv 1/\sqrt{a}$.

Summarizing, stability conditions lead us to

$$c_L \leq c < \tilde{c}, \quad 0 \leq f'(N^*) < \frac{1}{a}. \qquad (30)$$

Let us stress that the lower bound $c_L$ given by Eq. (29) is smaller than the one supplied in the absence of memory, i.e., $2\sqrt{f'(N^*)}$, and the upper bound $\tilde{c}$ is independent of the explicit form of the source term $f(n)$.

As an illustrative example, we apply the previous analysis to the logistic growth. There exist stable traveling wave fronts connecting the states $N^* = 1$ and $N^* = 0$ with speeds restricted to

$$\frac{2}{1+a} \leq c < \frac{1}{\sqrt{a}} \quad \text{and} \quad a < 1. \qquad (31)$$

Then in the classical version (no memory) $c_L = 2$, while in our model $c_L$ ranges from 2 at $a \to 0$ to 1 at $a \to 1$. The upper bound velocity $\tilde{c}$ bears also an interesting physical meaning. It may be written, with its dimensions, as $\tilde{c} = \sqrt{D/\tau}$. This is the maximum velocity of diffusive pulses [6], that is without reaction terms. Since the speed of fronts is always lower than $\tilde{c}$ ($c < \tilde{c}$), one concludes that the inclusion of a source term does not modify the maximum speed of propagation of the signal, and $\tilde{c}$ keeps being an upper bound to the speed of the signals with independence of a specific kinetic term $f(n)$.

*$ac^2 = 1$.* Now we analyze the stability of solutions, via linearization, for the case when the front speed coincides with $\tilde{c}$, i.e., the maximum possible front velocity. In this case, the nonlinear differential equation for the wave fronts reduces to

$$c\left(a\frac{df}{dN} - 1\right)N_z = f(N). \qquad (32)$$

Introducing a small perturbation $\varepsilon(z)$, $N = N^* + \varepsilon$, and expanding up to first order in $\varepsilon$, one has

$$\varepsilon(z) = \varepsilon_0 e^{\gamma z} \qquad (33)$$

with

$$\gamma=\frac{1}{c}\frac{f'(N^*)}{af'(N^*)-1}.$$

The stability condition $\gamma<0$ is fulfilled if and only if $0<f'(N^*)<1/a$, as also found in Eq. (30). Restricting to the logistic case, this means that the state $N^*=1$ is unstable and $N^*=0$ is stable provided that $a<1$. Hence, if $a<1$, there exist stable traveling fronts connecting $N^*=1$ to $N^*=0$ propagating with the maximum possible velocity $\tilde{c}=1/\sqrt{a}$.

#### *2. Benguria's method*

We apply now the method proposed recently by Benguria and Depassier [4] to our model equation to find a better bound, if possible, for the speed of fronts. Starting from Eq. (25) we define the variable $p(N)=-N_z>0$ such that $p(0)=0$ and $p(1)=0$. Introducing this variable, multiplying by $g/p$, and integrating, we obtain

$$\int_0^1\left(ph(1-ac^2)+\frac{gf}{p}\right)dN=c\int_0^1 g(1-af')dN, \quad (34)$$

where $h=-g'>0$. If $g'(1-ac^2)<0$ then it is possible to use the Swarzian inequality and write

$$ph(1-ac^2)+\frac{gf}{p}\geqslant 2\sqrt{h(1-ac^2)gf}.$$

So from Eq. (34) we find that

$$c\geqslant\frac{2\int_0^1\sqrt{fgh(1-ac^2)}dN}{\int_0^1 g(1-af')dN}, \quad (35)$$

where $g$ is positive definite. For the logistic case $f(N)=N(1-N)$, taking the arbitrary function $g(N)=(1-N)^2$, we find that the limit speed predicted by Benguria's method satisfies

$$c\geqslant\frac{64}{35}\frac{\sqrt{2(1-ac^2)}}{2-a}.$$

Then, there exists a lower bound for $c$ given by

$$c\geqslant c_L^*\equiv\frac{64\sqrt{2}}{\sqrt{1225(2-a)^2+8192a}}.$$

On the other hand, our choice for $g(N)$ implies $g'<0$, thus the inequality $g'(1-ac^2)<0$ leads to an upper limit for $c$, namely, $c\leqslant\tilde{c}\equiv 1/\sqrt{a}$, which coincides with the one found by means of the linearization method.

In summary, using Benguria's method the selected front speeds range from

$$c_L^*\leqslant c<\tilde{c}$$

in this case without any additional restriction on $a$.

It is easy to prove that $c_L^*<c_L$ for $a<1.436$ and $c_L^*>c_L$ for $a>1.436$. In the range of validity of the linearization method, that is for $a<1$, the lower bound predicted by Benguria's method ($c_L^*$) is always lower than that predicted by the linearization method ($c_L$). So, the linearization selection is stronger than the variational one. However, we have shown that from both methods the front speed has also an upper bound $\tilde{c}$, which does not exist in classical reaction-diffusion models.

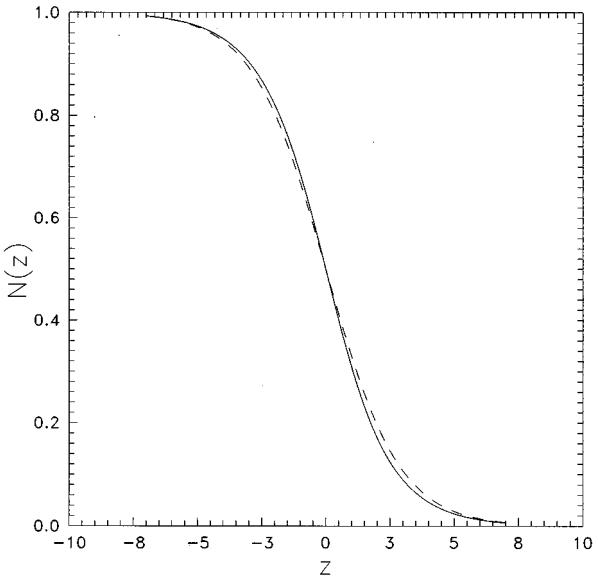


FIG. 1. Entropy production for the front wave solution obtained in the text. The solid line represents the entropy production supplied by EIT, $\sigma_{\mathrm{EIT}}$; the dashed line shows the entropy production in the stochastic description.

### B. Exact heteroclinic solutions

We focus on the special case when $ac^2=1$. In this case one finds the formal solution for Eq. (25):

$$e^{z-z_0/c}=f(N)^a e^{-\int dN/f(N)},$$

where $z_0$ is an integration constant. The problem is to invert this expression. It admits an inversion at least for one specific case as we show in turn. For the generalized logistic growth $f(N)=N(1-N^r)$ this formal solution may be written as

$$e^{z-z_0/c}=N^{a-1}(1-N^r)^{a+1/r}.$$

Choosing $r=2$ and $a=1/4$ the traveling stable wave front is written as

$$N(z)=\frac{1}{2}\left(\sqrt{e^{4(z-z_0)/3}+4}-e^{2(z-z_0)/3}\right), \quad (36)$$

which propagates at speed $c=2$ between the steady states $N=0,1$.

On the other hand, for $a=0$ and $r=2$, there exists an analytical solution for $c=3/\sqrt{2}\simeq 2.12$ given by [1]

$$N(z)=\frac{1}{1+e^{(z-z_0)/\sqrt{2}}}. \quad (37)$$

In Fig. 1, we compare both solutions. One observes that the delayed curve is steeper than the classical one.

## IV. NONEQUILIBRIUM THERMODYNAMICS

One can perform a comparison between the thermodynamic functions coming from the statistic description given in Sec. II A and the ones appearing in extended irreversible thermodynamics. Such a comparison has been done by Camacho and Zakari for the case when there is no source of particles [7].

At the statistic level, the entropy density is written as

$$\begin{aligned} s(x,t) &= -k_B(n_-\ln n_- + n_+\ln n_+) \\ &= -\frac{k_B}{2}\left[\left(n+\frac{J}{v}\right)\ln\frac{1}{2}\left(n+\frac{J}{v}\right)\right. \\ &\quad \left.+\left(n-\frac{J}{v}\right)\ln\frac{1}{2}\left(n-\frac{J}{v}\right)\right] \end{aligned} \tag{38}$$

and the entropy flux as

$$\begin{aligned} J^s(x,t) &= k_B v(n_-\ln n_- - n_+\ln n_+) \\ &= \frac{k_B}{2}\left[\left(n-\frac{J}{v}\right)\ln\frac{1}{2}\left(n-\frac{J}{v}\right)-\left(n+\frac{J}{v}\right)\ln\frac{1}{2}\left(n+\frac{J}{v}\right)\right]. \end{aligned} \tag{39}$$

Up to order $J^2$ both functions coincide with the ones supplied by EIT, as seen in [7]. The entropy production, on the other hand, differs if a generation of particles is present. Therefore, it seems reasonable to wonder if this entropy production obtained from the statistic description coincides, at the lowest orders, with the one proposed by EIT. The balance equation for the entropy, using Eqs. (38) and (39) and the mass balance equation (8), yields

$$\begin{aligned} \sigma_{\rm syst} = \frac{ds}{dt}+\nabla J^s &= -\frac{k_B}{2v}\left[\dot{J}+v^2\frac{\partial n}{\partial x}\right]\ln\left(\frac{nv+J}{nv-J}\right) \\ &\quad -\frac{k_B}{2}F(n)\ln\left[\frac{n^2-J^2}{2}+2\right]. \end{aligned} \tag{40}$$

Expanding the logarithm and keeping up to the lowest order in $J$, one obtains a term of the type of the first one in Eq. (18), namely,

$$\sigma_{\rm dif} \simeq -\frac{k_B}{nv^2}J\left[\dot{J}+v^2\frac{\partial n}{\partial x}\right]=\frac{k_B}{nD}J^2, \tag{41}$$

as already seen in [7]. The new term is the second one in Eq. (40) that, for consistency with EIT, should be recast as the second term in Eq. (19). Let us see that this is so by calculating the chemical potential $\mu T^{-1}$ from Eq. (38),

$$\mu T^{-1} = -\left.\frac{\partial s}{\partial n}\right|_J = \frac{k_B}{2}\ln\left[\frac{n^2-J^2}{2}+2\right].$$

Therefore, we obtain a full agreement between the stochastic description and EIT when one includes a source term.

To end this section, we compare the values of the exact expression for $\sigma_{\rm dif}$ as given by Eq. (40) and the approximate one, Eq. (41), supplied by EIT, for the wave front profile obtained in Sec. III B. For convenience, we write

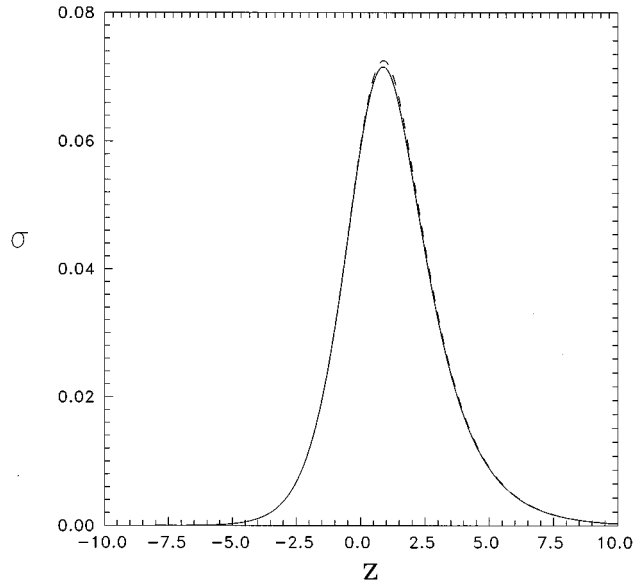


FIG. 2. Wave fronts for a logistic source term $f(N)=N(1-N^2)$ in the delayed case ($a=2, c=2$, solid line), and the classical case ($a=0, c=3/\sqrt{2}\simeq 2.12$, dashed line).

$\sigma^*_{\rm dif}\equiv\sigma_{\rm dif}/kk_B$ and $J^*\equiv J/v$ and omit asterisks. One has, with the help of the transport equation (6),

$$\sigma_{\rm dif}=\frac{J}{2a}\ln\left[\frac{n+J}{n-J}\right] \tag{42}$$

and

$$\sigma_{\rm EIT}\simeq\frac{J^2}{an} \tag{43}$$

for $J\ll n$ (EIT).

Then to evaluate these expressions for the entropy production $\sigma_{\rm dif}$ we need an expression for $J(z)$. By the dimensionless particle balance equation (8) and taking into account that $D=v^2\tau$, one easily finds

$$J(z)=\sqrt{a}\left(cn(z)+\int f(z)dz\right), \tag{44}$$

which, combined with the exact solution (36), yields after tedious calculations

$$J(z)=\frac{1}{4}e^{2z/3}-\frac{1}{8}e^{4z/3}\sqrt{4+e^{4z/3}}+\frac{1}{8}e^{2z}, \tag{45}$$

where $z_0=0$. With this expression for $J(z)$ and Eq. (36) for $N(z)$ we may calculate the entropy density, the entropy production density, etc. In Fig. 2 we plot the entropy production due to diffusion given in the EIT formalism, expression (43), versus the entropy production provided by the statistical description (42). One concludes that the differences are quite small and the entropy production has the form of a soliton. Since diffusion only occurs at the transient region—outside it the concentration is uniform—the entropy production only differs from zero in this region.

## V. CONCLUSIONS

We have proposed in this paper a population dynamic model that includes memory effects, a feature that is not present in other models discussed in the literature. The model presented is based in the inclusion of a relaxation term in the equation governing the flux of particles (or members of a species). We have showed three contexts in which such an equation would arise: a stochastic description, a phenomenological one, and extended irreversible thermodynamics. The combination with the balance of particles—which contains a source term describing, for instance, sexual reproduction—supplies a model equation of the hyperbolic type, having the key property of providing a finite velocity for the speed of a signal, in contrast to the previous models, which are parabolic, and lead to an infinite speed, what is not physically sensible. Let us mention, on the other hand, that the present paper is also of interest for people working in EIT, since it deals with a case where there exists a nonlinear source term, a situation that, as far as we know, has not been faced in the past.

We have performed a dynamical analysis and a thermodynamical one. In the first point, we have shown that the inclusion of memory decreases the lowest bound for the wave front velocities, and also that there exists an upper bound for it, which coincides with the maximum speed of diffusive pulses, i.e., in the absence of source terms. We have also found that Benguria's method for calculating the lowest speed limit is less restrictive than the linearization method. An exact solution for the front shape in the logistic case has also been calculated.

Finally, we have shown that there is a complete agreement between the thermodynamic functions obtained from the stochastic description exposed in Sec. II A—corresponding to a persistent random walk—and EIT in the presence of a source of particles. This extends the proof given by Camacho and Zakari for two-layer systems, where a source term was not considered.

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[1] J.D. Murray *Mathematical Biology* (Springer-Verlag, Berlin, 1989).
[2] C.K. Hayes, J. Math. Biol. **29**, 531 (1991).
[3] T.P. Witelski, J. Math. Biol. **33**, 1 (1994).
[4] R.D. Benguria and M.C. Depassier, Phys. Rev. Lett. **73**, 2272 (1994).
[5] A. Okubo, *Diffusion and Ecological Problems* (Springer-Verlag, Berlin, 1980).
[6] D. Jou, J. Casas-Vázquez, and G. Lebon, *Extended Irreversible Thermodynamics*, 2nd ed. (Springer, Berlin, 1996).
[7] J. Camacho and M. Zakari, Phys. Rev. E **50**, 4233 (1994).
[8] S. Goldstein, Quart. J. Mech. Appl. Math. **4**, 129 (1951); E. Zauderer, *Partial Differential Equations of Applied Mathematics*, 2nd ed. (Wiley, New York, 1989).
[9] G. I. Taylor, Proc. R. Soc. London, Ser. 2 **XX**, 196 (1921).
[10] S. Godoy, J. Chem. Phys. **94**, 6214 (1990); J. Masoliver, Phys. Rev. A **45**, 706 (1992); **45**, 2256 (1992); J. Masoliver and G.H Weiss, Physica A **193**, 469 (1993); **195**, 93 (1993); J. Masoliver, J.M. Porrà, and G.H. Weiss, Phys. Rev. E **48**, 939 (1993).
[11] P. Rosenau, Phys. Rev. E **48**, R655 (1993).
[12] A. Kolmogorov, I. Petrovsky, and N. Piskunov, Bull. Univ. Moscow, Ser. Int. A **1**, 1 (1937) .