Systematic derivation of reaction-diffusion equations with distributed delays and relations to fractional reaction-diffusion equations and hyperbolic transport equations: Application to the theory of Neolithic transition

Marcel Ovidiu Vlad[1,2] and John Ross[1]
[1]*Department of Chemistry, Stanford University, Palo Alto, California 94305-5080*
[2]*Center of Mathematical Statistics, Casa Academiei Romane, Calea Septembrie 13, 76100 Bucharest, Romania*
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We introduce a general method for the systematic derivation of nonlinear reaction-diffusion equations with distributed delays. We study the interactions among different types of moving individuals (atoms, molecules, quasiparticles, biological organisms, etc). The motion of each species is described by the continuous time random walk theory, analyzed in the literature for transport problems, whereas the interactions among the species are described by a set of transformation rates, which are nonlinear functions of the local concentrations of the different types of individuals. We use the time interval between two jumps (the transition time) as an additional state variable and obtain a set of evolution equations, which are local in time. In order to make a connection with the transport models used in the literature, we make transformations which eliminate the transition time and derive a set of nonlocal equations which are nonlinear generalizations of the so-called generalized master equations. The method leads under different specified conditions to various types of nonlocal transport equations including a nonlinear generalization of fractional diffusion equations, hyperbolic reaction-diffusion equations, and delay-differential reaction-diffusion equations. Thus in the analysis of a given problem we can fit to the data the type of reaction-diffusion equation and the corresponding physical and kinetic parameters. The method is illustrated, as a test case, by the study of the neolithic transition. We introduce a set of assumptions which makes it possible to describe the transition from hunting and gathering to agriculture economics by a differential delay reaction-diffusion equation for the population density. We derive a delay evolution equation for the rate of advance of agriculture, which illustrates an application of our analysis.

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I. INTRODUCTION

The nonlocal, space and time distributed, diffusion or reaction-diffusion processes can be described with the integral equations of the continuous-time random walk theory (CTRW [1]) or the generalized master equations (GME [2]) in which both transition times and transition displacements are governed by specified probability distributions. These two types of equations are equivalent to each other [3]. Unfortunately, both types of equations are nonlocal in space and time, and are for this reason very hard to solve for finite systems. In order to overcome this difficulty, different types of approaches have been developed. Hyperbolic diffusion and reaction-diffusion equations (HDE) have been derived by starting out from extended nonequilibrium thermodynamics [4]. A random walk approach [5], which also leads to hyperbolic diffusion equations, has been developed in connection with the study of the Neolithic transition in Europe [6]. A separate, complementary approach is based on the use of fractional diffusion equations (FDE [7]), with the use of the representation of the nonlocal terms by fractional derivatives in time or space.

Recently, attempts have been made in the literature to extend the to use of delay evolution equations to reaction-diffusion systems, based on the HDE and FDE approaches. Unfortunately both the HDE and FDE approaches are less general than the CTRW and GME theories, because they can accommodate only special types of delay functions. The purpose of this paper is the derivation of a generally valid local approach for the description of nonlocal diffusion and reaction-diffusion processes for which the transport component can accommodate any type of delay function. The approach presented in this study is general and can be applied to the study of a broad class of transport and interaction processes in physics, chemistry, biology and population dynamics. Our method is based on the use of the time interval between two jump events (the transition time) as an additional random variable. A similar approach has been introduced by one of us over a decade ago in connection with the computation of correlation functions in semiconductor statistics for the case of fast generation-recombination processes, which was based on the use of a system of age-dependent master equations (ADME [8]). The transport equations presented here are a nonlinear generalization of the ADME.

The structure of the paper is the following. In Sec. II we derive a system of nonlinear, age-dependent evolution equations, which describe the interaction between the transport and transformation processes for macroscopic systems made up of interacting, moving individuals. We transform these age-dependent master equations into a system of nonlinear continuous time and space random walk equations and finally into a system of nonlinear generalized master equations, and show that they include as particular cases various types of nonlinear delay equations, some of which have been discussed in the literature. In Sec. III we derive nonlinear, age-dependent evolution equations for more complex systems, for which it is still possible to derive nonlinear continuous time and space random walk equations; however, in general the derivation of nonlinear generalized master equations is no longer possible. Finally, in Sec. IV we illustrate our approach with the Neolithic transition.

II. NONLOCAL, NONLINEAR REACTION-TRANSPORT PROCESSES

We consider a macroscopic system containing different types of individuals (species) which can be atoms, molecules, quasiparticles, biological organisms, etc. We assume that the different types of individuals interact with each other and at the same time are involved in random walk motions in space and time, which can be described by the CTRW approach. We denote by $\rho_u(\mathbf{r};t)$, $u=1,2,...$ the concentrations of the different species at position $\mathbf{r}$ and time t, expressed in numbers of individuals per unit volume, and assume that the rate of change of the species u, $R_u(t)$, can be expressed as a local, nonlinear, non-negative function of the composition vector $\rho(\mathbf{r};t)=[\rho_u(\mathbf{r};t)]_{u=1,2,...}$ and of time t

$$R_u(t)=R_u(\rho(\mathbf{r};t),)\geqslant 0,u=1,2,... . \tag{1}$$

The motion of the species u can be described by a CTRW process characterized by a time homogeneous and generally space-inhomogeneous propagator:

$$\tilde{\psi}_u(\mathbf{r}',t'\to\mathbf{r},t)d\mathbf{r}\,dt=\psi_u(\mathbf{r}'\to\mathbf{r},\tau)d\mathbf{r}\,d\tau,$$

with

$$\int\int \psi_u(\mathbf{r}'\to\mathbf{r},\tau)d\mathbf{r}\,d\tau=1. \tag{2}$$

Here $\tilde{\psi}_u(\mathbf{r}',t'\to\mathbf{r},t)d\mathbf{r}\,dt$ is the probability that an individual from the u species, which has the position $\mathbf{r}'$ at time t', makes a jump in a time interval between t and $t+dt$ to a position between $\mathbf{r}$ and $\mathbf{r}+d\mathbf{r}$. The difference $\tau=t-t'$ is the transition time, that is, the time interval between two successive jumps (the age of the particle in the position $\mathbf{r}'$). In terms of this propagator we can introduce the survival function of an individual of type u at the position $\mathbf{r}'$

$$\ell_u(\mathbf{r}',\tau)=\int_{\mathbf{r}}\int_{r'=r}^{\infty}\psi_u(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}\,d\tau'. \tag{3}$$

The transition rate from the position $\mathbf{r}'$ to a position between $\mathbf{r}$ and $\mathbf{r}+d\mathbf{r}$ at an age between τ and $\tau+d\tau$ is

$$\mathcal{W}_u(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}\,d\tau'=\psi_u(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}\,d\tau'/\ell_u(\mathbf{r}',\tau'). \tag{4}$$

Now we introduce the notations $\xi_u(\mathbf{r},\tau;t)$ for the position and transition time densities of particles at time t and note that

$$\rho_u(\mathbf{r};t)=\int_0^{\infty}\xi_u(\mathbf{r},\tau;t)d\tau. \tag{5}$$

We can derive the following age-dependent balance equations for the loss of individuals of different types

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial\tau}\right)\xi_u(\mathbf{r},\tau;t)=-\xi_u(\mathbf{r},\tau;t)\int_{\mathbf{r}'}\mathcal{W}_u(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}'. \tag{6}$$

We can also derive the boundary condition

$$\xi_u(\mathbf{r},\tau=0;t)=R_u(\rho(\mathbf{r};t),t)+\int_{\mathbf{r}'}\int_{\tau'}\xi_u(\mathbf{r}',\tau';t)\times\mathcal{W}_u(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'\,d\tau', \tag{7}$$

which describes the jump of a particle from other positions to a position between $\mathbf{r}$ and $\mathbf{r}+d\mathbf{r}$ and the interaction of an individual from the species u with the individuals from the other species. The initial condition for Eq. (6) can be written as

$$\xi_u(\mathbf{r},\tau;t=0)=\rho_u(\mathbf{r},0)v_u^0(\tau|\mathbf{r}), \tag{8}$$

where $v_u^0(\tau|\mathbf{r})$ is the conditional probability of the jump time for a particle of species u placed at position $\mathbf{r}$ at time zero. Equations (6)–(8) determine completely the time evolution of the age-position particle density $\xi_u(\mathbf{r},\tau;t)$ and of the total particle density $\rho_u(\mathbf{r};t)$. They are nonlinear generalizations of the ADME derived in another physical context [8]. In the case of the ADME the unknown function is a probability density, whereas in our case the unknown function is the age-position particle density $\xi_u(\mathbf{r},\tau;t)$; on the other hand, in our equations $\mathbf{r}$ is a position vector in real space whereas the ADME depend on an abstract state vector. Another difference is that in the case of ADME the nonlinear term from Eq. (7) is missing. Nevertheless the mathematical structures of the equations are similar and thus we can generalize the results presented in the literature [8] for the study of our nonlinear problem. In the first place it is easy to show that Eqs. (6)–(8) lead to a nonlinear generalization of the integral equations of the CTRW theory [1]. We integrate Eq. (6) along the characteristics, resulting in

$$\xi_u(\mathbf{r},\tau;t)=\vartheta(t-\tau)\ell_u(\mathbf{r},\tau)Z_u(\mathbf{r},t-\tau)+\vartheta(\tau-t)\rho_u(\mathbf{r},0)\times v_u^0(\tau-t|\mathbf{r})\ell_u(\mathbf{r},\tau)/\ell_u(\mathbf{r},\tau-t), \tag{9}$$

where $Z_u(\mathbf{r},t)=\xi_u(\mathbf{r},\tau=0;t)$ and $\vartheta(x)$ is the Heaviside step function. By inserting Eq. (9) into the boundary condition (7) and into Eq. (5) we get an integral equation for $Z_u(\mathbf{r},t)$ and an expression for the population concentrations $\rho_u(\mathbf{r};t),u=1,2,...$:

$$Z_u(\mathbf{r},t)=R_u(\rho(\mathbf{r},t),t)+\int_0^t\int_{\mathbf{r}'}Z_u(\mathbf{r}',t-\tau')\times\psi_u(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'\,d\tau'+\int_t^{\infty}\int_{\mathbf{r}'}\rho_u(\mathbf{r}',0)\times v_u^0(\tau'-t|\mathbf{r}')\frac{\psi_u(\mathbf{r}'\to\mathbf{r},\tau')}{\ell_u(\mathbf{r}'\tau'-t)}d\mathbf{r}'\,d\tau', \tag{10a}$$

$$\rho_u(\mathbf{r},t)=\int_0^t \ell_u(\mathbf{r},\tau)Z_u(\mathbf{r},t-\tau)d\tau+\rho_u(\mathbf{r},0)\times\int_t^\infty v_u^0(\tau-t|\mathbf{r})\frac{\ell_u(\mathbf{r},\tau)}{\ell_u(\mathbf{r},\tau-t)}d\tau. \quad (10b)$$

Equations (10a) and (10b) determine the time and space evolution of the function $Z_u(\mathbf{r},t)$ and $\rho_u(\mathbf{r};t)$; they are nonlinear generalizations of the integral equations of the CTRW approach. Due to the nonlinear terms R_u no general analytical solutions of Eqs. (10a) and (10b) are available. However, these equations can be transformed into a nonlinear generalization of the generalized master equation. We use the method of Laplace transformation in time for eliminating the functions $Z_u(\mathbf{r},t)$ from Eqs. (10a) and (10b). The main steps of the derivation are outlined in Appendix A. After lengthy algebraic manipulations we obtain

$$\frac{\partial}{\partial t}\rho_u(\mathbf{r},t)=I_u(\mathbf{r},t)+R_u(\rho(\mathbf{r},t),t)+\int_0^t\int_{\mathbf{r}'}[\rho_u(\mathbf{r}',t')\times\psi_u(\mathbf{r}'\to\mathbf{r},t-t')-\rho_u(\mathbf{r},t')\times\psi_u(\mathbf{r}\to\mathbf{r}',t-t')]d\mathbf{r}'dt', \quad (11)$$

where

$$\omega_u(\mathbf{r}\to\mathbf{r}',t-t')=\mathcal{L}_{t-t'}^{-1}\left\{[s\overline{\psi}_u(\mathbf{r}\to\mathbf{r}',s)]\Big/\left[1-\int_{\mathbf{r}''}\overline{\psi}_u(\mathbf{r}\to\mathbf{r}'',s)d\mathbf{r}''\right]\right\} \quad (12)$$

are delayed rate densities, $\overline{\psi}_u(\mathbf{r}\to\mathbf{r}',s)=\mathcal{L}_s\psi_u(\mathbf{r}\to\mathbf{r}',\tau)$ are the Laplace transforms of the propagators attached to the different species, and

$$I_u(\mathbf{r},t)=\rho_u^0(\mathbf{r})\mathcal{L}_t^{-1}\left\{\int_0^\infty\int_{\tau'}^\infty\frac{s v_u^0(\tau-\tau'|\mathbf{r})\ell_u(\mathbf{r},\tau)e^{-s\tau'}}{[1-\int_{r''}\overline{\psi}_u(\mathbf{r}\to\mathbf{r}'',s)d\mathbf{r}'']\ell_u(\mathbf{r},\tau-\tau')}d\tau d\tau'\right\}-\rho_u^0(\mathbf{r})\delta(t)$$
$$+\mathcal{L}_t^{-1}\int_{\mathbf{r}'}\rho_u^0(\mathbf{r}')\int_0^\infty\int_t^\infty\frac{v_u^0(\tau'-\tau'|\mathbf{r}')}{\ell_u(\mathbf{r}',\tau'-\tau')}\left[\psi_u(\mathbf{r}'\to\mathbf{r},\tau')-\frac{s\overline{\psi}_u(\mathbf{r}'\to\mathbf{r},s)\ell_u(\mathbf{r}',\tau')}{1-\int_{\mathbf{r}''}\overline{\psi}_u(\mathbf{r}'\to\mathbf{r}'',s)d\mathbf{r}''}\right]e^{-s\tau'}d\tau d\tau' d\mathbf{r}', \quad (13)$$

where s is a Laplace variable, and the operators $\mathcal{L}_s$ and $\mathcal{L}_\tau^{-1}$ denote the direct and inverse Laplace transformations, respectively. $I_u(\mathbf{r},t)$ are terms which express the fact that the distribution of the transition time and the jump length of an individual at time zero is generally different from the one given by the propagator (2). In particular, if at time zero, the individuals are at the beginning of a waiting period, that is, if $v_u^0(\tau|\mathbf{r})=\delta(\tau)$, then from Eq. (14) it follows that $I_u(\mathbf{r},t)=0$. The contribution of $I_u(\mathbf{r},t)$ is a transient effect, which can be neglected in the analysis of long time behavior. This transient contribution is similar to the contribution of the first jump in the CTRW theory [1].

We notice that a particular case of Eq. (11) has been recently introduced by Feodotov and Okuda [9]. Their equation has the following form:

$$\frac{\partial n}{\partial t}=\int_0^t\int_{-\infty}^{+\infty}[K(x,z,t-s)n(s,z)-K(z,x,t-s)n(s,z)]dzds+Un(1-n), \quad (14)$$

where $n(x,t)$ is a continuous state variable depending on space and time, $K(x,z,t-s)$ is a suitable delay function, and U is a rate coefficient. This equation has been formally introduced as a nonlocal generalization of the classical Fisher equation $\partial n/\partial t=D\partial^2 n/\partial x^2+Un(1-n)$. Equation (14) is postulated without reference to a transport mechanism whereas our general equations (11) are derived by combining the CTRW theory with nonlinear dynamics.

Equations (11) are nonlinear generalizations of the so-called generalized master equation [2]. By considering different particular cases, they lead to various reaction-transport equations. By performing a Kramers-Moyal expansion in Eqs. (11) and neglecting the transient terms $I_u(\mathbf{r},t),u=1,2,...$ we come to

$$\frac{\partial}{\partial t}\rho_u(\mathbf{r},t)=R_u(\rho(\mathbf{r},t),t)+\int_0^t\sum_{m=1}^\infty(-1)^m\sum_{\mu_1}\cdots\sum_{\mu_m}\frac{\partial^m}{\partial r_{\mu_1}\ldots\partial r_{\mu_m}}\times\{\mathcal{D}^{u(m)}_{\mu_1\cdots\mu_m}(\mathbf{r},t-t')\rho_u(\mathbf{r},t')\}dt', \quad (15)$$

where

$$\mathcal{D}^{u(m)}_{\mu_1\cdots\mu_m}(\mathbf{r},t-t')=\frac{1}{m!}\int_{\mathbf{r}'}\prod_{N=1}^m(r_{\mu_u}-r'_{\mu_u})\times\omega_u(\mathbf{r}'\to\mathbf{r},t-t')d\mathbf{r}', \quad (16)$$

are delayed probability diffusion coefficients. By truncating the Kramers-Moyal series in Eqs. (15) to terms of order one and two we come to a nonlinear generalization of the Fokker-Planck equations with memory, used in condensed matter physics [2]. An important example of such equations corresponds to the case where the delayed drift coefficients $v_{\mu}^{u}(\mathbf{r},t-t')=\mathcal{D}_{\mu}^{u(1)}(\mathbf{r},t-t')$ are generated by a scalar force field $U(\mathbf{r})$:

$$v_{\mu}^{(u)}(\mathbf{r},t-t')=-\sum_{\mu'}\mathfrak{b}_{\mu\mu'}^{(u)}(t-t')[\partial U(\mathbf{r})/\partial r_{\mu'}], \quad (17)$$

where $\mathfrak{b}_{\mu\mu'}^{(u)}(t-t')$ are delayed mobility tensors attached to the different species. The evolution equations become

$$\frac{\partial}{\partial t}\rho_u(\mathbf{r},t)=R_u(\rho(\mathbf{r},t),t)+\int_0^t\sum_{\mu}\sum_{\mu'}\frac{\partial^2}{\partial r_{\mu}\partial r_{\mu'}}\times[\mathcal{D}_{\mu\mu'}^{u(2)}(\mathbf{r},t-t')\rho_u(\mathbf{r},t')]+\int_0^t\left\{\sum_{\mu}\sum_{\mu'}\mathfrak{b}_{\mu\mu'}^{u}(t-t')\left[\rho_u(\mathbf{r},t')\frac{\partial^2}{\partial r_{\mu}\partial r_{\mu'}}\times U(\mathbf{r})+\left[\frac{\partial^2}{\partial r_{\mu}}U(\mathbf{r})\right]\frac{\partial}{\partial r_{\mu'}}\rho_u(\mathbf{r},t')\right]\right\}dt'. \quad (18)$$

We suggest that Eqs. (18) can be used for the study of the propagation of reaction-diffusion waves in chemical systems in external force fields, for example in electrochemistry, plasma physics or for separation processes in centrifugal or gravitational fields.

An important particular class of cases is one for which the delayed transition rates $\omega_u(\mathbf{r}\to\mathbf{r}',t-t')$ can be factored into space-dependent terms, $W_u(\mathbf{r}\to\mathbf{r}')$, and time-dependent delay terms $\varphi_u(t-t')$

$$\psi_u(\mathbf{r}\to\mathbf{r}',t-t')=\varphi_u(t-t')W_u(\mathbf{r}\to\mathbf{r}'), \quad (19)$$

where $W_u(\mathbf{r}\to\mathbf{r}')$ are local (Markovian) transition rates. In this case the delayed diffusion coefficients are also factorizable:

$$\mathcal{D}_{\mu_1\cdots\mu_m}^{u(m)}(\mathbf{r},t-t')=\varphi_u(t-t')D_{\mu_1\cdots\mu_m}^{u(m)}(\mathbf{r}), \quad (20)$$

where $D_{\mu_1\cdots\mu_m}^{u(m)}(\mathbf{r})$ are Markovian probability diffusion coefficients and the nonlinear generalized master equations can be expressed as

$$\partial\rho_u(\mathbf{r},t)/\partial t=R_u(\rho(\mathbf{r},t),t)+\varphi_u(t)\otimes\mathbb{L}_u\rho_u(\mathbf{r},t), \quad (21)$$

where $\otimes$ denotes the temporal convolution product and

$$\mathbb{L}_u\ldots=\int_{\mathbf{r}'}[\ldots W_u(\mathbf{r}'\to\mathbf{r})d\mathbf{r}'-\ldots W_u(\mathbf{r}\to\mathbf{r}')d\mathbf{r}']=\sum_{m=1}^{\infty}(-1)^m\sum_{\mu_1}\ldots\sum_{\mu_m}\frac{\partial^m}{\partial r_{\mu_1}\ldots\partial r_{\mu_m}}\{D_{\mu_1\cdots\mu_m}^{u(m)}(\mathbf{r})\ldots\} \quad (22)$$

are linear, Markovian transport operators.

We distinguish three important particular subcases of Eqs. (21). The first subcase corresponds to a delay function having a long tail of the negative power law type:

$$\varphi_u(t-t')\sim-\frac{(1-H_u)}{(\sigma_u)^{1+H_u}\Gamma(H_u)}(t-t')^{-(1-H_u)},1>H_u>0, \quad (23)$$

where H_u are fractal exponents between zero and one, and σ_u are characteristic time scales attached to the different species, respectively. In this subcase Eqs. (22) become fractional transport equations

$$\frac{\partial^{H_u}}{\partial t^{H_u}}\rho_u(\mathbf{r},t)=\int_0^t\frac{\partial^{H_u}}{\partial t'^{H_u}}R_u(\rho(\mathbf{r},t'),t')dt'+(\sigma_u)^{1+H_u}\mathbb{L}_u\rho_u(\mathbf{r},t), \quad (24)$$

where

$$\frac{\partial^H}{\partial t^H}f(t)=\frac{1}{\Gamma(1-H)}\frac{d}{dt}\int_0^t\frac{f(t')}{(t-t')^H}dt',1>H>0, \quad (25)$$

is the fractional derivative of order H. Equations (24) are nonlinear generalizations of the fractional diffusion equations recently introduced in the literature [7] for the description of dispersive diffusion.

Another important subcase corresponds to exponential delay functions

$$\varphi_u(t-t')=(\sigma_u)^{-1}\exp[-(t-t')/\sigma_u]. \quad (26)$$

Here the transport equations (21) become hyperbolic

$$\left(\sigma_u\frac{\partial^2}{\partial t^2}+\frac{\partial}{\partial t}\right)\rho_u(\mathbf{r},t)=\left[1+\sigma_u\frac{\partial}{\partial t}+\sigma_u\sum_{u'}\frac{\partial\rho_{u'}(\mathbf{r},t)}{\partial t}\frac{\partial}{\partial\rho_{u'}}\right]\times R_u(\rho(\mathbf{r},t),t)+\mathbb{L}_u\rho_u(\mathbf{r},t). \quad (27)$$

A third subcase corresponds to the situation where the delay function is a combination of exponential terms:

$$\varphi_u(t-t')=\sum_v\pi_{uv}(\sigma_{uv})^{-1}\exp[-(t-t')/\sigma_{uv}], \quad (28)$$

where σ_{uv} are relaxation times and π_{uv} are weight factors. In this case we can introduce the auxiliary field functions:

$$\Xi_{uv}(\mathbf{r},t)=\mathcal{L}_t^{-1}\left[\frac{\mathcal{L}_s\rho_u(\mathbf{r},t)}{1+\sigma_{uv}s}\right]=\int_0^t\rho_u(\mathbf{r},t-t')(\sigma_{uv})^{-1}\exp[-t'/\sigma_{uv}]dt'. \quad (29)$$

By using these auxiliary field functions we can reduce Eq. (21) to a system of evolution equations local in time:

$$\frac{\partial}{\partial t}\rho_u(\mathbf{r},t)=R_u(\rho(\mathbf{r},t),t)+\sum_{v=1}^{m}\pi_{uv}\mathbb{L}_u\Xi_{uv}(\mathbf{r},t), \quad (30)$$

$$\sigma_{uv}\frac{\partial}{\partial t}\Xi_{uv}(\mathbf{r},t)+\Xi_{uv}(\mathbf{r},t)=\rho_u(\mathbf{r},t). \quad (31)$$

Equations (30) and (31) are nonlinear generalizations of telegrapher's equations from electrodynamics. By eliminating the auxiliary fields $\Xi_{uv}(\mathbf{r},t)$ from Eqs. (30) and (31) we come to an evolution equation which contains time derivatives of high order. We have

$$\prod_{w=1}^{m} \mathcal{D}_{uw}\left[\frac{\partial}{\partial t}\rho_u(\mathbf{r},t)-R_u(\rho(\mathbf{r},t),t)\right] = \sum_{v=1}^{m} \pi_{uv}\prod_{w\neq v}^{\mathcal{N}} \mathcal{D}_{uw}\mathbb{L}_u\rho_u(\mathbf{r},t), \tag{32}$$

where

$$\mathcal{D}_{uw}=1+\sigma_{uw}\frac{\partial}{\partial t}, \tag{33}$$

are differential operators. In the particular case of a single exponential, $v=1$, Eq. (34) reduces to the hyperbolic transport equation (27). Another interesting situation corresponds to the case where all relaxation times for a species are equal: $\sigma_{u1}=\sigma_{u2}=\ldots=\sigma_{um}=\sigma_u$. In this case the delay function (28) is replaced by

$$\varphi_u(t-t')=\frac{(\sigma_u)^{-1}}{(m-1)!}\left(\frac{t-t'}{\sigma_u}\right)^{m-1}\exp[-(t-t')/\sigma_u], \tag{34}$$

and Eq. (32) becomes

$$\left(1+\sigma_u\frac{\partial}{\partial t}\right)^m\left[\frac{\partial}{\partial t}\rho_u(\mathbf{r},t)-R_u(\rho(\mathbf{r},t),t)\right]=\mathbb{L}_u\rho_u(\mathbf{r},t). \tag{35}$$

A fourth subcase corresponds to a constant delay

$$\varphi_u(t-t')=\delta(t-t'-\sigma_u), \tag{36}$$

for which the evolution equations (21) turn into integro-differential equations with constant delays:

$$\partial\rho_u(\mathbf{r},t+\sigma_u)/\partial t=R_u(\rho(\mathbf{r},t+\sigma_u),t+\sigma_u)+\mathbb{L}_u\rho_u(\mathbf{r},t), \tag{37}$$

Equations similar to Eq. (37) are used at times in theoretical biology.

In conclusion, in this section we have introduced a general method for the derivation of transport equations with distributed time delays for a system containing different types of moving individuals. We have assumed that the motion of each individual is described by a continuous time random walk, whereas the interactions among individuals is described by a set of local, nonlinear transformation rates. We have introduced an additional state variable, the transition time, which makes it possible to derive a set of nonlinear, age-dependent evolution equations which are local in time. By eliminating the transition time from the evolution equations we derive a nonlinear generalization of the generalized master equation, which includes as particular cases various delay reaction-transport equations derived in literature, such as fractional transport equations and hyperbolic transport equations.

III. GENERALIZATIONS OF THE THEORY

The reduction of the nonlinear age-dependent transport equations to nonlinear generalized master equations is possible only if the net generation rates of individuals of different types are non-negative $R_u(\rho(\mathbf{r};t),t)\geqslant 0$, Eq. (1). However, for many physical, chemical and biological processes this condition is not satisfied. In this section we generalize the nonlinear, age-dependent transport equations to the case where the net generation rates can be negative. We assume that the net rate of production of species u is the difference between a generation rate $R_u^+(\rho(\mathbf{r};t),t)\geqslant 0$ and a consumption rate $R_u^-(\rho(\mathbf{r};t),t)\geqslant 0$:

$$R_u(\rho(\mathbf{r};t),t)=R_u^+(\rho(\mathbf{r};t),t)-R_u^-(\rho(\mathbf{r};t),t), \quad u=1,2,\ldots. \tag{38}$$

Although in Eq. (38) the individual generation and consumption rates are non-negative, $R_u^{\pm}(\rho(\mathbf{r};t),t)\geqslant 0$, their differences can be positive or negative. Under these circumstances the evolution equations (6) and (7) are replaced by

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial \tau}\right)\xi_u(\mathbf{r},\tau;t)=-\xi_u(\mathbf{r},\tau;t)\int_{\mathbf{r}'}\mathcal{W}_u(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}' - \frac{\xi_u(\mathbf{r},\tau;t)}{\rho_u(\mathbf{r};t)}R_u^-(\rho(\mathbf{r};t),t), \tag{39}$$

$$\xi_u(\mathbf{r},\tau=0;t)=R_u^+(\rho(\mathbf{r};t),t)+\int_{\mathbf{r}'}\int_{r'}\xi_u(\mathbf{r}',\tau';t)\times\mathcal{W}_u(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'d\tau'. \tag{40}$$

In Eq. (39) we have assumed that the rate of disappearance of the species u, $R_u^-(\rho(\mathbf{r};t),t)$ is uniformly distributed for all ages. This assumption is usually satisfied in physics or chemistry, because the rate processes are independent of age. In biology, however, this assumption is generally invalid and Eqs. (39) and (40) must be replaced by a more general evolution equation.

The nonlinear age-dependent equations can be transformed into a nonlinear generalization of the CTRW equations, similar to Eqs. (9)–(11) derived in Sec. II. We integrate Eq. (39) along the characteristics, and express the initial conditions in the form (8). We obtain

$$\begin{aligned}\xi_u(\mathbf{r},\tau;t)=&\,\vartheta(t-\tau)\ell_u(\mathbf{r},\tau)\times\exp\left[-\int_{t-\tau}^{t}\frac{R_u^-(\rho(\mathbf{r};t'),t')}{\rho_u(\mathbf{r};t')}dt'\right]Z_u(\mathbf{r},t-\tau)\\&+\vartheta(\tau-t)\rho_u(\mathbf{r},0)v_u^0(\tau-t|\mathbf{r})\frac{\ell_u(\mathbf{r},\tau)}{\ell_u(\mathbf{r},\tau-t)}\times\exp\left[-\int_0^t\frac{R_u^-(\rho(\mathbf{r};t'),t)}{\rho_u(\mathbf{r};t')}dt'\right],\end{aligned} \tag{41}$$

where $Z_u(\mathbf{r},t)=\xi_u(\mathbf{r},\tau=0;t)$. Now we insert Eq. (41) into Eq. (40) and Eq. (5). We come to

$$Z_u(\mathbf{r},t)=R_u^+(\rho(\mathbf{r},t),t)+\int_0^t\int_{\mathbf{r}'}Z_u(\mathbf{r}',t-\tau')\psi_u(\mathbf{r}'\rightarrow\mathbf{r},\tau')\exp\left[-\int_{t-\tau'}^t\frac{R_u^-(\rho(\mathbf{r}';t'),t)}{\rho_u(\mathbf{r}';t')}dt'\right]d\mathbf{r}'d\tau'$$
$$+\int_t^\infty\int_{\mathbf{r}'}\rho_u(\mathbf{r}',0)v_u^0(\tau'-t|\mathbf{r}')\frac{\psi_u(\mathbf{r}'\rightarrow\mathbf{r},\tau')}{\ell_u(\mathbf{r}',\tau'-t)}\exp\left[-\int_0^t\frac{R_u^-(\rho(\mathbf{r}';t'),t')}{\rho_u(\mathbf{r}';t')}dt'\right]d\mathbf{r}'d\tau', \quad (42)$$

$$\rho_u(\mathbf{r};t)=\int_0^t\ell_u(\mathbf{r},\tau)\exp\left[-\int_{t-\tau}^t\frac{R_u^-(\rho(\mathbf{r};t'),t')}{\rho_u(\mathbf{r};t')}dt'\right]Z_u(\mathbf{r},t-\tau)d\tau+\rho_u(\mathbf{r},0)\exp\left[-\int_0^t\frac{R_u^-(\rho(\mathbf{r};t'),t')}{\rho_u(\mathbf{r};t')}dt'\right]$$
$$\times\int_t^\infty v_u^0(\tau-t|\mathbf{r})\frac{\ell_u(\mathbf{r},\tau)}{\ell_u(\mathbf{r},\tau-t)}d\tau. \quad (43)$$

Equations (42) and (43) are nonlinear integral equations which determine the time and space dependence of the population densities $\rho_u(\mathbf{r};t)$ and of the functions $Z_u(\mathbf{r},t)=\xi_u(\mathbf{r},\tau=0;t)$; they are nonlinear generalizations of the CTRW theory for the case of a process with transport and transformation described by the propagator $\tilde{\psi}_u(\mathbf{r}',t'\rightarrow\mathbf{r},t)d\mathbf{r}\,dt$ and by the rates $R_u^\pm(\rho(\mathbf{r};t),t)$. In the particular case of a system without generation and consumption processes, $R_u^\pm(\rho(\mathbf{r};t),t)=0$, Eqs. (42) and (43) reduce to the classical evolution equations of the CTRW approach. Unfortunately, due to the exponential dependence on the integrals of the fractions R_u^-/ρ_u, in general Eqs. (42) and (43) can no longer be reduced to a nonlinear generalization of the generalized master equation. Such a reduction if possible if $R_u^-=0$, $u=1,2,...$; in this case Eqs. (42) and (43) reduce to Eqs. (9) and (10) derived in Sec. II.

A more complicated model corresponds to the case where the kinetics of the process itself is age-dependent. Such a situation is commonly encountered in biological population dynamics and population genetics, where the generation and consumption rates depend on the ages of the individuals involved in the process. In general we must make a distinction among the age of a jump event, the transition time τ, and the age a_u of an individual of type u. We introduce the notations $\zeta_u(\mathbf{r},a,\tau;t)$ for the position, age, and transition time densities of particles at time t and note that

$$\xi_u(\mathbf{r},\tau;t)=\int_0^\infty\zeta_u(\mathbf{r},a,\tau;t)da,$$

$$\rho_u(\mathbf{r};t)=\int_0^\infty\int_0^\infty\zeta_u(\mathbf{r},a,\tau;t)d\tau\,da. \quad (44)$$

An individual of type u is initially generated at an age $a_u=0$, and then ages as time goes on. We denote by $\mathcal{R}_u^+(0,\mathbf{r},t)$ the rate of generation of individuals of type u at position $\mathbf{r}$ and time t. We assume that $\mathcal{R}_u^+(0,\mathbf{r},t)$ is a functional of the vector of the density functions $\zeta(\mathbf{r},a,\tau;t)=[\zeta_u(\mathbf{r},a,\tau;t)]$ which also depends on the vector $\mathbf{a}=(a_1,a_2,\ldots)$ of the ages of the individuals involved in the generation process

$$\mathcal{R}_u^+(0,\mathbf{r},t)=\mathcal{R}_u^+[\mathbf{a},\zeta(\mathbf{r},a,\tau;t),t]. \quad (45)$$

Similarly, we denote by $\mathcal{R}_u^-(a_u,\mathbf{r},t)$ the rate of disappearance of individuals of type u at age a_u, position $\mathbf{r}$ and time t and assume that it is given by a nonlinear dependence similar to Eq. (45)

$$\mathcal{R}_u^-(a_u,\mathbf{r},t)=\mathcal{R}_u^-[a_u,\zeta(\mathbf{r},a,\tau;t),t]. \quad (46)$$

By using the age-dependent kinetic laws (45) and (46) we can derive the following nonlinear age-dependent master equations for the density functions $\zeta_u(\mathbf{r},a,\tau;t)$:

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a_u}+\frac{\partial}{\partial\tau}\right)\zeta_u(\mathbf{r},a_u,\tau;t)$$
$$=-\zeta_u(\mathbf{r},a_u,\tau;t)\int_{\mathbf{r}'}\mathcal{W}_u(\mathbf{r}\rightarrow\mathbf{r}',\tau)d\mathbf{r}'$$
$$-\delta(\tau)\mathcal{R}_u^-[a_u,\zeta(\mathbf{r},a,\tau;t),t], \quad (47)$$

$$\zeta_u(\mathbf{r},a_u,\tau=0;t)=\int_{\mathbf{r}'}\int_{r'}\zeta_u(\mathbf{r}',a_u,\tau';t)$$
$$\times\mathcal{W}_u(\mathbf{r}'\rightarrow\mathbf{r},\tau')d\mathbf{r}'d\tau', \quad (48)$$

$$\zeta_u(\mathbf{r},a_u=0,\tau;t)$$
$$=\delta(\tau)\int_{\tau'}\int_{a_1}\int_{a_2}\ldots\mathcal{R}_u^+[\mathbf{a},\zeta(\mathbf{r},a,\tau';t),t]d\mathbf{a}\,d\tau'. \quad (49)$$

By integrating the nonlinear age-dependent master equations (47)–(49) along the characteristics we can derive a system of nonlinear integral equations for the density functions $\zeta_u(\mathbf{r},a,\tau;t)$. These integral equations take two different continuous time walks into account: the first random walk describes the time evolution of the individuals and the second one the transport process itself. In general the evolution equations (47)–(49) cannot be reduced to a nonlinear generalized master equation. However, if the transit time, which describes the transport process, is related to the age of the individuals, which describes the population kinetics, the model can be reduced to a nonlinear generalized master equation. In particular, this is possible in the case of the theory of Neolithic transition, which is discussed in the following section.

IV. DISTRIBUTED DELAYS AND THE THEORY OF NEOLITHIC TRANSITION

For illustrating the theory as a test case we study the transition from hunting and gathering to agriculture economics. For the description of population dynamics we use a nonlinear generalization of Lotka's theory of stable population [10]. We consider that the maternity (natality) function of the population, λ, depends only on the age a, $\lambda=\lambda(a)$, and that the mortality function, μ, is made up of two components, an age dependent component, $\mu_0(a)$, and a density dependent component, $\delta\mu(\rho)$, which is a function of the population density ρ. Under these circumstances, after a transient regime of a few centuries, the population reaches a stable regime for which the fraction of individuals with a given age (the age profile)

$$c(a|\mathbf{r};t)da \quad \text{with} \quad \int_0^\infty c(a|\mathbf{r};t)da=1, \tag{50}$$

becomes stationary and position independent [10]

$$\begin{aligned} c\,da&=c_{st}(a)da\\ &=Z^{-1}(r)l(a)\exp(-ra)da \quad \text{independent of } \mathbf{r},t, \end{aligned} \tag{51}$$

and the rate of growth is given by a generalized logistic equation:

$$R(\rho)=\rho[r-\delta\mu(\rho)]. \tag{52}$$

where r, the intrinsic rate of growth, is the unique real root of the transcendental equation

$$\int_0^\infty \lambda(a)l(a)e^{-ra}da=1, \tag{53}$$

the function

$$l(a)=\exp\left(-\int_0^a \mu_0(a')da'\right) \tag{54}$$

is the survival function (the life table) evaluated from the density-independent component of the mortality function $\mu_0(a)$, and

$$Z(r)=\int_0^\infty l(a)\exp(-ra)da \tag{55}$$

is a partition function attached to the stable Lotka age profile (51).

We assume that the migration of the population can be described by a separable CTRW propagator:

$$\psi(\mathbf{r}'\to\mathbf{r},\tau)d\mathbf{r}d\tau=\psi_{\mathbf{r}}(\mathbf{r}-\mathbf{r}')d\mathbf{r}\psi_\tau(\tau)d\tau, \tag{56}$$

which can be expressed as the product of a space-dependent component and of a time-dependent component. It has been suggested [5] that the migration time, τ, is closely related to the time difference a between two successive generations. Denoting by $\overline{m}$ the number of migration events per generations, we have $\tau=a/\overline{m}$. Denoting by $g(a)da$ the probability that the duration of a generation is between a and $a+da$, we come to

$$\psi_\tau(\tau)d\tau=d\tau\int \delta(\tau-a/\overline{m})g(a)da=\overline{m}g(\overline{m}\tau)d\tau. \tag{57}$$

Now we have all elements necessary for building a generalized population model similar to the one described by Eqs. (47)–(49). We obtain a set of evolution equations for the age, position and transit time density function $\zeta(\mathbf{r},a,\tau;t)$:

$$\begin{aligned} &\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a}+\frac{\partial}{\partial \tau}\right)\zeta(\mathbf{r},a,\tau;t)\\ &\quad=-\zeta(\mathbf{r},a,\tau;t)\int_{\mathbf{r}'}\mathcal{W}(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}'-\delta(\tau)\vartheta(\mathbf{r},a;t)\\ &\qquad\times[\mu_0(a)+\delta\mu(\rho(\mathbf{r};t))], \end{aligned} \tag{58}$$

$$\zeta(\mathbf{r},a,\tau=0;t)=\int_{\mathbf{r}'}\int_{\tau'}\zeta(\mathbf{r}',a,\tau';t)\mathcal{W}(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'d\tau', \tag{59}$$

$$\zeta(\mathbf{r},a=0,\tau;t)=\delta(\tau)\int_0^\infty\int_0^\infty \lambda(a')\zeta(\mathbf{r},a',\tau';t)da'd\tau', \tag{60}$$

where

$$\vartheta(\mathbf{r},a;t)=\int_0^\infty \zeta(\mathbf{r},a,\tau;t)d\tau \tag{61}$$

is the age-position density of individuals at time t.

In Appendix B we show that, by assuming that the age profile of the population is given by the stable Lotka form (51), it is possible to eliminate the age variable a from the evolution equations (58)–(60). We obtain

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial \tau}\right)\xi(\mathbf{r},\tau;t)=-\xi(\mathbf{r},\tau;t)\int_{\mathbf{r}'}\mathcal{W}(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}', \tag{62}$$

$$\begin{aligned} \xi(\mathbf{r},\tau=0;t)&=R(\rho(\mathbf{r};t))\\ &\quad+\int_{\mathbf{r}'}\int_{\tau'}\xi(\mathbf{r}',\tau';t)\mathcal{W}(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'d\tau', \end{aligned} \tag{63}$$

where

$$\rho(\mathbf{r};t)=\int_0^\infty \xi(\mathbf{r},\tau;t)d\tau \tag{64}$$

is the total population density at position $\mathbf{r}$ and time t.

Equations (62) and (63) have the same structure as the general equations (6) and (7) derived in Sec. II. It follows that they can be reduced both to a system of nonlinear CRTW equations as well as to a nonlinear generalization of the master equation. We neglect the inhomogeneous term (13) and use the expressions (56) and (57) for the propagator $\psi(\mathbf{r}' \to \mathbf{r}, \tau) d\mathbf{r}\, d\tau$. We come to

$$\frac{\partial}{\partial t}\rho(\mathbf{r},t) = R(\rho(\mathbf{r},t)) + \Omega(t) \otimes \int_{\mathbf{r}'} [\rho(\mathbf{r}',t)\psi_{\mathbf{r}}(\mathbf{r}' \to \mathbf{r}) - \rho(\mathbf{r},t)\psi_{\mathbf{r}}(\mathbf{r} \to \mathbf{r}')] d\mathbf{r}', \tag{65}$$

where

$$\Omega(t) = \mathcal{L}_t^{-1}\left[\frac{s\overline{g}(s/\overline{m})}{1 - \overline{g}(s/\overline{m})}\right] \tag{66}$$

is a time-dependent frequency factor and

$$\overline{g}(s) = \int_0^\infty \exp(-sa) g(a) da, \tag{67}$$

is the characteristic function of the probability density of the time interval between two generations.

Mathematical demography [11] provides two different evaluations for the probability density of the time interval between two generations: an Eulerian, transversal (census type) evaluation, which expresses the distribution of the generation length at a given moment in time, and a Lagrangian, longitudinal (cohort type) evaluation, which expresses the distribution of the generation time for a group of individuals passing through life. Since the CTRW approach uses a Lagrangian description of motion, we should use the longitudinal evaluation, which in the case of a stable population leads to

$$g(a)da = \lambda(a) l(a) da \Big/ \int_0^\infty \lambda(a) l(a) da. \tag{68}$$

Unfortunately detailed demographic data for ancient populations are not available and thus Eq. (54) cannot be used directly. A common practice in mathematical population dynamics is the approximation of the delay functions by a superposition of exponentials [12]. For a developed population $g(a)$ is a bell-shaped curve, which increases from $g = 0$ for the minimum age of procreation, increases up to a maximum value, and then decreases and reaches again the value zero for the maximum age of procreation. A bell-shaped curve, which approximates such a behavior, can be easily generated by a combination of exponential functions. A crude representation of the growth and extinction of a generation can be given by a Markov process in continuous time with $N+1$ states $u = 1,...,N+1$, where $u = 1$ corresponds to a newly created generation, $u = 2,...,N$ to the process of growing and maturation of the generation, and the state $u = N+1$, which is a trap, corresponds to the extinction of the generation. We assume that at age zero the system is in the state $u = 1$, $p_u(0) = \delta_{u1}$ and that only N types of transitions can take place, $1 \to 2$, $2 \to 3$,...$N \to N+1$; we denote the rates of these transitions $k_1, k_2, \ldots, k_N$, respectively. Under these circumstances the probability density of the generation time, $g(a)$, is given by the probability density of the first passage time from the state 1 to the state $N+1$. By using the theory of Markov processes we can express $g(a)$ as the N-fold convolution product of the lifetime probability densities of the different states $k_u \exp(-ak_u)$, $u = 1,...,N$:

$$g(a) = \prod_{u=1}^{N} (k_u \exp(-ak_u) \otimes). \tag{69}$$

Since we have no detailed observations for $g(a)$, but only an estimate of the average value of the generation length, $\langle a \rangle \approx 25$ yr [6], in the following we assume that all transition rates are equal $k_1 = \cdots = k_N = k$. Under these circumstances the distribution of the generation length is given by a gamma probability density:

$$g(a) = [(N-1)!]^{-1} k^N a^{N-1} \exp(-ka) \quad \text{with } \langle a \rangle = N/k. \tag{70}$$

We assume that the random walk of the population is symmetric and isotropic and thus the moments of order one and two of the components of the displacement vector $\Delta\mathbf{r} = \mathbf{r} - \mathbf{r}'$ for a migration event are given in two dimensions by $\langle \Delta r_\alpha \rangle = 0$, $\alpha = 1,2$; $\langle \Delta r_\alpha \Delta r_{\alpha'} \rangle = 1/2\delta_{\alpha\alpha'} \langle |\Delta\mathbf{r}|^2 \rangle_m$, α, $\alpha' = 1,2$, where $\langle |\Delta\mathbf{r}|^2 \rangle_m$ is the dispersion of the displacement vector corresponding to a migration event. The numerical data reported in the literature refer to the dispersion of the displacement vector per generation, $\langle |\Delta\mathbf{r}|^2 \rangle_g$, which is related to $\langle |\Delta\mathbf{r}|^2 \rangle_m$ by a linear relation, $\langle |\Delta\mathbf{r}|^2 \rangle_g = \overline{m} \langle |\Delta\mathbf{r}|^2 \rangle_m$.

In the diffusion approximation the nonlinear generalized master equation (65) becomes

$$\frac{\partial}{\partial t}\rho(\mathbf{r},t) + \sum_{\varepsilon=2}^{N} \frac{(N-1)!}{\varepsilon!(N-\varepsilon)!}\left(\frac{\langle a \rangle}{N\overline{m}}\right)^{\varepsilon-1} \left\{\frac{\partial^\varepsilon}{\partial t^\varepsilon}\rho(\mathbf{r},t) - \frac{\partial^{\varepsilon-1}}{\partial t^{\varepsilon-1}} R[\rho(\mathbf{r},t)]\right\} = R[\rho(\mathbf{r},t)] + D\nabla^2\rho(\mathbf{r},t), \tag{71}$$

where $R(\rho) = \rho[r - \delta\mu(\rho)]$ and

$$D = \langle |\Delta\mathbf{r}|^2 \rangle_g / (4\langle a \rangle). \tag{72}$$

According to Refs. [5], [6] we assume that the intrinsic rate of growth for primitive populations is $r \approx 0.03\ \text{yr}^{-1}$ and the diffusion coefficient is $D \approx 15\ \text{km}^2/\text{yr}$. The rate constant k and the number of states N should be chosen in such a way that the gamma law (70) gives a biologically realistic estimate for the distribution of the generation length. One constraint results from the estimated value of the generation time reported in the literature, $k/N = \langle a \rangle \approx 25$ yr. A second constraint results by choosing biologically realistic figures for the modal value of the generation time, a_m. The gamma probability density (70) has a single maximum for the modal value $a = a_m = \langle a \rangle (N-1)/N$.

We evaluate the average number $\overline{m}$ of migration events per generation compatible with the rate of propagation of agriculture evaluated from archeological studies, $v \approx 1$ km/yr [6]. In order to check whether stable wave fronts of the Neolithic transition exist we must linearize Eq. (71) by considering small perturbations of the form $\rho = \exp(\lambda z)$ near $\rho = 0$ and, in order to rule out the existence of an oscillatory behavior, require that λ is real. In the following we consider three particular cases. For $N=1$ the sum in Eq. (71) disappears and our model reduces to Fisher's parabolic model [6], for which the velocity of propagation is $v = 2\sqrt{rD}$. The distribution of the generation time is exponential and the modal value of the generation time is equal to zero, $a_m = 0$. In this case the computed value of the propagation front, $v \approx 1.35$ km/yr, is bigger than the observed value and is independent of $\overline{m}$.

For $N=2$ Eq. (71) becomes hyperbolic and the velocity of the propagation front is given by

$$v = 4\overline{m}k\sqrt{rD}/[r + 2k\overline{m}] \quad \text{with} \quad r < 2k\overline{m}. \tag{73}$$

From Eq. (73) it follows that the mean number of migration events per generation compatible with the observed velocity is $\overline{m} \approx 0.55$, that is one migration event occurs in about two generations and the average migration time is $\langle \tau \rangle \approx 45$ yr. In this case the modal value of the generation time is $a_m = \langle a \rangle /2 \approx 12.5$ yr.

In the limit $N \to \infty$ the gamma probability density (70) tends towards a delta function

$$g(a) = \delta(a - \langle a \rangle), \tag{74}$$

the modal value of the generation time is equal to the average value $a_m = \langle a \rangle \approx 25$ yr, and the evolution equation (71) becomes a differential-delay equation

$$\frac{\overline{m}}{\langle a \rangle}\left\{ \rho\left(t + \frac{\langle a \rangle}{\overline{m}} \right) - \rho(t) \right\} = \frac{\overline{m}}{\langle a \rangle}\int_0^t \left\{ R\left[\rho\left(t' + \frac{\langle a \rangle}{\overline{m}} \right) \right] - R[\rho(t')] \right\} dt' + D\nabla^2 \rho. \tag{75}$$

Fort and Méndez [5] have shown that a delay-difference equation similar to Eq. (75) can be approximated, with a high degree of accuracy, by a hyperbolic differential equation for which the velocity of wave fronts can be easily evaluated. With our notations the velocity of the wave front is given by

$$v = 2\sqrt{rD}/[1 + (r\langle a \rangle)/(2\overline{m})] \quad \text{with} \quad \langle a \rangle r < 2\overline{m}. \tag{76}$$

Equation (76) leads to $\overline{m} \approx 1$ and $\langle \tau \rangle \approx 25$ yr; that is one migration occurs in about one generation.

Our systematic derivation of reaction diffusion equations shows that the dynamics of the neolithic transition depends strongly on the shape of the distribution of the generation time. The parabolic approximation $N=1$ has serious limitations because it corresponds to an exponential distribution of the generation time and overestimates the value of the velocity of wave front propagation. Under the assumption of a gamma distribution for the waiting times, the hyperbolic approximation $N=2$, leads to $a_m \approx 12.5$ yr, and to $\overline{m} \approx 0.55$; such small values are not consistent with the qualitative ideas of the neolithic transition [6]. Better results are obtained in the limit $N \to \infty$, which corresponds to the Fort and Méndez model [5], for which $a_m \approx 25$ yr and $\overline{m} \approx 1$. However, this limit corresponds to a delta distribution of the generation time, which cannot be exact in a real biological population, but can be a good approximation. Probably a more realistic model would correspond to large, but finite values of N for which the modal and average values of the generation time are close, but not identical. The choice of N is a difficult task because demographic data for ancient populations are missing.

V. CONCLUSIONS

In this paper we have derived a systematic method for the derivation of nonlinear delay transport equations for interacting particles involved in random motions described by the CRTW approach. Our method can be used for describing various nonlinear reaction-transport processes in physics, chemistry, and biology. As a test case of our approach we have discussed the problem of Neolithic transition in population genetics.

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APPENDIX A

In this appendix we show the main steps of the derivation which leads to the elimination of the transit time τ from the nonlinear CTRW equations (10a) and (10b). We apply the Laplace transform to Eqs. (10a) and (10b). We come to

$$\overline{\rho_u}(\mathbf{r},s) = \overline{\ell}_u(\mathbf{r},s)\overline{Z}_u(\mathbf{r},s) + \overline{\mathcal{A}}_u(\mathbf{r},s)\rho_u(\mathbf{r},0), \tag{A1}$$

$$\overline{Z}_u(\mathbf{r},s) = \mathcal{L}_s[R_u(\rho(\mathbf{r},t),t)] + \int_{\mathbf{r}'} \overline{Z}_u(\mathbf{r}',s)\overline{\psi}_u(\mathbf{r}' \to \mathbf{r},s)d\mathbf{r}' + \int_{\mathbf{r}'} \rho_u(\mathbf{r}',0)\overline{\mathcal{U}}_u(\mathbf{r}' \to \mathbf{r},s)d\mathbf{r}', \tag{A2}$$

where the overbar denotes the Laplace transformation

$$\overline{f}(s) = \int_0^\infty \exp(-st)f(t)dt,$$

with

$$f(t) = \rho_u(\mathbf{r},t), \ell_u(\mathbf{r},t), Z_u(\mathbf{r},t), \psi_u(\mathbf{r}' \to \mathbf{r},t) \tag{A3}$$

and

$$\overline{\mathcal{A}}_u(\mathbf{r},s)=\int_0^\infty\int_t^\infty \exp(-st)v_u^0(\tau-t|\mathbf{r})\frac{\ell_u(\mathbf{r},\tau)}{\ell_u(\mathbf{r},\tau-t)}d\tau\,dt, \tag{A4}$$

$$\overline{\mathcal{U}}_u(\mathbf{r}'\to\mathbf{r},s)=\int_0^\infty\int_t^\infty \exp(-st)v_u^0(\tau'-t|\mathbf{r}')\frac{\psi_u(\mathbf{r}'\to\mathbf{r},\tau')}{\ell_u(\mathbf{r}',\tau'-t)}\times d\tau'\,dt; \tag{A5}$$

other symbols have the same significance as in Sec. II.

We eliminate the functions $\overline{Z}_u(\mathbf{r},s)$ from Eqs. (A1) and (A2), resulting in

$$s\overline{\rho_u}(\mathbf{r},s)-\rho_u(\mathbf{r},0)=\overline{I_u}(\mathbf{r},s)+\mathcal{L}_s[R_u(\rho(\mathbf{r},t),t)]+\int_{\mathbf{r}'}[\overline{\rho_u}(\mathbf{r}',s)\overline{\omega_u}(\mathbf{r}'\to\mathbf{r},s)-\overline{\rho_u}(\mathbf{r},s)\overline{\omega_u}(\mathbf{r}\to\mathbf{r}',s)]d\mathbf{r}', \tag{A6}$$

where

$$\overline{\omega_u}(\mathbf{r}\to\mathbf{r}',s)=[s\overline{\psi_u}(\mathbf{r}\to\mathbf{r}',s)]/\left[1-\int_{\mathbf{r}''}\overline{\psi_u}(\mathbf{r}\to\mathbf{u}'',s)d\mathbf{r}''\right], \tag{A7}$$

$$\overline{I_u}(\mathbf{r},s)=\rho_u(\mathbf{r},0)\int_0^\infty\int_{r'}^\infty\frac{sv_u^0(\tau-\tau'|\mathbf{r})\ell_u(\mathbf{r},\tau)e^{-s\tau'}}{[1-\int_{r''}\overline{\psi_u}(\mathbf{r}\to\mathbf{r}'',s)d\mathbf{r}'']\ell_u(\mathbf{r},\tau-\tau')}d\tau\,d\tau'-\rho_u(\mathbf{r},0)+\int_{\mathbf{r}'}\rho_u^0(\mathbf{r}')\int_0^\infty\int_t^\infty\frac{v_u^0(\tau'-\tau'|\mathbf{r}')}{\ell_u(\mathbf{r}',\tau'-\tau')}\times\left[\psi_n(\mathbf{r}'\to\mathbf{r},\tau')-\frac{s\overline{\psi_u}(\mathbf{r}'\to\mathbf{r},s)\ell_u(\mathbf{r}',\tau')}{1-\int_{\mathbf{r}''}\overline{\psi_u}(\mathbf{r}'\to\mathbf{r}'',s)d\mathbf{r}''}\right]e^{-s\tau'}d\tau\,d\tau'\,d\mathbf{r}'. \tag{A8}$$

By applying the inverse Laplace transform to Eqs. (A6)–(A8) we come to Eqs. (11)–(13).

APPENDIX B

In order to eliminate the age structure from the evolution equations (54)–(56) we introduce the conditional age profile

$$c(a|\tau,\mathbf{r};t)=\frac{\zeta(\mathbf{r},a;\tau;t)}{\int da\,\zeta(\mathbf{r},a,\tau;t)}=\frac{\zeta(\mathbf{r},a,\tau;t)}{\xi(\mathbf{r},\tau;t)}. \tag{B1}$$

We insert Eq. (B1) into Eqs. (54)–(56), resulting in

$$c(a|\tau,\mathbf{r};t)\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial\tau}\right)\xi(\mathbf{r},\tau;t)+\xi(\mathbf{r},\tau;t)\times\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a}+\frac{\partial}{\partial\tau}\right)c(a|\tau,\mathbf{r};t)=-c(a|\tau,\mathbf{r};t)\xi(\mathbf{r},\tau;t)\int_{\mathbf{r}'}\mathcal{W}(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}'-\delta(\tau)\int_0^\infty c(a|\tau',\mathbf{r};t)\xi(\mathbf{r},\tau';t)\times[\mu_0(a)+\delta\mu(\rho(\mathbf{r};t))]d\tau', \tag{B2}$$

$$c(a|\tau=0,\mathbf{r};\tau)\xi(\mathbf{r},\tau=0;t)=\int_{\mathbf{r}'}\int_{r'}c(a|\tau',\mathbf{r}';t)\xi(\mathbf{r}',\tau';t)\mathcal{W}(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'\,d\tau', \tag{B3}$$

$$c(a=0|\tau,\mathbf{r};t)\xi(\mathbf{r},\tau;t)=\delta(\tau)\int_0^\infty\int_0^\infty\lambda(a')c(a'|\tau',\mathbf{r};t)\xi(\mathbf{r},\tau';t)da'\,d\tau'. \tag{B4}$$

By integrating Eqs. (B2) and (B3) over age from $a=0$ to $a=\infty$ and using Eq. (B4) we get the following evolution equations for the transit time-position population density $\xi(\mathbf{r},\tau;t)$:

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial\tau}\right)\xi(\mathbf{r},\tau;t)=-\delta(\tau)\int_0^\infty\int_0^\infty[\lambda(a')-\mu_0(a)-\delta\mu(\rho(\mathbf{r};t))]c(a'|\tau',\mathbf{r};t)\xi(\mathbf{r},\tau';t)\times da'\,d\tau'-\xi(\mathbf{r},\tau;t)\times\int_{\mathbf{r}'}\mathcal{W}(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}', \tag{B5}$$

$$\xi(\mathbf{r},\tau=0;t)=\int_{\mathbf{r}'}\int_{r'}\xi(\mathbf{r}',\tau';t)\mathcal{W}(\mathbf{r}\to\mathbf{r},\tau')d\mathbf{r}'\,d\tau'. \tag{B6}$$

Now we take into account that, after a transient regime of a few centuries, the age profile tends towards the stable Lotka form (51) and thus

$$\zeta(\mathbf{r},a,\tau;t)\sim c_{st}(a)\xi(\mathbf{r},\tau;t),\quad c(a|\tau,\mathbf{r};t)\sim c_{st}(a). \tag{B7}$$

We insert Eqs. (B7) into Eqs. (B5) and (B6) resulting in

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial \tau}\right)\xi(\mathbf{r},\tau;t)=\delta(\tau)\rho(\mathbf{r};t)[\langle\lambda\rangle-\langle\mu\rangle] - \xi(\mathbf{r},\tau;t)\int_{\mathbf{r}'}\mathcal{W}(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}', \tag{B8}$$

$$\xi(\mathbf{r},\tau=0;t)=\int_{\mathbf{r}'}\int_{\tau'}\xi(\mathbf{r}',\tau';t)\mathcal{W}(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'d\tau', \tag{B9}$$

where

$$\langle\lambda\rangle=\int_0^\infty \lambda(a')c_{st}(a')da', \tag{B10}$$

$$\langle\mu\rangle=\int_0^\infty[\mu_0(a')+\delta\mu(\rho(\mathbf{r};t))]c_{st}(a')da' \tag{B11}$$

are average natality and mortality functions, respectively. These two average vital functions can be easily evaluated. We have

$$\langle\lambda(a')\rangle=Z^{-1}(r)\int_0^\infty \exp(-ar)l(a')\lambda(a')da'=1/Z(r) \tag{B12}$$

and

$$\langle\mu(a)\rangle=\int_0^\infty c_{st}(a)[\mu^0(a)+\delta\mu[\rho(\mathbf{r};t)]]da = \int_0^\infty c_{st}(a)\mu^0(a)da+\delta\mu[\rho(\mathbf{r};t)]. \tag{B13}$$

The last integral in Eq. (B13) can be evaluated in a number of steps. We get

$$\int_0^\infty c_{st}(a)\mu^0(a)da = \frac{1}{Z(r)}\int_0^\infty \exp[-ra]\frac{\partial}{\partial a}\left\{-\exp\left[-\int_0^a\mu^0(a')da'\right]\right\}da = \frac{1}{Z(r)}\left[1-\int_0^\infty\left\{\frac{\partial}{\partial a}\exp[-ra]\right\}[-l(a)]da\right] = \frac{1}{Z(r)}-r. \tag{B14}$$

By collecting these results and inserting them into Eqs. (B5) and (B6) we come to

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial \tau}\right)\xi(\mathbf{r},\tau;t)=\delta(\tau)\rho(\mathbf{r};t)[r-\delta\mu(\rho(\mathbf{r};t))] - \xi(\mathbf{r},\tau;t)\int_{\mathbf{r}'}\mathcal{W}(\mathbf{r}\to\mathbf{r}',\tau)d\mathbf{r}', \tag{B15}$$

$$\xi(\mathbf{r},\tau=0;t)=\int_{\mathbf{r}'}\int_{\tau'}\xi(\mathbf{r}',\tau';t)\mathcal{W}(\mathbf{r}'\to\mathbf{r},\tau')d\mathbf{r}'d\tau'. \tag{B16}$$

We include the delta-dependent term in Eq. (B15) in the boundary condition (B16), resulting in Eqs. (62) and (63).

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