Evolution equation of population genetics: Relation to the density-matrix theory of quasiparticles with general dispersion laws

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(Received 24 June 2002; revised manuscript received 17 September 2002; published 27 February 2003)

The Waxman-Peck theory of population genetics is discussed in regard of soil bacteria. Each bacterium is understood as a carrier of a phenotypic parameter p. The central objective is the calculation of the probability density with respect to p, $\Phi(p,t;p_0)$, of the carriers living at time $t>0$, provided that initially at $t_0=0$, all bacteria carried the phenotypic parameter $p_0=0$. The theory involves two small parameters: the mutation probability μ and a parameter γ involved in a function $w(p)$ defining the fitness of the bacteria to survive the generation time τ and give birth to an offspring. The mutation from a state p to a state q is defined by a Gaussian with a dispersion σ_m^2. The author focuses our attention on a function $\varphi(p,t)$ which determines uniquely the function $\Phi(p,t;p_0)$ and satisfies a linear equation (Waxman's equation). The Green function of this equation is mathematically identical with the one-particle Bloch density matrix, where μ characterizes the order of magnitude of the potential energy. (In the x representation, the potential energy is proportional to the inverted Gaussian with the dispersion σ_m^2). The author solves Waxman's equation in the standard style of a perturbation theory and discusses how the solution depends on the choice of the fitness function $w(p)$. In a sense, the function $c(p)=1-w(p)/w(0)$ is analogous to the dispersion function $E(p)$ of fictitious quasiparticles. In contrast to Waxman's approximation, where $c(p)$ was taken as a quadratic function, $c(p)\approx\gamma p^2$, the author exemplifies the problem with another function, $c(p)=\gamma[1-\exp(-ap^2)]$, where γ is small but a may be large. The author shows that the use of this function in the theory of the population genetics is the same as the use of a nonparabolic dispersion law $E=E(p)$ in the density-matrix theory. With a general function $c(p)$, the distribution function $\Phi(p,t;0)$ is composed of a δ-function component, $N(t)\delta(p)$, and a blurred component. When discussing the limiting transition for $t\to\infty$, the author shows that his function $c(p)$ implies that $N(t)\to N(\infty)\neq 0$ in contrast with the asymptotics $N(t)\to 0$ resulting from the use of Waxman's function $c(p)\sim p^2$.

DOI: 10.1103/PhysRevE.67.021913 PACS number(s): 87.10.+e, 02.50.Ey, 05.10.Gg, 87.23.Cc

I. INTRODUCTION

During the last century, the development of the quantum theory has been paralleled with the development of the theory of stochastic processes. When comparing the time-dependent Schrödinger equation of the quantum mechanics with the Fokker-Planck equation of the stochastic dynamics, we may assert that both these equations are of the same kind. Mathematically speaking, both these equations are linear second-order partial differential equations of the parabolic type. The Fokker-Planck equation can be derived for any process that can be described by the Langevin equation $\eta dx(t)/dt-F[x(t)]=f(t)$ (cf., e.g., Refs. [1,2]). In the Langevin equation, $\eta>0$ is a deterministic constant, $F(x)$ is a deterministically defined real-valued function, and $f(t)$ is a stochastically defined zero-centered stationary Gaussian white-noise function. [As a rule, $x(t)$ and $f(t)$ are considered as real random functions of the real time variable t. The stationarity of $f(t)$ is meant in the stochastic sense.] Using the angular brackets $\langle\ \rangle$ for the averaging with respect to the randomness of $f(t)$, we assume that $\langle f(t)\rangle=0$ and $\langle f(t_1)f(t_2)\rangle=\Lambda\delta(t_1-t_2)$ at all time instants t,t_1,t_2. The initial value of $x(t)$, $x(0)=x_0$, is usually a deterministic value given in advance. The Fokker-Planck equation concerns the conditional probability density $P(x,t|x_0)=\langle\delta(x(t)-x)\rangle\geqslant 0$,

$$\frac{\partial P(x,t|x_0)}{\partial t}=\frac{\Lambda}{2\eta^2}\frac{\partial^2 P(x,t|x_0)}{\partial x^2}-\frac{1}{\eta}\frac{\partial}{\partial x}[F(x)P(x,t|x_0)], \tag{1}$$

$$P(x,+0|x_0)=\delta(x-x_0). \tag{2}$$

If $x(t)$ is the instantaneous position of a Brownian particle moving along a line, we may speak of the diffusion coefficient D (such that $2\eta^2 D=\Lambda>0$) and of the mobility $1/\eta$ of the particle. Then $F(x)=-dV_B(x)/dx$ is a driving force, $f(t)$ is the Langevin stochastic force, and Eq. (1) is the governing equation of the Brownian dynamics. Equation (1) can be transformed into an equation of the Schrödinger type by substituting

$$P(x,t|x_0)=\exp\left(\frac{\eta}{\Lambda}[V_B(x_0)-V_B(x)]\right)R(x,t|x_0). \tag{3}$$

The function $R(x,t|x_0)$ obeys the equation

$$\frac{\partial R(x,t|x_0)}{\partial t}=\frac{\Lambda}{2\eta^2}\frac{\partial^2 R(x,t|x_0)}{\partial x^2}-V(x)R(x,t|x_0), \tag{4}$$

where

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$$V(x)=\frac{1}{2\eta}\left[\frac{1}{\Lambda}\left(\frac{dV_{\mathrm{B}}(x)}{dx}\right)^2-\frac{d^2V_{\mathrm{B}}(x)}{dx^2}\right]$$
$$=\frac{1}{2\eta}\left[\frac{[F(x)]^2}{\Lambda}+\frac{dF(x)}{dx}\right]. \quad (5)$$

Equation (4) is known as the real Schrödinger equation. If t is replaced by $\hbar\beta$, where $k_{\mathrm{B}}T=1/\beta$, Eq. (4), with some change of symbols, becomes the Bloch equation for the one-particle canonical density matrix of boltzons of a constant (effective) mass in the thermodynamic equilibrium at the temperature T [3]. Thus, when comparing Eqs. (1) and (4), we can always juxtapose the Brownian dynamics and the quantum theory. (This juxtaposition can also be based on Feynman's path-integral theory [4,5].) The transition from the formalism of the Brownian theory to the formalism of the quantum theory is easy because if we define the driving force $F(x)=-dV_{\mathrm{B}}(x)/dx$, we can directly calculate the function $V(x)$ according to Eq. (5). [Vice versa, if one tries to find $F(x)$ corresponding to a given function $V(x)$, one has to solve Eq. (5) which is nonlinear. Equation (5) is known as the Riccati equation. Compare with any handbook on nonlinear differential equations—e.g., Ref. [6]. Recently, the usefulness of the Riccati equation in solving various problems of classical and quantum mechanics has been widely corroborated [7–11]. Nonetheless, except for the rare possibility to derive analytical solutions $F(x)$ of this equation, in some cases when $V(x)$ is chosen in a very simple and special form, Eq. (5) cannot be solved otherwise than numerically. Thus, the problem of finding a Brownian model to a given quantum-mechanical model is relatively difficult.]

In evolutionary theories of various populations, we may use $x(t)=\ln n(t)-\overline{\ln n(t)}$, taking $n(t)$ as the number of individuals of a certain kind at the time instant t and defining $\overline{\ln n(t)}$ as an average value of $\ln n(t)$. Since $n(t)$ may represent very large numbers, $n(t)$ may be treated as a continuous function so that the values of $x(t)$ may span the whole set of real numbers. Since mutations are random events, a formal stochastic theory of the population genetics can certainly be based on the use of the Langevin equation and, correspondingly, of the Fokker-Planck equation (1). If it is advantageous, we may also use the equivalent Schrödinger-type equation (4).

Notwithstanding, recently, Waxman has shown that there is also another mathematical relation between the population genetics and the quantum mechanics [12]. Waxman's theory concerns a simplified, but well-founded, model that we call the Waxman-Peck model. (Compare with Refs. [13,14], and references quoted therein.) Waxman's Schrödinger-type equation involves, in the x representation, the "potential-energy" function

$$V(x)\sim-\mu\exp\left(-\frac{\sigma_{\mathrm{m}}^2x^2}{2}\right), \quad (6)$$

with two mutation parameters $\mu>0$ and $\sigma_{\mathrm{m}}>0$. The "kinetic-energy" operator $\hat{T}$ in Waxman's equation was chosen in the usual form, $\hat{T}\sim-\partial^2/\partial x^2$.

In the present paper, we will generalize Waxman's theory. In the momentum representation, Waxman's kinetic energy is quadratic, $\langle p|\hat{T}|p\rangle\sim p^2$, as it is in the quantum mechanics. On the other hand, we assume that $\langle p|\hat{T}|p\rangle$, being a positive function, need not be quadratic; we only require its analyticity along the real p axis. This variability offers further possibilities to model the genetic evolution by adequate fitness functions (cf. Sec. II). Obviously, if $\langle p|\hat{T}|p\rangle>0$ is nonquadratic, the mathematical relation between the evolution equation of the population genetics and the quantum theory becomes somewhat more sophisticated than in Waxman's case. Namely, when paying heed to the x representation, we have generally to consider a more complicated equation than the real Schrödinger equation: in general, our equation, with the Hamilton operator $E(\hat{p})+V(x)$, where $E(p)\sim c(p)$, is a *functional* differential equation. [Note that $\hat{p}=-i\partial/\partial x$. The McLaurin development of $c(p)$ may involve an infinite number of terms]. For solid state theorists, such an equation is familiar as the transformed effective mass equation (cf., e.g., the monograph [15] or our paper [16]). This equation was invented for envelope wave functions of electrons in crystalline solids. [Synonymously, we may also speak of the real Schrödinger-Wannier equation. It is identical with the "one-particle Bloch equation" for the canonical density matrix with the Hamiltonian $E(\hat{p})+V(x)$.]

From the viewpoint of the effectiveness of calculations in the present paper, we deem the momentum representation better than the x representation. Under the assumption of the smallness of the parameter μ, we can apply the "plane-wave perturbation theory" (Sec. III) of the density-matrix theory. For a broad class of fitness functions, the distribution function of the theory of the population genetics can be expressed as a linear expression of the mutation parameter μ.

II. THE WAXMANN-PECK MODEL OF THE POPULATION GENETICS

Let us assume that a large enough habitat (such as a given volume of soil) hosts bacteria of a certain kind. The habitat yields space, food, moisture, temperature, inhibitory substances, and other needs for the survival of the bacteria in the sense that the total number of bacteria will never decrease to zero and will never increase to infinity. Most of the bacteria are free-living micro-organisms multiplying by simple fission. This means that their reproduction is asexual. In other words, each bacterial individual has only one parent. The typical number of bacteria may be huge indeed: 1 g of soil may contain several hundred million bacteria. Although the bacteria are small organisms—usually 0.3–2 μm in diameter—their morphology is well distinguishable microscopically.

There are two most frequent shapes of soil bacteria: short rods and (slightly deformed) spheres. In both these cases, we may characterize each bacterium by its size s. For instance, if the bacterium resembles a rod, we define s as the length of the rod. Denoting the average of $\ln s$ as $\overline{\ln s}$, we define the phenotypic parameter as $p=\ln s-\overline{\ln s}$. Recalling biology, we consider the phenotypic parameter as an inheritable value. If

there were no mutations in the reproduction of the bacteria, all the bacterial individuals in each generation would be equally long, i.e., p would be a constant equal to $p_0=0$. But then, the mutations—however infrequent they may be—account for a dispersal of the value p among the individuals, despite the fact that all individuals under consideration do still belong to the same biological type.

Generally, the theory has to respect both mutations caused by environmental effects and spontaneous mutations. For the sake of simplicity, we will consider no other than the spontaneous mutations. The spontaneous mutations are mainly due to transcription mistakes in the replication of the DNA, i.e., in the transmission of the genetic information just at the reproduction events. Let $\mu>0$ be the probability of the occurrence of such a mutation. In the case of soil bacteria, biologists have estimated the values of μ between 10^{-8} and 10^{-5}. If a mother bacterium is the carrier of the phenotypic value p, the daughter bacterium will carry the same value p with the probability equal to $1-\mu$. (We assume that a newborn daughter bacterium grows quickly enough to the adult size before becoming mature so that we need not distinguish between the size of young and adult bacteria.) If the birth of the daughter bacterium is accompanied with a mutation of the DNA, then there is a nonzero probability $M(q-p)dq$ for the possibility that the phenotypic value q of the daughter bacterium may lie in the interval $(q,q+dq)$, provided that the phenotypic value of the mother bacterium was equal to p. Following Waxman, we take the function $M(p)$ as a Gaussian,

$$M(p)\equiv M(p;\sigma_{\mathrm{m}})=\left(\frac{1}{2\pi\sigma_{\mathrm{m}}^2}\right)^{1/2}\exp\left(-\frac{p^2}{2\sigma_{\mathrm{m}}^2}\right). \tag{7}$$

Here, σ_{m}^2 is the dispersion of values of p.

Now, to formulate the evolution equation of the population genetics, we have to introduce the average generation time τ. Simplifying the problem, we may consider a discrete time variable as follows. Let the births of the bacteria happen at time instants $t_n=(n-1)\tau$, $n=1,2,\ldots$. Then we may say that the bacteria of the nth generation live between t_{n-1} and t_n. Thus, n is the generation index. The time discretization is an auxiliary, rather formal, mathematical trick which loses its significance if the time t is continualized. For each n, we define the distribution function $\Phi_n(p)$ so that $\Phi_n(p)dp$ may be interpreted as the probability of the occurrence of the phenotypic value p in the interval $(p,p+dp)$ in the nth generation. The basic problem is to relate the distribution function of the generation number $n+1$ (''generation of daughters'') with the distribution function of the generation number n (''generation of mothers'').

Before writing the recurrent formula between the functions $\Phi_{n+1}(p)$ and $\Phi_n(p)$, which is our primary objective in this section, we have still to mention one important point. Even if we have neglected the environmental influence upon the mutations, we do have to consider environmental effects in a Darwinian sense. Namely, we have to respect that not all bacteria, after their birth, are equally fit to survive over the whole generation time τ. Only those bacteria whose age is equal to τ give birth to an offspring. Some of the bacteria die before becoming mature. These bacteria do not take part in producing the individuals of the next generation. [However, we assume that even the fittest mother bacterium dies soon after giving birth to the daughter bacterium. Therefore, we do not include the mother bacteria in the number of the bacteria living in the time interval (t_n,t_{n+1}). The mother bacteria have been included in the number of the bacteria living in the time interval (t_{n-1},t_n)]. The fitness of the bacteria to live in their environment until their maturity can be modeled by a non-negative function $w(p)$. Requiring that

$$0<w(p)<1, \tag{8}$$

we may give the function $w(p)$ a probabilistic meaning. We assume that a newborn carrier of the phenotypic value p has the chance to live until maturity with the probability $w(p)$. The number of mature carriers of the phenotypic value p from the interval $(p,p+dp)$ in the nth generation is proportional to $w(p)\Phi_n(p)$. To determine the shape of the function, $w(p)$ should be a matter of thorough biological investigations from case to case. We assume, as Waxman and Peck did, that $w(p)$ behaves analytically around the value $p_0=0$ and that this value corresponds to the maximum value of $w(p)$. (Apparently, the fittest bacterial individuals are those whose phenotypic parameter p is equal to the average value $\overline{p}$. However, $\overline{p}=0$.)

Waxman and Peck have chosen the function $w(p)$ in the special form

$$w(p)=w(0)\exp(-\gamma p^2), \quad 0<w(0)<1, \tag{8a}$$

assuming that $0<\gamma\ll 1$. [In fact, expression (8a) *defines* the Waxman-Peck model. The value of $w(0)$ is insignificant since the distribution functions $\Phi_n(p)$ are independent of $w(0)$.]

There are, of course, many other possibilities to model $w(p)$ by slowly varying functions with the maximum at $p_0=0$. These functions need not tend to zero if $|p|\to\infty$. (The fitness function has been defined as a *probability*, not as a probability density.) In order to illustrate how the theory may depend on the choice of the function $w(p)$, we will treat, in addition to the Waxman-Peck model, also an alternative model. Our model (considered as an example) is defined by the fitness function

$$w(p)=w(0)\{1-\gamma[1-\exp(-ap^2)]\}. \tag{8b}$$

Here, we assume that $0<\gamma\ll 1$, admitting that $a>0$ need not be a small number. Expression (8b) tends to $w(0)(1-\gamma)>0$ if $|p|\to\infty$.

The distribution function $\Phi_{n+1}(p)$ of the generation of daughters is determined by two contributions from the generation of mothers. The first stems from the births without mutations. The phenotypic value p is unchanged at such births and the probability of occurrence of such births is equal to $1-\mu$. The first contribution to $\Phi_{n+1}(p)$ is proportional to $(1-\mu)w(p)\Phi_n(p)$. The second contribution to $\Phi_{n+1}(p)$ is proportional to $\mu\int_{-\infty}^{\infty}dqM(p-q;\sigma_{\mathrm{m}})w(q)\Phi_n(q)$. The interpretation of this expression is

clear: if the birth of the carrier of the phenotypic value p is accompanied with a mutation, we have to consider mature individuals, allowing all possible phenotypic values q of potential mothers. To exhaust all such possibilities, we have to integrate $M(p-q;\sigma_{\mathrm{m}})w(q)\Phi_n(q)$ with respect to q. Since both $\Phi_n(p)$ and $\Phi_{n+1}(p)$ are probability densities, we require that

$$\int_{-\infty}^{\infty} dp\Phi_n(p)=\int_{-\infty}^{\infty} dp\Phi_{n+1}(p)=1. \tag{9}$$

Therefore, we write the equality

$$\Phi_{n+1}(p)=\frac{(1-\mu)w(p)\Phi_n(p)+\mu\int_{-\infty}^{\infty} dqM(p-q;\sigma_{\mathrm{m}})w(q)\Phi_n(q)}{\int_{-\infty}^{\infty} dqw(q)\Phi_n(q)}. \tag{10}$$

The denominator on the right hand side of Eq. (10) warrants the fulfillment of condition (9). Since γ is small, it is convenient to introduce the complementary function $c(p)$ to $w(p)/w(0)$:

$$c(p)=1-\frac{w(p)}{w(0)}. \tag{11}$$

In the case of the Waxman-Peck model,

$$c(p)=1-\exp(-\gamma p^2), \tag{11a}$$

while in the case of the model defined by function (8b),

$$c(p)=\gamma[1-\exp(-ap^2)]. \tag{11b}$$

From the viewpoint of biology, the smallness of γ implies that the comparison of the survival fitness of the majority of the bacteria with the survival fitness of the fittest bacteria should not reveal too conspicuous differences. When using the function $c(p)$, we can rewrite formula (10) in the form

$$\Phi_{n+1}(p)=\frac{(1-\mu)[1-c(p)]\Phi_n(p)+\mu\int_{-\infty}^{\infty} dqM(p-q;\sigma_{\mathrm{m}})[1-c(q)]\Phi_n(q)}{1-\int_{-\infty}^{\infty} dqc(q)\Phi_n(q)}. \tag{10'}$$

With realistic values of p around $p_0=0$, the values of γp^2 are small. Thus, in the case of the Waxman-Peck model, the values of $c(p)$ are also small and

$$c(p)=\gamma p^2+O(\gamma^2). \tag{11a'}$$

On the other hand, in the case of the model defined by function (8b), we have to keep expression (11b) intact since a need not be a small parameter.

We may take advantage of the possibility to neglect all terms of the order of magnitude of γ^2, as well as of $\gamma\mu$. So we write

$$\frac{1}{1-\int_{-\infty}^{\infty} dqc(q)\Phi_n(q)}=1+\int_{-\infty}^{\infty} dqc(q)\Phi_n(q)+\cdots$$

and

$$\Phi_{n+1}(p)=\Phi_n(p)-\left[c(p)-\int_{-\infty}^{\infty} dqc(q)\Phi_n(q)\right]\Phi_n(p)-\mu\left[\Phi_n(p)-\int_{-\infty}^{\infty} dqM(p-q;\sigma_{\mathrm{m}})\Phi_n(q)\right]+\cdots. \tag{10''}$$

Now, in the approximation neglecting the terms symbolized by the dots, we are ready to go over into the formalism employing the continual time variable t, realizing that the value of the generation index n may be high. Typically, the generation time τ of soil bacteria is about 20 min. This means that after the elapse of 100 days, the genetic information passes over more than 7000 generations of the bacteria. If $n\gg 1$, we may identify $\Phi_n(p)$ with $\Phi(p,t)$ and approximate the difference $\Phi_{n+1}(p)-\Phi_n(p)$ as the time derivative

$$\Phi_{n+1}(p)-\Phi_n(p)=\tau\frac{\partial\Phi(p,t)}{\partial t}+\cdots \tag{12}$$

Thus, we can rewrite Eq. (10″) in the approximate integro-differential form

$$\frac{\partial\Phi(p,t)}{\partial t}=-\frac{1}{\tau}\left[c(p)-\int_{-\infty}^{\infty}dq\,c(q)\Phi(q,t)\right]\Phi(p,t)-\frac{\mu}{\tau}\left[\Phi(p,t)-\int_{-\infty}^{\infty}dq\,M(p-q;\sigma_{\mathrm{m}})\Phi(q,t)\right]. \tag{13}$$

This equation was derived in Ref. [12] (where, however, $c(p)$ was approximated as γp^2). Evidently, Eq. (13) is nonlinear. Fortunately, this nonlinearity does not mean a serious problem, since we may employ the substitution

$$\Phi(p,t)=\frac{\varphi(p,t)}{\int_{-\infty}^{\infty}dq\,\varphi(q,t)}, \tag{14}$$

and require the validity of the equation

$$\frac{\partial\varphi(p,t)}{\partial t}=-\frac{1}{\tau}c(p)\varphi(p,t)+\frac{\mu}{\tau}\int_{-\infty}^{\infty}dq\,M(p-q;\sigma_{\mathrm{m}})\varphi(q,t). \tag{15}$$

Equation (15) is linear. After integrating it with respect to p, we obtain the equation $d/dt\int_{-\infty}^{\infty}dq\,\varphi(q,t)=-(1/\tau)\int_{-\infty}^{\infty}dp\,c(p)\varphi(p,t)+(\mu/\tau)\int_{-\infty}^{\infty}dq\,\varphi(q,t)$ and when substituting expression (14) for $\varphi(p,t)$, we arrive at the identity

$$\frac{d}{dt}\int_{-\infty}^{\infty}dq\,\varphi(q,t)=\int_{-\infty}^{\infty}dq\,\varphi(q,t)\left[-\frac{1}{\tau}\int_{-\infty}^{\infty}dp\,c(p)\Phi(p,t)+\frac{\mu}{\tau}\right]. \tag{16}$$

The differentiation of expression (14) gives the identity

$$\frac{\partial\varphi(p,t)}{\partial t}=\frac{\partial\Phi(p,t)}{\partial t}\int_{-\infty}^{\infty}dq\,\varphi(q,t)+\Phi(p,t)\frac{d}{dt}\int_{-\infty}^{\infty}dq\,\varphi(q,t). \tag{17}$$

When equalizing the right hand sides of Eqs. (15) and (17) and when respecting identity (16), we obtain Eq. (l3) for the function $\Phi(p,t)$. Thus, instead of directly solving Eq. (13), we may solve Waxman's equation (15) at first. This task, as we will show in Sec. III, is not difficult. If the function $\Phi(p,t)$ obeys linear boundary conditions, the function $\varphi(p,t)$ has to obey the same boundary conditions. We will simply assume that

$$\Phi(p,t)\to 0 \quad \text{and} \quad \varphi(p,t)\to 0 \quad \text{if} \quad |p|\to\infty. \tag{18}$$

It remains still to discuss the initial condition. Whichever initial function

$$\Phi(p,0)=\Phi_0(p) \tag{19}$$

is chosen, the solution $\Phi(p,t)$ for $t>0$ of Eq. (13) is unique. Since Eq. (15) is linear, we may multiply $\varphi(p,t)$ by an arbitrary constant A. If $\varphi(p,t)$ gives the function $\Phi(p,t)$, then $A\varphi(p,t)$ does also give the same function $\Phi(p,t)$. Therefore, we may choose the integral $\int_{-\infty}^{\infty}dq\,\varphi(q,0)$ (which is a constant) equal to unity. Then formula (14) and equality (19) give us the initial condition

$$\varphi(p,0)=\Phi_0(p) \tag{20}$$

for the function $\varphi(p,t)$.

If $\Phi_0(p)$ is an even function, Eq. (15) implies that the function $\varphi(p,t)$ is also even in the variable p and $\Phi(-p,t)=\Phi(p,t)$ at all times $t>0$. In this case, the mean value of p is invariant in time (i.e., a constant),

$$\overline{p}=\int_{-\infty}^{\infty}dp\,p\Phi(p,t)=0. \tag{21}$$

Equation (15) is formally the same as the Schrödinger-Wannier equation in the momentum representation. It can easily be Fourier transformed. We define the function

$$\psi(x,t)=\frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty}dp\,\exp(\mathrm{i}px)\varphi(p,t). \tag{22}$$

This function is the solution of the functional differential equation

$$\frac{\partial\psi(x,t)}{\partial t}=-\frac{1}{\tau}c\left(-\mathrm{i}\frac{\partial}{\partial x}\right)\psi(x,t)+\frac{\mu}{\tau}\exp\left(-\frac{\sigma_{\mathrm{m}}^2x^2}{2}\right)\psi(x,t). \tag{23}$$

In Waxman's approximation, Eq. (23) reads

$$\frac{\partial\psi(x,t)}{\partial t}=\frac{\gamma}{\tau}\frac{\partial^2\psi(x,t)}{\partial x^2}+\frac{\mu}{\tau}\exp\left(-\frac{\sigma_{\mathrm{m}}^2x^2}{2}\right)\psi(x,t). \tag{23a}$$

If $c(p)$ is taken in the form of expression (11b), the functional differential equation for $\psi(x,t)$ reads

$$\frac{\partial\psi(x,t)}{\partial t}=\frac{\gamma}{\tau}\left[\exp\left(a\frac{\partial^2}{\partial x^2}\right)-1\right]\psi(x,t)+\frac{\mu}{\tau}\exp\left(-\frac{\sigma_{\mathrm{m}}^2x^2}{2}\right)\psi(x,t). \tag{23b}$$

III. THE PLANE-WAVE PERTURBATION THEORY

Instead of solving Eq. (23a) or Eq. (23b) and carrying out the integration

$$\varphi(p,t)=\frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty}dx\,\exp(-ipx)\psi(x,t), \tag{24}$$

we prefer to calculate the function $\varphi(p,t)$ directly. Defining the potential-energy operator $\hat{V}(p)$

$$\hat{V}(p)\varphi(p,t)=\frac{1}{\tau}\int_{-\infty}^{\infty}dqM(p-q;\sigma_{\mathrm{m}})\varphi(q,t), \tag{25}$$

let us write Eq. (15) in the form

$$\frac{\partial\varphi(p,t)}{\partial t}=-\frac{c(p)}{\tau}\varphi(p,t)+\mu\hat{V}(p)\varphi(p,t), \tag{26}$$

and define the Green function $G(p,t;p_0)$ of this equation. Employing the Green function, we write $\varphi(p,t)$ (for $t>0$) as the integral

$$\varphi(p,t)=\int_{-\infty}^{\infty}dp_0G(p,t;p_0)\varphi(p_0,0). \tag{27}$$

The initial function $\varphi(p,0)$ has been defined by equality (20). The Green function itself obeys the equation

$$\frac{\partial G(p,t;p_0)}{\partial t}=-\frac{c(p)}{\tau}G(p,t;p_0)+\mu\hat{V}(p)G(p,t;p_0). \tag{28}$$

According to equality (27), $G(p,t;p_0)$ satifies the initial condition

$$G(p,0;p_0)=\delta(p-p_0). \tag{29}$$

In the special case when $c(p)$ is approximated by the quadratic function, Eq. (28) is formally identical with the Bloch equation for the one-particle canonical density matrix $C_\beta(p,p_0)$ in the thermodynamic equilibrium. In the case of a general function $c(p)$, we have to speak of quasiparticles with a nonparabolic dispersion law. The function $C_{+0}(p,p_0)$ is equal to $\delta(p-p_0)$ for quantum-mechanical reasons. When transforming Eq. (28) into the *x*-representation form, one observes that the potential energy corresponds to a *well*: it is an inverted Gaussian [cf. expression (6)].

We can derive $G(p,t;p_0)$ as the series

$$G(p,t;p_0)=\sum_{j=0}^{\infty}\mu^jK_j(p,t;p_0). \tag{30}$$

The zero-order term is the solution of the equation

$$\frac{\partial G_0(p,t;p_0)}{\partial t}=-\frac{c(p)}{\tau}G_0(p,t;p_0) \tag{31}$$

with respect to the condition

$$G_0(p,0;p_0)=\delta(p-p_0). \tag{32}$$

When solving Eq. (31), we obtain, for $t>0$, the function

$$G_0(p,t;p_0)=\delta(p-p_0)\exp\left(-\frac{c(p)t}{\tau}\right). \tag{33}$$

With this function, we can write down the integral form of Eq. (28)

$$G(p,t;p_0)=G_0(p,t;p_0)+\mu\int_0^t dt_1\int_{-\infty}^{\infty}dp_1G\times(p,t-t_1;p_1)\hat{V}(p_1)G_0(p_1,t_1;p_0). \tag{34}$$

This gives a Dyson-type series (cf., e.g., Ref. [17].) The first-order term in this series (linear in μ) reads

$$\begin{aligned}\mu G_1(p,t;p_0)&=\mu\int_0^t dt_1\int_{-\infty}^{\infty}dp_1G_0(p,t-t_1;p_1)\times\hat{V}(p_1)G_0(p_1,t_1;p_0)\\&=\frac{\mu}{\tau}\int_0^t dt_1\int_{-\infty}^{\infty}dp_1G_0(p,t-t_1;p_1)\times\int_{-\infty}^{\infty}dqM(p_1-q;\sigma_{\mathrm{m}})G_0(q,t_1;p_0).\end{aligned} \tag{35}$$

After inserting expressions (7) and (33) here, we obtain the function

$$\mu G_1(p,t;p_0)=\frac{\mu}{\tau}\left(\frac{1}{2\pi\sigma_{\mathrm{m}}^2}\right)^{1/2}\exp\left(-\frac{(p-p_0)^2}{2\sigma_{\mathrm{m}}^2}\right)\times\int_0^t dt_1\exp\left(-\frac{c(p)(t-t_1)+c(p_0)t_1}{\tau}\right).$$

After performing the integration with respect t_1, we arrive, with respect to formula (7), at the final result

$$\mu G_1(p,t;p_0)=\mu M(p-p_0;\sigma_{\mathrm{m}})\times\frac{\exp[-c(p_0)t/\tau]-\exp[-c(p)t/\tau]}{c(p)-c(p_0)}. \tag{36}$$

In the same way, we could also calculate higher-order terms (i.e., the terms proportional to μ^j with $j>1$) in series (30). We expect, however, that higher-order terms are negligible, since the mutation probability μ is, as biologists have proved in their extensive studies, very small.

IV. DEVELOPMENT OF THE PHENOTYPIC DIVERSITY IN A POPULATION WHOSE INDIVIDUALS ARE INITIALLY EQUAL

If all individuals of a population are initially, at the time $t_0=0$, carriers of the same phenotypic value p_0, the initial distribution function $\Phi_0(p)$ is equal to the δ function:

$$\Phi_0(p)=\delta(p). \tag{37}$$

($p_0=\overline{p}=0$ according to our definition of the phenotypic parameter p.) In regard to identity (20), Eq. (27) allows us to assert that

$$\varphi(p,t)=G(p,t;0). \tag{38}$$

Since $c(0)=0$ [cf. expression (11)], formulas (33) and (36) imply, respectively, that

$$G_0(p,t;0)=\delta(p) \tag{39}$$

and

$$\mu G_1(p,t;0)=\mu M(p;\sigma_m)\frac{1-\exp[-c(p)t/\tau]}{c(p)} \tag{40}$$

at all times $t>0$. Hence, in the linear approximation with respect to μ, we have got the function

$$\varphi(p,t)=\delta(p)+\mu M(p;\sigma_m)\frac{1-\exp[-c(p)t/\tau]}{c(p)}. \tag{41}$$

The only problem that we have still left unsolved is the calculation of the integral

$$\int_{-\infty}^{\infty}dp\,\varphi(p,t)=1+\mu\left(\frac{1}{2\pi\sigma_m^2}\right)^{1/2}\int_{-\infty}^{\infty}dp\,\exp\left(-\frac{p^2}{2\sigma_m^2}\right)\times\frac{1-\exp[-c(p)t/\tau]}{c(p)}. \tag{42}$$

Recall that, according to Eq. (14),

$$\Phi(p,t)=N(t)\varphi(p,t), \tag{43}$$

where

$$N(t)=\left[\int_{-\infty}^{\infty}dp\,\varphi(p,t)\right]^{-1}. \tag{44}$$

We will calculate the function $N(t)$ approximately, assuming that $0<\sigma_m<1$. (In fact, it is probable that $\sigma_m\ll 1$). The most relevant values of p contributing to the value of the integral on the right hand side of formula (42) lie in the interval $(-\sigma_m,\sigma_m)$.

A. Distribution function $\Phi(p,t;0)$ in the model where $c(p)=1-\exp(-\gamma p^2)$ (the Waxman-Peck model)

Since $0<\gamma\sigma_m^2\ll 1$, we may use, when calculating integral (42), the approximation expressed by formula (11a′). Thus,

$$\int_{-\infty}^{\infty}dp\,\varphi(p,t)\approx 1+\mu\left(\frac{1}{2\pi\sigma_m^2}\right)^{1/2}\int_{-\infty}^{\infty}dp\,\exp\left(-\frac{p^2}{2\sigma_m^2}\right)\times\frac{1-\exp(-\gamma p^2 t/\tau)}{\gamma p^2}$$
$$=1+\frac{\mu}{\tau}\left(\frac{1}{2\pi\sigma_m^2}\right)^{1/2}\int_0^t dt_1\int_{-\infty}^{\infty}dp\times\left[-\exp\left(\frac{1}{2\sigma_m^2}+\frac{\gamma t_1}{\tau}\right)p^2\right].$$

After carrying out the integration with respect to p, we obtain the simple result

$$\int_{-\infty}^{\infty}dp\,\varphi(p,t)\approx 1+\frac{\mu}{\tau}\int_0^t\frac{dt_1}{(1+2\gamma\sigma_m^2 t_1/\tau)^{1/2}}=1+\frac{\mu}{\gamma\sigma_m^2}\left[\left(1+\frac{2\gamma\sigma_m^2 t}{\tau}\right)^{1/2}-1\right].$$

Hence, according to formula (14), we obtain the distribution function

$$\Phi(p,t;0)=N(t)\left[\delta(p)+\frac{\mu}{\gamma}M(p;\sigma_m)\frac{1-\exp(-\gamma p^2 t/\tau}{p^2}\right] \tag{43a}$$

with the normalizing coefficient

$$N(t)=\left\{1+\frac{\mu}{\gamma\sigma_m^2}\left[\left(1+\frac{2\gamma\sigma_m^2 t}{\tau}\right)^{1/2}-1\right]\right\}^{-1}. \tag{44a}$$

From the probabilistic viewpoint, the function $N(t)$ is well understood. When counting all the bacteria living at the time instant t, we have to distinguish whether they are carriers of the original phenotypic value $p_0=0$ or whether they carry other values, $p\neq 0$. Since $\int_{-\epsilon}^{\epsilon}dp\,\Phi(p,t;0)=N(t)$ (if $\epsilon\to+0$), we may say that a randomly chosen bacterium may be the carrier of the value $p_0=0$ with the probability equal to $N(t)$. If $t\to\infty$, the probability $N(t)$ decreases towards zero. However, this decreasing—the process influenced both by the mutations and by the fitness of the bacteria to live in their environment—is slow. Indeed, let us take $\gamma=0.02$, $\sigma_m=0.05$, and $\mu=10^{-5}$. Then $\mu/(\gamma\sigma_m^2)=0.2$ and $2\gamma\sigma_m^2 t/\tau=1$ for the generation number $t/\tau=10^4$. If these values of γ and σ_m, together with the value 20 min for the generation time τ, may be taken as realistic for some soil bacteria, the total time t comprising the lifetime of 10 000 generations of these bacteria equals about five months. If the time t is roughly ten times (or more than ten times) shorter, formula (44a) can be simplified:

$$N(t)\approx\left(1+\frac{\mu t}{\tau}\right)^{-1}\quad\text{if}\quad\frac{2\gamma\sigma_m^2 t}{\tau}\ll 1. \tag{45}$$

As a rule, the mutation probability μ is smaller than $2\gamma\sigma_m^2$. Thus, we may write

$$N(t)\approx 1-\frac{\mu t}{\tau} \quad \text{if} \quad \frac{2\gamma\sigma_m^2 t}{\tau}\ll 1. \tag{45'}$$

B. Distribution function $\Phi(p,t;0)$ in the model where $c(p)=\gamma[1-\exp(-ap^2)]$

Now we consider a small parameter γ $(0<\gamma\ll 1)$ and another parameter $a>0$, which need not be small. Only if $a\ll 1/\sigma_m^2$, we may accept the approximation $c(p)\approx\gamma a p^2$ and there is no essential difference from the Waxman-Peck model, only γ is replaced by γa.

Otherwise, if $a\sigma_m^2$ is comparable with unity, the integration of the function $\varphi(p,t)$ with respect to p is much more complicated but can be accomplished explicitly (it is presented in the Appendix).

Here, we confine ourselves to discussing what comes about if $a\sigma_m^2\gg 1$. Essentially, under this condition, we may approximate $1-\exp(-ap^2)$ by unity. Then we obtain the simple result

$$\int_{-\infty}^{\infty} dp\,\varphi(p,t)\approx 1+\frac{\mu}{\gamma}\left[1-\exp\left(-\frac{\gamma t}{\tau}\right)\right].$$

Correspondingly, if $a\sigma_m^2\gg 1$, then

$$\Phi(p,t;0)\approx N(t)\left\{\delta(z)+\frac{\mu}{\gamma}M(p;\sigma_m)\left[1-\exp\left(-\frac{\gamma t}{\tau}\right)\right]\right\}, \tag{43b}$$

where

$$N(t)=\left\{1+\frac{\mu}{\gamma}\left[1-\exp\left(-\frac{\gamma t}{\tau}\right)\right]\right\}^{-1}. \tag{44b}$$

In the short-time approximation, formulas (45) and (45′) are equally valid as in the case *A*. Note that expression (43b) for the distribution function $\Phi(p,t)$ would be correct if $c(p)=1-w(p)/w(0)$ might be approximated by a small constant $\gamma>0$. In this case, $N(t)$ may again be approximated as $1-\mu t/\gamma$ at short enough times. However, if $t\to\infty$, then $N(t)$ does not tend to zero (in contrast to the case analyzed in the preceding section):

$$\lim_{t\to\infty} N(t)=\frac{\gamma}{\gamma+\mu}.$$

V. CONCLUDING REMARKS

In the present paper, we have focused our attention on the importance of the fitness function $w(p)$ in the theory of the population genetics. Assuming that $0<c(p)=1-w(p)/w(0)\ll 1$, we have essentially followed Waxman and Peck who derived the distribution function $\Phi(p,t)$ of the population genetics as a functional of a function $\varphi(p,t)$ [cf. expression (14)] satisfying a *linear* integrodifferential equation [cf. Eq. (15)]. However, in contrast with Ref. [12], where $c(p)$ was approximated as γp^2 with some small parameter $\gamma>0$, we emphasize that $c(p)$ may be chosen from a wider class of functions. In particular, we have dealt with the model defined by the function $c(p)=\gamma[1-\exp(-ap^2)]$.

We have calculated the distribution function as a series with respect to the mutation probability μ. Our iteration scheme for calculating the Green function $G(p,t;p_0)$ of the equation for $\varphi(p,t)$ has been used in the same manner as in the density-matrix theory.

The replacement of $c(p)$ by $E(p)$, t by β (with $\hbar=1$), and $G_0(p,t;p_0)$ by the unperturbed canonical density matrix $C_\beta^{(0)}(p,p_0)$ yields the equation

$$-\frac{\partial C_\beta^{(0)}(p,p_0)}{\partial\beta}=E(p)C_\beta^{(0)}(p,p_0). \tag{46}$$

With adequately chosen function $E(p)$, this equation may concern conduction electrons in a homogeneous nondegenerate semiconductor. [Since $E(p)$ is not equal to the kinetic energy of an electron in vacuum, we may interpret the conduction electrons as quasiparticles defined by the dispersion law $E=E(p)$.]

Our second remark concerns analogy with the diffusion theory. The Fourier transform of the function $G(p,t;p_0)$ (multiplied by a constant) can be interpreted as the concentration $C(x,t;x_0)$ of diffusants which all were initially, at the time $t_0=0$, localized in the point x_0. In the approximation of the present paper, we may generally write the equation

$$\frac{\partial C_0(x,t;x_0)}{\partial t}=-\frac{1}{\tau}c\left(-\mathrm{i}\frac{\partial}{\partial x}\right)C_0(x,t;x_0)+\frac{\mu}{\tau}\exp\left(-\frac{\sigma_m^2 x^2}{2}\right)C(x,t;x_0). \tag{47}$$

If $c(p)=\gamma p^2$, the concentration $C(x,t;x_0)$ obeys the usual diffusion equation with the diffusion coefficient $D=\gamma/\tau$. If $c(p)\neq\gamma p^2$, the diffusion is anomalous. In any case, the positiveness of the potential-energy term means that Eq. (47) involves a *creation* of diffusants.

If $\mu=0$, we observe that $N_0=\int_{-\infty}^{\infty}dx C_0(x,t;x_0)$ is a quantity not varying in time. Therefore, we may define the probability density $P_0(x,t;x_0)=C_0(x,t;x_0)/N_0$ and put the theory on an equal footing with the theory of the Brownian motion.

If $c(p)=\gamma p^2$ and $\mu=0$, we may write down the Langevin equation $\dot{x}(u)=(2\gamma/\tau)^{1/2}\tilde{f}(u)$ for the stochastic paths $x(u)$ $(0\leqslant u\leqslant t)$ which all start from the common point $x(0)=x_0$ at the time instant $u_0=0$. The value of the end point $x(t)=x$ at a given time instant $t>0$ may be arbitrary and $P_0(x,t;x_0)=\langle\delta(x-x(t))\rangle$. In the terminology of the theory of stochastic processes, $x(u)$ is the Wiener process.

But then a natural question arises: which stochastic process corresponds to the case when the fitness function $w(p)$ is modeled by function (8b), with which we have exemplified our problem? About ten years ago, we dealt with the equation

$$\frac{\partial P_0(x,t;x_0)}{\partial t}=\frac{\gamma}{\tau}\left[\exp\left(a\frac{\partial^2}{\partial x^2}\right)-1\right]P_0(x,t;x_0)+D_0\frac{\partial^2 P_0(x,t;x_0)}{\partial x^2}. \tag{48}$$

[Compare with Eq. (48) in Ref. [18]; see also Ref. [19].] Equation (48) corresponds to a stochastic process with paths $x(u)$ defined by the stochastic equation $\dot{x}(u)=[(2D_0)^{1/2}+a\Sigma_j\delta(u-u_j)]\tilde{f}(u)$, where $\tilde{f}(u)$ is the standard zero-centered Gaussian white-noise function and where the sum represents a point process, in which u_j are random time instants distributed in the Poissonian way. The Poissonian process consists of equal δ pulses: all the pulses are taken with the same amplitude a. The average frequency of these pulses is equal to γ/τ. Clearly, we consider a *multiplicative* stochastic process $x(u)$ $(0\leqslant u\leqslant t)$. The probability density $P_0(x,t;x_0)=\langle\delta(x-x(t))\rangle$ is the fundamental solution of Eq. (48). Alternatively (as we have shown in Ref. [18]), Eq. (48) can be written in the equivalent integrodifferential form

$$\frac{\partial P_0(x,t;x_0)}{\partial t}=\frac{\gamma}{\tau}\int_{-\infty}^{\infty}dx'\times\left[\frac{1}{(2\pi a)^{1/2}}\exp\left(-\frac{(x-x')^2}{2a}\right)-\delta(x-x')\right]\times P_0(x,t;x_0)+D_0\frac{\partial^2 P_0(x,t;x_0)}{\partial x^2}. \tag{49}$$

In the case when $D_0=0$, Eq. (49) was employed by Laskin [20] in a theory of the channeling of high-energy particles in crystals. (The channeling occurs when a ray of equi-energy particles bombarding a crystal is collimated very precisely in a favorable direction.)

In the framework of the diffusion theory, we may conclude that the parameter γ of the theory of the population genetics corresponds to an environmental noise. If $\gamma=0$, the noise is absent.

Section IV of the present paper has been devoted to the problem of the evolution of a population in which all individuals are initially equal, being the carriers of the phenotypic value $p_0=0$. The distribution function $\Phi(p,t;0)$ of the population is the sum of a sharp δ-function component, $N(t)\delta(p)$, and a blurred component. Similarly, as in the thermodynamics, we may distinguish two phases in the population at any time $t>0$. Let us denote them as phase S and phase B. The phase S consist of the carriers of the initial phenotypic value $p_0=0$. The phase B consists of the individuals carrying the phenotypic values $p\neq p_0$. In the Waxman-Peck model [cf. expressions (43a) and (44a)], the probability $N(t)$ tends to zero if $t\to\infty$. Therefore, we may say that the phase S dissolves gradually in the phase B. In the model with the fitness function $w(p)$ defined by expression (8b) (or by another similar expression), the probability $N(t)$ does not tend asymptotically to zero: this model predicts that both the phases S and B may coexist if $t\to\infty$.

ACKNOWLEDGMENTS

This work has been supported by the Grant Agency VEGA of the Slovak Academy of Sciences and of the Ministry of Education of the Slovak Republic under Contract No. 1/7656/20. I thank D. Waxman for sending me some reprints of his papers. I thank R. Hlubina and A. Plecenik for their critical reading of my manuscript.

APPENDIX

In the model where $c(p)=\gamma[1-\exp(-ap^2)]$, we have to manage the function

$$\frac{1-\exp[-c(p)t/\tau]}{c(p)}=\frac{1-\exp\{-\gamma[1-\exp(-ap^2)]t/\tau\}}{\gamma[1-\exp(-ap^2)]}=\frac{1}{\tau}\int_0^t dt_1\exp\left(-\frac{\gamma[1-\exp(-ap^2)]t_1}{\tau}\right)=\frac{1}{\tau}\int_0^t dt_1\exp\left(-\frac{\gamma t_1}{\tau}\right)\times\exp\left(\frac{\gamma t_1}{\tau}\exp(-ap^2)\right).$$

We have to calculate the integral

$$\int_{-\infty}^{\infty}dp\,\varphi(p,t)=1+\frac{\mu}{\tau}\int_0^t dt_1\exp\left(-\frac{\gamma t_1}{\tau}\right)I(t_1),$$

where

$$I(t_1)=\left(\frac{1}{2\pi\sigma_{\mathrm{m}}^2}\right)^{1/2}\int_{-\infty}^{\infty}dp\,\exp\left(-\frac{p^2}{2\sigma_{\mathrm{m}}^2}\right)\times\exp\left(\frac{\gamma t_1}{\tau}\exp(-ap^2)\right).$$

When developing the second exponential in the MacLaurin series, we obtain the following sum of the Laplace integrals:

$$I(t_1)=\left(\frac{1}{2\pi\sigma_{\mathrm{m}}^2}\right)^{1/2}\sum_{j=0}^{\infty}\frac{t_1^j}{j!\,\tau^j}\int_{-\infty}^{\infty}dp\,\exp\left[-\left(\frac{1}{2\sigma_{\mathrm{m}}^2}+ja\right)p^2\right].$$

Hence,

$$I(t_1)=\sum_{j=0}^{\infty}\frac{t_1^j}{j!\,\tau^j(1+2ja\sigma_{\mathrm{m}}^2)^{1/2}}.$$

In this way, we have obtained the result

$$\int_{-\infty}^{\infty} dp\,\varphi(p,t) = 1 + \frac{\mu}{\tau}\sum_{j=0}^{\infty} \frac{1}{j!\,\tau^j (1+2ja\sigma_{\mathrm{m}}^2)^{1/2}} \int_0^t dt_1 \times \exp\left(-\frac{\gamma t_1}{\tau}\right) t_1^j .$$

The integral on the right hand side of this equality is easily calculable

$$\int_0^t dt_1 \exp\left(-\frac{\gamma t_1}{\tau}\right) t_1^j = \frac{j!\,\tau^{j+1}}{\gamma^{j+1}}\left[1 - \exp\left(-\frac{\gamma t}{\tau}\right)\sum_{k=0}^{j}\frac{\gamma^k t^k}{k!\,\tau^k}\right].$$

Thus, we have obtained the distribution function

$$\Phi(p,t;0) = N(t)\left[\delta(p) + \frac{\mu}{\gamma} M(p;\sigma_{\mathrm{m}}) \times \frac{1-\exp\{-\gamma[1-\exp(-ap^2)t/\tau]\}}{1-\exp(-ap^2 t/\tau)}\right],$$

where

$$N(t) = \left\{1 + \frac{\mu}{\gamma} \times \sum_{j=0}^{\infty} \frac{1}{\gamma^j (1+2ja\sigma_{\mathrm{m}}^2)^{1/2}} \times \left[1 - \exp\left(-\frac{\gamma t}{\tau}\right)\sum_{k=0}^{j}\frac{\gamma^k t^k}{k!\,\tau^k}\right]\right\}^{-1}.$$

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