Journal of Statistical Physics, Vol. 37, Nos. 3/4, 1984

Diffusion and Reaction in Random Media and Models of Evolution Processes

W. Ebeling,[1] A. Engel,[1] B. Esser,[1] and R. Feistel[1]

Received December 5, 1983; revision received June 5, 1984

A diffusion equation including source terms, representing randomly distributed sources and sinks is considered. For quasilinear growth rates the eigenvalue problem is equivalent to that of the quantum mechanical motion of electrons in random fields. Correspondingly there exist localized and extended density distributions dependent on the statistics of the random field and on the dimension of the space. Besides applications in physics (nonequilibrium processes in pumped disordered solid materials) a new evolution model is discussed which considers evolution as hill climbing in a random landscape.

KEY WORDS: Diffusion, disordered structures; evolution; localization; random processes.

1. INTRODUCTION

The phenomenon of a cooperative action of diffusion and reaction in random media has applications in diverse areas and arouses much interest. Many interesting results have been obtained already for the case that the rates of reaction (or replication) are independent of the space coordinates.[1] The basic equation governing reaction-diffusion problems is the following:

$$\frac{\partial}{\partial t} n(q, t) = n(q, t)\, w(q \mid n) + D \frac{\partial^2}{\partial q^2} n(q, t) \tag{1.1}$$

where n is the density of certain physical, chemical, or biological objects defined over the region Ω of an appropriate space of dimension d; further D is the constant of diffusion in that space and w the rate of reproduction of the objects located at the coordinate $q = \{q_1 \cdots q_d\}$. In many cases w

We dedicate this work to the memory of Ilya M. Lifshitz.

[1] Sektion Physik, Humboldt-Universität, Berlin, German Democratic Republic.

0022-4715/84/1100-0369$03.50/0

depends on q only via the density $n(q, t)$ itself; this leads to the usual reaction-diffusion problems which are well studied (see, e.g., Refs. 1 and 2). If however, $w(q \mid n)$ is a rather complicated function of q which is due to randomly changing properties of the medium in which the reaction and diffusion processes occur, another type of mathematical problem arises. This problem is closely related to the quantum theory of electrons moving in random potentials. This is a modern field of physics which has attracted much interest in recent times.[3–5] If the potential is spatially random, as first pointed out by Anderson,[6] there are eigenstates of the Schrödinger equation which are dying off away from particular regions of space. Such eigenstates are localized and do not conduct, whereas those with wave functions proportional to $\Omega^{-1/2}$ are extended and do conduct. There is a critical energy E_c, called the mobility edge separating localized states from extended states. For the class of problems considered here, diffusion and reaction in random media, the concepts of localized and extended states are of much interest too, since for a certain class of functionals $w(q \mid n)$ there is a transformation of Eq. (1.1) in such a way that the stationary solution of (1.1) and the Schrödinger equation are equivalent. This is the case for the evolution model we want to propose in the following. Despite the fact that the time behavior of both equations is quite different, many concepts and results of the quantum theory may be translated for use in our problem, as will be shown below. We are interested not only in the case of low dimension $d = 1, 2, 3$ but also in diffusion processes in high-dimensional spaces $d \geqslant 4$. This is connected with our interest in some new ideas and models about evolution processes.[7,8] Following these ideas evolution may be considered as a hill-climbing process in a random landscape. This process may formally be modeled by an equation of type (1.1), where q stands for a set of biological properties of a species and $n(q, t)$ is the population density of this species. The diffusion part models biological change (mutations). In this case the q space, called "phenotype space" is of very high dimension. Certainly the representation of mutations by Fickian diffusion is only a rough approximation, since "far mutations" are excluded in this way. However most of the biological mutations lead indeed to species with are "near" in respect to their phenotype and therefore the diffusion approximation is often used in genetical theories.[9] The theory given here may also be applied to ecological processes in real space as, e.g., the growth and migration of bacteria on a Petri dish covered with a nonuniform gel infected with bacteria ($d = 2$) or growth and migration processes of microorganisms in tanks without stirring ($d = 3$). Further possible applications of the equations discussed in this work are connected with transport processes or optical processes in active (pumped) disordered solid materials. One can model, e.g., by Eq. (1.1) the two-dimensional current distribution $i(q, t)$ of an electrical current crossing

perpendicularly a thin random layer (or boundary region) between two conductors. In this case q are the physical space coordinates, and the source term $i(q, t)\, w(q, i)$ describes the amplification of local currents according to favorable local properties. The result may be either a breakthrough at one place (localization of the current) or a uniform distribution (delocalized current).

The problems discussed above may show that the study of diffusion and reaction in random media is of interest for the modeling of different physical and nonphysical systems. Since we are interested here in processes in high-dimensional phenotype spaces ($d \gg 3$) and in processes in real physical spaces ($d = 1, 2, 3$) as well, we do not specify in the following the dimension d.

2. THE EVOLUTION MODEL

In a previous paper[7] it has been proposed to describe biological evolution formally as a drift process in a high-dimensional phenotype space nonlinearly driven by a fitness functional. The phenotype space is spanned by all possible combinations of phenotypic properties $q = \{q_1, \ldots, q_d\}$ where we could, e.g., imagine that q_1 fixes the height of the species, q_2 its weight, etc. To specify a biological species one has to choose $d = 10^2 \cdots 10^4$. The different values of the fitness functional at different loci (i.e., for different species) acts as a force to change the population distribution, leading that way to a changed landscape and so on. Any dependence on the physical space variables will be omitted, i.e., we consider only homogeneous populations.

Subject to such a description may be a simple ecological system, e.g., a homogeneous bacteria population in a tank reactor under controlled boundary conditions.

The basic equation for the population density $n(q, t)$

$$\frac{\partial}{\partial t} n(q, t) = n(q, t)[E(q) - F(t)] + D \frac{\partial^2}{\partial q^2} n(q, t) \tag{2.1}$$

is a generalization of R. A. Fisher's classical population genetical model[9] which was extensively studied by Eigen[10,2] and others for prebiotical models in the modified form

$$\frac{d}{dt} x_i(t) = (A_i - D_i)\, x_i + \sum_j (A_{ij} x_j - A_{ji} x_i) - F(t)\, x_i \tag{2.2}$$

Here A_i is the rate of correct reproduction, $A_{ji} x_i$ are the error copies j produced by i, D_i is the death rate, and $F(t)$ is a dilution flux controlled by

the boundary conditions. In relation of (2.1) and (2.2), the discrete species index i is appropriately replaced by the continuous phenotype vector q and $E(q) \triangleq A_i - D_i$ is the net reproduction rate. Supposing that the mutation rate is symmetrical, homogeneous, and of short range in the q space, it gives the diffusionlike expression in Eq. (2.1). In Fisher–Eigen models $F(t)$ is chosen as the population average fitness

$$F(t) = \int E(q)\, n(q, t)\, dq \Big/ \int n(q, t)\, dq \tag{2.3}$$

in order to keep the total occupation $N = \int n(q, t)\, dq$ constant. Thus Eq. (2.1) is of the type (1.1) with a linear functional

$$w(q \mid n) = E(q) - N^{-1} \int E(q')\, n(q', t)\, dq' \tag{2.4}$$

Note that in this case the interaction of the different species is modeled only by an overall dilution flux which correspondes to the mean field concept in the physics of many-body systems. The problem is that the fitness function $E(q)$, which gives the "selective value" of a species with the properties q, is practically unknown. There are reasons to believe that $E(q)$ has a very complicated structure. One is that living beings can only approach to a certain compromise between several physical, chemical, and biological requirements and conditions, to find the "fittest" is a so-called "frustrated problem." This was underlined by Anderson,[11] who suggested a prebiotic model and argued that the valuation function is necessarily chaotically shaped, comparable with the multimodality of a spin glass Hamiltonian. In such a system many states of local stability (read: high fitness) compete, which can cause, following Landauer,[12] that classical maximum principles may fail (say the "fittest" principle of Darwin).

To get some properties of the solution of Eq. (2.1) we shall assume that at least statistical properties of the function $E(q)$ are given by a functional probability density $P[E(q)]$. It is reasonable to assume that the correlations in $E(q)$ vanish for very distant points in the q space. Further we shall simplify the problem by treating macroscopically homogeneous random fields $E(q)$.

For the case without the diffusion part in Eq. (2.1) and a Gaussian distribution $P[E(q)]$ an explicit time-dependent solution was given by Zeldovich.[13] Using percolation theory he showed that with increasing time the population concentrates in islands where particular high values of the random function $E(q)$ are realized. In the presence of diffusion, however, the behavior of the solution of (2.1) is more complicated, as will be shown in the following section.

3. TIME BEHAVIOR OF SOLUTIONS

We assume that $E(q)$ is a random function and derive some approximate expressions for the time-dependent solution $n(q, t)$ of (2.1) by using the analogy to the Schrödinger equation for an electron in a random field. To make this analogy explicit we use in Eq. (2.1) the transformation

$$y(q, t) = n(q, t) \exp\left[\int_0^t F(t')\, dt'\right] \tag{3.1}$$

to get

$$\begin{aligned} \partial_t y(q, t) &= \left[E(q) + D\frac{\partial^2}{\partial q^2}\right] y(q, t) \\ y(q, 0) = n_0(q), \quad \frac{\partial y}{\partial q}(q, t) &= 0, \qquad \forall q \in \partial\Omega,\ \forall t \end{aligned} \tag{3.2}$$

Consequently we may write $y(q, t)$ in the form

$$y(q, t) = \sum_n c_n \exp(E_n \cdot t)\, \psi_n(q) \tag{3.3}$$

$$c_n = \int dq\, n_0(q)\, \psi_n(q) \tag{3.4}$$

where the E_n and ψ_n are given by the eigenvalue problem

$$\left[D\frac{\partial^2}{\partial q^2} + E(q)\right] \psi_n(q) = E_n \psi_n(q) \tag{3.5}$$

Therefore ψ_n and E_n are the eigenfunctions and negative eigenvalues, respectively, of a stationary Schrödinger equation of a particle of mass

$$m = \frac{\hbar^2}{2D} \tag{3.6}$$

in a potential

$$u(q) = -E(q) \tag{3.7}$$

For the continuous part of the spectrum the sum in Eq. (3.3) has to be replaced by an integral. Note that $y(q, t)$ in Eq. (3.2) is a probability distribution and not a quantum mechanical wave function. The main following differences to ordinary quantum mechanics are $y(q, t) \geqslant 0\ \forall q\ \forall t$ and linear averages, calculated with $y(q, t)$ alone (not with $y^* \cdot y$).

Inserting (3.3) into (3.1), integrating over q, and using (2.3) we get

$$\sum_n c_n a_n e^{E_n \cdot t} = N \exp\left[\int_0^t F(t')\, dt'\right]$$

$$N = \int dq\, n_0(q)$$

$$a_n = \int dq\, \psi_n(q)$$

and therefore

$$n(q, t) = N \frac{\sum_n c_n e^{E_n \cdot t} \psi_n(q)}{\sum_n c_n e^{E_n \cdot t} a_n} \tag{3.8}$$

Equation (3.8) represents the solution of (2.1) by the eigenfunctions and eigenvalues of the equivalent Schrödinger problem (3.5)–(3.7). For various random field models with different statistics for $E(q)$ this problem was intensively investigated in the last years.[3–5] In particular a basic result proved by Pastur[3,4] is that for a given statistics of $E(q)$ all the realization of $E(q)$ generate the same spectrum of eigenvalues E_n with probability 1. Hence for given statistics of $E(q)$ definite conclusions concerning the energy spectrum, i.e., the density of states, and other self-averaging quantities are possible.[3–5] Another important point concerns the very nature of the states $\psi_n(q)$ entering the right-hand side of (3.3), i.e., the question whether these states are localized or extended. From (3.5)–(3.7) it is immediately clear that this is the problem of Anderson localization of a particle in a random potential $U(q) = -E(q)$ (considered by Anderson in case of a lattice Hamiltonian[6]). In the last years the scaling theory of localization has added much to our understanding of localization in random potentials.[14] For space dimensions $d \geqslant 3$ the existence of a mobility edge separating extended from localized states is now certain. However the dependence of the transition from extended to localized states from other parameters of the problem such as the strength of the random field and its correlation length seems to be still an open problem. This dependence must obviously be connected with the space dimension, e.g., it is well known that the white noise limit (vanishing correlation length) must be taken with special care when treating fluctuation states produced by the random field for space dimensions $d \geqslant 4$.[3,15] Here we shall assume the existence of localized states in the eigenvalue problem set by Eq. (3.5). As will be seen the existence of localized states is important for the long-time behavior of the solution of (2.1).

We consider two approximate solutions of Eq. (2.1). The first approximation is a short time expansion based on a semiclassical calculation of the

Green's function equivalent to (3.5). This approximation is particularity useful for a smooth random relief $E(q)$ or equivalently small diffusion. For $D \to 0$ we obtain the result of Zeldovich[13] from this solution.

The second approximation is derived from (3.8) for the long-time behavior by using approximative expressions for the localized states.

3.1. Smooth Variations of $E(q)$

Here we assume that $E(q)$ is a slowly varying function and the solution of (3.2) can be calculated by an expansion of derivatives of $E(q)$ and powers of D of rising order. This is equivalent to the semiclassical expansion in rising powers of $\hbar^2$ in the corresponding quantum problem.[5] In this case it is convenient to start with the Green's function equivalent to (3.2), (3.5). Using the initial condition

$$n_0(q) = N \cdot \delta(q - q')$$

we get

$$\left[p - D \frac{\partial^2}{\partial q^2} - E(q) \right] G(q, q'; p) = N \cdot \delta(q - q') \tag{3.9}$$

where $G(q, q'; p)$ is the Laplace transform of the Green's function. With the Fourier representation of the δ function in the right-hand side of Eq. (3.9) one obtains

$$G(q, q'; p) = \frac{N}{(2\pi)^d} \int d^d k \frac{1}{p - D(\partial^2/\partial q^2) - E(q)} e^{ik(q-q')} \tag{3.10}$$

In the zeroth order of the expansion we neglect the derivatives of $E(q)$ altogether and find

$$G^0(q, q'; p) = \frac{N}{(2\pi)^d} \int d^d k \frac{1}{p + Dk^2 - E(q)} e^{ik(q-q')} \tag{3.11}$$

Now the Laplace transform is easily reversed and the k integral done. One obtains

$$G^{(0)}(q, q'; t) = \frac{N}{(4\pi Dt)^{d/2}} \exp\left[t \cdot E(q) - \frac{(q - q')^2}{4Dt} \right] \tag{3.12}$$

According to (3.1) the corresponding expression for $n^{(0)}(q, t)$ is

$$n^{(0)}(q, t) = \exp\left\{ \int_0^t [E(q) - F(t')]\, dt' \right\} \frac{N}{(4\pi Dt)^{d/2}} \exp\left[- \frac{(q - q^2)^2}{4Dt} \right] \tag{3.13}$$

The role of the two factors in the right-hand side of Eq. (3.13) is obvious. The first factor exponentially increases (decreases) for space regions where $E(q)$ is greater (smaller) than the mean value $F(t)$. The second factor describes ordinary diffusion from the initial value q' into space regions q. The combined effect of both factors results in a shift of $n(q, t)$ to regions with high-valued $E(q)$. An improvement of (3.13) is easily performed along the lines of the semiclassical approximation (Appendix XII of Ref. 5). Keeping terms up to the second derivatives in $E(q)$ one obtains

$$G^{(1)}(q, q'; t) = \frac{N}{(4\pi Dt)^{d/2}} \times \exp\left[t \cdot E(q) + \frac{t^2}{2} D \frac{\partial^2}{\partial q^2} E(q) + \frac{t^3}{3} D \left(\frac{\partial}{\partial q} E(q)\right)^2\right] \times \exp\left\{-\frac{[q - q' + t^2(\partial/\partial q)\, E(q)]^2}{4Dt}\right\} \tag{3.14}$$

In the next orders terms with higher powers in t will appear which become significant with increasing time. Hence (3.14) represents a short time expansion. The time region of validity of (3.10) is however the larger the smaller the derivatives of $E(q)$ or equivalently the diffusion coefficient D are. For $D \to 0$ and a homogeneous initial condition $n(q, t = 0) = n_0$ the result of Zeldovich[13] is easily obtained. Indeed, from (3.13) we get for a homogeneous initial distribution

$$n^{(0)}(q, t) = n_0 \exp\left\{\int_0^t [E(q) - F(t')]\, dt'\right\} \tag{3.15}$$

Now $F(t)$ introduced by (2.3) insures a constant total occupation, $\int n^{(0)}(q, t)\, dq = N$. Hence integration of Eq. (3.15) over q yields

$$\exp\left[\int_0^t F(t')\, dt'\right] = \frac{1}{\Omega} \int dq \exp[E(q) \cdot t] \tag{3.16}$$

The right-hand side of Eq. (3.16) is a spatial average which is equivalent to the ensemble average performed with the distribution $P[E(q)]$ of $E(q)$. Assuming Gaussian statistics for $P[E(q)]$ with a zero mean value $\langle E \rangle = 0$, one obtains from (3.16)

$$F(t) = \langle E^2 \rangle \cdot t \tag{3.17}$$

where $\langle E^2 \rangle$ is the mean square of $E(q)$. Inserting (3.17) into (3.15) the solution given in Ref. 13 results.

3.2. Evolutionary Hopping

Now we consider the evolution of $n(q, t)$ after that part of $n(q, t)$ connected with the extended states has relaxed out and the localized states dominate in (3.8). Such a time region is always reached (if localized states exist) because in the present problem the E_n are the negative eigenvalues of the corresponding Schrödinger problem, see (3.7). Hence the eigenvalues E_n of the localized solution of (3.5) are higher than the eigenvalues of the extended states and the contribution of the latter becomes negligible in the sums in (3.8) after some time. Note that for $d \geqslant 4$ the field $E(q)$ has to be not δ correlated to ensure the existence of localized states.[15] Otherwise the spectrum is purely continuous and there is no concentration of the distribution in the long time region but a diffusion-like spreading takes place.

We assume exponentially localized states characterized by a localization center q_n and the localization length $l(E_n)$, i.e., the asymptotic dependence of $\psi_n(q)$ is

$$\psi_n(q) \sim \exp\left[-\frac{|q-q_n|}{l(E_n)}\right] \tag{3.18}$$

The localization length l is generally a function of the eigenvalue E_n. The selection processes are described by the falling into the "ground state" of a local maximum of $E(q)$ (establishing local equilibrium), whereas the diffusion appears as tunneling to other local maxima of $E(q)$ (see Fig. 1). This is schematically shown in Fig. 2.

Now it is interesting to consider which states effectively contribute to the sum in Eqs. (3.3), (3.8). Taking once more the initial condition $n_0(q) = N \cdot \delta(q-q')$, i.e., $c_n = \psi_n(q')$ we get from (3.3)

$$y(q, q'; t) = \sum_n \exp\left\{-\frac{1}{l(E_n)}\left[|q-q_n| + |q'-q_n|\right] + t \cdot E_n\right\} \tag{3.19}$$

and from (3.1)

$$n(q, q'; t) = \sum_n \exp\left\{\int_0^t dt'(E_n - F(t')) - \frac{1}{l(E_n)}\left[|q-q_n| + |q'-q_n|\right]\right\} \tag{3.20}$$

For small times the time dependent integral in Eq. (3.20) is negligible and the coordinate dependent part dominates. Hence the states effectively present are states nearby q', for which $|q'-q_n| \sim |q-q_n| \sim l(E_n)$. For intermediate times the time dependent integral is a fastly rising function for terms corresponding to states with the largest E_n. However the factor $[l(E_n)]^{-1}$ in

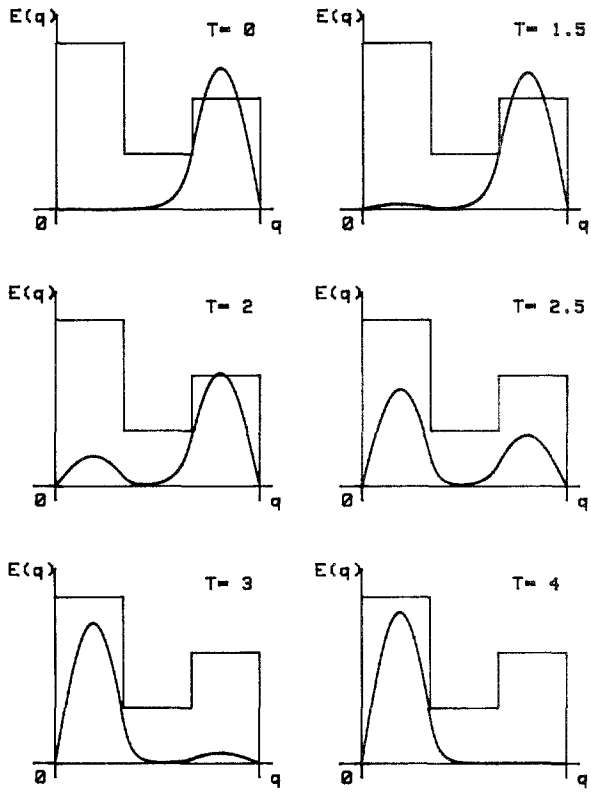

Fig. 1. Numerical solution of Eq. (3.2) for a simple double-well shape of the function $E(q)$. Initial condition $n_0(q) = \psi_0 + 0.0001 \cdot \psi_2$ time units $\tau = (E_0 - E_2)^{-1}$ [cf. Eq. (3.8)].

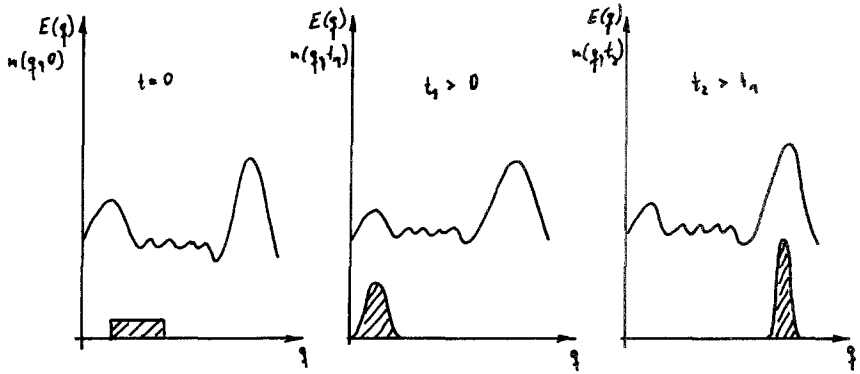

Fig. 2. Schematic picture of the evolution according to Eq. (3.8): Falling into the local ground state (establishing local equilibrium) at t_1 followed by a "tunneling" to the next higher maximum of $E(q)$ at t_2.

the coordinate dependent part will also be large for such states and a competition of these two tendencies takes place. As a result, states with lower values of E_n are left and those with higher ones are entered up to the final time region discussed above. The competition between time and coordinate dependent part in Eq. (3.20) makes it difficult to decide wether the transition from the initial state to the final one is a rather direct process or if there are a lot of intermediate states involved. This can be clarified in the following way. From (3.18) it is clear that only a few of the c_n's will be of order unity. We define

$$E_0 = \max_{n, c_n \approx 1} E_n$$

as the maximum among the eigenvalues corresponding to an eigenfunction with $c_n \approx 1$. The majority of the c_n's will be exponentially small, since $|q_n - q'| \gg l(E_n)$. With (3.18) we have approximately

$$\frac{c_n}{c_0} \simeq \exp\left[-\frac{|q_n|}{l(E_n)}\right] \tag{3.21}$$

where we have chosen q_0 as origin of our coordinate system. So for small time $n(q, t)$ is dominated by ψ_0. At the time

$$t_n = \frac{\ln(c_0/c_n)}{(E_n - E_0)} \tag{3.22}$$

we get

$$c_0 e^{E_0 \cdot t_n} = c_n e^{E_n \cdot t_n} \tag{3.23}$$

i.e., $n(q, t)$ is no longer dominated by ψ_0 alone and there is a transition into other space regions (see Fig. 1). From (3.21) and (3.22) results

$$t_n = \frac{|q_n|}{l(E_n)(E_n - E_0)} \tag{3.24}$$

We try to find the mean transition time $\bar{t}$ for such a transition into other space regions.

Because $E(q)$ is macroscopically homogeneous the probability of finding the localization center q_i of a function ψ_i corresponding to an eigenvalue out of the interval $(E, E + dE)$ in the d-dimensional sphere with radius r is

$$w(e, r)\, dE\, dr = \rho(E)\, dE\, S_d r^{d-1}\, dr$$

$$S_d = \frac{2\pi^{d/2}}{\Gamma(d/2)} \tag{3.25}$$

$$\rho(E) = \lim_{V \to \infty} \frac{1}{V} \sum_n \delta(E - E_n) \tag{3.26}$$

is the density of states of the operator on the left-hand side of Eq. (3.5) and $\rho(E)\,dE$ gives therefore the number of eigenvalues out of the interval $(E, E+dE)$ per unit volume. In Eq. (3.25) we have neglected possible correlations between the states.

From (3.25) and (3.24) we get

$$w(E,t)\,dE\,dt = \rho(E)\,dE\,S_d[l(E)(E-E_0)]^d\,t^{d-1}\,dt \tag{3.27}$$

as probability for a transition in the time interval $(t, t+dt)$ to a state with eigenvalue out of $(E, E+dE)$. Hence

$$w(t)\,dt = \left[S_d\int_{E_0}^{\infty}[l(E)(E-E_0)]^d\,\rho(E)\,dE\right]t^{d-1}\,dt \tag{3.28}$$

gives the probability for a transition during $(t, t+dt)$ to any other state.

Using the abbreviation

$$K_d = S_d\int_{E_0}^{\infty}[l(E)(E-E_0)]^d\,\rho(E)\,dE$$

we get for the probability density $P(t)$ of the time of first escape:

$$\begin{aligned} P(t) &= \left(1-\int_0^t P(t')\,dt'\right)K_d t^{d-1} \\ \frac{d}{dt}\left[\frac{P(t)}{K_d t^{d-1}}\right] &= -P(t) = -K_d t^{d-1}\left[\frac{P(t)}{K_d t^{d-1}}\right] \\ P(t) &= K_d\cdot t^{d-1}\exp\left(-\frac{1}{d}K_d t^d\right) \end{aligned} \tag{3.29}$$

For $\bar{t}$ we find

$$\bar{t} = \int_0^{\infty} t\cdot P(t)\,dt = \Gamma\left(\frac{d+1}{d}\right)\left[\frac{S_d}{d}\int_{E_0}^{\infty}[l(E)(E-E_0)]^d\,\rho(E)\,dE\right]^{-1/d} \tag{3.30}$$

Usually $\rho(E)$ falls off exponentially for great E so $K_d < \infty$ and $\bar{t} > 0$. Putting $\rho(E) = \bar{\rho}(E_n)\cdot\delta(E-E_n)$ in (3.30) we get for the mean transition time to a state with eigenvalue E_n:

$$\bar{t}_{E_n} = \frac{\Gamma[(d+1)/d]}{l(E_n)(E_n-E_0)}\cdot\left[\frac{d}{S_d\cdot\bar{\rho}(E_n)}\right]^{1/d} \tag{3.31}$$

Consequently t_E is for great E a monotonically increasing function of E, i.e., transitions to states with smaller eigenvalues will be on the whole quicker

then those to states with higher ones, because their mean distance to q_0 is sufficiently shorter. So the evolution from the initial state to the final one will be a stepwise rather than a straight process. This is of special interest in sight of frustrated valuation functions,[11,12] because then there are many states with practically the same maximum $E(q)$, but located relatively far from each other. Then the transition probability is dominated by these distances instead of the $E(q)$ value. Especially in a high-dimensional space there is a large number of neighboring states with the same "attractiveness," and for a sample process the decision between them depends sensitively on random influences. Then the evolution turns out to be a random walk rather than a directed process (sometimes called non-Darwinian evolution).

Note also that from (3.31) follows $t_E \to \infty$ if $E \to E_0$. Therefore $t_E(E)$ has a minimum at some value $E_{\min}$ (see Fig. 3) and the evolution process will consist of successive small jumps in the phenotype space connected with an average fitness increase of $\delta E = E_{\min} - E_0$. This is pictured in Fig. 4. Taking into account the correlations of the different states ψ_i in (3.25) makes this feature even more distinct.[16]

In most cases $\rho(E)$ is a very complicated function. But if we start with a sufficiently high developed master species ψ_0 (i.e., $E_0 \gg \langle E^2 \rangle$), we may use asymptotic formulaes for $\rho(E)$ which are known for a wide class of random potentials.[16,3]

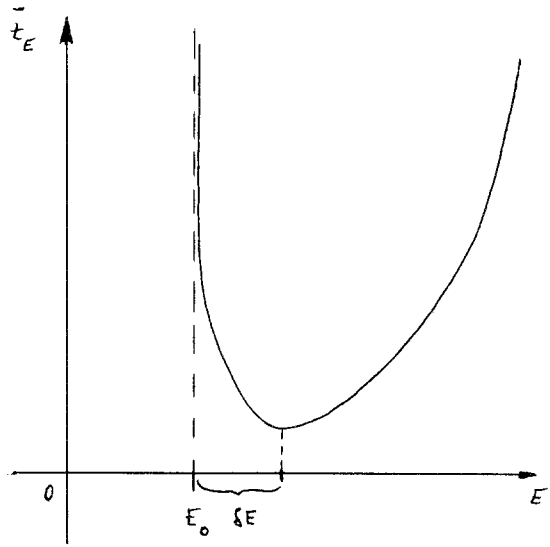

Fig. 3. Qualitative plot of the mean transition time $\bar{t}_E$ from a state with fitness eigenvalue E_0 to another one with eigenvalue E as function of E.

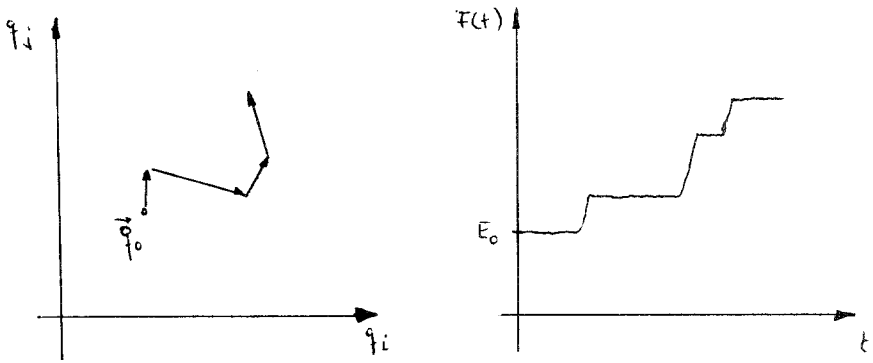

Fig. 4. Possible evolution pathway in a two-dimensional phenotype space and associated increase of the population average fitness $F(t)$ with time.

As an simple example we consider here a Gaussian ensemble

$$P[E(q)] = \frac{1}{\mathscr{N}} \exp\left[-\frac{1}{2}\iint dq\, dq'\, E(q)\, A(q, q')\, E(q')\right]$$

with zero mean value $\langle E(q)\rangle \equiv 0$ and the correlation function

$$B(q-q') = \langle E(q)\, E(q')\rangle$$

given by

$$\int B(q-q')\, A(q'-q'')\, dq' = \delta(q-q'')$$

The asymptotic form of $\rho(E)$ is[16,3]

$$\rho(E) \sim \exp\left(-\frac{E^2}{2B}\right) \qquad (3.32)$$

$$B = B(0)$$

Furthermore for $E^2 \gg B$ we have[5]

$$l(E) = \left(\frac{D}{E}\right)^{1/2} \qquad (3.33)$$

Inserting (3.32) and (3.33) into (3.30) we find for $E_0^2 \gg B \cdot d$

$$\bar{t} = \text{const} \cdot \Gamma\left(\frac{d+1}{d}\right)\left[\frac{d \cdot \Gamma(d/2)}{\Gamma[(d+1)/2]}\right]^{1/d}\left(\frac{E_0}{BD}\right)^{1/2} \exp\left(\frac{E_0^2}{2Bd}\right) \qquad (3.34)$$

Equation (3.34) gives the explicit dependence of $\bar{t}$ on the parameters of the problem. Note that the curves $\bar{t}(D, d) = \text{const}$ in the D–d plane are given by $D^d = \text{const}$ and that in the "white noise limit" $B \to \infty$ we get $\bar{t} \to 0$.

4. DISCUSSION

Let us discuss the main results of this paper in connection with the model of biological evolution introduced in Section 2. Similar conclusions of course hold for other physical and chemical examples. In the evolution model the vector $q \in R^d$ denotes a biological species by fixing all its phenotypical properties q_i, $i = 1 \cdots d$. ($d \gg 10$). The model appears as a continuous generalization of the well-known Fisher–Eigen equation, where mutation is modeled by the diffusion term.[7] The fitness $E(q)$ of the species q as function of the phenotypic properties q_i forms a random landscape, its detailed shape is unknown. Assuming it to be a random field and following the lines of this paper we find that the interaction of selection and diffusion enables the system to reach the most favorable regions of the q space, where the fitness $E(q)$ exhibits its greatest maxima (Darwin's principle). So the evolution process reminds hill-climbing in the fitness landscape $E(q)$. For small times this causes the development of an island structure in the phenotyp space, that means only certain combinations of the phenotypic properties represent viable organisms. Such combinations define a biological species. In the long-time region the hill-climbing proceeds via small but discrete steps (see Fig. 4). The quickest and therefore mostly realized transitions from an initial state with fitness E_0 occur to states with fitness eigenvalues $E = E_0 + \delta E$, $\delta E > 0$. That such a discontinuous character is found in a model where the phenotypic properties are allowed to change continuously may serve as indication, that the stepwise character of evolution as observed in nature is not a direct consequence of the discretness of mutations but a rather general feature of selection–diffusion processes.

Note that these statements are only true if the field $E(q)$ admits the existence of localized states, i.e., if $E(q)$ is not δ correlated ($d \geqslant 4$ is surely satisfied). Otherwise the spectrum of the operator in Eq. (3.5) will be purely continuous and a diffusion-like spreading of the initial distribution takes place. The necessity of a smooth landscape was first pointed out by Conrad.[18] It can be understood as premise to the development of a strategy by the system. The special role of the δ correlated field is connected with our diffusion approximation of the mutation process. Usually the mutation mechanism will set a length scale l_m and the discussed spreading of the distribution will occur in high dimensions whenever the correlation length of $E(q)$ is less than l_m. The diffusion approximation implies $l_m \to 0$ and thus these effects can only be observed if the correlation length vanishes too.

Therefore several interesting features of evolution processes can be understood using the model of a random field for $E(q)$. Furthermore characteristic parameters of the processes are completely determined by the statistical properties of this field alone. This is an essential point because for any real biological system the function $E(q)$ is practically not measurable and we may get at most some qualitative information about its shape. In this sense it is natural to assume that $E(q)$ is a random landscape and to relate its statistical and correlation properties to the characteristics of the evolution process like the velocity of phenotypical change, the dispersion of the gene pool of a species, etc. As we demonstrated, there is an interesting analogy in modeling of evolution processes on the one hand and disordered solid states on the other, which may support the further investigation in this field of biophysics.

REFERENCES

1. G. Nicolis and I. Prigogine, *Self-organization in Nonequilibrium Systems* (Wiley, New York, 1977); Yu. M. Romanovsky, N. V. Stepanova, and D. S. Chernavsky, *Mathematical Models in Biophysics* (in Russian) (Nauka, Moscow, 1975); H. Haken, *Synergetics. An Introduction* (Springer, New York, 1978).
2. W. Ebeling and R. Feistel, *Physik der Selbstorganisation und Evolution* (Akademie-Verlag, Berlin, 1982).
3. I. M. Lifshitz, S. A. Gredeskul, and L. A. Pastur, *Introduction into the Theory of Disordered Systems* (in Russian) (Nauka, Moscow, 1982).
4. L. A. Pasteur, *Commun. Math. Phys.* **75**:179 (1980); *Usp. Math. Nauk* **28**:3 (1973).
5. V. L. Bonch-Bruevich, R. Enderlein, B. Esser, R. Keiper, A. G. Mironov, and I. P. Zvyagin, *Elektronentheorie ungeordneter Halbleiter* (VEB Deutscher Verlag der Wissenschaften, Berlin, 1984).
6. P. W. Anderson, *Phys. Rev.* **109(5)**:1492 (1958).
7. R. Feistel and W. Ebeling, *BioSystems* **15**:291 (1982).
8. R. Feistel and W. Ebeling, in *Thermodynamics and Regulation in Biological Processes*, A. I. Zotin, ed. (Nauka, Moscow, 1984).
9. R. A. Fisher, *The Genetical Theory of Natural Selection* (Clarendon Press, Oxford, 1930).
10. M. Eigen, *Naturwiss.* **58**:465 (1971).
11. P. W. Anderson, *Proc. Natl. Acad. Sci.* **80**:3386 (1983).
12. R. Landauer, *Helv. Phys. Acta* **56**:847 (1983).
13. Ya. B. Zel'dovich, *Dokl. Akad. Nauk USSR* **270**:1369 (1983).
14. E. Abrahams, P. W. Anderson, D. C. Licciardello, and T. V. Ramakrishnan, *Phys. Rev. Lett.* **42**:673 (1979).
15. D. J. Thouless, *J. Phys. C* **9**:L603 (1976); J. L. Cardy, *J. Phys. C* **11**:L321 (1978).
16. A. Engel, in *Proceedings of the 5th UNESCO-Meeting on System Theory* (Akademie-Verlag, Berlin, 1984).
17. I. M. Lifshitz, *Usp. Fiz. Nauk* **83**:617 (1964).
18. M. Conrad, *Lect. Notes Biomath.* **21**:147 (1978); *Adaptability* (Plenum Press, New York, 1983).