

## Solvable biological evolution model with a parallel mutation-selection scheme

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Based on the connection between a quantum spin model and an asexual biological evolution model with a single-peak fitness function in parallel mutation-selection scheme, we solve exactly both static and dynamics of the evolution model. We find that relaxation in such a parallel scheme is faster than that in a connected scheme of Eigen model. Our method can also be extended to other fitness functions.

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Classical and quantum spin models [1,2] have been considered to be related to a variety of physical, mathematical, and biological problems. Thus a better understanding or solution of the former can often lead to a better understanding of the latter. Exact solutions of microscopic models often reveal important developments of theory, which cannot be matched in approximate solutions of the same models. In the present paper we will show that the method used in the solution of quantum spin models can be applied to solve exactly an asexual biological evolution model and answer some important open questions of biological evolution.

Biological evolution and associated genetic models have attracted the attention of researchers across various fields for more than a century [3–15]. In the popular microscopic Eigen model of asexual evolution [5,6], individuals have offspring that are subjected to mutation that connects with a selection. In the parallel mutation-selection model, a mutation mechanism and a selection mechanism are two independent processes that take place concurrently [7]. The proper choice of the mutation-selection scheme is an important open question in modern evolutionary biology [8–10]. It has been suggested that for the case of low mutation rates two schemes are similar [11]. In both cases there is a replication in the system with some rate. In the parallel case there are mutations with some rate uniform in time. In the connected case these mutations are strictly located at the replication events. In this paper we will show that for both low and high mutation rates, the relaxation in the parallel scheme is faster than that in the connected scheme (Fig. 1).

Statistical mechanics has been applied to investigate the discrete time version of the Eigen model [12,13]. Recently, Baake *et al.* [14] mapped equations of the parallel model into the Schrödinger equation in imaginary time for quantum spins in a transverse magnetic field. The model with a ferromagnetic fitness function proportional to the square of the total magnetization has been solved for both static and dynamics [14,15]. Based on the connection between the parallel model and the quantum spin model [14], here we derive an exact solution of the parallel model with a single-peaked fitness function, which is more relevant for biology, and compare it with the result for the connected (Eigen) model

obtained by exact [16] or approximate [17,18] methods.

*Biological Evolution Model.* In both connected and parallel mutation-selection models, a genome configuration is specified by a sequence of  $N$  spin values  $s_k = \pm 1$ ,  $1 \leq k \leq N$ . We denote the  $i$ th genome configuration by  $S_i \equiv (s_1^i, s_2^i, \dots, s_N^i)$  and  $S_1 = (1, 1, \dots, 1)$ , i.e., all spins are 1; the probability of the  $i$ th genome at time  $t$  is given by  $p_{S_i} \equiv p_i(t)$  and the fitness  $r_i$  is the average number of offsprings per unit time, which is a function  $f$  of  $S_i$ , i.e.,  $r_i = f(S_i)$ .

In the Eigen model, elements of the mutation matrix  $Q_{ij}$  represent probabilities that an offspring produced by state  $j$  changes to state  $i$ , and the evolution is given by the set of  $2^N$  coupled equations for  $2^N$  probabilities  $p_i$ :

$$\frac{dp_i}{dt} = \sum_{j \neq i}^{2^N} Q_{ij} r_j p_j + p_i \left( Q_{ii} r_i - \sum_{j=1}^{2^N} r_j p_j \right), \quad (1)$$

where  $p_i$  satisfies  $\sum_{i=1}^{2^N} p_i = 1$ . The mutation matrix is defined as  $Q_{ij} = q^{N-d(i,j)}(1-q)^{d(i,j)}$ , where  $d(i,j) \equiv (N - \sum_{k=1}^N s_k^i s_k^j)/2$  is the Hamming distance between configurations  $S_i$  and  $S_j$ . The parameter  $1-q$  is a probability per site for mutation. The simplest choice of  $f$  is the single-peaked function with

$$r_1 = A; \quad r_i = 1, \quad i \neq 1. \quad (2)$$

For this fitness function, Eigen used information theory to derive the exact error threshold:

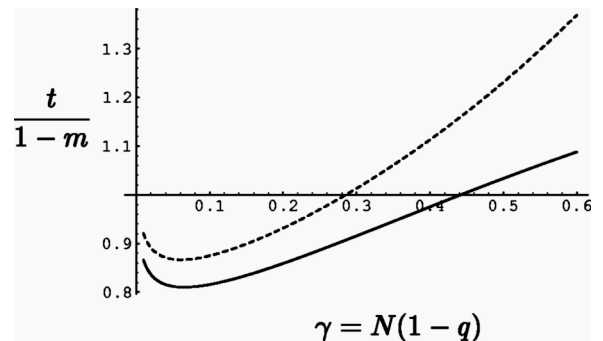


FIG. 1. Relaxation periods as a function of mutation rates. Dashed and solid lines are for connected and parallel schemes, respectively.

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$$A > e^\gamma. \tag{3}$$

Here  $\gamma \equiv N(1-q)$  is the number of mutations per genome per replication. It is important to note that while Eq. (3) allows  $\gamma > 1$ , it has been observed that  $\gamma$  is less than one in asexual evolution [19–21].

For the parallel mutation-selection model, the dynamics is given by

$$\frac{dp_i}{dt} = \sum_{j=1}^{2^N} m_{ij} p_j + p_i \left( r_i - \sum_{j=1}^{2^N} r_j p_j \right), \tag{4}$$

where  $m_{ij}$  are the elements of the mutation matrix. By comparing Eq. (1) with Eq. (4) one can notice that for Eq. (1) the mutation is connected with the replication, therefore we denote this model as a connected one; for Eq. (4) two processes (replication with the rate  $r_i$  and mutation with the rate  $m_{ij}$ ) are independent, thus we call it a parallel model.

In the following we adopt the following mutation matrix after Baake *et al.* [14]:  $m_{ij} = \gamma_0$  for  $d(i,j)=1$ ,  $m_{ij}=0$  for  $d(i,j) > 1$ , and  $m_{ij} = -N\gamma_0$  for  $i=j$ . Here  $\gamma_0$  reflects the mutation rate. Baake *et al.* [14] realized that, for the fitness  $r_i = f(S_i)$ , Eq. (4) is equivalent to the evolution of the quantum-mechanical spin system described by the Hamiltonian

$$-H = \gamma_0 \sum_{i=1}^N (\sigma_i^x - 1) + f(\sigma_1^z, \dots, \sigma_N^z), \tag{5}$$

$$\frac{d}{dt} \sum_{i=1}^{2^N} p_i(t) |S_i\rangle = -H \sum_{i=1}^{2^N} p_i(t) |S_i\rangle,$$

where  $\sigma$  denotes the Pauli spin operator and  $|S\rangle$  is the standard notation for the spin state. It follows from Eq. (5) that, starting at  $t=0$  from the initial distribution  $p_j^0$ , after a time  $t$  the new distribution  $p_i$  can be computed as

$$p_i = \frac{\sum_j \langle S_i | e^{-Ht} | S_j \rangle p_j^0}{Z}, \tag{6}$$

$$Z = \sum_{ij} p_j^0 Z_{ij}, \quad Z_{ij} = \langle S_i | e^{-Ht} | S_j \rangle,$$

where  $\langle S_i | e^{-Ht} | S_j \rangle$  is the standard notation for the transition matrix from configuration  $S_j$  to configuration  $S_i$ , and  $T(t) \equiv e^{-Ht}$  is the time evolution operator. Equation (6) is invariant under the transformation

$$f(S) \rightarrow f(S) + c. \tag{7}$$

Solving Eqs. (5) and (6) one can rescale the results to compare those in the connected model:

$$f(S) \rightarrow f(S)/L, \quad \gamma_0 \rightarrow \gamma_0/L, \quad t \rightarrow tL. \tag{8}$$

For the single-peaked fitness function, we take  $f(S) = J_0 N$  when  $S = S_1$  and  $f(S) = 0$ , otherwise, which is equivalent to the choice of Eq. (2) for the Eigen model.

What are the differences between two models? For the parallel case, both mutation and replication terms are characterized by rates with dimension of inverse time, and for the connected scheme mutation matrix  $Q_{ij}$  is dimensionless [10]. Eigen model does not have symmetries like Eqs. (7) and (8). Due to such symmetries actually the parallel model has only one free parameter  $\gamma_0/J_0$ , while Eigen model has two:  $A$  and  $q$ . Thus Eigen model can describe wider situations compared with the parallel case.

*Error Threshold.* Now we proceed to derive the error threshold of the parallel model and consider the following fitness function:

$$f(S) = J_0 N \left[ \frac{\sum_{k=1}^N \sigma_k^z}{N} \right]^p, \tag{9}$$

where  $p$  is a positive integer. As  $p \rightarrow \infty$ ,  $f(S)$  of Eq. (9) becomes the single-peaked fitness function defined above,  $f(S)$  of Eq. (9) for  $p=2$  was studied by Baake *et al.* [14]. For any value of  $p$  an exact method of Suzuki-Trotter formalism [22,23] can map the system of Eq. (5) to the problem in classical statistical mechanics. A simple presentation of the formalism for the model defined by Eqs. (5) and (9) is given in the Appendix of the present paper. Moreover, for the large values of  $p$  the problem is drastically simplified. For the quantum spins with  $p$ -spin interactions in a transverse magnetic field it has been found [23] that all the order parameters (magnetizations) are either 1 or 0 and one should take either only transverse interaction [ $\gamma_0 \sum_{k=1}^N (\sigma_k^x - 1)$ ] or only the longitudinal one [ $J_0 N [(\sum_{k=1}^N \sigma_k^z)/N]^p - N\gamma_0$ ]. We take the form of interactions, which gives a larger contribution to  $Z$  of Eq. (6). The ferromagnetic phase for the model of Eq. (5) has been studied in Ref. [24]. We need only slightly change those results to calculate matrix elements. In the Appendix we present a rigorous derivation of this trick. Here we only outline the main ideas.

To derive error threshold let us consider a situation, when originally all the individuals are just in the peak configuration. We take

$$\langle S_1 | e^{-Ht} | S_1 \rangle \sim \exp[N(J_0 - \gamma_0)t]. \tag{10}$$

With exponential accuracy we have for the other matrix elements

$$\langle S_i | e^{-Ht} | S_j \rangle = \langle S_i | \exp \left[ \gamma_0 \sum_{k=1}^N (\sigma_k^x - 1) \right] t | S_j \rangle. \tag{11}$$

The last expression can be factorized as the Cartesian product of matrices  $T_{\alpha,\beta}^1$  in the two-dimensional space, whose matrix elements are defined by  $T_{12}^1 = T_{21}^1 = \exp(-\gamma_0 t) \sinh(\gamma_0 t)$  and  $T_{11}^1 = T_{22}^1 = \exp(-\gamma_0 t) \cosh(\gamma_0 t)$ . Thus,

$$\begin{aligned} \langle S_i|T|S_j \rangle &= \prod_{k=1}^N \langle s_k^i|T^1|s_k^j \rangle \\ &= [\exp(-\gamma_0 t) \sinh(\gamma_0 t)]^{n_d} [\exp(-\gamma_0 t) \cosh(\gamma_0 t)]^{n_f}, \end{aligned} \quad (12)$$

where  $n_d$  and  $n_f$  are, respectively, the number of unchanged and flipped spins. With exponential accuracy we have that

$$\sum_{j \neq 1} \langle S_1|T|S_j \rangle \approx 1. \quad (13)$$

The contribution of the peak configuration to  $Z$  is  $\exp[N(J_0 - \gamma_0)t]p_0$ , the other  $2^N - 1$  configurations give a contribution  $\sim 1$  to  $Z$ . In the limit of large  $t$ , the peak configuration dominates and we have the error threshold.

$$J_0 > \gamma_0. \quad (14)$$

In the Appendix, we obtain the error threshold for  $f(S)$  of Eq. (9) for finite  $p$ ; the result for  $p=2$  is consistent with the result of Baake *et al.* [14].

*Relaxation Periods.* Let us calculate relaxation periods in the parallel scheme. In the case of a uniform distribution of initial probabilities  $p_j^0$ , system will relax to a steady distribution in  $t_{flat}$ , when the contribution of the peak configuration to the  $Z$  function  $e^{(J_0 - \gamma_0)Nt}$  will dominate in  $Z$  over  $e^{N \ln 2}$ :

$$t_{flat} = \frac{\ln 2}{J_0 - \gamma_0}. \quad (15)$$

To derive the relaxation period from a more general initial configuration to the peak configuration, we assume that initially only one configuration ( $S_i \equiv |m\rangle$ ) is occupied, which has an  $m$  overlap with the peak configuration  $S_1 \equiv |1\rangle$ :  $\sum_{k=1}^N s_k^i = Nm$ . To calculate rigorously the matrix element  $\langle 1|T(t)|m\rangle$  one should calculate the matrix element in Suzuki-Trotter formalism considering the sum along all trajectories (intermediate configurations)  $S_i \cdots S_j \cdots S_1$ . It is easy to check that the contributions are dominated by expressions such as  $S_i \cdots S_1, S_1 \cdots S_1$ , where the intermediate spin state  $S_1$  appears first time at the moment  $t_0$  and for  $t > t_0$  the system remains at  $S_1$ . The contribution from such series of configurations is larger than the sum of contributions of other configurations, where after having  $S_1$  at the moment  $t_0$  there are some  $S_j \neq S_1$  at the later moments. To calculate the principal contribution to  $\langle 1|T(t)|m\rangle$  one should find the maximal value of contributions by the trajectories with  $S_j(t) = S_1$  for  $t \geq t_0$ . In the bulk approximation,

$$\begin{aligned} \langle 1|T(t)|m \rangle &\sim \exp[N(J_0 - \gamma_0)(t - t_0)] \langle 1| \\ &\quad \times \exp \left[ \gamma_0 \sum_{k=1}^N (\sigma_k^x - 1) \right] t_0 |m \rangle \\ &\sim \exp \left[ N \left( \frac{1+m}{2} \ln \cosh(t_0 \gamma_0) \right. \right. \\ &\quad \left. \left. + \frac{1-m}{2} \ln \sinh(t_0 \gamma_0) + J_0(t - t_0) - \gamma_0 t \right) \right]. \end{aligned} \quad (16)$$

The saddle point condition (with respect to  $t_0$ ) leads to

$$\tanh[\gamma_0 t_0] = \frac{1-m}{k + \sqrt{k^2 - 1 + m^2}}, \quad (17)$$

with  $k = J_0 / \gamma_0$ . There is a macroscopic concentration in the configuration  $S_1$ , when the contribution of Eq. (16) to  $Z$  is larger than 1 and the total contributions of other configurations [according to Eq. (13)] is of order 1. Thus for a transition period  $t_1$  we deduce a condition

$$\begin{aligned} \frac{1+m}{2} \ln \cosh(\gamma_0 t_0) - t_1 \gamma_0 + \frac{1-m}{2} \ln \sinh(\gamma_0 t_0) \\ + J_0(t_1 - t_0) \geq 0. \end{aligned} \quad (18)$$

Therefore, the relaxation time  $t_1(m, J_0, k)$  can be obtained from Eq. (18) as

$$\begin{aligned} t_1(m, J_0, k) &= \frac{1}{J_0 - \gamma_0} \\ &\quad \times \left[ ky - \frac{1+m}{2} \ln \cosh(y) - \frac{1-m}{2} \ln \sinh(y) \right], \end{aligned} \quad (19)$$

where  $y \equiv t_0 \gamma_0$ . In the case  $\gamma \rightarrow J_0$ , Eq. (19) implies that  $t_1$  diverges:  $t_1 \sim 1/(J_0 - \gamma_0)$ . For the typical biological case  $\gamma_0(1-m) \ll J_0$ , Eq. (19) gives an asymptotic for the parallel scheme relaxation:

$$t_{par} = (1-m) \frac{\ln \frac{2eJ_0}{(1-m)\gamma_0}}{2(J_0 - \gamma_0)}. \quad (20)$$

Let us compare relaxations in two schemes. For the Eigen model, we give an asymptotic formula from our exact solution [16] (consistent with earlier approximate results [17]):

$$t_{Eig} = (1-m)N \frac{\ln \frac{2e \ln(A+1)}{(1-m)\gamma}}{2(Ae^{-\gamma} - 1)}. \quad (21)$$

Since  $t_{par}$ ,  $t_{Eig}$ , and mutation rates depend on parameters of the models, i.e.,  $J_0$  and  $r_0$  for the parallel model, and  $A$  and  $\gamma = N(1-q)$  for the Eigen model, to compare relaxation times and mutation rates between two models, we should first establish the correspondence between parameters of two models. For this purpose let us consider the parallel and connected schemes with equivalent fitness function:  $J_0 N = (A - 1)$ . For the distribution  $p_i$ , the Eigen model has the mutation rate  $N(1-q) \sum_i p_i r_i$ . In parallel scheme the total number of mutations is  $\gamma_0 N$ , which is independent of frequencies  $p_i$ . One reasonable choice is to take  $A \gamma$  (Eigen model's mutation rate in peak configuration  $p_1 = 1$ ) and put it as a parallel scheme mutation rate  $N \gamma_0$ ,

$$N \gamma_0 = A \gamma \quad (22)$$

(this is the maximal mutation rate among different distributions  $p_i$ ). For this choice, we have

$$t_{1,par} = (1-m)N \frac{\ln \frac{2e(A-1)}{(1-m)\gamma A}}{2(A-1-A\gamma)}, \quad (23)$$

and error threshold of Eq. (4) transforms to

$$\gamma < \frac{A-1}{A}. \quad (24)$$

In observed biological species mutation schemes as a rule are fixed: either parallel or connected. Let us assume that in a hypothetical system (it is possible to organize such situation in digital life) transitions between different mutation schemes are possible and we are looking for the survival condition. Our choice of Eq. (22) corresponds to the worst case with highest mutation rate. Therefore we have the condition of Eq. (24) instead of the Eigen condition of Eq. (3). It is interesting that real data for asexual biological evolution are consistent with Eq. (24).

Let us consider the second more realistic mapping between mutation rates of two schemes. We take as a mutation rate the mean mutation rate in steady state distribution in Eigen model. For the large values of  $A$ , one can derive that  $p_1 = e^{-\gamma}$  [12,16], and we take

$$N\gamma_0 = \gamma(Ap_1 + 1 - p_1) \equiv \gamma[(A-1)e^{-\gamma} + 1], \quad (25)$$

$$t_{2,par} = (1-m)N \frac{\ln \frac{2e(A-1)}{(1-m)\gamma[(A-1)\exp(-\gamma) + 1]}}{2[(A-1)(1-\gamma e^{-\gamma}) - \gamma]}.$$

For error threshold at large  $A$ , we have

$$(A-1) > \frac{\gamma}{1 - \gamma \exp[-\gamma]}. \quad (26)$$

Let us now compare relaxation periods in both schemes. At low mutation rates, Eqs. (23), (25), and (21) diverge logarithmically and there is a finite difference:

$$\lim_{\gamma \rightarrow 0} (t_{Eig} - t_{1,par}) = \lim_{\gamma \rightarrow 0} (t_{Eig} - t_{2,par})$$

$$= (1-m)N \frac{\ln \ln(A+1) - \ln \frac{A-1}{A}}{2(A-1)}. \quad (27)$$

Thus the two schemes are different even at very small mutation rates and the parallel scheme is slightly faster. In Fig. 1 we plot  $t_{2,par}$  and  $t_{Eig}$  as a function of  $\gamma$ ; dash and solid lines represent, respectively, the relaxation periods for connected and parallel schemes. We note that the connected scheme relaxes more slowly at large values of  $\gamma$  and  $t_{Eig}(\gamma)/t_{2,par}(\gamma) \approx 1.77$  at  $\gamma=1$ , which is qualitatively similar to the case that classical simulation annealing is slower than the quantum one [25]. For very large  $\gamma$ , we have

$$t_{Eig}/t_{2,par} \sim \exp(\gamma). \quad (28)$$

In conclusion, we have derived the error threshold of Eq. (14) and relaxation times of Eqs. (15) and (19) for a simple single-peak fitness function. The same method could be applied to solve exactly other evolution models in both parallel and connected schemes with several choice of fitness functions: Random energy [12], isolated peaks with some widths, mixture of royal road [26] and generalized random energy [27] like fitness functions. The last case is realistic for evolution of  $B$  cells [28], and a good approximation for other fitness functions. All these situations have a  $m^p$  like interaction with  $p \rightarrow \infty$  ( $m$  is the magnetization). For the case of models with a finite  $p$  the solution is becoming highly involved. We could not derive the analytical dynamics of the  $p=2$  case, solved in Ref. [14] with an alternative method, while in the Appendix we derive the correct error threshold.

We compared the results of parallel and connected schemes to conclude that even at the limit of vanishing mutation rates two mutation schemes give a finite (nonvanishing) difference in relaxation periods as shown in Eq. (27). Our rigorous result contradicts widely accepted opinion that two schemes are equivalent, at least for low mutation rates. Therefore our exact solution gives unexpected result. Exact solutions of microscopic models can clarify other principal moments in biology, complementing two other sources of reliable scientific results in this area: experiments with real or artificial organisms [29,30].

We have derived our results for infinite populations. For the finite case we should consider separately the random diffusion (before peak configuration has been discovered) and evolution with at least one individual in peak genome. Our approach is still valid for the second period ( $t_0 < t < t_1$ ) for very general fitness functions. The treatment of the first diffusion period ( $0 < t < t_0$ ) is more complicated.

For some biological systems, e.g., virus or immune system [18,31], to function or survive in changing environments, fast relaxations are necessary. In such situations the choice of parallel scheme is preferable. In observed species  $\gamma \sim 1$  or less in asexual evolution [19–21] (even for  $\gamma=1$  parallel scheme is faster almost twice), but there are other situations: quantum simulated annealing at low temperatures, origin of life, and digital life [32] where the *mutation rates* could be much larger than 1. In such cases the parallel scheme with exponentially fast relaxation of Eq. (28) is preferable. While we derived Eq. (28) for the case of single-peak fitness function, perhaps it is valid for more general situation.

Eigen model is the paradigm of complex adaptive systems [33], therefore it is interesting to look for the whole range of parameters in that model as well as in the parallel model. Page and Nowak [34] considered nonlinear generalization of Eigen model with applications to evolutionary games and language evolution. It would be interesting to consider the similar generalization of the parallel model and compare their relaxation periods.

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### APPENDIX: SUZUKI-TROTTER METHOD FOR THE QUANTUM SPIN SYSTEM

*Formalism.* To calculate formulas of Eq. (6) and  $Z = \sum_j Z_{ij} p_j(0)$  based on Hamiltonian defined by Eqs. (5) and (9), we need to evaluate  $Z_{ij} \equiv \langle S_j | e^{-H\beta} | S_i \rangle$ , where  $S_i \equiv \{s_k^i\}$ ,  $S_j \equiv \{s_k^j\}$ ,  $1 \leq k \leq N$ , and we used notation  $t \equiv \beta$  ( $t$  resembles inverse temperature in quantum statistical mechanics).

For the Hamiltonians  $H \equiv A + B$ , where  $A$  and  $B$  do not commute, we can use the Suzuki-Trotter method [22],

$$\begin{aligned} & \langle S_j | \exp[-\beta(A+B)] | S_i \rangle \\ &= \lim_{L \rightarrow \infty} \langle S_j | \left[ \exp\left(-\frac{\beta}{L}A\right) \exp\left(-\frac{\beta}{L}B\right) \right]^L | S_i \rangle \\ &\equiv \lim_{L \rightarrow \infty} \langle S_j | \left[ \exp\left(-\frac{\beta}{L}A\right) \exp\left(-\frac{\beta}{L}B\right) \right] \cdots \\ & \quad \times \left[ \exp\left(-\frac{\beta}{L}A\right) \exp\left(-\frac{\beta}{L}B\right) \right] | S_i \rangle. \end{aligned} \quad (\text{A1})$$

To transform the quantum statistical mechanical problem into the one in classical mechanics, instead of quantum spins  $\sigma_k$ , we introduce  $L+1$  classical spins  $v_k^l$ ,  $1 \leq k \leq N$ ,  $1 \leq l \leq L+1$  (corresponding to introduction of the identity  $\hat{1} = \sum_\alpha |\alpha\rangle\langle\alpha|$  between any pair of brackets) [22]. We take for the boundary configuration  $v_k^1 = s_k^i$ ,  $v_k^{L+1} = s_k^j$  and use a representation of  $\sigma^x$  in the basis of  $|v\rangle$ ,  $v = \pm 1$ :

$$\begin{aligned} \langle v_i | e^{\sigma_x \beta \gamma_0 / L} | v_j \rangle &= \sqrt{\sinh\left(\frac{\gamma_0 \beta}{L}\right) \cosh\left(\frac{\gamma_0 \beta}{L}\right)} e^{B v_i v_j}, \\ e^{-2B} &= \tanh\left(\frac{\gamma_0 \beta}{L}\right). \end{aligned} \quad (\text{A2})$$

For the partition  $Z_{ij}$  at the limit  $L \rightarrow \infty$  it is possible to derive [23,24]

$$\begin{aligned} Z(S_i, S_j) &= A \text{Tr}_v \exp \left[ \sum_{l=1}^L \sum_{k=1}^N B v_k^l v_k^{l+1} - \gamma_0 \beta N \right. \\ & \quad \left. + \frac{\beta J_0 N}{L} \sum_{l=1}^L \left( \frac{\sum_{k=1}^N v_k^l}{N} \right)^p \right], \end{aligned} \quad (\text{A3})$$

where  $A = \left[ \frac{1}{2} \sinh(2\beta\gamma_0/L) \right]^{(1/2)LN}$ . The ‘‘Tr’’ means a summation over all spin configurations  $\sum_{v_k^l = \pm 1}$ ,  $1 < l \leq L$ . In Eq. (A3), the interaction is only via magnetizations  $m_l \equiv \sum_{k=1}^N v_k^l / N$ . We introduce magnetization variable  $m_l$  and corresponding Lagrange coefficient  $\beta h_l$ . To derive the next equation, we need the integral representation for a  $\delta$  function:

$$\begin{aligned} & \frac{\beta}{2\pi i L} \int_{-i\infty}^{i\infty} dh_l \exp \left[ -\frac{N\beta}{L} h_l m_l + \frac{\beta}{L} h_l \sum_{k=1}^N v_k^l \right] \\ &= \delta \left( N m_l - \sum_{k=1}^N v_k^l \right). \end{aligned} \quad (\text{A4})$$

We use the identity  $\prod_l N \int dm_l \delta(N m_l - \sum_{k=1}^N v_k^l) = 1$  and derive

$$\begin{aligned} Z(S_i, S_j) &= A \exp[-\gamma_0 \beta N] \prod_{l=1}^L \frac{\beta N}{2\pi i L} \int_{-i\infty}^{i\infty} dh_l \int_{-\infty}^{\infty} dm_l \\ & \quad \times \text{Tr}_v \exp \left[ -\frac{N\beta}{L} \sum_l h_l m_l + \frac{N J_0 \beta}{L} \sum_l m_l^p \right. \\ & \quad \left. + \frac{\beta}{L} \sum_l h_l \sum_{k=1}^N v_k^l + B \sum_l \sum_{k=1}^N v_k^l v_k^{l+1} \right]. \end{aligned} \quad (\text{A5})$$

In the last expression spins  $v_k^l$  with different  $k$  decouple and we can perform calculations, considering the saddle point via  $m_l, h_l$ , giving the maximal value for the exponent:

$$\begin{aligned} Z(S_i, S_j) &= A \prod_{l=1}^L \frac{\beta N}{2\pi i L} \int_{-i\infty}^{i\infty} dh_l \int_{-\infty}^{\infty} dm_l \exp \left[ -\frac{N\beta}{L} \sum_l h_l m_l \right. \\ & \quad \left. + \frac{N J_0 \beta}{L} \sum_l m_l^p - \gamma_0 \beta N + \ln z[B, \{h_l\}, N, L] \right], \\ z[B, \{h_l\}, N, L] &= z_+(B, \{h_l\}, L)^{N(1+m)/2} z_-(B, \{h_l\}, L)^{N(1-m)/2}. \end{aligned} \quad (\text{A6})$$

Here  $z_+[B, \{h_l\}, L]$  and  $z_-[B, \{h_l\}, L]$  are, respectively, the partition function of the one-dimensional (1D) Ising model with symmetric and asymmetric boundary conditions at inverse temperature  $B$  and magnetic field  $h_l/L$  at position  $l$ , and  $m$  is an overlap of configurations  $S_i$  and  $S_j$ . We should consider different saddle point solutions for  $m_l$  and  $h_l$  and choose the one with maximal value in the exponent.

For the case that there is no magnetization  $m_i = 0$  and  $h_i = 0$ , we have

$$Z(S_j, S_i) = A z_+(B, 0, L)^{N(1+m)/2} z_-(B, 0, L)^{N(1-m)/2} \exp[-N\gamma_0 \beta]. \quad (\text{A7})$$

From Eq. (A2), we derive

$$\begin{aligned} \cosh(B) &= \frac{e^{\gamma_0 \beta / L}}{2 \sqrt{\sinh\left(\frac{\gamma_0 \beta}{L}\right) \cosh\left(\frac{\gamma_0 \beta}{L}\right)}}, \\ \sinh(B) &= \frac{e^{-\gamma_0 \beta / L}}{2 \sqrt{\sinh\left(\frac{\gamma_0 \beta}{L}\right) \cosh\left(\frac{\gamma_0 \beta}{L}\right)}}. \end{aligned} \quad (\text{A8})$$

For the large  $L$ , we have

$$\sinh(B) \approx \cosh(B) \approx \frac{1}{2} \sqrt{\frac{L}{\beta\gamma_0}}, \quad (\text{A9})$$

$$\lim_{L \rightarrow \infty} e^B \sqrt{\sinh\left(\frac{\beta\gamma_0}{L}\right) \cosh\left(\frac{\beta\gamma_0}{L}\right)} = 1.$$

Using equations for the Ising model with boundary conditions  $v_k^1 = \pm v_k^{L+1}$  [2]:

$$\begin{aligned} z_+(B, 0, L) &= [\cosh(B)^L + \sinh(B)^L] 2^{L-1}, \\ z_-(B, 0, L) &= [\cosh(B)^L - \sinh(B)^L] 2^{L-1}, \end{aligned} \quad (\text{A10})$$

we derive for  $Z(S_i, S_i)$  as well as for  $Z_0 = \sum_i Z(S_i, S_i)$ :

$$\begin{aligned} N \ln z_+ + \ln A &= N \ln \cosh(\beta\gamma_0), \\ N \ln z_- + \ln A &= N \ln \sinh(\beta\gamma_0), \end{aligned} \quad (\text{A11})$$

In  $Z(S_i, S_i) = N \ln z_+ + \ln A - N\beta\gamma_0 = N[\ln \cosh(\beta\gamma_0) - \gamma_0\beta]$ ,

$$\ln Z_0 = N[\ln 2 + \ln \cosh(\beta\gamma_0) - \gamma_0\beta].$$

For the nondiagonal  $Z_{ij}$  we will give an expression later. We have that

$$\lim_{\beta \rightarrow \infty} \ln Z_0 \rightarrow 0. \quad (\text{A12})$$

This is a solution for a paramagnetic phase without magnetization ( $m_i=0$ ).

*The thermodynamics.* In the thermodynamic limit one should consider the saddle point for the exponent of Eq. (A6). As  $p \rightarrow \infty$ , one should take either  $m_l=0$  or  $m_l=1$  ( $m_l < 1$  is equivalent to the choice  $m_l=0$ ). To calculate relaxation period we should calculate  $Z_{ij}$ , then use formula (6). To find error threshold, we need only investigate  $Z_0 = \text{Tr} \exp[-\beta H]$ , because  $Z$  and  $Z_0$  have the same bulk singularity, connected with error threshold. Calculation of  $Z_0$  is an easier problem, as there is a translation symmetry  $l \rightarrow l+1$ , and we can choose  $m_l=m, h_l=h$ .

Let us consider the case, when  $m_l=m, h_l=h$ . Then we consider an expression for  $Z_0 \equiv \sum_i Z(S_i, S_i)$ :

$$\begin{aligned} Z_0 &= A \frac{N\beta}{2\pi i} \int_{-\infty}^{\infty} dm \int_{-\infty}^{i\infty} dh \\ &\times \exp \left[ J_0 N \beta m^p + N h \beta m - \gamma_0 \beta N + N \ln z \left( B, \frac{h}{L}, L \right) \right]. \end{aligned} \quad (\text{A13})$$

We have an expression for the 1D Ising  $L$  spin partition function in a magnetic field  $h/L$  [2] at inverse temperature  $B$ :

$$z \left( B, \frac{h}{L}, L \right) = \sum_{s_l} \exp \left[ B \sum_l s_l s_{l+1} + \frac{\beta h}{L} \sum_l s_l \right] = \lambda_+^L + \lambda_-^L, \quad (\text{A14})$$

$$\lambda_{\pm} = e^B \cosh \left( \frac{\beta h}{L} \right) \pm \sqrt{e^{2B} \sinh^2 \left( \frac{\beta h}{L} \right) + e^{-2B}}.$$

For the large  $L$ , from Eq. (A9) we have

$$\begin{aligned} z \left( B, \frac{h}{L}, L \right) &= e^{BL} \left[ \left( 1 + \frac{\beta}{L} \sqrt{h^2 + \gamma_0^2} \right)^L + \left( 1 - \frac{\beta}{L} \sqrt{h^2 + \gamma_0^2} \right)^L \right] \\ &= 2e^{BL} \cosh(\beta \sqrt{h^2 + \gamma_0^2}). \end{aligned} \quad (\text{A15})$$

In Eq. (A14), we consider a sum over  $L$  spins, while in Eq. (A10) there is a sum over  $L-1$  spins.

Equations (A2), (A13), and (A15) imply that

$$\begin{aligned} Z_0 &= \frac{N\beta}{2\pi i} \int_{-\infty}^{\infty} dm \int_{-\infty}^{i\infty} dh \exp[N[\ln 2 \cosh(\beta \sqrt{h^2 + \gamma_0^2}) \\ &+ J_0 \beta m^p - \beta h m - \beta \gamma_0]]. \end{aligned} \quad (\text{A16})$$

The saddle point condition via  $m$  and  $h$  gives

$$\ln Z_0 = N \ln 2 \cosh[\beta \sqrt{h^2 + \gamma_0^2}] + J_0 N \beta m^p - N h \beta m - \gamma_0 \beta N, \quad (\text{A17})$$

$$h = J_0 p m^{p-1}, \quad m = \frac{h}{\sqrt{h^2 + \gamma_0^2}} \tanh[\beta \sqrt{h^2 + \gamma_0^2}].$$

Let us consider the limit of large  $p$  and finite  $\beta$ :

$$h = J_0 p, \quad m = 1, \quad \ln Z_0 = N J_0 \beta - N \gamma_0 \beta. \quad (\text{A18})$$

This is the ferromagnetic phase of the model [24]. The phase transition can be found, when  $\ln Z_0$  in Eq. (A18) with  $m=1$  and  $\ln Z_0$  in Eq. (A11) with  $m=0$  coincide:

$$J_0 \beta = \ln 2 + \ln \cosh(\beta \gamma_0). \quad (\text{A19})$$

At the limit of  $\beta \rightarrow \infty$  (this corresponds to the infinite relaxation period) we have

$$J_0 = \gamma_0. \quad (\text{A20})$$

This is an error threshold condition. The ferromagnetic phase of Eq. (A18) corresponds to the effective selection and the paramagnetic phase of Eq. (A11) to absence of selection. Thus the thermodynamic approach gives accurately the bulk characteristics. To calculate relaxation dynamics we should calculate  $Z(S_i, S_i)$  instead of the simpler expression  $Z_0 \equiv \sum_i Z(S_i, S_i)$ .

*Correlators in Suzuki-Trotter method.* Let us calculate now our main objects,  $\langle S_1 | T(t) | S_i \rangle$  and  $\langle S_j | T(t) | S_i \rangle, j \neq 1$  with  $T(t) \equiv e^{-Ht}$ . From now on, we take  $t$  instead of  $\beta$  in previous equations of the Appendix.

While looking via the saddle point the maximum of  $Z$ , one should divide the total period of time  $t$  into  $K$  pieces and as a saddle point solution take either  $m_l < 1$  or  $m_l = 1$  for  $1 \leq l \leq K$ . The choice  $m_l = 0$  is connected with the random diffusion, the choice  $m_l = 1$  corresponds to the evolution in peak configuration. One should take a scheme, giving maximal value of  $\langle S_j | T(t) | S_i \rangle$ .

To calculate  $\langle S_1 | T(t) | S_i \rangle$ , we simply take  $K=2$ . We divide the total time  $t$  into two periods: for period  $[0, t_0]$  there is a random diffusion from the original configuration  $S_i$  to the peak one, then an evolution in  $S_1$  for the period  $[t_0, t]$ . Thus,

while calculating  $\langle S_1|T(t)|S_i \rangle$  we consider an ansatz for the saddle point solution:

$$m_l = 0, \quad 1 \leq l < L_0; \quad m_l = 1, \quad l > L_0, \quad (\text{A21})$$

where  $L_0 = t_0 L / t$ . We should consider all possible values of  $L_0$ .

For the part  $m_l = 0$  we denote  $T(t) = T_{diff}$  and for the part  $m_l = 1$  we denote  $T(t) = T_{int}$ . Thus

$$\langle S_1|T(t)|S_i \rangle \rightarrow \langle S_1|T_{int}(t-t_0)|S_1 \rangle \langle S_1|T_{diff}(t_0)|S_i \rangle. \quad (\text{A22})$$

To calculate  $\langle S_1|T_{int}(t-t_0)|S_1 \rangle$ , we take Eq. (A5) with the boundary conditions  $m_1 = 1, m_L = 1$ . Then  $h_j \rightarrow \infty$  like the ones in Eq. (A18) and all the diffusion terms disappear and we have a result of Eq. (10):

$$\langle S_1|T_{int}(t-t_0)|S_1 \rangle = e^{N(J_0 - \gamma_0)(t-t_0)}. \quad (\text{A23})$$

Let us consider  $\langle S_j|T_{diff}(t)|S_i \rangle$ . We have for  $i \neq 1, j \neq 1$ ,

$$m_l = 0, \quad 1 \leq l \leq L, \quad (\text{A24})$$

and therefore we miss the interaction term in Eq. (A5) [according to Eq. (A17) interaction term disappears for any finite  $m < 1$ ]. Using Eqs. (A7) and (A11), we derive

$$\langle S_j|T_{diff}(t)|S_i \rangle = \exp \left[ N \left( \frac{1+m}{2} \ln \cos(\gamma_0 \beta) + \frac{1-m}{2} \ln \sinh(\gamma_0 \beta) - \gamma_0 \beta \right) \right], \quad (\text{A25})$$

where  $m$  is an overlap of configurations  $S_i$  and  $S_j$ .

For the situation of Eq. (A21) we derive the result of Eq. (16):

$$\langle S_1|T(t)|S_i \rangle = e^{N(J_0 - \gamma)(t-t_0)} \langle S_1 | \exp \left[ \sum_i \gamma_0 (\sigma^x - 1) t_0 \right] | S_i \rangle, \quad (\text{A26})$$

where  $t_0$  gives a maximum of Eq. (A26).

For other matrix elements we take as in Eq. (12),

$$\langle S_j|T(t)|S_i \rangle = \langle S_j|T_{diff}(t)|S_i \rangle. \quad (\text{A27})$$

*Other fitnesses function.* What other models can be solved with the same method? Quantum random energy model

(REM) has been considered in Refs. [23,24]. In that model there is also  $m^p$ -type random spin-spin interaction at  $p \rightarrow \infty$ . This situation is similar to the case considered in the current work, only calculations are more involved. In the similar way it is possible to solve ferromagnetic REM with multi-spin interactions. The close hierarchic models such as royal road [26] or generalized random energy model [27] are also solvable in this approach.

The case of finite  $p$  in Eq. (9) is too complicated. In Suzuki-Trotter formalism one should consider different finite  $m_l, h_l$  and deal with a partition function of the 1D Ising model, where the magnetic field changes along the chain of Eq. (A6). There are self-consistent nonlinear equations. For the bulk values of  $h_l$  and  $m_l$ , we can take the result of Eq. (A17), but there is a nontrivial boundary slice:  $h_l = h(l/L)$ , where  $h(x)$  is a nontrivial function. Even the analytical solution of the case  $p=2$  is a highly nontrivial task [for the finite values of  $p$  we derive field theoretical equations for the source  $h(x)$ ]. For  $p=2$  the method of Ref. [14] is preferable to investigate the steady state distribution.

What about error threshold? We guess that from Eq. (A16) we can derive correct phase transition point, when the expression for  $\ln Z_0$  at  $\beta \rightarrow \infty$ ,  $\ln Z_0 = \beta N [\gamma_0^2 / \sqrt{h^2 + \gamma_0^2} + J_0 m^p - \gamma_0]$  coincides with the corresponding expression of Eq. (A11) and we thus have

$$1 = \frac{J_c p m^{p-2}}{\sqrt{(J_c p m^{p-1})^2 + \gamma_0^2}}, \quad \gamma_0 = \frac{\gamma_0^2}{\sqrt{(J_c p m^{p-1})^2 + \gamma_0^2}} + J_c m^p. \quad (\text{A28})$$

The error threshold condition is

$$J_0 > J_c. \quad (\text{A29})$$

For the case of  $p=2$ , Eq. (A28) gives  $J_c = \gamma_0/2$ , which is consistent with the result of Baake *et al.* [14]. For  $J_0 > J_c$ , the magnetization  $m$  can be written as

$$m = \sqrt{1 - \left( \frac{\gamma_0}{2J_0} \right)^2}, \quad (\text{A30})$$

which is also consistent with the result of Ref. [14] for the magnetization (nonzero  $m$  is an indicator of successful selection, but  $m$  does not have serious biological meaning [15]).

We guess that Eq. (A28) gives error threshold  $J_c$  for  $p > 2$  as well.

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- [1] *Phase Transitions and Critical Phenomena*, edited by C. Domb and M. S. Green (Academic, London, 1972), Vols. 1–6; *Phase Transitions and Critical Phenomena*, edited by C. Domb and L. S. Lebowitz, (Academic, London, 1977–1988), Vols. 7–22; S. K. Ma, C. Dasgupta, and C.-K. Hu, Phys. Rev. Lett. **43**, 1434 (1979); C.-K. Hu, Phys. Rev. B **29**, 5103 (1984); **29**, 5109 (1984)
- [2] R. J. Baxter, *Exactly Solvable Models in Statistical Mechanics*

(Academic Press, London, 1982).

- [3] R. A. Fisher, *The Genetical Theory of Natural Selection* (Dover, New York, 1930).
- [4] S. Wright, Genetics **16**, 97 (1931).
- [5] M. Eigen, Naturwissenschaften **58**, 465 (1971).
- [6] M. Eigen, J. Mc Caskill, and P. Schuster, Adv. Chem. Phys. **75**, 149 (1989).
- [7] J. F. Crow and M. Kimura, *An Introduction to Population Ge-*

- netics Theory* (Harper Row, New York, 1970).
- [8] J. H. Gillespie, *The Cause of Molecular Evolution* (Oxford University Press, Oxford, 1991).
- [9] T. Ohta, Proc. Natl. Acad. Sci. U.S.A. **90**, 10676 (1993).
- [10] E. Baake and W. Gabriel, Annu. Rev. Comput. Phys. **7**, 203 (2000).
- [11] J. Hofbauer, J. Math. Biol. **23**, 41 (1985).
- [12] L. Franz and L. Peliti, J. Phys. A **30**, 4481 (1997).
- [13] I. Leuthausser, J. Stat. Phys. **48**, 343 (1987); P. Tarazona, Phys. Rev. A **45**, 6038 (1992).
- [14] E. Baake, M. Baake, and H. Wagner, Phys. Rev. Lett. **78**, 559 (1997).
- [15] H. Wagner, E. Baake, and T. Gerisch, J. Stat. Phys. **92**, 1017 (1998).
- [16] D. B. Saakian and C.-K. Hu, Phys. Rev. E **69**, 021913 (2004).
- [17] M. Nilsson and N. Snoad, Phys. Rev. Lett. **84**, 191 (2000).
- [18] C. Kamp and S. Bornholdt, Phys. Rev. Lett. **88**, 068104 (2002); C. Kamp *et al.*, Complexity **8**, 28 (2002).
- [19] J. W. Drake *et al.*, Genetics **148**, 1667 (1998).
- [20] J. W. Drake and J. J. Holland, Proc. Natl. Acad. Sci. U.S.A. **96**, 13910 (1999).
- [21] S. C. Manrubia, E. Lazaro, and J. Perez-Mercader, Phys. Rev. Lett. **90**, 188102 (2003).
- [22] M. Suzuki, *Quantum Monte Carlo Methods* (Springer-Verlag, Berlin, 1986).
- [23] Y. Y. Goldschmidt, Phys. Rev. B **41**, 4858 (1990).
- [24] D. B. Saakian, J. Math. Phys. **94**, 123 (1993).
- [25] G. E. Santoro *et al.*, Science **295**, 2427 (2002).
- [26] E. V. Nimwegen, J. P. Crutchfield, and M. Mitchell, Phys. Lett. A **229**, 144 (1997).
- [27] B. Derrida and E. Gardner, J. Phys. C **19**, 2253 (1986); E. Bittner, W. Janke, and D. B. Saakian, Phys. Rev. E **67**, 016105 (2003).
- [28] A. S. Perelson and C. A. Macken, Proc. Natl. Acad. Sci. U.S.A. **97**, 9657 (1995).
- [29] R. Lenski and M. Travisano, Proc. Natl. Acad. Sci. U.S.A. **91**, 6808 (1994).
- [30] C. O. Wilke *et al.*, Nature (London) **412**, 331 (2001).
- [31] T. B. Kepler and A. S. Perelson, J. Theor. Biol. **164**, 37 (1993).
- [32] Here both connected and parallel schemes of evolution are possible, C. Wilke (private communications).
- [33] H. G. Schuster, *Complex Adaptive Systems* (Scator Verlag, Saarbrücken, 2001).
- [34] K. M. Page and M. A. Nowak, J. Theor. Biol. **219**, 93 (2002).