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A modified Crow–Kimura evolution model with reduced fitness for the smooth distribution of population

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ABSTRACT

We investigate an evolution model in which the fitness depends on the steepness of population distribution via Hamming classes (the absolute value of the logarithm of the probability ratios for the neighbor Hamming classes). The model has a rather rich phase structure with observed oscillations of the mean fitness in the dynamics. Specifically, the fitness is reduced (compared to the standard Crow–Kimura model) when the steepness is less than a certain value, d. We compare the mean fitness of our model with the mean fitness of Crow–Kimura model with the same parameters. Our work reveals that there is a threshold value, d_c for which $d > d_c$, there are no oscillations of the mean fitness, and it is less than the corresponding fitness in the Crow–Kimura model with the same parameters. For $d < d_c$, the mean fitness oscillates with time. The time averaged mean fitness is identical to the mean fitness in Crow–Kimura model, and there is a wider distribution than in the case of Crow–Kimura model. This is a significant advantage in dynamic environment.

1. Introduction

Over the past decades, interdisciplinary applications of statistical physics methods have led to significant progress in the investigation of asexual evolution [1–13]. Most classical models use fixed mutation rates and static fitness landscapes which do not depend on population structure. For cases like virus or cancer evolution, modifications of these models allow for realistic predictions and research is ongoing to make the analysis more accurate, especially in the case of strong collective phenomena [14–16]. The analogy between models of asexual evolution and models of statistical physics allows expanded use of existing analytical results in biological context. Notions like energy or magnetization can be re-defined in evolutionary terms.

The Crow–Kimura [2,8,9] and Eigen [1,5] models of molecular evolution are described by nonlinear differential equations, albeit with weak nonlinearity. One of the key features is that these systems can be mapped to the system of linear differential equations using a nonlinear algebraic transformation [6]. The simple Crow–Kimura model with L nucleotides is equivalent to the Ising model with L spins. For small mutation rates, the genetic sequence space assemblies around the genomes with high fitness. The system state where selective pressure favors the fittest and replication is

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accurate enough to transfer genetic information, is called a selective phase [5]. This is similar to the ferromagnetic phase in the Ising model. At high mutation rates, there is no grouping of the population around the peak sequence, and the system behavior corresponds to the absence of the mean magnetization in the paramagnetic phase of the Ising model. The transition between the two phases is the error threshold point in the evolution model.

The quasispecies models, initially introduced to explain the origin of life [1] and later applied to virus evolution [17], have wider applications than population genetics [18]. It is possible to develop classical models with new characteristics to model advanced evolution phenomena like strong evolution-ecology interaction [18], evolvability [19], learning [20], cancer [21–24].

The concept of frustration in statistical physics was first introduced by Anderson to describe the essential features of the spin-glass phenomenon, including the impossibility of satisfying a large fraction of the exchange interactions with any spin structure [25,26]. The investigation of models of evolution under "frustration" is one of the key directions in evolutionary research [27–29]. In the models with frustration in selection [28,29], there is a conflict between the different contributions to fitness when we try to optimize the total fitness, similar to the definition of frustration in Spin-glasses. In Ref. [28], there is contribution to the fitness for molecules participating in the auto-catalytic reactions and protocells; and their results suggest conflicting multilevel evolution as a key cause of the origin of genetic complexity. Version related to striped glasses and self-organized criticality has also been discussed in Ref. [29], where the role of conflicting contributions to the total fitness in biological complexity is investigated. Instead of converging to a steady-state, as in the classical case, the population structure can oscillate if we include similar concept of frustration [27]. This feature could be responsible for the origin of genetic code [28] or even play a key role in multi-cellular organization [29]. In the current paper, we consider a simple modification of the Crow–Kimura model by examining the model with a frequency-dependent fitness. We assume that fitness function is a discontinuous function of population structure and sometimes decreases due to distribution. In Ref. [28], there is a conflict between the fitness contributions for the protocell and molecules, whereas there is a conflict between the fitness of replicators and duets of Hamming classes in the present context. We also observe oscillations in our model, similar to Ref. [27]. In [30,31], we have investigated a model where the mutation rate is conditioned by reducing from the higher occupied Hamming class (a collection of sequences with the same number of mutations) to the lower occupied class [30]. We have calculated the mean fitness, and also found the phase structure and derived the steady-state distribution. Significant plateaus were discovered in the population distribution, whereas in the standard Crow–Kimura model there is a normal distribution around the maximum. The existence of mutants at large Hamming distances from the wild-type in population certainly increases the adaptation potential of the population in dynamic environments. Motivated by both the statistical physics and biological perspectives, our goal here is to formulate and solve a modification of the quasispecies model with the simplest version of frustration in selection as described earlier. The proposed model assumes an adaptive property, complementary to the one in Ref. [30]. We have found a new mechanism for increasing the adaptability in evolving systems with cooperative interactions [32]. Bacteria and viruses are examples of such systems [32,33]. Our model is related to the Hamilton–Jacobi equation (HJE) with discontinuous Hamiltonian [34,35] (we give the Hamilton–Jacobi equation method in the Appendix). The adaptive system [32,33] can modulate both the mutation rate (similar to Ref. [30]) and fitness (in the current case). Our current work is motivated by the study of evolution with conflicting contributions to the fitness [28,29], as well as by [32,33]. We first use a toy model for the evolution with conflicting interactions in the fitness, similar to the approach used in Refs. [27,28]. Our work is also related to the advanced HJE problems [34,35].

2. The investigation of the evolution model with conditioned fitness

2.1. The model

Consider the genome as a sequence of L letters (spins) taking values ± 1, so there are 2^L different genotypes in the sequence space. We take the configuration with only $+1$ spins as a reference sequence. To describe fitness, we first introduce a reproduction rate $r_l \equiv f(x)$, $x = 1-2l/L$, where l is the number of -1 letters in the given sequence. We collect all the sequences with the same l number of -1 states into the lth Hamming class and define their total probability as P_l.

2.2. Our previous model

In previous articles [30,31], we have considered another model:

$$\frac{dP_l}{dt} = r_l P_l + \mu \left(P_{l-1}\frac{L-l+1}{L}J(P_{l-1}/P_l) + P_{l+1}\frac{l+1}{L}J(P_{l+1}-P_l) - P_l\frac{L-l}{L}J(P_l/P_{l+1}) + \frac{l}{L}J(P_l/P_{l-1})\right) - P_l R, \quad (1)$$

where $R = \sum_{n=0}^{L} r_n P_n$, $J(y) = 1,\ y > 1$ and $J(y) = c,\ y < 1$, where $c < 1$.

For the model due to Eq. (1), we have found a bell-shaped like distribution with a plateau at the top (see Fig. 1). In the case of the model by Eq. (1), the HJE approach gives the mean fitness of the model.

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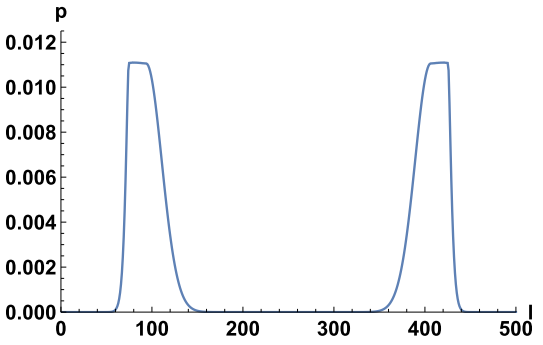

Fig. 1. The steady-state probability distribution $P = P_l$ versus the l for the model by Eq. (1) with $L = 500, f(x) = kx^2/2, \mu = 1, k = 0.15, c = 0.5$. We give the probability distribution via Hamming classes. We now have two peaks of distribution due to the symmetry of the function $f(x)$.

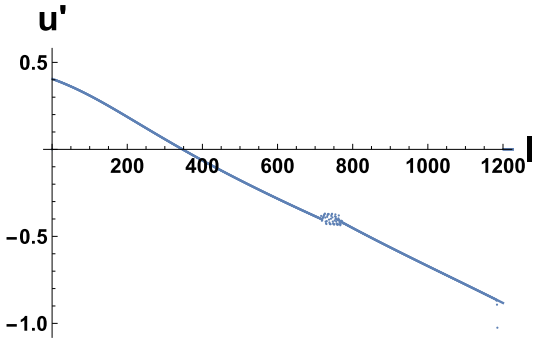

Fig. 2. Plot of the u' for $L = 2000, f(x) = kx, k = 2, d = 0.4, c = 0.8$ for the model by Eq. (3). We define $u(x) = \ln P_l$, x = 1-2l/L. We see oscillations in the interval $[l_1, l_2] = [715, 755]$. We compare the numerics with two branches of our solution. Our analytics (A.6), (A.8) are well confirmed by the numerics outside the interval l_1, l_2. These points are derived from Eqs. (A.9).

2.3. Our new model

In our system, there is a mutation with unit rate, growth of the population with rate (fitness) $\hat{r}_l = f(1-2l/L)J(P_l/P_{l-1})$, where the function J describes how the fitness is affected by the population distribution. There is also a dilution of population to hold a probability balance $\sum_l P_l = 1$. We have the following system of equations:

$$\frac{dP_l}{dt} = \hat{r}_l P_l + \mu \left(P_{l-1}\frac{L-l+1}{L} + P_{l+1}\frac{l+1}{L} - P_l \right) - P_l R, \tag{2}$$

where

$$R = \sum_{nl=0}^{L} \hat{r}_l P_l. \tag{3}$$

Thus the fitness $\hat{r}_l$ depends on the population distribution.

We choose the function $J(y)$, to reduce the fitness for cases with certain smooth distributions (the ratio of P_l for the neighbor classes is less than some threshold):

$$J\left(\frac{P_l}{P_{l-1}}\right) = 1 - (1-c)\theta\left(2\log(d) - |\log\left(\frac{P_l}{P_{l-1}}\right)|\right) \tag{4}$$

where d is some threshold value, and $\theta(x)$ is the step function. We consider $|\log\left(\frac{P_l}{P_{l-1}}\right)|$ as the steepness of the distribution; for smooth distribution, the considered expression tends to zero, and it is large when P_l is substantially different from the neighbor classes. Eq. (4) means that the fitness is attenuated when the steepness of the population is very small (less than critical value). For the borderline cases with $l = 0$ or $l = L$, we can omit J in Eq. (2), as there is no term P_{l-1} at $l = 0$ and there is no term P_{l+1} at $l = L$.

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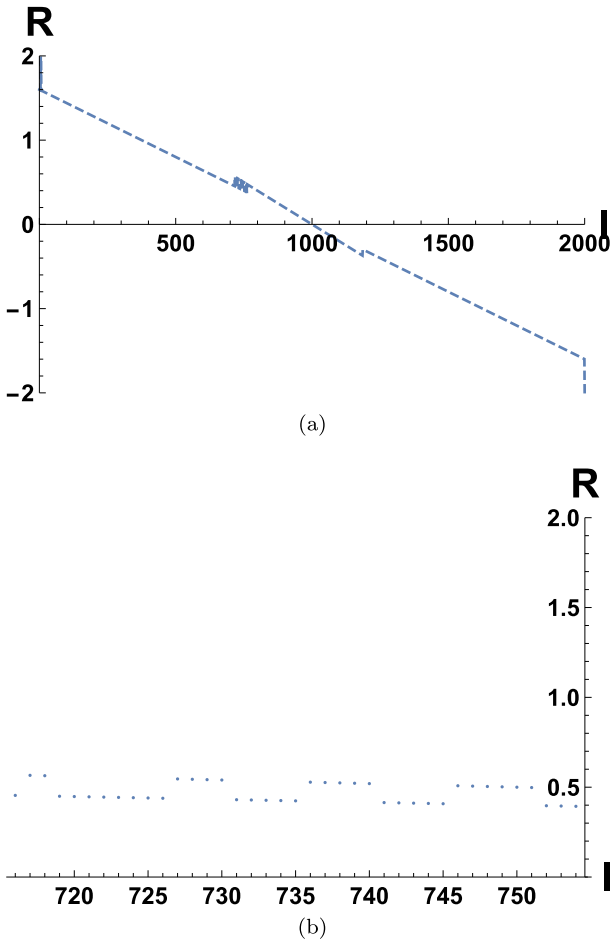

Fig. 3. The conditioned fitness model. Plot of the $\hat{r}_l$ for $L = 2000, f(x) = kx, k = 2, d = 0.4, c = 0.8$. Smooth behavior can be observed in most regions. (a) In the interval $[0, 2000]$ (b) In the interval $[715, 755]$. There are oscillations in the interval $[715, 755]$.

Eq. (1) gives the evolutionary dynamics of our model. Clearly, the case of $c = 1, J(x) = 1$ corresponds to the Crow–Kimura model. Here, μ is the mutation rate per genome and r_l is the fitness of the sequences with l mutations. The combinatorial coefficients $\frac{L-l+1}{L}$, $\frac{L-l}{L}$ arise from the consideration of the Hamming class probabilities [7, 9]. We use the function $f(1 - 2l/L) \equiv f(x) = r_l, \quad x \equiv 1 - 2l/L$. This is a system of strongly nonlinear equations. We then introduce our modification to get wide distribution in the steady-state. We now ask an important question: whether it is possible to get wide distribution (compared to the Crow–Kimura model), and whether there is a cost to mean fitness.

2.4. The numerical results

We now numerically solve the steady-state of the model and identify the phase structure. The results shown in Figs. 2, 3, 4, 5, 6 illustrate the important behavior of the distribution in our model. We have a situation similar to the one in the model by Eq. (5), see Fig. 2 for the distribution of $u' = 0.5 \ln(P_l/P_{l+1})$ ($u(x)$ and $u'(x)$ is defined in the Appendix). It is worth noting that there exists a singular solution in the interval $[l_1, l_2]$ in Fig. 2, as well as a smooth solution from the left and right parts. The smooth solution is well described by the Hamilton–Jacobi equation, similar to the case due to the model given by Eq. (4). In Figs. 3, 4a, we give the results for the fitness distribution in the steady-state and we describe the steady-state distribution via Hamming classes in Fig. 4b. We see the areas with a singular behavior (oscillations) in the intervals $[l_1, l_2]$ and $[l_3, l_4]$, some peak values near the point $l = 0$, and smooth behavior elsewhere.

The existence of a phase transition via the steepness threshold parameter d is worth exploring. There is a critical value d_c, for which the considered case is equal to $d_c \approx 0.055$. For $d < d_c$, there is no steady-state. We have observed stochastic oscillations without damping for the mean fitness as shown in Figs. 6–7, with the minimal and maximal values given by dashed lines in Fig. 5a. The amplitude of oscillations decreases with N, so it is some finite size effect, like the plateaus width found in [28]. The value of mean fitness, averaged via oscillations, corresponds to the case of the Crow–Kimura model for $d < d_c$, while the variance of distribution is larger, see Fig. 5b.

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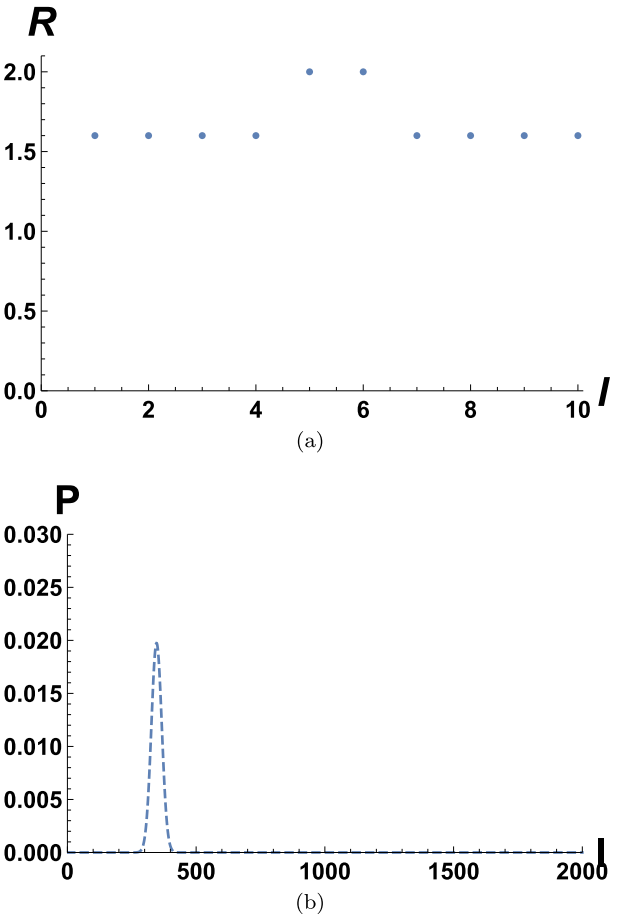

Fig. 4. The conditioned fitness model. (a) Plot of the $R = \hat{r}_l$ versus l for $L = 2000$, $f(x) = kx$, $k = 2$, $d = 0.4$, $c = 0.8$. There are peaks near $l = 0$. (b) The distribution of probabilities $P = P_l$ versus l.

After the critical value $d > d_c$, the mean fitness decreases with the growth of d. We see that there is an optimal value of d for our model, $d = d_c$. Our mechanism provides an important evolutionary advantage for the system, as the wide distribution is favorable during the evolution in dynamic environment, without any cost in the mean fitness of population.

The evolution models are related to both the statistical physics [6] and Hamilton–Jacobi equation (Hamiltonian mechanics) [12], and they have specific features typical of statistical physics models [9]. Consider the standard Crow–Kimura model with symmetric fitness landscape and smooth fitness function $\hat{f}(x)$. As has been found in [12], the model can be mapped to the Hamilton–Jacobi equation, with some Hamiltonian. Then the steady-state mean fitness corresponds to the minimum of the energy for the particle in related potential. First the system selects for the mean fitness value by searching for the maximum of [10,12],

$$R = \frac{\sqrt{1-x^2}}{2} - 1 + \hat{f}(x). \tag{5}$$

Then the peak of distribution s is derived using the equation [9],

$$\hat{f}(s) = R. \tag{6}$$

Hence, the mean fitness is defined without investigating the peak of distribution in the original Crow–Kimura model.

As we have small u' near the peak, we have the following conditions for our model:

$$cf(s) = R. \tag{7}$$

Eq. (7) is well-validated numerically in the case of our model.

The scenario with the mean fitness is much more involved than before. In the case of the model [30,31], we can derive the mean fitness by analyzing the peaks of steady-state distribution in Fig. 1.

We have some intervals with singular behavior, and a peak of distribution far from these singularities. We also observe the peak values of fitness near $l = 0$. All these factors should be taken into account while solving for the model.

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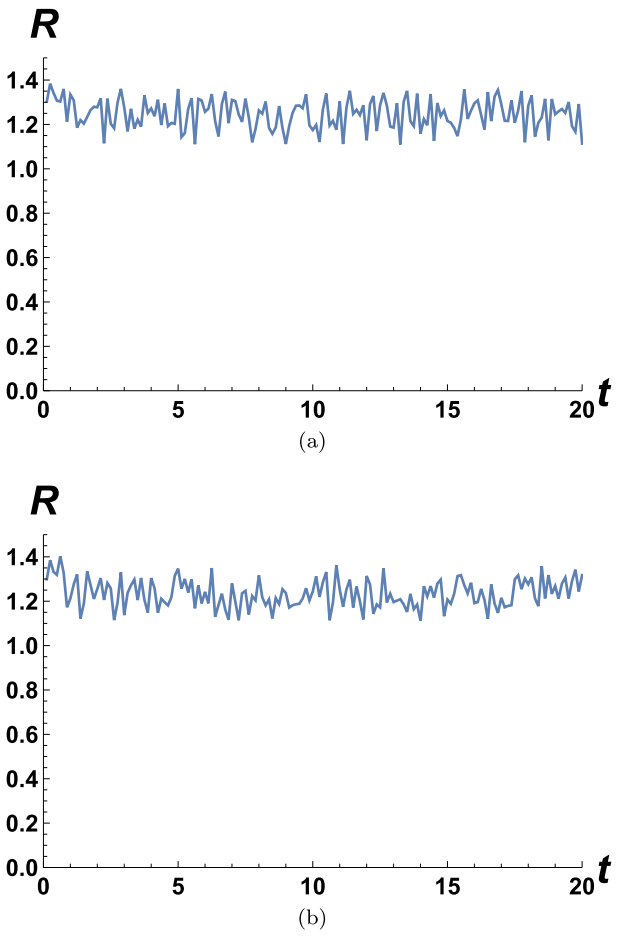

Fig. 5. The mean fitness of population versus the time. $L = 1000$, f(x) = 2x, c = 0.8, d = 0.025 (a) The results of numerics by the Runge–Kutta method $\delta t = 0.00125$ (b) $\delta t = 0.0003125$.

Attempts have been made to connect the phase transition point with the situation when the singularity interval (the interval where u' or $\hat{r}_l$ oscillates) coincides with the point of maximum in Eq. (5) for the choice $\hat{f}(x) = f(x)$. However, there is only limited success.

Then we analyze the peaks of the fitness near $l = 0$ point by taking $\hat{f}(1) = f(1)$. The model is similar to the single peak fitness case. We obtain:

$$R = f(1) - 1. \tag{8}$$

The region in Fig. 3a near the transition point motivates future work. The peculiar character of the model is related to the behavior of the model near $l = 0$. If we modify the model by removing the condition near $l = 0$, then the model will be described well by Eq. (5).

2.5. The sensitivity of numerics to discretization scheme

We have carried out the numerics using the Runge–Kutta method. For the discretization step $\delta t = 0.00125$ in Fig. 5a, we obtain for the mean fitness $R = 1.231$, the variance of distribution $V = 0.32$. For $\delta t = 0.0003125$ in Fig. 5b, we obtain $R = 1.2331$, $V = 0.230$. The mean fitness for the Crow–Kimura model is 1.236. This shows that the time averaged mean fitness coincides with the result by Crow–Kimura model within the accuracy of our numerics.

3. Discussion

We have investigated an important evolution model with conditioned fitness function, by starting from the frequency dependent fitness in the Crow–Kimura model. The system controls the steepness of the distribution via the Hamming class. When the steepness (the absolute value of the logarithm of the probability ratios for the neighbor Hamming classes) is

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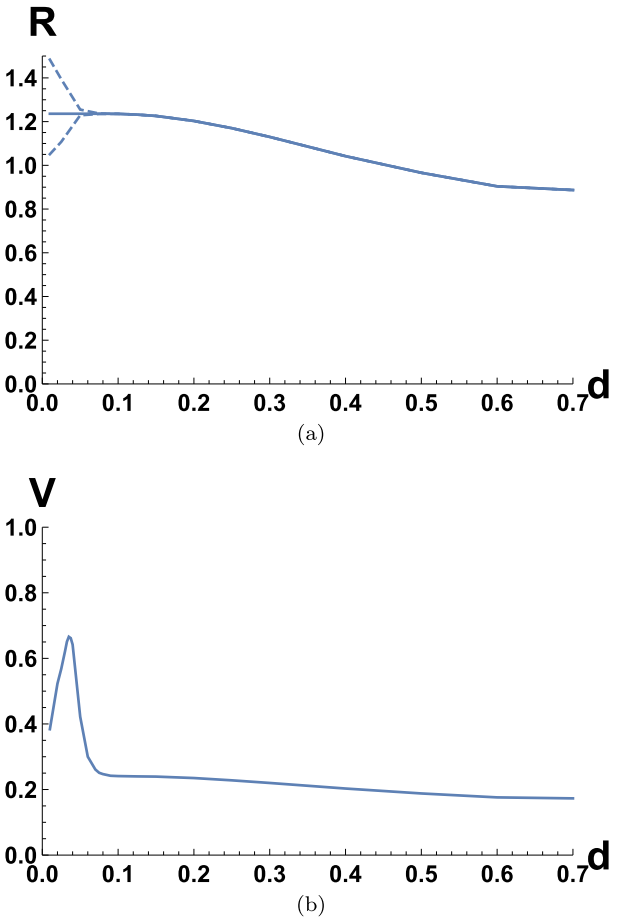

Fig. 6. The conditioned fitness model. (a) Plot of the mean fitness $R\langle\sum_l \hat{r}_l P_l\rangle$ versus the parameter d for $L = 1000, f(x) = kx, k = 2, c = 0.8$. The dashed lines gives the minimal and maximum values of mean fitness during the oscillations. The smooth line is the time averaged value of the mean fitness. Below the transition point the latter coincides with the Crow–Kimura model result $R = \sqrt{k^2 + 1} - 1$. For the large value of d we get $R = \sqrt{c^2k^2 + 1} - 1$. (b) Variance of distribution $V = < (l - < l >)^2 > /L$ versus d. For the Crow–Kimura model $< (l - < l >)^2 > /L \approx 0.154$.

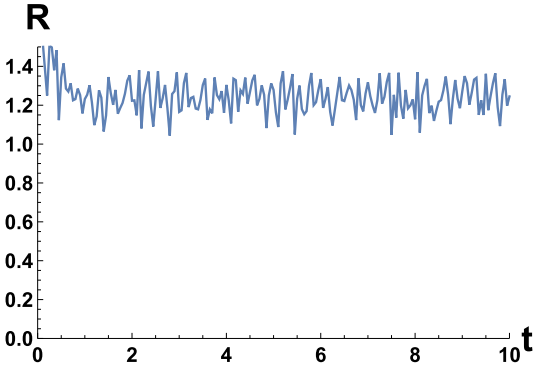

Fig. 7. The conditioned fitness model. Plot of the $R = \langle\sum_l \hat{r}_l P_l\rangle$ versus the time t for $L = 1000, f(x) = kx, k = 2, d = 0.025, c = 0.8$.

above a particular threshold value, the system reduces the fitness. In our model, different parts of the system are in conflict when we look at the total replication rate; that is why we define our model as a version analogous to frustration, similar to Refs. [28,29]. In our model, we preserve the value of mean fitness of the population, while increasing the variance of the distribution. The latter is essential for the case involving dynamic environment. The numerics support our intuition. There

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is a critical value for the parameter d. When $d < d_c$, the time-averaged mean fitness is unchanged, and we can increase the variance of the distribution. Below d_c, oscillations can be observed in the system, and there is no steady-state. The state of the system oscillates. Similar oscillations have been found in another evolution model with frustration [28]. We assume that the suggested mechanism, attenuation of fitness for some sequences, brings to the increase of mean fitness in dynamics environment. Our main contribution is in the numerical investigation of the model, as we have found a new phase transition. Success in the analytical solution is limited as neither the maximum principle by E. Baake [10] nor the HJE method [12] can succeed with the derivation of the mean fitness of the model. The Baake–Wagner relation between mean fitness and surplus is valid for our model, Eq. (9) as it supports the mean-field like character of our model. We have also obtained steady-state distribution and surplus, using the result of mean fitness derived from our numerics.

We now provide some words of caution on why the solution to the model is mathematically intractable. In the solving of the Crow–Kimura model, we first find the mean fitness R from the maximum principle, then calculate the maximum of distribution s from the equation $R = f(s)$. The first step is independent of the second. In the previous version of the conditioned model, we have solved both mean fitness and surplus altogether, because there are some singularity intervals in the steady-state distribution, so the location of the distribution maximum influences the mean fitness as well, a situation that is well known in other nonlinear models (eg. the evolution with recombination [36,37], where two solutions have been found for the distribution depending on initial distribution). The current situation is even more complicated; there are singularity intervals, peaks of fitness near $l = 0$, and the maximum of distribution is far from these mentioned intervals and the $l = 0$ point.

In conclusion, our model represents a new statistical physics phase in evolutionary dynamics because it describes an evolutionary advantage without reducing mean fitness. The asexual evolution models have a lot of different applications ranging from the origin of life [1] to virus evolution [32,33]. There is also potential application in artificial intelligence system and genetic algorithms, in which the evolutionary dynamics can be highly nonlinear with adaptation abilities; and this highlights the applicability of our model. We have analyzed the evolving population of agents with the distribution having increased variance of fitness. Previously, it has been analyzed the interaction between learning and evolution [38–41]. It was assumed that any agent of the population has the genotype and phenotype, which are optimized using learning (phenotypes) and evolution (genotypes). Genotypes determine initial phenotypes. Agents are selected into the population of a new generation following final phenotypes. According to Refs. [38,40], strong learning can hinder the finding of optimal genotype. The optimal phenotype can be found using learning for the wide distribution of genotypes. Hence, the wide distribution of genotypes is selected; this is similar to the current model described above. The present study suggests a framework for developing mathematical tools to realistically capture wide and nonlinear distributions that are found in natural selective landscapes of the evolutionary process at multiple scales of biological complexity.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Disclosure of potential conflicts of interest—ethical and financial

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Appendix. The HJE approach

Let us assume an ansatz [11,12]

$$P_l = \exp[Lu(x,t)], x = 1 - 2l/L \tag{A.1}$$

We derive the following Hamilton–Jacobi equation (HJE) from Eq. (3):

$$\frac{\partial u(x,t)}{\partial t} + H(x,u') = 0.$$
$$-H(x,u') = \mu(\frac{1+x}{2}e^{2u'} + \frac{1-x}{2}e^{-2u'} - 1) +$$
$$f(x)\theta(|u'(x,t)| - d) + cf(x)\theta(d - |u'(x,t)|)$$
$$- cf(s)\theta(d - |u'(s,t)|), \tag{A.2}$$

where s corresponds to the maximum of distribution. While writing the last term, we take into account that near the maximum point we should take a fitness function $cf(x)$. Eq. (A.2) corresponds to the singular Hamiltonian, like the one in [30,31].

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Let us now look at the regions with smooth solutions. We have two branches of the Hamiltonian:

$$-H_+(x,u') = \mu(\frac{1+x}{2}e^{2u'} + \frac{1-x}{2}e^{-2u'} - 1) + f(x) - cf(s),$$
$$-H_-(x,u') = \mu(\frac{1+x}{2}e^{2u'} + \frac{1-x}{2}e^{-2u'} - 1) + f(x)c - f(s)c. \tag{A.3}$$

We choose $\mu = 1$. The Crow–Kimura model has a well defined asymptotic (steady-state) solution

$$u(x,t) = u(x). \tag{A.4}$$

It is related to the existence of single maximum eigenvalue. Similar situation exists at some regions in our model.

We obtain for such a solution

$$R = \frac{1+x}{2}e^{2u'} + \frac{1-x}{2}e^{-2u'} - 1 + f(x). \tag{A.5}$$

Thus we have for the $u'(x)$ the following equation

$$u' = \frac{1}{2}\log(\frac{R+1-f(x) \pm \sqrt{(R+1-f(x))^2 - 1 + x^2}}{1+x}). \tag{A.6}$$

For the second choice of our Hamiltonian, we analyze the equations

$$R = (\frac{1+x}{2}e^{2u'} + \frac{1-x}{2}e^{-2u'} - 1) + cf(x). \tag{A.7}$$

We have $u'(x)$:

$$u' = \frac{1}{2}\log(\frac{R+1-f(x)c + \sqrt{(R+1-f(x)c)^2 - 1 + x^2}}{1+x}). \tag{A.8}$$

Let us find the point where $u' = d$:

$$d = \frac{1}{2}\ln\frac{R+1-f(m_2) + \sqrt{(R+1-f(m_2))^2 - 1 + (m_2)^2}}{1+m_2},$$
$$d = \frac{1}{2}\ln\frac{R+1-cf(m_1) + \sqrt{(R+1-cf(m_1))^2 - 1 + (m_1)^2}}{1+m_1}. \tag{A.9}$$

We define m_1, m_2 from last two equations. Finally, we can use m_1 and m_2 to define l_1, l_2 in our figures.

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