

# Exact solution of a model of time-dependent evolutionary dynamics in a rugged fitness landscape

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A simplified form of the time dependent evolutionary dynamics of a quasispecies model with a rugged fitness landscape is solved via a mapping onto a random flux model whose asymptotic behavior can be described in terms of a random walk. The statistics of the number of changes of the dominant genotype from a finite set of genotypes are exactly obtained confirming existing conjectures based on numerics.

In evolution, long periods of stasis or inactivity are punctuated by bursts of rapid activity. Fossil records [1] reveal this basic pattern in the evolution of biological species and the same behavior is observed in the development of microbial populations [2] and artificial life [3]. Not surprisingly, the dynamics of genetic algorithms [4] also exhibits this punctuated behavior. In this paper we will show how a simple model of biological evolution can be exactly solved using a mapping onto a random flux model. The important asymptotic details of this random flux model can then be determined in terms of the first passage time distribution of a random walk.

The model we study was introduced in [5] as a simplified version of the quasispecies model which is used for the study of large populations of replicating macromolecules [6]. In [5], the quasispecies model was studied in the strong selection limit where the location in the space of genotypes is defined as the genotype having the largest population. A shell model [5] may be derived in the strong selection limit and a further simplification of this model leads to the i.i.d. (independent and identically distributed) shell model where the natural space of genotypes, which is that of binary sequences, is replaced by a one dimensional lattice. Rather than re-derive the model we shall describe it and the reader will immediately see that it can be reinterpreted in terms of a simple evolutionary process.

We consider an ensemble of  $N$  different genotypes labeled by  $i = 1, 2, \dots, N$ . The fitness of a genotype is given by its effective rate of reproduction per individual  $v_i \geq 0$  and thus the size of the population at time  $t$  is given by  $n_i(t) = n_i(0) \exp(v_i t)$ . In terms of logarithmic variables,  $y_i(t) = \ln(n_i(t)) = \ln(n_i(0)) + v_i t$ . One can interpret  $y_i(t)$  as the trajectory of a particle moving ballistically with a non-negative velocity  $v_i$ , starting from its initial position  $y_i(0)$ . The i.i.d. version of the shell model [5], which we will call the leader model, is defined as follows: we draw  $N$  velocities  $\{v_i\}_{1 \leq i \leq N}$  independently from the same probability distribution  $p(v)$  (which has positive support only). We then consider the semi-infinite lines of slope  $v_i$  describing the evolution of genotype  $i$  (up to

an overall constant)

$$y_i(t) = -i + v_i t. \quad (1)$$

At any time  $t > 0$ , the leader is defined as the genotype  $i$  having the maximum  $y_i(t)$ , the corresponding  $i$  is thus the most populated genotype at time  $t$ . The choice of  $y_i(0) = -i$  comes from the details of the original quasispecies model [5]. Thus, the evolution of the trajectories is completely deterministic, the only randomness comes from the velocities. Obviously at  $t = 0$ ,  $y_1$  is the leader; however if  $v_1$  is not the maximal velocity, then  $y_1$  will ultimately be overtaken by a faster/fitter genotype. At each of these overtaking events the number of genotypes which have been leaders increases by one, finally the fastest genotype will become the final leader and no more leader changes will occur. In the general context of evolutionary processes these overtakings correspond to punctuation events.

The total number of lead changes is denoted by  $l_N$  and we denote by  $w_k$  the velocity of the leading genotype after the  $k$ -th lead change. Clearly  $l_N$  is a random variable, varying from one realization of velocities to another. Based on simulations, it was observed [5] that for large  $N$ ,  $\langle l_N \rangle \approx \beta \ln N$ . where, remarkably, the coefficient  $\beta$  is rather robust and depends only on the tails of the distribution  $p(v)$ . Based on numerics, Krug and Karl [5] made some conjectures about the value of  $\beta$  and also showed how a comparison with record statistics gives the upper bound  $\beta < 1$ . Similar logarithmic growth of the average number of lead changes has also been reported [7] recently in the context of growing networks where the leader is the maximally connected node.

In this letter, we present an exact solution to this problem, confirming the conjectures of [5]. Moreover, we calculate the variance of  $l_N$  and show that  $\langle (l_N - \langle l_N \rangle)^2 \rangle \approx \gamma \ln N$  for large  $N$ , where the coefficient  $\gamma$  is calculated exactly and shown to be as robust as  $\beta$ . We also show that the full distribution of  $l_N$  around its mean is asymptotically Gaussian. The key observation that leads to the exact solution of this model is a mapping onto a *random flux* model whose late time properties are iden-

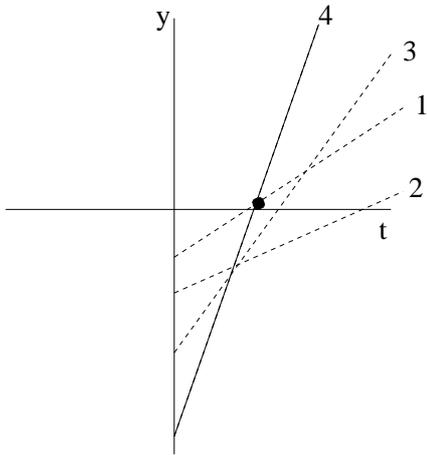


FIG. 1: Model trajectory for  $N = 4$ . Genome 4 becomes the ultimate leader and there is only one leadership change indicated by the black dot.

tical to those of the original model. Here, the velocity distribution is chosen as before but instead of fixing the initial positions  $y_i(0)$  of the genotype  $i$  at  $-i$ , we chose it to be a random variable uniformly distributed on  $[0, -N]$ . From a coarse grained point of view, for a large number of genotypes, this difference in the initial condition is not expected to change the asymptotic properties. In the context of the quasispecies model, this random initial condition translates to having the initial population of each genotype having a probability distribution:  $\text{Prob}(n_i(0) = x) = (xN)^{-1}$ , with  $\exp(-N) \leq x \leq 1$ . An example set of trajectories for  $N = 4$  and where  $l_N = 2$  is shown in Fig. (1). If  $w_k$  is the velocity of the  $k$ -th leader then clearly only genotypes with velocities greater than  $w_k$  can become subsequent leaders. From the rest frame of the leader, in the next time interval  $\Delta t$  the genotype  $i$ , with velocity  $v_i (> w_k)$ , will overtake the leader if it is at a distance  $\Delta x = (v_i - w_k)\Delta t$  behind the leader. The rate at which the genotype  $i$  becomes the new leader is thus given by

$$r_i = (v_i - w_k) \langle \delta(y_k(0) - y_i(0) - (v_i - w_k)t) \rangle, \quad (2)$$

where the angled brackets indicate the average over the initial conditions. Given that  $y_k(0) > y_i(0)$  the initial distance  $d_{ik} = y_k(0) - y_i(0)$ , between the genotypes  $i$  and  $k$ , is a random variable also uniformly distributed over  $[0, N + y_k(0)]$  and consequently the average of the delta function in the above expressions is equal to one and independent of time. The probability that the genotype  $i$  (with  $v_i > w_k$ ) becomes the next leader is given by  $r_i / \sum_j r_j$  which we write as a transition probability

$$p_{k \rightarrow i} = \frac{(v_i - w_k)\theta(v_i - w_k)}{\sum_{j=1}^N (v_j - w_k)\theta(v_j - w_k)}, \quad (3)$$

This rather intuitive rule appears in a simple traffic model studied in [8], although the physics is different

to that here because on catching up with a slower car the faster one then adopts the same speed. We next show that this model can be mapped onto a first-passage problem for a random process. Notice that, once the  $k$ -th leader is selected with velocity  $w_k$ , the number  $N_k$  of possible future leaders is

$$\frac{N_k}{N} = \frac{\sum_{j=1}^N \theta(v_j - w_k)}{N}, \quad (4)$$

where  $N$  is the total number of genotypes. In the limit of large  $N$ , one can replace the right hand side of Eq. (4) by the integral over  $v$ ,

$$\frac{N_k}{N} \rightarrow \int_{w_k}^{v_{\max}} p(v) dv = P(w_k), \quad (5)$$

which is exact up to  $O(1/\sqrt{N})$  corrections and where  $P(v) = \int_v^{v_{\max}} p(u) du$  is the cumulative velocity distribution. Clearly, the number of lead changes  $l_N$  is the value of  $k$  where  $N_k = 1$ . This gives,  $P(w_{l_N}) = 1/N$  and hence

$$-\ln[P(w_{l_N})] = \ln N. \quad (6)$$

We define  $Y_k = -\ln[P(w_k)]$  whose evolution is given by

$$Y_{k+1} = Y_k + \xi_k, \quad (7)$$

where clearly

$$\xi_k = -\ln[P(w_{k+1})/P(w_k)]. \quad (8)$$

Thus  $Y_k$  can be interpreted as the position of a random walker at time  $k$  and its time evolution is given by the Langevin equation (7) where  $\xi_k$  is the noise at step  $k$ . This redefinition is not yet very useful since the noise at step  $k$  depends on  $Y_{k+1}$  and  $Y_k$ . However, as we will see, for large  $k$  the probability distribution of the noise  $\xi_k$  becomes independent of  $k$  and  $w_k$  and has a finite mean  $\langle \xi_k \rangle = \mu$  and variance  $\langle [\xi_k - \langle \xi_k \rangle]^2 \rangle = \sigma^2$ , that can be computed explicitly for arbitrary velocity distribution  $p(v)$ . For large  $k$ , Eq. (7) represents a discrete time random walk with a positive drift  $\mu$ , i.e.,

$$Y_{k+1} = Y_k + \mu + \sigma \eta_k \quad (9)$$

where  $\eta_k$  is a noise with zero mean  $\langle \eta_k \rangle = 0$  and unit variance. We will also see that  $\eta_k$ 's are not only completely independent of  $w_k$  for large  $k$ , they are also uncorrelated at different times. Thus Eq. (9) is a true Markovian evolution of a discrete time random walker with a positive drift  $\mu$ . Obviously then, by central limit theorem,  $Y_k$  will have a Gaussian distribution with mean  $\langle Y_k \rangle = \mu k$  and variance  $\langle Y_k^2 \rangle - \langle Y_k \rangle^2 = \sigma^2 k$ .

Once we have the Markovian random walker evolution as in Eq. (9), it follows from Eq. (6) that the number of lead changes  $l_N$  is just the first time the process  $Y_k$  (starting at some initial value  $Y_0$ ) hits the level  $Y = \ln(N)$ .

Thus the distribution of  $l_N$  is simply the distribution of the first-passage time to the level  $Y = \ln(N)$ . To compute this, it is convenient to define  $Z_k = \ln N - Y_k$ . Then  $Z_k$ 's evolve via,  $Z_{k+1} = Z_k - \mu - \sigma\eta_k$  starting from  $Z_0 = \ln N - Y_0$ . Thus  $Z_k$  is the position of a random walker at step  $k$  with a negative drift  $-\mu$  towards the origin and  $l_N$  now represents the first-passage time to the *origin* starting from the initial position  $Z_0$ . Now, for large  $k$ , the discrete-time random walker can be replaced by a continuous-time Brownian motion,

$$\frac{dZ}{dt} = -\mu + \sigma\eta(t) \quad (10)$$

where  $\eta$  is a white noise with  $\langle\eta(t)\rangle = 0$  and  $\langle\eta(t)\eta(t')\rangle = \delta(t-t')$ . For such a process, the distribution  $P(t_f|Z_0)$  of the first-passage time  $t_f$  to the origin is known exactly [9] and we can apply it here to obtain the probability that  $l_N = k$  is given by

$$Q(k) = \frac{\ln N}{\sigma\sqrt{2\pi k^3}} \exp\left[-\frac{\mu^2}{2\sigma^2 k} (k - (\ln N)/\mu)^2\right]. \quad (11)$$

Note that this distribution of  $l_N$  is non-Gaussian. However, we expect this result to be valid only in the vicinity of  $k \approx \ln N/\mu$ , i.e., near its mean. This can be traced back to the fact that in deriving this result we replaced a discrete-time random walk by a continuous-time Brownian process. Near its mean, using  $k \approx \ln N$  in Eq. (11), the distribution of  $l_N$  becomes a Gaussian

$$Q(k) \approx \frac{\mu^{3/2}}{\sigma\sqrt{2\pi \ln N}} \exp\left[-\frac{\mu^3}{2\sigma^2 \ln N} (k - (\ln N)/\mu)^2\right] \quad (12)$$

with mean and variance (for large  $N$ ) given by

$$\langle l_N \rangle = \beta \ln N; \quad \text{where } \beta = \frac{1}{\mu} \quad (13)$$

$$\langle (l_N - \langle l_N \rangle)^2 \rangle = \gamma \ln N; \quad \text{where } \gamma = \frac{\sigma^2}{\mu^3}. \quad (14)$$

Thus, irrespective of the velocity distribution  $p(v)$ , the distribution of  $l_N$  near its mean is a universal Gaussian characterized by two parameters  $\mu$  and  $\sigma$ . The only dependence on  $p(v)$  appears through the two constants  $\mu$  and  $\sigma$ .

To calculate the mean  $\mu$  and the variance  $\sigma^2$  of the noise  $\xi_k$  defined in Eq. 8, we note that for a given  $w_k$ ,  $\xi_k$  is a random variable since  $w_{k+1}$  is a random variable drawn from the distribution in Eq. (3). We define

$$J(v) = \int_v^{v_{\max}} P(u) du \quad (15)$$

$$K(v) = \int_v^{v_{\max}} [P'(u)/P(u)]J(u) du \quad (16)$$

$$L(v) = \int_v^{v_{\max}} [P'(u)/P(u)]K(u) du. \quad (17)$$

Using the definition in Eq. (8) and the transition probability in Eq. (3), the mean of  $\xi_k$  (for a given  $w_k$ ) is

$$\langle \xi_k \rangle = -\frac{\int_{w_k}^{v_{\max}} [\ln(P(v)) - \ln(P(w_k))](v - w_k)p(v) dv}{\int_{w_k}^{v_{\max}} (v - w_k)p(v) dv}. \quad (18)$$

Using integration by parts, in both the numerator and denominator above we find

$$\langle \xi_k \rangle = 1 - \frac{K(w_k)}{J(w_k)}, \quad (19)$$

where the function  $K(v)$  is defined in Eq. (16). The second moment is given by

$$\langle \xi_k^2 \rangle = \frac{\int_{w_k}^{v_{\max}} [\ln(P(v)) - \ln(P(w_k))]^2 (v - w_k)p(v) dv}{\int_{w_k}^{v_{\max}} (v - w_k)p(v) dv}, \quad (20)$$

and a similar calculation leads to

$$\langle (\xi_k - \langle \xi_k \rangle)^2 \rangle = 1 + 2\frac{L(w_k)}{J(w_k)} - \left[\frac{K(w_k)}{J(w_k)}\right]^2, \quad (21)$$

where the functions  $J$ ,  $K$  and  $L$  are defined in Eqs. (15), (16) and (17) respectively.

We now consider the three classes of distributions considered by [5].

(i) **Fast decaying distribution with  $v_{\max} = +\infty$ :** In this case, it is easy to see that for large  $u$ ,

$$\frac{P'(u)}{P(u)} \approx \frac{J'(u)}{J(u)} \quad (22)$$

Thus, using this result in the definition of  $K(v)$  in Eq. (16) one finds that for large  $w_k$

$$K(w_k) = \int_{w_k}^{\infty} \frac{P'(u)}{P(u)} J(u) du \approx -J(w_k) \quad (23)$$

Similarly, for large  $w_k$ ,

$$L(w_k) = \int_{w_k}^{\infty} \frac{P'(u)}{P(u)} K(u) du \approx J(w_k) \quad (24)$$

Using these results in Eqs. (19) and (21) we find for large  $k$

$$\langle \xi_k \rangle = \mu = 2 \quad (25)$$

$$\langle (\xi_k - \langle \xi_k \rangle)^2 \rangle = \sigma^2 = 2. \quad (26)$$

Thus, as stated earlier, we see the variance become independent of  $k$  and  $w_k$ .

(ii) **Distribution with a finite  $v_{\max}$ , with  $p(v) \sim |\ln(v_{\max} - v)|^\gamma (v_{\max} - v)^\alpha$ :** In this case, for  $u$  close to  $v_{\max}$ , we find

$$\frac{P'(u)}{P(u)} \approx \left(\frac{1 + \alpha}{2 + \alpha}\right) \frac{J'(u)}{J(u)}. \quad (27)$$

and it follows that for  $w_k$  close to  $v_{\max}$

$$\begin{aligned} K(w_k) &\approx -\left(\frac{1+\alpha}{2+\alpha}\right) J(w_k) \\ L(w_k) &\approx \left(\frac{1+\alpha}{2+\alpha}\right)^2 J(w_k) \end{aligned} \quad (28)$$

Using these results in Eqs. (19) and (21) we get

$$\langle \xi_k \rangle = \mu = \frac{2\alpha + 3}{\alpha + 2} \quad (29)$$

$$\langle (\xi_k - \langle \xi_k \rangle)^2 \rangle = \sigma^2 = \frac{2\alpha^2 + 6\alpha + 5}{(\alpha + 2)^2}. \quad (30)$$

**(iii) Power-law decaying distribution with  $v_{\max} = +\infty$ , and  $p(v) \sim \ln(v)^\gamma v^{-\alpha}$  with  $\alpha > 2$ :** In this case, for large  $u$

$$\frac{P'(u)}{P(u)} \approx \left(\frac{\alpha - 1}{\alpha - 2}\right) \frac{J'(u)}{J(u)} \quad (31)$$

Using this result in the definition of  $K(v)$  and  $L(v)$  one easily finds that for large  $w_k$

$$\begin{aligned} K(w_k) &\approx -\left(\frac{\alpha - 1}{\alpha - 2}\right) J(w_k) \\ L(w_k) &\approx \left(\frac{\alpha - 1}{\alpha - 2}\right)^2 J(w_k) \end{aligned} \quad (32)$$

Using these results in Eqs. (19) and (21) we get

$$\langle \xi_k \rangle = \mu = \frac{2\alpha - 3}{\alpha - 2} \quad (33)$$

$$\langle (\xi_k - \langle \xi_k \rangle)^2 \rangle = \sigma^2 = \frac{2\alpha^2 - 6\alpha + 5}{(\alpha - 2)^2}. \quad (34)$$

One can also demonstrate [10] that for all these velocity distributions, and for large  $k$  and  $k' \langle \xi_k \xi_{k'} \rangle - \mu^2 \rightarrow 0$ , indicating that the noise  $\xi_k$ 's become completely uncorrelated in time. Thus Eq. (9) truly represents a Markovian random walk with drift  $\mu$ . Knowing the exact values of  $\mu$  and  $\sigma$ , we then find that distribution of  $l_N$ , near its mean, is given by the Gaussian in Eq. (12) with mean and variance given by Eqs. (14). The coefficients  $\beta$  and  $\gamma$  are thus calculated exactly knowing  $\mu$  and  $\sigma$  and are given, for each of the cases mentioned above, by

$$(i) : \beta = 1/2 ; \gamma = 1/4 \quad (35)$$

$$(ii) : \beta = \frac{\alpha + 2}{2\alpha + 3} ; \gamma = \frac{(\alpha + 2)(2\alpha^2 + 6\alpha + 5)}{(2\alpha + 3)^3} \quad (36)$$

$$(iii) : \beta = \frac{\alpha - 2}{2\alpha - 3} ; \gamma = \frac{(\alpha - 2)(2\alpha^2 - 6\alpha + 5)}{(2\alpha - 3)^3} \quad (37)$$

The results for the coefficient  $\beta$  are in complete agreement with those conjectured in [5] in all three cases and we have further verified all our results by simulating the

original i.i.d. shell model with an algorithm which permits us to simulate up to  $N = 10^{200}$  genotypes [10]. Moreover, we have also calculated the variance exactly and shown that near its mean, the distribution of  $l_N$  is a universal Gaussian. In [5] it was pointed out that the variance of  $l_N$  is typically smaller than the mean indicating the temporal correlation between leadership changes, this is clearly seen in our exact results. Away from its mean, one expects to see departures of the distribution of  $l_N$  away from the Gaussian form. To compute the full distribution one needs to solve the first-passage problem for the discrete-time process without resorting to the continuous-time approximation. Fortunately, for our discrete-time process, this can be achieved by observing that the evolution of  $Y_k$  with  $k$ , though random, is actually a strictly monotonic process. This follows from Eq. (8) that shows that the noise  $\xi_k$  is always positive. The distribution of the first-passage time  $l_N$  to the level  $\ln(N)$  then satisfies the identity [10]

$$\text{Prob}(l_N \leq k) = \text{Prob}(Y_k \geq \ln(N)). \quad (38)$$

This gives  $Q(k) = \text{Prob}(l_N = k) = \text{Prob}(l_N \leq k + 1) - \text{Prob}(l_N \leq k) = \text{Prob}(Y_{k+1} \geq \ln(N)) - \text{Prob}(Y_k \geq \ln(N))$ . Thus, a knowledge of the distribution of  $Y_k$  (which is usually much simpler to compute) provides us with an exact distribution of lead changes  $Q(k)$  for all  $k$ . For example, for an exponential velocity distribution  $p(v) = e^{-v}$ , the probability density function of  $Y_k$  can be found explicitly for all  $k$

$$\rho_k(y) = \frac{y^{2k-1}}{(2k-1)!} \exp(-y). \quad (39)$$

This result is in fact asymptotically valid for any rapidly decaying distribution  $p(v)$  [10]. Using this result we thus obtain the full probability distribution of  $l_N$  for the exponential velocity distribution as

$$Q(k) = \frac{(\ln(N))^{2k}}{N(2k)!} \left[ 1 + \frac{\ln(N)}{2k+1} \right] \quad (40)$$

In Fig. (2) we show the predictions of Eq. (40) versus the results of extensive simulations and the agreement is perfect. The above use of the monotonicity of  $Y_k$  also enables one to obtain analytical results, away from the Gaussian regime, for generic fitness distributions [10].

To summarize we have solved exactly the asymptotic statistics of lead changes in a quasispecies evolution model by mapping the model to a random flux model. Our results confirm previous conjectures about the mean number of leader changes. We have also computed the variance exactly and shown that the distribution is generically Gaussian in the region around the mean. Finally, we remark that the evolution time  $\tau$  defined as the time when the last leader change occurs can be shown to have a distribution  $q(\tau) \sim \tau^{-2}$  for large  $\tau$  [10], as found in more realistic models [5].

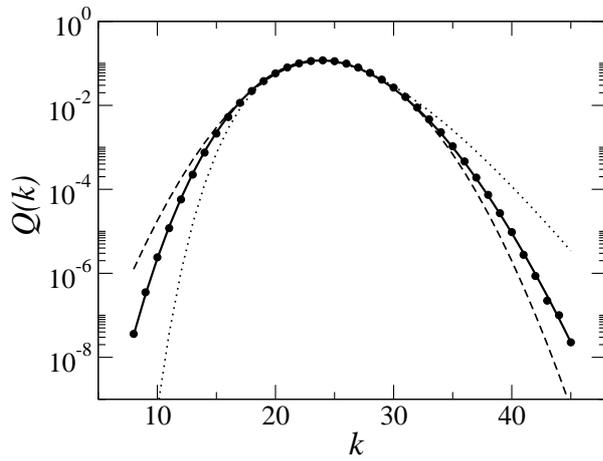


FIG. 2: Plot of the distribution  $Q(k)$  of and  $l_N$  (circles), for  $N = 10^{20}$  generated from  $2 \cdot 10^8$  samples with velocities taken from an exponential distribution. Also shown is the result Eq. (40) (solid line), the result Eq. (11) (dotted lines) and the Gaussian result Eq. (12) (dashed line).

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