Breaking records in the evolutionary race

Joachim Krug and Kavita Jain

Institut für Theoretische Physik, Universität zu Köln
Zülpicher Strasse 77, 50937 Köln, Germany

Abstract

We explore some aspects of the relationship between biological evolution processes and the mathematical theory of records. For Eigen’s quasispecies model with an uncorrelated fitness landscape, we show that the evolutionary trajectories traced out by a population initially localized at a randomly chosen point in sequence space can be described in close analogy to record dynamics, with two complications. First, the increasing number of genotypes that become available with increasing distance from the starting point implies that fitness records are more frequent than for the standard case of independent, identically distributed random variables. Second, fitness records can be bypassed, which strongly reduces the number of genotypes that take part in an evolutionary trajectory. For exponential and Gaussian fitness distributions, this number scales with sequence length $N$ as $\sqrt{N}$, and it is of order unity for distributions with a power law tail. This is in strong contrast to the number of records, which is of order $N$ for any fitness distribution.

Key words: Biological evolution, punctuated equilibrium, record dynamics, extremal statistics, quasispecies model

1 Records and evolution

In the Darwinian view of nature [1], biological evolution is a fierce competition among different organisms in which the winners are rewarded by copious offspring while the losers perish. It should therefore be no surprise to see metaphors from the world of athletics turn up in the description of evolutionary dynamics. Indeed, every evolutionary innovation that is fixed in a population has to be a record, in the sense that it solves some problem encountered by the organism in a way that is superior to all existing solutions. A possible mathematical relationship between evolution models and the theory of records was suggested by Kauffman and Levin in the context of long-jump adaption on correlated fitness landscapes [2], and has more recently been elaborated by Sibani and coworkers [3].
The basic problem of record statistics can be formulated as follows \[4,5\]: Given an ordered sequence \( \{X_n\}_{n=1,2,3...} \) of real random variables (RV’s), a record occurs at \( r \) iff
\[
X_r = \max_{n \leq r} \{X_n\}.
\] (1)

By convention, \( X_1 \) is always a record, and through application of (1) a series of record times \( \{r_k\}_{k=1,2,3...} \) and record values \( \{X_{r_k}\} \) is generated from the underlying sequence \( \{X_n\} \), with \( r_k \) denoting the time of the \( k \)'th record and \( r_1 = 1 \). Many properties of records are known for the case when the \( X_n \) are independent and identically distributed (i.i.d.). In particular, the statistics of the record times is completely independent of the underlying probability distribution. This is largely a consequence of a simple symmetry argument \[6\]. Denote by \( P_n \) the probability that a record occurs at \( n \). In the i.i.d. case, each of the \( n \) RV’s \( \{X_1, X_2, ..., X_n\} \) is equally likely to be the largest, and hence \( P_n = 1/n \). In particular, the expected number of records \( \langle R(n) \rangle \) up to time \( n \) is equal to
\[
\langle R(n) \rangle = \sum_{i=1}^{n} \frac{1}{i} \approx \ln(n) + 0.57721566... + O(1/n).
\] (2)

The full distribution of \( R(n) \) becomes Poissonian for large \( n \), and the record sequence can be described as a Poisson process in logarithmic time \( \ln(n) \) \[3\]. Furthermore, it can be shown that the ratios of subsequent record times \( r_k/r_{k+1} \) become uniformly distributed, independent random variables for large \( k \) \[4\]. This implies that the sequence \( \{r_k\} \) of record times has some rather counterintuitive properties; for example, given the time \( r_k \) of the \( k \)'th record, the expected time of the preceding record is \( \langle r_{k-1} \rangle = r_k/2 \), while the expected time \( \langle r_{k+1} \rangle \) of the next record is infinite\(^1\).

The record sequence is distinctly non-stationary: With increasing time, it becomes exponentially harder to beat the current record. For this reason record dynamics and the associated log-Poisson process has been invoked to describe the nonstationary aspects of macroevolutionary dynamics \[3\] (as evidenced e.g. by extinction and origination rates of taxa in the fossil record \[7\]), as well as the relaxation of disordered systems such as spin glasses \[8\]. The pattern of static periods of exponentially increasing duration interspersed by rare events of rapid change (new records) is a simple realization of punctuated equilibrium, an important paradigm of evolutionary theory \[9,10\].

\(^1\) The latter property invalidates an argumentation based on the average waiting time for the next record, which has lead Kauffman and Levin to conclude (erroneously) that the number of records grows as \( \log_2(n) \) rather than as \( \ln(n) \) \[2\].
Here we approach the relation between evolution and records from the point of view of population dynamics on the space of genetic sequences [11,12]. We show how the properties of sequence space introduce modifications to the standard record problem, which are of interest in their own right, and only partly understood at present. Some basic notions are introduced in the next section, and the remaining sections summarize the main results of a detailed investigation, which will be published elsewhere [13].

2 Sequence space and fitness landscape

The proper arena in which to describe evolutionary dynamics is the space of genotypes, which are represented as sequences $\sigma = (\sigma_1, \sigma_2, ..., \sigma_N)$ of $N$ symbols taken from an alphabet of $\ell$ letters; for DNA sequences $\ell = 4$, but in many theoretical studies binary sequences ($\ell = 2$) are considered for simplicity. The total number of possible sequences is $S = \ell^N$. The nearest neighbors of a given sequence $\sigma$ are those sequences $\sigma'$ that can be reached from $\sigma$ by a single point mutation, which alters one of the $N$ symbols. More generally, the Hamming distance $d(\sigma, \sigma')$ between two sequences $\sigma$ and $\sigma'$ is the number of symbols in which the two differ. An important quantity in what follows is the number $\alpha_k$ of sequences at distance $k$ from a given sequence, which takes the form

$$\alpha_k = \binom{N}{k} (\ell - 1)^k.$$  

(3)

This can be derived by noting that there are $\binom{N}{k}$ ways of choosing $k$ mutation sites on the sequence, and at each site $\ell - 1$ different symbols are available. The maximum distance between two sequences is $N$. For large $N$ (3) takes the form of a Gaussian of width $\sqrt{N}$ centered around the distance $k_{\text{max}} = N(\ell - 1)/\ell$ at which the majority of sequences reside.

Next we have to associate a fitness with each sequence $\sigma$. We define the fitness $W(\sigma)$, in the Wrightian sense [14], to be proportional to the expected number of offspring of an individual carrying the genotype $\sigma$ [15,16]. This implies that $W(\sigma) \geq 0$, and only ratios of fitnesses matter. We can thus write $W(\sigma) = e^{\beta F(\sigma)}$ to introduce an inverse selective temperature $\beta$ [16] for later use. In the following both $W$ and $F$ will be referred to as “fitness”.

The mapping from genotype to fitness is largely unknown, but it is expected to be very complicated. We therefore follow a common practice and assume the $F(\sigma)$ to be quenched i.i.d. RV’s drawn from some distribution $p(F)$; in statistical physics this is known as the random energy model (REM) of spin
glasses [15,17], while in the context of evolutionary biology it has been referred to as the house of cards model [14] or the uncorrelated fitness landscape [2]. Many properties of the REM fitness landscape, such as the number of local fitness maxima and the length of uphill adaptive walks [2,18], can be derived using simple ideas from order statistics [19]. It is of particular interest to find properties that are independent of the fitness distribution. For example, the probability that a given sequence is a local maximum is equal to the probability that it has the largest fitness in the set of sequences comprising its \((\ell - 1)N\) nearest neighbors and itself; by the symmetry argument of Sect.1, this is just \([((\ell - 1)N + 1)^{-1}].\)

Important characteristics of the REM landscape needed in the following discussion are the expected maximum fitness value \(F_{\text{max}}(S)\) that occurs among the \(S\) independent sequences, and the fitness gap \(\epsilon\), which is the difference between the largest and the second largest fitness value [11]. A simple estimate for the maximum fitness is obtained by setting the cumulative fitness distribution \(p_c(F)\) equal to \(1 - 1/S\) [20],

\[
p_c(F_{\text{max}}) = \int_{-\infty}^{F_{\text{max}}} dF p(F) = 1 - 1/S,
\]

and the fitness gap is of the order of \(\epsilon \sim [S p(F_{\text{max}}(S))]^{-1} [11,12].\)

3 Records in sequence space

Kauffman and Levin [2] found record statistics to be applicable in a situation where a population, assumed to be localized at a single sequence at all times, explores sequence space by random mutations of arbitrarily long range, and moves to a new location whenever the fitness of the mutant exceeds that of the present position. To highlight the role of the geometry of sequence space, we consider here a variant of their model where the range of mutations is restricted but grows in the course of time. At time \(t = 0\) the entire population resides at a randomly chosen “seed” sequence \(\sigma_0\). At the integer time \(t > 0\), the population has access to all genotypes within Hamming distance \(k = t\) of \(\sigma_0\), and it always resides in its entirety at the sequence of maximum fitness within the accessible region. Thus the current position of the population in sequence space jumps whenever a fitness record occurs among the \(\alpha_k\) sequences which become newly available at time \(t = k\).

The analysis of this model requires a slight generalization of the basic symmetry argument of record statistics outlined above, which is adapted to a situation where a variable number of new i.i.d. RV’s is introduced at each
time step\footnote{This generalization was originally introduced to investigate whether the frequent breaking of records in the Olympic games can be attributed to the fact that the athletes are selected from exponentially growing populations \cite{21}. The conclusion was that population growth is not sufficient to explain the data.} \cite{5,21}: As the newly introduced RV’s are indistinguishable from those that have appeared at earlier times, the probability that a record occurs among them is simply equal to

\begin{equation}
P_k = \frac{\alpha_k}{\sum_{j=1}^{k} \alpha_j} \approx 1 - \frac{k}{(\ell - 1)(N - k)}. \tag{5}\end{equation}

In the last step the expression (3) has been inserted and an expansion for \(k, N \to \infty\) at fixed \(k/N\) has been carried out \cite{13}. The probability \(P_k\) starts out at unity and dwindles to zero as \(k\) approaches the value \(k_{\text{max}}\) of the Hamming distance at which the majority of sequences reside; the process stops at \(t = k_{\text{max}}\), when the globally fittest sequence \(\sigma^{(f)}\) (which is located with certainty at \(k_{\text{max}}\) for large \(N\)) is reached. In contrast to the logarithmic increase (2) in the i.i.d. case, here new records are found quite frequently, at least when \(k \ll N\). This is because of the exponential growth of the number of available sequences with increasing distance from the seed, which compensates the scarcity of new records.

Integrating (5) from \(k = 0\) to \(k_{\text{max}}\) one finds that the mean of the total number of records \(R\) that are encountered during the evolution is given by

\begin{equation}\langle R \rangle = \left(1 - \frac{\ln \ell}{\ell - 1}\right) N. \tag{6}\end{equation}

It can be shown that the occurrences of records are independent events in this model \cite{5,13}, and hence the variance and higher moments of \(R\) can also be computed from the \(P_k\). The variance is

\begin{equation}\langle R^2 \rangle - \langle R \rangle^2 = \sum_{k=1}^{N} P_k - P_k^2 \approx \frac{N}{\ell - 1} \left(\frac{\ell + 1}{\ell - 1} \ln \ell - 2\right) \tag{7}\end{equation}

for large \(N\), which decreases with increasing \(\ell\). Thus asymptotically \(R\) is a normal RV with fluctuations of order \(\sqrt{N}\). In addition, analytic results for the the spacings between records are reported in \cite{13}.
4 Quasispecies evolution in the strong selection limit

For a somewhat more realistic description of the population dynamics, we turn to Eigen’s quasispecies model [22,23], arguably the simplest mathematical model that implements the basic mechanisms of selection and mutation for a genetically heterogeneous population on the level of the sequence space [14]. The model was introduced to describe the population dynamics of asexually reproducing entities like self-replicating macromolecules. It can be applied whenever the population size is large, so that the number of individuals occupying a given site in sequence space can be represented by a continuous variable. Because of the exponential proliferation of the number of sequences with increasing \( N \), real populations are very sparse in sequence space, which severely limits the applicability of a continuum description. We nevertheless believe that it is important to first understand the long time dynamics of sequence space evolution in the continuum setting, before taking into account the effects of the discreteness of real populations.

In the quasispecies model, the population \( Z(\sigma, t) \) of genotype \( \sigma \) at time \( t \) evolves in discrete time according to the linear recursion relation

\[
Z(\sigma, t + 1) = \sum_{\sigma'} p(\sigma' \rightarrow \sigma) W(\sigma') Z(\sigma', t),
\]

where \( p(\sigma' \rightarrow \sigma) \) is the mutation probability that sequence \( \sigma \) appears as offspring of sequence \( \sigma' \). Assuming that single point mutations occur with probability \( \mu \) per generation, the mutation probability takes the form

\[
p(\sigma' \rightarrow \sigma) = \mu^{d(\sigma, \sigma')}(1 - \mu)^{N - d(\sigma, \sigma')}.
\]

Consider a population that is initially localized at a seed sequence \( \sigma_0 \), i.e., the initial condition for (8) is \( Z(\sigma, 0) = Z_0 \delta_{\sigma, \sigma_0} \). Then after one time step we have

\[
Z(\sigma, 1) = Z_0 W(\sigma_0)(1 - \mu)^N [\mu/(1 - \mu)]^{d(\sigma, \sigma_0)} \sim \exp[-d(\sigma, \sigma_0)/\lambda].
\]

The population density is now nonzero everywhere, with a magnitude decaying exponentially with increasing distance from the seed sequence, where the decay length is \( \lambda = 1/\ln[1/\mu - 1] \). At this point individuals with genotypes far away from the seed start to compete with the majority of the population still located at \( \sigma_0 \). To quantify this competition, we follow the location of the current leader \( \sigma^*(t) \), which is defined as the sequence at which \( Z(\sigma, t) \) is maximal. The path of \( \sigma^*(t) \) describes an evolutionary trajectory in sequence space [11,12]. Along such a trajectory the fitness \( F(\sigma^*) \) increases in a stepwise fashion, similar to the fitness trajectories observed in experimental studies of microbial populations [24,25].
The dynamics of evolutionary trajectories is simple in a strong selection limit modeled after the zero temperature limit of the statistical physics of disordered systems [11,12]. Writing \( \mu = e^{-\beta \gamma} \) and taking the inverse selective temperature \( \beta \to \infty \), one obtains a recursion relation for the logarithmic population variable \( E(\sigma, t) \) defined by \( Z(\sigma, t) = e^{\beta E(\sigma, t)} \). As was shown in [12], the behavior remains essentially unchanged if the mutational part of the dynamics is turned off after the first time step. This implies that for \( t \geq 2 \) the population at each site \( \sigma \) grows independently, at its own logarithmic rate \( F(\sigma) \), according to

\[
E(\sigma, t) = E(\sigma, 1) + F(\sigma)(t - 1) = F(\sigma_0) - \gamma d(\sigma, \sigma_0) + F(\sigma)(t - 1). \tag{11}
\]

Here the initial condition (10) has been inserted. Equation (11) is a particularly transparent representation of the evolutionary race. Each genotype advances at its own speed \( F(\sigma) \), from an initial position determined by its distance from the seed sequence \( \sigma_0 \). In the course of time, the leadership in the population changes from sequences with relatively low fitness located close to \( \sigma_0 \) to more distant sequences of larger fitness, until eventually the globally fittest sequence is reached and the race comes to an end. At any given time the current leader \( \sigma^*(t) \) satisfies \( E(\sigma^*(t), t) = \max_{\sigma} \{E(\sigma, t)\} \); that is, \( E(\sigma^*(t), t) \) is the upper envelope of the family of straight lines defined by (11), and leadership changes correspond to the corners of the envelope. The leadership changes are precisely the jumps in the punctuated evolutionary trajectory, and their statistics will be discussed in the next section.

5 Bypassing

Several properties of evolutionary trajectories follow immediately from the representation (11). First, since all sequences within a shell of constant distance \( d(\sigma, \sigma_0) \) start with the same population at \( t = 1 \), only the sequence with the largest fitness within each shell has a chance of ever attaining the leadership. Second, in order to become the new leader, the fitness of a sequence has to exceed that of the current leader, i.e. the sequence has to be a record in the sense of Sect.3. Thus, among the \( \ell^N \) available genotypes only a small fraction given by the mean number of records (6) is eligible to become part of the evolutionary trajectory.

However, not every record will become a leader. To see this, suppose the current leader is at \( \sigma \), and let \( \sigma' \) be a subsequent record with \( F(\sigma') > F(\sigma) \) and \( d(\sigma_0, \sigma') > d(\sigma_0, \sigma) \). Then \( E(\sigma, t) \) and \( E(\sigma', t) \) will cross at time

\[
T(\sigma, \sigma') = \frac{\gamma [d(\sigma_0, \sigma') - d(\sigma_0, \sigma)]}{F(\sigma') - F(\sigma)}. \tag{12}
\]
Fig. 1. Simulation data for the probability $Q_k$ for an evolutionary jump to occur at distance $k$ from the seed site. Main figure shows data for Gaussian (O, Δ) and exponential (+, ×) fitness distributions, two different sequence lengths $N$, and alphabet size $\ell = 2$, on a double logarithmic scale. Inset shows data for exponential fitness distribution, $N = 512$, and three different values of $\ell$ on a linear scale. The data were averaged over $10^5$ (main figure) and $10^4$ (inset) disorder configurations, respectively.

The leadership will be taken over by the sequence $\sigma'$ that minimizes the crossing time (12), which does not need to be the next record in line. We say that a sequence $\sigma_1$ is bypassed by a sequence $\sigma_2$ with $d(\sigma_0, \sigma) < d(\sigma_0, \sigma_1) < d(\sigma_0, \sigma_2)$, if $T(\sigma, \sigma_2) < T(\sigma, \sigma_1)$. Because of bypassing, the number of records (6) is only an upper bound on the number of leadership changes.

In contrast to the properties of the records discussed in Sects. 1 and 3, which are independent of the underlying fitness distribution, the prevalence of bypassing depends on $p(F)$ [13]. We can get some insight into the behavior by estimating the typical time $T^* = T(\sigma^{(f-1)}, \sigma^{(f)})$ at which the penultimate leader $\sigma^{(f-1)}$ is overtaken by the sequence $\sigma^{(f)}$ with globally maximal fitness [12]. As both $\sigma^{(f)}$ and $\sigma^{(f-1)}$ are expected to reside within a belt of thickness $\sqrt{N}$ around $k_{\text{max}}$, we have $d(\sigma_0, \sigma^{(f)}) - d(\sigma_0, \sigma^{(f-1)}) \sim \sqrt{N}$. The fitness difference $F(\sigma^{(f)}) - F(\sigma^{(f-1)})$ should be of the order of the fitness gap of the landscape. For example, for a fitness distribution with a power law tail $p(F) \sim F^{-\mu+1}$, we have according to (4) that $F_{\text{max}} \sim S^{1/\mu} = \ell^{N/\mu}$, and the fitness gap is of the same order. This implies that the crossing time $T^* \sim \sqrt{N/\ell^{N/\mu}}$ decreases with increasing $N$; for large $N$ all intermediate records are bypassed, and the globally fittest sequence immediately takes over the leadership.

---

3 Due to the rare occurrence of landscapes with a very small fitness gap, the mean crossing time is nevertheless infinite: The distribution of $T^*$ has a universal $1/(T^*)^2$ tail with a prefactor that vanishes for $N \to \infty$ for power law fitness distributions [12].
Nontrivial behavior is found when the fitness gap decreases with \( N \), or increases more slowly than \( \sqrt{N} \). In Fig.1 we show numerical data for Gaussian and exponential fitness distributions, for which the gap is of order unity independent of \( N \). Very large sequence lengths can be treated by using the shell fitness \( F_k \), which is the largest of \( \alpha_k \) i.i.d. RV’s [12]; in this way the number of RV’s that are needed for each realization reduces from \( \ell^N \) to \( N \). The generation of the \( F_k \) is feasible despite the astronomically large values of \( \alpha_k \) because the maximum of \( \alpha_k \) exponential or Gaussian RV’s is only of order \( \ln \alpha_k \) or \( \sqrt{\ln \alpha_k} \), respectively [compare to (4)]. The key result illustrated in Fig.1 is the scaling form

\[
Q_k \approx N^{-1/2} f(k/N) \tag{13}
\]

for the probability \( Q_k \) for an evolutionary jump to occur at distance \( k \) from the seed. The total number of jumps is of order \( \sqrt{N} \), and hence most of the \( O(N) \) records are bypassed. The scaling function \( f(x) \) is cut off at \( k_{\text{max}}/N = 1 - 1/\ell \), but its shape appears to be independent of the alphabet size \( \ell \) (inset of Fig.1). For both Gaussian and exponential fitness distributions, the behavior of the scaling function at small arguments is close to \( f(x) \sim x^{-1/2} \). This behavior would imply that \( Q_k \sim 1/\sqrt{k} \) independent of \( N \) for \( k \ll N \), and that the number of jumps grows as \( \sqrt{k} \) with increasing distance from the seed site. We expect these results to be generally valid for fitness distributions in the Gumbel universality class of extreme value theory [20]. The case of bounded fitness distributions should also be interesting, but has not been treated so far because of the difficulty in creating the shell fitnesses for large \( N \).

An analytic understanding of (13) is lacking at present, and must be left to future work. In fact, as is explained in detail in [13], the statistics of bypassing is difficult to handle analytically even for the simple case when the geometry of sequence space is ignored and the shell fitnesses are replaced by i.i.d. RV’s. It is remarkable that the innocuous generalization of the basic record model, defined by the family (11) of lines with random slopes, leads to a rather involved and rich probabilistic problem.

**Acknowledgements**

We acknowledge useful discussions with Andreas Engel and Luca Peliti. This work has been supported by DFG within SFB/TR 12 *Symmetries and Universality in Mesoscopic Systems.*
References

[1] C. Darwin, The Origin of Species by Means of Natural Selection, John Murray, London, 1859.

[2] S.A. Kauffman, S. Levin, J. theor. Biol. 128 (1987) 11.

[3] P. Sibani, M. Brandt, P. Alstrøm, Int. J. Mod. Phys. 12 (1998) 361.

[4] N. Glick, Amer. Math. Monthly 85 (1978) 2.

[5] V. B. Nevzorov, Theory Probab. Appl. 32 (1987) 201.

[6] W. Feller, Introduction to Probability Theory and Its Applications, Vol.2, Wiley, New York, 1971.

[7] M.E.J. Newman, P. Sibani, Proc. Roy. Soc. London B 266 (1999) 1593.

[8] P. Sibani, J. Dall, Europhys. Lett. 64 (2003) 8.

[9] S.J. Gould, N. Eldredge, Nature 366 (1993) 223.

[10] N. Eldredge, Macroevolutionary Dynamics, McGraw-Hill, New York, 1989.

[11] J. Krug, in: M. Lässig, A. Valleriani (Eds.), Biological Evolution and Statistical Physics, Springer, Berlin, 2002, p. 205.

[12] J. Krug, C. Karl, Physica A 318 (2003) 137.

[13] K. Jain, J. Krug (to be published).

[14] E. Baake, W. Gabriel, in: D. Stauffer (Ed.), Annual Reviews of Computational Physics VII, World Scientific, Singapore, 2000, pp. 203-264.

[15] L. Peliti, in: T. Riste, D. Sherrington (Eds.), Physics of Biomaterials: Fluctuations, Self-Assembly and Evolution, Kluwer, Dordrecht, 1996, p. 267.

[16] L. Peliti, cond-mat/9712027.

[17] S. Franz, M. Sellitto, L. Peliti, J. Phys. A 26 (1993) L1195.

[18] H. Flyvbjerg, B. Lautrup, Phys. Rev. A 46 (1992) 6714.

[19] H.A. David, Order Statistics, Wiley, New York, 1970.

[20] D. Sornette, Critical Phenomena in Natural Sciences, Springer, Berlin, 2000.

[21] M.C.K. Yang, J. Appl. Prob. 12 (1975) 148.

[22] M. Eigen, Naturwissenschaften 58 (1971) 465.

[23] M. Eigen, J. McCaskill, P. Schuster, Adv. Chem. Phys. 75 (1989) 149.

[24] R.E. Lenski, M. Travisano, Proc. Natl. Acad. Sci. USA 91 (1994) 6808.

[25] C.L. Burch, L. Chao, Genetics 151 (1999) 921.