Why do Evolutionary Systems Stick to the Edge of Chaos

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Abstract

The long-term behaviour of dynamic systems can be classified in two different regimes, regular or chaotic, depending on the values of the control parameters, which are kept constant during the time evolution. Starting from slightly different initial conditions, a regular system converges to the same final trajectory, whereas a chaotic system follows two distinct trajectories exponentially diverging from each other.

In spite of these differences, regular and chaotic systems share a common property: both arrive exponentially fast to their final destiny, becoming trapped there. In both cases one has finite transient times. This is not a profitable property in what concerns evolutionary strategies, where the eternal search for new forms, better than the current one, is imperative. That is why evolutionary dynamic systems tend to tune themselves in very particular situations in between regular and chaotic regimes. These particular situations present eternal transients, and the system actually never reaches its final destiny, preserving diversity. This feature allows the system to visit other regions of the space of possibilities, not only the tiny region covered by its final attractor.

Key words: evolution, critical slowing down, self organized criticality

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I) Introduction

Any dynamic system has its dynamic variables which evolve as time goes by, and also its constant parameters. An example is the so-called logistic map

$$x_{t+1} = a x_t (1 - x_t) \quad , \tag{1}$$

where x_t is the dynamic variable which follows the trajectory $x_0, x_1, x_2...$ after starting from the initial seed x_0 . The time t = 0, 1, 2... is discrete. The control parameter a is kept constant during the dynamic evolution. This map was introduced a century and a half ago in order to model population growth dynamics [1], by considering $x_t = P_t/P_{\text{max}}$, where P_t is the current population at time (or generation) t, and P_{max} is the maximum population the environment can support. Within this model, a represents the birth rate per generation, allowing population growth if a > 1 for small values of x_t (i.e. $P_t <<< P_{\text{max}}$). The Verhulst death factor $(1 - x_t)$ avoids population explosion whenever P_t approaches the maximum environment capacity P_{max} , provided $a \leq 4$.

Other dynamic systems cannot be put in a simple, compact analytic language as in equation (1). Nevertheless, the dynamic variable as well as the rules governing its time evolution exist, and must be described according to some other language. For instance, the genetic pool of a real population evolves in time, but cannot be expressed by a single number x_t . At least one needs to count the frequency of each possible allele for all genes, among the current population at time (or generation) t, storing the results on a onedimensional array of frequencies. In this case, instead of a number, the dynamic variable is this array. In order to consider possible correlations between these genes, for instance how many individuals share the same set of D alleles, the frequencies must be stored on a D-dimensional array which becomes the dynamic variable. Instead of frequencies, the most complete representation is to store, for each individual, a bit 1 or 0 for each possible present or absent allele: in this case, the current populations is represented by a variable number of bit-arrays, or bit-strings, one for each alive individual, i.e. the dynamic variable becomes a P-dimensional array of bit-strings, where the population size P varies. Also the rules allowing to determine the current genetic status of the population from the knowledge of its past history depends on its reproduction and death behaviour, environment changes, and so on. Hardly these rules can be translated into equations relating the current and previous arrays. Perhaps other more detailed genetic information cannot even be stored in arrays of numbers, and the mathematical description of the system becomes very difficult. Many other non-biological evolutionary systems, as the behaviour of an economy with its various individual agents, or the development of a human language, fall into the same class of problems, with more or less the same difficulties.

A very powerful language to express the rules governing the evolution of such a system, is computer modeling. Let's consider a diploid population, as a simple example. Each individual is represented by two *B*-bit-strings storing, say, B = 1024 bits each. These two ordered *B*-strings will be called the individual's genome, kept fixed during its whole life. It inherits one *B*-string from its mother, and the other from its father. First, before its birth, the mother's genome is copied, and a random crossover is performed on the copy: both *B*-strings are cut in the same random position, and a new *B*-string is constructed by joining one random piece with the complementary piece taken from the other string. This is the *B*-string inherited from the mother, and the other is constructed by performing the same process on the father's genome. Then, *M* random mutations are introduced, say M = 1, by flipping *M* randomly chosen bits (from 0 to 1, or vice-versa) of the newborn genome. Besides its genome, each newborn also inherits the mother's family name, without mutations. During each time step, each individual reproduces *F* times as mother, say F = 1. This breeding process is sequentially performed for each alive individual, with the father being another one, randomly chosen.

The population size P (the number of alive individuals) is kept nearly constant, always fluctuating around some number P_0 , say $P_0 = 1000$, by applying the following death rule after the whole population breeding is over. Each individual *i* survives with probability $p = x^{N_i+1}$, where N_i is the number of homozygous 1-bit pairs in its genome (1-bits in the same position of both *B*-strings). Before to kill anybody, the value of *x* is determined in order to give an overall death rate compensating the appearance of newborns, i.e. by solving equation

$$x \sum_{i=1}^{P} x^{N_i} = P_0 \quad , \tag{2}$$

where the sum runs over all individuals (including newborns), or alternatively

$$x \sum_{N=0}^{\infty} H(N) x^N = P_0$$
, (3)

where H(N) counts the current number of individuals with N homozygous 1-bit pairs. Once the value of x is already known, the death roulette is applied sequentially to each individual *i*, according to its N_i . We count one more time step (one generation) after this complete process, breeding and deaths, is applied to the whole population. This simple rule strictly follows Darwin's principles [2]. First, the offspring genomes are slightly modified copies of the parents', with the additional crossing mechanism observed in diploid real organisms. These minor modifications from parent to offspring are performed at random. No further genome modification is performed during each individual's lifetime (no somatic mutations are considered). Second, again following Darwin, selection acts through the different survival probabilities, depending on some characteristics of the individual's genome. Here, specifically, the larger the number of homozygous 1-bits it has, the lower is its life expectancy, and thus the lower is the number of offspring it is supposed to breed. In this case, 1-bits represent harmful mutations. Many different versions of such a rule can be invented, the first one being the famous Eigen model [3]. The details of each model are not relevant here, the important feature is their common purpose to mimic Darwin's evolution working in real time. A few among them allow analytic treatments by translating the rules into differential equations, and solving them.

These analytic successes are rare. For most models, like the present one, analytic approaches are hard or impossible: in spite of its simplicity, one cannot translate the above rules into differential equations. Then, another language is necessary. For instance, C, FORTRAN, PASCAL or any other computer language which allows one to program the machine to follow strictly the dynamic rules, starting from some given population, during many time steps. By using some tricks [4], one can repeat this routine many times with different randomnesses, in a very fast way. Thus, one can measure the various properties of interest, their averages and correlations, how much they fluctuate due to randomness, etc. More important is the possibility to follow the historical evolution, time after time, an impossible task concerning most examples of real biological evolution. Moreover, one can even **repeat** the historical path introducing some controlled modifications, in order to study their influences. We were able to follow the above defined model for S = 1000 different samples, with $P_0 = 1000$ individuals each, with a length genome of B = 1024, during t = 8192 time steps (generations). First, we have performed some preliminary computer runs starting from a population with only 0-bits (no harmful mutations), storing at the end the corresponding populations in order to use them later, as starting points. We observed the same probability distribution of 0 and 1-bits, for all these final populations, after t = 8192 generations, in spite of the different randomnesses during their past evolutions. This statistical equilibration is always achieved, provided the number of generations is a few times larger than P_0 , even starting from different initial populations (with randomly assigned harmful mutations, instead of only 0-bits).

Now, re-setting t = 0 for the already equilibrated populations obtained from the preliminary runs, we performed the S = 1000 observation runs. A different family name

is given to each individual at generation t = 0. Different randomnesses were used during the time evolution of each sample. For all of them, we observed that all final individuals at generation t = 8192 share the same family name (inherited without mutations from the mother). In other words, after t = 8192 generations, all the $P \approx 1000$ alive individuals are relatives of each other, all descendents from the same original grand-grand-...mother. Let's call this lineage founder individual, which lived at generation t = 0, the Eve. Each sample has its own Eve, different from sample to sample. Even by starting just from the same initial population, different randomnesses lead to different Eves. This is not a novelty, it is in complete agreement with the coalescence theory, a mathematically well established set of branching-processes theorems concerning genetic behaviour (see, for instance [5], for a soft an excellent review). Other similar models also present this behaviour [6,7], as expected. Some results of our computer simulations are in figure 1a. The open circles show how the number of not-yet extinct family names evolves in time, averaged for all S = 1000samples. This number monotonically decreases from the initial value (≈ 1000) at t = 0, reaches the value 1 after ≈ 1000 generations, and remains constant thereafter. The values on the vertical axis, figure 1a, are normalised (divided) by the initial population. Also, only the first 64 generations are shown, but the monotonic decay goes on.

The obvious question concerns the population genetic diversity. Is it compromised by the fact that all final individuals are relatives, belonging to the same family? Is the final population genetic pool dominated by Eve's genome in some sense? In order to answer these questions, we have measured the correlation between each individual's genome and that of Eve, during all the time. In order to perform this task, we have profited from the possibility of repeating the whole evolution again, starting from exactly the same initial population and following exactly the same randomness, after knowing who was Eve from a first run. Only computer modeling allows such a procedure. We simply count the number of coincident bits at the same position in both genomes of Eve and the individual i. We performed this counting twice, first comparing the first (second) B-string of Eve with the first (second) B-string of i. Then, we repeated the counting by comparing the first Bstring of Eve with the second B-string of i, and vice-versa. The largest between these two counters is normalised (divided) by B. The result (a number in between 0 and 2) is the genome correlation. It measures how much the genome of i is "similar" to Eve's. At each generation, we measured the average of this quantity for all alive individuals, and subtracted this from the restricted average performed only among Eve's descendents. The absolute value of this quantity is shown by pluses in figure 1a. It decays to zero much faster than the number of family names. This means that, within Eve's family, the same genetic diversity of the whole population is reached in few generations, far before it becomes the only survival family. Nature is smart enough to preserve (and fast restore, if necessary) genetic diversity, even being forced to follow the coalescence theorems which dictate that all individuals belong to the same family, at the end.

We invented the above defined (toy) model only in order to analyse the deep mathematical differences between the two decaying curves in figure 1a. The reader can forget the model hereafter. Later, we will return to the much simpler time-evolution defined by equation (1), which nevertheless presents all the essential features one can study about dynamic systems, at least within the purpose of the present work. This purpose is to discuss how Nature knows to deal with the two possibilities exemplified in figure 1a, profiting from one or other mathematical behaviour, in what seems to be a universal law governing all evolutionary systems. This curious mathematical issue attracts the attention of researchers at least since [8]. The text is divided as follows. In section II, we analyse the mathematical properties of both "experimental" curves shown in figure 1a, and some implications in what concerns evolutionary behaviour. In section III, we return to equation (1) which also presents both mathematical behaviours, depending on the value of the parameter afixed by the user. This equation has the advantages of allowing some analytical treatment and of being much more easily programmed on a computer. In section IV, we present our main argument. Conclusions are in section V.

II) Fast \times Slow Decays, or Exponential \times Power Law Behaviours

Figure 1a shows two decaying quantities, one fast (pluses), and the other slow (circles). They are different averaged quantities concerning the same dynamic population model, and were measured from a series of computer simulations. Pluses display the genetic similarity between a founder individual (Eve) which lived at generation t = 0 and all its descendents alive at generation t. Let's call g this quantity. Its fast decay gives rise to a fast spread of genetic diversity among the whole population. Eve's descendents fast "forget" their genetic origin: the in-family differences between their genomes fast become statistically the same as the whole population. In order to infer the mathematical form of this "experimental" curve, we adopted the trick of showing the same data in figure 1b, now plotted according to a logarithmic vertical scale (equally spaced powers of 10). The first obvious effect of this trick is to enhance for the eyes the g-fluctuations appearing after generation $t \approx 20$, hardly observable in figure 1a. These fluctuations will remain forever, and are due to the simple

fact that both the population size ($P_0 = 1000$) and the number of statistically distinct samples (S = 1000) are finite. Indeed, from the product $P_0S = 10^6$, one can expect fluctuations around $1/\sqrt{P_0S} = 10^{-3}$, as really observed in figure 1b. These fluctuations are not important at all in what concerns our conceptual interpretation: would we have simulated a larger population size with a larger number of samples, they would be pushed to below any previously defined tolerance one wants.

The really important feature of adopting a non-linear, logarithmic vertical scale in figure 1b is the straight line observed before the fluctuations dominate the scenario. From it, we can infer that g follows an exponential decay, i.e.

$$g_t = g_0 \,\mathrm{e}^{-\lambda t} \quad , \tag{4}$$

where e = 2.718282... is the natural basis for logarithms, and the constant $g_0 = 1$ is unimportant. From the slope of this plot, fitted between t = 0 and t = 20 (dotted line), we can also obtain the "experimental" value for the constant λ which depends on the mutation rate M. In this case, we found $\lambda \approx 0.21$.

Circles display the fraction of yet-alive families (lineages) relative to the founder population at t = 0 (each individual at t = 0 is a family founder, and pass its family name to its descendents). Let's call f this fraction. It decays much slower than g, and certainly does not fit to an exponential function. The mere 64 generations shown along the horizontal axis common to both figures 1a and 1b are not enough to fully observe the decay of f. Considering the observed fact that only one family eventually survives, among the initial number $P_0 = 1000$, we can conclude that the current value of f, at t = 64, is still far above the final, definitive figure 10^{-3} . Thus, in order to better observe the slow decay of f, let's adopt the trick once more, now also along the horizontal axis. Figure 1c shows the same data again, with logarithm scale in both axis. The difference is the much larger number of generations shown now, in figure 1c, up to t = 8192. This is a too large number of points for a plot, thus we show only a few of them, namely those corresponding to generations which are integer powers of 2 (t = 1, 2, 4, 8 ... 8192), for clarity.

Now, in figure 1c, the fraction f of alive families fits to a straight (continuous) line after some few initial generations, leading to the mathematical relation

$$f_t = f_1 t^{-\alpha} \quad , \tag{5}$$

called a power law, where f_1 is another unimportant constant. What matters is the universal value $\alpha = 1$, predicted by coalescence theory for a very wide class of systems to which our toy model belongs. Measuring the slope of our "experimental" curve, at

its inflection point, we get $\alpha \approx 0.98$ in agreement with the theory. One can modify the particular, naive dynamic rules described in last section for our toy model, as one wants, and the universal value $\alpha = 1$ will insistently re-appear. More important, it also describes many actually observed real population data. It is our first example of universality, thanks to which some naive models can describe real situations. We will return to this fundamental point, later.

The important concept to be taken into account is the deep difference concerning the fast exponential behaviour $e^{-\lambda t}$ versus the slow power law $t^{-\alpha}$. It is so deep, as we will see later, that it is rather a qualitative distinction, not merely a quantitative difference. It concerns the distinction between any time interval, no matter how long it is, and eternity. Any evolutionary process must be eternal (if it stops after some finite time, it no longer evolves). Thus, evolution is expected to be mathematically described by some power laws. It is interesting to note that, besides power laws, Nature also uses the fast exponential behaviours, when necessary within each particular evolutionary system (for instance, in order to restore genetic diversity in our model). However, the quantities related with these exponential behaviours are not universal, as the value $\lambda \approx 0.21$, equation (4). It depends on the mutation rate M: the larger M, the larger is λ and faster Eve's genome is "forgotten". These quantities also depend on the particular rule one adopts. For instance, would we have considered haploid, as exual populations, then the value of λ would be smaller: driven only by mutations, without recombination (crossing) within two distinct parents' genomes, the genetic diversity spreads slower, although yet exponentially fast. On the other hand, the exponents defining the power laws, as $\alpha = 1$ in equation (5), are insensitive to particular parameters and universally valid for wide classes of different systems and models.

Also important is to note that a power law, equation (5) for instance, never appears alone. When a given system presents such a mathematical dependence between two particular variables, many other quantities also depend on each other by power law relations with universal exponents. In our model simulations, we have also measured the size of each family, i.e. the total number of individuals which belonged to this family during all its history. Then, we classified these families according to their sizes, counting how many of them presented just 1 individual (no descendents at all, the smallest conceivable size), how many presented 2 or 3 individuals (second smallest size), how many presented 4, 5, 6 or 7 individuals, and so on. We choose family size intervals increasing as the integer powers of 2, a traditional procedure usually adopted in order to improve statistics. The occurrence of families according to their sizes is plotted in figure 2, again a power law. A similar counting was performed half a century ago by Gutenberg and Richter [9], in what concerns the occurrence of earthquakes according to their intensities. The number of already extinct biological genera as a function of their lifetime [10] is another example. Many others can be found in [11].

Denoting by s the family size and by n their counter per size, our "experimental" data in figure 2 leads to

$$n = n_1 s^{-\beta} \quad , \tag{6}$$

where the new exponent $\beta = 1/2$ can be related to the previous one, $\alpha = 1$, by following the same coalescence theory. By fitting our data (dotted line in figure 2), we find $\beta \approx 0.50$ again in agreement with the theory. Normally, the various exponents α , β , etc, governing the universal behaviour of a whole class of systems are not independent, but related to each other by some simple relations.

One can argue that, in practical terms, the power law behaviour in equation (5) cannot continue eternally, once the number of alive families eventually drops to a single, definitive one. However, this is only due to the finite population size $P_0 = 1000$ of our example. Would we have considered a 10-fold larger population, and the waiting time for coalescence to a single family would also be multiplied by 10. Accordingly, 10-fold larger family sizes would appear, and the plot of figure 2 (or 1c) would suffer a translation to the right by adding one more 0-digit to each horizontal axis label. A further equivalent translation would occur for a 100-fold larger population, and so on. For an "ideal" infinite population, coalescence will never occur, and all family sizes and lifetimes would be expected to appear. In other words, the absence of a size scale gives rise to the corresponding absence of a time scale, and vice-versa. Other quantities also become scaleless. On the other hand, the finite-size of a given system necessarily limits also its characteristic scales of time, energy, mass, etc.

III) Lessons from a Simple Example

Let's return to the logistic map, equation (1), restricting ourselves to the intervals $0 < x_0 < 1$ for the initial seed, and 0 < a < 4 for the control parameter. This last restriction forces the dynamic variable x_t to stay forever within the same interval $0 < x_t < 1$ as the initial seed, in agreement with the population problem for which this map was invented [1]. The reader can easily program equation (1) on her/his pocket calculator,

and appreciate the many different dynamic behaviours one can get for the variable x_t , by choosing distinct values for the fixed control parameter a. Indeed, this is just what was done two decades ago by the now-famous physicist M.J. Feingenbaum. Experimenting with equation (1) on his pocket calculator, Feigenbaum discovered the so-called period-doubling route to chaos and the universal behaviour valid for a huge class of distinct dynamic systems [12]. This is another example of universality: precisely the same universal values obtained by Feigenbaum from equation (1) were later measured in a lot of real, different systems, as well as a lot of other, more complicated computer models. Reference [13] is a friendly reading about this discovery. Here, we will use the logistic map as a guiding example. One can follow all our reasonings through numerical tests performed on a pocket calculator or computer (indeed, I strongly recommend the reader to do so). The concepts and conclusions, however, are completely general, independent of equation (1).

A first observation is that the (normalised) population x_t vanishes for large values of t, when one chooses a < 1. On the other hand, x_t reaches a stable long-term value if 1 < a < 3. There is a transition between population stability and extinction, by crossing the critical point $a = a_0 = 1$. In both cases, stability or extinction, the attractor (i.e. the final destiny) is a single fixed point: $x^* = 0$ for a < 1; or $x^* = 1 - 1/a$ for 1 < a < 3. The transient time roughly corresponds to the number of iterations one needs to perform from the initial seed x_0 until reaching the final fixed point x^* , within the machine accuracy. The closer the control parameter a is to the critical value $a_0 = 1$, the larger is this transient time. The particular behaviour **at** the critical point will be discussed later. For the moment, let's choose a **near** 1. One can verify that x_t evolves according to an exponential decaying function

$$x_t - x^* \sim e^{-|a-1|t}$$
, (7)

where \sim means proportionality, and $|\ldots|$ represents the absolute value. This form can be obtained numerically, for instance by plotting the logarithm of $x_t - x^*$ versus t, verifying that this corresponds to a straight line (for large values of t), then measuring its slope and comparing the result with |a - 1|. We have already followed this numerical recipe in figure 1b and the corresponding equation (4). In the present case, alternatively, one can rewrite equation (1) as

$$\frac{\mathrm{d}y}{\mathrm{d}t} = -|a-1|y-ay^2 \quad , \tag{8}$$

by introducing a new variable $y_t = x_t - x^*$, where the difference $y_{t+1} - y_t$ was identified with the derivative dy/dt (this procedure is valid for large values of t). Provided $a \neq 1$, i.e. the system is **near** but **not at** the critical point, one can neglect the quadratic term ay^2 in (8), compared with the other, larger term |a-1|y. Then, the solution of this simple differential equation is just expression (7).

The exponential decay (7) allows us to define precisely the transient time

$$\tau = \frac{1}{|a-1|} = |a-1|^{-1} \quad , \tag{9}$$

as the time during which the difference $x_t - x^*$ decays by a factor of $e \approx 2.7$. Alternatively, we can resort to an analogy with a radioactive sample, for which τ corresponds also to the mean lifetime

$$\tau = \frac{\int_0^\infty dt \ t \ e^{-|a-1|t}}{\int_0^\infty dt \ e^{-|a-1|t}} = \frac{1}{|a-1|} \quad , \tag{10}$$

i.e. the time one needs to wait for the radioactive emission from a particular nucleus to occur, on average. In practice, τ is roughly the time one needs to wait for the radioactive sample become dangerless. In general, any system obeying an exponential decay has a characteristic time τ well defined by equation (10), representing its natural time scale, during which all important phenomena occur. One does not need to consider times much larger than τ , because they have no effect on the system behaviour. In other words, τ roughly measures the system's lifetime, after which all activities cease.

Nature was kind enough to choose the exponential mathematical form for radioactive decays: because of that, the integrals in equation (10) converge, and we get a **finite** value for τ (maybe large, but finite). This is not the case for other dynamic systems at critical situations, for instance the logistic map with $a = a_0 = 1$. In this case, one can no longer neglect the quadratic term y^2 in equation (8), because the other term |a - 1|y vanishes, and the solution of this differential equation is now the power law decay

$$x_t - x^* \sim t^{-1}$$
 , (11)

instead of the exponential form (7) valid for non-critical situations. Trying to replace the exponential form appearing twice in equation (10) by the power law (11), one would be in trouble because the integrals no longer converge to finite values. Accordingly, one can no longer perform the division in equation (9): the transient time is now **infinite**. These critical dynamic systems do not have a characteristic time: all time scales are important. Nature is not always so kind as in the case of radioactivity. For instance, the probability of having an earthquake decays for increasing intensities, obeying a power law (in this case, earthquake intensity replaces the time). This means that there is not a characteristic earthquake intensity beyond which the probability of occurrence can be neglected. All intensities are expected to occur some day. Would this distribution be an exponential, engineers could design buildings strong enough to support the characteristic intensity, and earthquakes would be not such a big problem as they are. Unfortunately, this characteristic earthquake intensity does not exist, according to the power law behaviour reported by Gutenberg and Richter [9]. Again, due to the fact that the Earth itself is finite, some earthquake intensity upper bound certainly exists, beyond which the Gutenberg and Richter law is no longer valid. However, nobody knows what could be this finite-size characteristic intensity: large, extremely destructive earthquakes could occur still below this unknown bound.

The distinguishing feature of the isolated critical point $a = a_0 = 1$, among all continuous distributed possibilities 0 < a < 3, is the eternal transient followed by the dynamic system, equation (1). Mathematically, instead of an ordinary exponential decay which limits the system history to a finite lifetime, at critical situations one has power law decays without time limits. This mathematical feature is completely general for all dynamic systems, and is indeed taken as the definition of criticality. At these situations, the system presents **long-term memory**, i.e. its current state is a consequence of many features accumulated during a long past history. Many "strange" properties appear only at these situations. For instance, a widespread class of numerical devices called relaxation methods consist in finding the true solution of some problem by gradually performing small modifications (or mutations) on an initially posed approximation. It is a dynamic path to the solution. In principle, it would be enough to design a dynamic rule whose attractor has been previously shown to coincide with the desired solution. However, if the chosen dynamic rule is critical, the user will be in trouble. First, because the critical slowing down forces the computer time to be prohibitively large. Second, and much worse, because the final (finite precision) numeric answer will be wrong! The reader can verify both characteristics within the logistic map with $a = a_0 = 1$. In particular, in case the reader is patient enough to wait for convergence, the final reached value x_{∞} will differ from the right answer $x^* = 0$ by half the digit precision of her/his pocket calculator — half of the digits will be wrong because of the square in equation (8). Also, the wrong digits depend on the initial seed introduced at the very beginning, a symptom of the long-term memory.

The concepts of short *versus* long-term memory can be better understood by performing a simple exercise on both equations (4) and (5): try to express the next value g_{t+1} (or f_{t+1}) as a function of only the current one, g_t (or f_t). In the exponential case (4), this is possible, and the result is simply $g_{t+1} = e^{-\lambda}g_t$. This means that g_0, g_1, g_2, \ldots is a Markovian sequence, i.e. each term depends only on the previous one, not on remote past terms like g_0 . The system "remembers" only one past step. In the power law case (5), however, the exercise is fruitless: the best one can do is to write $f_{t+1} = [f_t^{-1/\alpha} + f_1^{-1/\alpha}]^{-\alpha}$, i.e. the next term f_{t+1} depends not only on the previous one, f_t , but also on the very first, f_1 . The system always "remembers" its birth, no matter how old it is. Note, however, that both g and f are quantities concerning the same dynamic system, namely our toy population model treated before. Note also that the system itself is Markovian, because the next generation is constructed exclusively from the current one. Thus, even a Markovian system can exhibit long-term memory behaviour concerning some particular quantities which follow power law decays. Other exponentially decaying quantities could also coexist within the same system, for which the memory is instead short term. Of course, this simultaneous occurrence of both forms is not possible for simple systems as the logistic map, which presents only one varying quantity, x_t : for some values of the fixed parameter a its memory is short, as in equation (7), for others it is long-term, as in (11).

Critical, long-term memory situations normally occur at precisely tuned transition points where the system behaviour changes qualitatively, such as the temperature above which a magnet can no longer retain its spontaneous magnetisation, or a fluid can no longer be found in both (coexisting) liquid and vapour forms. These examples are static, in the sense that thermal equilibrium is supposed to be already reached for both the magnet and the fluid: universal power laws in space (instead of time) govern the system behaviour. Of course, also the path previously followed towards thermal equilibrium was governed by a universal power law decay in time. As before, the term "universal" means the same numerical values for some characteristic exponents, like the -1 in equation (11), holding for completely distinct systems. Both the fluid compressibility and the magnetic susceptibility diverge at the critical point according to the same critical exponent, valid for a huge class of fluids and magnets. This universality is a consequence of the lack of both a characteristic time and length scales: most microscopic or short term details are not important for those scaleless (critical) systems. Often, a very simplified model is enough to reproduce, even in a quantitative sense, the complex behaviour observed in a much more complicated, real system. For instance, as we have already treated, simplified mathematical models based on Darwin's principles could allow one to follow evolution features step by step, in real time — see [14] for a review.

The theoretical explanation for the universality observed in equilibrium critical phenomena is due to the Nobel laureate K.G. Wilson [15]. Concerning critical dynamics, an equivalent complete theory is still lacking. Nevertheless, it is well known that systems evolving according to a critical dynamics (i.e. a time decay to equilibrium according to a power law) normally also present static critical behaviour (i.e. power law relations between quantities other than time). Due to the long times involved in such situations, the dynamic critical behaviour of many systems can only be observed indirectly, through these other timeless power law relations. Biological evolution is an example, where the already quoted statistics of mass extinction are found to obey power laws, both from fossil records data [10] and mathematical models [16]. Earthquakes intensity distribution is another example. In most cases the dynamical criticality is the fundamental one, although hard or impossible to follow step by step. The long-term memory of the system is responsible for its whole critical behaviour. Although very interesting and important, the universal features found in critical systems are not directly linked to our main argument concerning evolution strategies. Before entering into this point, let's stress that many dynamic systems are able to adapt themselves according to the environment, by self organizing some of their own control parameters, with no need to resort to external tuning mechanisms. In particular, a very common feature is the so-called self organized criticality, where the system keeps itself at critical situations [17]. Among others, biological evolution was proposed to belong to this class of system [18] (see also [19] for an excellent explanation).

Back to the logistic map, there are other critical points. The next one is $a = a_1 = 3$, beyond which the attractor is no longer a single fixed point. Instead, for $3 < a < 1 + \sqrt{6}$ the attractor is a cycle with period 2, i.e. a sequence of two alternating values $x_1^*, x_2^*, x_1^*, x_2^*, x_1^*, x_2^*, x_1^*$ x_2^* The next critical point is $a = a_2 = 1 + \sqrt{6} \approx 3.449$, after which the attractor become a 4-period cycle. There is a cascade of critical points $a_0, a_1, a_2, a_3 \ldots$, where successive period doublings occur. This cascade ends at $a_{\infty} \approx 3.570$, after which one can find chaotic behaviour, with no longer periodic repetitions. Even inside the chaotic region $a_{\infty} < a < 4$ some periodic "windows" appear again, as one just after $a = A_3 = 1 + \sqrt{8} \approx 3.828$ where a period-3 cycle holds. Thus, one has a series of transitions from one kind of attractor to another (vanishing population, fixed point, periodic cycles, chaotic attractors, oddperiodic cycles, chaotic again, and so on). The system is critical only at these transition points, but still presents exponential decays (and thus finite transients) in between two such transition points, including the chaotic intervals. The chaotic behaviour concerns the diverging character of two initially neighbouring trajectories, having nothing to do with how fast both reach the attractor. In what concerns the transient lifetime, both regular (fixed points or periodic cycles) and chaotic systems are not critical, both approaching the corresponding attractor exponentially fast, according to short term memories. So, we are not interested in classifying dynamic systems in chaotic or regular, but in distinguishing the very particular critical, long-term memory situations among the whole set of possibilities. For the logistic map, for instance, these situations occur only at the very precise values $a_0, a_1, a_2, a_3 \ldots a_{\infty} \ldots A_3 \ldots$ of the control parameter. Figure 3 shows the so-called Lyapunov exponent measuring the exponential rate of convergence (negative values) or divergence (positive) of two initially slightly different trajectories, as a function of the control parameter a. The critical situations correspond to zero Lyapunov exponent, at the particular positions where the plot crosses (or touches) the horizontal axis. At these situations, the rates of convergence or divergence no longer follow the fast exponential way. Instead, it is replaced by the power law way, and further mathematical analysis [20] is needed. This analysis is similar to what we have done by keeping explicitly the term $-y^2$ in equation (8) for the particular case a = 1, obtaining the power law (11). For most values of a, however, the system is either regular (below the horizontal axis, in figure 3) or chaotic (above), both cases corresponding to non critical, short term memory behaviour.

IV) Why do Evolutionary Systems Stick to the Edge of Chaos

Evolution is an eternal, endless process. Thus, it cannot occur in a closed, finite system because size limits correspond also to time limits, according to our previous analysis. Any dynamic activity occurring within a finite system completely isolated from the rest of the universe will eventually cease, after a finite time. This ephemeral activity is rather a transient before reaching final static equilibrium, not evolution. A single species never evolves in isolation, it is always under the influence of other species. Nevertheless, it is hard to conceive the whole universe as the evolving system to be studied. The practical approach is to follow only the behaviour of a small part of the universe. Then, one needs to consider also the environment in which this finite system is embedded. Such a system is finite, but not closed. Instead, it is an **open dynamic system**, constantly fed from outside with mass, energy, heat, information, etc. It also constantly throws away these same entities, after processing them in some way. It is a **dissipative** system. One needs to have always in mind that this separation of a small part of the universe is only a working procedure, an artificial approximation which could be very good up to certain limit scales of time, size, energy, etc. Beyond these limits, this approximation fails, and some parts of the former "environment" must be included into a new, enlarged "system" to be studied.

Being dissipative, this kind of dynamic evolution tends to converge to some attractor, becoming irreversibly trapped there forever. One of the dissipated quantities during this process is the entropy, which measures the number of available states, related to the current options the system could follow from now on. Considering the whole initial space of states, only a shrinking subset of them remain available, as time goes by. The system continuously looses its ability to explore the whole space of states. Eventually reaching the attractor, it becomes restricted to a subspace of the whole initial set of possibilities. Compared with the whole, this subspace is a null measure set, like a needle in a haystack: by tossing a random state among all the initially available options, the probability to become inside the final subspace is null. In other words, the dimension of the final subspace of states is smaller than the dimension of the initially available space, like a line inside a plane, or a plane inside the 3-dimensional space. Note that such a dimensional reduction is much drastic than a finite-fraction decrement, because what remains at the end is a **null fraction** of the whole. The final attractor may also be a fractal, i.e. it may have a non-integer dimension, anyway smaller than that of the whole space.

Within the mathematical description of evolutionary systems, the dimension of the space of states is normally very high, as we have exemplified in section I. Even the simplest approach of counting the frequencies of all possible alleles for each gene, storing the results on an array, would correspond to a high dimension, namely the total number of possible alleles. In order to study also correlations between these alleles, a larger vet dimension arises. By storing separate informations concerning each individual, as in our population dynamic model discussed before, the dimension increases even more. As time goes by, the mere extinction of a single allele would correspond to a dimension reduction with its huge and irreversible trapping effect. Concerning evolution strategies, such a dissipative dynamics is not convenient. Indeed, after being trapped into the tiny attractor, the probability of exploring the remainder set of possibilities (searching for forms better than the current one) is null. On the other hand, evolution within a limited size system cannot be described by a non-dissipative, conservative dynamics which theoretically could solve the problem by keeping it forever visiting all possible options. This situation would correspond to a closed object, isolated from the rest of the universe, not to a finite-but-open dynamic system we need in order to take the environment into account.

How Nature solves this puzzle? Let's consider a wonderful example, extracted from [21], an amazing text which treats exactly the same subject as the present work, namely the importance of diversity, from a completely distinct (and much more interesting) point of view. A recessive genetic disease affects homozygous individuals carrying twice the defective allele. An example is phenylketonuria, for which the current frequency of the defective allele p in France is estimated to be x = 0.95%. Let's suppose that all homozygous pp individuals die before reproduction, and that heterozygous Np individuals do not present any handicap at all (N represents the normal allele). It is obvious that the frequency x of this harmful allele p will decrease, eventually becoming extinct. However, only after 6 generations, i.e. one and a half century from now, the current frequencing from the frequency drop.

to x = 0.90%. Moreover, after 95 generations, i.e. more than twenty centuries from now, the defective allele frequency would drop to x = 0.50%, still a very small "improvement". This extremely slow time decay for the frequency of a defective allele could seem paradoxical, if one adopts the restricted reasoning of considering the evolution of this allele alone, separated from the whole set of genes within each individual. Natural selection, however, acts on each individual as a whole, according to its global characteristics. Within this example, pp individuals die but the much more numerous Np individuals remain untouched, avoiding the extinction of allele p (by delaying it *sine die*). Taking the opposed reasoning of considering the survival of the whole species, one can argue that instead of a paradox, the slow frequency decay of p is just the expected behaviour, because this allele could have some beneficial function in some far future, under unpredictable modified environment conditions. Indeed, some examples of imune behaviour against some diseases are known to hold among individuals affected by other genetic diseases. According to this reasoning, Nature adopts the precaution of preserving these (nowadays) "bad" genes.

The figures given by Albert Jacquard [21] concerning the frequency x of phenylketonuria allele p came from the Hardy-Weinberg fundamental law of genetics. He simply supposes random parent pairings, according to the frequencies $(1 - x_t)^2$ for NN and $2x_t(1 - x_t)$ for Np individuals, at the current generation t, composing from these pairings the next generation. For instance, one can sum up the probabilities corresponding to all pp-offspring possibilities, equating the result to x_{t+1}^2 , from which one can obtain the frequency

$$x_{t+1} = \frac{x_t}{1 + x_t} \cong x_t (1 - x_t)$$
(12)

for the p allele at the next generation t + 1. The Lyapunov exponent of this equation is exactly zero, i.e. it corresponds to a critical dynamics. The approximation on the righthand side of (12) is valid for small values of x. It is amazing, but not a surprise, to verify that it is just the logistic map (1) **at its critical point** $a = a_0 = 1$. Thus, Nature's strategy to avoid the extintion of p consists in adopting a critical dynamic evolution for it, according to which its frequency power law decay is very slow, following an **infinite** transient time. Within the genetic high-dimensional space of the evolving population, the particular direction corresponding to p allele remains always available, due to a small but never null occupation. The critical dynamics avoids the dimensional reduction which would be caused by an eventual p extinction. Under a practical point of view, as the population is finite, the extinction time for p would be also finite, nevertheless proportional to the average number of individuals, as we have already analysed, and so very large.

For evolutionary purposes, it is imperative to avoid the tiny attractor provided by the

dissipative dynamics, and this is an automatic feature at the critical situations for which the system evolves forever in transients. The evolutionary system naturally tune their internal parameters in order to stay at such a critical situation. The tiny attractor can be interpreted as the current "best" form, in singular. However, the selection mechanism needs diversity in order to obtain the current "best" forms, in plural, i.e. some enlarged neighbourhood around the tiny attractor. Critical dynamics provides just this feature: one stays forever **near** the current "best", but never trapped into their tiny cage. In this way, any environment modification which slightly changes the "best" position of the space of possibilities, is likely to match some other neighbouring form kept alive together the former "best". Any eugenic attempt to de-tune the evolving system out from its critical situation, performed in order to accelerate the selection of the "best" form, again in singular, could be disatrous [22]. Indeed, this procedure would replace a broad, critical distribution of many coexisting forms by a sharp distribution of only one "best" form. The de-tuned non-critical dynamics drives the system to this optimized, single form, according to a fast exponential decay. This process could be considered an efficient, short term optimization strategy, but it definitely does not correspond to evolution. The selection mechanism cannot proceed from this point on, due to the lack of diversity: the now-extinct neighbouring forms could miss under some future environment change. Critical dynamics provide the degree of diversity the selection process needs. If the dynamic process is not critical, one has no diversity, thus no selection, and finally no evolution.

In short, evolutionary systems stick to critical situations (the edge of chaos), because within all other possibilities (regular or chaotic regimes) they rapidly become trapped into low-dimensional attractors, loosing diversity. This trapping feature forbids the system to explore the whole set of available possibilities inside its higher-dimensional space of states. Although being of fundamental importance, this feature is only the beginning of the whole story about evolutionary strategies. In order to design an efficient dynamic evolutionary strategy, one must first be sure to stay always at critical situations. But this is not enough! By simply following a critical one-dimensional trajectory, one would not explore the whole space of possibilities. It would be very hard to explore a high-dimensional space by following one-dimensional trajectories: infinitely many of them must be tested. In order to overcome this difficulty, a lot of alternative optimization strategies exist: some famous are simulated annealing [23], its generalizations [24] and genetic algorithms [25]. Among these and many others, we will quote only the one Nature has chosen for biological evolution, namely the endless mutation/selection approach discovered by Darwin more than a century and half ago [2] — see also [26].

According to Darwin, random mutations occur during reproduction, the offspring

being slightly different from their parents. Translated to our language, and considering only asexual reproduction for simplicity, this means a single point (the parent) in our space of possibilities generating many other neighbouring points (the offspring), in a branching process. Considering the offspring's offspring, and so on, this would generate a ramified tree eventually covering the whole space of possibilities in parallel, optimizing the search for better forms. However, this would cause population explosion, and some branches of this tree are actually cut by natural selection, i.e. the individuals best adapted to the current environment have more offspring (growing branches), while the worst adapted ones tend to die without generating offspring (dangling branches). Instead of a single onedimensional trajectory, this tree is a low-dimensional object avoiding populations explosion, the growing branches exploring the most promising parts of the whole space of possibilities. The dimension of this tree is itself a varying quantity, allowing the occurrence of suddent large events. Of course, this evolution strategy would not work at all if the dynamic would not be a critical one. Thus, the natural selection process also acts in driving the dynamic evolution to critical situations, avoiding trappings. This can be done in many ways. Within an evolving population, for instance, the average birth rate (equivalent to the logistic map parameter a) can be self-organized into critical values. Other parameters can also play the same role, and after some external modification, they can be re-tuned according to the new environment conditions. This automatic re-tuning mechanism towards criticality introduces a new level into the whole dynamic process. However, this re-tuning must be performed according to a fast rate, not to be confused with the low rate observed when criticality is already achieved. Once more, Nature is challenged to deal with both exponential (fast) and power law (slow) decaying rates.

As we have already discussed, the reasoning of last paragraph is not complete. The particular evolving species we considered is not alone. Think about the coevolution of many species. The space of possibilities where one particular species evolves is not a static landscape. This search is a branching process performed over an **evolving landscape**, because the environment itself depends on the evolution of other species. Thus, the search for better forms is an endless process: one can be comfortably sit on an optimum state today, i.e. the best possible situation among the whole neighbourhood, but tomorrow this same state may be worse than some neighbouring competitor, due to the slow movement of the underlying landscape. Under the global point of view, the above quoted re-tuning mechanism of parameters within each species is actually an internal job belonging to the evolution of the global system. They are not parameters controling the behaviour of each species separately, they are dynamic variables internal to the whole set of coevolving species. Under a larger yet point of view, a whole system of interacting species, for instance

the ones living in Madagascar, is also influenced by other similar systems. Thus the very particular set of "parameters" allowing for the odd wildlife observed in Madagascar is only, actually, part of the current state of the flora and fauna evolving in larger Africa. Moreover, the oddness of Africa itself is part of the current state of the evolving Earth or Gaia, again increasing once more the time and size scales, and so on (instead, we would have written earth and gaia). That is why evolution occurs in a scaleless, critical way, both in time and space.

Together with random mutations and natural selection, this self-organized criticality in now considered as a third leg needed to keep stable the basis for biological evolution theory, as reviewed in [19]. Although catastrophic events are crucial for the behaviour of critical dynamic systems, they do not play any special role as compared to small events (both follow the same scale-free probability distribution power law). However, the study of this amazing subject goes beyond the scope of the present work. Indeed, only recently it was recognized as an inportant new scientific deep stuff, as beautifully presented in [11]. The important role played by extremal dynamics is reviewed in [27].

Nevertheless, this third leg is not a further ingredient, being a consequence of the other two. Mutations and selection act on the individual, microscopic level, following a gradual smooth rate. However, it is not correct to conclude that their effect on the macroscopic level of the whole population would be also gradual and smooth. This wrong conclusion is based on the usual linear reasoning according to which the sum of small increments will be also small. However, this reasoning does not hold when one adds infinitely many small increments, whose sum may be very large. This is just the case of long-term memory systems, which "remember" infinitely many small steps from the past. Evolution is not a linear system. Indeed, this is an old puzzle since Darwin, due to the fact that fossil data show some catastrophic biological extinctions as well as periods of large speciation activity, the so-called punctuated equilibrium [28]. Due to the long-term, critical memory, small modifications at the microscopic level can accumulate themselves during long periods of time, suddently overflowing into a fast catastrophic event. This feature, however, is not due to a third, independent ingredient which would be missing in original Darwin's principles. On the contrary, criticality is a long-term consequence of the short-term mutation/selection process repeated ad infinitum. Of course, the idea of catastrophic, fast events being a consequence of infinitely many small steps, accumulated during an infinite past, has emerged only after computers allow us to follow evolution models step by step, in real time. Darwin could not imagine such a non-linear mechanism at his time, not because it would not be a consequence of his principles (it is!), but because he missed the right instrument, i.e. the computer, to drive his imagination a little bit further.

A very common argument against evolution theory is based on some estimates of the time needed to get the biological complexity observed nowadays, comparing them with the age of the universe. The counter-argument is that, in performing such estimates, one cannot take into account all the set of potential possibilities, but only the ones already selected by the critical branching process, at each step. As a consequence, the estimated times are actually much smaller [19].

V) Conclusions

We have proposed here that evolutionary strategies must follow critical dynamics in which slow power law decays replace the wide spread fast exponential way to reach equilibrium. Equilibrium situations, even in chaotic systems, represent a tiny fraction of the whole set of possibilities. Thus, any system which rapidly reaches its equilibrium looses the chance of searching for new, better forms in the high-dimensional space of possibilities. On the other hand, by following a critical dynamics, the system actually never reaches its equilibrium situation, staying forever in transients. This opens for the system the chance of eternal search for better forms, i.e. opens the whole space of possibilities instead of only the tiny fraction represented by the equilibrium states. This is a pre-condition for any efficient evolutionary strategy, and can be fulfilled by self-organization of the parameters controling the system's behaviour. The evolutionary strategy itself starts at this point (the dynamic criticality already assured), and deals with the problem of efficiently walking around a high-dimensional space through low-dimensional trajectories. Many such strategies exist, including the biological one discovered by Darwin, which naturally leads to a critical dynamics. The important here is that none of these strategies would be efficient if the corresponding dynamic rule would not be a critical one.

Natural selection is based on the available diversity of options. Both regular and chaotic dynamics drive the system quickly to its tiny attractor, where diversity is then irreversibly lost. Critical dynamics, on the other hand, keep the system forever **near** but **never restricted** to the tiny attractor, providing the necessary diversity which allows the selection process to goes on, eternally. In practical terms, for a finite system, "eternity" means some large time of the same order of magnitude of the populations itself. Within a non-critical dynamics, however, any activity ceases much before such a time, independently of the population size.

Aknowledgements

I am indebted to Suzana Moss, Jorge Sá Martins, Kris Stenzel, Américo Bernardes, Antônio Toledo Piza, Per Bak, Alaor Chaves, Jean Lobry, Dietrich Stauffer and Moysés Nussenzveig for helpful discussions and critical readings of the manuscript. This work was partially supported by Brazilian agencies CAPES, CNPq and FAPERJ, and dedicated to the late J.J. Giambiagi.

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Figure Captions

- fig. 1 Time decaying of two different quantities f and g, both concerning the same population dynamics. Each founder individual at generation t = 0 inaugurates a family, and all its descendents carry its family name: f (circles) measures the still alive fraction of families. After thousands of generations, only one family remains alive, all current individuals being descendents from the same family founder, Eve. The correlation (similarity) between Eve's genome and all other individuals were also measured. Genetically, Eve is more similar to its own descendents than the average among all individuals of the same generation. The difference g (pluses), however, decays with time much faster than the number of families. Genetic diversity evolves very fast, even within a very slow family number decay. 1a) linear scale in both axis; 1b) vertical logarithm scale, same data; 1c) logarithm scale in both axis, same data again, within a much larger time scale.
- fig. 2 For the same population dynamics corresponding to figure 1, we measured the number n of families classified according to their sizes s (total number of individuals sharing the same family name).
- fig. 3 Lyapunov exponent for the logistic map, equation (1), as a function of the control parameter a. Below, a detail inside the interval 3 < a < 4. This dynamic system is regular below the horizontal axis (negative exponents), and chaotic above (positive). Instead, the present text concerns only the relatively few critical situations where the plot crosses (or touches) the horizontal axis.





figure 1a



figure 1b









