Evolutionary Computer Simulations

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Abstract

Computer modelling for evolutionary systems consists in: 1) to store in the memory the individual features of each member of a large population; and 2) to update the whole system repeatedly, as time goes by, according to some prescribed rules (reproduction, death, ageing, etc) where some degree of randomness is included through pseudo-random number sequences. Compared to direct observation of Nature, this approach presents two distinguishing features. First, one can follow the characteristics of the system in real time, instead of only observing the current, static situation which is a long-term consequence of a remote past completely unknown except for some available fossil snapshots. In particular, one can repeat the whole dynamical process, starting from the same initial population, using the same randomness, changing only some minor contingency during the process, in order to study its long-term consequences. Second, evolution necessarily follows a critical dynamics with long-term memory characteristics, equivalent to the long-range correlations responsible for the well known universality properties of static critical phenomena. Accordingly, some strong simplifications can be applied, allowing one to obtain many characteristics of real populations from toy models easily implementable on the computer.

Key words: evolution, computer simulations, critical dynamics
What nowadays we call evolution — the theory describing how living beings behave under permanent changes, the whole dynamical system never reaching any final, absorbing state — was introduced by Jean Lamarck [1] two centuries ago. He also invented the name “biologie”. According to him, the many currently observed biological species are not static, independent entities, but derive from ancient ones after small modifications accumulated during very long times. Lamarck fell into disgrace under the religious/conservative power dominating his lifetime. Reference [2] presents an amusing and intriguing discussion concerning these subjects. The mechanism leading to this forever-changing scenario is Charles Darwin’s natural selection [3]. Each individual inherits the characteristics of its parents, with some small modifications, being similar but not identical to neither the parents nor the siblings. Among the latter, the ones better adapted to survive under the current environment are more likely to breed, their offspring carrying the naturally selected traits from their grand-parents.

A simple way to interpret evolution is to imagine the high-dimensional space of all possible living forms. Each individual is a point in this space, and their offspring are neighbouring points. Considering asexual reproduction, for simplicity, each offspring can also produce its own offspring, and so on, according to a branching dynamical process. Some selected branches of the resulting tree continue to grow further, whereas others are dangling ends without offspring, avoiding population explosion. Under a large-scale overview, a snapshot of this space of all possible living forms shows a very sparsely, highly inhomogeneous occupation pattern: many neighbouring occupied points form a cloud localised in some small region, separated from other equivalent clouds. Each such a cloud is a species. Following such a cloud during a short-term time interval, i.e. some few generations, its many occupied points are continuously replaced by other neighbouring points: the whole cloud seems to stay immobile. Only under a long-term point of view, i.e. after a large number of generations, one can observe the extremely slow movement of the cloud as a whole. Tracing back the movement of two nowadays separated clouds, one would discover that both derive from the same ancient, possibly no-longer existing, parent cloud, the so-called speciation process. Thus, evolution occurs according to a branching process not only under the local point of view of each individual and its offspring, but also under the much larger scale of species as a whole.

Under a coarse-grained point of view, the same space of all possible living forms can be re-interpreted: now each cloud (species) corresponds to a single slowly moving Point (capital P to distinguish it from a single individual). Neighbouring occupied Points form a Cloud, i.e. a set of neighbouring species, called a genus. Stretching once more the scale, each genus can be interpreted as a single PPoint (double PP, since my keyboard does not
provide anything larger than capital letters) within the same space of all possible living forms. A CCloud of PPoints is called a family. An order is a CCloud of PPPPoints. A class is a CCCCCloud of PPPPPPPoints. Note that each step along this hierarchical sequence of scalings involves not only larger and larger scales of length (distances measured within the space of all possible living forms), but also larger and larger scales of time!

For statistical physicists, the above description has certainly a feeling of “déjà-vu”. It is just the basic reasoning used in order to study critical, scale-free phenomena, the fundamental concept being the renormalisation-group theory [4] for which Kenneth Wilson was awarded with the 1982 Nobel prize. These phenomena are normally described by power-law decays of the various correlations as functions of both length and time. Indeed, there is a lot of evidence in favour of this scenario also governing biological evolution (see, for instance, [5] and original references therein). However, the above iterative-scaling reasoning (individual – species – genus – family – order – class) has only an illustrative purpose.

An argument showing that evolution necessarily follows a critical dynamics was presented in [6]. In short, it is as follows (six paragraphs). One always needs to separate some part of the universe (a species, a geographic region, etc), in order to study its evolutionary behaviour. This artificially separated part cannot be considered a closed object, because it is always under some influence of the rest of the universe, its environment. Thus, the system under study must necessarily be considered as an open dynamic system. Some ingredients (mass, energy, information, etc) feed continuously the system, and in some way are processed therein. Also, as a by-product of this procedure, the same kind of ingredients are continuously thrown out. That is why the dynamic evolution of such a system is always dissipative, irreversible: the would-be final situation, i.e. the attractor, is a low-dimensional object, a null measure set compared to the whole initially available set of possibilities. Among the many directions of the high-dimensional space of all possible living forms, only a few remain available after the system is trapped forever inside its tiny attractor. After that, all other directions are extinct. This is not a profitable feature, in what concerns evolution by natural selection, which demands the eternal possibility of visiting new forms.

The difference between the so-called regular or chaotic behaviours is the following. Starting from two slightly distinct initial conditions, the distance $\Delta$ from each other will evolve as

$$\Delta(t) \sim e^{\lambda t}$$

as the time $t$ goes by. The so-called Lyapunov exponent $\lambda$ may be negative, which corre-
sponds to the regular case: both trajectories eventually converge to a single one, a simple attractor. Otherwise, for positive values of $\lambda$, the system is chaotic: both trajectories diverge from each other inside a complicated object (anyway a low-dimensional one), usually called a strange attractor. In both cases, regular or chaotic, after a finite transient time $\tau \sim |1/\lambda|$ the system becomes trapped, loosing forever its ability to explore the whole set of possibilities. Again, evolution is not compatible with this scenario.

The question now is: how to preserve diversity of options, i.e. the ability to reach any part of the high-dimensional space of possibilities, while the dynamic process itself traps the system more and more close to a low-dimensional destiny? It is not a simple matter of loosing some fraction of the whole space. It is worse than that: one looses entire directions! Nature is smart enough to avoid this catastrophe by postponing it forever: Nature “chooses” $\lambda = 0$, the complex, critical case. The above equation misses sub-dominant terms (not-shown), which in this case become the dominant ones imposing a much slower decaying rate. Normally they are power-laws, sometimes slower-yet-decaying relations, anyway lacking any typical time (and length) scale. The difference is not a mere quantitative one, it is rather qualitative: the difference between any finite time interval, no matter how long it could be, and eternity. In order to better understand this concept, consider an analogy with a radioactive decay described just by the above equation: $\tau \sim |1/\lambda|$ is the so-called waiting time, the time one needs to wait for the decay of some particular nucleus, in average. After some finite time interval (say $2\tau$, $4\tau$) the whole sample looses its radioactivity. In other cases for which this characteristic scale is lost, i.e. $\lambda = 0$, the system’s activity never ceases. This is just what evolution needs.

Here, the precise mathematical meaning of the word never is the following. For an exponential decay, the waiting time does not depend on the system’s size: one can make the system larger and larger, and the waiting time will stay at the same finite value. For the scale-free case $\lambda = 0$, however, the waiting time grows indefinitely for larger and larger systems. In other words, the lifetime of a critical system is limited only by its size. The lack of any typical size scale implies the corresponding lack of any typical time scale, and vice-versa. For purists, another reasoning leading to the same conclusion follows. In order to keep finite the minority number of individuals carrying some rare trait, avoiding its extinction, one needs to keep alive a large enough whole population. Tolerating some fixed, large-but-finite extinction time $T$, one needs to keep a population which increases exponentially with the extinction rate $|\lambda|$. For the scale-free case $\lambda = 0$, however, it increases according to some other slower-than-exponential rate, say a power-law, which requires a not-so-large population. In this case, extinction can always be postponed beyond $T$ only by keeping some moderate population, i.e. effectively forever. A nice example
of how Nature adopts this strategy is the extremely slow rate of extinction observed for recessive diseases [7,6], where diploidism plays a major role.

Nature does not choose anything. In reality, natural selection itself tunes to the critical, complex case $\lambda = 0$: only those situations avoid their own extinction, among all other possibilities which die out along the process. That is why so many examples of fossil data seem to agree with this scenario: the other possibilities, if any, did not survive long enough. Also, the Lyapunov exponent $\lambda$ is not just one, their number coincides with the system’s dimensionality. Natural selection tunes as many of them as possible to the critical value $\lambda = 0$.

Another interesting interpretation of the same concept, namely the preservation of diversity, is as follows. In separating the system under study from its environment, only an artificial working procedure, one needs to realise that the environment itself is not constant, that it also evolves (normally under a slower rate). The attractor of the dynamical process can be viewed as the current best option. However, future environment modifications will slightly displace this optimum to neighbouring positions. Thus, evolution needs to keep the current attractor’s neighbourhood always populated, in order to fit these unpredictable future displacements. In other words, some degree of diversity near but outside the current attractor must be kept forever. This feature is automatically provided by critical dynamics, according to which the system continuously approaches its attractor but never reaches it. Evolution is not an eugenic optimisation process where only the current “best” is selected to survive: this would forbid natural selection itself to proceed, due to the consequent lack of future options. Any non-critical dynamics, where the “best” form is reached after some finite transient time, rules out evolution. Indeed, according to [8], eugenics leads to extinction.

Probably, the reader is not confortable with the expression “space of all possible living forms”, in which all previous reasoning is based. How to define such an object? The first to address this question was Gregor Mendel [9], the founder of genetics, in his famous two lectures of 1865. By breeding sexually reproducing plants, he discovered that particular individual traits are inherited as a whole, all or nothing, yes or not, 1 or 0. Each individual inherits half of its traits from the father, half from the mother. Mendel provided the basic “software” theory for genetics. His work was completely forgotten for decades. Much later, chromosomes and diploidism were discovered, confirming his original findings and providing the “hardware” for parent’s inheritance mechanism. Mendel’s “traits” were then physically associated with genes, small pieces of the chromossomes. Since then, it becomes clear that characteristics acquired during the lifetime of an individual are not genetically passed on to its offspring. Before that, missing this molecular-based genetic mechanism,
both Lamarck and Darwin did not ruled out the possibility of passing acquired traits to the offspring (which indeed occurs, but not genetically, except for rare cases of damaged germ cells).

Thanks to Mendel’s idea, one can easily conceive an array of bits 1 or 0, each one meaning whether some particular gene is present or not in a particular individual belonging to the population under study. Thus, each conceivable individual is represented by such an array, its total number of bits being the dimension of the quoted “space of all living forms”. Indeed, sexually reproducing individuals must be represented by two bit-arrays each, one inherited from the father, other from the mother. Also, the same gene can appear in a few different forms, alleles: in order to deal with this further complication, one can simply allocate more than one bit per gene. Anyway, our “space of all living forms” is now well defined: its elements are bit-strings, each one corresponding to a possible existing individual (its “genome”). The population dynamics corresponds to the evolution of a variable number of these individuals which are alive at each time step \( t \). The dynamic evolution follows some rules concerning birth, death, interaction with the environment, etc. All biological issues are included in such rules. The first mathematical description of evolution based on this bit-string representation was the famous Eigen model [10].

At this point, after a long and dangerous digression over other fields of knowledge, concerning which I hope the reader did not notice my complete ignorance, I am back to the main subject of the title. Being a computer physicist without access to powerful computers, I learned many tricks useful to save computer time and memory. One particularly important strategy is to operate directly on the bits of each computer word (a sequence with 32 bits), through bitwise, parallel operations [11]. These tricks allow one to perform incredible, otherwise impossible jobs. Computer modelling consists simply in programming such rules on the computer, let them work as time goes by, and observe the outcome. As biological issues are an enormous source of complications, one needs to simplify these rules. In reality, one plays with toy models, opening the way for criticisms related to reductionism. On the other hand, they are very convenient in order to analyse which ingredients are really important and which are not, concerning particular population features. Within a complex subject as biology, this approach could contribute with some light for questions particularly difficult to answer by other means, moreover due to the advantages of following the evolution in real time and the possibility of repeating the whole history under controlled contingencies.

An example is a conjecture raised by Stephen J. Gould [12]: would some contingency have occurred a long time ago, even a small one, slightly different than the historical truth, then we could observe nowadays a different scenario concerning the current existing
species. The true evolutionary tree historically followed since the onset of life on Earth is not the only possible one, many others could also have occurred. Obviously, this issue cannot be verified by observation, however, it can easily be simulated on computers in the way described above. There is a set of arguments against evolution based on probabilistic estimatives of the time needed to reach the enormous biological complexity we can observe nowadays, resulting in values many orders of magnitude larger than the Universe age! However, one needs at least to divide these estimatives by the number of possible alternative scenarios, not just by the single one we observe today. How many they are? This is a problem very difficult or impossible to be solved by other means than computer simulations. Another way to understand this puzzle is to consider only a small step of the evolutionary time, a snapshot of the evolutionary tree and all its subsequent potentially possible scenarios a little bit later: among them, many can be discarded immediately, presenting no growing branches at all. Thus, only the remainders which present some possibility of further growing need to be taken into account, not the whole potential set. This dissipative feature goes on at each new time step, cumulatively. It challenges the estimatives of the age of life on Earth obtained by a direct comparison between the currently observed scenario and some plausible starting condition, disregarding all dissipated possibilities in between.

In order to construct an evolutionary computer model, the first ingredient to be taken into account is the reproductive behaviour, for instance: the bit-string of the parent is copied into its offspring, with some possible random mutations (to flip a small number of bits). For a sexual population, with two parallel bit-strings per individual, first one cuts both bit-strings of the mother at the same random position, and then form one bit-string by joining two complementary pieces to be inherited by the offspring. The other is obtained by performing the same on the father’s genome. The second ingredient concerns death, for instance: the death roulette randomly kills individuals at every new time step, in order to keep constant the population. Further ingredients can be included. For instance, the mutation rate can vary for different genes (different positions along the bit-string). One can also give some preference for the position where the crossing is performed. Also, diverse correlations between different genes can be included. Birth and death rates can be genome-dependent. Geographic concerns and migrations can also be adopted. I am a very lucky guy, because I know how to efficiently implement such rules on the computer, and also because one has a virtually infinite number of new biological ingredients to be tested. Nowadays, for every physics problem there are a thousand physicists working behind, while for every thousand problems in biology there is one biologist [13]. I invite everybody to contribute.
I will finish with a single example of an evolutionary computer model, which was invented in our Institute [14]. For a review, see [15] and [16]. A further fundamental ingredient is ageing. One can keep the age of each alive individual, updating it every new time step, i.e. every new “year”. Instead of the whole genome, one can store only a reduced chronological projection of it, say a 128-bit string: each bit corresponds to one year, during the individual’s lifetime. We will call this bit-string “genome”, anyway, since it is not modified during life. A bit 0 at position $a$ means that no disease will appear at this age. Otherwise, a harmful genetic disease corresponds to a bit 1: for instance, an individual starting to be affected by Alzheimer disease since 60 years old has a bit 1 at position $a = 60$. Note that Alzheimer disease starts to be harmful only after 60, but it was already present in the individual’s genome since birth. A child suffering from Down’s syndrome has a bit 1, say, at position $a = 2$. At each new year, every alive individual whose age is above some minimum reproduction age $R$, say $R = 15$, is allowed to breed $B$ offspring, say $B = 1$, without or with sex [17]. Also each individual with more than $T$ genetic diseases accumulated up to its current age, say $T = 3$, dies. Another set of individuals also dies at random, independently of age or genome, in order to mimic non-genetic deaths avoiding population explosion.

This model makes concrete the evolutionary theory of ageing [18]. According to this theory, we age due to inheritance from our ancestors: would they have too much genetic diseases programmed in their genomes to occur at youth, then they would die before breeding. Thus, our true ancestors had their genomes “clean” enough (without or with only few genetic diseases) up to their reproduction age. However, they could be our ancestors even presenting very “dirty” genomes after their reproduction age. Being descendents of them, so we are: almost free of genetic diseases before the reproduction age. That is why we start to suffer from more and more diseases when we become old, i.e. after the reproduction age. A guy like Dietrich Stauffer, who has no known offspring, is supposed to live forever, according to his own (wrong) interpretation of the theory. A striking consequence of this theory is: a species which, besides the minimum reproduction age, has also a maximum reproduction age $M$ (for menopause), evolves to a situation such that nobody survives beyond age $M$. This is just the case of the pacific salmon, for instance. This behaviour is nicely reproduced [19] by the Penna model, simply by introducing this new ingredient: a maximum reproduction age. Women present menopause around 50 years old, contrary to men who are in principle able to reproduce until death. Thanks to men, women were allowed by Nature to live beyond 50. Is menopause explainable from evolutionary arguments? According to Williams [20] the answer is yes. His theoretical argument concerns a compromise between child care and reproduction risk for the mother:
it would be better for the mother to stop reproduction at some age, avoiding the risk of death during future childbirths, in order to be able to take care of the already born offspring. Indeed, including these two ingredients, namely child care and reproduction risk, a menopause age naturally arises from the Penna model [21]. According to data collected by Sir Thomas Perls and colleagues [22], longevity is inheritable. Again, the Penna model reproduces quite well these data [23].

Many similar models consider characteristics other than ageing, some of them in [24].

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