Ploidy, sex and crossing over in an evolutionary aging model

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Abstract

Nowadays, many forms of reproduction coexist in nature: Asexual, sexual, apomictic and meiotic parthenogenesis, hermaphroditism and parasex. The mechanisms of their evolution and what made them successful reproductive alternatives are very challenging and debated questions. Here, using a simple evolutionary aging model, we give a possible scenario. By studying the performance of populations where individuals may have diverse characteristics—different ploidies, sex with or without crossing over, as well as the absence of sex—we find an evolution sequence that may explain why there are actually two major or leading groups: Sexual and asexual. We also investigate the dependence of these characteristics on different conditions of fertility and deleterious mutations. Finally, if the primeval organisms on Earth were, in fact, asexual individuals we conjecture that the sexual form of reproduction could have more easily been set and found its niche during a period of low-intensity mutations.

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1. Introduction

Aging or senescence is a phenomenon characterized by a decline in the physical capabilities of individuals. Many theories have been suggested to explain why there is senescence [1], when it occurs, and what are the biological processes responsible for it. We can divide these theories into two main branches: Biochemical and evolutionary. The first invokes damages on DNA, cells, tissues, and organs and connects senescence with imperfections in the biochemical processes. A kind of this biochemical imperfection is the presence of free radicals that can cause death of the cells or may even lead to cancer. The evolutionary theory [2], on the other hand, explains senescence as a competitive result of the reproductive rate, mutation, heredity, and natural selection.

There are actually two different evolutionary aging models proposed by statistical physicists: Penna [3,4] and the modified Heumann–Hötzl model [5] (MHH). Both work, essentially, with the so-called chronological genome. In the former case this genome is composed of 0 and 1 which indicates the absence or the presence of one disease, respectively. An individual who has accumulated more than a certain (fixed) number $T$ of diseases dies in the next time step. So this threshold $T$ plays the role of natural selection. In the MHH model, the genome is composed of real numbers representing the survival probability of an individual at some age. Here, natural selection works in the following way: A random number is drawn and if it is higher than the survival probability of the individual, then it dies. Due to its bit-string characteristic, the Penna model is simpler to simulate in computers and, perhaps for this reason, it has been studied much more. In this paper, we study the MHH model, for which far less results are known.

During the evolution of life, nature has developed many different forms of reproduction, some more successful than others. Today, the sexual and the asexual forms are dominant but there exist several intermediate forms. How these forms evolved, what were the conditions that led to such an evolution and what kind of mechanisms nature discovered to implement evolution are very fundamental questions. We have tried to contribute to the theme, using exclusively the elementary facts associated with life as we know it: Birth, reproduction with some possible mutations, the omnipresent natural selection and death. We did not add any kind of external or social motives like parasites [6] or child protection [7] and neither did we place different types of population to interact together [8] since these actions presuppose the introduction of new parameters, and the system, as we shall see, is already full of them. Instead, we compare the performance of populations composed of different kinds of individuals evolving under the same set of parameters and starting with identical initial conditions.

In order to study ploidy, we first compare a population made up of asexual (haploid) individuals with that of diploid individuals reproducing by apomictic parthenogenesis (which is also an asexual form of reproduction). To investigate sex, we analyze diploid individuals with (asexual) apomictic parthenogenesis reproduction and the simplest case of sexed diploid individuals, i.e., those in which the gametes are generated without crossing over. Naturally, in the next step, we compare
sexual reproduction with and without crossing over. Finally, we investigate under which conditions the prevalent forms of reproduction, sexual and asexual, perform better. All forms of reproduction were studied at low and high levels of fertility and submitted to low, medium and high intensities of deleterious mutations.

2. Evolutionary aging model

In 1993, Partridge and Barton [9] proposed a very simple evolutionary model which incorporated antagonistic pleiotropy into a structured population with three ages [10]. Antagonistic pleiotropy arises when the same gene is responsible for multiple effects. For instance, genes enhancing early survival by promotion of bone hardening might prejudice later survival by causing arterial hardening. Dasgupta [11] removed the antagonistic pleiotropy restriction of the Partridge–Barton model and Heumann and Hötzl [12] tried to generalize it to a many ages structured population model. They tried but failed. Even on starting with several ages (11, in their work), the final stationary regime ended with only 3 ages, like in the Partridge–Barton and Dasgupta models. Recently, Medeiros and Onody [5] have altered the Heumann–Hötzl model in terms of two essential points: The incidence of mutations, originally occurring at all ages, were restricted to the offspring (as it should be in the case of hereditary mutations) and a mutation rate was introduced as, for example, in the Redfield model [13]. With these changes, the modified Heumann–Hötzl model (MHH) was capable of reproducing many interesting behaviors like the Gompertz law, catastrophic senescence and the effect “later is better”. Let us explain these. Based on actuarial observations, in 1825 Gompertz found that the human mortality grows exponentially with age in the age interval 40–60 years. This exponential behavior is called the Gompertz law. Semelparous are those individuals which breed only once, like the Pacific salmon. This fish exhibits a dramatic manifestation of aging—it dies just after its first reproduction, which is the so-called catastrophic senescence phenomenon. Finally, some experiments [14] done with the fruit fly Drosophila melanogaster unequivocally demonstrated that postponing reproduction favors the population. In these experiments, male and female flies were placed together some time later after they had reached their sexual maturity. The result was an improved population, with both male and female flies living longer.

Let us now describe the MHH model. The initial population at time \( t = 0 \) amounts to \( N_0 \) individuals. Each individual carries a “chronological genome” of size \( k_{\text{max}} \). It can be composed of 1 or 2 chromosomes depending on whether the individual is haploid or diploid. Each chromosome has at the position \( k \) (\( 1 \leq k \leq k_{\text{max}} \), where \( k \) is an integer) a real number which corresponds to the survival probability \( G(k) \) of that individual at that age \( k \). Individuals with age in the interval \([R_{\text{min}}, R_{\text{max}}]\) (\( 1 \leq R_{\text{min}} \leq R_{\text{max}} \leq k_{\text{max}} \)) are fertile and can reproduce, giving birth to children. Let \( f \) (a real positive number) be its fertility at each time step, in the following sense: The individual has \( \text{int}(f) \) (the integer part of \( f \)) offspring plus one additional offspring with probability \( f - \text{int}(f) \). So, \( f = 1.4 \) indicate that the individual will have 1 or 2 offspring with probabilities 0.6 and 0.4, respectively. Likewise, in nature, an
offspring does not undergo a mutation always. Let $F$ be the mutation rate, i.e., the fraction of babies that will undergo one mutation by chromosome at some random position (or age) $k'$. This mutation can be beneficial or deleterious in such a way that the new survival probability $G'(k')$ is given by

$$G'(k') = G(k')e^{u},$$

where $u$ is a real number randomly chosen from a uniform distribution in the interval $-|d| \leq u \leq |b|$, and $|d|$ and $|b|$ correspond to the maximum deleterious and beneficial mutation intensities, respectively.

Representing the pressure of the environment (e.g., food restrictions), at each time step $t$, every individual will survive with probability $V(t)$ (the so-called Verhulst factor)

$$V(t) = 1 - \frac{N(t)}{N_{\text{max}}},$$

where $N(t)$ is the number of individuals at time $t$ and $N_{\text{max}}$ correspond to the maximum population allowed. Naturally, besides mutations, the model must embrace the natural selection mechanism, the two masterpieces of a truly Darwinian theory. We implement natural selection in the following way: A random number $r \in [0, 1]$ is drawn from a uniform distribution. A haploid (diploid) individual with survival probability $G(k)$ ($G_1(k)$ and $G_2(k)$) at age $k$ dies if $r > G(k)$ ($r > (G_1(k) + G_2(k))/2$). Every individual of age $k = k_{\text{max}}$ dies in the next time step. To date, the MHH was only studied in its asexual form [5] and the sexual form for the particular case $F = 1$ [15].

In the resume, we saw that the MHH model has 5 fundamental elements of a good evolutionary theory: Genome, reproduction, mutation, natural selection and environmental influence. In the next section, we discuss different forms of reproduction.

3. Forms of reproduction

There are two fundamental forms of reproduction: Sexual and asexual. Nature sometimes favors sexual reproduction and sometimes asexual reproduction. Apparently, the initial form chosen by the first living organisms on Earth was asexual reproduction.

Besides sexual (SX) and asexual (AS) reproduction, there are many other intermediate forms such as apomictic parthenogenesis, meiotic parthenogenesis, hermaphroditism and parasex [16]. Parthenogenesis is a form of asexual reproduction that involves the development of a female gamete without fertilization. In apomictic (meiotic) parthenogenesis the diploid offspring is produced without (with) crossing over. Parasex, present in fungi and bacteria, involves the exchange of haploid genome parts between different organisms. As we wish to study how ploidy, sex and crossing over affect an age-structured population, we restricted our
investigations to the following cases: Asexual (AS), apomictic parthenogenesis (AP), sexual with (SX) and without crossing over (SXW).

In asexual reproduction, individuals are haploid and an offspring may differ from its parent only by some possible mutation (see Fig. 1(a)). In the apomictic parthenogenesis reproduction, the individuals are diploid and, again, an offspring may eventually differ from its parent by a possible mutation. There is no sex or crossing over (Fig. 1(b)). Fig. 1(c) shows sexual reproduction without crossing over (SXW). In this regime, there are male and female individuals. To form the male’s or the female’s gamete, one of the two chromosomes is randomly chosen with equal probability. These gametes may undergo mutation at some point (age) and then they are blended into the new offspring’s genome. The sex of the new offspring is

Fig. 1. Schematic representations of the reproduction regimes: (a) Asexual (AS); (b) apomictic parthenogenesis (AP); (c) sexual without crossing over (SXW) and (d) sexual with crossing over (SX). Symbols X indicate the positions in the genome where mutations occurred.
randomly chosen with a probability of 50%. The sexual reproduction with crossing over (SX), shown in Fig. 1(d), is almost identical to the SXW except that there is an additional phase called crossing over: At the moment of gamete formation, a position is randomly chosen along the genome, both chromosomes are then cut at that place and their pieces are interchanged.

4. Simulations

In order to know how ploidy, sex and crossing over affect an age-structured population many parameters must be fixed and we need to wait until the stationary regime is reached. In our simulations, we kept the following constant: \( N_0 = 45,000, \) \( N_{\text{max}} = 150,000, k_{\text{max}} = 15, R_{\text{min}} = 5, R_{\text{max}} = 10, b = 0.01 \) and \( F = 0.1. \)

We studied the system in two levels of fertility: Low, with \( f = 0.5 \) and high, with \( f = 1.5. \) Keep in mind that \( f \) is the average fertility of an individual by time step. Moreover, as we discuss asexual as well as sexual reproduction, we must guarantee that the outcome takes into account the number of partners involved in the process, so a fertility \( f \) means that the average number of offspring by fertile individual is \( f. \) To investigate the role played by the mutations, we attribute the following values to the deleterious mutations \( d_1 = -0.05, d_2 = -0.30 \) and \( d_3 = -0.50. \) In order to achieve the stationary state we simulated the system for very long times, actually, up to \( t = 3,000,000. \)

In Fig. 2, we study the aspect of haploidy versus diploidy utilizing the asexual (AS) and apomictic parthenogenesis (AP) forms of reproduction. The reason for our choice is very simple—the only difference between them lies in their ploidies: The asexual includes haploid individuals while the apomictic parthenogenesis includes diploid individuals. Anything else evolves identically. In Fig. 2(a) fertility is low. Individuals reproducing through AP die. On the other hand, asexual individuals reach a stable population (see the discussion in the next paragraph). Fig. 2(b) shows the effect of increasing fertility. In general, as expected, there is an overall population growth. Observe that although \( |d_3| > |d_1|, \) the
population with the highest deleterious mutation intensity $d_3$ is more robust in both cases—diploid or haploid populations. A very intensive deleterious mutation is more likely to kill an individual at the mutated age than a small mutation. An individual with a more intense deleterious mutation is rapidly eliminated by natural selection without leaving behind offspring. This fact, together with the small mutation rate $F$ ($F = 0.1$ in our simulations), gives us the following scenario for the offspring: In the case of high intensive mutations almost all survivals arise from the fraction $(1 - F)$ which are free of mutations; in the case of mutations of small intensity, the survivals arise from almost all offspring including those with small deleterious mutations. So, a more intensive deleterious mutation is harmful for a single organism but it is advantageous for the population as a whole.

We conclude that haploidy is better than diploidy. A similar result was found for the Penna model [17]. Diploid individuals undergo, effectively, a less intense mutation since the survival probability at a given age is an average of both chromosomes and, hardly will mutations occur in both chromosomes in the same position. Individuals with less intense mutations escape from the natural selection and, after a long time, degenerate the population. In resume, diploid organisms may enjoy an immediate advantage over haploid in masking harmful mutations, avoiding the fitness cost such mutations impose on haploid individuals. This advantage is, however, elusive and it disappears over the long term. Note that we have carefully imposed random mutations occurring in haploid and diploid individuals at the same rate, i.e., the mutation probability per gene is constant. Since diploid organisms have twice as many genes, the overall effect is that they have 2 times more mutations per genome per generation.

It is worth mentioning that the final result of a mutation on a single individual may be altered by epimutations. Epigenetics study changes in gene expression determined by how the DNA of a gene is packed. Within tightly packed DNA, genes are not readily available to the transcription machinery and epimutations can be different for haploid and diploid organisms [18].

Our next step is to find out how can sex be consolidated in a given population of diploid individuals. Males carry a very degenerated chromosome, the Y chromosome, that almost does not recombine with its counterpart, the X chromosome. The Y chromosome is much smaller than the X chromosome and it is composed of many repeated sectors. In a recent paper [19], we have shown that the degeneration of the Y chromosome occurs even in a complete absence of crossing over between the X and X or X and Y pairs. The only necessary ingredient is the existence of a male chromosome (Y); the proportion of 1:3 between Y and X chromosomes is enough to degenerate Y.

It is possible that sexual reproduction without crossing over preceded sexual reproduction with recombination of genetic material. For this reason, we think that it will be instructive to compare the following cases: Sexual without crossing over with the asexual diploid individuals, i.e., with the apomictic parthenogenesis reproduction. In Fig. 3, we have plotted the SXW reproduction versus AP. In both cases, all the individuals are diploid and the only difference lies in the existence of two sexes in the former. Under a very small mutation intensity, $d_1$, and low fertility, both forms
of reproduction lead to a population meltdown. However, by increasing the fertility or the intensities of mutations, contrary to what happens with AP, the SXW form of reproduction reaches a steady state.

Now it is time to see what are the effects of crossing over between the chromosomes. In Fig. 4, we show SX versus SXW reproduction. For any value of the chosen deleterious mutations or fertility, sexual reproduction with crossing over results in a total population larger than that of sexual reproduction without crossing. The exchange of genetic material guarantees genetic variability. So, nature found out a very inventive and efficient mechanism to push sexual reproduction forward.

Finally, the last question: Is complete sexual reproduction, that is, the one with crossing over, meiosis and mutations better than simple asexual reproduction? In the MHH model the answer is: It depends. It depends, basically, on the mutation intensities. In Fig. 5, we have plotted SX versus AS reproduction. For the lowest value of the deleterious mutation, $d_1 = -0.05$, the sexual form prevails. Asexual individuals are haploid and, in a regime of small mutation intensity, natural selection is not very effective. It is blinded by the very small fitness differences between the

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**Fig. 3.** Reproduction in a population of diploid individuals. The total population for the sexual regime without crossing over (apomictic parthenogenesis) is indicated in black (gray).

**Fig. 4.** The crossing-over mechanism produces a very strong effect on the total population. The time evolution of the SX (SXW) reproduction is plotted in black (gray).
individuals so it lets them pass, affecting the quality and the size of the final population. On the other hand, sexual reproduction has strong mechanisms to compensate the negative presence of small mutations: Crossing over, meiosis and fusion of the gametes. Indeed, sexual reproduction in the MHH model is more or less insensitive to the mutation intensities. However, as the mutation intensity is increased, asexual reproduction becomes better than the sexual form. For example, in the case of our higher mutation intensity $d_3 = -0.5$, the sexual mean populations are $11,380 \pm 890$ and $17,924 \pm 811$ while the asexual mean populations are $12,135 \pm 811$ and $18,141 \pm 792$ for the fertilities $f = 0.5$ and $1.5$, respectively.

Last but not the least, it is necessary to state that we did not treat here the case where some mutation positions in the genome are dominant. In the MHH model this means that, at those positions (ages), it is the allele with the smallest survival probability that one should submit to natural selection. Although such dominant positions exist in less than 10% of the genome, they will certainly weaken the sexual reproduction performance.

5. Conclusions

Some hundreds of million of years ago, life was spreading over earth probably in its simplest form of haploid individuals. All evolutionary mechanisms were operational: Reproduction, mutations and natural selection. Nature was doing its indefatigable work of trying and testing things when it happened to fuse two haploid individuals into one diploid organism. In the light of the evolutionary aging model discussed here, such a development should be followed up by the discovery of sex and the crossing-over mechanism between the chromosomes; otherwise, the diploid organisms would be in serious disadvantage compared to the haploid forms.

Certainly, with the simple MHH model used here, it is out of question to estimate how long nature took to implement sex and crossing over after the diploid
individuals were created, but our analysis gives us a hint of how the asexual supremacy could have been broken—in a less intensive deleterious mutations scenario, which is indeed the Achilles’ heel of asexual reproduction.

In our investigation, fertility plays the role of a population stabilizer—the population dies if it is very small. Of course, nature should have found an optimal compromise between extinction and environmental conditions.

Regarding the aspects studied in this paper (ploidy, sex and crossing over), the Penna model and the MHH model exhibit essentially the same behavior [16]. There is, however, a very important difference between the Penna model and MHH. In a recent paper [19], it was shown that in a population with sexual reproduction and recessive mutations, the final stationary state has a numerical predominance of female (male) individuals in the case of the MHH (Penna) model. It is the first example where the two models have opposite behavior.

We did not try justifying sex evolution through any external or social reasons like parasites, changing environment or child protection. Our approach does not preclude the existence of these reasons but follows the Occam’s razor principle. William of Occam, a Franciscan monk, philosopher, and political writer who was born in England in the thirteenth century, believed that for every phenomenon occurring in the universe we need to look at the simplest explanation first—complexity should not be assumed without necessity.

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