

Simulated coevolution in a mutating ecology

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The bit-string Penna model is used to simulate the competition between an asexual parthenogenetic and a sexual population sharing the same environment. A newborn of either population can mutate and become a part of the other with some probability. In a stable environment the sexual population soon dies out. When an infestation by rapidly mutating genetically coupled parasites is introduced, however, sexual reproduction prevails, as predicted by the so-called Red Queen hypothesis for the evolution of sex.

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The question of why sexual reproduction prevails among an overwhelming majority of species has resisted a century-long investigation. It is clear that its appearance is rather ancestral for metazoan, multicellular animals. Recombination probably originated some three thousand million years ago, and eukaryotic sex one thousand million years ago. But the mechanisms through which simple haploid organisms mutated into diploid sexual forms (the origins of meiosis and the haploid cycle) remain one of the great puzzles of evolution theory [1]. We can speculate about these origins, but cannot test our speculations. In contrast, selection must be acting today to maintain sex and recombination. We have to concentrate on maintenance rather than origins, because only thus can we have any hope of testing our ideas.

From a theoretical point of view, the selective advantages of a sexual population over a simple asexual one are well understood, and could be established through a variety of approaches. The bases for these advantages derive first from the covering up, by complementation, of deleterious genes, then from the ability to recombine genetic material, which haploid asexual reproduction lacks. But serious difficulties arise when sexual reproduction is compared with meiotic parthenogenesis, which is a kind of diploid asexual regime that also involves genetic recombination. In this case, the two-fold advantage of not having to produce males could give parthenogenetic populations the upper hand against a competing sexual variety, since recombination is present in both.

The theoretical problem thus posed to evolutionary biologists is indeed very difficult. The observation of this competition in natural habitats is not feasible, in general. One must rely on very indirect and often questionable data. It should be pointed out that this is a feature shared by many of the most important problems in the theory of evolution. This situation is certainly one of the main reasons for the recent boost of activities in physics directed towards biology, since the same methods and approaches could prove once again fruitful [2]. In particular, physicists have pioneered the use of techniques derived from the availability of powerful low-cost computers to fulfill the lack of and complement experimentation [3]. Computer simulations of natural systems can provide much insight into their fundamental mechanisms, and can be used to put to a test theoretical ideas that could be otherwise viewed as too vague to deserve the status of scientific knowledge. The scientific literature of this decade is strong testi-

mony to the success of this approach, in various and apparently disconnected fields; for a recent, although partial, survey of nonphysical applications I direct the reader to Ref. [4]. It is against this background that this work is being reported.

Investigations of evolutionary problems by physicists have in fact boomed in the last few years. In that which concerns biological aging, this boom can be traced back to the introduction of Penna's bit-string model [5] which was quickly adopted as referential in most studies, as a sort of "Ising model" of the field. Its simplicity and early successes in reproducing observed features of real populations, such as the Gompertz law [6], the Azbel phenomenology [7], and the catastrophic senescence of semelparous animals [8], unleashed a burst of efforts in its application to a number of different phenomena. In some simple cases, analytical solutions could even be provided, shedding some light on the simulation results; recent reviews can be found in Ref. [9], and an extensive list of references in Ref. [4].

Other models have been examined in the recent literature. Of particular interest is the Redfield model [10], which assumes a constant population and does not allow mutational meltdown.

The Penna model has also been used to address the problem in question here, namely, the reasons for the maintenance of sexual reproduction [11]. Simulations with this model showed that a genetical catastrophe could eliminate a parthenogenetical population, whereas sexually reproducing species survived. This result had the merit of pointing out a measurable effect of the greater genetic diversity created by sex, but the occurrence in nature of catastrophes of that kind seems rather unlikely. Its introduction in the simulation is prone to be thought of as too artificial to be convincing. Another drawback should also be mentioned. All previous comparisons between sexual and asexual reproduction have come from results where each population evolved by itself, as if each one lived in a separate environment. This is biologically improbable, and a simultaneous study of both regimes, sharing the same resources, is needed. This has been already done, in the context of the Redfield model. There, it was shown that sexual reproduction has a short-term advantage over the haploid asexual regime if the female mutation rate is high enough [12].

The present work represents a step in the direction of endowing the artificial world in which the populations

evolve in Penna model simulations with more realistic features. Its purpose is again to verify measurable effects of sexual genetic diversity when compared to parthenogenetic reproduction. The simulations here reported are based on the recent field work of biologist Lively, in which he observed the effect of parasitic infestation of a freshwater snail's (*Potamopyrgus antipodarum*) natural habitat on its dominant reproductive regime [13]. This observation can be considered as an illustration of one of the theories in the debate over the reasons for the prevalence of sex, the so-called "Red Queen" hypothesis. This is a variation of the idea that sex serves to assemble beneficial mutation, and so creates a well-adapted lineage in the face of a rapidly changing environment. Because parasites adapt to the most common host genotype, evolution will favor hosts with a rare combination of resistant genes. Thus, the Red Queen predicts that selection will favor the ability to generate diversity and rare genotypes, exactly the abilities conferred by sex and recombination.

I describe in what follows the model used in the simulations, the Penna bit-string model with recombination, and the representation of a parasitic infestation in its context. The genome of each (diploid) organism is represented by two computer words. In each word, a bit set to 1 at a position ("locus") corresponds to a deleterious mutation; a "perfect" strand would be composed solely of zeros. The effect of this mutation may be felt at all ages equal to or above the numerical order of that locus in the word. As an example, a bit set to 1 at the second position of one of the bit-strings means that a harmful effect may become present in the life history of the organism to which it corresponds after it has lived for two periods ("years"). The diploid character of the genome is related to the effectiveness of the mutations. A mutation in a position of one of the strands is felt as harmful either because of homozygosity or because of dominance. For the former, a mutation must be present in both strings at the same position to be effective. The concept of dominance on the other hand relates to loci in the genome in which a mutation in just one strand is enough to make it affect the organism's life. The life span of an individual is controlled by the amount of effective mutations active at any instant in time. This number must be smaller than a specified threshold to keep the individual alive; it dies as soon as this limit is reached.

Reproduction is modeled by the introduction of new genomes in the population. Each female becomes reproductive after having reached a minimum age, after which it generates a fixed number of offspring at the completion of each period of life. The meiotic cycle is represented by the generation of a single-stranded cell out of the diploid genome. To do so, each string of the parent genome is cut at a randomly selected position, the same for both strings, and the left part of one is combined with the right part of the other, thus generating two new combinations of the original genes. The selection of one of these completes the formation of the haploid gamete coming from the mother.

The difference between sexual and parthenogenetic reproduction appears at this stage. For the first, a male is selected in the population and undergoes the same meiotic cycle, generating a second haploid gamete out of his genome. The two gametes, one from each parent, are now combined to form

the genome of the offspring. Each of its strands was formed out of a different set of genes.

For parthenogenesis, all genetic information of the offspring comes from a single parent. Its gamete is cloned, composing an homozygous genome for the offspring. For both regimes, the next stage of the reproduction process is the introduction of m independent mutations in the newly generated genetic strands. In this kind of model it is normal to consider only the possibility of harmful mutations, because of their overwhelming majority in nature. For sexual populations, the gender of the newborn is then randomly selected, with equal probability for each sex.

A last ingredient of the model is a logistic factor, called the Verhulst factor, which accounts for the maximum carrying capacity of the environment for this particular (group of) species. It introduces a mean-field probability of death for an individual, coming from nongenetic causes, and for computer simulations has the benefit of limiting the size of populations to be dealt with.

The passage of time is represented by the reading of a new locus in the genome of each individual in the population(s), and the increase of its age by 1. After having accounted for the selection pressure of a limiting number of effective (harmful) mutations and the random action of the Verhulst dagger, females that have reached the minimum age for reproduction generate a number of offspring. The simulation runs for a prespecified number of time steps, at the end of which averages are taken over the population(s). A more detailed description of the standard Penna model can be found in Ref. [4], together with a sample computer code that implements its logic.

The extension of the original Penna model to simulate the coevolution of populations is rather straightforward. In this Rapid Communication, I focus on the coevolution of different varieties of the same species, sharing the same ecological range. This implies that the maximum carrying capacity relates to the total population, summing up all varieties. I use this simple extension to study the effect of introducing a small probability p for a mutation to transform offspring of one variety into the other. This implies an extra stage for the reproduction logic. After a new-born genome is generated from the sexual population, it mutates into a parthenogenetic female and becomes part of the asexual population with probability p . Accordingly, the offspring of an asexual female can mutate to the sexual form, with the same probability p ; if it does, a gender is randomly chosen for it.

Further extension is needed to simulate the conditions of a parasitic infestation. I chose a very simple strategy to reproduce Lively's observation. Parasites are represented by a memory genetic bank of a fixed size M . At each time step, every female of the species establishes contact with a fixed number P of elements of the parasite population. If the female's genome is completely matched by the genome already memorized by the parasite, it loses its ability to procreate. This simulates the action of the parasite *Microphallus* on the fresh water snail: this trematode renders the snail sterile by eating its gonads. The parasite memory bank has, on the other hand, a dynamic evolution. If an element of the parasite population contacts the same genome a certain number of times n in a row, this particular genetic configuration is "learned" by the parasite, and turns it active against this

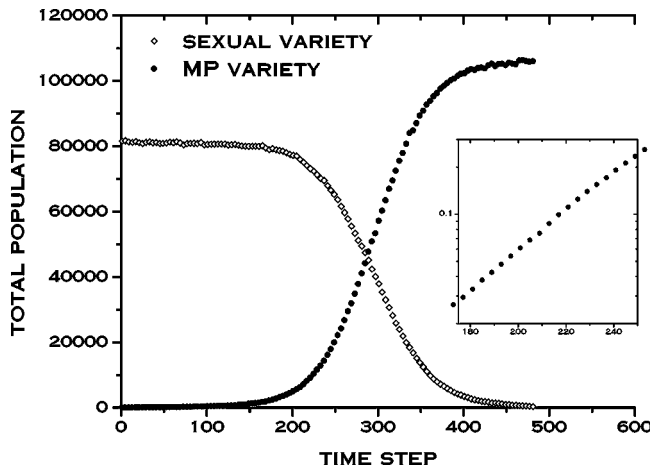


FIG. 1. Total population of each variety is plotted against time, measured in the number of Monte Carlo steps. After a short transient, the parthenogenetic (MP) variety dominates. The inset shows a semilog plot of the fraction of asexual females in the population as a function of time, exhibiting the expected exponential increase. See text.

genome, until a new pattern is found repetitively. Note that the same genome can be present in a number of different females, so the action of the parasite is not restrained by being randomly “chosen” by the same female the required number of times. Rather, the effectiveness of this simulated parasitic infestation is an indirect measure of the genetic variability (actually, of the lack of this variability) within the female population of each variety.

It must be remarked that this is not the only possible choice for the dynamic evolution of the parasite population. Nonetheless, it captures the essential features of parasitism; in particular, parasites that match frequently occurring female’s genomes will spread out through the population, showing that the above dynamical rules succeed in giving them an effective handicap.

All the species, the two varieties of the snail and the parasites, evolve as fast as they can, but neither gets far ahead, hence the theory’s name, after the Red Queen’s remark to Alice in Wonderland: “It takes all the running you can do, to keep in the same place.” The extra constraint that the two varieties of snail are competing for the same resources of the environment may eventually cause one of them to collapse. And Lively’s observations match this expectation: environments with few parasites tend to have mostly asexual snail populations, while a larger number of parasites is correlated to a predominant sexual variety. This pattern strongly suggests that the parasites prevent the elimination of sexual populations.

The two-fold short-term disadvantage of sexual reproduction is the object of the first result shown. The initial population is composed of a single sexual variety in which each reproductive female gives birth to a parthenogenetic female with a small probability $p=0.0001$. The minimum age for reproduction $R=10$ and the birth rate per female $b=1$ are fixed, and do not suffer the effect of mutations. Figure 1 shows the time evolution of the total population of each variety. In this run, the environment is kept fixed; there is no parasite infestation. The burden of having to produce males in the population is responsible for the quick establishment

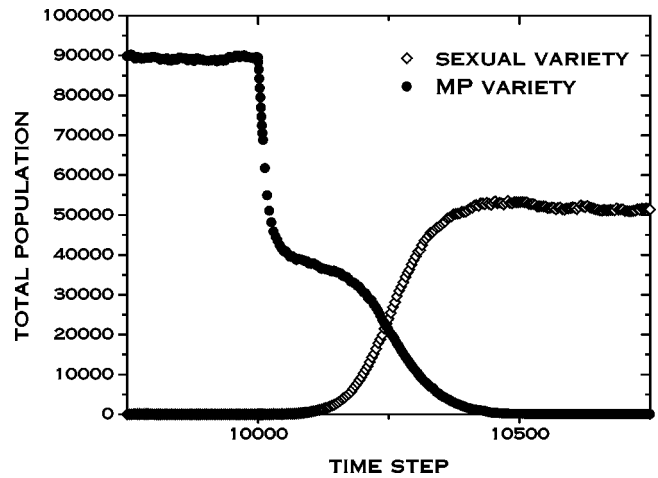


FIG. 2. Total population of each variety is plotted against time, measured in the number of Monte Carlo steps. The sexual population is nearly vanishing at first, and is kept alive only because of back-mutations from the parthenogenetic (MP) one. At time step 10 000 a parasitic infestation is turned on, with an exposure of 60 patterns per female per time step. The sexual population rebounds after that, and becomes the dominant variety.

of a dominant asexual variety. The inset shows the time evolution of the fraction of asexual females in the total population once a parthenogenetic lineage appears for the first time. A simple argument that underlies this result goes as follows [1]: suppose there are A asexual females and S sexual ones (and also S males) that have already reached reproduction age in a generation. In the next one, there will be bA and $bS/2$ of each variety; the factor of 2 of the latter comes up because of equal probabilities to give birth to males and females. The fraction of parthenogenetic females in the total population increases from $A/A+2S$ to $A/A+S$; when A is small, this is a doubling in each generation. This reasoning presupposes an unbounded increase in the total population and no overlapping between generations, which are not realistic assumptions in general. Instead, one should expect a smaller factor for this growth. The simulation shows clearly this exponential effect in a semilog plot, albeit with a factor close to 1.05.

The results described in what follows were obtained from runs where the basic parameters of the model for the infestation had values $M=1000$ and $n=2$. The use of different values does not, however, change any of the conclusions, which are essentially qualitative.

Figure 2 shows the effect of the parasite infestation. This infestation appears at time step 10 000, and is simulated by an exposure of each female to $P=60$ genomic imprints of the parasite bank before trying to give birth. After having almost vanished, and being kept alive solely by the infrequent back-mutations, the sexual variety becomes rapidly more abundant as soon as the infestation is unleashed and eventually dominates. In accordance with the Red Queen hypothesis, the greatest diversity of genomes that sexual reproduction engenders [11] is showing one of its measurable consequences.

The density of the parasite infestation, measured by the number of exposure patterns, drives a transition between dominating reproductive regimes. This transition can be

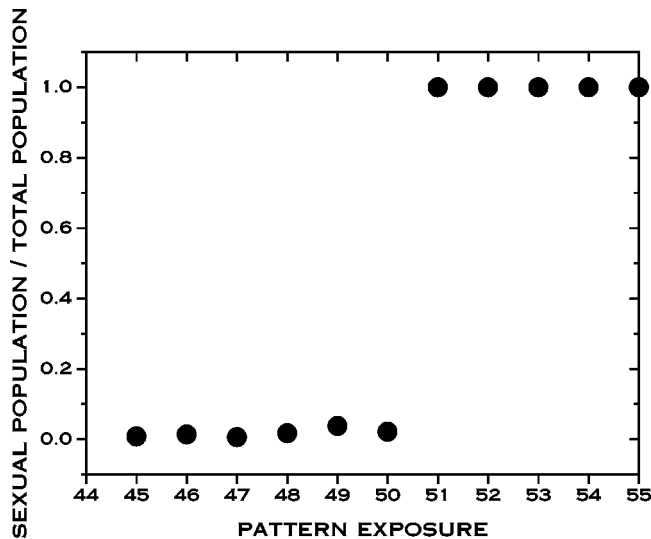


FIG. 3. Final fraction of sexual population in the total is plotted against parasite exposure, the number of parasite patterns with which a female's genome is compared at each time step. The former plays the role of the order parameter of the parasitic-driven transition, while the exposure is related to parasite density. The sharp jump signals a first-order transition.

measured through the fraction of total sexual population over the total population. This number acts as an order parameter for this transition. Figure 3 shows this fraction as a function of parasite exposure after a stationary population has been reached. The sudden jump in the order parameter is signaling a first-order transition. This claim is further supported by the

observation that some runs near the transition, differing only by the sequence of pseudorandom numbers used, had unusually long relaxation times. These long relaxations can be understood as related to metastable states, typical of first-order transitions.

This paper reports on a simulation of the coevolution of sexual and parthenogenetic varieties of a same species, competing for the same resources, in the framework of the Penna bit-string model. The two-fold disadvantage of having to produce males shows its deadly effect on the sexual population, in a static environment. On the other hand, the introduction in the model of an infestation of rapidly mutating parasites, tailored to reproduce recent observations of existing species, can revert the outcome of this competition. This result is in complete accordance with those observations, and acts as support for the Red Queen hypothesis for sex maintenance in the natural world. A transition, conjectured to be of first-order, between dominant reproductive regimes observed in nature could be simulated. The selective pressure of a mutating ecology is enough to enhance the genetic diversity promoted by sexual reproduction, giving it the upper hand against competing asexual populations. The results reported show that very simple simulational models can in fact be explored as testing ground for theories in biology where observational evidence is lacking or insufficient.

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