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On the evolutionary benefit of recombination: progress acceleration or degradation slowdown?

Technical paper

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Abstract. The article presents the author's proposed classification of hypotheses explaining the positive role of genetic recombination induced by sexual reproduction for biological evolution. It has been hypothesized that both progressive and conservative theories may be proper, but they have to be applied to different stages of a species' evolutionary history. The results of computational experiments with an agent-based simulation model are presented to determine the "optimal" number of sexes for quickly achieving the genotype of maximum fitness under natural selection.

Keywords: diploidy, “the queen of evolutionary problems”, recombination, population dynamics, optimal number of sexes

1. Introduction

Despite the rapid development of experimental biology and genetics (especially at the micro-level), many fundamental problems of theoretical biology and evolutionary theory still remain unsolvable. An exceptional place among them is occupied by the so-called "queen of evolutionary problems". It is formulated very simply by two principal questions: 1) how did the mechanism of sexual reproduction arise in the course of natural selection, and 2) why did this mechanism take root and remain so widespread? In other words, what is the global evolutionary advantage of having two sexes or, from a genetic point of view, diploidy? Why is the process of genetic recombination so important for the formation of any new organism from two parent organisms? To answer these questions, one needs a very powerful hypothesis that explains how the profit of sexual reproduction compensates for the "two-fold cost of males". The last term means that the theoretical growth rate of the sexual population is expected to be half that of the population that has chosen asexual reproduction (apomixis).

The article will examine the advantages of sexual reproduction solely and exclusively from the perspective of genetic recombination. We ignore here the possible differentiation of genders determined by the resources they invest in the birth and upbringing of a common child and their various social roles. A large number of impressive studies and papers have addressed these specific issues (Geodakyan, 1999). We will focus on answering a single question: why did evolution require that the genotype of an offspring not copy the genotype of a single parent (except for rare and random mutations, which in this case would be the only mechanism of variability for natural selection), but represent a new combination of genes obtained by genes obtained from two (and, in general case, ***from several***) parents?

There is a huge number of often mutually exclusive hypotheses (Kondrashov, 1993; Felsenstein, 1974), but neither experimental nor theoretical (mathematical) biology can yet give an unambiguous answer to this question. At the same time, the entire variety of explanatory approaches and models can be divided into

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two classes. The first class consists of models that consider the usefulness of recombination from the point of view of ***accelerating positive evolution*** - that is, improving the genotype to increase the average fitness of a heterogeneous population. Hypotheses related to this type will be called ***progressive*** here. Such approaches include the Vicar of Bray hypothesis, the Black Queen hypothesis, and the clonal interference effect (Ridley, 2011). Let’s talk about the last idea in a little more detail.

The concept of clonal interference was first presented by Muller in 1932 (Muller, 1932). Figure 1 is a copy of a diagram from the original paper illustrating the principal idea. It compares the dynamics of the spreading of new genes resulting from advantageous mutations in sexual and asexual organisms. In asexual organisms these genes compete and hinder one another's spread; while in sexual organisms they spread through one another. As a result, the ideal combination of different positive genes in a single genotype through natural selection can be achieved much earlier under sexual reproduction. Diagrams of such type have since been reproduced in a huge number of publications. These beautiful illustrative images explain the clonal interference effect intuitively and qualitatively. However, surprisingly, no simple and clear quantitative analytical model or unambiguous mathematical interpretation has yet been proposed. Perhaps the most famous complete mathematical formalization of such statements is the model (Crow, Kimura, 1965), which obtained a mathematical expression for the relative intensity of the emergence and consolidation of useful traits in a population of infinite size in cases of sexual and asexual reproduction. But both the mathematical apparatus and the set of assumptions underlying this model are much more non-trivial than a simple graphical interpretation like Fig. 1.

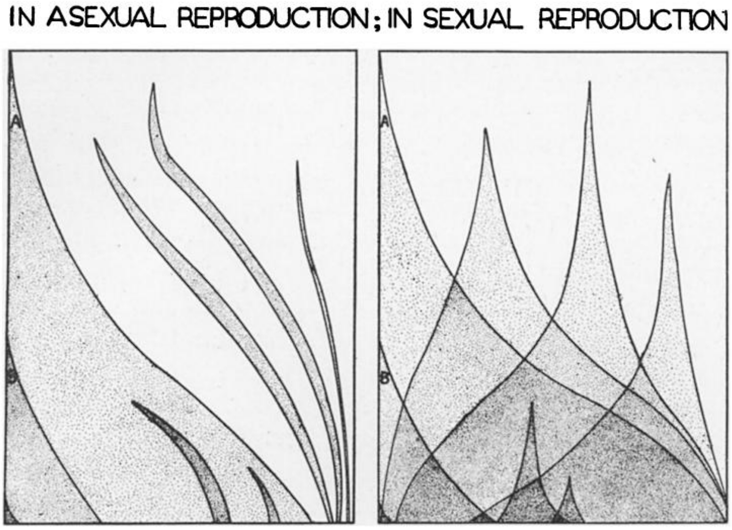

Figure 1. Evolutionary spread of advantageous mutations (copied from Muller, 1932)

The second class includes models that, on the contrary, prove the evolutionary advantage of recombination for ***slowing down negative evolution*** – the irreversible accumulation of harmful mutations in the gene pool of a population, leading to the degradation and extinction of a species. The most famous hypotheses of this kind are Möller's ratchet and Kondrashov's axe (Popadyin, 2003). We, in turn, will call them ***conservative***.

This discussion paper presents the author's subjective classification of existing hypotheses and suggests which stages of a species' evolutionary history they are most applicable to. The research tools utilize both analytical equations for the dynamics of a heterogeneous population under natural selection and an agent-based simulation model.

2. Models of evolutionary population dynamics: ecological vs. genetic approach

Mathematical models describing changes in the structure of heterogeneous populations during evolution can also be divided into two broad groups. These groups correspond to the ecological or genetic views on population dynamics. The main difference between such paradigms is the semantics of the main dynamic variable. In ecologically-oriented models, variables are the numbers of individuals of the corresponding genotypes, while in genetically-oriented models they are the frequencies of these genotypes in the overall heterogeneous population. Let's give general definitions. Let $L(\mathbf{x},t)$ be the number of individuals of genotype $\mathbf{x}$ at time t. Then the total number of individuals in the population is calculated as $N(t)=\int\limits_{\mathbf{X}} L(\mathbf{x},t)\cdot d\mathbf{x}$, and the proportion or frequency of clone $\mathbf{x}$ in the entire population is equal to $P(\mathbf{x},t)=L(\mathbf{x},t)/N(t)$. The general form of the equation for describing the dynamics in terms of numbers in this case looks like

$$\dot{L}(\mathbf{x},t)=F_{\mathbf{x}}\cdot L(\mathbf{x},t), \tag{1}$$

where $F_{\mathbf{x}}$ is the current fitness of clone $\mathbf{x}$, which may depend on its genotype, on time, and, in the general case, on the number of this and all other clones in the population. But if we choose not the number but the frequency of clones as the variable of interest, then the formula (1) goes into the form of the so-called basic replicator equation (Page, Novak, 2002) and looks as:

$$\dot{P}(\mathbf{x},t)=P(\mathbf{x},t)\cdot\left(F_{\mathbf{x}}-\bar{F}\right), \tag{2}$$

where $\bar{F}$ is the average fitness of the population, i.e. $\bar{F}=\int\limits_{\mathbf{X}} F_{\mathbf{x}}\cdot P(\mathbf{x},t)\cdot d\mathbf{x}$. It is evidently clear from (2) that clones with a current fitness above the average value increase their frequency, while less fit clones, on the contrary, are gradually eliminated from the population. Despite the apparent similarity of ecological (1) and genetic (2) formulations, both the necessary mathematical framework for the study and the interpretation of the results obtained can differ significantly. It seems that the ecological equation operating on clone numbers is more universal and informative. Indeed, consider the simplest example, where each clone has its own fitness, dependent only on its genotype. This fitness differs for each clone, but all are negative. Then, according to equation (2), over time the population should degenerate to a steady state, where it contains only one clone having the highest fitness. However, this would be a very dubious evolutionary success for this clone, because, in fact, according to the Malthusian equation (1), it would also die out, just like the others.

Perhaps the simplest non-degenerate model of evolutionary dynamics in terms of sub-population sizes is the so-called non-homogeneous logistic equation. It is an extension of the standard scalar logistic growth equation (or Verhulst's model) for a non-homogeneous population and is written as

$$\dot{L}(\mathbf{x},t)=b(\mathbf{x})\cdot L(\mathbf{x},t)\cdot\left(1-\frac{N(t)}{N_{LIM}}\right), \tag{3}$$

where N_{LIM} – the maximum capacity of an ecological niche. Within this model, competition between clones is achieved by limiting the total population size. The model (3) can be solved numerically or even analytically using an approach based on Karev's reduction theorem (Karev, 2010). The mentioned approach provides an effective method for solving replication-selection systems; it reduces the initial complex model to a special system of ordinary differential equations (the escort system). For example, in the case under consideration, the dynamics of the non-homogeneous logistic equation coincide with the usual Malthusian one if the "normal" time t is replaced by the "internal" time q(t), where

$$q(t)=1-N(t)/N_{LIM} \quad ; \quad q(0)=0 .$$

The solution leads to rather strange results. The final distribution of genotypes within the population turns out to be nondegenerate. Every clone existing at the initial moment will also be present in the final state of the system. "All survive," not just the "fittest".

A numerical study provides a simple explanation for the resulting contradiction. The fact is that, for the model under consideration, the limiting capacity of the ecological niche for **all** clones is reached much faster than the elimination of less adapted clones from the population under the pressure of natural selection. Apparently, this result should be considered a simulation artifact, caused by the intrinsic properties of the model used.

The problem becomes clear if we open the parentheses in (3) and interpret the terms as birth and death rates, respectively. It turns out that the specific fertility and mortality of a given genotype are controlled by the same parameter $b(\mathbf{x})$. That is, more fertile clones are somehow more sensitive to resource shortages caused by overpopulation. To resolve this unnatural limitation, it is proposed to rewrite Equation 3 in form

$$\dot{L}(\mathbf{x},t) = L(\mathbf{x},t)\cdot\left(b(\mathbf{x}) - d(\mathbf{x})\cdot N(t)\right), \qquad (4)$$

where the coefficients that determine the birth (b) and death (d) rates of a particular clone are clearly identified and separated. As a result, the maximum capacity of an ecological niche in terms of total population size also turns out to be specific for each clone (see Figure 2A):

$$N_{LIM}(\mathbf{x}) = {}^{b(\mathbf{x})}\!\big/_{d(\mathbf{x})} \; .$$

Figure 2 presents the results of the numerical analysis of equation (4). For this purpose, a simple simulation model of system dynamics has been implemented, in which the only dynamic variable was a vector of several clones comprising a common population and differing in the values of clone-specific parameters d and b. It is evident that at the initial moments of time (when the total population size is small and the ecological niche is far from saturation), the clone with the highest specific fertility exhibits the highest growth rate. However, this stage ends quickly, and the population enters a rather long stage of comparatively slow integral growth (the final filling of the ecological niche). During this stage, under the pressure of natural selection, its internal structure is restructured in favor of clones with a higher N_{LIM} value. Ultimately, survives not the locally "fittest" clone, but the globally the "most tolerant" one (the clone with a larger value of limiting total population size).

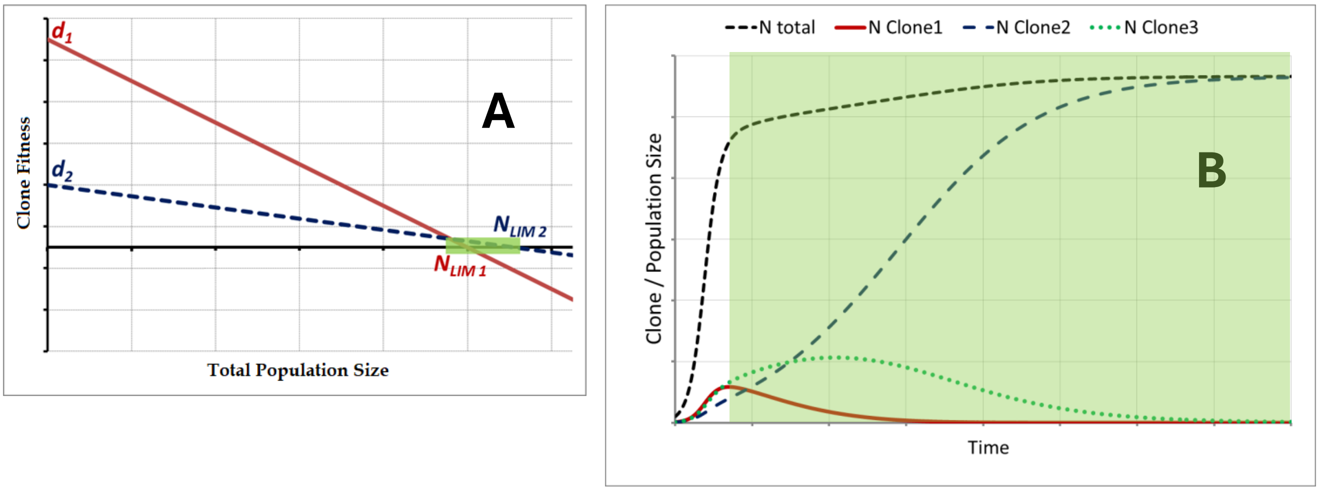

Figure 2. Numerical solution of the equation for the growth of a genetically heterogeneous population with different ecological niche capacities for clones.

From a qualitative analysis of the results presented in Figure 2, we can attempt to cautiously formulate conclusions about which of the two fundamental hypotheses regarding the advantage of sexual reproduction over apomixis (progressive or conservative) can be considered preferable, depending on the current stage of population or species evolution.

In simplest terms, three periods can be distinguished in the evolutionary history of a species or individual population. The first is the occupation of an empty ecological niche, accompanied by rapid population size growth and the displacement of competing species. This can occur, for example, due to migration or a sharp change in environmental conditions, altering the established "rules of the game" and conferring significant fitness advantages on certain new traits. The only adequate mathematical framework here is classical ecological models of population dynamics, albeit with a "genetic" component.

The second period is the internal restructuring of the population within an already occupied and limited ecological niche or in the context of a slowly changing external environment under the pressure of intra-population competition and natural selection (green rectangles in Fig. 2). Here, genetic models demonstrating the benefits of genetic recombination in accelerating the achievement of an "optimal" genotype and explaining the pattern of the emergence of sexual reproduction (i.e. progressive hypotheses) seems to be most prospective.

Finally, the third period is maintaining the stable existence of a population or species in a closed and saturated ecological niche. It is characterized by a roughly constant population size and an achieved "optimal" internal genetic structure, ensuring maximum fitness. In general, this optimal structure does not necessarily boil down to the dominance of a single clone with a specific genotype; it can involve the stable coexistence of several different clones (like an evolutionary stable set in evolutionary games). During that period, the focus of interest shifts to the role of recombination in protecting the population from the accumulation of harmful mutations during genetic drift, that is, to explain the persistence of sexual reproduction from a conservative point of view. Agent-based simulation models with a stochastic component offer a promising research tool here.

This spirally repeating "life cycle" of evolution is demonstrated in Fig. 3. Thus, both the choices of model or research tool, as well as the class of hypothesis explaining the advantages of sexual reproduction, are determined by the stage of evolutionary development of the species or population being implicitly discussed.

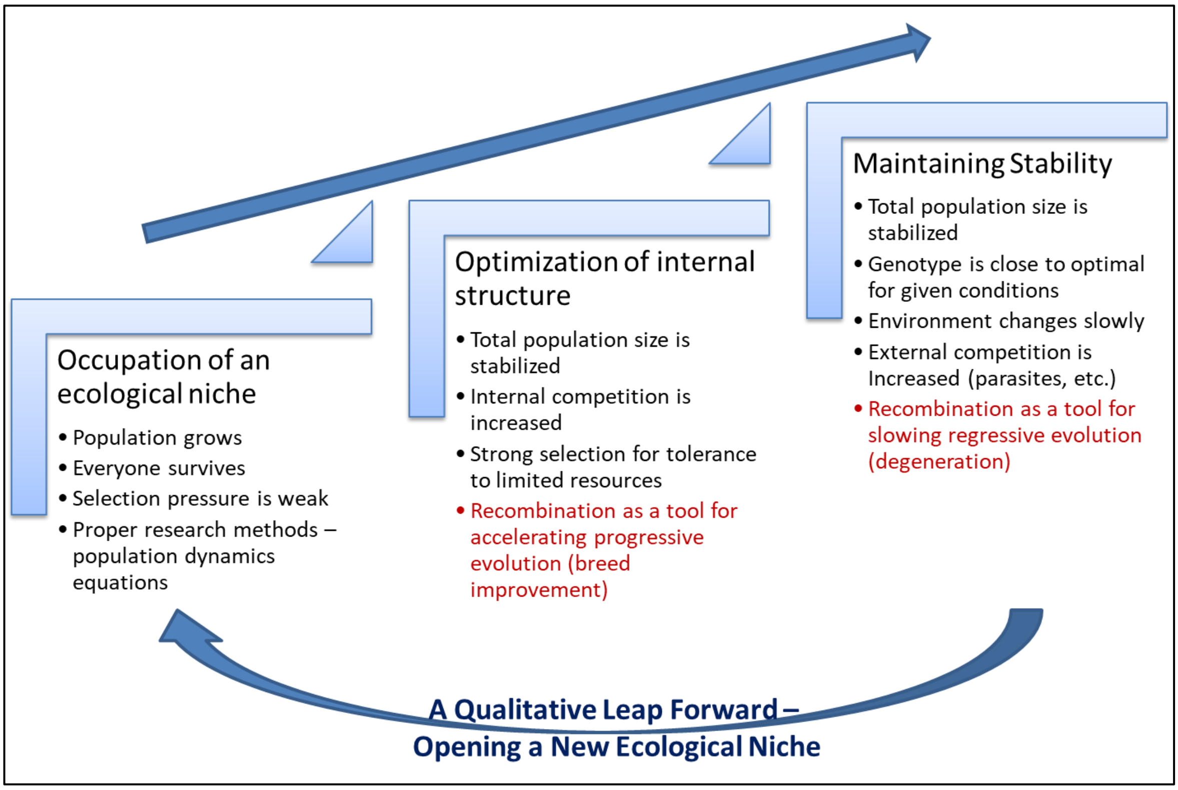

Figure 3. Life cycle of species evolution

3. How many sexes are needed for efficient recombination?

Let's consider the theoretical advantage of sexual reproduction from the perspective of the progressive-type hypothesis, that is, for populations in the second stage of development according to the classification given above. An interesting problem can then be posed and solved: how many sexes are needed for the most effective genetic recombination, that is, to maximize the rate of genotypic improvement? In other words, what should be the optimal number of parents, each transmitting part of their genotype to a common offspring, to accelerate the accumulation and consolidation of beneficial mutations in the population? This is not a trivial question. On the one hand, the greater the number of parental genotypes mixed in a single offspring, the sooner independently acquired random beneficial mutations can meet. But, on the other hand, the less likely it is that they will acquire the desired optimal combination in a particular child. This formulation of the problem is not original (Iwasa & Sasaki, 1987; Hurst, 1996). However, unlike the aforementioned works, we will not investigate abstract mathematical formalization using analytical methods but will run a series of simulation experiments with stochastic repetitions by means of the specially developed agent-based simulation model.

The model implemented describes the evolution process within the population of individuals (active agents). The model has been implemented in the AnyLogic© Personal Learning Edition software framework. This platform supports the paradigms of agent-based and discrete-event simulation.

Each agent that makes up a population is characterized by its own “genotype,” which in this case is presented as an array of binary values. The value (0 or 1) in the *i*-th position of the array is interpreted as the allele of the gene at the corresponding locus. The fitness of each agent is uniquely determined by its genotype and, for simplicity, is calculated proportionally to the number of unit elements of the array. At the initial moment of time, the genotypes of all individuals in the population contain zero values at all loci, that is, their fitness is minimal.

The sequence of generational changes and changes in genotypes under the pressure of natural selection (evolutionary game) is simulated. The model runs in discrete time; one step corresponds to one generation. At each step of the process, the following operations are performed sequentially:

1. Random formation of "families" (the sets of parent individuals) of a given size;
2. Birth of a given number of offspring in each family;
3. Assigning the genotype of each offspring by randomly selecting a gene from one of the parents at each locus;
4. Modeling the possible random mutation at a random locus of the offspring genome (switching from 0 to 1 or vice versa);
5. Calculation of the conditional fitness of the offspring for the obtained genome;
6. Random selection of representatives for the next generation from the general offspring pool, maintaining the overall population size. The probability of selection (survival) of an offspring is determined by its conditional fitness.
7. Calculation of current integral indicators for the entire population (average fitness, genotype distribution, etc.)

The model's graphical interface allows users to observe, during its execution, the dynamics of the accumulation of beneficial mutations and the "improvement" of the genotype of both individuals and the average fitness of the population due to natural selection. The speed of this improvement is considered an indicator of the progressive power of evolution.

The model has the following control parameters: stationary size of population N_{LIM}, number of sexes (parental individuals making up a family) N_{SEX}, mutation frequency R_{MUT}, number of offspring per individual/family N_{CHILD}, and genome size *G.* AnyLogic platform includes the built-in tools for automating multiple runs of simulation experiments. It permits to perform the sensitivity analysis of the model result under consideration (the rate of positive evolution in the case) to any of the model's parameters. To solve the stated problem —determining the optimal number of sexes — we need to carry out such an analysis for the variable N_{SEX}. Value a N_{SEX}=1 in this case can be considered as asexual reproduction (apomixis).

Selected results of such a sensitivity analysis are presented in Fig. 4A. Other model parameters are fixed and, for the given example, are: N_{LIM} = 1000; R_{MUT} = 10^{-5} per individual per locus; N_{CHILD} = 8 per family; *G* = 100. Specifically, Fig. 4a shows the dynamics of the increase in average population fitness for different numbers of parents making up the "family" (N_{SEX}). A striking finding is that a difference is observed only between the value 1 (i.e., asexual reproduction) and all other values. Moreover, the difference in the rate of progressive evolution for any number of sexes greater than or equal to two is within the margin of statistical error. Genetic recombination does indeed significantly increase the rate of breed improvement, but the number of sexes does not play any significant role!

To explore this issue in more detail, we run the developed model with a **fractional number of sexes**. This sounds very strange, but in fact, it conceals a very simple realization. This exotic variant is simulated in the model as follows: in the studied population, only a certain predetermined proportion of individuals in each generation choose sexual reproduction (forming a two-parent family), while the remainder prefer apomixis.

The corresponding results are presented in Fig. 4B. They allow us to draw a rather surprising conclusion: the fundamental factor influencing the rate of positive evolution in a heterogeneous population is the very **presence** of recombination, not its **strength**. That is, for rapid "breed improvement," two or, formally speaking, even a smaller (non-integer!) number of sexes (for instance 1.08) is quite sufficient. One can only be glad that nature did not choose this «economical», but fortunately technically difficult, mode.

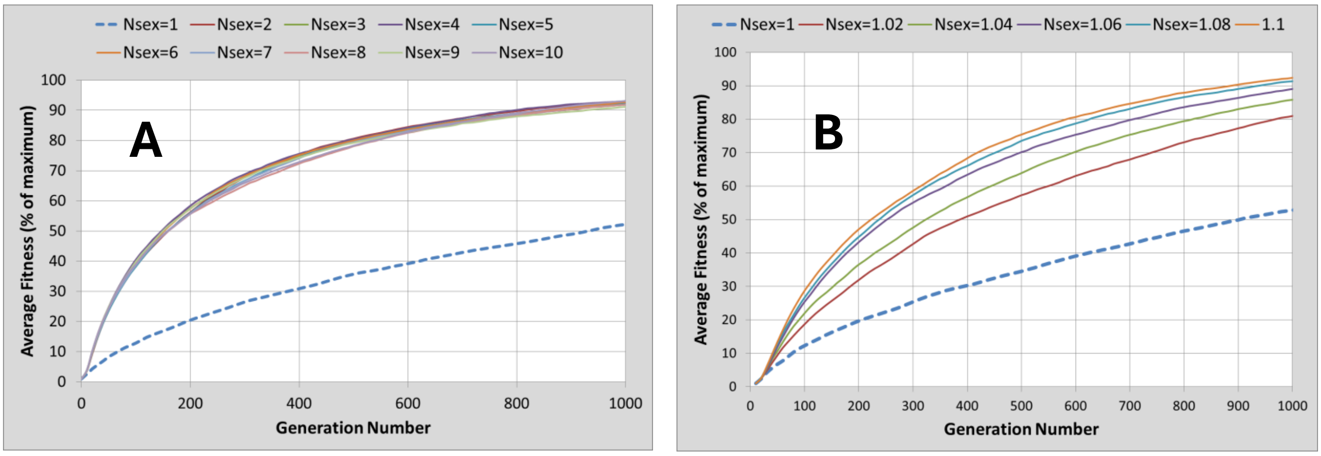

Figure 4. Sensitivity analysis of the rate of positive evolution on the number of sexes in genetic recombination.

4. Conclusions & Prospects

This article briefly addressed two issues. First, a new formalization was proposed for a simple ecological-genetic model of dynamics of heterogeneous population under natural selection. Based on its numerical analysis, a hypothesis was advanced regarding conservative or progressive theory explaining the advantages of sexual reproduction is most appropriate for which stage of species evolution. The second issue addressed was determining the theoretically optimal number of sexes to achieve the maximum rate of positive evolution. The main conclusion reached in this study is that the presence of genetic recombination itself, rather than its intensity, is of primary importance.

The results obtained and the conclusions drawn are, of course, subjective, somewhat speculative, and require further verification. However, this does not negate the need for further development of quantitative approaches and numerical methods applied to the theory of biological evolution. In particular, a promising direction for research is the creation and analysis of a comprehensive agent-based simulation model capable of describing all three stages of the "life cycle" of the evolutionary process of a heterogeneous population. Such a model should simultaneously consider environmental factors (resource limitations, population dynamics, environmental variability, Interspecific competition) and genetic aspects (frequency dynamics, recombination, intraspecific competition, selection, etc.).

In particular, to extend the results obtained using the proposed model, it is important to study the influence of other parameters (population size, mutation frequency, average number of offspring, that is, possibly a different effect of genetic recombination for species with r-strategy and K-strategy of reproduction). A separate challenge is incorporating epistasis into the model and its study. The term "epistasis" means here the non-additive effects of the combined influence of beneficial or harmful mutations in different parts of the genome on the fitness of an individual organism.

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