

The Origin of Two Sexes Through Optimization of Recombination Entropy Against Time and Energy

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Abstract Sexual reproduction in nature requires two sexes, which raises the question why the reproductive scheme did not evolve to have three or more sexes. Here we construct a constrained optimization model based on the communication theory to analyze trade-offs among reproductive schemes with arbitrary number of sexes. More sexes on one hand lead to higher reproductive diversity, but on the other hand incur greater cost in time and energy for reproductive success. Our model shows that the two-sexes reproduction scheme maximizes the recombination entropy-to-cost ratio, and hence is the optimal solution to the problem.

Keywords Sexual reproduction · Asexual reproduction · 1:1 sex ratio · Chromosomal crossover · Meiosis · Mitosis · Information entropy · Reproductive cost · Constrained optimization · Communication model of DNA replication · Evolutionarily stable strategy

1. Introduction

DNA replication is a stochastic process by which genomes mutate over time. The planetary environment of Earth is also a dynamical process which harbors life. Since these dynamical processes are otherwise uncoordinated, the time scale alignment between them are important—DNA replication must operate at a faster time scale than Earth's environmental changes so that life can establish itself in a seeming constant environment, relatively speaking, or more accurately, in punctuated equilibrium environments (Gould and Eldredge, 1977). As a result, organisms will accumulate too many unusable mutations during such punctuated equilibrium states to keep their replication machinery running indefinitely. Reproduction comes as a logical and, apparently, a practical solution to this necessary problem of replication—leaving a working copy behind to continue the DNA replication process.

Reproduction did not stop at cloning. There is a net information gain to reproduce sexually. This observation is self-evident when examining the difference between somatic

cell division (mitosis) and reproductive cell division (meiosis). The critical difference is the crossover process of homologous chromosomes employed by the latter. As a result, each gamete (sperm and ovum) acquires one set of haploid chromosomes consisting of exchanged gene alleles or DNA segments, gene or otherwise, from both parents. Instead of one working copy, sexually reproductive species give their offspring a combination of two working copies of genomes—enhancing the genetic diversity of individuals within species. At the organismic level however, there is a variety of costs to sexual reproduction. The immediate ones are in time and energy. The purpose of this paper is to quantify in what sense the sexual reproduction strategy is better and why the logic of having a greater reproductive diversity does not extend to three or more sexes.

2. Mathematical model

It is assumed in this paper that DNA recombination is the principle payoff of sexual reproduction and that information entropy at each segment of chromosomal exchange is the measurement to quantify the payoff. The biological importance of using entropy lies in the fact that it measures recombinatorial diversity at the molecular level. The scientific importance of using entropy lies in the fact it is observer and sampling time independent, a property necessary for being a physical law.

Recombinatorial entropy increases with the number of sexes, but it also incurs greater cost in time and energy for reproductive success. Our model is to find the number of sexes so that the entropy payoff per each unit of time and energy cost is maximal, or equivalently, the time and energy cost for each bit of recombinatorial entropy is minimal. In other words, it is to show that the 2-sexes reproduction scheme is the optimal solution to a constrained optimization problem. We begin with the constraints in terms of the following hypotheses, characterizing the crossover process.

Recombination Model:

1. There are n sexes and gametes (reproductive cells) from all n sexes are required to produce a zygote. Gametes contain haploid chromosomes and zygotes contains polyploid chromosomes, one set of haploid chromosomes from each parental sex.
2. Each gamete autosome (nonsex-determining chromosome) is a mixture of n parental homologous chromosomes (analogous to the crossover process in the case of two sexes).
3. The mixing probability at any exchanging site along any gamete autosome is the same for all parental sexes, i.e., the equiprobability $1/n$ from each parent's contribution to the mixing.
4. The sex ratio of any pair of sexes is 1:1.
5. The time and energy required to produce a zygote is proportional to the average number of randomly grouping n individuals that has exactly one sex each, called a *reproductive grouping* below. In other words, the time and energy cost for one reproductive success is inversely proportional to the probability that a random group of n individuals would be a reproductive grouping.

Hypotheses 1 and 2 are true for $n = 2$ as mentioned in the Introduction. As for Hypothesis 3, an exchanging segment can be a sequence of many bases or genes. The analysis

below applies to whatever length a segment may actually be. For this reason, an exchange site can be taken as a single nucleotide base for definitiveness throughout the discussion. The equiprobability part of Hypothesis 3 follows from the following facts. First, when a pair of mixed homologous chromosomes split, at any mixing segment one copy is from one sex and the other copy is from the opposite sex. Thus, there is always an equal number of exchanged copies from all sexes at any site and in any population of gametes. Second, the chromosomal crossover is independent from segment to segment so that each gamete contains a unique mix of its contributing sex's parental DNA. Further factoring the fact that it usually takes an overwhelming number of gametes for each fertilization, we can indeed assume the mixing to be completely thorough and thus the equiprobability. As a consequence, the information entropy (Shannon, 1948a, 1948b) of the chromosomal mixing is maximal, denoted by $H_n = \log_2 n$ in bits per segment. It can be considered to quantify the *per-site crossover diversity*, referred to as the *recombination entropy* below. The quantification applies to every crossover site of all gamete autosomes. As expected, the more parental sexes there are, the greater the recombinatorial diversity is. As a result of this hypothesis, the model does not discriminate against any sex's genetic contribution to reproduction.

Hypothesis 4 can be considered to be the 0th order approximation (in the sense of Shannon, 1948a, 1948b) to the sex ratio. In fact, for $n = 2$ it is a structural consequence to the fact that the sex-determining chromosomes, X and Y , are equally distributed in male gametes. It is not hard to concoct hypothetical schemes to maintain the equiratio for $n \geq 3$ cases. It should be noted that the equiratio condition is used below to calculate the reproductive cost in a definitive way. Changing the ratio alters the cost function from Hypothesis 5, that in turn results in alternative models which will not be considered further.

Hypothesis 5 should be treated as a possible scenario at an early evolutionary stage of sexual reproduction when the sexual identity of individual organisms was about to be well-defined and the main cost for reproduction was to get together a reproductive group mostly by chance. It can also be treated as a possible scenario at a later stage of the evolution when well-defined sexual characteristics cut down the chance encounter factor of the cost (e.g. opposite sexes attract) which on the other hand is off-set by like-sex interactions such as competition for mates and cooperation for offspring rearing. Nevertheless, the hypothesis should be treated as a "0th order" approximation of the cost. Cost reduction and cost overrun mechanisms can be treated as higher order corrections to the 0th order approximation. An analysis on the robustness of the model against corrections is given shortly. Notice that except for Hypothesis 5 all hypotheses are based on empirical, textbook facts for $n = 2$ (Becker et al., 2002).

The optimization objective is to maximize the recombination entropy H_n constrained to each unit of reproductive cost in time or/and energy. When combined the problem is to maximize the dimensionless *recombination entropy-to-cost* ratio $S_n = H_n/E_n$ over the number n of possible sexes, where E_n is the cost in dimensionless form (without the proportionality from Hypothesis 5). Equivalently, the problem is to minimize the time/energy cost for each unit of recombination entropy, $1/S_n = E_n/H_n$.

We already have $H_n = \log_2 n$ as mentioned above. To derive E_n , we proceed as follows. Without loss of generality from Hypothesis 4, assume each sex has the same number, M , of individuals with M being any large integer. Then there are $\binom{nM}{n} = \frac{(nM)!}{n!(nM-n)!}$ many ways to choose a group of n individuals from the total nM many individuals of all sexes.

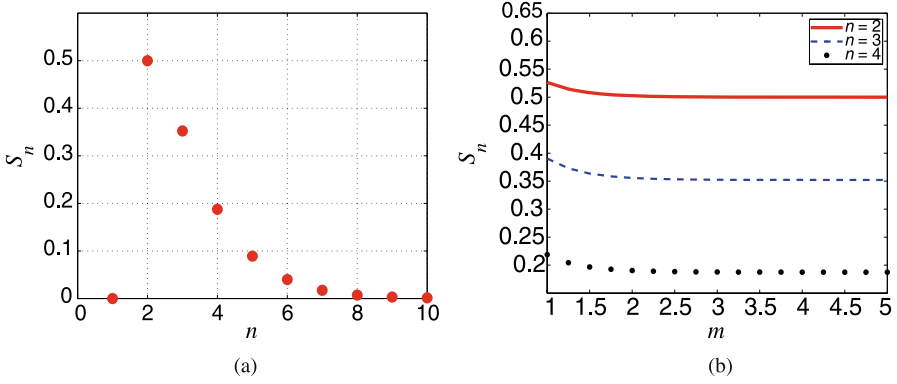


Fig. 1 (a) Infinite population. (b) Finite population with equal sex population $M = 10^m$.

Of which only M^n many are reproductive groupings by Hypothesis 1. Hence, for each reproductive grouping there are on average $\binom{nM}{n}/M^n$ many random ways to have a group of n individuals.

Throughout the discussion, all cost functions are for large population size when $M \sim \infty$ unless stated otherwise. So

$$E_n = \lim_{M \rightarrow \infty} \frac{\binom{nM}{n}}{M^n}.$$

To simplify, we have

$$\begin{aligned} E_n &= \lim_{M \rightarrow \infty} \frac{\binom{nM}{n}}{M^n} = \lim_{M \rightarrow \infty} \frac{nM(nM-1) \cdots (nM-n+1)}{n!M^n} \\ &= \lim_{M \rightarrow \infty} \frac{(n - \frac{1}{M})(n - \frac{2}{M}) \cdots (n - \frac{n-1}{M})}{(n-1)!} = \frac{n^{n-1}}{(n-1)!}. \end{aligned}$$

Note that the time and energy cost of producing a zygote is kE_n for some proportionality k by Hypothesis 5. Also, $1/E_n$ is the probability that a random group of n individuals would be a reproductive grouping. For $n = 1$, $E_1 = 1$ as it should be for asexual reproductive cost. For $n = 2$, $E_2 = 2$. That is, for each reproduction from two opposite sexes, there is one nonreproductive interaction between like sexes. Like-sex interactions can be in the forms of competition for mate or cooperation for offspring rearing or just plain random encountering. Thus E_n is a reasonable functional form for reproductive cost at the population level. Similar interpretation applies to $n > 2$ cases.

As a result, the recombination entropy-to-cost ratio is

$$S_n = \frac{H_n}{E_n} = \frac{(n-1)! \log_2 n}{n^{n-1}} = 0, 0.5, 0.3522, 0.1875, 0.0892, 0.0399, 0.0072,$$

for $1 \leq n \leq 7$, respectively. Figure 1a shows the graph of S_n (with $M = \infty$). Clearly, S_2 is the maximal solution. That $S_1 = 0$ is expected since asexual reproduction has zero recombination entropy. Figure 1b shows the graph of $S_n = M^n \log_2 n / \binom{nM}{n}$ as a function

of a finite equal sex population $M = 10^m$. The limiting ratios are good approximations beyond a modest size $M = 100$. Surprisingly, the 2-sexes reproductive strategy remains optimal even when the population size is small, $M = 10$. Notice also that the optimal solution S_2 is quite robust against the next best solution S_3 . In fact, the difference between S_2 and S_3 is about 30% and 43% against S_2 , S_3 , respectively. It implies that the model can tolerate high order corrections of considerable magnitude, especially to Hypothesis 5, and still keep S_2 as the optimal solution.

3. Discussion

The prediction that S_2 is the optimal solution is expected from any reasonable model. Some immediate implications of our model are nevertheless surprising. With the caveat that our recombination model is only a 0th order approximation, we have the following extrapolations. Since $S_2/S_3 \sim 1.43$, a 3-sexes reproductive strategy will reduce the per-exchange-site diversity that is due to sexual reproduction by 43% at every evolutionary stage. Equivalently, since the reciprocal $1/S_n$ measures the minimal time or/and energy required for each bit of sexual recombination entropy, a 3-sexes strategy will set back the evolutionary clock that is due to sexual reproduction by 1.5 billion years assuming life started 3.5 billion years ago (Schopf et al., 2002). All these are good reasons why a pure 3-sexes reproductive machinery (characterized by the crossover process of meiosis) has not been found in nature.

There are two ways to use the recombination model to compare and contrast the asexual and 2-sexes reproductive strategies since Hypotheses 1–5 can be thought either to apply trivially to the asexual case or not at all. In the first case, take for an example the case of multiparous mammals which could have their litters effortlessly cloned from one fertilized egg but did not. For them, each gamete's recombination entropy-to-cost remains at $S_2 = 0.5$ in bits per segment per cost v.s. $S_1 = 0$ for the would-be cloned embryos. Since $1/S_n$ measures the minimal time or/and energy required at the organismic level for each bit of sexual reproductive diversity, that $1/S_1 = \infty$ implies that such species, all mammals included, would never appeared if they adopted the asexual reproductive strategy. In this regard, our model is consistent with this known sexual reproductive reality.

In the second case, S_n cannot be used to quantify differences between the asexual and 2-sexes reproductive strategies because there is no recombinatorial entropy to begin with for the former. Therefore, they must be treated as two distinct categories second only to the primary purpose of DNA replication. Nevertheless, our model can offer one insight into the asexual reproductive strategy. Its continued usage can be explained by the principle reason that sexual reproduction is not a necessary but only a sufficient way to increase genetic diversities. Less complex organisms, such as some bacteria which under certain conditions can speed up their mutation rate, may be able to generate enough genomic diversity by DNA replication alone to compensate their lack of recombinatorial diversity. In this regard, asexual reproductive realities do not contradict our model.

This paper takes the view that evolution is a process of time percolation. Spacial percolation follows the least resistive passage through a porous space. Time percolation does the same except for the aspect that there are no predetermined or known optimal passages in time evolution. Biological processes appeared for their own right as optimal solutions to their immediate constraints that came before them. It is because of this modular view

on evolution that leads one to believe that life can be stripped down to its bare minimum, say to the “RNA world” in which single-strand RNA replicates itself without any of the functions that evolved later. It is also because of this idea of branched optimal modularization about evolution that constrained optimization models for biological systems can be constructed one piece a time. To demonstrate this methodology and to stay close to the main subject of this paper, we consider two more phenomena of reproduction.

Although a pure 3-sexes reproduction scheme (characterized by the crossover of three parental chromosomes) does not exist in nature, there are indications that sexual reproduction is not purely 2-sexual either. Under certain conditions some bacteria can freely exchange genetic materials. It is a plausible theory that bacterial life form was an earlier branch of all life forms on Earth (with a possible exception of viruses) and its genetic exchange mechanism was the precursor to the sexual reproduction scheme. Such schemes may be modeled by the following model.

Exchange Model:

- (a) Any two individual organisms can exchange genetic materials.
- (b) The information gain to exchange one nucleotide base among n individuals is $\log_2 n$ bits per base.
- (c) The time and energy needed to exchange one nucleotide base among n individuals is proportional to the maintenance or existential cost of the n individuals.

Similar to the recombination model, the entropy-to-cost ratio, without the dimensional proportionality is,

$$S_n = \frac{H_n}{E_n} = \frac{\log_2 n}{n} = 0, 0.5, 0.5283, 0.5, 0.4644, 0.4308, 0.4011, 0.3750,$$

for $1 \leq n \leq 8$, respectively. It shows having 3 exchanging partners is about 6% better than having 2 or 4 exchanging partners.

After bacteria on the evolutionary tree came fungi. Although there are no male or female fungi, sexually reproducing fungi reproduce by fusing two nuclei of hyphae to produce diploid zygote which undergoes meiosis to form haploid spores. The cost function is not strictly that of the exchange model because the mating strains need to come together before nuclei fusion can take place. It is not that of the recombination model either because of the lack of sex distinction. The cost function can be thought as a combination of both. More specifically, we can consider the weighted cost function of the following form:

$$E_n = (1 - p) \frac{n^{n-1}}{(n-1)!} + pn,$$

where $0 \leq p \leq 1$. That $E_1 = 1$ holds since it must satisfy the asexual reproduction cost condition as a default. The corresponding reproductive entropy-to-cost ratio is

$$S_n = \frac{H_n}{E_n} = \frac{\log_2 n}{(1 - p) \frac{n^{n-1}}{(n-1)!} + pn}.$$

Figure 2a shows that S_2 is optimal for a significant range of the weighting parameter $0 \leq p < 0.8870$, and that S_3 is optimal only when the exchange model is weighted heavily

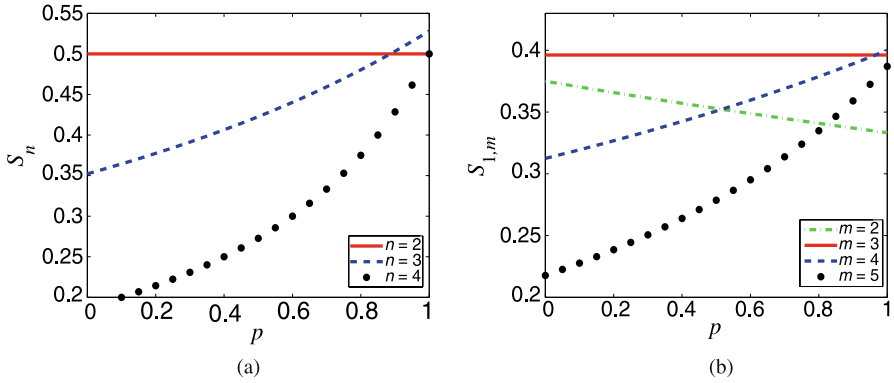


Fig. 2 (a) The Recombination Model with mixed cost. (b) The Multiparous Model with mixed cost.

with $0.8870 < p \leq 1$. Thus as sexual differentiation further developed so that forming a reproductive group became critical for reproductive success, the recombination cost must weigh more heavily, and the exchange-recombination mixed model predicted the emerging of the pure 2-sexes scheme as the optimal reproductive strategy.

Even after the establishment of the pure 2-sexes reproductive machinery for higher organisms, reproduction is not purely monogamous. Multiparous females mate with several males so that members of each litter may have different fathers. The exchange-recombination model does not apply to this phenomenon because the latter evolved well after the establishment of the 2-sexes mechanism. According to our time percolation modeling methodology, the multiparous mechanism should be modeled based on the *existence* of 2-sexes, but not entangled with the *origin* of 2-sexes. Moreover, the information gain to have more male mates for one litter is for the members of the litter at the whole individual level while the recombination entropy gain remains the same for each member at the molecular level. Specifically, we have the following model:

Multiparous Model:

- (i) Each member of a multiparous litter is the offspring of one of $m \geq 1$ many equally probable fathers.
- (ii) The male and female sex ratio is 1:1.
- (iii) The time and energy needed to produce a zygote is inversely proportional to the probability that a random group of $1 + m$ individuals has one female and m males.

In this case, the *multiparous entropy* is simply

$$H_{1,m} = \log_2 m,$$

because of the equal probability assumption of Hypothesis (i). Thus, with one father ($m = 1$), there is no multiparous entropy gain ($H_{1,1} = 0$) as expected. As for the cost, assume there are M individuals of each sex for large $M \sim \infty$. There are $\binom{2M}{m+1}$ many ways to have a group of $m + 1$ individuals, of which there are $M \binom{M}{m}$ many ways to have

a group of 1 multiparous female and m multiparous males. Thus, the dimensionless cost function is approximately

$$E_{1,m} = \lim_{M \rightarrow \infty} \frac{\binom{2M}{m+1}}{M \binom{M}{m}} = \frac{2^{m+1}}{m+1},$$

after canceling out same factors and taking the limit in a way similar to the derivation of the recombination model's cost function. $E_{1,m}$ satisfies the pure 2-sexes condition $E_{1,1} = E_2 = 2$ when there is only one father. The reproductive entropy-to-cost ratio is

$$S_{1,m} = \frac{(m+1) \log_2 m}{2^{m+1}} \\ = 0, 0.3750, 0.3962, 0.3125, 0.2177, 0.1414, 0.0877, 0.0527,$$

for $1 \leq m \leq 8$, respectively. That is, having 3 fathers maximizes the multiparous payoff over cost. Similar to the mixed exchange-recombination cost assumption, it is reasonable to consider the mixed multiparous cost function which is a weighted combination of the reproductive grouping cost, $\frac{2^{m+1}}{m+1}$, and the maintenance cost, $m+1$, both in dimensionless forms,

$$E_{1,m} = (1-p) \frac{2^{m+1}}{m+1} + p(m+1).$$

Figure 2b shows that having 3 fathers is optimal for the range of $0 \leq p < 0.9661$ and having 4 fathers is optimal for the rest of the weight parameter.

With regard to the concept of biological diversity, we take the view that the grand scope of it is the sum of many constituent parts, e.g., the constituent diversity from the combination of nucleotides for DNA, that from the 20 amino acids for proteins, that from the recombination of chromosomes for reproduction, and so on. The grand term is inevitably vague, but its individual parts can be made precise, such as the DNA replication entropy we used for the DNA replication and the various reproductive entropies we used here for reproduction. In addition to their definitiveness, the constituent parts are intrinsically independent from the others in the evolutionary time percolation sense discussed above. For example, any reproductive entropy is delineated from the replication entropy and the dependence of the former on the latter is only insofar as that reproduction evolved after replication rather than the other way around.

Arguably, in addition to these constituent diversities mentioned, there are many more mechanistic sources contributing to biological diversity, such as gene splicing, post-transcriptional editing, post-translational editing, small RNA interference and regulation, retroviral reverse transcription, heritable regulators of expression such as methylation and acetylation, and the rate of mutations, etc. Some of which may or may not be constant in time. Nevertheless, the approach adopted in this paper can conceivably be applied to construct compartmentalized models for these functions and processes. Each can be modeled alone or in combinations with others. To do so, one presumably has to consider some mean averages to quantify the information exchanged within or gained by the processes, or even to define some time dependent diversity measurements. In such models, aggregating varying quantities or over different phases is probably inevitable, at least for the initial

approximations of these processes. In any case, to incorporate these processes into new models or to expand them into larger ones, one has to formulate their mechanics in terms of hypotheses like we did here. Each new formulation can bring out a different payoff measurement. If the measurement is for diversity, it will be simply added to the grand notion of diversity, with no or little effect to other constituent parts.

The conceptual model for our model is essentially the same as that for DNA replication introduced in (Deng, 2005, 2006). We treated the latter as a communication channel when the DNA bases, A, T, G, C , are paired one at a time with their complementary bases along the single strands of the double helix. We treated it further as an all-purpose channel for which the mean base distribution $1/n = \sum_{k=1}^n p_k/n$ is used for the ensemble of all genomes, each with a particular distribution p in n bases. As the 0th order approximation (Shannon, 1948a, 1948b), the equiprobability gives rise to the maximal per-base diversity in entropy $\log_2 n$, exactly the same quantity as the per-exchange-site reproduction entropy H_n . We then showed that the mean transmission/replication rate $R_n = \log_2 n/T_n$, with T_n the mean base pairing time, is maximal for $n = 4$ provided that the pairing time of the hydrogen bonds of the GC pair is between 1.65 and 3 times that of the AT pair. Although our reproduction models here do not mechanistically fit to a communication model as neatly as the replication model does, the apparent analogy is hard to miss. For example, each reproduction from the recombination model can be thought as one packet transmission, and each packet contains a total information $H_n \times L$, where L is the number of mixing sites along gamete chromosomes. Since it is more natural to consider the whole reproduction cost E_n in time or/and energy rather than to unitize it, E_n/L , we are led to the normalized recombination entropy-to-cost ratio $S_n = H_n/E_n$, which is now clearly proportional to the mean transmission rate R_n if we think the reproduction as a channel and E_n as the time.

Based on the game theory (Owen, 1968; Bomze and Pötscher, 1989), the idea of evolutionarily stable strategy (ESS, Smith, 1982) was also used to explain sex evolution at the phenotypic level, in particular the problem of 1:1 sex ratio. Our method is based on Shannon's communication theory (Shannon, 1948a, 1948b). However, both methods are rooted in constrained optimizations. The game theory is about maximizing fitness payoffs with play rule constraints. The communication theory is about maximizing information with constraints in transmission time or storage space or energy consumption. Our view is that ESS is a more plausible theory for species behavioral interaction at the community level. In contrast, the 1:1 sex ratio strategy most sexually reproducing organisms adopt has a more fundamental root at the molecular level for reproduction. Otherwise, ESS would have to predict unequal sex ratio for species such as African lions and elephants for which a large portion of males do not procreate.

The stochastic formulation of both replication and reproduction models implies the following. (1) Since parents cannot choose the genetic composition of their offspring (Hypothesis 3) and offspring cannot choose its parents (Hypothesis 5), the notion of "individual ownership of DNA" cannot be well defined. Thus each organism is only an accidental and temporary carrier of the protogenic DNA at the origin or origins of life, echoing with Darwin's "common descent" theory (Darwin, 1859). (2) The maximal recombination entropy in bits per base or segment resides in every organism in a suspended probabilistic state and at every moment of recombination in time, in the averaged sense of the entropy definition. It is by replication and reproduction that the maximal entropies are expressed

through time, expanded in length, and multiplied in space. (3) Because the 4-base replication strategy and the 2-sexes reproduction strategy are optimal strategies, evolution is where it should be in time as far as the part of the biological diversity due to replication and reproduction is concerned, though individual organisms and species are accidental. (4) Since Hypothesis 5 leads to the notion of minimizing reproductive cost, our model is consistent with the observation that sex-specific features have the effect of cost reduction from same sex interactions.

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