

Neutral Mutations Are Substituted at the Rate They Arise, Whatever the Size of the Population

— a larger population produces more mutations, but the probability that each spreads through falls in exactly the same proportion — the separator is whether one asks about the probability that one mutation spreads through or the number of substitutions per generation — [Paper 879]

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Abstract

It is easy to assume that larger populations evolve faster because more mutations arise in them. This paper counts the rate at which mutations spread through a whole population, varying population size and advantage. No new theorem or law is claimed. First, neutral mutations are substituted at the rate they arise: the substitution rate divided by μ is **0.946667**, **1.041667** and **0.983333** for population sizes 10, 50 and 200 (Section 2). Second, and this is the core. Making the population 20 times larger does not change the neutral rate: the ratio of rates between sizes 200 and 10 is **1.038732** (Section 2). Third, advantageous mutations are faster in larger populations: with selection coefficient $+0.01$ the rate over μ is **1.121667**, **1.568333** and **3.914167**, and the ratio between 200 and 10 is **3.489599** (Section 3). Fourth, harmful mutations are slower in larger populations: with -0.01 it is **0.977500**, **0.598333** and **0.082500**, a ratio of **0.084399** (Section 3). Fifth, the counts agree with the formula: population size $\times \mu \times$ fixation probability gives 1 for neutral, **1.092371**, **1.566262** and **4.034153** for advantageous, and **0.912425**, **0.587835** and **0.075381** for harmful, matching the counts in direction and size (Section 3). Sixth, the separator is whether one asks about the probability that one mutation spreads through or the number of substitutions per generation: the probability falls in larger populations, but the number arising rises in the same proportion, so the count does not change (Section 4). **Keywords:** neutral mutation, substitution rate, fixation probability, population size, genetic drift.

Scope of this paper (scope note): No new theorem or law is claimed: that the substitution rate of neutral mutations equals the mutation rate independent of population size, and that for advantageous or harmful mutations the fixation probability changes with the product of population size and selection coefficient, are both known in population genetics. No real values are claimed: μ , selection coefficients and population sizes are model values matching no gene and no species. The model is not widened: a population with one set of genes (haploid) and non-overlapping generations is assumed; diploidy, overlapping generations and linkage between genes are not included. No dates are estimated: deriving divergence dates from substitution counts is not treated. Relation to earlier papers: Paper 478 showed that whether being advantageous matters is decided by the size of the population. This paper stands beside it. There, the probability that one advantageous mutation spreads through was counted. Here, the number of substitutions per generation is counted, showing that for neutral mutations it does not depend on population size. What is added is counting 60000 generations for three population sizes and three levels of advantage, measuring a ratio of 1.038732 for a 20 times larger population in the neutral case, measuring ratios of 3.489599 and 0.084399 for advantageous and harmful mutations, and placing the separator on one probability versus the number per generation.

1. Notation and the Question

Setting: in a population of N individuals, on average $N\mu$ new mutations arise each generation, each in one individual. The share p of individuals carrying a mutation becomes $p(1+s)/(1+ps)$ under selection coefficient s , then N individuals are drawn binomially for the next generation. A mutation that has spread through the whole population is counted as substituted.

$$\text{substitution rate} \approx N\mu \times u(s, N), \quad u(0, N) = \frac{1}{N}, \quad u(s, N) = \frac{1 - e^{-2s}}{1 - e^{-2Ns}}$$

u is the probability that one mutation spreads through. With $\mu = 0.02$ and 60000 generations, the number of substitutions divided by the number of generations gives the rate.

Question: are substitutions faster in larger populations?

2. Neutral Mutations

Computation 2.1: with $s = 0$, substitutions were counted for different population sizes.

population size	substitutions	rate $\div \mu$	formula
10	1136	0.946667	1.000000
50	1250	1.041667	1.000000
200	1180	0.983333	1.000000

Observation 2.2

this is the core. Making the population 20 times larger does not change the neutral rate. The rate over μ is near 1 for all three, and the ratio between sizes 200 and 10 is 1.038732: a larger population produces more mutations, $N\mu$ per generation, but the probability that each spreads through falls as $1/N$ in exactly the same proportion. Multiplied together, μ remains.

3. Advantageous and Harmful Mutations

Computation 3.1: the same counts were made with $s = +0.01$ and $s = -0.01$.

selection coefficient	population size	rate $\div \mu$	formula
+0.01	10	1.121667	1.092371
+0.01	50	1.568333	1.566262
+0.01	200	3.914167	4.034153
-0.01	10	0.977500	0.912425
-0.01	50	0.598333	0.587835
-0.01	200	0.082500	0.075381

Observation 3.2

for advantageous and harmful mutations, the rate changes greatly with population size. The ratio between sizes 200 and 10 is 3.489599 for advantageous and 0.084399 for harmful mutations: advantageous mutations are less often lost by chance in large populations, and harmful ones almost never spread through by chance there. The counts matched the formula in direction and size.

4. The Separator

Observation 4.1

the separator is whether one asks about the probability that one mutation spreads through or the number of substitutions per generation. The probability that one neutral mutation spreads through falls as $1/N$ in larger populations: the number per generation is its product with the number arising, $N\mu$, so N cancels. Ask about the probability and population size matters; ask about the number and it does not.

Observation 4.2

placed beside Paper 478.478 showed that whether being advantageous matters is decided by population size. There the probability that one advantageous mutation spreads through was counted. Here the number per generation was counted, showing that population size cancels only for neutral mutations. For advantageous or harmful ones, 478's difference in probability appears directly as a difference in rate.

Observation 4.3

what is not said. Real evolutionary rates of genes or species, diploidy, overlapping generations and date estimation are not treated. What is shown is that the substitution rate of neutral mutations does not depend on population size.

5. Census and Closing

1. rate $\approx N\mu \times u$ (Section 1): number arising times probability.
2. neutral $u = 1/N$ (Section 1): smaller when larger.

3. neutral: **0.946667**, 1.041667, 0.983333 (Computation 2.1): **divided by μ** .
4. ratio **1.038732** for 20 times the size (Observation 2.2): **the core**.
5. advantageous: **3.914167** (Computation 3.1): **size 200**.
6. advantageous ratio **3.489599** (Observation 3.2): **faster when larger**.
7. harmful: **0.082500** (Computation 3.1): **size 200**.
8. harmful ratio **0.084399** (Observation 3.2): **slower when larger**.
9. counts and formula agree in direction (Observation 3.2): **independent**.
10. one probability, or number per generation (Observation 4.1): **the separator; Paper 478**.

Closing: Neutral mutations are substituted at the rate they arise, whatever the size of the population. Over 60000 generations, the rate divided by μ is 0.946667, 1.041667 and 0.983333 for sizes 10, 50 and 200, and even 20 times the size gives a ratio of 1.038732, because a larger population produces more mutations, but the probability that each spreads through falls in exactly the same proportion. For advantageous mutations the ratio is 3.489599 and for harmful ones 0.084399, changing greatly with population size: population size cancels only for neutral mutations. Placed among the earlier papers: beside the probability of one mutation that Paper 478 counted, we placed the number of substitutions per generation. To be honest: the model is haploid with non-overlapping generations, and μ and the selection coefficients are model values.

References

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