

With Overlapping Generations, Time to Fixation and the Chance a Favourable Mutation Fixes Both Approach Half

— the generations until a neutral mutation fixes come near half those of a population without overlap, the ratio of fixation probabilities of a favourable mutation approaches 0.5 from above, and the neutral fixation probability does not change —the separator is whether a quantity is counted by the fluctuation per generation, or is the neutral $1/N$ that does not move — [Paper 983]

Yuuki YAMAGISHI (山岸 勇輝)

Yamagishi Complexity Torus Lab, Japan

September 2026

YOI: <https://www.yamagishiyuuki.com/yoi/983>

— *From thinking to syncing.* —

Abstract

Neutral mutations are substituted at the rate they arise, whatever the size of the population (Paper 879). Only populations with non-overlapping generations were treated there, and overlapping generations were not included. For haploid populations of N individuals, this paper compares, by exact solution of the transition matrix, the model with non-overlapping generations (Paper 879) and a model with overlapping generations in which one individual is born and one dies at each step (the Moran model, N steps to a generation). No new theorem or law is claimed. First, the generations until a neutral mutation fixes come near half when generations overlap: counting only runs that fixed, the overlapping model took $N - 1$ generations (9, 19, 49) and the non-overlapping model 17.495620, 37.272064 and 96.971198, non-overlapping over overlapping being 1.943958, 1.961688 and **1.979004** ($N = 10, 20, 50$) (Section 3). Second, the ratio of fixation probabilities of a favourable mutation approaches 0.5 from above: overlapping over non-overlapping ran from **0.957342** ($N = 10, s = 0.01$) to **0.508654** ($N = 200, s = 0.05$) over six settings, all above 0.5, and smaller for larger Ns between groups of different Ns (Section 2). Third, the ratio is not set by Ns alone: of the two settings with $Ns = 0.5$, $N = 10, s = 0.05$ gave 0.825819 and $N = 50, s = 0.01$ gave 0.807811, differing by **0.018007** (Section 2). Fourth, the neutral fixation probability does not change, and the fluctuation per generation is larger with overlap: the neutral fixation probability agreed with $1/N$ within 10^{-10} in both models. The variance of frequency after one generation from frequency $1/2$ was 1.829272 times larger with overlap ($N = 10$) and **1.961297** times ($N = 50$) (Section 4). Fifth, the separator is whether a quantity is counted by the size of the fluctuation in frequency per generation, or is the neutral $1/N$ that does not move: in the same direction as the variance ratio per generation approaching 2, the ratio of generations to fixation approached 2 and the ratio of fixation probabilities of a favourable mutation approached 0.5. The neutral $1/N$ did not move. It is not shown that the two quantities are set by the variance ratio alone (Section 5). **Keywords:** overlapping generations, Moran model, fixation probability, generations to fixation, population genetics, transition matrix.

Scope of this paper (scope note): No new theorem or law is claimed: the closed form for the fixation probability in the Moran model, the number of steps a neutral mutation takes to fix in the Moran model, and that in models with overlapping generations the chance fluctuation per generation is larger so that the effective population size counts smaller, are known in population genetics. No real values are claimed: population sizes of 10, 20, 50 and 200 and advantages of 0.01 and 0.05 are model values and correspond to no gene or species. Counting a generation as N steps is a convention of this paper. The model is not extended: haploids only; diploids, age structure, differing generation lengths and linkage between genes are not included. The mechanism is not asserted: the variance ratio per generation was measured, but it is not shown that generations to fixation and fixation probabilities are set by that ratio alone. Relation to earlier papers: Paper 879, in its scope note, did not extend the model, taking haploids with non-overlapping generations and leaving out diploids, overlapping generations and linkage between genes; this paper sits in the seat of overlapping generations (no earlier occupant; the diploid seat of the same scope note was taken by Paper 982). Paper 879 showed that neutral mutations are substituted at the rate they arise, whatever the size of the population. Here the change in generations to fixation and in the fixation probability of a favourable mutation when generations overlap is counted. Paper 982 showed that in diploids the degree of dominance divides the fixation probability of a favourable mutation, and that additive ones come near half the haploid value: the non-overlapping values compared here were, as in Paper 982, solved exactly with the transition matrix. What is added: finding fixation probabilities exactly for both models in six settings, measuring that the ratio is not set by N s alone, finding the generations until a neutral mutation fixes, over runs that fixed, exactly, comparing the variance of frequency per generation, and placing the separator on “counted by the fluctuation, or the unmoving $1/N$ ”.

1. Notation and the Question

Two models: in a haploid population of N individuals, let k be the number of mutants, s the advantage and $r = 1 + s$. The non-overlapping model (Paper 879) takes $p = k/N$ to $p' = pr/(1 + ps)$ in a generation and redraws N individuals binomially. The overlapping model (the Moran model) at each step has one individual, chosen in proportion to fitness, leave one offspring, and one individual, chosen uniformly, die. The probabilities that k rises or falls by one in a step are

$$\frac{rk}{rk + N - k} \cdot \frac{N - k}{N}, \quad \frac{N - k}{rk + N - k} \cdot \frac{k}{N}$$

and N steps are counted as a generation. The closed form for fixation from one copy in the Moran model is $(1 - 1/r)/(1 - r^{-N})$.

Method: for both, absorption probabilities of the transition matrix were solved as linear equations. The mean number of steps over runs that fixed was solved with the matrix reweighted as $Q_{ij}u_j/u_i$ by the absorption probability u (the Doob transform). The variance of frequency per generation was found from $k = N/2$ after one generation of the non-overlapping model and after N steps of the overlapping model.

Question: when generations overlap, how do the fixation probability of a favourable mutation and the generations until a neutral mutation fixes change?

2. Fixation Probability of a Favourable Mutation

Computation 2.1: probability of fixation from one copy (exact transition-matrix solution).

N	s	Ns	non-overlapping	overlapping	overlapping over non-overlapping
10	0.01	0.1	0.109195	0.104537	0.957342
10	0.05	0.5	0.149352	0.123338	0.825819
50	0.01	0.5	0.031270	0.025260	0.807811
50	0.05	2.5	0.094116	0.052168	0.554301
200	0.01	2.0	0.020097	0.011469	0.570671
200	0.05	10.0	0.093623	0.047622	0.508654

The overlapping values agreed with the closed form within 10^{-10} in four settings ($N = 10, 50$). Using the diffusion formula of Paper 879 for the non-overlapping model gives 0.109237 and 0.150545 for $N = 10$ and 0.020171 and 0.095163 for $N = 200$, and overlapping over that formula ran from 0.956971 ($N = 10, s = 0.01$) to 0.500426 ($N = 200, s = 0.05$).

Observation 2.2

the ratio approaches 0.5 from above and is not set by Ns alone. All six ratios were above 0.5, and between the five groups of different Ns the ratio was smaller for larger Ns : the two with $Ns = 0.5$ gave 0.825819 and 0.807811, differing by 0.018007, the larger N being smaller.

3. Generations Until a Neutral Mutation Fixes

Computation 3.1: neutral ($s = 0$) mean generations from one copy over runs that fixed.

N	overlapping	non-overlapping	diffusion formula for non-overlapping	non-overlapping over overlapping
10	9.000000	17.495620	18.964893	1.943958
20	19.000000	37.272064	38.982904	1.961688
50	49.000000	96.971198	98.993266	1.979004

The overlapping model agreed with $N - 1$ generations within 10^{-8} for all three N . The diffusion formula is $-2N(1 - p) \ln(1 - p)/p$ with $p = 1/N$, and was longer than the exact generations for all three N .

Observation 3.2

generations to fixation come near half with overlap. Non-overlapping over overlapping was 1.943958, 1.961688 and 1.979004 for $N = 10, 20$ and 50 , approaching 2 as N grows: fixation takes fewer generations with overlap, and the neutral fixation probability was $1/N$ in both (Section 4).

4. Neutral Fixation Probability and Fluctuation per Generation

Computation 4.1: neutral fixation probability and variance of frequency after one generation from $k = N/2$.

N	neutral fixation (overlapping)	(non- overlapping)	variance (overlapping)	variance (non- overlapping)	ratio
10	0.100000	0.100000	0.04573180	0.02500000	1.829272
50	0.020000	0.020000	0.00980649	0.00500000	1.961297

The neutral fixation probability agreed with $1/N$ within 10^{-10} in both models. The non-overlapping variance is $p(1 - p)/N$.

5. The Separator

Observation 5.1

the separator is whether a quantity is counted by the size of the fluctuation in frequency per generation, or is the neutral $1/N$ that does not move when that fluctuation changes. The variance ratio per generation was 1.829272 for $N = 10$ and 1.961297 for $N = 50$, approaching 2, and in the same direction the ratio of generations to fixation approached 2 and the ratio of fixation probabilities of a favourable mutation approached 0.5: the neutral fixation probability $1/N$ was the same in both models. It is not shown that the two quantities are set by the variance ratio alone. The favourable-mutation ratio was not set by Ns alone (a difference of 0.018007), and the variance ratio per generation also changed with N (1.829272 and 1.961297).

Observation 5.2

what is not said. Diploids, age structure, differing generation lengths, generations and lifespans of real organisms, and limit formulas are not treated. What is shown is how far, for the same number of individuals, generations to fixation and the fixation probability of a favourable mutation differ between the two models in exact transition-matrix solutions.

6. Roll Call and Closing

1. transition matrices of the two models (Section 1): exact solution and the Doob transform.
2. ratio of generations to fixation **1.979004** ($N = 50$) (Computation 3.1): near half with overlap.
3. ratio of fixation probabilities **0.957342** to **0.508654** (Computation 2.1): approaches 0.5 from above.
4. a difference of **0.018007** at $Ns = 0.5$ (Observation 2.2): not set by Ns alone.
5. variance ratio per generation **1.961297** (Computation 4.1): the neutral $1/N$ is the same.
6. counted by the fluctuation, or the unmoving $1/N$ (Observation 5.1): the separator; the scope note of Paper 879.

Closing: With overlapping generations, time to fixation and the chance a favourable mutation fixes both approach half. Solved exactly with transition matrices, a neutral mutation that fixed took $N - 1$ generations in the overlapping model and 1.943958 to 1.979004 times that in the non-overlapping model: the ratio of fixation probabilities of a favourable mutation (overlapping over non-overlapping) ran from 0.957342 to 0.508654, all above 0.5, and the two settings with $Ns = 0.5$ differed by 0.018007. The neutral fixation probability was $1/N$ in both, and the variance of

frequency per generation was 1.961297 times larger with overlap ($N = 50$). The separator is whether a quantity is counted by the size of the fluctuation in frequency per generation, or is the neutral $1/N$ that does not move when that fluctuation changes. Placed among the earlier papers: to the model of haploids with non-overlapping generations counted in Paper 879, the overlapping generations Paper 879 did not include were added. The diploid seat of the same scope note was filled by Paper 982. To be honest: two models with the same number of individuals were solved with transition matrices and set side by side. The mechanism is not reduced to the variance ratio alone. How much fixation changes when generations overlap, and no further.

References

1. Ewens, W. J. (2004). *Mathematical Population Genetics I: Theoretical Introduction* (2nd ed.). Springer.
 2. Moran, P. A. P. (1958). Random processes in genetics. *Proceedings of the Cambridge Philosophical Society*.
 3. Yamagishi, Y. (2026). *Neutral Mutations Are Substituted at the Rate They Arise, Whatever the Size of the Population* [Paper 879]. YOI: <https://www.yamagishiyuuki.com/yoi/879>
 4. Yamagishi, Y. (2026). *Dominance Divides the Fixation of Favourable Mutations in Diploids, and Additive Ones Come Near Half the Haploid Value* [Paper 982]. YOI: <https://www.yamagishiyuuki.com/yoi/982>
-

— *From thinking to syncing.* —

Yuuki YAMAGISHI (山岸 勇輝)

© 2026 Yamagishi Complexity Torus Lab, Japan · Licensed under Creative Commons Attribution 4.0 International (CC BY 4.0)