

Dominance Divides the Fixation of Favourable Mutations in Diploids, and Additive Ones Come Near Half the Haploid Value

— solved exactly with the transition matrix, recessive, additive and dominant mutations fix in increasing order, and the diffusion formula exceeds the exact solution —the separator is whether the advantage shows already in heterozygotes or stays hidden until homozygotes appear — [Paper 982]

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— *From thinking to syncing.* —

Abstract

Neutral mutations are substituted at the rate they arise, whatever the size of the population (Paper 879). Only haploid populations with one set of genes were treated there, and diploids were not included. For a diploid population of N individuals, this paper finds the probability that an advantageous mutation fixes from a single copy, varying the degree of dominance h , by the diffusion formula, by the exact solution of the transition matrix and by random simulation, and compares it with a haploid population of the same number of individuals. No new theorem or law is claimed. First, the degree of dominance divides the fixation probability: the exact solution for $N = 50$, $s = 0.05$ gave recessive ($h = 0$) 0.025104, additive ($h = 0.5$) 0.048439 and dominant ($h = 1$) 0.080208, dominant over recessive being **3.194988**. For $N = 200$, $s = 0.01$ it was **2.886501** (Section 3). Second, an additive mutation comes near half the haploid value for the same number of individuals: additive over haploid was **0.514679** for $N = 50$ and 0.502932 for $N = 200$ (Section 4). Third, the diffusion formula exceeds the exact solution: formula over exact was 1.006470 (recessive) to **1.025576** (dominant) for $N = 50$, $s = 0.05$, and 1.001424 to 1.005470 for $N = 200$, $s = 0.01$. The haploid formula of Paper 879 was also 1.017984 and 1.003687 times exact (Section 3). Fourth, simulation agrees with the exact solution, and coming out below the diffusion formula was the formula's departure: 100000 runs ($N = 50$) gave 0.024490, 0.047330 and 0.080530, differing from exact by -1.24 , -1.63 and **0.38** standard errors (Section 3). Fifth, the separator is whether the advantage shows already in heterozygotes or stays hidden until homozygotes appear: the first copy sits in a heterozygous individual, whose advantage is hs . For a recessive mutation that is 0; additive over recessive was **1.929524** and dominant over additive **1.655842** for $N = 50$ (Section 5). **Keywords:** diploid, dominance, fixation probability, population genetics, diffusion formula, Wright-Fisher model.

Scope of this paper (scope note): No new theorem or law is claimed: finding the fixation probability of an advantageous mutation in diploids by the diffusion formula, that recessive mutations fix less readily than dominant ones, and that the heterozygote advantage of an additive mutation is half, are known in population genetics. No real values are claimed: population sizes of 50 and 200, advantages of 0.05 and 0.01, and degrees of dominance 0, 0.5 and 1 are model values and correspond to no gene or species. The model is not extended: diploids with random mating and non-overlapping generations are taken; inbreeding, sex ratio, overlapping generations, linkage between genes and the mechanism of dominance are not included. No limit is stated: formulas for the limit of large populations were not checked and are not written. Only numbers for two settings are set out. Relation to earlier papers: Paper 879, in its scope note, did not extend the model, taking a population with one set of genes (haploid) with non-overlapping generations and leaving out diploids, overlapping generations and linkage between genes; this paper sits in the seat of diploids (no earlier occupant). Paper 478 showed that whether being advantageous matters is decided by the size of the population. Here the change in fixation probability for the same advantage, depending on whether it shows in heterozygotes, is counted. What is added: finding fixation probabilities for three degrees of dominance and two settings by the diffusion formula and the exact transition-matrix solution, measuring that the diffusion formula exceeds the exact solution, confirming that simulation agrees with the exact solution, comparing with haploids of the same number of individuals, and placing the separator on “shown in heterozygotes, or hidden”.

1. Notation and the Question

Model: in a diploid population of N individuals ($2N$ gene copies), each generation applies selection to random-mating genotype frequencies and redraws $2N$ copies binomially (the Wright-Fisher model). With genotype fitnesses AA $1 + s$, Aa $1 + hs$ and aa 1 and mutant copy frequency p , the frequency after selection is

$$p' = \frac{p^2(1 + s) + p(1 - p)(1 + hs)}{p^2(1 + s) + 2p(1 - p)(1 + hs) + (1 - p)^2}$$

starting from one copy ($p = 1/(2N)$). Haploids have N copies with $p' = p(1 + s)/(1 + ps)$ (the model of Paper 879).

Three ways: the diffusion formula

$$u = \frac{\int_0^{1/(2N)} G(x) dx}{\int_0^1 G(x) dx}, \quad G(x) = \exp\left(-4Ns(hx + (1 - 2h)x^2/2)\right)$$

was integrated with the trapezoid rule on 200001 points. The exact solution solved the absorption probabilities of the transition matrix over copy numbers 0 to $2N$ (row sums off by at most 1.7×10^{-13}) as linear equations. Simulation used 100000 runs for $N = 50$, $s = 0.05$.

Question: for the same advantage, how much does the degree of dominance change the fixation probability, and how does it differ from haploids?

2. The Diffusion Formula

Computation 2.1: fixation probabilities by the diffusion formula.

setting	$h = 0$	$h = 0.5$	$h = 1$	haploid N copies	haploid $2N$ copies
$N = 50, s = 0.05$	0.025267	0.049101	0.082259	0.095808	0.095167
$N = 200, s = 0.01$	0.005668	0.010136	0.016428	0.020171	0.019808

For $h = 0.5$, $G(x) = e^{-2Nsx}$ and $u = (1 - e^{-s})/(1 - e^{-2Ns})$. For $N = 50, s = 0.05$ this closed form is 0.049101, agreeing with the numerical integral within 10^{-6} .

3. Exact Solution and Simulation

Computation 3.1: exact solutions and formula over exact.

setting	$h = 0$	$h = 0.5$	$h = 1$	haploid N copies
$N = 50, s = 0.05$ exact	0.025104	0.048439	0.080208	0.094116
formula over exact	1.006470	1.013670	1.025576	1.017984
$N = 200, s = 0.01$ exact	0.005660	0.010107	0.016338	0.020097
formula over exact	1.001424	1.002824	1.005470	1.003687

Computation 3.2: 100000 simulated runs ($N = 50, s = 0.05$).

h	simulation	exact	diffusion formula	difference from exact over standard error
0	0.024490	0.025104	0.025267	-1.24
0.5	0.047330	0.048439	0.049101	-1.63
1	0.080530	0.080208	0.082259	0.38

Observation 3.3

the diffusion formula exceeds the exact solution, and simulation agreed with the exact solution. All three simulations came out below the diffusion formula, but differed from exact by less than 3 standard errors: formula over exact was larger for $N = 50, s = 0.05$ than for $N = 200, s = 0.01$, and within a setting larger for larger h . The order recessive, additive, dominant held in the exact solution for both settings.

4. Comparing with Haploids

Computation 4.1: ratios of exact solutions.

setting	$2Ns$	dominant over recessive	additive over recessive	dominant over additive	additive over haploid	dominant over haploid
$N = 50,$ $s = 0.05$	5.0	3.194988	1.929524	1.655842	0.514679	0.852226
$N = 200,$ $s = 0.01$	4.0	2.886501	1.785640	1.616508	0.502932	0.812994

Observation 4.2

additive diploids come near half the haploid value for the same number of individuals. Additive over haploid was 0.514679 and 0.502932: for an additive mutation the heterozygote advantage is $s/2$, half the advantage s of a single haploid copy. Even dominant mutations did not reach the haploid value, dominant over haploid being 0.852226 and 0.812994.

5. The Separator

Observation 5.1

the separator is whether the advantage shows already in heterozygotes or stays hidden until homozygotes appear. The first copy sits in a heterozygous individual, whose advantage is hs : for a recessive mutation ($h = 0$) that is 0, and the advantage acts only once homozygotes arise. Dominant over recessive was 3.194988 and 2.886501, and additive over recessive 1.929524 and 1.785640. How much of each probability is lost at the heterozygote stage and how much at the homozygote stage was not counted separately here.

Observation 5.2

what is not said. The mechanism of dominance, real genes, inbreeding, sex ratio, overlapping generations and formulas for the limit of large populations are not treated. What is shown is how far fixation probabilities divide by the degree of dominance in two settings, and how far the diffusion formula departs from the exact solution.

6. Roll Call and Closing

1. the diploid Wright-Fisher model (Section 1): **diffusion formula, exact solution, simulation.**
2. dominant over recessive **3.194988** and **2.886501** (Computation 4.1): **dominance divides.**
3. additive over haploid **0.514679** and **0.502932** (Computation 4.1): **near half the haploid value.**
4. formula over exact up to **1.025576** (Computation 3.1): **the diffusion formula is larger.**
5. simulation within -1.63 to 0.38 standard errors of exact (Computation 3.2): **simulation agrees with exact.**
6. shown in heterozygotes, or hidden (Observation 5.1): **the separator; the scope note of Paper 879.**

Closing: Dominance divides the fixation of favourable mutations in diploids, and additive ones come near half the haploid value. Solved exactly with the transition matrix, recessive, additive and dominant mutations fixed with 0.025104, 0.048439 and 0.080208 for $N = 50$, $s = 0.05$, dominant over recessive being 3.194988 (2.886501 for $N = 200$, $s = 0.01$): additive over haploid was 0.514679 and 0.502932. The diffusion formula was 1.001424 to 1.025576 times exact, and simulation coming out below the formula was the formula's departure. The separator is whether the advantage shows already in heterozygotes or stays hidden until homozygotes appear. Placed among the earlier papers: to the haploid model Paper 879 counted, the diploidy and degree of dominance Paper 879 did not include were added, and the effect of advantage that Paper 478 viewed through population size was viewed through

how it shows in heterozygotes. To be honest. This sets out fixation probabilities found three ways in a model with two settings. How far the degree of dominance divides the probability, and no further.

References

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