

Selfing Lowers the Fixation of Dominant Mutations, the Opposite of What an Inbreeding-Coefficient Model Gives

— drawing selfed offspring individual by individual from a multinomial and solving the transition matrix, recessive mutations are lifted and dominant ones pushed down, and under full selfing a mutation starting in a homozygote takes the haploid value for the same number of individuals —the separator is whether copies are drawn one at a time or individuals are drawn whole — [Paper 993]

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Abstract

Inbreeding lifts recessive fixation most, and at inbreeding coefficient 1 dominance stops mattering (Paper 984). There the inbreeding coefficient entered only the genotype frequencies, and the chance fluctuation in the number of copies was not changed. For a diploid population of 50 individuals with some offspring made by selfing, this paper solves exactly by the transition matrix a model that draws genotype counts from a multinomial, and compares it with the inbreeding-coefficient model of Paper 984. No new theorem or law is claimed. First, selfing lowers the fixation probability of dominant mutations: a dominant mutation starting in one heterozygote fixed with 0.080004 at selfing rate 0 and 0.049281 at 1, falling to **0.615984** times. In the model of Paper 984 it rises 1.166348 times over the same range (Section 2). Second, the lift for recessive mutations is smaller than in the inbreeding-coefficient model: recessive mutations went from 0.024597 to 0.045052, **1.831588** times, against 3.726468 times in the model of Paper 984. Additive mutations hardly moved at 0.982352 times (Section 2). Third, the more selfing, the more the inbreeding-coefficient model overstates fixation: the genotype model over the model of Paper 984 was 0.979811 to 0.997453 at selfing rate 0, **0.538466** to 0.567902 at 0.9 and 0.481585 to 0.526785 at 1 (Section 3). Fourth, under full selfing, starting in a homozygote matches the haploid value: a mutation starting in one homozygote fixed with **0.094116** for all three degrees of dominance, agreeing within 10^{-9} with the transition matrix for 50 haploid individuals. Starting in one heterozygote gave 0.478692 to 0.523621 times that (Section 4). Fifth, the separator is whether copies are drawn one at a time or individuals are drawn whole: the model of Paper 984 draws 100 copies one at a time, with inbreeding changing only genotype frequencies. In the model drawing individuals, the two copies of a selfed individual enter the next generation together. The direction split between the two models for dominant mutations (Section 5). **Keywords:** selfing, inbreeding coefficient, dominance, fixation probability, genotype, population genetics.

Scope of this paper (scope note): No new theorem or law is claimed: that selfing sets an equilibrium inbreeding coefficient $S/(2-S)$, that selfing reduces effective population size, and that selfing exposes recessive mutations to selection and changes the effect of dominant advantage, are known in population genetics. No real values are claimed: a population of 50, advantage 0.05, degrees of dominance 0, 0.5 and 1, and selfing rates from 0 to 1 are model values and correspond to no plant. The model is not extended: generations do not overlap, selection weights parents by count times fitness, and offspring genotypes are set by the shares of selfed and randomly mated offspring. Inbreeding depression, pollen or ovule limitation and separate sexes are not included. The mechanism is not asserted. It is not shown that the difference between the two models is explained by a change in effective population size alone. Only fixation probabilities are set out. Relation to earlier papers: Paper 984, in its scope note, did not change chance fluctuation, putting the inbreeding coefficient only into genotype frequencies and not including the fall in effective population size under inbreeding, and did not extend the mechanism, leaving out how inbreeding builds up over generations; this paper sits in that seat (no earlier occupant). Paper 984 showed that inbreeding lifts recessive fixation most, and that at inbreeding coefficient 1 dominance stops mattering. Here, building inbreeding generation by generation as selfing and drawing individuals whole, the change in that lift is counted. Paper 982 and Paper 983 found exactly by transition matrices the fixation probability for 50 haploid individuals. Here whether full selfing from a homozygote matches it is examined. What is added: solving the genotype model exactly for six selfing rates and three degrees of dominance, comparing it with the model of Paper 984, measuring that dominant mutations turn the other way, confirming that full selfing matches the haploid value, and placing the separator on “copies, or individuals”.

1. Notation and the Question

Genotype model: for a diploid population of $N = 50$ with counts $(i, j, N - i - j)$ of AA, Aa and aa, and fitnesses AA $1 + s$, Aa $1 + hs$, aa 1 ($s = 0.05$), parents are weighted by count times fitness. With p the A frequency and f_{AA}, f_{Aa}, f_{aa} the genotype frequencies under that weighting, offspring genotype probabilities are

$$q_{AA} = S\left(f_{AA} + \frac{f_{Aa}}{4}\right) + (1 - S)p^2, \quad q_{Aa} = S\frac{f_{Aa}}{2} + (1 - S)2p(1 - p), \quad q_{aa} = S\left(f_{aa} + \frac{f_{Aa}}{4}\right) + (1 - S)(1 - p)^2$$

and the next N individuals are drawn from this multinomial. There are 1326 states; all AA is fixation and all aa loss. Row sums were off by at most 3.8×10^{-14} .

Model compared: the model of Paper 984, putting the inbreeding coefficient $F = S/(2 - S)$ into genotype frequencies and drawing $2N$ copies binomially.

Question: when selfing is counted individual by individual, how does the fixation probability differ from the inbreeding-coefficient model?

2. Selfing Rate and Fixation Probability

Computation 2.1: fixation probability starting from one heterozygote (model of Paper 984 in parentheses).

selfing S	F	recessive	additive	dominant
0	0.000000	0.024597 (0.025104)	0.047974 (0.048439)	0.080004 (0.080208)
0.25	0.142857	0.029158 (0.032720)	0.047756 (0.054953)	0.071740 (0.082852)
0.5	0.333333	0.034121 (0.044415)	0.047543 (0.063647)	0.063873 (0.085822)
0.75	0.600000	0.039435 (0.063008)	0.047334 (0.075734)	0.056392 (0.089278)
0.9	0.818182	0.042771 (0.079431)	0.047210 (0.085504)	0.052082 (0.091710)
1	1.000000	0.045052 (0.093550)	0.047127 (0.093550)	0.049281 (0.093550)

As selfing increased, recessive fixation rose through all six S and dominant fixation fell through all six. In the model of Paper 984 dominant fixation rose throughout. Factors from selfing 0 to 1 were recessive 1.831588, additive 0.982352 and dominant **0.615984** in the genotype model, and 3.726468, 1.931289 and 1.166348 in the model of Paper 984.

3. Ratio of the Two Models

Computation 3.1: genotype model over the model of Paper 984.

selfing S	recessive	additive	dominant
0	0.979811	0.990387	0.997453
0.25	0.891127	0.869038	0.865873
0.5	0.768241	0.746987	0.744249
0.75	0.625867	0.625004	0.631643
0.9	0.538466	0.552135	0.567902
1	0.481585	0.503761	0.526785

Observation 3.2

the more selfing, the more the inbreeding-coefficient model overstated fixation. Even at selfing 0 the ratio is not 1 (recessive 0.979811), a difference due only to drawing copies versus individuals: at selfing 1 the ratio was 0.481585 to 0.526785.

4. Full Selfing

Computation 4.1: at selfing 1, starting from one homozygote (AA) gave 0.094116 for all three degrees of dominance, agreeing within 10^{-9} with the transition-matrix value 0.094116 for 50 haploid individuals ($p' = p(1 + s)/(1 + ps)$, binomial over N). The same value appears in the exact haploid solutions of Paper 982 and Paper 983. Starting from one heterozygote gave 0.478692 (recessive), 0.500735 (additive) and 0.523621 (dominant) times the homozygote value.

Observation 4.2

a fully selfing population behaved as haploids numbering its individuals. An AA individual leaves only AA offspring and carries the advantage s as one unit: the value 0.093550 of the model of Paper 984 at coefficient 1 is the value for 100 haploid copies, a different number from this value drawn by individuals.

5. The Separator

Observation 5.1

the separator is whether copies are drawn one at a time or individuals are drawn whole. The model of Paper 984 draws 100 copies independently, with inbreeding changing only genotype frequencies. In the model drawing individuals, the two copies of a selfed individual enter the next generation together: the direction split between the two models for dominant mutations, and the size of the recessive lift also differed (1.831588 against 3.726468). Whether that difference is explained by a change in effective population size alone was not measured separately here.

Observation 5.2

what is not said. Inbreeding depression, pollen or ovule limitation, overlapping generations, separate sexes, the shape for larger populations, and real plants are not treated. What is shown is how far, and in which direction, fixation probabilities depart from the inbreeding-coefficient model when selfing is counted individual by individual, in one setting of 50 individuals.

6. Roll Call and Closing

1. a multinomial genotype model with selfing (Section 1): a transition matrix of 1326 states.
2. dominant falls to **0.615984** times (Computation 2.1): rises in the model of Paper 984.
3. recessive **1.831588** times (Computation 2.1): smaller than **3.726468** in the model of Paper 984.
4. ratio **0.538466** at selfing **0.9** (Computation 3.1): the coefficient model overstates.
5. **0.094116** from a homozygote under full selfing (Computation 4.1): matches 50 haploid individuals.
6. copies, or individuals (Observation 5.1): the separator; the scope note of Paper 984.

Closing: Selfing lowers the fixation of dominant mutations, the opposite of what an inbreeding-coefficient model gives. Drawing selfed offspring individual by individual from a multinomial for 50 diploids, a dominant mutation starting in one heterozygote fell to 0.615984 times from selfing 0 to 1, opposite to the 1.166348 times of the inbreeding-coefficient model of Paper 984: the recessive lift was 1.831588 times against the model's 3.726468, and at selfing 0.9 the ratio of the two models was 0.538466 to 0.567902. Under full selfing, starting from a homozygote matched the 0.094116 of 50 haploid individuals. The separator is whether copies are drawn one at a time or individuals are drawn whole. Placed among the earlier papers: the inbreeding Paper 984 put only into genotype frequencies was recounted with the generation-by-generation building by selfing and the individual-level chance that Paper 984 did not include. To be honest: fixation probabilities of two models were set side by side for one population size and one advantage. The mechanism was not separated. How the direction changes when selfing is counted by individuals, and no further.

References

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