Appendix 3: Approximate distribution of fixed effects

The distribution of fixed effects s_f is that of beneficial effects, conditional on escaping drift loss, with probability $\pi(s_f)$. The pdf of fixed mutation effects, $f_{fix}(s_f)$, is therefore

$$f_{fix}(s_f) = \frac{\pi(s_f)\, f_b(s_f)}{\int_{x=0}^{s_o} \pi(x)\, f_b(x) ds}, \tag{A.3.1}$$

ignoring the fixation of deleterious mutations. In the general case, this expression cannot be explicitly derived. However, when the pdf $f_b(s_b)$ of beneficial mutations follows the Jaschke tail approximation of eq. (A.2.1), a simple approximation for $f_{fix}(s_f)$ can be derived. To do so, one simply replaces f_b (.) in eq. (A.3.1) by the tail approximation f_b*(.) (in A.2.4) and uses the weak selection, large population approximation for the fixation probability : $\pi(s) \approx 2s$ (HALDANE 1927). As all beneficial mutations are below s_o which is assumed to be small, this weak selection approximation should always be fairly accurate whenever the Jaschke tail approximation is valid (wild-type well adapted). The pdf of the distribution of fixed effects is approximately

$$f_{fix}(s_f) \underset{s_o \to 0}{\approx} f_{fix}^*(s_f) = \frac{2s_f\ f_b^*(s_f)}{\int_{x=0}^{s_o} 2x\, f_b^*(x) dx} = \frac{m\,(2+m)}{4{s_o}^2}\left(1-\frac{s_f}{s_o}\right)^{\frac{m}{2}-1} s_f\,, \tag{A.3.2}$$

Which means that the distribution of s_f/s_o is a beta with shape parameters 2 and $m/2$:

$$\frac{s_f}{s_o} \sim Beta\left(2, \frac{m}{2}\right). \tag{A.3.3}$$

Note that for populations of finite (though not too small) size N and effective size N_e (and still with weak selection as assumed here), the probability of fixation of a beneficial allele becomes approximately $2s^*N_e/N$ (WHITLOCK 2000). This scaling factor does not affect eq. (A.3.2) so that the distribution of fixed mutation effects is not affected by finite population sizes (i.e. only the probability of a beneficial mutation fixing is affected, not its effect distribution). Note, however, that for smaller N, the above approximation is inaccurate *a priori*; in particular, deleterious mutations can fix, which was neglected here.

As a comparison, we compute, in the same way, the distribution of fixed effects when the distribution of beneficial mutation effects is exponential with rate λ (note that the integral in the numerator of (A.3.2) is over the range $[0,\infty]$ for the exponential). The distribution of fixed mutation effects is then

$$f_{\exp}(s_f) = \lambda^2 s_f\ e^{-\lambda\, s_f}\,, \tag{A.3.4}$$

and the average fitness effect of fixed mutations when beneficial effects are exponentially distributed is

$$E_{\exp}(s_f) = \frac{2}{\lambda}, \tag{A.3.5}$$

where in the limiting case of a large m, $\lambda = m/2s_o$ is the rate of the exponential distribution of beneficial effects s_b (as $x = s_b/s_o$ is exponential with rate $m/2$, see eq. (A.2.6)).

References:

HALDANE, 1927 A mathematical theory of natural and artificial selection V. Selection and mutation. Proceedings of the Cambridge Philosophical Society **26:** 220-230.

WHITLOCK, M. C., 2000 Fixation of new alleles and the extinction of small populations: Drift load, beneficial alleles, and sexual selection. Evolution **54:** 1855-1861.