

Appendix A from S. Peischl et al., “Expansion Load and the Evolutionary Dynamics of a Species Range” (Am. Nat., vol. 185, no. 4, p. 000)

Probability of Fixation on the Wave Front

We derive here the probability of fixation of a new mutation occurring on the wave front under the analytical model described in the main text. We use a diffusion approximation to calculate the probability of fixation of a new mutation (Kimura 1964). Note that fixation means here that the mutation becomes fixed at the front of the expansion wave; that is, we do not consider the fate of mutations that fall back into the wake of the wave.

First, we follow the fate of a mutation introduced at the time of the colonization of the new deme. We then generalize our results to mutations that occur at an arbitrary stage of the colonization process. The selective advantage of an individual carrying a single copy of the mutation is denoted s . Let Δx denote the change in mutant allele frequency x during the colonization of a new deme, and let $E[\Delta x]$ and $V[\Delta x]$ denote its mean and variance, respectively. The probability of fixation of the mutant allele is then given by

$$p = \frac{\int_0^{x_0} g(x) dx}{\int_0^1 g(x) dx},$$

where x_0 is the initial frequency of the mutation and $g(x) = \exp(-\int 2E[\Delta x]/V[\Delta x] dx)$ (Kimura 1964).

Let t denote the generation at which the mutation appears. For the sake of simplicity, we omit the dependence on t , and we denote the growth rate and the carrying capacity of the population at generation t by R and K , respectively. We assume that changes in mean fitness are caused exclusively by fluctuations in the allele frequency of the focal mutation. For instance, this is the case if allele frequencies at other loci remain, on average, constant. Let x denote the current frequency of the mutation. We denote by $\xi(x, s, \tau)$ the expected frequency of the mutation after τ generations of selection. Assuming that selection acts deterministically and that relative fitness is density independent, the frequency of the mutation after a single generation of selection is $x' = x(1+s)/[x(1+s) + (1-x)]$ (e.g., Ewens 2004), and after τ generations of selection, we obtain

$$\xi(x, s, \tau) = \frac{x(1+s)^\tau}{x(1+s)^\tau + (1-x)}.$$

The expected change in allele frequency during the colonization of a single deme is then

$$E[\Delta x] = \xi(x, s, T) - x,$$

where T is the length of the growth phase during which we assume that selection operates. Assuming exponential growth, the length of each growth phase is given implicitly by the equation

$$FR^T e^{\int_0^T \log[1+s\xi(x, s, t)] dt} = K[1 + s\xi(x, s, T)], \quad (\text{A1})$$

where F is the number of founder individuals.

Binomial sampling of individuals during migration does not change the expected frequency of the mutation, but it increases sampling variance around x' . We ignore stochastic variation during the growth phase and assume that all variation is from choosing the founders (see also Heffernan and Wahl 2002). Hence the variance of Δx is

$$V[\Delta x] = \frac{1}{2F} \xi(x, s, T) [1 - \xi(x, s, T)],$$

where $2F$ is the number of genes founding the new deme on the wave front.

Under weak selection (i.e., $|s| \ll 1$), we find that $g(x) \approx \exp(1 - 4FTsx)$, and straightforward integration yields

$$p \approx \frac{\exp(-4FTsx_0) - 1}{\exp(-4FTs) - 1}. \quad (\text{A2})$$

An alternative way to obtain this result is by observing that

$$E[\Delta x] = x(1 - x)Ts + O(s^2),$$

which is the expected per generation change in allele frequency of a mutation with selection coefficient Ts in a single panmictic population. Furthermore,

$$V[\Delta x] = \frac{1}{2F}x(1 - x) + O(s),$$

which implies that the probability of fixation is given by the standard formula for a single panmictic population (Kimura 1964), with selection coefficient Ts and population size F .

If the mutation appears during the colonization of a new deme, its initial frequency is $x_0 = 1/(2F)$, and we find that the fixation probability is

$$p \approx \frac{\exp(-2Ts) - 1}{\exp(-4FTs) - 1}.$$

We next consider a mutation with effect s that occurs in a deme of age τ (in generations) and denote the probability of fixation of this mutation by $p(s, \tau)$. The population size of the deme on the wave front is denoted $N(\tau)$. The mutation's expected frequency in generation T (i.e., when the deme at the edge is at carrying capacity and before colonization of a new deme) is $\xi[1/(2N(\tau)), s, T - \tau]$, and the probability of fixation is thus given by equation (A2), with $x_0 = \xi[1/(2N(\tau)), s, T - \tau]$.

Note that equation (A2) is a generalization of the probability of fixation on the wave front derived by Peischl et al. (2013). Assuming soft selection, exponential growth within demes, and $F = Km/2$, the solution of equation (A2) is $T = \log(2/m)/\log(R)$. Then, $FTs = K(m/2)[\log(2/m)/\log(R)] = Ks_e$ in the parameterization used by Peischl et al. (2013).