

Appendix A from J. Masel et al., “The Loss of Adaptive Plasticity during Long Periods of Environmental Stasis” (Am. Nat., vol. 169, no. 1, p. 38)

Sojourn Time $\bar{\tau}$ within a Deme

Mean Sojourn Time

Consider a population of size N that has the trait. Mutants that lack the trait appear at rate m per replication, with a negligible back-mutation rate. At a given point in time, there are $N - i$ individuals with and i individuals without the trait, and we denote these types $plastic^+$ and $plastic^-$, respectively. At each time step, one individual is chosen at random to reproduce and one to die, where $plastic^-$ individuals have a selective advantage s in reproduction. The probability that the new individual is $plastic^-$ is therefore given by

$$\frac{i(1 + s) + (N - i)m}{N + is}.$$

The probability that the next individual chosen to die is $plastic^-$ is given by i/N . The probability that the number of $plastic^-$ variants increases from i by 1 is then given by the probability that a $plastic^-$ individual is produced by reproduction while a $plastic^+$ individual is chosen to die:

$$\lambda_i = \frac{[i(1 + s) + (N - i)m](N - i)}{(N + is)N}.$$

The probability that the number of $plastic^-$ variants decreases from i by 1 is given by the probability that a $plastic^+$ individual is produced by reproduction while a $plastic^-$ individual is chosen to die:

$$\mu_i = \frac{(N - i)(1 - m)i}{(N + is)N}.$$

The ratio is given as

$$\rho_j = \frac{\mu_j}{\lambda_j} = \frac{(1 - m)j}{j(1 + s) + (N - j)m}.$$

Then the mean sojourn time $\bar{\tau}_{0i}$ during which there are i $plastic^-$ individuals, given that there are none initially, is given by equation (2.161) of Ewens (2004): for $i = 0, \dots, N - 1$,

$$\begin{aligned} \bar{\tau}_{0i} &= \frac{1 + \sum_{k=0}^{N-i-2} \prod_{j=i+1}^{N-1-k} \rho_j}{\lambda_i} \\ &= \frac{1 + \sum_{k=0}^{N-i-2} [(1 - m)/(1 - m + s)]^{N-1-k-i}}{N\lambda_i} \times \frac{(N - 1 - k)! \Gamma\{i + 1 + [mN/(1 - m + s)]\}}{i! \Gamma\{N - k + [mN/(1 - m + s)]\}}, \end{aligned} \quad (A1)$$

where Γ is the gamma function and the unit of time is 1 generation, corresponding to N rounds in the Moran model, each of which involve a single death and a single reproduction. The mean total sojourn time before all individuals are $plastic^-$, given an initial population of pure $plastic^+$, is

$$\bar{\tau}_0 = \sum_{i=0}^{N-1} \bar{\tau}_{0i}. \quad (\text{A2})$$

When N is large, the summations in equations (A1) and (A2) are performed by interpolation using an adaptive algorithm.

Equation (A2) can be used to calculate the mean sojourn time exactly for arbitrary values of m , s , and N . In certain circumstances, much simpler, more intuitive approximations are available. When $s = 0$, we have, from equation (9.11) of Ewens (2004),

$$\bar{\tau}_0 = N \left(N + \frac{mN}{1-m} \right) \sum_{j=1}^N \frac{1}{j \{ j + [mN/(1-m)] - 1 \}}.$$

When $mN \gg 0$ and $m \ll 1$, this is well approximated by

$$\bar{\tau}_0 \approx \frac{\ln(mN) + \gamma}{m}, \quad (\text{A3})$$

where γ is Euler’s constant, with numerical value 0.577216. When selection dominates the sojourn time, that is, $s \gg m$ and $mN \gg 1$, we have a second limiting case from equation (A17) of Hermisson and Pennings (2005),

$$\bar{\tau}_0 \approx 2 \frac{\ln(sN) + \gamma}{s}. \quad (\text{A4})$$

Based on equations (A3) and (A4), we therefore attempted to fit the approximate solution

$$\bar{\tau}_{\text{approx}} \approx \frac{1}{mN p_{\text{fix}}} + \begin{cases} \frac{\ln[(m+s)N] + \gamma}{m+s/2} & \text{if } [(m+s)N] > 0, \\ N-1 & \text{otherwise,} \end{cases} \quad (\text{A5})$$

where p_{fix} is the probability of fixation, beginning with a single *plastic*⁻ mutant and not returning to having zero mutants. The first term captures the expected waiting time until the appearance of the first mutant destined for fixation and hence the behavior of the system when $mN \ll 1$. The second term captures the expected sojourn time once such a mutant has appeared both in the limiting case of $mN \gg 1$ and/or $sN \gg 1$ and in the neutral limiting case of $mN \ll 1$ and $sN \ll 1$. From equation (2.158) of Ewens (2004), we have

$$p_{\text{fix}} = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{j=1}^k \rho_j}.$$

We see in figure 2 that the approximation given in equation (A5) performs reasonably well in practice. For $s < m$, the exact and approximate solutions converge very quickly for large N . For $s > m$, the approximation was good but retained systematic biases. For some parameter combinations, a denominator of $(m+s)$ performed better than the $(m+s/2)$ given in equation (A5), but overall the latter seemed to give a closer approximation for a greater range of the parameter space.

Variance in Sojourn Time

From equation (2.145) of Ewens (2004), the variance of the sojourn time, given that there are initially no *plastic*⁻ individuals, is equal to

$$\sigma_0^2 = 2 \sum_{j=1}^{N-1} \bar{\tau}_0 \bar{\tau}_j - \bar{\tau}_0 - (\bar{\tau}_0)^2. \quad (\text{A6})$$

As a generalization of equation (A1), the mean sojourn time $\bar{\tau}_i$ during which there are i *plastic*⁻ individuals,

given that there are j initially, can also be derived from equation (2.161) of Ewens (2004) and used to calculate $\bar{\tau}_j$ and hence equation (A6). These calculations were performed (data not shown) and confirmed numerically that the variance in the sojourn time is negligible for $mN \gg 1$, hence justifying our assumption of fixed $\tau = \bar{\tau}$ in this case. Since increasingly large values of N yield many more time steps in the Moran model but only slight increases in $\bar{\tau}$ measured in generations, the variance scales approximately with the average of an increasing number of random waiting times. The law of large numbers therefore applies, making the total sojourn time highly deterministic.

Appendix B from J. Masel et al., “The Loss of Adaptive Plasticity during Long Periods of Environmental Stasis” (Am. Nat., vol. 169, no. 1, p. 38)

Exact Solution for a Single Population

Consider states E_i and E'_i for $i = 0, \dots, N$, where i represents the number of individuals lacking the trait, and E and E' represent the original and the new environment, respectively. We define a Markov chain on this state space as follows: for $0 \leq i < N$, from state E_i the chain moves to state E'_i with probability $1 - e^{-\theta/N}$ (corresponding to an environmental change), moves to state E_{i-1} with probability $e^{-\theta/N}\lambda_i$, moves to state E_{i+1} with probability $e^{-\theta/N}\mu_i$, and remains in state E_i otherwise. State E_N is an absorbing state, corresponding to trait loss. From state E'_i , the chain moves to state E'_{i-1} with probability 1, unless $i = 0$, in which case it moves to state E_0 with probability 1. Figure 3 shows the states and the allowable transitions between them.

Let $p(X, Y)$ denote the probability of moving from state X to state Y in one step of the Markov chain, which corresponds to $1/N$ generation. Then the expected number of generations until trait loss starting from state X , which we denote $f(X)$, is the solution to the following systems of $2N + 1$ linear equations (see, e.g., sect. 2.1.2 of Ewens 2004):

$$\begin{aligned} f(X) &= \sum_Y p(X, Y)f(Y) + 1/N & X \neq E_N, \\ f(X) &= 0 & X = E_N. \end{aligned}$$

If we order the states $E_0, E'_0, E_1, E'_1, \dots, E_{N-1}, E'_{N-1}, E_N$, then this system of equations is pentadiagonal and so can be solved directly with requirements in memory and computational time of order N (see, e.g., sec. 4.3 of Golub and van Loan 1996). The expected time until trait loss is given by $f(E_0)$. This reduces to the expected sojourn time $\bar{\tau}_0$ of equation (A2) when $\theta = 0$.

Note that this formulation differs slightly from the formulation introduced above, in which the system jumps immediately to state E_0 after an environmental change. This formulation captures the time required for the population to regrow after ill-adapted individuals lacking the trait die after environmental change. The resulting difference in the time until trait loss is less than a single generation per environmental change event. But note that the solution to the modified system of equations

$$\begin{aligned} f(X) &= \sum_Y p(X, Y)f(Y) + 1/N & X \in \{E_0, \dots, E_{N-1}\}, \\ f(X) &= \sum_Y p(X, Y)f(Y) & X \in \{E'_0, \dots, E'_{N-1}\}, \\ f(X) &= 0 & X = E_N. \end{aligned}$$

gives the expected time until trait loss in the case where the state immediately jumps to E_0 after an environmental change while retaining the pentadiagonal structure. For consistency with the approximate solution, the calculations shown in figure 4 use this modified system, although in practice it makes very little difference.

Literature Cited Only in Appendix B

Golub, G. H., and C. F. van Loan. 1996. Matrix computations. John Hopkins University Press, Baltimore.

Appendix C from J. Masel et al., “The Loss of Adaptive Plasticity during Long Periods of Environmental Stasis”

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Metapopulations with Exponentially Distributed Sojourn Times within Demes

Consider a metapopulation of n demes that initially bear the trait. At a given a point in time, there are $n - j$ demes with and j demes without the trait. Each time step is an environmental change event or a trait loss, whichever occurs first. The probability that the number of demes without the trait increases by 1 is given by the probability that in the next time step a deme with the trait undergoes a trait loss event,

$$\Lambda_j = \frac{1/\bar{\tau}}{1/\bar{\tau} + \theta} \frac{n - j}{n}.$$

Note that in this appendix, we have $mN \ll 1$ and can therefore make the approximation that the sojourn time is dominated by time waiting for a mutation destined for fixation. This means that at a given moment in time, we can make the approximation that all individuals in trait-bearing demes bear the trait. We therefore take the probability that the number of demes without the trait decreases by 1 as the probability that in the next time step a deme without the trait undergoes an event and is recolonized by a deme that bears the trait,

$$M_j = \frac{\theta}{1/\bar{\tau} + \theta} \frac{j(n - j)}{n(n - 1)}.$$

We now have the ratio

$$P_j = \frac{M_j}{\Lambda_j} = \frac{\theta j \bar{\tau}}{n - 1}.$$

Then the mean sojourn time \bar{T}_{0j} during which there are j demes without the trait, given that all demes initially have the trait, is given by equation (2.161) of Ewens (2004): for $j = 0, \dots, n - 1$,

$$\begin{aligned} \bar{T}_{0j} &= \frac{1 + \sum_{k=0}^{n-j-2} \prod_{x=j+1}^{n-1-k} P_x}{\Lambda_j} \\ &= \frac{n(1 + \theta \bar{\tau})}{n - j} \left[1 + \sum_{k=0}^{n-j-2} \frac{(n - k - 1)!}{j!} P_1^{n-j-k-1} \right], \end{aligned} \quad (C1)$$

where the unit of time is 1 time step in the Markov process, which corresponds to an environmental change event or a potential trait loss, whichever occurs first, with combined rate $n(1/\bar{\tau} + \theta)$ events per generation. The total sojourn time before all demes lose the trait, given that all initially bear it, is

$$\bar{T}_0 = \sum_{j=0}^{n-1} \bar{T}_{0j}. \quad (C2)$$

When n is large, the summations in equations (C1) and (C2) are performed by interpolation using an adaptive algorithm.

Appendix D from J. Masel et al., “The Loss of Adaptive Plasticity during Long Periods of Environmental Stasis”

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Metapopulations with Fixed Sojourn Times within Demes

Approximate Solution

Fixed sojourn times are more difficult to capture within a Markov model, since although the environmental change events follow a Markov process, trait loss events do not. As an approximation, each time environmental change occurs, we check whether trait loss will occur before the next environmental change event in that deme. If so, we then approximate trait loss as rapid for all but the last deme to undergo trait loss. We make adjustments at the beginning and the end of the Markov process used for the analytical model. At the beginning, we check all n demes bearing the trait to see if they lose it before they have their first environmental change event. At the end, we consider the additional time for the last deme to lose the trait. Now our quantity of interest, instead of being \bar{T}_0 , is

$$\bar{T} = \sum_{i=0}^{n-1} \binom{n}{i} e^{-\theta\bar{\tau}i} (1 - e^{-\theta\bar{\tau}})^{n-i} \bar{T}_i / n\theta + \bar{\tau}, \quad (\text{D1})$$

where the unit of time is generations and the denominator corrects for the fact that in this Markov process, each time step is an environmental change event. We now go on to calculate the sojourn time \bar{T}_i before all demes lose the trait, given that i demes initially lack it. The probability that the number of demes without the trait increases by 1 is given by the probability that a deme with the trait undergoes an environmental change event and is destined to lose the trait before the next event in that deme:

$$\Lambda_j = e^{-\theta\bar{\tau}} \frac{n-j}{n}.$$

The probability that the number of demes without the trait decreases by 1 is given by the probability that a deme without the trait undergoes an event and is recolonized by a deme that bears the trait, multiplied by the probability that the newly colonized deme is not destined to lose the trait before the next event in that deme,

$$M_j = \frac{j(n-j)}{n(n-1)} (1 - e^{-\theta\bar{\tau}}).$$

Note that this is an approximation. On the one hand, not all colonizing individuals from a trait-bearing deme are trait-bearing individuals, making M an overestimate. On the other hand, some recolonization may come from demes that are destined to lose the trait before their deme encounters an event, but they have not yet lost the trait when another deme encounters an event. This makes M an underestimate. The model was verified by numerical simulations to test the effects of these two factors, as described in “Simulated Exact Solution.” Figure 5 shows fairly good agreement between the analytical model and the simulations, suggesting that the two effects largely cancel each other out.

Now the mean sojourn time \bar{T}_{ij} during which there are j demes without the trait, given that i demes initially lack it, is given by equation (2.161) of Ewens (2004),

$$\bar{T}_{ij} = \begin{cases} \prod_{x=j}^{i-1} \frac{M_{x+1}}{\Lambda_x} \bar{T}_{ii} = \prod_{x=j}^{i-1} \frac{x(n-x-1)}{(n-1)(n-x)} (e^{\theta\bar{\tau}} - 1) \bar{T}_{ii} = \frac{(n-i)!}{(n-j)j!} \left(\frac{e^{\theta\bar{\tau}} - 1}{n-1} \right)^{i-j} \bar{T}_{ii} & j = 0, 1, \dots, i-1, \\ \frac{1 + \sum_{k=0}^{n-j-2} \prod_{x=j+1}^{n-1-k} (M_x/\Lambda_x)}{\Lambda_j} = \frac{ne^{\theta\bar{\tau}}}{n-j} \left[1 + \sum_{k=0}^{n-j-2} \frac{(n-k-1)!}{j!} \left(\frac{e^{\theta\bar{\tau}} - 1}{n-1} \right)^{n-j-k-1} \right] & j = i, i+1, \dots, n-1, \end{cases} \quad (\text{D2})$$

where the unit of time is one step in the Markov process, which corresponds to one environmental change event, with rate $n\theta$ events per generation. The total sojourn time before all demes lose the trait, given that i demes initially lack it, is

$$\bar{T}_i = \sum_{j=0}^{n-1} \bar{T}_{ij}. \quad (\text{D3})$$

When n is large, the summations in equations (D1)–(D3) are performed by interpolation using an adaptive algorithm.

Simulated Exact Solution

We performed simulations according to the following algorithm. Initialize time $t = 0$, and set up n demes with both trait-bearing status and the value $x_1 = x_2 = \dots = x_n = \bar{\tau}$ to specify the time at which they are due to undergo trait loss. Sample the time of the next environmental change event from the exponential distribution with mean $1/n\theta$. Increment t and switch any deme j for which $x_j < t$ to trait loss status. Choose a new deme j at random to undergo the environmental change event. If deme j bears the trait, reset x_j to $t + \bar{\tau}$. If deme j lacks the trait, assume that it is destroyed, and choose a second deme i at random to recolonize it. If deme i bears the trait, reset x_j to x_i ; this assumes that recolonization involves a representative sample of the colonizing population rather than a single individual. Then repeat this procedure for the next environmental change event, stopping when all demes lack the trait.

Calculating the minimum number of demes needed for the mean sojourn time to be less than 10^8 generations is computationally expensive, since it is difficult to find an algorithm that avoids calculating very long sojourn times greatly in excess of 10^8 generations. We truncated our simulations at 10^8 generations and found a minimum deme number according to how often simulations were truncated. When the trait was lost, we incremented the deme number by 1, and when the simulation was truncated because the trait was not lost, we decremented the deme number by 1. We then calculated the average deme number sampled by this procedure over a large number of iterations.