

Appendix C from H. Uecker et al., “Evolutionary Rescue in Structured Populations”

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Levene Model

We now consider $D \geq 1$, but focus on the limiting case $m = 1$. In a first step, we furthermore restrict the analysis to $\beta = 0$. As derived in the main text equation (10), the effective growth parameter of a mutant in the metapopulation in a period with d deteriorated demes is given by

$$s_{\text{eff}}(t) = \frac{d}{D}(1 + s) + \frac{D - d}{D} \alpha \frac{K}{N_w^{(\text{total})}(t)/D} - 1. \quad (\text{C1})$$

The total number of wildtypes $N_w^{(\text{total})}(t) = N_w^{(\text{new})}(t) + K(D - d)$ is a function of time. However, after another deme has turned bad, it will quickly decay to its new steady state (until the next deme deteriorates). For sufficiently large values of ϑ , we can therefore approximate s_d as constant by taking the equilibrium value $\hat{N}_{w,d}^{(\text{total})}$ of the total wildtype population size in the period within which d demes are perturbed. The stationary value of the total wildtype population size $\hat{N}_{w,d}^{(\text{new})}$ in the bad environment is found by solving the equation

$$0 = (1 - r) \frac{d}{D} [\hat{N}_{w,d}^{(\text{new})} + (D - d)K] - \hat{N}_{w,d}^{(\text{new})}. \quad (\text{C2})$$

This yields

$$\hat{N}_{w,d}^{(\text{new})} = \frac{(1 - r)(d/D)(D - d)K}{1 - (1 - r)(d/D)}. \quad (\text{C3})$$

And we obtain

$$\hat{N}_{w,d}^{(\text{total})} = \hat{N}_{w,d}^{(\text{new})} + K(D - d). \quad (\text{C4})$$

Inserting equation (C4) into equation (C1) yields s_d as in equation (11). With equation (11), we can now use equation (A7) with $\Phi = \vartheta$ to determine the establishment probability of a new mutant.

The probability of evolutionary rescue in a Levene model can be approximated by (cf. eq. [5]):

$$P_{\text{rescue}} \approx 1 - \exp \left[-u \sum_{t=-\infty}^{-1} KD \alpha p_{\text{est}}(t + 1) - u \sum_{t=0}^{(D-1)\vartheta-1} N_w^{(\text{total})}(t)(1 + s_{\text{eff}}(t))p_{\text{est}}(t + 1) \right] \\ \times \exp \left[-u \frac{N_w^{(\text{total})}((D-1)\vartheta)}{r} (1 + s) \frac{2\hat{s}}{1 + \hat{s}} \right], \quad (\text{C5})$$

where $N_w^{(\text{total})}((D-1)\vartheta)$ is the wildtype population size immediately after the last deme has deteriorated. The first sum captures the contributions of mutations that arose before time $t = 0$. The second sum takes all mutations into account that are generated as the degradation proceeds across the demes. From time $(D-1)\vartheta$ on, the population size decays geometrically, which leads to the last term in equation (C5).

We now allow for density-dependent mutant fitness ($\beta \geq 0$). We assume that the periods of environmental stasis are very long. As discussed in the main text, it is in that case sufficient to consider the two phases where either one or no deme is unperturbed. We can approximate $S(t)$ during the phase where all but one deme have deteriorated by its steady state value:

$$\bar{S} = \max \left[-z, s \left(1 - \beta \frac{\hat{N}_{w,D-1}^{(\text{total})}}{K} \right) \right] \quad (\text{C6})$$

with

$$\hat{N}_{w,D-1}^{(\text{total})} = \frac{KD}{(D-1)r + 1}. \quad (\text{C7})$$

Analogously to equation (11), we then obtain equation (13) for the effective growth parameter during that period. In the main text, we pointed out that the situation corresponds to an unstructured population with a single environmental change. We can thus use equation (B3) with the following substitutions to calculate the probability of evolutionary rescue:

$$\begin{aligned} K &\text{ is substituted by } \hat{N}_{w,D-1}^{(\text{total})}, \\ \alpha &\text{ is substituted by } 1 + s_{D-1}, \\ \beta &\text{ is substituted by } \frac{\beta \hat{N}_{w,D-1}^{(\text{total})}}{DK}. \end{aligned} \tag{C8}$$

We close the section with a comparison of $P_{\text{rescue}}(\vartheta \rightarrow 0)$ and $P_{\text{rescue}}(\vartheta \rightarrow \infty)$ if $\beta = 0$. In order to do so, we approximate the amount of genetic variation which is present at the time when the last deme deteriorates by its expected value. We only consider the case $s_{D-1} < 0$. For $\vartheta = 0$ and $\vartheta \rightarrow \infty$, we obtain

$$E[\text{sgv}_0] = uDK \frac{\alpha}{1 - \alpha} \text{ and } E[\text{sgv}_\infty] = u\hat{N}_{w,D-1}^{(\text{total})} \frac{1 + s_{D-1}}{-s_{D-1}}, \tag{C9}$$

respectively. Analogously, we introduce

$$E[\text{dnm}_0] = \frac{uKD(1 + s)}{r} \text{ and } E[\text{dnm}_\infty] = \frac{u\hat{N}_{w,D-1}^{(\text{total})}(1 + s)}{r} \tag{C10}$$

for the expected number of de novo mutations that are generated after deterioration of the last deme in both scenarios. With this notation,

$$P_{\text{rescue}}(\vartheta = 0) \approx 1 - \exp \left[-(E[\text{sgv}_0] + E[\text{dnm}_0]) \frac{2\hat{s}}{1 + \hat{s}} \right], \tag{C11a}$$

$$P_{\text{rescue}}(\vartheta \rightarrow \infty) \approx 1 - \exp \left[-(E[\text{sgv}_\infty] + E[\text{dnm}_\infty]) \frac{2\hat{s}}{1 + \hat{s}} \right]. \tag{C11b}$$

We now compare the exponents:

$$\begin{aligned} \frac{E[\text{sgv}_\infty] + E[\text{dnm}_\infty]}{E[\text{sgv}_0] + E[\text{dnm}_0]} &= \frac{\hat{N}_{w,D-1}^{(\text{total})}}{DK} \cdot \frac{(1 + s_{D-1})(-s_{D-1}) + 1/r}{[\alpha/(1 - \alpha)] + 1/r} \\ &= \frac{\hat{N}_{w,D-1}^{(\text{total})}}{DK} \cdot \frac{1 - \alpha}{-s_{D-1}} \cdot \frac{r - s_{D-1}(1 - r)}{1 - \alpha + \alpha r} \left(\text{Note: This expression gets minimal when } -s_{D-1} \text{ gets maximal.} \right. \\ &\quad \left. -s_{D-1} \text{ as a function of } s \text{ gets maximal for } s \rightarrow 0. \right) \\ &= \frac{1}{1 + r(D - 1)} \cdot \frac{1}{1 + (D - 1)r - [(s + r)/(1 - \alpha)](D - 1)} \cdot \frac{[r + s + (1 - \alpha)(1 - r)][1 + (D - 1)r] - sD}{1 - \alpha + \alpha r} \\ &= \frac{1}{1 + (D - 1)r - [(s + r)/(1 - \alpha)](D - 1)} \cdot \frac{1 - \alpha + \alpha r + s - sD/[1 + r(D - 1)]}{1 - \alpha + \alpha r} \stackrel{s \rightarrow 0}{\geq} \frac{1}{1 - [\alpha/(1 - \alpha)](D - 1)r} \geq 1. \end{aligned} \tag{C12}$$

This means that for $\beta = 0$, $P_{\text{rescue}}(\vartheta \rightarrow \infty) \geq P_{\text{rescue}}(\vartheta = 0)$. For $\alpha = 0$, we obtain equality. The approximation thus suggests that for arbitrary values of r , the probability of evolutionary rescue is approximately the same for a very fast and a very slowly progressing change if $\alpha = 0$ and s small, which is confirmed by computer simulations (not shown). This implies in particular, that for $\alpha = 0$, s small, and ϑ large, $P_{\text{rescue}}(m = 0) \approx P_{\text{rescue}}(m = 1)$, as can be seen in figure 10A.