

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

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Panmictic Populations with $D = 1$ and Scenarios Where Habitat Structure Is Immaterial

We first treat the case $D = 1$ and show at the end of the section that the results coincide with the results for $D > 1$, replacing K with K_{total} , if either $m = 0$ or $\vartheta = 0$.

After the shift in the environment, the wildtype population size decays geometrically:

$$N_{\text{w}}^{(\text{total})}(t) = \begin{cases} K & \text{for } t < 0, \\ K(1-r)^t & \text{for } t \geq 0. \end{cases} \quad (\text{B1})$$

As we model the population size deterministically, the selection coefficient, too, becomes a deterministic function of time:

$$s_{\text{eff}}(t) = \begin{cases} \alpha - 1 = z_0 & \text{for } t < 0, \\ S(N_{\text{w}}^{(\text{total})}(t)) = S(t) & \text{for } t \geq 0. \end{cases} \quad (\text{B2})$$

For the calculation of establishment probabilities, we approximate $s_{\text{eff}}(t)$ in continuous time as a stepped function with each step lasting one generation. We can then use equation (A7) with $\Phi = 1$ to calculate the establishment probability of a mutation, setting $s_{\text{eff}}(t) = s$ (accordingly $\hat{s}_{\text{eff}}(t) = \hat{s}$) when $K(1-r)^t < 1$. Calculations based on a continuous change in $s_{\text{eff}}(t)$ (see app. E) work well for small r but break down as r increases, since for large r the differences between discrete and continuous time dynamics become significant.

Following equation (5), the overall probability of evolutionary rescue reads:

$$P_{\text{rescue}} \approx 1 - \exp \left[- \sum_{t=-\infty}^{-1} uK\alpha p_{\text{est}}(t+1) - \sum_{t=0}^{\infty} uN_{\text{w}}^{(\text{total})}(t)(1+S(t))p_{\text{est}}(t+1) \right], \quad (\text{B3})$$

where for numerical evaluation we again set $N_{\text{w}}^{(\text{total})}(t) = 0$ when $K(1-r)^t < 1$.

For $\beta = 0$, formula (A7) for the establishment probability reduces to

$$p_{\text{est}}(T) = \begin{cases} \frac{2}{1 + \exp[-\hat{z}_0 T](1/\hat{s} + 1/\hat{z}_0) - 1/\hat{z}_0} & \text{for } T < 0, \\ \frac{2\hat{s}}{1 + \hat{s}} & \text{for } T \geq 0, \end{cases} \quad (\text{B4})$$

with

$$\hat{z}_0 = \max[-\ln(1-z_0), 1]. \quad (\text{B5})$$

We can give an explicit formula for the probability of evolutionary rescue:

$$\begin{aligned} P_{\text{rescue}} &\approx 1 - \exp \left[- \sum_{t=-\infty}^{-1} uK\alpha p_{\text{est}}(t+1) - \sum_{t=0}^{\infty} uK(1-r)^t(1+s) \frac{2\hat{s}}{1+\hat{s}} \right] \\ &\approx 1 - \exp \left[- \int_{t=-\infty}^0 uK\alpha p_{\text{est}}(t) - \sum_{t=0}^{\infty} uK(1-r)^t(1+s) \frac{2\hat{s}}{1+\hat{s}} \right] \\ &= 1 - \exp \left[-2uK \frac{\alpha}{1-\hat{z}_0} \ln \left(\frac{\hat{s} + \hat{z}_0}{(1+\hat{s})\hat{z}_0} \right) - u \frac{K}{r} (1+s) \frac{2\hat{s}}{1+\hat{s}} \right] \quad \text{for } \hat{z}_0 \neq 1. \end{aligned} \quad (\text{B6})$$

For $\hat{z}_0 = 1$ (i.e., $\alpha \leq \exp[-1]$), we obtain

$$P_{\text{rescue}} \approx 1 - \exp\left[-2\alpha u K \frac{\hat{s}}{1 + \hat{s}} - u \frac{K}{r} (1 + s) \frac{2\hat{s}}{1 + \hat{s}}\right]. \quad (\text{B7})$$

Returning to equation (B6), the respective contributions of mutations from standing genetic variation and de novo mutations are given by

$$P_{\text{rescue}}^{\text{sgv}} \approx 1 - \exp\left[-2uK \frac{\alpha}{1 - \hat{z}_0} \ln\left(\frac{\hat{s} + \hat{z}_0}{(1 + \hat{s})\hat{z}_0}\right)\right] \approx 1 - \exp\left[-2uK \ln\left(\frac{s + z_0}{z_0}\right)\right] \quad (\text{B8})$$

$$= 1 - \left(\frac{s + z_0}{z_0}\right)^{-2uK}, \quad (\text{B9})$$

$$P_{\text{rescue}}^{\text{dnm}} \approx 1 - \exp\left[-u \frac{K}{r} (1 + s) \frac{2\hat{s}}{1 + \hat{s}}\right] \approx 1 - \exp\left[-u \frac{K}{r} 2s\right], \quad (\text{B10})$$

where the approximation is valid for small s and z_0 . For small s and z_0 , our results coincide with formulas (3) and (5) in Orr and Unckless (2008; note that the absolute fitness of a mutant is $1 + s$ in our model, while it is $1 + s_b - r$ in Orr and Unckless 2008; z_0 corresponds to s_d in Orr and Unckless 2008) and are similar to formula (8) for $P_{\text{rescue}}^{\text{sgv}}$ in Hermisson and Pennings (2005).

For $\beta > 0$, the formula for the probability of evolutionary rescue does not reduce to a compact expression. Evaluation of the complex formula and comparison to computer simulations shows that it yields highly accurate results. In particular, figure B1 demonstrates that the kinks in the graphs are not an artifact of our analytical approximation, but that the theory accurately reproduces the correct behavior. The existence of kinks can be understood if we consider the generation T_c at which for the first time $S(t) > -z$:

$$T_c = \max\left[0, \left\lfloor \frac{1}{r} \ln\left(\frac{s\beta}{s + z}\right) \right\rfloor + 1\right], \quad (\text{B11})$$

where $\lfloor \cdot \rfloor$ denotes the floor function, which maps a real number to the largest previous integer. T_c takes only discrete values and therefore jumps as a function of r . As a consequence, $P_{\text{rescue}}(r)$ is not everywhere differentiable.

We pointed out in the main text that the decay of the rescue probability as a function of r is not completely monotonic in figure 5C. This can be seen in more detail in figure B2, which zooms in on larger r . A slight local minimum exists at $r = 0.7$. This is precisely the point where $T_c = T_c(r)$ jumps from 1 to 2 giving a little advantage to values of r larger than 0.7.

In the main text, we have discussed scenarios where the probability of evolutionary rescue either decays with r or exhibits a minimum for intermediate values of r . In addition to these patterns, a third pattern is possible: the probability of evolutionary rescue attains a minimum, then a maximum, and decays afterwards (fig. B3). This pattern can arise, because the probability that a mutation generated between time 0 and τ_0 , at which $S(t)$ turns from negative to positive, rescues the population has a maximum for intermediate r : For large r , only few mutations are generated; for small r , they have a low establishment probability. If this maximum is pronounced enough, it shapes the overall curve. This is the case if β is extremely large such that the period between 0 and τ_0 is long and z small such that the establishment probability is high. The maximum gets masked if α is very large. The overall effect on the curve is generally weak, however.

It remains to prove that the results for a structured population with $m = 0$ or $\vartheta = 0$ reduce to the unstructured case with $D = 1$ (replacing K by K_{total}). To do so, we consider the general formula equation (5).

We start with $m = 0$: the dynamics in the single demes are then independent from each other. Thus, $N_w^{(i)'}(t) = N_w^{(i)'}(t -$

$(i-1)\vartheta$) and $S_i(t) = S_1(t - (i-1)\vartheta)$. The latter implies furthermore $p_{\text{est}}^{(i)}(t) = p_{\text{est}}^{(1)}(t - (i-1)\vartheta)$. Plugging this into the formula for P_{rescue} yields

$$\begin{aligned}
 P_{\text{rescue}} &\approx 1 - \exp \left(- \sum_{i=1}^D \left[\sum_{t=-\infty}^{(i-1)\vartheta-1} u\alpha K p_{\text{est}}^{(1)}[t - (i-1)\vartheta + 1] \right. \right. \\
 &\quad \left. \left. + \sum_{t=(i-1)\vartheta}^{\infty} u[1 + S_1(t - (i-1)\vartheta)] N_w^{(1)'}(t - (i-1)\vartheta) p_{\text{est}}^{(1)}(t - (i-1)\vartheta + 1) \right] \right) \\
 &= 1 - \exp \left[- \sum_{i=1}^D \left[\sum_{t=-\infty}^{-1} u\alpha K p_{\text{est}}^{(1)}(t+1) + \sum_{t=0}^{\infty} u(1 + S_1(t)) N_w^{(1)'}(t) p_{\text{est}}^{(1)}(t+1) \right] \right] \\
 &= 1 - \exp \left[- \sum_{t=-\infty}^{-1} u\alpha D K p_{\text{est}}^{(1)}(t+1) + \sum_{t=0}^{\infty} u(1 + S_1(t)) D N_w^{(1)'}(t) p_{\text{est}}^{(1)}(t+1) \right]. \tag{B12}
 \end{aligned}$$

For the wildtype population size, $N_w^{(1)'}(t) = N_w^{(1)}(t) = K(1-r)^t$. Using this, $S_1(t) = \max\{-z, s[1 - \beta(1-r)^t]\}$. Consequently, the mutant fitness and along with it the establishment probability p_{est} of a mutation are independent of the carrying capacity. A comparison of equations (B12) and (B3) completes the proof.

We now turn to $\vartheta = 0$. In that case, the wildtype population size decays simultaneously on all demes, and we have $N_w^{(i)'}(t) = N_w^{(i)}(t) = K(1-r)^t$ and consequently $S_i(t) = \max\{-z, s[1 - \beta(1-r)^t]\}$ for all $i \in \{1, \dots, D\}$. This implies in particular that the establishment probability is the same in every deme and again the same as in a population of size KD . We immediately obtain from equation (5)

$$P_{\text{rescue}} \approx 1 - \exp \left[- \sum_{t=-\infty}^{-1} u\alpha D K p_{\text{est}}^{(1)}(t+1) + \sum_{t=0}^{\infty} u(1 + S_1(t)) D N_w^{(1)'}(t) p_{\text{est}}^{(1)}(t+1) \right], \tag{B13}$$

which again coincides with equation (B3).

The formulas imply that for $m = 0$ or $\vartheta = 0$, P_{rescue} depends only on the product DK (i.e., the carrying capacity of an equivalent unstructured population) and not on D and K separately.

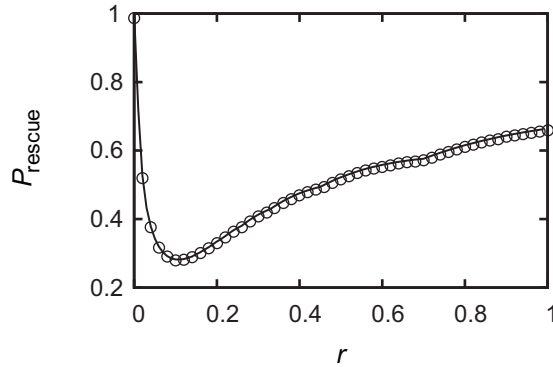


Figure B1: Probability of evolutionary rescue as a function of r with a single deme ($D = 1$). The plot shows a detailed comparison between theory and simulation results. The parameters are chosen as in figure 5D. The theoretical curve is based on equations (B3) and (A7). Simulation results are denoted by circles. Each simulation point is the average of 10^6 replicates.

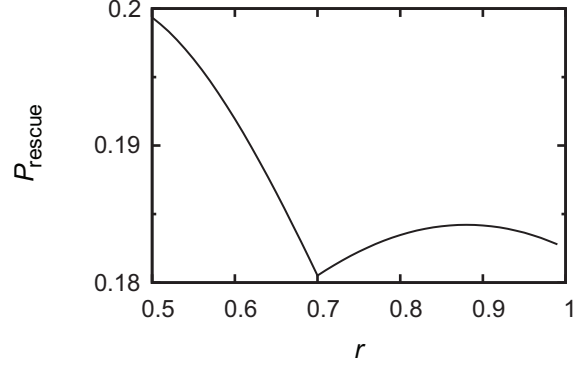


Figure B2: Probability of evolutionary rescue as a function of r with a single deme ($D = 1$). The plot expands figure 5C for large values of r , showing a minimum for $r = 0.7$. The theoretical curve is based on equations (B3) and (A7).

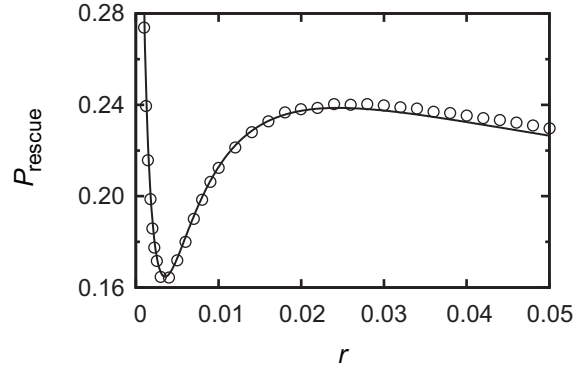


Figure B3: Probability of evolutionary rescue in an unstructured population ($D = 1$). We see that the probability of evolutionary rescue can attain a minimum, followed by a maximum. Parameter values: $\alpha = 0.9$, $z = 0.005$, $s = 0.01$, $\beta = 40$, $K = 10^6$, and $u = 1 \cdot 10^{-6} = 1/K$. The theoretical curve is based on approximation (E1). Circles denote simulation results. Each simulation point is the average of 10^6 replicates.