

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

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General Notes on the Analysis

The Wildtype Population Size

We model the dynamics of the wildtype population size deterministically and assume that mutants are rare enough to be ignored. For the submodels considered in this article, it is not necessary to determine the number of wildtype individuals in each single deme. It is sufficient to determine the total number of wildtypes in the unperturbed (or “old”) and the total number of wildtypes in the deteriorated (or “new”) part of the habitat. Let $N_w^{(\text{new})}(t)$ be the total number of wildtype individuals that live in the new habitat at time t before migration and selection. Using equation (3) and ignoring the effects of mutation, for $t + 1 > 0$,

$$E[N_w^{(\text{new})}(t + 1) | N_w^{(\text{new})}(t)] = (1 - r) \left(1 - m + \frac{d_t}{D} m \right) N_w^{(\text{new})}(t) + m \frac{d_t}{D} (1 - r) (D - d_t) K + K \delta((t + 1) \bmod \vartheta), \quad (\text{A1})$$

where d_t is the number of demes in the new environmental state at time t and $\delta(0) = 1$ and $\delta(x) = 0$ otherwise. The function δ takes into account that every ϑ generations a new island turns bad, bringing with it approximately K new wildtype individuals. As demes in the old environmental state get filled up to carrying capacity every generation, the number of wildtypes in the old part of the habitat is

$$N_w^{(\text{old})}(t) = K(D - d_t).$$

Establishment Probabilities

As explained in the main text, we restrict our analytical results to scenarios where we deal with only one type of mutant individual. Across the entire life cycle (except for density regulation), each mutant produces a Poisson distributed number of offspring with mean $1 + s_{\text{eff}}(t)$, where the effective growth parameter $s_{\text{eff}}(t)$ depends on the specific scenario. To make use of analytical theory, we approximate the discrete-time branching process by a continuous-time branching process. As selection can be strong in scenarios of population decline and evolutionary rescue, details matter in the transition from discrete to continuous time. For the continuous-time branching process, we use the following per capita birth and death rates:

$$\lambda(t) = 0.5 + 0.5 \cdot \text{sign}[\ln(1 + s_{\text{eff}}(t))] \cdot \min[|\ln(1 + s_{\text{eff}}(t))|, 1], \quad (\text{A2a})$$

$$\mu(t) = 0.5 - 0.5 \cdot \text{sign}[\ln(1 + s_{\text{eff}}(t))] \cdot \min[|\ln(1 + s_{\text{eff}}(t))|, 1], \quad (\text{A2b})$$

and define

$$\hat{s}_{\text{eff}}(t) := \text{sign}[\ln(1 + s_{\text{eff}}(t))] \cdot \min[|\ln(1 + s_{\text{eff}}(t))|, 1]. \quad (\text{A3})$$

With the logarithm, we assure that the average long-term growth $\hat{s}_{\text{eff}}(t) = \lambda(t) - \mu(t)$ is the same as in the discrete-time process. The restriction to values between -1 and 1 is necessary for rates to remain nonnegative. Last, drift has to be scaled appropriately. In the continuous-time process, the sum $\lambda(t) + \mu(t)$ measures the strength of drift. In the diffusion limit, $\lambda(t) + \mu(t)$ must be 1 in order to match continuous-time and discrete-time dynamics. This leaves some freedom for the incorporation of selection (affecting the death rate or the birth rate or both). While this choice is irrelevant in the diffusion limit (and hence for weak selection), it matters if the growth parameter is large as it can be in our model. Comparison to computer simulations shows that the best agreement is obtained if we equally distribute it between the death and the birth rate, as above.

If $\exp[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau] \xrightarrow{t \rightarrow \infty} 0$, the establishment probability of a mutation arising at time T is given by (Uecker and Hermisson 2011)

$$p_{\text{est}}(T) = \frac{2}{1 + \int_T^\infty \exp\left[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau\right] dt}. \quad (\text{A4})$$

In the following sections, we will encounter effective growth rates that change stepwise in time:

$$s_{\text{eff}}(t) = \begin{cases} s_0 & \text{for } t < 0, \\ s_l & \text{for } t \in [(l-1)\Phi, l\Phi], \quad l \in \{1, \dots, L-1\}, \\ s_L = s & \text{for } t \geq (L-1)\Phi, \end{cases} \quad (\text{A5})$$

where the steps occur at regular intervals Φ , depending on the model. The term $\hat{s}_{\text{eff}}(t)$ is defined accordingly, with

$$\begin{aligned} \hat{s}_i &= \text{sign}[\ln(1 + s_i)] \cdot \min[|\ln(1 + s_i)|, 1] \quad \text{for } i \in 0, \dots, L, \\ \hat{s} &= \hat{s}_L. \end{aligned} \quad (\text{A6})$$

Assuming that $\hat{s}_k \neq 0$ for all $k \in 0, \dots, L$, we obtain (see below for a derivation)

$$p_{\text{est}}(T) = \begin{cases} \frac{2}{1 + I_0(T)} & \text{for } T < 0, \\ \frac{2}{1 + I_l(T)} & \text{for } T \in [(l-1)\Phi, l\Phi[, \\ \frac{2\hat{s}_L}{1 + \hat{s}_L} & \text{for } T \geq (L-1)\Phi, \end{cases} \quad (\text{A7})$$

with

$$I_l(T) = \frac{1}{\hat{s}_l} + \exp[\hat{s}_l \Delta T_l] \sum_{k=l}^{L-1} \frac{\hat{s}_k - \hat{s}_{k+1}}{\hat{s}_k \hat{s}_{k+1}} \exp\left[-\sum_{j=l}^k \hat{s}_j \Phi\right], \quad (\text{A8})$$

where $\Delta T_l = T - (l-1)\Phi$. For $l > 0$, ΔT_l is the time that has elapsed since the l th island deteriorated. If one or more of the $\hat{s}_k$ are 0, the result is obtained by taking the limit $\hat{s}_k \rightarrow 0$.

We turn to the derivation of equation (A7) with equation (A8). We need to evaluate the integral

$$\int_T^\infty \exp\left[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau\right] dt. \quad (\text{A9})$$

For $T \geq (L-1)\Phi$, the calculation is straightforward. So, we focus on $T < (L-1)\Phi$. We assume throughout the derivation that $\hat{s}_k \neq 0$ for all $k \in 0, \dots, L$. For $T < l\Phi$, if $l = 0$, or $T \in [(l-1)\Phi, l\Phi]$, if $l \in \{1, \dots, L-1\}$, we have

$$\begin{aligned} I_l(T) &= \int_T^\infty \exp\left[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau\right] dt \\ &= \int_T^{l\Phi} \exp\left[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau\right] dt + \sum_{k=l+1}^{L-1} \int_{(k-1)\Phi}^{k\Phi} \exp\left[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau\right] dt + \int_{(L-1)\Phi}^\infty \exp\left[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau\right] dt. \end{aligned} \quad (\text{A10})$$

The first integral gives

$$\int_T^{l\Phi} \exp\left[-\int_T^t \hat{s}_{\text{eff}}(\tau) d\tau\right] dt = \int_T^{l\Phi} \exp\left[-\int_T^t \hat{s}_l d\tau\right] dt = \int_0^{l\Phi-T} \exp[-\hat{s}_l t] dt = \frac{1 - \exp[-\hat{s}_l(l\Phi - T)]}{\hat{s}_l}. \quad (\text{A11})$$

The components of the sum ($k \in \{l+1, \dots, L-1\}$) are

$$\begin{aligned}
 \int_{(k-1)\Phi}^{k\Phi} \exp \left[- \int_T^t \hat{s}_{\text{eff}}(\tau) d\tau \right] dt &= \int_{(k-1)\Phi}^{k\Phi} \exp \left[- \int_T^{l\Phi} \hat{s}_{\text{eff}}(\tau) d\tau - \sum_{j=l+1}^{k-1} \int_{(j-1)\Phi}^{j\Phi} \hat{s}_{\text{eff}}(\tau) d\tau - \int_{(k-1)\Phi}^t \hat{s}_{\text{eff}}(\tau) d\tau \right] dt \\
 &= \exp \left[- \hat{s}_l(l\Phi - T) - \sum_{j=l+1}^{k-1} \hat{s}_j \Phi \right] \int_0^\Phi \exp[-\hat{s}_k t] dt \\
 &= \exp \left[- \hat{s}_l(l\Phi - T) - \sum_{j=l+1}^{k-1} \hat{s}_j \Phi \right] \frac{1 - \exp[-\hat{s}_k \Phi]}{\hat{s}_k}.
 \end{aligned} \tag{A12}$$

For the last integral, we obtain

$$\begin{aligned}
 \int_{(L-1)\Phi}^\infty \exp \left[- \int_T^t \hat{s}_{\text{eff}}(\tau) d\tau \right] dt &= \int_{(L-1)\Phi}^\infty \exp \left[- \int_T^{l\Phi} \hat{s}_l d\tau - \sum_{j=l+1}^{L-1} \int_{(j-1)\Phi}^{j\Phi} \hat{s}_j d\tau - \int_{(L-1)\Phi}^t \hat{s}_L d\tau \right] dt \\
 &= \exp[-\hat{s}_l(l\Phi - T)] \exp \left[- \sum_{j=l+1}^{L-1} \hat{s}_j \Phi \right] \frac{1}{\hat{s}_L}.
 \end{aligned} \tag{A13}$$

We now use the transformation $T \rightarrow \Delta T_l = T - (l-1)\Phi$. With this, we obtain for $l \in \{0, \dots, L-1\}$:

$$\begin{aligned}
 I_l(T) &= \frac{1}{\hat{s}_l} - \frac{1}{\hat{s}_l} \exp[\hat{s}_l \Delta T_l] \exp[-\hat{s}_l \Phi] + \exp[\hat{s}_l \Delta T_l] \sum_{k=l+1}^{L-1} \exp \left[- \sum_{j=l}^{k-1} \hat{s}_j \Phi \right] \frac{1 - \exp[-\hat{s}_k \Phi]}{\hat{s}_k} \\
 &\quad + \exp[\hat{s}_l \Delta T_l] \exp \left[- \sum_{j=l}^{L-1} \hat{s}_j \Phi \right] \frac{1}{\hat{s}_L} \\
 &= \frac{1}{\hat{s}_l} - \frac{1}{\hat{s}_l} \exp[\hat{s}_l \Delta T_l] \exp[-\hat{s}_l \Phi] + \exp[\hat{s}_l \Delta T_l] \sum_{k=l}^{L-2} \exp \left(- \sum_{j=l}^k \hat{s}_j \Phi \right) \frac{1 - \exp[-\hat{s}_{k+1} \Phi]}{\hat{s}_{k+1}} \\
 &\quad + \exp[\hat{s}_l \Delta T_l] \exp \left[- \sum_{j=l}^{L-1} \hat{s}_j \Phi \right] \frac{1}{\hat{s}_L} \\
 &= \frac{1}{\hat{s}_l} - \frac{1}{\hat{s}_l} \exp[\hat{s}_l \Delta T_l] \exp[-\hat{s}_l \Phi] + \exp[\hat{s}_l \Delta T_l] \sum_{k=l}^{L-2} \left[\frac{\exp[-\sum_{j=l}^k \hat{s}_j \Phi] - \exp[-\sum_{j=l}^{k+1} \hat{s}_j \Phi]}{\hat{s}_{k+1}} \right] \\
 &\quad + \exp[\hat{s}_l \Delta T_l] \exp \left[- \sum_{j=l}^{L-1} \hat{s}_j \Phi \right] \frac{1}{\hat{s}_L} \\
 &= \frac{1}{\hat{s}_l} + \exp[\hat{s}_l \Delta T_l] \sum_{k=l}^{L-1} \frac{\hat{s}_k - \hat{s}_{k+1}}{\hat{s}_k \hat{s}_{k+1}} \exp \left[- \sum_{j=l}^k \hat{s}_j \Phi \right],
 \end{aligned} \tag{A14}$$

as given by equation (A8).