

# Appendix from J. H. Peniston et al., “Pulsed Immigration Events Can Facilitate Adaptation to Harsh Sink Environments” (Am. Nat., vol. 194, no. 3, p. 316)

## A1. Derivation of Term in Brackets in Equation (4a)

Assume the genotype at the start of a generation is normally distributed over the population with mean  $\bar{g}$  and variance  $G$ , so the genotype probability density function (PDF) is  $f_G(g) = (1/(2\pi G)^{1/2}) \exp\{-(g - \bar{g})^2/2G\}$ . The phenotype  $z$  (trait) of an individual is the sum of its genotype and a zero-mean normal random variable with variance  $E$ , so its conditional PDF given  $g$  is  $f_{z|G}(z|g) = (1/(2\pi E)^{1/2}) \exp\{-(z - g)^2/2E\}$  ( $z$  overall is normal, with mean  $\bar{g}$  and variance  $P = G + E$ ). The joint PDF of phenotype and genotype is then

$$f_{z,G}(z, g) = f_{z|G}(z|g)f_G(g) = \frac{1}{\sqrt{2\pi E}} \exp\left\{-\frac{(z - g)^2}{2E}\right\} \frac{1}{\sqrt{2\pi G}} \exp\left\{-\frac{(g - \bar{g})^2}{2G}\right\}.$$

The survival as a function of  $z$  is  $\exp\{-(z - \theta)^2/2\omega^2\}$ . The joint PDF after selection is proportional to the product of the survival and the joint PDF before selection, which is

$$k_1 \exp\left\{-\frac{(z - g)^2}{2E}\right\} \exp\left\{-\frac{(g - \bar{g})^2}{2G}\right\} \exp\left\{-\frac{(z - \theta)^2}{2\omega^2}\right\},$$

where  $k_1$  is the reciprocal of the integral of the rest of the expression over all  $g$  and  $z$ . Note that it is only necessary to follow the form of the distributions (which are normally distributed), so terms not involving  $g$  or  $z$  will be absorbed into the leading constant (at which point the subscript of this constant will change). The value of the constant will always be the value needed to make the PDF have an integral of 1. The PDF of the postselection genotype is the integral of the postselection joint PDF over all  $z$ , which is

$$\begin{aligned} f_G^*(g) &= \int_{-\infty}^{\infty} k_1 \exp\left\{-\frac{(z - g)^2}{2E}\right\} \exp\left\{-\frac{(g - \bar{g})^2}{2G}\right\} \exp\left\{-\frac{(z - \theta)^2}{2\omega^2}\right\} dz \\ &= k_1 \exp\left\{-\frac{(g - \bar{g})^2}{2G}\right\} \int_{-\infty}^{\infty} \exp\left\{-\frac{1}{2}\left[\frac{(z - g)^2}{E} + \frac{(z - \theta)^2}{\omega^2}\right]\right\} dz. \end{aligned}$$

Multiplying out the squared terms in the integral and removing terms not involving  $z$  gives

$$f_G^*(g) = k_1 \exp\left\{-\frac{(g - \bar{g})^2}{2G}\right\} \exp\left\{-\frac{1}{2}\left(\frac{\theta^2}{\omega^2} + \frac{g^2}{E}\right)\right\} \int_{-\infty}^{\infty} \exp\left\{-\frac{1}{2}\left[z^2\left(\frac{1}{\omega^2} + \frac{1}{E}\right) - 2z\left(\frac{\theta}{\omega^2} + \frac{g}{E}\right)\right]\right\} dz.$$

Completing the square in the integral gives

$$\begin{aligned} f_G^*(g) &= k_2 \exp\left\{-\frac{(g - \bar{g})^2}{2G}\right\} \exp\left\{-\frac{1}{2}\left[\frac{\theta^2}{\omega^2} + \frac{g^2}{E} - \left(\frac{\omega^2 + E}{\omega^2 E}\right)\left(\frac{\theta E + g\omega^2}{\omega^2 + E}\right)^2\right]\right\} \\ &\quad \times \int_{-\infty}^{\infty} \sqrt{\frac{\omega^2 + E}{2\pi E \omega^2}} \exp\left\{-\frac{1}{2}\left(\frac{\omega^2 + E}{\omega^2 E}\right)\left[z^2 - 2z\left(\frac{\theta E + g\omega^2}{\omega^2 + E}\right) + \left(\frac{\theta E + g\omega^2}{\omega^2 + E}\right)^2\right]\right\} dz. \end{aligned}$$

The integrand is now in the form of normal PDF, and the integral equals 1. The genotype PDF is therefore the first line of the equation just above, which can be simplified to

$$f_G^*(g) = k_2 \exp\left\{-\frac{(g - \bar{g})^2}{2G}\right\} \exp\left\{-\frac{(g - \theta)^2}{2(E + \omega^2)}\right\}.$$

Combining the exponentials and expanding the squares gives

$$\begin{aligned}
 f_G^*(g) &= k_2 \exp \left\{ -\frac{1}{2} \left[ \frac{g^2 - 2g\bar{g} + \bar{g}^2}{G} + \frac{g^2 - 2g\theta + \theta^2}{E + \omega^2} \right] \right\} \\
 &= k_3 \exp \left\{ -\frac{1}{2} \left[ \left( \frac{1}{G} + \frac{1}{E + \omega^2} \right) g^2 - 2 \left( \frac{\bar{g}}{G} + \frac{\theta}{E + \omega^2} \right) g \right] \right\} \\
 &= k_3 \exp \left\{ -\frac{E + \omega^2 + G}{2G(E + \omega^2)} \left[ g^2 - 2 \left( \frac{\bar{g}(E + \omega^2) + G\theta}{E + \omega^2 + G} \right) g \right] \right\}.
 \end{aligned}$$

Completing the square gives

$$f_G^*(g) = k_4 \exp \left\{ -\frac{E + \omega^2 + G}{2G(E + \omega^2)} \left[ g - \left( \frac{\bar{g}(E + \omega^2) + G\theta}{E + \omega^2 + G} \right) \right]^2 \right\}.$$

This is of the form of a normal distribution, with a mean  $g$  of  $[\bar{g}(E + \omega^2) + G\theta]/[E + \omega^2 + G] = \bar{g} + [G(\theta - \bar{g})/(\omega^2 + P)]$ , which is the term in brackets in equation (4a). (The postgenetic variance is decreased by selection, and from this equation it is  $[G(E + \omega^2)]/[E + \omega^2 + G] = G - (G^2/\omega^2 + P)$ ; this does not violate our assumption of constant genetic variance, because that is only assumed at the offspring stage.)

## A2. Derivation of the Equilibrium Population Sizes in the Haploid and Diploid Models with Constant Immigration ( $A_2$ Allele Only)

Here we show the derivation of the equilibrium value of the single-locus haploid model if all individuals are  $A_2$  and there is immigration every generation. If there is no density dependence, as shown in Holt and Gomulkiewicz (1997), the equilibrium value of  $N_2$  is

$$\begin{aligned}
 \hat{N}_2 &= \hat{N}_2 w_2 + I, \\
 \hat{N}_2 &= \frac{I}{1 - w_2}.
 \end{aligned} \tag{A1}$$

To solve for the equilibrium sink population size with density dependence, we start with the recursion

$$\hat{N}_2 = \hat{N}_2 \frac{w_2}{1 + c\hat{N}_2} + I. \tag{A2}$$

We then multiply both sides of this equation by  $1 + c\hat{N}_2$  and rearrange:

$$\begin{aligned}
 \hat{N}_2(1 + c\hat{N}_2) &= w_2 \hat{N}_2 + I(1 + c\hat{N}_2), \\
 c\hat{N}_2^2 + \hat{N}_2(1 - cI - w_2) - I &= 0.
 \end{aligned} \tag{A3}$$

After applying the quadratic formula, the equilibrium population size is

$$\hat{N}_2 = \frac{cI + w_2 - 1 + \sqrt{(1 - cI - w_2)^2 + 4cI}}{2c}. \tag{A4}$$

Because we are assuming that all individuals have only the  $A_2$  allele, the results for the diploid model are identical to the above, with  $N_2$  and  $w_2$  replaced by  $N_{22}$  and  $w_{22}$ , respectively.

## A3. Equations for Adapted States

For analysis of the deterministic models, we considered a population locally adapted when its mean fitness was greater than 1. This would allow a population to persist in the (formerly) sink environment without recurrent immigration. Below are the equations determining critical values in the density-independent models, above which the population is adapted for the haploid, diploid, and quantitative genetic models, respectively.

$$P_{\text{adapt}} = \frac{1 - W_2}{W_1 - W_2},$$

$$P_{\text{adapt}} = \frac{-W_{12} + W_{22} + \sqrt{W_{11} - W_{11}W_{22} + W_{12}^2 + W_{22} - 2W_{12}}}{W_{11} - 2W_{12} + W_{22}}, \quad (\text{A5})$$

$$\bar{g}_{\text{adapt}} = \theta - \sqrt{-2(\omega^2 + P) \ln(1/Bv)},$$

where  $v = [\omega^2/(\omega^2 + P)]^{1/2}$ . For the density-dependent cases, the mean population fitness was also dependent on population size, so there is not a single threshold value. In these cases, population fitness must be calculated.

#### A4. Equilibria for the Diploid Model with No Density Dependence (Both Alleles)

Equilibria for the diploid model with no density dependence and constant immigration can be found by setting  $N' = N$  and  $p' = p$  in equation (2b), giving  $p = (N/N)\bar{w}_1 p = \bar{w}_1 p$ , which has solutions  $\hat{p}_a = 0$  and  $\hat{p}_b = 1 - w_{12}/(w_{11} - w_{12})$  (the latter gives  $\bar{W}_1 = 1$ ). The corresponding equilibrium population sizes are  $\hat{N}_a = I/(1 - w_{22})$  and  $\hat{N}_b = I/[1 - \bar{W}(\hat{p}_b)]$ , where an argument has been appended to  $\bar{W}$  to indicate the  $p$  value at which it is evaluated. The first equilibrium is stable if  $w_{12} < 1$ , while the second equilibrium is unstable. If the system is started near the unstable equilibrium but with  $p$  slightly below  $\hat{p}_b$ , the system goes to the stable equilibrium (persistent maladaptation). If instead the system is started with  $p$  slightly above  $\hat{p}_b$ , assuming  $w_{11} > 1$ ,  $p$  continuously increases until it approaches 1, and  $N$  increases without bound (the adapted state). When  $p$  approaches 1, then mean fitness of the population and of  $A_1$  is  $w_{11}$ , so the recursions are  $N' = w_{11}N + I$  and  $p' = pNw_{11}/(Nw_{11} + I)$ . Since by assumption  $w_{11} > 1$ ,  $N$  increases each generation, as does  $p$ , which approaches 1. However,  $p$  is kept slightly below 1 by the gene flow, which becomes increasingly small as  $N$  increases.

When the period of the immigration cycle is two generations (each generation with immigration is followed by one without immigration), the recursions for  $p$  are

$$p' = N\bar{w}_1(p)p/N', \quad (\text{A6})$$

$$p'' = N'\bar{w}_1(p')p'/N'' = \bar{w}_1(p')[N\bar{w}_1(p)p]/N'', \quad (\text{A7})$$

where an argument has been appended to  $\bar{w}_1$  to indicate the  $p$  value at which it is evaluated (the double prime indicates the generation after that indicated by a single prime). If  $p$  and  $N$  are periodic, then after one cycle (two generations) the values must repeat, so setting  $p'' = p$  and  $N'' = N$  in the last equation yields either  $p = 0$  or  $\bar{w}_1(p')\bar{w}_1(p) = 1$ .

The recursions for  $N$  are

$$N' = N[p^2w_{11} + 2p(1-p)w_{12} + (1-p)^2w_{22}] + I, \quad (\text{A8})$$

$$N'' = N'[p'^2w_{11} + 2p'(1-p')w_{12} + (1-p')^2w_{22}]. \quad (\text{A9})$$

If  $p = 0$ ,  $p' = 0$ ,  $N = w_{22}I/(1 - w_{22}^2)$ , and  $N' = Nw_{22} + I = w_{22}^2I/(1 - w_{22}^2) + I = I/(1 - w_{22}^2)$ . This is the persistent maladapted state. Substituting the equilibrium  $N$  and assuming  $p$  and  $p'$  are slightly above zero gives the recursion  $p'' = w_{12}^2p$ , which indicates that  $p$  can increase from this equilibrium only if  $w_{12} > 1$ . Therefore, the maladapted equilibrium is stable only if  $w_{12} < 1$ . There is also an adapted state, which is periodic, the recursions for which are  $N'' = w_{11}(w_{11}N + I)$  and  $p'' = pNw_{11}/(Nw_{11} + I)$ . The only difference from constant immigration is that  $N$  goes up more slowly because immigration is only half as often, and so  $p$  approaches 1 more slowly.

To find a periodic solution with  $p > 0$ , recall from above that this requires  $\bar{w}_1(p')\bar{w}_1(p) = 1$ . Expanding the mean fitnesses yields an expression that can be solved for  $p'$  in terms of  $p$ :

$$[p'w_{11} + (1-p')w_{12}][pw_{11} + (1-p)w_{12}] = 1,$$

$$p' = \frac{1 - w_{12}(ps + w_{12})}{s(ps + w_{12})}, \quad (\text{A10})$$

where  $s = w_{11} - w_{12}$ . Equation (A6) can now be expanded to

$$p' = \frac{N[pw_{11} + (1-p)w_{12}]p}{N[p^2w_{11} + 2p(1-p)w_{12} + (1-p)^2w_{22}] + I}. \quad (\text{A11})$$

This can be combined with equation (A10) to give a relation between  $N$  and  $p$ :

$$\frac{1 - w_{12}(ps + w_{12})}{s(ps + w_{12})} = \frac{N(ps + w_{12})p}{N[p^2w_{11} + 2p(1-p)w_{12} + (1-p)^2w_{22}] + I},$$

which can be solved for  $N$ , giving

$$N = \frac{[w_{12}(ps + w_{12}) - 1]I}{[1 - w_{12}(ps + w_{12})]\bar{w}(p) - (ps + w_{12})^2ps}. \quad (\text{A12})$$

Substituting  $N$  from equation (A8) into equation (A9), letting  $N'' = N$ , and solving for  $N$  gives

$$N = [N\bar{w}(p) + I]\{p^2w_{11} + 2p'(1-p)w_{12} + (1-p')^2w_{22}\}. \quad (\text{A13})$$

Using equation (A12), equation (A13) can be written in terms of  $p$  and  $p'$  only:

$$\begin{aligned} \frac{[w_{12}(ps + w_{12}) - 1]}{[1 - w_{12}(ps + w_{12})]\bar{w}(p) - (ps + w_{12})^2ps} &= \left[ \frac{[w_{12}(ps + w_{12}) - 1]\bar{w}(p)}{[1 - w_{12}(ps + w_{12})]\bar{w}(p) - (ps + w_{12})^2ps} + 1 \right] \\ &\times \{p^2w_{11} + 2p'(1-p)w_{12} + (1-p')^2w_{22}\}. \end{aligned}$$

Now we can use equation (A10) to put the equation in terms of  $p$  only:

$$\begin{aligned} w_{12}(ps + w_{12}) - 1 &= -(ps + w_{12})^2ps\{p^2w_{11} + 2p'(1-p)w_{12} + (1-p')^2w_{22}\}, \\ w_{12}(ps + w_{12}) - 1 &= -(ps + w_{12})^2 \times ps \left\{ \left[ \frac{1 - w_{12}(ps + w_{12})}{s(ps + w_{12})} \right]^2 w_{11} \right. \\ &\quad + 2 \left[ \frac{1 - w_{12}(ps + w_{12})}{s(ps + w_{12})} \right] \left[ \frac{w_{11}(ps + w_{12}) - 1}{s(ps + w_{12})} \right] w_{12} \\ &\quad \left. + \left[ \frac{w_{11}(ps + w_{12}) - 1}{s(ps + w_{12})} \right]^2 w_{22} \right\} \\ s[1 - w_{12}(ps + w_{12})] &= p\{[1 - w_{12}(ps + w_{12})]^2w_{11} + 2[1 - w_{12}(ps + w_{12})] \\ &\quad \times [w_{11}(ps + w_{12}) - 1]w_{12} + [w_{11}(ps + w_{12}) - 1]^2w_{22}\}. \end{aligned}$$

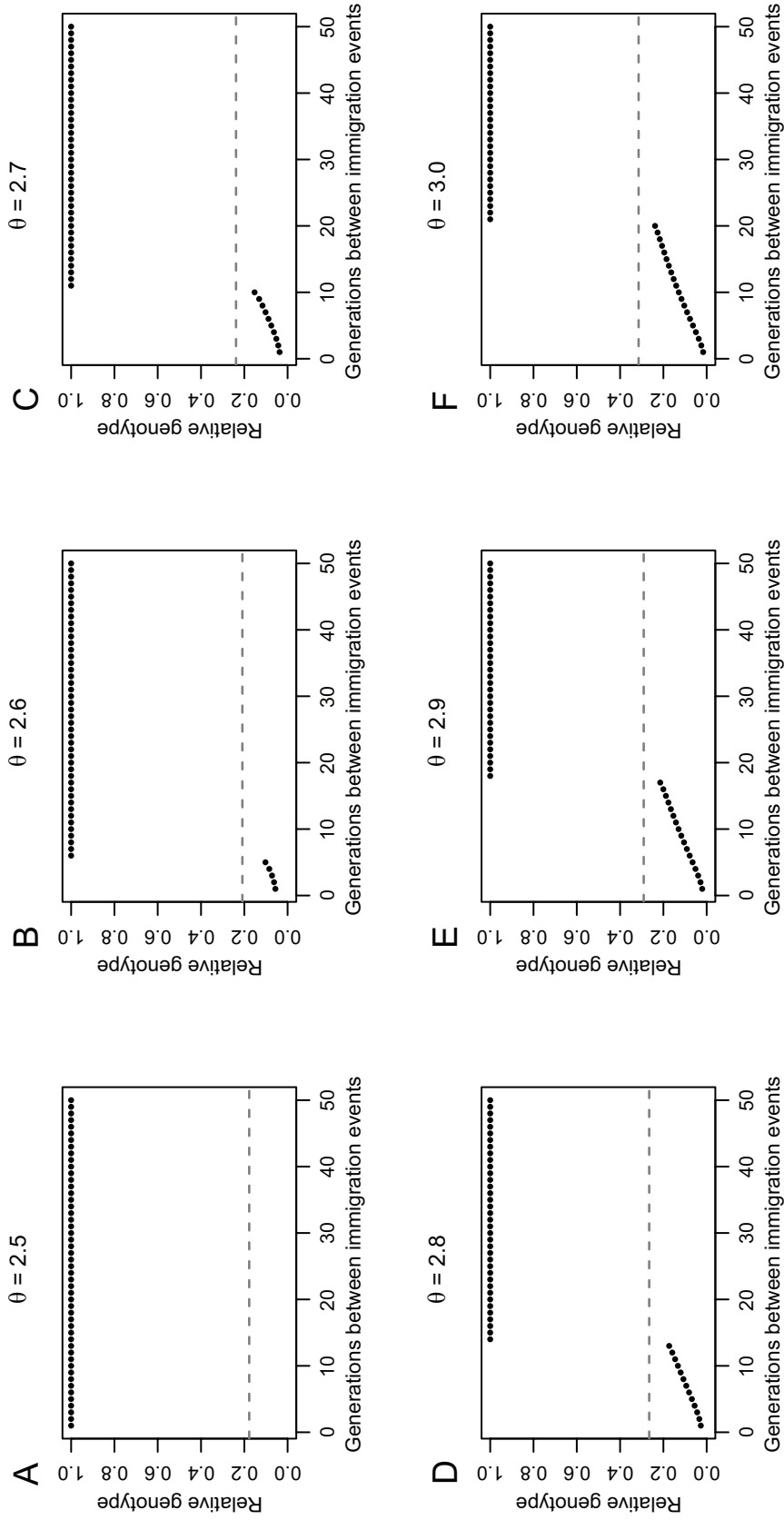
This is a cubic equation and therefore has no simple closed-form solution. However, we solved it numerically to verify that it gives a periodic solution and then started  $p$  just above and below the numerical solution (with  $N$  at the corresponding value from eq. [A12]). As in the constant immigration case, with  $p$  slightly above the periodic value the system went to the adapted state ( $p$  approaching 1 and  $N$  increasing without bound), and with  $p$  slightly lower the system went to the maladapted state.

The derivations for longer immigration cycles would be more complex and were not attempted.

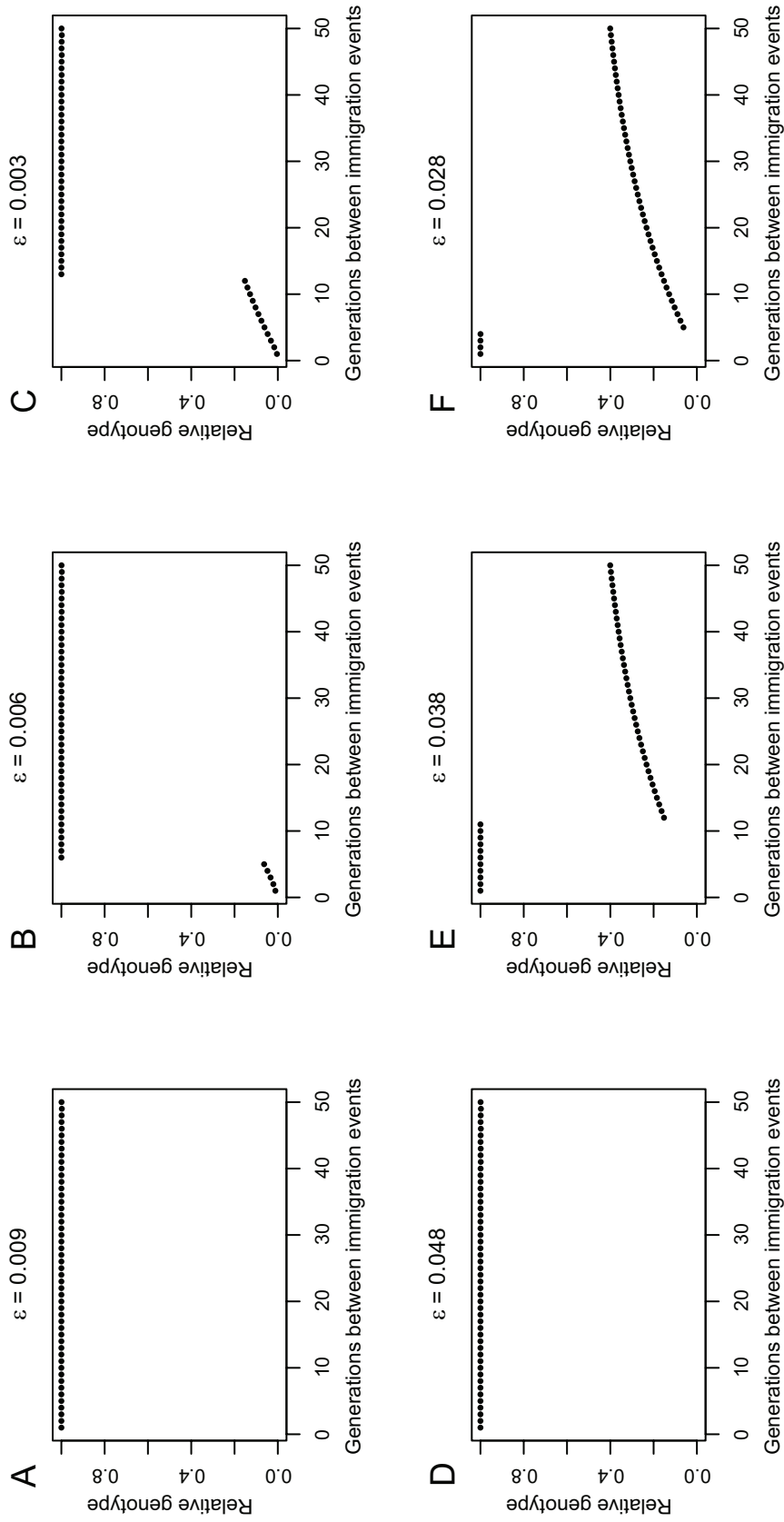
## A5. Explanation of Decline in Diploid Individual-Based Simulations with a Fixed Cumulative Number of Immigrants

As mentioned in the main text, in the diploid individual-based simulations with a fixed cumulative number of immigrants, there was a decline in the probability of adaptation when immigration events became very infrequent, especially when  $w_{12} = 0.4$  (fig. 2C). Because of the low relative abundance of the  $A_1$  allele in the source and the harshness of the sink, immigrant populations decline too rapidly for the relative abundance of  $A_1$  to become high before extinction is approached. Therefore, adaptation requires the persistence of at least one  $A_1$  allele until this point, at which demographic stochasticity could allow  $\bar{w}_1$  to sometimes exceed 1. Most  $A_1$  alleles come from immigrants (rather than mutations in

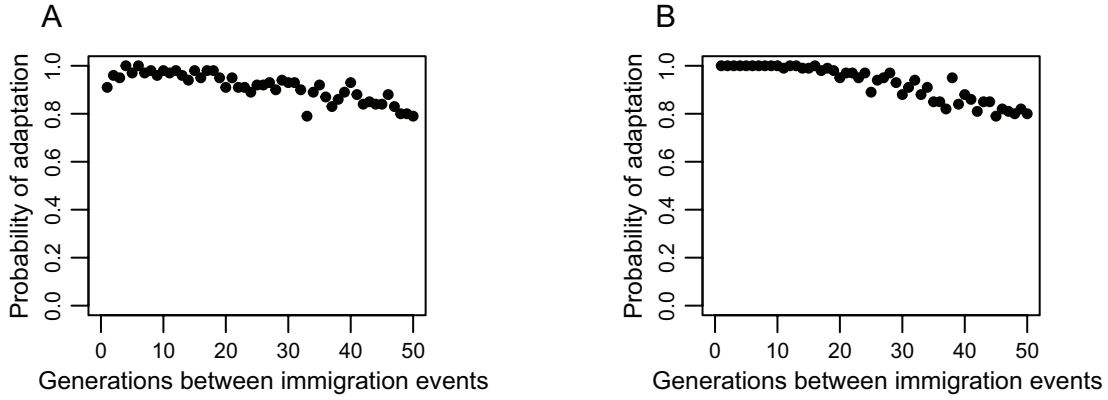
the sink) and are in heterozygotes with fitness  $<1$ . Therefore, their numbers tend to decrease each generation. For a larger immigrant number, the population takes longer to reach a low level, and so fewer  $A_1$  alleles are expected to survive until this point. This can be easily seen by comparing immigration every 10 generations with immigration every 50 generations. In both cases, without adaptation the sink population is expected to become extinct before the next immigration event, so we assume that from one immigration pulse to the next the sink population became extinct (if it did not adapt). With immigration every 50 generations, there were 200 immigrants per event, almost all  $A_2A_2$ , so the population is expected to decline to very near 40 adults the generation after immigration (because  $w_{22,\text{sink}} = 0.2$ ), which is the population size per immigration event for immigration every 10 generations. The relative abundance of  $A_1$  in immigrants is 0.0138, so in 200 immigrants there are expected to be 5.52  $A_1$  alleles, but this should decline to 2.21 after one generation assuming they are all in heterozygotes (since  $w_{22,\text{sink}} = 0.4$ ). There would also be an average of 0.16  $A_1$  alleles produced by mutation that survive to adulthood, for a total of 2.37  $A_1$  alleles in adults when the population size is about 40. With immigration every 10 generations, there are 40 immigrant adults, which are expected to have 1.10  $A_1$  alleles. When  $A_1$  is rare, the probability of adaptation starting with 40 adults should be approximately linearly related to the number of  $A_1$  alleles (we have done simulations to confirm this; for the number of  $A_1 = x$  between 0 and 4, the linear regression for probability of adaptation is  $0.0293x + 0.0032$ , with  $R^2 = 0.988$ ). So the probability of adaptation per immigration event is about twice as high (2.05 using the regression) with immigration every 50 generations as it is with immigration every 10 generations. Let  $p_{40}$  and  $p_{200}$  be the probabilities of adaptation for one event of 40 and 200 immigrants, respectively. If we assume that adaptation for different immigration events is independent and that if adaptation occurs at least once the population at the end is adapted, then the probabilities of adaptation over the entire 1,000 generations are  $1 - (1 - p_{40})^{100}$  and  $1 - (1 - p_{200})^{20}$ , respectively. In our results, the former is higher, which requires  $1 - (1 - p_{40})^{100} > 1 - (1 - p_{200})^{20}$  or  $(1 - p_{40})^5 < (1 - p_{200})$ , which implies that  $p_{200} < 1 - (1 - p_{40})^5 \approx 5p_{40}$ . Based on the number of  $A_1$  alleles,  $p_{200}$  is about twice as high as  $p_{40}$ , which is much less than five times, explaining the drop. This can help explain differences in adaptation probabilities in figure 2C. However, the assumption that adaptation in different pulses is independent is likely incorrect, because probabilities of adaptation over 1,000 generations assuming independence are too high for both one immigration pulse every 10 generations and one immigration pulse every 50 generations. In both cases, there is enough time between pulses so that the vast majority of immigrant pulses become extinct, but there is likely insufficient time for a population to become adapted enough to withstand the next immigrant pulse.



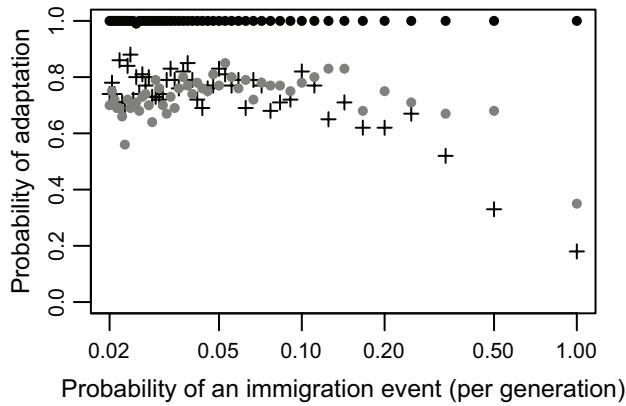
**Figure A1:** Results of the quantitative genetic model without density dependence for different optimum phenotypes in the sink,  $\theta$ . The relative genotype is the mean genotype of the sink population at the end of 1,000 generations divided by the optimum phenotype in the sink (a perfectly adapted population has a relative genotype of 1). The dashed gray lines denote the threshold value for the adapted state, above which the population will have a positive growth rate. Here we assume that the cumulative number of immigrants over 1,000 generations is fixed at about 4,000 individuals. Parameters:  $\omega = 1$ ,  $G = 0.067$ ,  $P = 1.067$ ,  $B = 4$ .



**Figure A2:** Quantitative genetic model with different strengths of an Allee effect  $\epsilon$ . The relative genotype is the mean genotype of the sink population at the end of 1,000 generations divided by the optimum phenotype in the sink (a perfectly adapted population has a relative genotype of 1). *A–C* show results with a fixed cumulative number of immigrants over 1,000 generations (about 4,000). *D–F* show results where there is a fixed number of immigrants each immigration event ( $I_1 = 4$ ). Parameters:  $\theta = 1.05$ ,  $B = 4$ ,  $G = 0.067$ ,  $\omega = 1$ ,  $P = 1.067$ .



**Figure A3:** Diploid (A) and quantitative genetic (B) individual-based simulations with a fixed cumulative number of immigrants over the 1,000 generations of the simulations (about 4,000), continuous density dependence, and mild sink environments. Each point represents the proportion of 100 runs of the simulation in which adaptation occurred. Figure 4D and figure 4F show comparable results for harsher sink environments. Parameters: for A,  $w_{11,sink} = 2.0$ ,  $w_{12,sink} = 0.98$ ,  $w_{22,sink} = 0.2$ ,  $B = 4$ ,  $\mu = 0.001$ ,  $c = 0.0015$ ; for B,  $\theta = 2.6$ ,  $\omega = 1$ ,  $B = 4$ ,  $\mu = 0.001$ ,  $c = 0.0015$ .



**Figure A4:** Probability of adaptation for the haploid (black circles), diploid (gray circles), and quantitative genetic (crosses) versions of the individual-based simulations as a function of per-generation probability of an immigration event (with random timing of immigration events). Each point represents the proportion of 100 runs of the simulation in which adaptation occurred. Note that the abscissas are on logarithmic scales and are average immigration frequencies, whereas other figures use immigration cycle period, the reciprocal of frequency. Parameters: for haploid,  $w_{1,sink} = 1.6$ ,  $w_{2,sink} = 0.2$ ,  $B = 4$ ,  $\mu = 0.001$ ,  $K = 200$ ,  $I_1 = 4$ ; for diploid,  $w_{11,sink} = 2.0$ ,  $w_{12,sink} = 0.65$ ,  $w_{22,sink} = 0.2$ ,  $B = 4$ ,  $\mu = 0.001$ ,  $K = 200$ ,  $I_1 = 4$ ; for quantitative genetic,  $\theta = 3.2$ ,  $\omega = 1$ ,  $B = 4$ ,  $\mu = 0.001$ ,  $K = 200$ ,  $I_1 = 4$ .