

Appendix from R. D. Holt et al., “Temporal Variation Can Facilitate Niche Evolution in Harsh Sink Environments” (Am. Nat., vol. 164, no. 2, p. 187)

Equilibria for Continuous-State Model

Without density dependence, the finite-population equilibria are given by

$$\hat{N} = \frac{BI}{1 - B\hat{W}}, \quad (\text{A1})$$

$$\hat{g} = \theta \frac{G/(\omega^2 + P)}{(B\hat{W})^{-1} - (\omega^2 + E)/(\omega^2 + P)}, \quad (\text{A2})$$

where the mean viability when $\bar{g} = \hat{g}$ is $\hat{W} = \sqrt{\omega^2/(\omega^2 + P)} \exp[-\hat{g} - \theta)^2/2(\omega^2 + P)]$. Equation (A2) is independent of \hat{N} but defines \hat{g} only implicitly, since \hat{W} depends on \hat{g} . Given \hat{g} , \hat{N} can be found from equation (A1). Equation (A2) is independent of I , so the genotypic state \hat{g} is independent of the immigration rate in the absence of density dependence (see Holt and Gomulkiewicz 1997a, 1997b; Gomulkiewicz et al. 1999; Tufto 2000). As defined in the main text, a measure of gene flow is the fraction of breeding adults comprised of immigrants. At equilibrium, after a little manipulation, this fraction can be shown to be $1 - B\hat{W}$, which is independent of the absolute rate of immigration from the source. Note that as fitness goes up, this measure of gene flow decreases, reflecting the dependence of population size on fitness (see eq. [A1]). Many of the results discussed in the main text reflect this interdependence of fitness, population size, and gene flow. In particular, the existence of alternative equilibria rests on this interdependence.

All biologically meaningful solutions of equations (A1) and (A2) require that $B\hat{W} < 1$. Given this inequality, if immigration were cut off and evolution precluded (e.g., by setting heritability to 0), the population would decline inexorably to extinction, which is a defining attribute of a sink environment. However, with evolution (nonzero heritability), an isolated population would eventually adapt and persist without immigration, because the model is deterministic. With $I = 0$, equations (2)–(4) predict that the population moves inexorably toward the optimal phenotype in the sink environment. Because we have assumed that a well-adapted population has mean fitness > 1 , the model predicts adaptation and persistence in the absence of the recurrent immigration. So adaptation in this model is prevented by recurrent gene flow from the source.

When a ceiling form of density dependence is included, it has no effect on the finite equilibria, as long as the equilibrium population calculated in the absence of this density dependence (eq. [A1]) satisfies $\hat{N} < BK$, since in this case the population never reaches the ceiling. However, for the adapted state, without density dependence the population size becomes infinite, and therefore with ceiling density dependence, the ceiling always limits an adapted population. In this case (and in the case in which a finite equilibrium reaches the ceiling), $\hat{N} = BK$ and

$$\hat{g} = \theta \frac{BK\hat{W}G/(\omega^2 + P)}{I + BK\hat{W}G/(\omega^2 + P)}.$$

This degree of maladaptation is less than that of new immigrants, but the population cannot become perfectly adapted, that is, $\hat{g} < \theta$, because of the impact of gene flow on the population.

With continuous density dependence (the average survival probability is the viability in eq. [1] divided by $1 + cN$), the equilibria are given by

$$\hat{N} = \frac{BI(1 - v_{\max}^2 \hat{d})}{(1 - v_{\max}^2 \hat{d}) \hat{d}}, \quad (\text{A3})$$

$$Bv_{\max} \exp \left[\frac{-\hat{d}^2 \theta^2}{2(\omega^2 + P)} \right] = \frac{(\omega^2 + P)(1 - \hat{d})}{\omega^2 + P - (\omega^2 + E)\hat{d}} + cIB \frac{(\omega^2 + P)(1 - \hat{d})}{G\hat{d}}, \quad (\text{A4})$$

where $\hat{d} = (\theta - \hat{g})/\theta$ is the relative distance of the mean from the local optimum phenotype. The equations cannot be directly solved for the equilibria, but these implicit expressions can be readily studied nonetheless. Equation (A4) can be solved numerically for \hat{d} , which can then be used to find \hat{N} using equation (A3). Equation (A4) with $c = 0$ is equivalent to equation (A2). The left-hand side of equation (A4) is the shape of a normal probability density function centered at 0 and has a value of $Bv_{\max} > 1$ at $\hat{d} = 0$. The right-hand side is independent of θ , and without density dependence ($c = 0$), equals 1 at $\hat{d} = 0$ and 0 at $\hat{d} = 1$ and is monotonically decreasing and concave down. Therefore, with no density dependence, the left-hand side is greater than the right-hand side for both extremes of \hat{d} . For low values of θ , the left side is greater than the right at all values, so there is no positive solution to equation (A2), and the only “equilibrium” is the adapted one. As θ is increased, the left side falls more rapidly, and eventually a value of θ is reached (θ_c) at which the curves (the two sides plotted as functions of \hat{d}) touch at one point. For higher values of θ , the curves cross twice (since the left side is greater at both ends, the curves must cross an even number of times), and there are two solutions of equation (A2).

The right-hand side in equation (A4) has a second term added (due to the density dependence, $c > 0$), which is 0 for $\hat{d} = 1$, approaches infinity as \hat{d} approaches 0 from the right, and is positive for \hat{d} between 0 and 1 (the right side still does not depend on θ). Since the left-hand side is now less than the right-hand side at 0 and greater at 1, the two sides must be equal for at least one point in between. If the density dependence is weak, or the immigration rate is low, there will be a solution to the above equation at a low value of \hat{d} , which means \hat{g} close to but lower than θ . This equilibrium is stable and corresponds to the sink becoming adapted (but not perfectly adapted because of gene flow and finite population size).

Note that when θ gets very large (i.e., a sink that is very maladaptive from the perspective of the immigrants), the left side of equation (A4) goes to 0 (because we have assumed that $Bv_{\max} > 1$, which in turn implies that $\hat{d} = 0$ is not a solution of the equation). The right side of equation (A4) in general goes to 0 if and only if \hat{d} goes to unity, which in turn implies that \hat{g} goes to 0. In other words, if the sink is sufficiently maladapted, there will be an equilibrium comprised essentially just of immigrants, with a genotypic value identical to that of the source. If population size is bounded due to density dependence, this will be the only equilibrium in very severe sinks.

There may be additional solutions to equations (A3) and (A4). Without density dependence, there is a value of θ (θ_c) for which curves representing the two sides of the equation touch but do not cross. At this value of θ , if density dependence is added, the right-hand side is increased; if the increase is small (low cBI), the two curves will cross twice in this region, so θ_c is reduced in value by the density dependence. Where there are two maladapted roots, the stable one is moved to a more maladapted value by the density dependence, while the unstable one (the “separatrix”) is moved toward greater adaptation. If θ is increased beyond θ_c , at some point the left-hand side will become less than the right-hand side for all values of \hat{d} other than those very close to 1 (where the right side goes to 0). Therefore, for small cBI , as θ is increased, we can go from one solution to three, and then back to one (fig. 1A; $c = 0.001$). If cBI is high enough, however, there will be only a single solution to the above equation for each θ (fig. 1A; $c = 0.002$). A higher \hat{d} inserted into equation (A3) gives a lower \hat{N} , so the maladapted equilibrium population size is also smaller with density dependence.

Increasing negative density dependence thus makes adaptation less likely, by enhancing the inhibitory effect of gene flow upon selection, and decreases the degree of adaptation maintained, if it occurs (Gomulkiewicz et al. [1999] discuss this in detail for a single-locus model). Also, increased density dependence decreases the range of θ for which there are two stable equilibria. This can make the impact of temporal variation less significant in niche evolution at least when gene flow hampers selection.

Note that genetic variance enters into the denominator on the right-hand side of equation (A4). An increase in genetic variance has a parallel effect to a decrease in the strength of density dependence, which means that alternative stable states are more readily generated for traits under selection with higher genetic variances.

A comparable argument regarding the number of equilibria can be developed for ceiling density dependence. Given a sufficiently high carrying capacity, there is a zone of low sink maladaptation, where only adapted equilibria exist; a zone of intermediate sink maladaptation, in which there are alternative stable equilibria, one maladapted, and one adapted; and finally, some level of sink maladaptation, θ' , above which only a maladapted equilibrium is found. In the main text, a numerical example of alternative equilibria existing only for an intermediate band of sink maladaptation with ceiling density dependence is shown in figure 1B.