

MUTLILOCUS GENETICS AND THE COEVOLUTION OF QUANTITATIVE TRAITS
(MICHAEL KOPP and SERGEY GAVRILETS)

Appendix 3: The haploid case

If both species are haploid equations (5) to (8) remain valid, but the definitions of phenotypic means and variances change to $\bar{x} = x_m + \sum_i \alpha_i (p_i - 1/2)$ and $G_x = \sum_i \alpha_i^2 p_i (1 - p_i)$, respectively.

Similarly, the per locus variances at equilibrium are now given by $\tilde{V}_x = \alpha^2 \hat{p}(1 - \hat{p})$ and $\tilde{V}_y = \beta^2 \hat{q}(1 - \hat{q})$.

Stability analysis of the model with equal locus effects and no mutation leads to the following results: The eigenvalues associated with monomorphic loci are identical to those in the diploid case, which are given in equations (A1-2). If both species are polymorphic in m and n loci, respectively, there are $m + n$ additional eigenvalues. These are the eigenvalues of the block matrix

$$\mathbf{S} = \begin{pmatrix} \mathbf{A} & \mathbf{B} \\ \mathbf{C} & \mathbf{D} \end{pmatrix}, \quad (\text{A3-1})$$

where the submatrices \mathbf{A} , \mathbf{B} , \mathbf{C} and \mathbf{D} have dimensions $m \times m$, $m \times n$, $n \times m$ and $n \times n$, respectively, and the elements

$$a_{ii} = -2\alpha^2(\gamma_x + \sigma_x)\hat{p}(1 - \hat{p})(1 - \delta_{ij}), \quad (\text{A3-2a})$$

$$b_{ij} = 2\alpha\beta\gamma_x\hat{p}(1 - \hat{p}), \quad (\text{A3-2b})$$

$$c_{ij} = 2\alpha\beta\gamma_y\hat{q}(1 - \hat{q}), \quad (\text{A3-2c})$$

$$d_{ij} = -2\beta^2(\gamma_y + \sigma_y)\hat{q}(1 - \hat{q})(1 - \delta_{ij}), \quad (\text{A3-2d})$$

with δ_{ij} being the Kronecker delta ($\delta_{ii} = 1$, $\delta_{ij} = 0$ for $i \neq j$). The real eigenvalues of \mathbf{S} are

$$\boldsymbol{\lambda} = 2(\gamma_x + \sigma_x)\tilde{V}_x \quad m - 1 \text{ times}, \quad (\text{A3-3a})$$

$$= 2(\gamma_y + \sigma_y)\tilde{V}_y \quad n - 1 \text{ times} \quad (\text{A3-3b})$$

(i.e., they are identical to those given in equations A1-5 for the diploid case). In addition, there is a pair of potentially complex eigenvalues satisfying the quadratic equation

$$\left[\boldsymbol{\lambda} + 2(m - 1)(\gamma_x + \sigma_x)\tilde{V}_x \right] \left[\boldsymbol{\lambda} + 2(n - 1)(\gamma_y + \sigma_y)\tilde{V}_y \right] - 4mn\tilde{V}_x\tilde{V}_y\gamma_x\gamma_y = 0. \quad (\text{A3-3c})$$

These eigenvalues have negative real part if

$$-2(m - 1)(\gamma_x + \sigma_x)\tilde{V}_x < 2(n - 1)(\gamma_y + \sigma_y)\tilde{V}_y \quad (\text{A3-4a})$$

$$mn\gamma_x\gamma_y < (m - 1)(n - 1)(\gamma_x + \sigma_x)(\gamma_y + \sigma_y) \quad (\text{A3-4b})$$

If only species X is polymorphic (i.e., $m > 0, n = 0$), there are m eigenvalues in addition to those in (A1-2). These are the eigenvalues of matrix \mathbf{A} :

$$\lambda = -2(m-1)(\gamma_x + \sigma_x)\tilde{V}_x \quad \text{once,} \quad (\text{A3-5a})$$

$$= 2(\gamma_x + \sigma_x)\tilde{V}_x \quad m-1 \text{ times.} \quad (\text{A3-5b})$$

If only species Y is polymorphic (i.e., $m = 0, n > 0$), there are n additional eigenvalues. These are the eigenvalues of matrix \mathbf{D} :

$$\lambda = -2(n-1)(\gamma_y + \sigma_y)\tilde{V}_y \quad \text{once,} \quad (\text{A3-6a})$$

$$= 2(\gamma_y + \sigma_y)\tilde{V}_y \quad n-1 \text{ times.} \quad (\text{A3-6b})$$

As one can see from these results, there are only two classes of polymorphic equilibria that are potentially stable. First, equilibria with $m = 1, n = 0$ or $m = 0, n = 1$ do not exist generically, but if they exist they are neutrally stable ($\lambda = 0$ according to equations (A3-5a) and (A3-6a)). Second, equilibria with $m = n = 1$ are potentially stable in the one-locus case or for either $-1 < e_x < 0, e_y > 0$ or $e_x > 0, -1 < e_y < 0$. In these cases, all real eigenvalues are negative and the eigenvalues defined by equation (A3-3c) are purely imaginary, meaning that stability is determined by higher-order terms. Simulations show that (in the multilocus case) double polymorphic equilibria can be either stable or be surrounded by stable limit cycles involving one polymorphic locus per species. Note that if e_x and e_y have equal signs then condition (A3-4b) is not fulfilled. In this case, the eigenvalues defined by equation (A3-3c) are real and one of them is positive. Thus, equilibria with $m = n = 1$ cannot be stable in a mutualistic or competitive interaction. All other classes of polymorphic equilibria are unstable for all parameter combinations. In particular, there can be no stable equilibria with the maximal number of polymorphic loci in the victim and one polymorphic locus in the exploiter (e.g., $m = L_x > 1, n = 1$), as these cannot fulfill condition (A3-4a). This is the most important difference to the diploid case. In the haploid case, equilibria with net disruptive selection in the victim (EQ_{DIS}) cannot be stable, because net stabilizing selection in the exploiter destroys all genetic variation.

In the following, we derive the structure of (potentially) stable equilibria for various ranges of e_x and e_y .

Case 1: $e_x, e_y > -1$.— Using the approach and the definitions from Appendix 2 (available online only), monomorphic equilibria can be shown to be stable if inequalities (A2-2) are fulfilled. At double polymorphic equilibria (with $m = n = 1$), the polymorphic loci have allele frequencies

$$\hat{p} = \varepsilon_y(1/2 + \delta_y^*), \quad (\text{A3-7a})$$

$$\hat{q} = \varepsilon_x(1/2 + \delta_x^*). \quad (\text{A3-7b})$$

Such equilibria exist if

$$\Theta_x + \frac{\alpha}{2}(1 + e_x) - \beta e_x < \theta_x < \Theta_x + \frac{\alpha}{2}(1 + e_x) \quad \text{if } e_x > 0, \quad (\text{A3-8a})$$

$$\Theta_x + \frac{\alpha}{2}(1 + e_x) < \theta_x < \Theta_x + \frac{\alpha}{2}(1 + e_x) - \beta e_x \quad \text{if } -1 < e_x < 0, \quad (\text{A3-8b})$$

$$\Theta_y + \frac{\beta}{2}(1 + e_y) - \alpha e_y < \theta_y < \Theta_y + \frac{\beta}{2}(1 + e_y) \quad \text{if } e_y > 0, \quad (\text{A3-8c})$$

$$\Theta_y + \frac{\beta}{2}(1 + e_y) < \theta_y < \Theta_y + \frac{\beta}{2}(1 + e_y) - \alpha e_y \quad \text{if } -1 < e_y < 0. \quad (\text{A3-8d})$$

These inequalities define rectangular areas in the plane (θ_x, θ_y) , which, for various values of M_1 and N_1 , can be shown to cover the whole parameter space. For a victim-exploiter interaction (i.e., if e_x and e_y have different signs), these areas are non-overlapping. Therefore, for each parameter combination, the system approaches a unique class of equilibria (defined in terms of (M_0, m, N_0, n)). For a mutualistic or competitive interaction (i.e., if e_x and e_y have equal sign), the double polymorphic equilibria are unstable. In these cases, the areas corresponding to the classes of monomorphic equilibria can be shown to cover the whole parameter space. However, for any given parameter combination, the class of equilibria (in terms of M_1 and N_1) reached by the system is not unique. (The areas for the existence of unstable double polymorphic equilibria are also areas of overlap for the regions of two different classes of stable monomorphic equilibria.)

Case 2: $e_x < -1, e_y > -1$ or $e_x > -1, e_y < -1$.— It is sufficient to consider the case $e_x < -1, e_y > -1$. A reasoning similar to the one applied in the diploid case shows that the only possible stable equilibria are those where the victim is fixed for an extreme trait value. The exploiter then is subject to net stabilizing selection, which in the haploid case, cannot maintain genetic variation. Thus the exploiter gets fixed for the monomorphic genotype whose trait value is closest to the optimum $\tilde{\theta}_y$.

Case 3: $e_x, e_y < -1$.— As in the diploid case, both species must be fixed for a pair of extreme trait values that maximizes the phenotypic distance between them.