MUTLILOCUS GENETICS AND THE COEVOLUTION OF QUANTITATIVE TRAITS
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Appendix 1: Stability analysis of the weak-selection approximation with equal locus effects

Here, we analyze the dynamical system (7) for $\alpha_i = \alpha$, $\beta_j = \beta$ for all i, j. At equilibrium, each locus can be either monomorphic for allele 0, monomorphic for allele 1, or polymorphic, with the frequencies of polymorphic loci being equal within each species:

$$p_i = \hat{p} = 1/2 + \delta_x, \tag{A1-1a}$$

$$q_i = \hat{q} = 1/2 + \delta_y. \tag{A1-1b}$$

Here, the variables

$$\delta_x = \frac{\bar{x} - \tilde{\theta}_x(\bar{y})}{\alpha}, \quad \delta_y = \frac{\bar{y} - \tilde{\theta}_y(\bar{x})}{\beta} \tag{A1-1c}$$

are the distances of the mean phenotypes from $\tilde{\theta}_x$ and $\tilde{\theta}_y$, relative to the corresponding locus effects (cf., Barton 1986). A polymorphic equilibrium exists if $|\delta_x| < 1/2$ and $|\delta_y| < 1/2$. In the following, we derive the eigenvalues of the stability matrix. Let M_0, M_1 and m be the number of loci in species X that are monomorphic for allele 0, allele 1, and polymorphic, respectively. Let N_0, N_1 and n be the corresponding numbers for species Y. Each monomorphic locus contributes one line to the stability matrix in which the only non-zero entry is on the main diagonal and, hence, is an eigenvalue. Thus, monomorphic loci contribute the following eigenvalues:

$$\boldsymbol{\lambda} = -2\alpha^2(\gamma_x + \sigma_x)(1/2 + \delta_x) \quad M_0 \text{ times} \tag{A1-2a}$$

$$= -2\alpha^2(\gamma_x + \sigma_x)(1/2 - \delta_x) \quad M_1 \text{ times} \tag{A1-2b}$$

$$= -2\beta^2(\gamma_y + \sigma_y)(1/2 + \delta_y) \quad N_0 \text{ times} \tag{A1-2c}$$

$$= -2\beta^2(\gamma_y + \sigma_y)(1/2 - \delta_y) \quad N_1 \text{ times} \tag{A1-2d}$$

If both species are polymorphic (i.e., $m > 0, n > 0$), there are $m+n$ additional eigenvalues. These are the eigenvalues of the block matrix

$$\mathbf{S} = \begin{pmatrix} \mathbf{A} & \mathbf{B} \\ \mathbf{C} & \mathbf{D} \end{pmatrix}, \tag{A1-3}$$

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

$$a_{ij} = -2\alpha^2(\gamma_x + \sigma_x)\hat{p}(1 - \hat{p})(2 - \delta_{ij}), \tag{A1-4a}$$

$$b_{ij} = 4\alpha\beta\gamma_x\hat{p}(1 - \hat{p}), \tag{A1-4b}$$

$$c_{ij} = 4\alpha\beta\gamma_y\hat{q}(1 - \hat{q}), \tag{A1-4c}$$

$$d_{ij} = -2\beta^2(\gamma_y + \sigma_y)\hat{q}(1 - \hat{q})(2 - \delta_{ij}), \tag{A1-4d}$$

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

$$\boldsymbol{\lambda} = (\gamma_x + \sigma_x)V_x \qquad m-1 \text{ times,} \tag{A1-5a}$$
$$= (\gamma_y + \sigma_y)V_y \qquad n-1 \text{ times,} \tag{A1-5b}$$

and a pair of potentially complex eigenvalues satisfying the quadratic equation

$$[\boldsymbol{\lambda} + (2m-1)(\gamma_x + \sigma_x)V_x]\,[\boldsymbol{\lambda} + (2n-1)(\gamma_y + \sigma_y)V_y] - 4mnV_xV_y\gamma_x\gamma_y = 0. \tag{A1-5c}$$

Here,

$$V_x = 2\alpha^2\hat{p}(1-\hat{p}), \quad V_y = 2\beta^2\hat{q}(1-\hat{q}) \tag{A1-6}$$

are the contributions to genetic variance of each polymorphic locus. These last two eigenvalues have negative real part if the trace of the corresponding submatrix is negative and the determinant is positive, that is if

$$-V_x(2m-1)(\gamma_x + \sigma_x) < V_y(2n-1)(\gamma_y + \sigma_y), \tag{A1-7a}$$
$$4mn\gamma_x\gamma_y < (2m-1)(2n-1)(\gamma_x + \sigma_x)(\gamma_y + \sigma_y) \tag{A1-7b}$$

The eigenvalues simplify if only one species is polymorphic. 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 $\mathbf{A}$:

$$\boldsymbol{\lambda} = -(2m-1)(\gamma_x + \sigma_x)V_x \qquad \text{once,} \tag{A1-8a}$$
$$= (\gamma_x + \sigma_x)V_x \qquad m-1 \text{ times.} \tag{A1-8b}$$

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

$$\boldsymbol{\lambda} = -(2n-1)(\gamma_y + \sigma_y)V_y \qquad \text{once,} \tag{A1-9a}$$
$$= (\gamma_y + \sigma_y)V_y \qquad n-1 \text{ times.} \tag{A1-9b}$$

The eigenvalues can be used to determine the stability of the various equilibria. Only certain classes of equilibria have the potential to be stable. Here and in the following, it will be convenient to use the composite parameters

$$e_x = \gamma_x/\sigma_x, \quad e_y = \gamma_y/\sigma_y. \tag{A1-10}$$

From (A1-5a), stability of an equilibrium requires that $m \in \{0, 1\}$ if $e_x > -1$, and from (A1-2a), that $m \in \{0, L_x\}$ if $e_x < -1$. Similarly, from (A1-5b), $n \in \{0, 1\}$ if $e_y > -1$, and from (A1-2c), $n \in \{0, L_y\}$ if $e_y < -1$. Furthermore, equilibria with $m = L_x, n = 0$ cannot be stable according to (A1-8), and equilibria with $m = 0, n = L_y$ cannot be stable according to (A1-9). Finally, equilibria with $m = L_x, n = L_y$ cannot be stable according to (A1-5) (see A1-5a for $e_x > -1$, A1-5b for $e_y > -1$ and A1-7a for $e_x, e_y < -1$).

This leaves the following classes of potentially stable equilibria in terms of (m, n):

- $(0, 0)$,
- $(0, 1)$: stability possible only for $e_y > -1$ because of (A1-9a),
- $(1, 0)$: stability possible only for $e_x > -1$ due to (A1-8a),
- $(1, 1)$: in the multilocus case ($L_x > 1$ or $L_y > 1$), stability is possible only for $e_x, e_y > -1$ due to (A1-2); stability is guaranteed (given an equilibrium exists) for either $-1 < e_x < 0$ and $e_y > 0$ or $e_x > 0$ and $-1 < e_y < 0$, because of (A1-2) and (A1-7),
- $(L_x, 1)$: for $e_x < -1, e_y > 0$ due to (A1-5a) and (A1-7), and
- $(1, L_y)$: for $e_x > 0, e_y < -1$ due to (A1-5b) and (A1-7).

Furthermore, for $e_x < -1$, stability of an equilibrium with $m = 0$ requires that all loci of species X are fixed for the same allele ($M_0 = L_x$ or $M_1 = L_x$), because the eigenvalues defined by (A1-2a) and (A1-2b) cannot be negative simultaneously. Similarly, for $e_y < -1$, equilibria with $n = 0$ require that all loci in species Y are fixed for the same allele, because of (A1-2c) and (A1-2d). These results directly lead to the different dynamic regimes discussed in the main text.

References

Barton, N. H., 1986. The maintenance of polygenic variation through a balance between mutation and stabilizing selection. Genet. Res. 47:209–216.