MUTLILOCUS GENETICS AND THE COEVOLUTION OF QUANTITATIVE TRAITS (Michael Kopp and Sergey Gavrilets)

Appendix 2: Stable equilibria in the weak-selection approximation with equal locus effects

In this Appendix, we use the results from Appendix 1 (available online only) in order to derive more details about the structure of stable equilibria in the weak-selection approximation with equal locus effects. Unlike in the main text, we structure our discussion not according to the type of ecological interaction – that is to the signs of e_x and e_y (see eq. A1-10) – but rather according to the mathematically more relevant signs of $e_x + 1$ and $e_y + 1$.

Case 1: $e_x, e_y > -1$.— This scenario comprises EQ_{STA} equilibria in the victim-exploiter interaction, as well as the mutualistic interaction and a special case of the competitive interaction. In all these cases, both species are subject to net stabilizing selection, and the system evolves to a stable equilibrium at which each species is polymorphic in no more than one locus. In the following, we will derive the classes of stable equilibria (as identified by the numbers (M_1, m, N_1, n)) as a function of θ_x and θ_y, the physiological optima of the two species. Our results are illustrated in Figure A1.

If a species is monomorphic at equilibrium, the stability of this state (given the state of the other species) is determined by the eigenvalues defined in equations (A1-2). If a species has one polymorphic locus at equilibrium, the equilibrium allele frequency is given by one of equations (A1-1). If such an equilibrium exists (i.e., if the allele frequency is between 0 and 1), the state of the polymorphic species is always stable (as the eigenvalues defined by (A1-8a) and (A1-9a) for equilibria with one polymorphic species are negative and the eigenvalues defined by equation (A1-5c) for equilibria with two polymorphic species have negative real parts according to conditions (A1-7a) and (A1-7b); we will show below that the latter condition, (A1-7b), holds true whenever a double polymorphic equilibrium exists). Thus, the conditions for existence and stability of equilibria with no more than one polymorphic locus per species are

$$|\delta_x| < 1/2, \quad |\delta_y| < 1/2. \tag{A2-1}$$

Assume for the moment that M_1 and N_1 are fixed at a certain value. Then there are four classes of potentially stable equilibria, which are defined by the values of m and n. First, consider the class of monomorphic equilibria with $m = n = 0$. Let us denote the average trait values at this equilibrium as $\bar{x}^*$ and $\bar{y}^*$ and the corresponding values of δ_x and δ_y as δ_x^* and δ_y^*. From equations (A2-1) and (A1-1c), equilibria of this class are stable if

$$\Theta_x - \frac{\alpha}{2}(1 + e_x) < \theta_x < \Theta_x + \frac{\alpha}{2}(1 + e_x) \tag{A2-2a}$$

$$\Theta_y - \frac{\beta}{2}(1 + e_y) < \theta_y < \Theta_y + \frac{\beta}{2}(1 + e_y) \tag{A2-2b}$$

where

$$\Theta_x = (1 + e_x)\bar{x}^* - e_x\bar{y}^* \qquad \text{(A2-3a)}$$

$$\Theta_y = (1 + e_y)\bar{y}^* - e_y\bar{x}^* \qquad \text{(A2-3b)}$$

Note that both Θ_x and Θ_y are functions of M_1 and N_1. On the plane (θ_x, θ_y), inequalities (A2-2) define a rectangular area with the center at the point (Θ_x, Θ_y) (see Fig. A1). Note that the above conditions are relaxed if one species has an extreme trait value. For example, if the victim has the minimum possible trait value (i.e., $M_0 = L_x, m = M_1 = 0$) the eigenvalue defined by (A1-2b) does not exist, and therefore, the first inequality in (A2-2) does not apply. (This qualification also applies to the monomorphic species in the next two classes of equilibria).

Next, consider the class of equilibria where only species X is polymorphic (i.e., $m = 1, n = 0$). Now $\bar{x} = \bar{x}^* + 2\alpha\hat{p}$ with $\hat{p} = -(1/2 + \delta_x^*)$, $\delta_x = \delta_x^* + 2\hat{p}$ and $\delta_y = \delta_y^* - 2\hat{p}\varepsilon_y$, where $\varepsilon_y = \alpha/\beta \cdot \gamma_y/(\gamma_y + \sigma_y)$. Equilibria of this class exist and are stable if $-1/2 < \delta_x^* < -3/2$ and $2\hat{p}\varepsilon_y - 1/2 < \delta_y^* < 2\hat{p}\varepsilon_y + 1/2$, and these conditions are fulfilled for

$$\Theta_x + \frac{\alpha}{2}(1 + e_x) < \theta_x < \Theta_x + 3\frac{\alpha}{2}(1 + e_x), \qquad \text{(A2-4a)}$$

$$\Theta_y - 2\alpha e_y\hat{p} - \frac{\beta}{2}(1 + e_y) < \theta_y < \Theta_y - 2\alpha e_y\hat{p} + \frac{\beta}{2}(1 + e_y). \qquad \text{(A2-4b)}$$

As p is linear in θ_x, the area described by these inequalities on the plane (θ_x, θ_y) has the shape of a parallelogram.

Next, consider the class of equilibria where only species Y is polymorphic (i.e., $m = 0, n = 1$). In this case, we have $\bar{y} = \bar{y}^* + 2\beta\hat{q}$ with $\hat{q} = -(1/2 + \delta_y^*)$, $\delta_y = \delta_y^* + 2\hat{q}$ and $\delta_x = \delta_x^* - 2\hat{q}\varepsilon_x$, where $\varepsilon_x = \beta/\alpha \cdot \gamma_x/(\gamma_x + \sigma_x)$. Equilibria of this class exist and are stable if $2\hat{q}\varepsilon_x - 1/2 < \delta_x^* < 2\hat{q}\varepsilon_x + 1/2$ and $-1/2 < \delta_y^* < -3/2$, leading to the conditions

$$\Theta_x - 2\beta e_x\hat{q} - \frac{\alpha}{2}(1 + e_x) < \theta_x < \Theta_x - 2\beta e_x\hat{q} + \frac{\alpha}{2}(1 + e_x) \qquad \text{(A2-5a)}$$

$$\Theta_y + \frac{\beta}{2}(1 + e_y) < \theta_y < \Theta_y + 3\frac{\beta}{2}(1 + e_y). \qquad \text{(A2-5b)}$$

On the plane (θ_x, θ_y), these inequalities again describe a parallelogram.

Finally, consider the class of double polymorphic equilibria with $m = n = 1$. This implies $\bar{x} = \bar{x}^* + 2\alpha\hat{p}$, $\bar{y} = \bar{y}^* + 2\beta\hat{q}$, $\delta_y = \delta_y^* + 2\hat{q} - 2\varepsilon_y\hat{p}$, $\delta_x = \delta_x^* + 2\hat{p} - 2\varepsilon_x\hat{q}$, $\hat{p} = -(1/2 + \delta_x^* - 2\varepsilon_x\hat{q})$, and $\hat{q} = -(1/2 + \delta_y^* - 2\varepsilon_y\hat{p})$. Equilibria of this class exist and are stable if $2\hat{q}\varepsilon_x - 3/2 < \delta_x^* < 2\hat{q}\varepsilon_x - 1/2$ and $2\hat{p}\varepsilon_y - 3/2 < \delta_y^* < 2\hat{p}\varepsilon_y - 1/2$, which holds true if

$$\Theta_x - 2\beta e_x\hat{q} + \frac{\alpha}{2}(1 + e_x) < \theta_x < \Theta_x - 2\beta e_x\hat{q} + 3\frac{\alpha}{2}(1 + e_x) \qquad \text{(A2-6a)}$$

$$\Theta_y - 2\alpha e_y\hat{p} + \frac{\beta}{2}(1 + e_y) < \theta_y < \Theta_y - 2\alpha e_y\hat{p} + 3\frac{\beta}{2}(1 + e_y). \qquad \text{(A2-6b)}$$

These conditions can only be fulfilled if $2\beta e_x \hat{q}\big|_{\hat{p}=0} < -2\beta e_x \hat{q}\big|_{\hat{p}=1} + \alpha/2 \cdot (1+e_x)$. From this, it is straightforward to show that double polymorphic equilibria can only exist for

$$e_y < \frac{(e_x+1)}{(3e_x-1)} \quad \text{and } e_x > 1/3 \quad \text{or} \tag{A2-7a}$$

$$e_y > \frac{(e_x+1)}{(3e_x-1)} \quad \text{and } e_x < 1/3 \tag{A2-7b}$$

If conditions (A2-7) hold, inequalities (A2-6) define a parallelogram on the plane (θ_x, θ_y). Note that these conditions also assure fulfillment of stability condition (A1-7b).

If double polymorphic equilibria exist the areas defined by inequalities (A2-2) to (A2-6) are non-overlapping and contiguous (see Fig. A1a). Furthermore, by choosing different values for M_1 and N_1 (leading to different Θ_x and Θ_y), the whole (θ_x, θ_y) plane can be divided into non-overlapping areas like the ones described above (see Fig. A1b). Thus, for each parameter combination, the system reaches a unique class of equilibria.

If double polymorphic equilibria do not exist – which is only possible in mutualistic or competitive interactions, but not in victim-exploiter interactions – the (θ_x, θ_y) parameter space is completely covered by areas corresponding to classes of equilibria with at most one polymorphic species [defined by inequalities (A2-2) to (A2-5)]. In this case, however, the class of equilibria reached by the system is not unique (not shown).

Case 2: $e_x < -1, e_y > -1$ **or** $e_x > -1, e_y < -1$.— Stable equilibria in this case comprise EQ_{DIS} and EQ_{DIR} equilibria in the victim-exploiter interaction, as well as a special case of the competitive interaction. Assume for definiteness that, in the victim-exploiter case, species X is the victim (i.e., $e_x < -1, e_y > -1$). We first derive the equilibrium allele frequencies, $\hat{p}$ and $\hat{q}$, for EQ_{DIS} equilibria (equilibria with L_x polymorphic loci in the victim and 1 polymorphic locus in the exploiter). These can be expressed in terms of the variables $Q_x = \alpha(1-2\hat{p})$ and $Q_y = \beta(1-2\hat{q})$, which (from equations 7 and after several algebraic manipulations) can be shown to be

$$Q_x = -2[(1+e_y)F_x + 2e_x F_y]/T \tag{A2-8a}$$

$$Q_y = 2[2L_x e_y F_x + (1+e_x)(2L_x-1)F_y]/T \tag{A2-8b}$$

with

$$F_x = [\theta_x - x_m - e_x(x_m - \tilde{y}_m)] \tag{A2-9a}$$

$$F_y = [\theta_y - \tilde{y}_m + e_y(x_m - \tilde{y}_m] \tag{A2-9b}$$

$$T = (1+e_x)(1+e_y)(2L_x-1) - 4e_x e_y L_x \tag{A2-9c}$$

$$\tilde{y}_m = y_m + \beta(N_1 - N_0)) \tag{A2-9d}$$

Stability conditions for these equilibria follow from inequalities (A1-7) and are given in the main text (inequalities 10).

In general, there can be up to L_y such equilibria, which differ in the number of loci fixed for allele 0 and allele 1 in the exploiter, and several of these equilibria can be stable simultaneously. This is best seen in the limiting case without direct stabilizing selection ($\sigma_x = \sigma_y = 0$), where equations (A2-8a) simplify to

$$Q_x = Q_y = Q \equiv \frac{|x_m - \tilde{y}_m|}{L_x + 1/2}, \tag{A2-10}$$

and an equilibrium exists if

$$Q < \max(\alpha, \beta). \tag{A2-11}$$

With large L_x, a number of different values of $\tilde{y}_m$ will be compatible with this inequality. Furthermore, without direct stabilizing selection, such an equilibrium is stable if

$$\frac{\gamma_y}{|\gamma_x|} > (2L_x - 1)\frac{\alpha^2 - Q^2}{\beta^2 - Q^2} \tag{A2-12}$$

For example, if $\alpha = \beta$, all feasible equilibria are stable if $\gamma_y/|\gamma_x| > 2L_x - 1$.

During complex heteroclinic cycles, the system temporarily approaches equilibria with more than one polymorphic locus in the exploiter (see Fig. 2B). Oscillations around such equilibria are converging (i.e., the eigenvalues defined by eq. A1-5c have negative real part) if

$$R < \frac{L_x}{n}\frac{2n-1}{2L_x-1} \tag{A2-13}$$

(from A1-7). Here, n is the number of polymorphic exploiter loci and R is defined as in condition (10b). Indeed, condition (A2-13) is a generalized version of condition (10b). It is more easily satisfied for larger n (note that R increases with $G_y = 2n\beta^2 q(1-q)$, which increases with n).

Next, consider equilibria where the victim is fixed for an extreme trait value (EQ_{DIR}). For definiteness, assume that $\bar{x} = x_{\max}$. The exploiter is subject to net stabilizing selection with an optimum trait value $\tilde{\theta}_y = \theta_y + \frac{e_y}{e_y+1}(x_{\max} - \theta_y)$. The possible trait values in a monomorphic exploiter form a sequence in which the subsequent entries differ by 2β. Assume that $\tilde{\theta}_y$ is between two such values $\tilde{y}_m - \beta$ and $\tilde{y}_m + \beta$, where $\tilde{y}_m$ is defined as in (A2-9d) and denotes the phenotype of an individual with N_0 loci homozygous for allele 0, N_1 loci homozygous for allele 1, and one locus heterozygous. If $\tilde{\theta}_y$ is closer to a boundary of this interval than to its center the exploiter population evolves to a monomorphic state at which the trait value coincides with the boundary. Otherwise, the population evolves to a state with a single locus polymorphic at frequency

$$\hat{q} = 1/2 + (\tilde{\theta}_y - \tilde{y}_m)/\beta. \tag{A2-14}$$

In this case, the mean phenotype is

$$\bar{y} = \tilde{y}_m + 2(\tilde{\theta}_y - \tilde{y}_m). \tag{A2-15}$$

This analysis also applies to a competitive interaction with $-1 < e_y < 0$.

Case 3: $e_x, e_y < -1$.— This case corresponds to a competitive interaction. For each species, only one of the eigenvalues defined by equations (A1-2) can be negative. Therefore, both species must be fixed for an extreme trait value with maximal possible phenotypic distance between the two species.

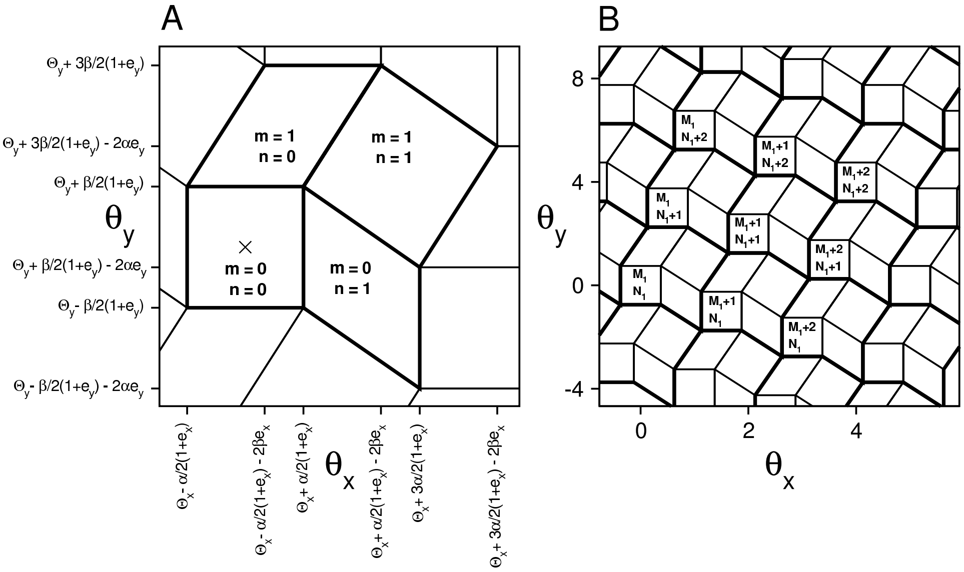

Figure A1: Stable classes of equilibria between victim and exploiter in the multilocus model with equal locus effects, for the case of strong direct stabilizing selection in the victim (i.e., $-1 < e_x < 0, e_y > 0$). The graphs show the stable class of equilibria in the parameter space spanned by θ_x and θ_y, the trait values favored by direct stabilizing selection in the two species. Classes of equilibria are identified by m and n, the respective numbers of polymorphic loci in the victim and exploiter, and M_1 and N_1, the numbers of loci fixed for the 1 allele. (**A**) A subset of the parameter space, showing the areas of stable classes of equilibria in terms of pairs (m, n) for a specific pair (M_1, N_1). The boundaries of the various areas are derived in Appendix 2. The $\times$ marks the point (Θ_x, Θ_y) as defined in (A2-3). (**B**) A larger subset of parameter space, showing the areas of stable classes of equilibria for different pairs (M_1, N_1).The thick lines enclose areas like the one shown in **a**, that is belonging to a single pair (M_1, N_1). The thin lines separate the areas belonging to different pairs (m, n). Parameter values chosen for both figures where $e_x = -1/4, e_y = 1/2, \alpha = \beta = 1$.