Invasion fitnesss in genetic models and the adaptive dynamics of infinite number of alleles and infinite number of loci models

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1 One locus, two allele models: population dynamical formalism

Two alleles A and a, with corresponding phenotypes X_{aa}, X_{aA} and X_{AA}.

Individuals reproduce in summer and then die.

Sampling is done immediately after reproduction and the death of the parent generation.
The densities of newborns will be denoted as n_{aa}, n_{aA} and n_{AA}.

Female ferilities are denoted as $\lambda(X, E_{\mathrm{e}}(t))$, and male fertilities as $\mu(X, E_{\mathrm{e}}(t))$, E_{e} the ecological environment (which includes the overall availability of mating opportunities).

(Arguments will be dropped when there is no need to have them shown, and $\lambda(X_A, E_{\mathrm{e}})$ will be further abreviated to λ_A, etc..)

Gametes combine effectively randomly.

The corresponding population dynamical recurrences:

$$\begin{aligned}
n'_{aa} &= p'_a(\lambda_{aa}n_{aa} + \frac{1}{2}\lambda_{aA}n_{aA}), \\
n'_{aA} &= p'_A(\lambda_{aa}n_{aa} + \frac{1}{2}\lambda_{aA}n_{aA}) + p'_a(\frac{1}{2}\lambda_{aA}n_{aA} + \lambda_{AA}n_{AA}) \\
&= p'_A\lambda_{aa}n_{aa} + \frac{1}{2}\lambda_{aA}n_{aA} + p'_a\lambda_{AA}n_{AA} \\
n'_{AA} &= p'_A(\frac{1}{2}\lambda_{aA}n_{aA} + \lambda_{AA}n_{AA}) \qquad (1)
\end{aligned}$$

with

$$p'_A = \frac{m_A}{m_a + m_A}, \qquad p'_a = \frac{m_a}{m_a + m_A},$$
$$m_a = \mu_{aa}n_{aa} + \frac{1}{2}\mu_{aA}n_{aA}, \qquad m_A = \frac{1}{2}\mu_{aA}n_{aA} + \mu_{AA}n_{AA}. \qquad (2)$$

m_a and m_A together form the genetic environment E_{g} for a female centered model formulation of the form

$$N(t+1) = A(E(t))N(t). \tag{3}$$

with

$$E = \begin{bmatrix} E_{\mathrm{g}} \\ E_{\mathrm{e}} \end{bmatrix} \tag{4}$$

and

$$A = \begin{bmatrix} p'_a\lambda_{aa} & \frac{1}{2}p'_a\lambda_{aA} & 0 \\ p'_A\lambda_{aa} & \frac{1}{2}\lambda_{aA} & p'_a\lambda_{AA} \\ 0 & \frac{1}{2}p'_A\lambda_{aA} & p'_A\lambda_{AA} \end{bmatrix} \tag{5}$$

The effective male and female fertilities, μ and λ, may be interpreted either as

the probability that an X individual happens to have a male of female phenotype - whatever the sex determination mechanism -
times the survival of that phenotype,
times its gamete production,
times the per gamete probability of fertilisation,

or else as

the effective gametic outputs of hermaphrodites, calculated in a similar manner.

In Diekmann O, Gyllenberg M and Metz JAJ (2003) Steady-state analysis of structured population models, *Theoretical Population Biology* 63: 309-338 it is shown that

for any structured population in which everybody is born equal (i.e., everybody has to pass through a single f(ysiological)- as well as h(eterogeneity)-state at birth)

the equilibria satisfy a formula of the form (1) with the primes removed,

with the quantities λ and μ replaced by the lifetime production of newborns, respectively the lifetime sperm production, or, depending on the mating system, the lifetime male mating propensity,

and n_{aa}, n_{aA} and n_{AA} interpreted as the rates at which the various genotypes are born into the population.

One possible example of how E_{e} may be generated:

$$E_{\mathrm{e}} = F\left(\sum_{\mathcal{A}_1\mathcal{A}_2=aa,aA,AA} g_1(X_{\mathcal{A}_1\mathcal{A}_2})n_{\mathcal{A}_1\mathcal{A}_2}, \sum_{\mathcal{A}_1\mathcal{A}_2=aa,aA,AA} g_2(X_{\mathcal{A}_1\mathcal{A}_2})n_{\mathcal{A}_1\mathcal{A}_2}\right). \tag{6}$$

2 One locus, two allele models: population genetical formalism

Population genetics uses a different coordinate system consisting of

the total population density

$$N = n_{aa} + n_{aA} + n_{AA}, \tag{7}$$

the male gametic frequencies p_a and p_A,
and
the female gametic frequencies

$$q'_A = \frac{\frac{1}{2}\lambda_{aA} n_{aA} + \lambda_{AA} n_{AA}}{\lambda_{aa} n_{aa} + \lambda_{aA} n_{aA} + \lambda_{AA} n_{AA}}, \qquad q'_a = 1 - q'_A. \tag{8}$$

From these quantities the genotype densities can be reconstructed as

$$n_{aa} = p_a q_a N, \quad n_{aA} = (p_A q_a + p_a q_A) N, \quad n_{AA} = p_A q_A N. \tag{9}$$

The population genetical recurrences:

$$\begin{aligned} N' &= \bar{\lambda} N, \\ \bar{\mu} p'_A &= \mu_{AA} p_A q_A + \frac{1}{2}\mu_{aA}(p_A q_a + p_a q_A), \\ \bar{\lambda} q'_A &= \lambda_{AA} p_A q_A + \frac{1}{2}\lambda_{aA}(p_A q_a + p_a q_A), \end{aligned} \tag{10}$$

with

$$\begin{aligned} \bar{\mu} &= p_a q_a \mu_{aa} + (p_A q_a + p_a q_A)\mu_{aA} + p_A q_A \mu_{AA}, \\ \bar{\lambda} &= p_a q_a \lambda_{aa} + (p_A q_a + p_a q_A)\lambda_{aA} + p_A q_A \lambda_{AA}. \end{aligned}$$

These recurrences will look unfamiliar to anybody brought up on the Hardy-Weinberg principle. The difference derives from the fact that μ and λ were not assumed to be proportional, as is done implicitly in the textbooks.

If such a proportionality holds, p_A becomes equal to q_A, and the equations collapse to the familiar pattern.

However, as soon as one looks at more realistic biological situations there is little ground for a proportionality assumption.

Equation (10) has an elegance that can fruitfully be exploited for a number of purposes. One disadvantage is that the transformation from the analog of (1) and (2) to an analog of (10) is less than obvious for models of physiologically structured populations expressed in matrix, ODE or PDE form. This can be remedied only by reverting to a generally less accessible integral equation formalism. The necessary formalism is worked out at the population dynamical side in Diekmann et al (1998, 2001), and at the population genetical side, under the Hardy-Weinberg assumption, in Norton (1928) and, in discretised form, in Charlesworth (1980). The combination of the two is developed in Diekmann et al (2003), but only with respect to the special problem of calculating point attractors, where the calculations regain the elegant simplicity of (10).

To calculate the invasion fitness of A into a monomorphically a population, first the long term dynamics of the resident population is calculated from

$$N' = \lambda_{aa} N, \tag{11}$$

together with the rule for determining E_{e}, in the example

$$E_{\mathrm{e}} = F(g_1(X_{aa})N, g_2(X_{aa})N). \tag{12}$$

Next, p_a is replaced with $1 - p_A$ and q_a with $1 - q_A$ in the recurrences for p_A and q_A, and the smaller terms are dropped:

$$p'_A = \frac{1}{2}\frac{\mu_{aA}}{\mu_{aa}}(p_A + q_A), \quad q'_A = \frac{1}{2}\frac{\lambda_{aA}}{\lambda_{aa}}(p_A + q_A). \tag{13}$$

Adding the two equations in (13) gives

$$(p_A + q_A)' = \frac{1}{2}\left[\frac{\mu_{aA}}{\mu_{aa}} + \frac{\lambda_{aA}}{\lambda_{aa}}\right](p_a + q_A). \tag{14}$$

Therefore the invasion fitness of A in an a environment is equal to

$$\rho_A(E(X_{aa})) = \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \ln\left(\frac{1}{2}\left[\frac{\mu_{aA}(E_{\mathrm{e},a}(t))}{\mu_{aa}(E_{\mathrm{e},a}(t))} + \frac{\lambda_{aA}(E_{\mathrm{e},a}(t))}{\lambda_{aa}(E_{\mathrm{e},a}(t))}\right]\right). \qquad (15)$$

In the special case that the monomorphic attractor leads to a constant environment, $E_{\mathrm{e},a}(t) = \bar{E}_{\mathrm{e},a}$:

$$\rho_A(\bar{E}_{\mathrm{e},a}) = \ln(R_{0,A}(\bar{E}_{\mathrm{e},a})) = \ln\left(\frac{1}{2}\left[\frac{\mu_{aA}}{\mu_{aa}} + \frac{\lambda_{aA}}{\lambda_{aa}}\right]\right), \qquad (16)$$

[The right equality of (16) also holds for structured populations.]

Shaw RF and Mohler JD (1953) The selective advantage of the sex ratio. *American Naturalist* 87: 337-342.

Parsons PA (1961). The initial progress of new genes with viability differences between the sexes and with sex linkage. *Heredity* 16: 103-107.

3 Invasion in a genetically variable resident population I: more alleles

Consider a new allele α that appears in a dimorphic (a, A) population, characterised by an internal attractor of (10) with, say (9) and (6):

$$\begin{aligned} p'_\alpha &= \frac{1}{2}\left[\tilde{\mu}_{\alpha a}(p_\alpha q_a + p_a q_\alpha) + \tilde{\mu}_{\alpha A}(p_\alpha q_A + p_A q_\alpha)\right], \\ q'_\alpha &= \frac{1}{2}\left[\tilde{\lambda}_{\alpha a}(p_\alpha q_a + p_a q_\alpha) + \tilde{\lambda}_{\alpha A}(p_\alpha q_A + p_A q_\alpha)\right], \end{aligned} \tag{17}$$

with

$$\tilde{\lambda} = \lambda/\bar{\lambda}, \qquad \tilde{\mu} = \mu/\bar{\mu}, \tag{18}$$

and $\mu_{\alpha a}$, $\mu_{\alpha A}$, $\lambda_{\alpha a}$, $\lambda_{\alpha A}$, p_a, q_a, p_A, q_A, $\bar{\mu}$, and $\bar{\lambda}$ determined by the resident population dynamics.

In vector-matrix form:

$$\begin{bmatrix} p_\alpha \\ q_\alpha \end{bmatrix}' = A_\alpha(E_{a,A}) \begin{bmatrix} p_\alpha \\ q_\alpha \end{bmatrix}$$

with

$$\begin{aligned} A_\alpha &= \frac{1}{2}\begin{bmatrix} (\tilde{\mu}_{\alpha a} q_a + \tilde{\mu}_{\alpha A} q_A) & (\tilde{\mu}_{\alpha a} p_a + \tilde{\mu}_{\alpha A} p_A) \\ (\tilde{\lambda}_{\alpha a} q_a + \tilde{\lambda}_{\alpha A} q_A) & (\tilde{\lambda}_{\alpha a} p_a + \tilde{\lambda}_{\alpha A} p_A) \end{bmatrix} \\ &= \frac{1}{2}\left(\begin{bmatrix} \tilde{\mu}_{\alpha a} \\ \tilde{\lambda}_{\alpha a} \end{bmatrix} [q_a \;\; p_a] + \begin{bmatrix} \tilde{\mu}_{\alpha A} \\ \tilde{\lambda}_{\alpha A} \end{bmatrix} [q_A \;\; p_A] \right). \end{aligned} \tag{19}$$

In a constant resident environment the invasion fitness of α equals $\ln(R_{0,\alpha})$, $R_{0,\alpha}$ the dominant eigenvalue of A_α.

Let the invariant b-state distribution corresponding to $R_{0,\alpha}$ be

$$U_\alpha = \begin{bmatrix} \hat{p}_\alpha \\ \hat{q}_\alpha \end{bmatrix}, \tag{20}$$

with $\hat{p}_\alpha + \hat{q}_\alpha = 1$.

Then $R_{0,\alpha}$ can be written as

$$R_{0,\alpha} = 1^{\mathrm{T}} A_\alpha U_\alpha =$$

$$\frac{1}{2}\left[(\hat{p}_\alpha q_a + \hat{q}_\alpha p_a)\tilde{\mu}_{\alpha a} + (\hat{p}_\alpha q_A + \hat{q}_\alpha p_A)\tilde{\mu}_{\alpha A} + (\hat{p}_\alpha q_a + \hat{q}_\alpha p_a)\tilde{\lambda}_{\alpha a} + (\hat{p}_\alpha q_A + \hat{q}_\alpha p_A)\tilde{\lambda}_{\alpha A}\right]. \tag{21}$$

[Eshel I and Feldman M (1984) Initial increase of new mutants and some continuity properties of ESS in two-locus systems. *American Naturalist*124: 631-640

Liberman U (1988) External stability and ESS: criteria for the initial increase of a new mutant allele. *Journal of Mathematical Biology* 26: 477-485]

The invasion fitness of α is negative, i.e., $R_{0,\alpha} < 1$, if and only if

$$\frac{1}{2}(q_a\tilde{\mu}_{\alpha a} + q_A\tilde{\mu}_{\alpha A} + p_a\tilde{\lambda}_{\alpha a} + p_A\tilde{\lambda}_{\alpha A}) - \frac{1}{4}(p_Aq_a - p_aq_A)(\tilde{\mu}_{\alpha a}\tilde{\lambda}_{\alpha A} - \tilde{\mu}_{\alpha A}\tilde{\lambda}_{\alpha a}) \;<\; 1 \tag{22}$$

and

$$\frac{1}{2}(q_a\tilde{\mu}_{\alpha a} + q_A\tilde{\mu}_{\alpha A} + p_a\tilde{\lambda}_{\alpha a} + p_A\tilde{\lambda}_{\alpha A}) \;<\; 2 \tag{23}$$

Conversily, $R_{0,\alpha} > 1$ if one or the other of the inequalities (22) and (23) hold in the opposite direction.

Whenever the resident population is in Hardy-Weinberg equilibrium, or when in the invader heterozygotes μ and λ are proportional, the second term of (22) is zero, so that (22) simplifies to an explicit averaged Shaw-Mohler formula, and (23) becomes redundant.

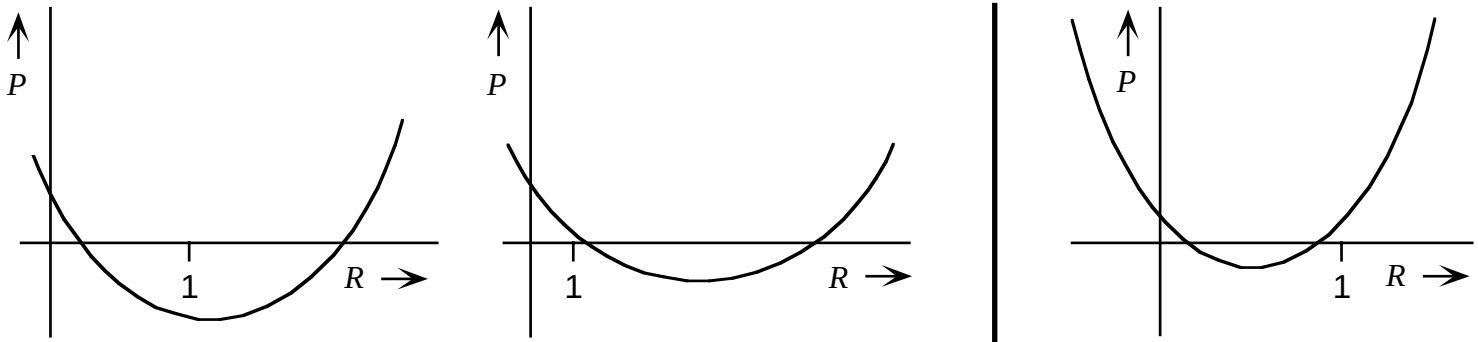
Proof: The characteristic polynomial of A_α equals

$$P_\alpha(R) = R^2 - \text{trace}(A_\alpha)R + \det(A_\alpha).$$

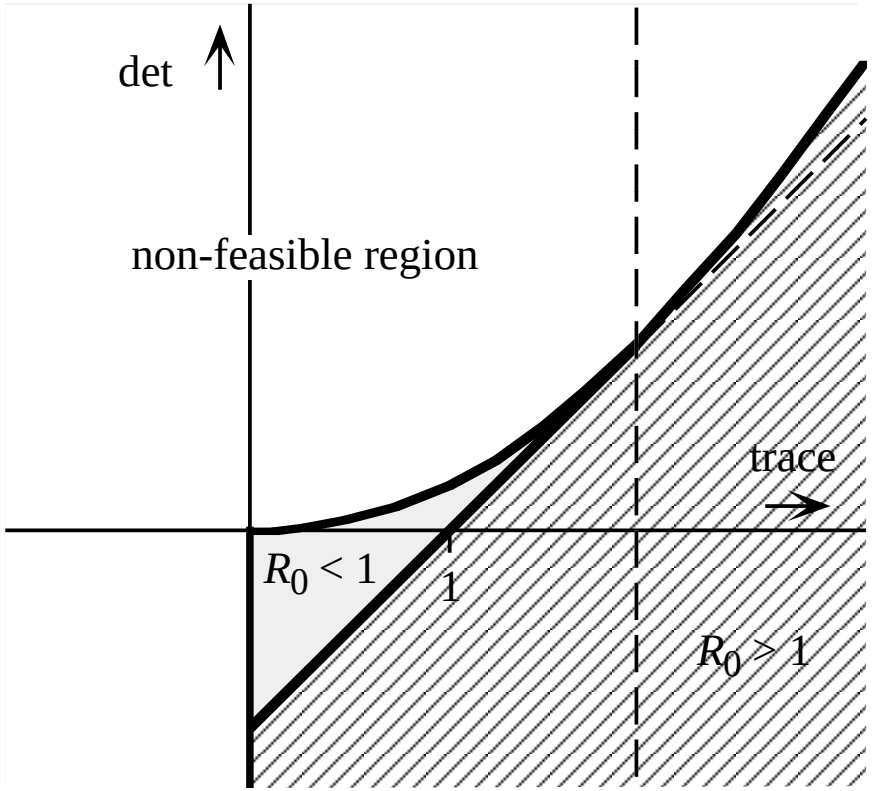
A_α is nonnegative. Therefore P_α has at least one positive real root. Moreover, P_α has positive leading coefficient.

Therefore, P_α has a root to the right of 1, if and only if

$$P_\alpha(1) < 0 \qquad \text{or} \qquad P'_\alpha(1) < 0.$$

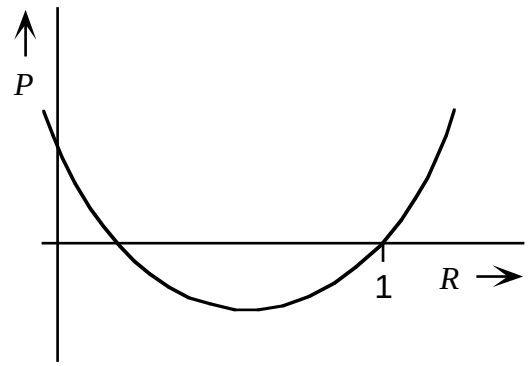


$R_0 > 1$ $R_0 < 1$


det
non-feasible region
trace
$R_0 < 1$
1
$R_0 > 1$

If the interest is in the $R_{0,\alpha}$ of mutants with allelic trait values X_α close to that of some resident allele $X_\mathcal{A}$, for which necessarily $R_{0,\mathcal{A}} = 1$, it suffices to consider (22).

The same result can also be reached by the following direct graphical argument: As $R_{0,\mathcal{A}} = 1$ is by definition the rightmost root of $P_\mathcal{A}$, $P_\mathcal{A}(1) = 0$ and $P'_\mathcal{A}(1) > 0$. Hence, for sufficiently small $|X_\alpha - X_\mathcal{A}|$, $P'_\alpha(1) > 0$, so that (23) is implied by (22).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Allelic Adaptive Dynamics

Assume that alleles carry a trait X, so that $\mathcal{A}$ corresponds to $X_{\mathcal{A}}$.

The phenotype is generated through the map

$$\Phi : (X_{\mathcal{A}_1}, X_{\mathcal{A}_2}) \mapsto X_{\mathcal{A}_1\mathcal{A}_2} = \Phi(X_{\mathcal{A}_1}, X_{\mathcal{A}_2}). \tag{24}$$

which is assumed to be smooth and symmetric:

$$\Phi(X, Y) = \Phi(Y, X). \tag{25}$$

As a consequence for a small mutational step from $X_{\mathcal{A}}$ to X_{α}

$$X_{\alpha\alpha} - X_{\mathcal{A}\mathcal{A}} \approx 2(X_{\alpha\mathcal{A}} - X_{\mathcal{A}\mathcal{A}}). \tag{26}$$

(Andrea Pugliese, personal communication)

Proof: Let

$$\left.\frac{\partial\Phi}{\partial X}(X,Y)\right|_{X=Y} = \left.\frac{\partial\Phi}{\partial Y}(X,Y)\right|_{X=Y} =: \Phi'(X,X).$$

Then, if $X_\alpha = X_\mathcal{A} + \varepsilon Z$, $|Z| = 1$, ε small,

$$X_{\alpha\mathcal{A}} = \Phi(X_\mathcal{A}, X_\mathcal{A} + \varepsilon Z) = X_{\mathcal{A}\mathcal{A}} + \varepsilon\Phi'(X_\mathcal{A}, X_\mathcal{A})Z + \mathrm{O}(\varepsilon^2),$$

and

$$\begin{aligned} X_{\alpha\alpha} &= \Phi(X_\mathcal{A} + \varepsilon Z, X_\mathcal{A} + \varepsilon Z) \\ &= X_{\mathcal{A}\mathcal{A}} + \varepsilon\Phi'(X_\mathcal{A}, X_\mathcal{A})Z + \varepsilon\Phi'(X_\mathcal{A}, X_\mathcal{A})Z + \mathrm{O}(\varepsilon^2) \\ &= X_{\mathcal{A}\mathcal{A}} + 2\varepsilon\Phi'(X_\mathcal{A}, X_\mathcal{A})Z + \mathrm{O}(\varepsilon^2), \end{aligned}$$

and therefore

$$X_{\alpha\alpha} - X_{\mathcal{A}\mathcal{A}} = 2(X_{\alpha\mathcal{A}} - X_{\mathcal{A}\mathcal{A}}) + \mathrm{O}(\varepsilon^2).$$

We can now formulate an adaptive dynamics for the coevolution of the two allelic "species" X_a and X_A.

Assume that mutational steps are small. Then, if α is a mutant of, say, a, so that $X_\alpha = X_a + \varepsilon Z$, with $|Z| = 1$ and ε small:

$$\begin{aligned}\ln(R_{0,\alpha}) &= \varepsilon \sum_{\mathcal{A}=a,A} \left[\frac{\partial R_{0,\alpha}}{\partial \mu_{\alpha\mathcal{A}}}(\mu_{aa}, \mu_{aA}, \lambda_{aa}, \lambda_{aA}) \, \frac{\mathrm{d}\mu}{\mathrm{d}X_{\alpha\mathcal{A}}}(X_{a\mathcal{A}}) + \right. \\ &\left. \frac{\partial R_{0,\alpha}}{\partial \lambda_{\alpha\mathcal{A}}}(\mu_{aa}, \mu_{aA}, \lambda_{aa}, \lambda_{aA}) \frac{\mathrm{d}\lambda}{\mathrm{d}X_{\alpha\mathcal{A}}}(X_{a\mathcal{A}}) \right] \frac{\partial \Phi}{\partial X_\alpha}(X_a, X_\mathcal{A}) \; Z + \mathrm{O}(\varepsilon^2),\end{aligned} \tag{27}$$

where terms like $\frac{\partial \Phi}{\partial X_\alpha}(X_a, X_\mathcal{A})$ should be interpreted as $\frac{\partial \Phi}{\partial X_\alpha}(X_\alpha, X_\mathcal{A})$ evaluated at $X_\alpha = X_a$.

The term between the summation sign and Z is the (transpose of) the selection gradient for $X_\mathcal{A}$ appearing in the canonical equation.

From e.g. Caswell (2001):

$$R_{0,\alpha} = R_{0,a} + (V_a U_a)^{-1} V_a (A_\alpha - A_a) U_a + \mathrm{O}(\varepsilon^2) = (V_a U_a)^{-1} V_a A_\alpha U_a + \mathrm{O}(\varepsilon^2). \tag{28}$$

with A_a defined as in (19) with α replaced by a, and with V_a and U_a the left and right eigenvectors of A_a corresponding to the eigenvalue $R_{0,a} = 1$.

From (28) the derivative of $R_{0,\alpha}$ for $\mu_{\alpha\mathcal{A}}$ respectively $\lambda_{\alpha\mathcal{A}}$ can be calculated as

$$\frac{\partial R_{0,\alpha}}{\partial \mu_{\alpha\mathcal{A}}} = (V_a U_a)^{-1} \sum_{i,j} u_{a,i} v_{a,j} \frac{\partial a_{\alpha,ij}}{\partial \mu_{\alpha\mathcal{A}}}, \quad \frac{\partial R_{0,\alpha}}{\partial \lambda_{\alpha\mathcal{A}}} = (V_a U_a)^{-1} \sum_{i,j} u_{a,i} v_{a,j} \frac{\partial a_{\alpha,ij}}{\partial \lambda_{\alpha\mathcal{A}}}. \tag{29}$$

From the interpretation it is immediately guessed that

$$U_a = \begin{bmatrix} p_a \\ q_a \end{bmatrix}. \tag{30}$$

This guess is corroborated by multiplying U_a with A_a and using the equilibrium equation corresponding for the resident.

Calculating the left eigenvector takes a little more work:

$$V_a = [1 - \delta\tilde{\lambda}_{aa} + \delta\tilde{\lambda}_{aA}, \quad 1 + \delta\tilde{\mu}_{aa} - \delta\tilde{\mu}_{aA}] \tag{31}$$

with

$$\delta = \frac{1}{2}(p_a - q_a) = \frac{1}{2}(q_A - p_A).$$

Note that the combination of (28), (30) and (31) is nothing but a weighted sum of $\tilde{\lambda}_{\alpha a}$ and $\tilde{\lambda}_{\alpha A}$ with weights summing to $\frac{1}{2}$ plus a weighted sum of $\tilde{\mu}_{\alpha a}$ and $\tilde{\mu}_{\alpha A}$, again with weights summing to $\frac{1}{2}$, in other words, an explicit averaged Shaw-Mohler formula.)

Note also that in the hardy-Weinberg case $\delta = 0$.

As mutational steps are assumed to be small, away from the singular resident combinations and from bifurcations of the population dynamics, invasion implies fixation (Geritz et al. 2002; Dercole 2002).

Therefore, as long as at least one of the selection gradients, at $X_\alpha = X_a$ and at $X_\alpha = X_A$, are nonzero, (27) to (31) together with the distribution of mutational steps around X_a and X_A tell the direction of evolutionary movement.

Combinations of resident alleles for which both selection gradients are zero, which includes all ESSes, are called evolutionarily singular.

For evolutionarily singular combinations of alleles the first order criterion (28) to (31) can no longer decide even whether nearby alleles can invade that particular combination.

To decide whether or not a combination of alleles is globally impervious to invasion it is necessary to fall back on (22) and (23).

$$\frac{1}{2}(q_a\tilde{\mu}_{\alpha a} + q_A\tilde{\mu}_{\alpha A} + p_a\tilde{\lambda}_{\alpha a} + p_A\tilde{\lambda}_{\alpha A}) - \frac{1}{4}(p_A q_a - p_a q_A)(\tilde{\mu}_{\alpha a}\tilde{\lambda}_{\alpha A} - \tilde{\mu}_{\alpha A}\tilde{\lambda}_{\alpha a}) \;<\; 1 \tag{22}$$

and

$$\frac{1}{2}(q_a\tilde{\mu}_{\alpha a} + q_A\tilde{\mu}_{\alpha A} + p_a\tilde{\lambda}_{\alpha a} + p_A\tilde{\lambda}_{\alpha A}) \;<\; 2 \tag{23}$$

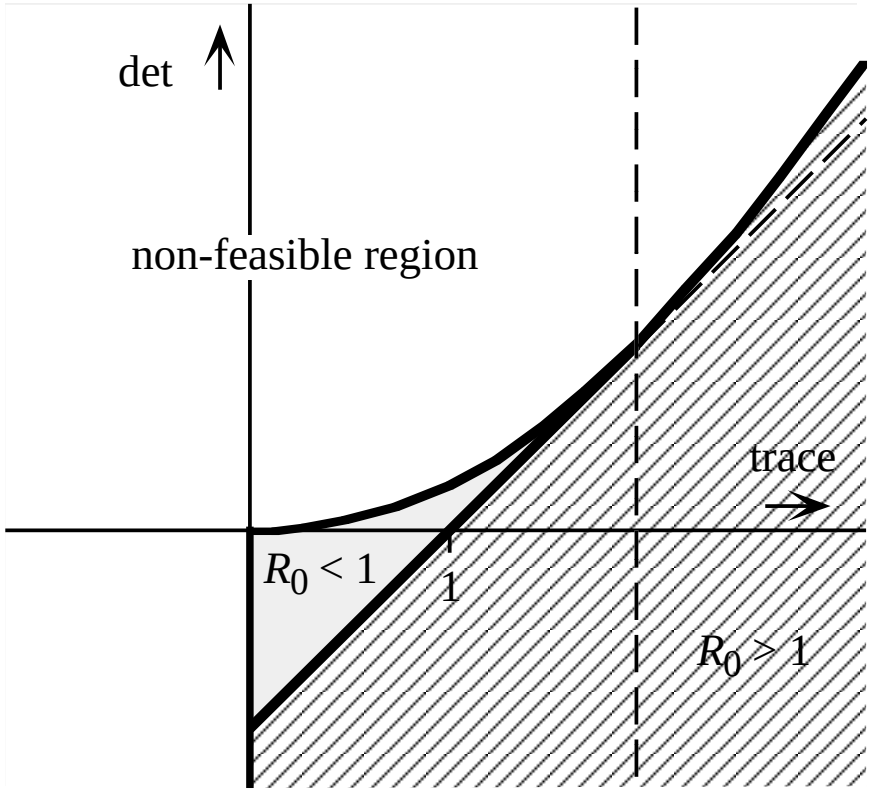
Result:
If the set of trait values realisable by mutants is connected and (22) holds good for *all* potential mutants, then the combination (a, A) is impervious to invasion.

The combination fails to be an ESS if potential mutants exist such that the inequality (22) holds in the opposite direction.

Proof:

That such is the case can be seen by looking at figure XXX2.A2. Any mutant α_0 such that X_{α_0} is equal to either X_a or X_A necessarily maps onto the line segment where $R_0 = 1$. Now take any other mutant α_1 and connect X_{α_1} with a continuous curve to X_{α_0}. If (22) holds good for all possible mutants, other than α_0, the curve always stays left of the line segment separating the regions labeled $R_0 < 1$ and $R_0 > 1$, and therefore $R_{0,\alpha_1} < 1$.

Another graphical way of phrasing the previous argument is by observing how the likes of figure XXX2.A1 change by moving X_α through allelic trait space away from X_{α_0}. For the candidate ESS to make any chance, the first small change in X_α should lift up $P_\alpha(1)$. Condition (22) then says that $P_\alpha(1)$ nowhere sinks below 0 again, except when $X_\alpha = X_a$ or $X_\alpha = X_A$. Therefore, with those two exceptions, the rightmost root of $P_\alpha(R)$ cannot but stay to the left of 1.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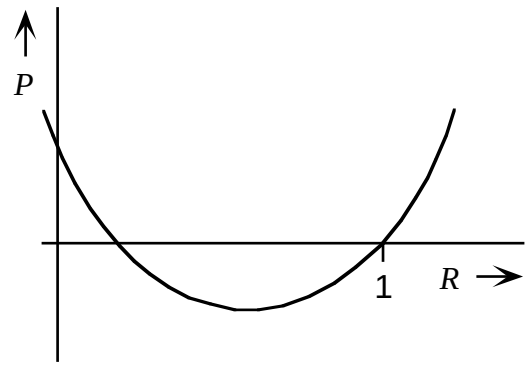
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Of course, if the set of potential allelic trait values is not connected, but can be made connected by adding virtual allleles such that for all allelic trait values in the so enlarged set (22) applies in the environment set by the allelic combination under consideration, then that combination is also an ESS. Furthermore it is not necessary that all $R_{0,\alpha}$ other than for $\alpha = a$ or $\alpha = A$ are smaller than 1. Generic bifurcation theory tells that in general the resident combination of alleles will still be uninvadable if $R_{0,\alpha} < 1$ but for some isolated points in trait space where $R_{0,\alpha} = 1$.

4 Invasion in genetically variable resident populations II: two loci

Once again assume that the resident population is dimorphic at the $\mathcal{A}$-locus, with two resident alleles, a and A, and is otherwise effectively genetically homogeneous, so that the ecological and genetic environments are captured by the attractor of (10) and, for example (6).

Now assume that a mutant allele B arises at another locus that formerly carried the allele b only.

In the gametes, B occurs together with either a or A, so that four gamete types have to be distinguished, occurring with frequencies

$$p_{B,a}, \quad q_{B,a}, \quad p_{B,A} \quad \text{and} \quad q_{B,A}$$

For a recombination probability r:

$$\begin{aligned}
p'_{B,a} &= \frac{1}{2}[\tilde{\mu}_{B,aa}(q_a p_{B,a} + p_a q_{B,a}) \\
&\quad + \tilde{\mu}_{B,aA}((1-r)(q_A p_{B,a} + p_A q_{B,a}) + r\tilde{\mu}_{B,aA}(q_a p_{B,A} + p_a q_{B,A})], \\
q'_{B,a} &= \frac{1}{2}[\tilde{\lambda}_{B,aa}(q_a p_{B,a} + p_a q_{B,a}) \\
&\quad + \tilde{\lambda}_{B,aA}((1-r)(q_A p_{B,a} + p_A q_{B,a}) + r\tilde{\lambda}_{B,aA}(q_a p_{B,A} + p_a q_{B,A})], \\
p'_{B,A} &= \frac{1}{2}[\tilde{\mu}_{B,AA}(q_A p_{B,A} + p_A q_{B,A}) \\
&\quad + \tilde{\mu}_{B,aA}((1-r)(q_a p_{B,A} + p_a q_{B,A}) + r\tilde{\mu}_{B,aA}(q_A p_{B,a} + p_A q_{B,a})], \\
q'_{B,A} &= \frac{1}{2}[\tilde{\lambda}_{B,AA}(q_A p_{B,A} + p_A q_{B,A}) \\
&\quad + \tilde{\lambda}_{B,aA}((1-r)(q_a p_{B,A} + p_a q_{B,A}) + r\tilde{\lambda}_{B,aA}(q_A p_{B,a} + p_A q_{B,a})],
\end{aligned} \tag{32}$$

with p_a, p_A, q_a, and q_A the frequencies of ab and Ab in the micro- resp. macro-gametes, $\tilde{\mu} = \mu/\bar{\mu}$, $\tilde{\lambda} = \lambda/\bar{\lambda}$, and $\bar{\mu}$ and $\bar{\lambda}$, as well as E_{e}, and therefore $\mu_{B,aa} = \mu_{aabB}$ etc., determined by the resident (a, A) polymorphism.

$$\begin{bmatrix} p_{B,a} \\ q_{B,a} \\ p_{B,A} \\ q_{B,A} \end{bmatrix}' = A_B(E_{a,A}) \begin{bmatrix} p_{B,a} \\ q_{B,a} \\ p_{B,A} \\ q_{B,A} \end{bmatrix} \tag{33}$$

with

$$A_B = A_{B,\mathrm{sel}} + A_{B,\mathrm{rec}}, \qquad A_{B,\mathrm{sel}} = \begin{bmatrix} A_{B,\mathrm{sel},a} & 0 \\ 0 & A_{B,\mathrm{sel},A} \end{bmatrix},$$

$$A_{B,\mathrm{sel},a} = \frac{1}{2} \begin{bmatrix} \tilde{\mu}_{B,aa} q_a + \tilde{\mu}_{B,aA} q_A & \tilde{\mu}_{B,aa} p_a + \tilde{\mu}_{B,aA} p_A \\ \tilde{\lambda}_{B,aa} q_a + \tilde{\lambda}_{B,aA} q_A & \tilde{\lambda}_{B,aa} p_a + \tilde{\lambda}_{B,aA} p_A \end{bmatrix},$$

$$A_{B,\mathrm{sel},A} = \frac{1}{2} \begin{bmatrix} \tilde{\mu}_{B,AA} q_A + \tilde{\mu}_{B,aA} q_a & \tilde{\mu}_{B,AA} p_A + \tilde{\mu}_{B,aA} p_a \\ \tilde{\lambda}_{B,AA} q_A + \tilde{\lambda}_{B,aA} q_a & \tilde{\lambda}_{B,AA} p_A + \tilde{\lambda}_{B,aA} p_a \end{bmatrix},$$

$$A_{B,\mathrm{rec}} = \frac{r}{2} \begin{bmatrix} -\tilde{\mu}_{B,aA} \\ -\tilde{\lambda}_{B,aA} \\ \tilde{\mu}_{B,aA} \\ \tilde{\lambda}_{B,aA} \end{bmatrix} [q_A \quad p_A \quad -q_a \quad -p_a]. \tag{34}$$

The likeness of the formulas for $A_{B,\mathrm{sel},a}$ and $A_{B,\mathrm{sel},A}$ with (19) can be understood from the fact that without crossing over the combinations Ba and BA act as pseudo-alleles.)

The invasion fitness of the B-allele is the dominant Lyapunov exponent of the matrix sequence $A_B(E_{a,A}(t))$.

In a constant resident environment the invasion fitness of B equals $\ln(R_{0,B})$, $R_{0,B}$ the dominant eigenvalue of $A_B(\bar{E}_{a,A})$.
Let the invariant b-state distribution corresponding to $R_{0,B}$ be

$$U_B = \begin{bmatrix} \hat{p}_{B,a} \\ \hat{q}_{B,a} \\ \hat{p}_{B,A} \\ \hat{q}_{B,A} \end{bmatrix}, \tag{35}$$

(with $\hat{p}_{B,a} + \hat{p}_{B,A} + \hat{q}_{B,a} + \hat{q}_{B,A} = 1$). Then $R_{0,B}$ can be written as

$$R_{0,B}(\bar{E}_{a,A}) = 1^{\mathrm{T}} A_B U_B = 1^{\mathrm{T}} A_{B,\mathrm{sel}} U_B, \tag{36}$$

since $1^{\mathrm{T}} A_{B,\mathrm{rec}} = 0$. And (36) can be rewritten as

$$R_{0,B} = \frac{1}{2}(w_1\tilde{\mu}_{B,aa} + w_2\tilde{\mu}_{B,aA} + w_3\tilde{\mu}_{B,AA} + w_1\tilde{\lambda}_{B,aa} + w_2\tilde{\lambda}_{B,aA} + w_3\tilde{\lambda}_{B,AA})$$

with

$$w_1 = \hat{p}_{B,a}q_a + p_a\hat{q}_{B,a},\ w_2 = \hat{p}_{B,a}q_A + \hat{p}_{B,A}q_a + p_a\hat{q}_{B,A} + p_A\hat{q}_{B,a},\ w_3 = \hat{p}_{B,A}q_A + p_A\hat{q}_{B,A}, \tag{37}$$

[Eshel I and Feldman M (1984) Initial increase of new mutants and some continuity properties of ESS in two-locus systems. *American Naturalist*124: 631-640

Liberman U (1988) External stability and ESS: criteria for the initial increase of a new mutant allele. *Journal of Mathematical Biology* 26: 477-485]

(37) has the same advantages and disadvantages as (21). It supports the intuition that new mutants can only invade if they increase Shaw-Mohler fitness in some averaged manner. However, (37) is of no help for doing concrete calculations, such as calculating ESSes.

Once more assume that all mutations have only small phenotypic effect. Then (e.g. Caswell 2001), since $A_{B,\mathrm{rec}}U_b = 0$:

$$R_{0,B} = (V_b U_b)^{-1} V_b A_B U_b + \mathrm{O}(\varepsilon^2) = (V_b U_b)^{-1} V_b A_{B,\mathrm{sel}} U_b + \mathrm{O}(\varepsilon^2), \qquad (38)$$

with

$$U_b = \begin{bmatrix} p_a \\ q_a \\ p_A \\ q_A \end{bmatrix}. \qquad (39)$$

$$\begin{aligned} V_b \;=\; & [(\tilde{\mu}_{aA}(1+\delta\tilde{\lambda}_{AA}) + \tilde{\lambda}_{aA}(1-\delta\tilde{\mu}_{AA}))(1-\delta\tilde{\lambda}_{aa} + \delta\tilde{\lambda}_{aA}), \\ & (\tilde{\mu}_{aA}(1+\delta\tilde{\lambda}_{AA}) + \tilde{\lambda}_{aA}(1-\delta\tilde{\mu}_{AA}))(1+\delta\tilde{\mu}_{aa} - \delta\tilde{\mu}_{aA}), \\ & (\tilde{\mu}_{aA}(1-\delta\tilde{\lambda}_{aa}) + \tilde{\lambda}_{aA}(1+\delta\tilde{\mu}_{aa}))(1+\delta\tilde{\lambda}_{AA} - \delta\tilde{\lambda}_{aA}), \\ & (\tilde{\mu}_{aA}(1-\delta\tilde{\lambda}_{aa}) + \tilde{\lambda}_{aA}(1+\delta\tilde{\mu}_{aa}))(1-\delta\tilde{\mu}_{AA} + \delta\tilde{\mu}_{aA})]. \end{aligned} \qquad (40)$$

(NB $\tilde{\mu}_{b,aA} = \tilde{\mu}_{aA}$, etc..)

Note that the combination of (38), (39) and (40) does not contain r. For sufficiently small selection the relaxation to linkageequilibrium takes place on a faster time scale than the selective changes.

V_b and U_b are the left and right eigenvectors of A_b corresponding to the eigenvalue $R_{0,b} = 1$, A_b defined as in (34) with B replaced with b, and with ε defined in a manner similar to that in the allelic case.

The formula for U_v is immediately guessed from the interpretation.

This guess is corroborated by observing that $A_{b,\mathrm{sel}}$ has two eigenvectors $[p_a, q_a, 0, 0]^{\mathrm{T}}$ and $[0, 0, p_A, q_A]^{\mathrm{T}}$ with eigenvalue 1 (use the equilibrium equation corresponding to (10)). Among all weighted sums of these two vectors only those with equal weights are annihilated by $A_{b,\mathrm{rec}}$.

V_b can be calculated by a similar strategy.

$$A_b = A_{b,\mathrm{sel}} + A_{b,\mathrm{rec}}, \qquad A_{b,\mathrm{sel}} = \begin{bmatrix} A_{b,\mathrm{sel},a} & 0 \\ 0 & A_{b,\mathrm{sel},A} \end{bmatrix},$$

$$A_{b,\mathrm{sel},a} = \frac{1}{2}\begin{bmatrix} \tilde{\mu}_{aa}q_a + \tilde{\mu}_{aA}q_A & \tilde{\mu}_{aa}p_a + \tilde{\mu}_{aA}p_A \\ \tilde{\lambda}_{aa}q_a + \tilde{\lambda}_{aA}q_A & \tilde{\lambda}_{aa}p_a + \tilde{\lambda}_{aA}p_A \end{bmatrix},$$

$$A_{b,\mathrm{sel},A} = \frac{1}{2}\begin{bmatrix} \tilde{\mu}_{AA}q_A + \tilde{\mu}_{aA}q_a & \tilde{\mu}_{AA}p_A + \tilde{\mu}_{aA}p_a \\ \tilde{\lambda}_{AA}q_A + \tilde{\lambda}_{aA}q_a & \tilde{\lambda}_{AA}p_A + \tilde{\lambda}_{aA}p_a \end{bmatrix},$$

$$A_{b,\mathrm{rec}} = \frac{r}{2}\begin{bmatrix} -\tilde{\mu}_{aA} \\ -\tilde{\lambda}_{aA} \\ \tilde{\mu}_{aA} \\ \tilde{\lambda}_{aA} \end{bmatrix}[q_A \quad p_A \quad -q_a \quad -p_a].$$

$A_{b,\mathrm{sel}}$ has two eigenvectors with eigenvalue 1 (use the equilibrium equation for the resident:

$$[p_a, q_a, 0, 0]^{\mathrm{T}} \quad \text{and} \quad [0, 0, p_A, q_A]^{\mathrm{T}}$$

Among all weighted sums of these two vectors only those with equal weights are annihilated by $A_{b,\mathrm{rec}}$.

V_b can be calculated by a similar strategy.

(39) to (40) together allow a first check whether some single locus polymophism is impervious to change through the invasion of so-called modifiers, i.e., new alleles on other loci that induce only small phenotypic changes. (Notice that, in the same manner as in the one locus case, (38) can be read as an averaged Shaw-Mohler formula.)

When the resident polymorphism is such that the resident μ's are all equal and so are the resident λ's,

$$V_b = [2, 2, 2, 2], \quad \text{and} \quad p_a = q_a,\ p_A = q_A, \tag{41}$$

so that

$$\begin{aligned} &R_{0,B}(\bar{E}_{a,A}) = \\ &\frac{1}{2}(p_a^2\tilde{\mu}_{B,aa} + 2p_a p_A\tilde{\mu}_{B,aA} + p_A^2\tilde{\mu}_{B,AA} + p_a^2\tilde{\lambda}_{B,aa} + 2p_a p_A\tilde{\lambda}_{B,aA} + p_A^2\tilde{\lambda}_{B,AA}) \\ &\qquad\qquad + \mathrm{O}(\varepsilon^2). \end{aligned} \tag{42}$$

ESSes such that all μ's are equal and all λ's are equal are called

ideal free.

Under the (commonly made, but silly) proportionality restriction

$$\lambda(X) = \theta\mu(X),$$

θ fixed, the ideal free property of ESSes appears as consequence of the assumption that there are no genetic constraints, i.e., any allowed phenotype can occur through mutation.

Proof: Whenever, say, $\lambda(X_{aa}) = \theta\mu(X_{aa}) < \lambda(X_{aA}) = \theta\mu(X_{aA})$, a mutant at some other locus that changes $X_{b,aa} = X_{aa}$ into $X_{B,aa} = X_{aA}$ can invade.

Without the proportionality restriction a similar argument applies when the sexes are separate, and male and female traits can vary independently due to sex dependent gene expression:

$$X = (X_{\text{male}}, X_{\text{female}}), \quad \text{and} \quad \lambda(X) = \lambda_{\text{f}}(X_{\text{female}}),\ \mu(X) = \mu_{\text{m}}(X_{\text{male}}).$$

The term "ideal free", originates from behavioural ecology (Fretwell and Lucas 1970; Bulmer 1994).

The etymology comes from the fact that under the commonly made proportionality restriction the ideal free property appears as consequence of the assumption that there are no genetic constraints, i.e., any allowed phenotype can occur through mutation.

Without the proportionality restriction this argument is no longer valid without further assumptions, since if, say, λ_{aa} and μ_{aa} are both lowest, there is in general no need that there exist a mutant that improves both.

The most important special case where a similar argument applies is when (i) the sexes are separate, and male and female traits can vary independently due to sex dependent gene expression and (ii) there are no genetic constraints.

The previous considerations imply that any ideal free genetically dimorphic ESS can be found through the use of the simple averaged Shaw-Mohler formula (42).

A modifier Adaptive Dynamics

Modifiers, i.e., mutants on other loci, generically to be referred to as $\mathcal{B}$, with b as resident and B as mutant, are supposed to effect the following phenotypic changes:

$$X_{aabB} = X_{aa} + \varepsilon Z_{aa}, \quad X_{aAbB} = X_{aA} + \varepsilon Z_{aA}, \quad X_{AAbB} = X_{AA} + \varepsilon Z_{AA},$$

where $X_{aa} = X_{aabb}$ etc..

Then

$$\begin{aligned} \ln(R_{0,B}) \;\; = \;\; \varepsilon \sum_{\mathcal{A}\mathcal{A}=aa,aA,AA} \Bigg[& \frac{\partial R_{0,B}}{\partial \mu_{\mathcal{A}\mathcal{A}}} \;\; \frac{\partial \mu}{\partial X_{\mathcal{A}\mathcal{A}}}(X_{aa}, X_{aA}, X_{AA}) + \\ & \frac{\partial R_{0,B}}{\partial \lambda_{\mathcal{A}\mathcal{A}}} \;\; \frac{\partial \lambda}{\partial X_{\mathcal{A}\mathcal{A}}}(X_{aa}, X_{aA}, X_{AA}) \Bigg] \;\; Z_{\mathcal{A}\mathcal{A}} \;\; + \mathrm{O}(\varepsilon^2). \end{aligned} \tag{43}$$

It is now possible to formulate an adaptive dynamics through modifier effects in (X_{aa}, X_{aA}, X_{AA})-space.

The appropriate selection gradient corresponds to the combination of the three terms, for $\mathcal{AA} = aa, aA, AA$, between the square brackets.

Genetic resident dimorphisms for which the selection gradient is 0 are called evolutionarily singular.

As modifiers are supposed to have only small effect, it may be assumed that $X_{aaBB} \approx X_{aa} + 2Z_{aa}$, etc., and that, away from evolutionarily singular resident combinations and population dynamical bifurcations, invasion implies fixation (Geritz et al. 2002; Dercole 2002).

This means that the direction of evolution is essentially determined by the selection gradient and the distribution of mutational steps in (X_{aa}, X_{aA}, X_{AA})-space.

To see whether evolutionarily singular dimorphisms are impervious to invasion and therefore can be classified as ESSes, additional tools are needed.

For modifiers the genotype to phenotype map for the modifier allelic effects X_b and $X_B = X_b + \varepsilon V$, is made conditional on the $\mathcal{A}$-locus,

$$X_{\mathcal{A}_1\mathcal{A}_2,\mathcal{B}_1\mathcal{B}_2} = \Phi_{\mathcal{A}_1\mathcal{A}_2}(X_{\mathcal{B}_1}, X_{\mathcal{B}_2}),$$

with $\Phi_{\mathcal{A}_1\mathcal{A}_2}(X,Y) = \Phi_{\mathcal{A}_1\mathcal{A}_2}(Y,X)$ and $\Phi_{\mathcal{A}_1\mathcal{A}_2}$ smooth, so that

$$\left.\frac{\partial\Phi_{\mathcal{A}_1\mathcal{A}_2}}{\partial X}(X,Y)\right|_{X=Y} = \left.\frac{\partial\Phi_{\mathcal{A}_1\mathcal{A}_2}}{\partial Y}(X,Y)\right|_{X=Y} =: \Phi'_{\mathcal{A}_1\mathcal{A}_2}(X,X).$$

Therefore

$$X_{\mathcal{A}_1\mathcal{A}_2,bB} = \Phi_{\mathcal{A}_1\mathcal{A}_2}(X_b, X_b+\varepsilon V) = X_{\mathcal{A}_1\mathcal{A}_2,bb} + \varepsilon\Phi'_{\mathcal{A}_1\mathcal{A}_2}(X_b,X_b)V + \mathrm{O}(\varepsilon^2),$$

$$\begin{aligned} X_{\mathcal{A}_1\mathcal{A}_2,BB} &= \Phi_{\mathcal{A}_1\mathcal{A}_2}(X_b+\varepsilon V, X_b+\varepsilon V) \\ &= X_{\mathcal{A}_1\mathcal{A}_2,bb} + 2\varepsilon\Phi'_{\mathcal{A}_1\mathcal{A}_2}(X_b,X_b)V + \mathrm{O}(\varepsilon^2), \end{aligned}$$

or, after renaming $\Phi'_{\mathcal{A}_1\mathcal{A}_2}(X_b,X_b)V + \mathrm{O}(\varepsilon) =: Z$,

$$\text{if} \quad X_{\mathcal{A}_1\mathcal{A}_2,bB} - X_{\mathcal{A}_1\mathcal{A}_2,bb} = \varepsilon Z_{\mathcal{A}_1\mathcal{A}_2}, \quad \text{then} \quad X_{\mathcal{A}_1\mathcal{A}_2,BB} - X_{\mathcal{A}_1\mathcal{A}_2,bb} \approx 2\varepsilon Z_{\mathcal{A}_1\mathcal{A}_2}.$$

If the set of trait values realisable by mutants is connected, a genetic dimorphism (a, A) is impervious to invasion by any modifiers, if

- the dimorphism is uninvadable by pseudo-alleles, consisting of an allele on a different locus, inexorably linked to the $\mathcal{A}$-locus, and
- for all mutants on other loci, generically to be called B, as opposed to a resident allele b,

$$\begin{aligned} 1 \;>\; & \frac{1}{2}\,(q_a\tilde{\mu}_{B,aa} + p_a\tilde{\lambda}_{B,aa} + q_A\tilde{\mu}_{B,AA} + p_A\tilde{\lambda}_{B,AA}) \\ & - \frac{1}{4}\,[(q_a\tilde{\mu}_{B,aa} + p_a\tilde{\lambda}_{B,aa})(q_A\tilde{\mu}_{B,AA} + p_A\tilde{\lambda}_{B,AA}) \\ & \qquad - (q_a\tilde{\mu}_{B,aA} + p_a\tilde{\lambda}_{B,aA})(q_A\tilde{\mu}_{B,aA} + p_A\tilde{\lambda}_{B,aA})] \\ & - \frac{1}{8}\,[(p_aq_A - p_Aq_a)[(q_A\tilde{\mu}_{B,aA} + p_A\tilde{\lambda}_{B,aA})(\tilde{\mu}_{AA}\tilde{\lambda}_{aA} - \tilde{\lambda}_{AA}\tilde{\mu}_{aA}) \\ & \qquad - (q_a\tilde{\mu}_{B,aA} + p_a\tilde{\lambda}_{B,aA})(\tilde{\mu}_{aa}\tilde{\lambda}_{aA} - \tilde{\lambda}_{aa}\tilde{\mu}_{aA})] \\ & - \frac{1}{16}\,(p_aq_A - p_Aq_a)^2(\tilde{\mu}_{aa}\tilde{\lambda}_{aA} - \tilde{\lambda}_{aa}\tilde{\mu}_{aA})(\tilde{\mu}_{AA}\tilde{\lambda}_{aA} - \tilde{\lambda}_{AA}\tilde{\mu}_{aA}). \end{aligned} \tag{44}$$

When invasion by pseudo-alleles is possible, or mutations are possible on some freely recombining $\mathcal{B}$-locus such that inequality (44) holds good in the opposite direction, the evolutionarily singular genetic dimorphism is not an ESS.

The first term at the right hand side of (44) is once again the averaged Shaw-Mohler formula familiar from the previous subsection. Otherwise (44) is substantially different.

In the case of candidates for ideal free ESSes, imperviousness to any invasion by (pseudo-)alleles implies also guarantees imperviousness to invasion by alleles on other loci.

Therefore, ideal free Evolutionarily Stable genetic dimorphisms are characterisedd by the fact that the Shaw-Mohler expression

$$\frac{1}{2}(p_a\tilde{\mu}(X_{\alpha a}, E_{\rm e}) + p_A\tilde{\mu}(X_{\alpha A}, E_{\rm e}) + p_a\tilde{\lambda}(X_{\alpha a}, E_{\rm e}) + p_A\tilde{\lambda}(X_{\alpha A}, E_{\rm e})) \qquad (45)$$

is maximised as a function of $(X_{\alpha a}, X_{\alpha A})$ at (X_{aa}, X_{aA}), and at (X_{aA}, X_{AA}), while in addition the following population dynamical equilibrium conditions are satisfied

$$\lambda(X_{aa}, E_{\rm e}) = \lambda(X_{aA}, E_{\rm e}) = \lambda(X_{AA}, E_{\rm e}) = 1 \qquad (46)$$

$$\mu(X_{aa}, E_{\rm e}) = \mu(X_{aA}, E_{\rm e}) = \mu(X_{AA}, E_{\rm e}) \qquad (47)$$

together with, say,

$$E_{\rm e} = F\left(\sum_{\mathcal{A}_1,\mathcal{A}_2=a,A} g_1(X_{\mathcal{A}_1\mathcal{A}_2})p_{\mathcal{A}_1}p_{\mathcal{A}_2}N, \sum_{\mathcal{A}_1,\mathcal{A}_2=a,A} g_2(X_{\mathcal{A}_1\mathcal{A}_2})p_{\mathcal{A}_1}p_{\mathcal{A}_2}N\right). \qquad (48)$$

Notice that

$$\frac{1}{2}(p_a\tilde{\mu}(X_{\alpha a}) + p_A\tilde{\mu}(X_{\alpha A}) + p_a\tilde{\lambda}(X_{\alpha a}) + p_A\tilde{\lambda}(X_{\alpha A})) \tag{49}$$

is maximised as a function of $(X_{\alpha a}, X_{\alpha A})$ at (X_{aa}, X_{aA}), and at (X_{aA}, X_{AA}), if and only if

$$\frac{1}{2}(p_a^2\tilde{\mu}(X) + 2p_ap_A\tilde{\mu}(Y) + p_A^2\tilde{\mu}(Z) + p_a^2\tilde{\lambda}(X) + 2p_ap_A\tilde{\lambda}(Y) + p_A^2\tilde{\lambda}(Z)) \tag{50}$$

is maximised as a function of (X, Y, Z) at (X_{aa}, X_{aA}, X_{AA}).

$$A_B = A_{B,\mathrm{sel}} + A_{B,\mathrm{rec}}, \qquad A_{B,\mathrm{sel}} = \begin{bmatrix} A_{B,\mathrm{sel},a} & 0 \\ 0 & A_{B,\mathrm{sel},A} \end{bmatrix},$$

$$A_{B,\mathrm{rec}} = \frac{r}{2} \begin{bmatrix} -\tilde{\mu}_{B,aA} \\ -\tilde{\lambda}_{B,aA} \\ \tilde{\mu}_{B,aA} \\ \tilde{\lambda}_{B,aA} \end{bmatrix} [q_A \quad p_A \quad -q_a \quad -p_a].$$

The characteristic equation of A_B can be relatively easily obtained by making use of the decomposition (34):

If a column vector is added to one of the columns of a matrix, the determinant of the resulting matrix equals the sum of the original determinant plus the determinant of a matrix constructed from the original matrix by replacing the changed column with the column vector that was added.

The determinant of a matrix of which one of the columns can be expressed as a linear combunation of the remaining columns, equals zero.

These two facts combine into the result that the determinant of a matrix $F = G + H$ with $\mathrm{rank}(H) = 1$ equals the determinant of G plus a sum over the determinants of all matrices constructed from G by replacing g_{ij} with h_{ij}, and replacing the other components on i-th row and j-th column of G with zeros. In the case of $A_B - RI = (A_{B,\mathrm{sel}} - RI) + A_{B,\mathrm{rec}}$ choosing i and j in the lower left and upper right blocks of $A_{B,\mathrm{sel}} - RI$ produces a matrix with determinant 0. Making use of these facts gives

$$P_B(R) = \det(A_B - RI) = D_a D_A + \frac{r}{2}(C_A D_a + C_a D_A), \tag{51}$$

with

$$D_a(R) = \det(A_{B,\mathrm{sel},a} - RI), \quad D_A(R) = \det(A_{B,\mathrm{sel},A} - RI),$$

and

$$C_a(R) = (q_A \tilde{\mu}_{B,aA} + p_A \tilde{\lambda}_{B,aA})R + \frac{1}{2}(p_a q_A - p_A q_a)(\tilde{\lambda}_{B,aA}\tilde{\mu}_{B,aa} - \tilde{\mu}_{B,aA}\tilde{\lambda}_{B,aa}),$$

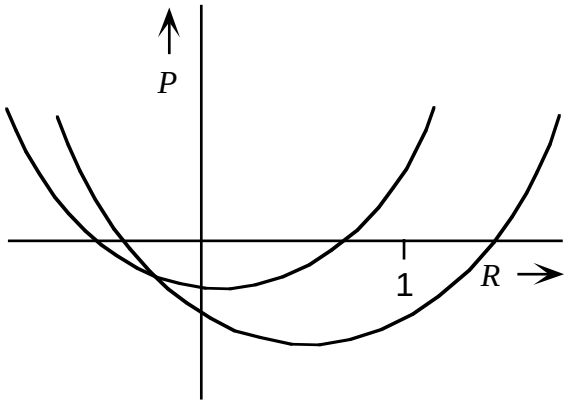
$$C_A(R) = (q_a \tilde{\mu}_{B,aA} + p_a \tilde{\lambda}_{B,aA})R + \frac{1}{2}(p_A q_a - p_a q_A)(\tilde{\lambda}_{B,aA}\tilde{\mu}_{B,AA} - \tilde{\mu}_{B,aA}\tilde{\lambda}_{B,AA}).$$

P_B, and hence $R_{0,B}$ depends on the recombination fraction r.

For modifiers with small effect, which generally are the ones of most interest, (38) to (40) already show that this dependence becomes negligible, at least up to first order in the mutational change.

However, from a general evolutionary perspective it is also of interest whether a given genetically realised phenotypic polymorphism is impervious to mutations of any type.

Therefore it pays to study the characteristic equation $P_B = 0$ in a little more depth.


P
1
R

As the interest is in imperviousness to any mutation, it is only necessary to look at those values of r that engender the highest $R_{0,B}$.

$R_{0,B}$ equals the rightmost intersection of the graph of P_B with the R-axis. (4) shows that the leading coefficient in P_B is positive.
Therefore $P'_B(R_{0,B})$ is positive, which in turn tells that decreasing P_B as far as possible by changing r leads to the largest possible value of $R_{0,B}$.

From (4) it can also be seen that P_B is linear in r. This implies that $P_B(R)$ considered as a function of r takes its extreme values at the extremes of its domain, i.e., at $r = 0$ and $r = \frac{1}{2}$. Therefore it is only necessary to study $P_B = 0$ for these two values of r.

The invasion of modifiers for which $r = 0$ is comparable to the invasion of a new allele on the $\mathcal{A}$-locus. B can either be linked to a or to A.

So there are two new pseudo-alleles that have to be considered, one with $X_{\alpha a} = X_{B,aa}$ and $X_{\alpha A} = X_{B,aA}$ and one with $X_{\alpha a} = X_{B,aA}$ and $X_{\alpha A} = X_{B,AA}$. This is reflected in the decomposition of $P_B(R) = D_a(R)D_A(R)$.

The dimorphism a with A is impervious to invasion by fully linked modifiers if any such modifier cannot invade according to (22).

Remains the study of P_B for $r = \frac{1}{2}$. Working out (4) gives

$$
\begin{aligned}
P_b(R) = R^4 \;&-\; \frac{1}{2}\left(q_a\tilde{\mu}_{B,aa} + p_a\tilde{\lambda}_{B,aa} + q_A\tilde{\mu}_{B,AA} + p_A\tilde{\lambda}_{B,AA}\right) R^3 \\
&+\; \frac{1}{4}\left[(q_a\tilde{\mu}_{B,aa} + p_a\tilde{\lambda}_{B,aa})(q_A\tilde{\mu}_{B,AA} + p_A\tilde{\lambda}_{B,AA})\right. \\
&\qquad\left. - (q_a\tilde{\mu}_{B,aA} + p_a\tilde{\lambda}_{B,aA})(q_A\tilde{\mu}_{B,aA} + p_A\tilde{\lambda}_{B,aA})\right] R^2 \\
&+\; \frac{1}{8}\left[(p_aq_A - p_Aq_a)\left[(q_A\tilde{\mu}_{B,aA} + p_A\tilde{\lambda}_{B,aA})(\tilde{\mu}_{AA}\tilde{\lambda}_{aA} - \tilde{\lambda}_{AA}\tilde{\mu}_{aA})\right.\right. \\
&\qquad\left.\left. - (q_a\tilde{\mu}_{B,aA} + p_a\tilde{\lambda}_{B,aA})(\tilde{\mu}_{aa}\tilde{\lambda}_{aA} - \tilde{\lambda}_{aa}\tilde{\mu}_{aA})\right] R \right. \\
&+\; \frac{1}{16}\left.(p_aq_A - p_Aq_a)^2(\tilde{\mu}_{aa}\tilde{\lambda}_{aA} - \tilde{\lambda}_{aa}\tilde{\mu}_{aA})(\tilde{\mu}_{AA}\tilde{\lambda}_{aA} - \tilde{\lambda}_{AA}\tilde{\mu}_{aA}).\right.
\end{aligned}
\tag{52}
$$

At first sight (52) only intimidates. However, the earlier argument makes clear that for ascertaining whether a particular genetic dimorphism produces an environment that shields it from invasion, one only has to study the sign of $P_B(1)$.

$$P_B(R) = \det(A_B - RI) = D_a D_A + \frac{r}{2}(C_A D_a + C_a D_A), \tag{51}$$

with

$$D_a(R) = \det(A_{B,\mathrm{sel},a} - RI), \quad D_A(R) = \det(A_{B,\mathrm{sel},A} - RI),$$

and

$$C_a(R) = (q_A \tilde{\mu}_{B,aA} + p_A \tilde{\lambda}_{B,aA})R + \frac{1}{2}(p_a q_A - p_A q_a)(\tilde{\lambda}_{B,aA}\tilde{\mu}_{B,aa} - \tilde{\mu}_{B,aA}\tilde{\lambda}_{B,aa}),$$

$$C_A(R) = (q_a \tilde{\mu}_{B,aA} + p_a \tilde{\lambda}_{B,aA})R + \frac{1}{2}(p_A q_a - p_a q_A)(\tilde{\lambda}_{B,aA}\tilde{\mu}_{B,AA} - \tilde{\mu}_{B,aA}\tilde{\lambda}_{B,AA}).$$

In the case of an ideal free candidate ESS, the condition that this candidate is impervious to invasion by pseudo-alleles imparting certain phenotypes implies that for any modifier imparting the same phenotypes, both $D_a(1) > 0$ and $D_A(1) > 0$. Moreover, $p_a q_A - p_A q_a = 0$, so $C_a(1) > 0$ and $C_A(1) > 0$. Therefore, $P_B(1)$ increases in r, and thus, if $P_B(1) > 0$ for $r = 0$, then $P_B(1) > 0$ for all $r > 0$. In other words, if the invasion of pseudo-alles with different phenotypes is ruled out, then invasion by any other modifiers is ruled out as well.

On the other hand:

In the case of candidates for ideal free ESSes the last two terms of (44) become zero; moreover, (44) can be simplified by writing

$$\tilde{\mu}_{B,\mathcal{A}_1\mathcal{A}_1} - \tilde{\mu}_{b,\mathcal{A}_1\mathcal{A}_1} =: \Delta\tilde{\mu}_{\mathcal{A}_1\mathcal{A}_1}, \quad \tilde{\lambda}_{B,\mathcal{A}_1\mathcal{A}_1} - \tilde{\lambda}_{b,\mathcal{A}_1\mathcal{A}_1} =: \Delta\tilde{\lambda}_{\mathcal{A}_1\mathcal{A}_1}. \tag{53}$$

After some rearangements this leads to

$$\begin{aligned} 0 \;>\; & [p_a^2(\Delta\tilde{\mu}_{aa} + \Delta\tilde{\lambda}_{aa}) + 2p_a p_A(\Delta\tilde{\mu}_{aA} + \Delta\tilde{\lambda}_{aA}) + p_A^2(\Delta\tilde{\mu}_{AA} + \Delta\tilde{\lambda}_{AA})] \\ & + \frac{1}{2}\, p_a p_A\, [(\Delta\tilde{\mu}_{aA} + \Delta\tilde{\lambda}_{aA})^2 - (\Delta\tilde{\mu}_{aa} + \Delta\tilde{\lambda}_{aa})(\Delta\tilde{\mu}_{AA} + \Delta\tilde{\lambda}_{AA})]. \end{aligned} \tag{54}$$

How does this square with the previous argument???