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Additive Genetic Variation under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study

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Contents

Abstract

A diallelic two-locus model is investigated in which the loci determine the genotypic value of a quantitative trait additively. Fitness has two components: stabilizing selection on the trait and a frequency-dependent component, as induced for instance if the ability to utilize different food resources depends on this trait. Since intraspecific competition induces disruptive selection, this model leads to a conflict of selective forces. We study how the underlying genetics (recombination rate and allelic effects) interacts with the selective forces, and explore the resulting equilibrium structure. For the special case of equal effects, global stability results are proved. Unless the locus effects are sufficiently different, the genetic variance maintained at equilibrium displays a threshold-like dependence on the strength of competition. For loci with equal effects, the equilibrium fitnesses of genotypic values exhibit disruptive selection if and only if competition is strong enough to maintain a stable two-locus polymorphism. For unequal effects, disruptive selection can be observed for weaker competition and in the absence of a stable polymorphism.

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Additive Genetic Variation under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study

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1 Introduction

Both stabilizing selection on quantitative traits and intraspecific competition are frequently observed phenomena. Yet, surprisingly few studies have been performed to elucidate their interaction and the consequences for the maintenance of genetic variation. Moreover, competition leads to disruptive selection by favoring genotypes that deviate from the most frequent ones, but disruptive selection on quantitative traits appears to be rare compared with stabilizing or directional selection (Endler 1986). This seems to contradict the wide-spread belief among ecologists that frequency-dependent selection is ubiquitous. Therefore, it may be worthwhile to investigate how strong competition must be in order that it leads to detectable disruptive selection on a trait.

A Gaussian phenotypic model with competition and density-dependent selection was investigated by Slatkin (1979). He considered a phenotypic character in a population of size $N(t)$, and assumed that the fitness of an individual with phenotype z is given by

$$W(z,t) = 1 + R - \frac{RN(t)}{k(z)} \int \alpha(z-y)P(y,t)d\nu(y) , \qquad (1.1)$$

where $1+R$ is the maximum fitness in the absence of competition, $k(z)$ represents resources that can be utilized by an individual of type z, $\alpha(z-y)$ represents the competition between individuals of type z and y for the limiting resource, and P denotes the Gaussian density of the trait which has variance σ_z^2. This functional form of W is related to the Lotka–Volterra competition equations (cf. Roughgarden 1979). As a model for $k(z)$, Slatkin used a function proportional to a Gaussian density with mean z_0, which is the value of the character for which the maximum resources are available, and variance σ_k^2, which measures the range of available resources. Thus, small σ_k^2 means strong stabilizing selection. Similarly, as an example of α he uses

$$\alpha(z-y) = \exp\left[-\tfrac{1}{2}(z-y)^2/\sigma_\alpha^2\right], \qquad (1.2)$$

where σ_α^2 measures the extent of competition between individuals. With these choices, the fitness function (1.1) leads to disruptive selection on the character if $\sigma_z^2 < \sigma_k^2 - \sigma_\alpha^2$, and to stabilizing selection otherwise (including the case $\sigma_k^2 < \sigma_\alpha^2$).

Slatkin (1979) showed that for these specific functions a stable equilibrium with positive variance exists if $\sigma_k^2 - \sigma_\alpha^2 > \sigma_e^2$, where σ_e^2 is the environmental variance of the trait, and $R < 2$. The latter condition is necessary for demographic stability of the difference

equation describing population growth. At this equilibrium, the population mean satisfies $\bar{z} = z_0$ and the variance is $\sigma_z^2 = \sigma_k^2 - \sigma_\alpha^2$. Hence, competition can maintain genetic variation if it is strong enough relative to the stabilizing selection induced by the resources that can be utilized. However, he also proved that for less flexible genetic models (e.g., two alleles at a single locus), often no polymorphism is maintained.

Bulmer (1980, pp. 171–172) studied a related model, in which he assumed that

$$W(z) = \left(\rho - \frac{1}{\kappa} \int \alpha(z - y) P(y) d\nu(y) \right) \exp\left[-\frac{(z - z_O)^2}{2V_{\mathrm{s}}} \right] . \tag{1.3}$$

Furthermore, the population size was assumed to be constant and at its equilibrium value determined by the condition that mean fitness satisfies $\bar{W} = 1$ (from this condition it is straightforward to derive the corresponding value of κ). Bulmer proved that a diallelic locus that contributes an infinitesimally small amount to the trait is maintained polymorphic if and only if

$$(\sigma_z^2 + V_{\mathrm{s}} + \sigma_\alpha^2)(\sigma_z^2 + V_{\mathrm{s}})^{3/2} < \rho V_{\mathrm{s}}^{5/2} . \tag{1.4}$$

This implies that no polymorphism can be maintained, whatever the phenotypic variance σ_z^2 of the trait, if

$$\frac{\sigma_\alpha^2}{V_{\mathrm{s}}} \geq \rho - 1 , \tag{1.5}$$

i.e., if stabilizing selection is strong (V_{s} small) relative to competition. Otherwise, the locus is maintained polymorphic if the variance σ_z^2 of the trait is below the critical value defined by (1.4).

Christiansen and Loeschke (1980) investigated a multiallelic one-locus model based on the Lotka-Volterra-like functional form (1.1) for the fitnesses. They found that if $\sigma_k^2 > \sigma_\alpha^2$, i.e., if competition is sufficiently strong, and if the resource optimum is within the range of genotypic values, then the two alleles with the most extreme effects will persist in the population, whereas if the resource optimum is outside this range, so that there is directional selection, a polymorphism is maintained only if the effect of the allele that deviates most from the optimum is sufficiently large. In this case, this extreme allele will be maintained in the population together with the allele that is closest to the optimum. Conversely, if $\sigma_\alpha^2 > \sigma_k^2$, then a polymorphism will be maintained only if the resource optimum is within the range of allelic effects, and the two alleles closest two the optimum, but on opposite sides, will be persist. Dominance does not fundamentally alter these conclusions (Christiansen 1988).

In 1984, Loeschke and Christiansen extended their previous model to two linked loci. Their study concentrates on the case of tight linkage and strong competition relative to stabilizing selection. They investigated the equilibrium structure for a number of scenarios, mainly by numerical computation. We shall discuss the relation between the present work and their work in the final section.

The present article focuses on the population-genetic consequences of the interaction of competition and stabilizing selection. Therefore, we shall ignore density dependence and adopt the fitness function of Bulmer, but approximate the Gaussian functions by quadratic functions to make the model analytically tractable. We shall study how genetic assumptions about recombination rate and allelic effects influence the equilibrium structure obtained from a balance between the selective forces. For the special case of equal effects, global stability results are derived for arbitrary recombination rates. We shall further explore how the genetic variance depends on the parameters of the model, and

when the equilibrium fitness of genotypic values exhibits disruptive selection. The results are derived under the assumption that selection acts on diploids, but we shall also outline the case of selection on haploids.

2 The Model

We consider a randomly mating population with discrete generations and equivalent sexes that is sufficiently large so that random genetic drift can be ignored. Here we assume that selection acts on diploids, and in Section 5 we shall briefly deal with selection on haploids. Fitness is determined by two components: (i) by a quantitative character that is under stabilizing selection, and (ii) by competition between individuals, as may result, for instance, if different phenotypes utilize different food resources. Selection acts only through differential viabilities. We ignore environmental variation and deal directly with the fitnesses of genotypic values.

We adopt the functional form (1.3) and posit that the fitness of an individual with genotypic value g is given by

$$W(g) = \left(\rho - \frac{1}{\kappa} C(g) \right) S(g) , \tag{2.1}$$

where $C(g)$ represents the strength of intraspecific competition experienced by individuals of genotypic value g, ρ and κ are positive parameters, and $S(g)$ represents stabilizing selection on g. In the context of density-dependent growth models, the parameter ρ in (2.1) is related to the growth rate of the population and κ to the carrying capacity. Since we are mainly interested in the population-genetic consequences of the interaction of competition and stabilizing selection, we assume throughout that the population size is constant and at the equilibrium value resulting from the condition that mean fitness, $\bar{W}$, is unity. We assume that competition between genotypes g and h can be described by the function

$$\alpha(g, h) = 1 - \frac{1}{2\sigma_\alpha^2}(g - h)^2 , \tag{2.2}$$

with the obvious constraint that the maximum difference between genotypic values must be less than $\sqrt{2\sigma_\alpha^2}$. Then the competition function $C(g)$ is defined as

$$C(g) = \sum_h \alpha(g, h)P(h) , \tag{2.3}$$

where $P(h)$ is the relative frequency of individuals with genotypic value h.

Stabilizing selection is modeled by the quadratic function

$$S(g) = 1 - g^2/(2V_s) , \tag{2.4}$$

where V_s is an inverse measure for the strength of stabilizing selection. Of course, $S(g)$ is assumed to be positive on the range of possible genotypic values, thus restricting the admissible values of V_s. In the articles cited in the introduction, the functions α and S specified in (2.2) and (2.4) are Gaussian, but the quadratic functions used here will be adequate approximations, unless selection or competition are very strong. In particular, the present choice enables us to analyze the model analytically.

The genetic assumptions are as follows: the trait values g are determined additively by two loci (no dominance or epistasis), each with two alleles, A_1 and A_2, B_1 and B_2. The

four gametes A_1B_1, A_1B_2, A_2B_1, A_2B_2 have relative frequencies p_1, p_2, p_3, p_4, respectively. Let the contributions of the alleles A_1, A_2, B_1, and B_2 to the genotypic value g of the trait be $\beta - \frac{1}{2}\gamma_1$, $\beta + \frac{1}{2}\gamma_1$, $-\beta - \frac{1}{2}\gamma_2$, and $-\beta + \frac{1}{2}\gamma_2$, respectively, where β is an arbitrary constant. We assume that the alleles determine the genotypic value g purely additively. Then the effects of the gametes A_1B_1, A_1B_2, A_2B_1, and A_2B_2 are $-\frac{1}{2}(\gamma_1+\gamma_2)$, $-\frac{1}{2}(\gamma_1-\gamma_2)$, $\frac{1}{2}(\gamma_1 - \gamma_2)$, and $\frac{1}{2}(\gamma_1 + \gamma_2)$. The resulting genotypic values are shown in Table 2.1. For notational simplicity, we will use the same symbol g for a genotype and its genotypic value, and we shall write g_{ij} for the genotype composed of the gametes i and j.

Table 2.1. The genotypic values in the additive model.

	B_1B_1	B_1B_2	B_2B_2
A_1A_1	$-\gamma_1 - \gamma_2$	$-\gamma_1$	$-\gamma_1 + \gamma_2$
A_1A_2	$-\gamma_2$	0	γ_2
A_2A_2	$\gamma_1 - \gamma_2$	γ_1	$\gamma_1 + \gamma_2$

For definiteness, we assume $\gamma_1 \geq \gamma_2$ and refer to these loci as major and minor, respectively. The parameters γ_1 and γ_2 are the effects of allelic substitution at locus one and two, respectively. For brevity, we call them the effects of the loci. Let us introduce the following quantities:

$$\gamma = \tfrac{1}{2}(\gamma_1 + \gamma_2), \quad e = \frac{\gamma_1 - \gamma_2}{2\gamma}, \quad s = \frac{\gamma^2}{2V_s}, \tag{2.5}$$

where γ^2 may be called the average (substitutional) effect on the trait, e measures the disparity of effects, and s ($0 < s < \frac{1}{4}$ because $S(g)$ must be positive) is a measure for the strength of stabilizing selection on genotypes. This yields a special case of the so-called symmetric viability model (Karlin and Feldman 1970) with the genotypic fitness values given in Table 2.2.

Table 2.2. The fitnesses of genotypes, $S(g)$, caused by stabilizing selection.

	B_1B_1	B_1B_2	B_2B_2
A_1A_1	$1 - 4s$	$1 - (1+e)^2 s$	$1 - 4e^2 s$
A_1A_2	$1 - (1-e)^2 s$	1	$1 - (1-e)^2 s$
A_2A_2	$1 - 4e^2 s$	$1 - (1+e)^2 s$	$1 - 4s$

Moreover, it will be convenient to introduce the following new variables:

$$x = p_1 + p_4, \quad y = p_1 - p_4, \quad z = p_2 - p_3. \tag{2.6}$$

Because $p_1 + p_2 + p_3 + p_4 = 1$, these are sufficient to describe the genetic composition of the population.

Next, a straightforward calculation shows that

$$C(g) = 1 - \frac{1}{2\sigma_\alpha^2}[(g - \bar{g})^2 + \sigma_g^2], \tag{2.7}$$

where

$$\bar{g} = 2\gamma(y + ez) \tag{2.8}$$

denotes the mean genotypic value, and

$$\sigma_g^2 = 2\gamma^2[x - y^2 - 2eyz + e^2(1 - x - z^2)] \tag{2.9}$$

is the (additive) genetic variance. It will be convenient to write $C(g)$ as

$$C(g) = 1 - \frac{\gamma^2}{2\sigma_\alpha^2}\,\varphi(g)\,, \tag{2.10}$$

where explicit formulas for $\varphi(g)$ are given in Table 2.3.

Table 2.3. The values of $\varphi(g)$.

$$
\begin{aligned}
\varphi(-\gamma_1 - \gamma_2) &= 2[2 + x - 4y + y^2 - 2ez(2 - y) + e^2(1 - x + z^2)] \\
\varphi(\gamma_1 + \gamma_2) &= 2[2 + x + 4y + y^2 + 2ez(2 + y) + e^2(1 - x + z^2)] \\
\varphi(-\gamma_1) &= 1 + 2x - 4y + 2y^2 + 2e(1 - 2y - 2z + 2yz) + e^2(3 - 2x - 4z + 2z^2) \\
\varphi(\gamma_1) &= 1 + 2x + 4y + 2y^2 + 2e(1 + 2y + 2z + 2yz) + e^2(3 - 2x + 4z + 2z^2) \\
\varphi(-\gamma_1 + \gamma_2) &= 2[x + y^2 - 2ey(2 - z) + e^2(3 - x - 4z + z^2)] \\
\varphi(\gamma_1 - \gamma_2) &= 2[x + y^2 + 2ey(2 + z) + e^2(3 - x + 4z + z^2)] \\
\varphi(-\gamma_2) &= 1 + 2x - 4y + 2y^2 - 2e(1 - 2y + 2z - 2yz) + e^2(3 - 2x + 4z + 2z^2) \\
\varphi(\gamma_2) &= 1 + 2x + 4y + 2y^2 - 2e(1 + 2y - 2z - 2yz) + e^2(3 - 2x - 4z + 2z^2) \\
\varphi(0) &= 2[x + y^2 + 2eyz + e^2(1 - x + z^2)]
\end{aligned}
$$

Let

$$c = \frac{\gamma^2/(2\sigma_\alpha^2)}{\rho\kappa - 1}\,, \tag{2.11}$$

which we call the coefficient of competition ($c > 0$), and let

$$w(g) = [1 + c\varphi(g)]S(g)\,; \tag{2.12}$$

then $W(g) = (\rho - 1/\kappa)w(g)$. Since in the recurrence relations for the gamete frequencies multiplicative constants cancel, we shall denote the (scaled) fitness $w(g_{ij})$ of genotype g_{ij} by w_{ij}. The w_{ij} are calculated from (2.12) by resorting to Tables 2.2 and 2.3. Denoting the marginal fitness of gamete i by $w_i = \sum_{j=1}^{4} w_{ij}p_j$, and the resulting mean fitness by $\bar{w} = \sum_{i,j=1}^{4} w_{ij}p_ip_j = \sum_{i=1}^{4} w_ip_i$, the dynamics of gamete frequencies is given by the four recurrence relations

$$\bar{w}p_i' = p_iw_i - \eta_i r w_{14} D \tag{2.13}$$

(e.g. Bürger 2000, Chap. II.1), where $\eta_1 = \eta_4 = 1$, $\eta_2 = \eta_3 = -1$, r is the recombination fraction, and $D = p_1p_4 - p_2p_3$ measures linkage disequilibrium. The expressions for the w_i and $\bar{w}$ are formidable in general, and given in Appendix 1 for the case $e = 0$.

3 Equal Effects and Arbitrary Recombination

If both loci have equal effects, $\gamma_1 = \gamma_2$, then fairly complete analytic results can be derived. For unequal effects, even in the absence of competition, global convergence results have not yet been proved. Nevertheless, in this case ($c = 0$) the model is fairly well understood and the possible equilibria and their local stability properties have been derived (see Gavrilets and Hastings 1993, and Bürger 2000, Chap. VI.2). It should also be noted that

in the absence of competition, but for Gaussian instead of quadratic stabilizing selection, the possible equilibrium structure has not yet been fully explored. Nagylaki's (1989) analysis, which is based on the assumption of linkage equilibrium, suggests that for strong selection, the equilibrium structure may be more complex than for quadratic selection (see the Discussion). This is one of the reasons why we chose a quadratic fitness function.

In this section, we assume $\gamma = \gamma_1 = \gamma_2$, i.e., $e = 0$. This simplifies the expressions for the fitnesses and the recursion relations substantially. In particular, the marginal fitnesses of the gametes A_1B_2 and A_2B_1 are equal, i.e., $w_2 = w_3$. We also assume $r > 0$ and relegate the degenerate case $r = 0$ to the end of this section.

We begin by demonstrating how the equilibria can be found. Because $r > 0$, no equilibrium can exist in the interior of the boundary planes, i.e., equilibria involving three gametes are impossible. Therefore, at every boundary equilibrium at least one locus is monomorphic, and we leave the calculation of the possible boundary equilibria to the interested reader.

Determination of the interior equilibria is more cumbersome. From the recurrence relations we obtain immediately

$$\frac{p_2'}{p_3'} = \frac{p_2 w_2 + r w_{14} D}{p_3 w_2 + r w_{14} D} \ . \tag{3.1}$$

Since for an equilibrium with $p_3 > 0$, $p_2'/p_3' = p_2/p_3$ must hold, any equilibrium lies either at one of the boundary planes $p_2 = 0$ or $p_3 = 0$, in the plane $p_2 = p_3$, or at the Wright manifold $D = 0$. In addition, it follows that each of the regions $p_2 > p_3$, $p_2 = p_3$, and $p_2 < p_3$ is invariant.

Next, Lemma A.5 in the Appendix implies that

$$\frac{p_1'}{p_4'} = \frac{p_1}{p_4} \tag{3.2}$$

can hold only if $D > 0$ or $p_1 = p_4$ (or $p_4 = 1$). Therefore, any interior equilibrium with $D \le 0$ is located in the plane $p_1 = p_4$ and those with $D < 0$ must even be symmetric, i.e., satisfy $p_1 = p_4$ and $p_2 = p_3$. Finally, Lemma A.7 informs us that equilibria with $D > 0$ (hence $p_2 = p_3$) must also be symmetric.

It is now straightforward to calculate the coordinates of all possible equilibria. Their stability properties are derived in Appendix A. In the following we summarize these results. Figure 1 gives a graphical representation. For simplicity (and with little loss of generality and relevance), we shall posit $s < \frac{1}{5}$, although this is necessary only if $c \ge s/(1 - 5s)$ is assumed.

The main result: equilibria and their stability properties

1. There always exist the four corner equilibria. Of these, the equilibria $\hat{p}_1 = 1$ (fixation of A_1B_1) and $\hat{p}_4 = 1$ (fixation of A_2B_2) are always unstable. Both of the equilibria $\hat{p}_2 = 1$ (fixation of A_1B_2) and $\hat{p}_3 = 1$ (fixation of A_2B_1) are (locally) asymptotically stable if and only if

$$c \le \frac{s}{1 - s} \ . \tag{3.3}$$

In this case, $\hat{p}_2 = 1$ is globally attractive for the half space $p_2 > p_3$, and $\hat{p}_3 = 1$ for $p_3 > p_2$.
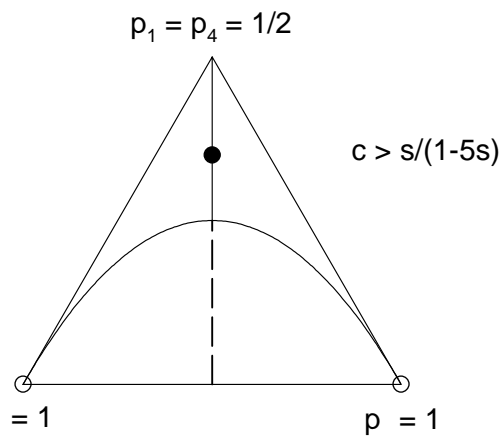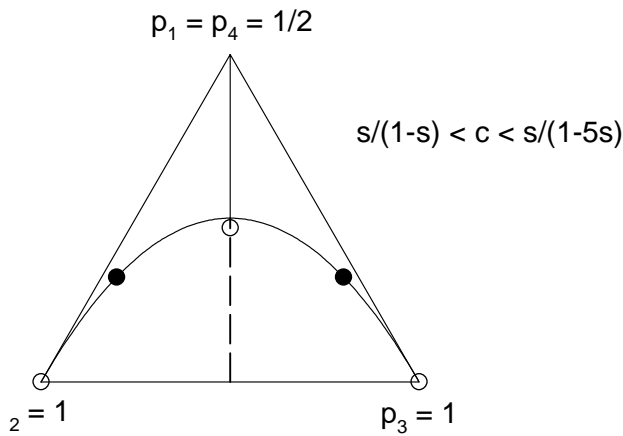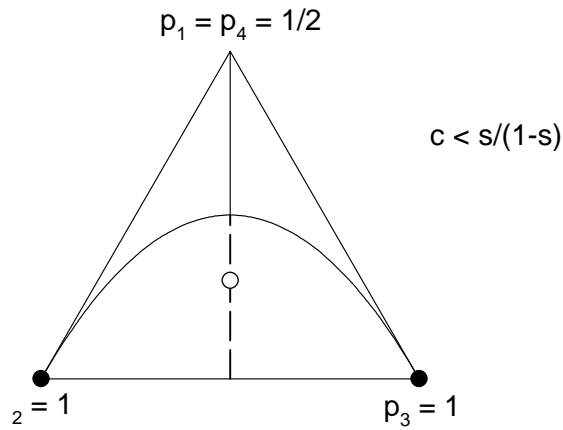
Figure 1: The three possible equilibrium structures for equal effects, corresponding to the cases (3.3), (3.4), and (3.8). Displayed is the plane $y = 0$ with the curve $D = 0$, the symmetric line $\{p_1 = p_4, p_2 = p_3\}$ (dashed, where the symmetric equilibrium is always unstable), the stable equilibria (filled circles), and the unstable equilibria (open circles). Other stable equilibria do not exist, but unstable single-locus polymorphisms may exist.

2. If
$$\frac{s}{1-s} < c < \frac{s}{1-5s} , \qquad (3.4)$$

then the following pair of equilibria exists and is asymptotically stable:

$$\hat{p}_1 = \hat{p}_4 = \frac{c(1-s)-s}{16cs} , \qquad (3.5a)$$

$$\hat{p}_2(\pm) = \frac{s - c(1-9s)}{16cs} \pm \frac{1}{4}\sqrt{\frac{s - c(1-5s)}{cs}} , \quad \hat{p}_3(\pm) = \hat{p}_2(\mp). \qquad (3.5b)$$

Both equilibria satisfy $D = 0$ and, therefore, do not depend on r. Numerical iterations of the recurrence relations suggest that the first is globally attractive for the half space $p_2 > p_3$, and the second for $p_3 > p_2$. If c is taken as bifurcation parameter, then they emerge from the corner equilibria $\hat{p}_2 = 1$ or $\hat{p}_3 = 1$ by an exchange-of-stability bifurcation at $c = s/(1-s)$. As c increases, they converge to the center of the simplex $(p_1 = p_2 = p_3 = p_4 = \frac{1}{4})$, where, for $c = s/(1-5s)$, they merge with the unstable symmetric equilibrium and cease to exist. For large c, the symmetric equilibrium described below becomes stable; thus, a pitchfork bifurcation occurs at $c = s/(1-5s)$.

3. If $c > s/(1-s)$, then there exist four equilibria with one locus monomorphic and one locus polymorphic. For instance, if the B-locus is fixed at B_1, i.e., $p_1 + p_2 = 0$, then $\hat{p}_1$ is the unique solution of the equation

$$4csp_1^3 - 18csp_1^2 + 2p_1(c + s + 6cs) - c(1+s) + s = 0 . \qquad (3.6)$$

This equilibrium always satisfies $\hat{p}_1 < \frac{1}{2}$, and $\hat{p}_1$ increases as c/s increases. The positions of the three other equilibria of this type are given by analogous conditions (with p_1 replaced by p_4 if A_1 is absent. These equilibria are always unstable with respect to the whole simplex, but they are globally attractive for the corresponding single-locus systems.

4. There always exists one symmetric equilibrium, $\hat{p}_1 = \hat{p}_4$ and $\hat{p}_2 = \hat{p}_3$. It is the uniquely determined solution of the equation

$$32csp_1^3 + 2[s - c(1 + 2r + 7s)]p_1^2 - [r + s - c(1 + r - s)]p_1 + \frac{r}{4} = 0 \qquad (3.7)$$

such that $0 \le \hat{p}_1 \le \frac{1}{2}$. If $c < s/(1-5s)$, then $0 < \hat{p}_1 < \frac{1}{4}$, hence $D < 0$, and the equilibrium is unstable. If $c = s/(1-5s)$, then $\hat{p}_1 = \frac{1}{4}$. If $c > s/(1-5s)$, then $\frac{1}{4} < \hat{p}_1 < \frac{1}{2}$ and $D > 0$. If

$$c \ge s/(1-5s) , \qquad (3.8)$$

then this equilibrium is asymptotically stable, and numerical iterations suggest that it is globally stable. Global stability (with respect to the interior of the simplex) can be proved if $s < \frac{1}{6}$ and $c \ge s/(1-6s)$.

For the symmetric equilibrium it is easy to show that its position $\hat{p}_1$, and therefore the amount of linkage disequilibrium D, is an increasing function of c, but a decreasing function of s and r. For every $s \ge 0$, $\hat{p}_1$ approaches an upper limit $< \frac{1}{2}$ as $c \to \infty$. For $s = 0$, this limit is $\lim_{c\to\infty} \hat{p}_1(c) = \frac{1}{2}\frac{1+r}{1+2r}$; for larger s, it is smaller (cf. Figure 3). Positive linkage disequilibrium is maintained only at the symmetric equilibrium if (3.8) holds. Because, in this case $\hat{D} = \hat{p}_1 - \frac{1}{4}$, strong (positive) linkage disequilibrium is maintained only if the loci are tightly linked (cf. Figure 3).

The genotypic fitnesses at equilibrium

Next, we investigate the fitnesses of the genotypes at equilibrium, in particular, when they experience stabilizing or disruptive selection. In the present symmetric case with equal effects there are only five different genotypic values: $\pm 2\gamma$, $\pm\gamma$, and 0. We refrain from giving the formulas for the fitnesses, which are complicated, but summarize the results verbally and graphically (Figure 2). If (3.3) holds, i.e., competition is weak relativ to stabilizing selection, then the net selection on genotypic values is stabilizing, i.e.,

$$w(0) > w(\gamma) = w(-\gamma) > w(2\gamma) = w(-2\gamma) \,. \tag{3.9a}$$

If $c = s/(1-s)$, then

$$w(0) = w(\gamma) = w(-\gamma) > w(2\gamma) = w(-2\gamma) \,. \tag{3.9b}$$

(But note that in these two cases, at equilibrium only genotypes with value 0 are maintained in the population.) If (3.4) holds, i.e., the pair of interior equilibria with $D = 0$ is stable, then there is disruptive selection and the genotypes with one homozygous locus and one heterozygous locus have highest fitness, and the 'extreme' genotypes have the lowest fitness.

$$w(\gamma) = w(-\gamma) > w(0) > w(2\gamma) = w(-2\gamma) \,. \tag{3.9c}$$

If $c = s/(1-5s)$, then

$$w(\gamma) = w(-\gamma) > w(0) = w(2\gamma) = w(-2\gamma) \,. \tag{3.9d}$$

If $c = s/(1-5s-6s\hat{p}_1)$, where $\hat{p}_1$ the coordinate of the symmetric equilibrium, then

$$w(2\gamma) = w(-2\gamma) = w(\gamma) = w(-\gamma) > w(0) \,. \tag{3.9e}$$

Finally, if competition is even stronger, then the extreme genotypes have the highest fitness and those with genotypic value zero have the lowest, i.e.,

$$w(2\gamma) = w(-2\gamma) > w(\gamma) = w(-\gamma) > w(0) \,. \tag{3.9f}$$

The equilibrium genetic variance

The equilibrium variance is zero, of course, if the monomorphic equilibria are stable, i.e., if (3.3) holds. In general, it is given by $\hat{\sigma}^2 = 4\gamma^2\hat{p}_1$, because all equilibria satisfy $p_1 = p_4$; cf. (2.9). As c increases beyond $c = s/(1-s)$, the genetic variance increases rapidly to high values. It is independent of r if $c \leq s/(1-5s)$, and decreases with increasing r, otherwise. Figure 3 displays the equilibrium genetic variance as a fraction of the maximum possible variance, which is $2\gamma^2$ and is obtained if $x = p_1 + p_4 = 1$ and $x = y = 0$. Therefore, the equilibrium variance relative to the maximum possible variance is $2\hat{p}_1$. This shows that frequency-dependent selection caused by intraspecific competition can maintain high levels of genetic variation in situations where stabilizing selection alone depletes all variation, provided competition is sufficiently strong. Figure 3 shows an almost threshold like dependence of the variance upon the coefficient of competition: the increase from no variance to a very high value occurs within the, typically small, interval $[s/(1-s), s/(1-5s)]$ in which the equilibria with $D = 0$ move from the corners to the center.
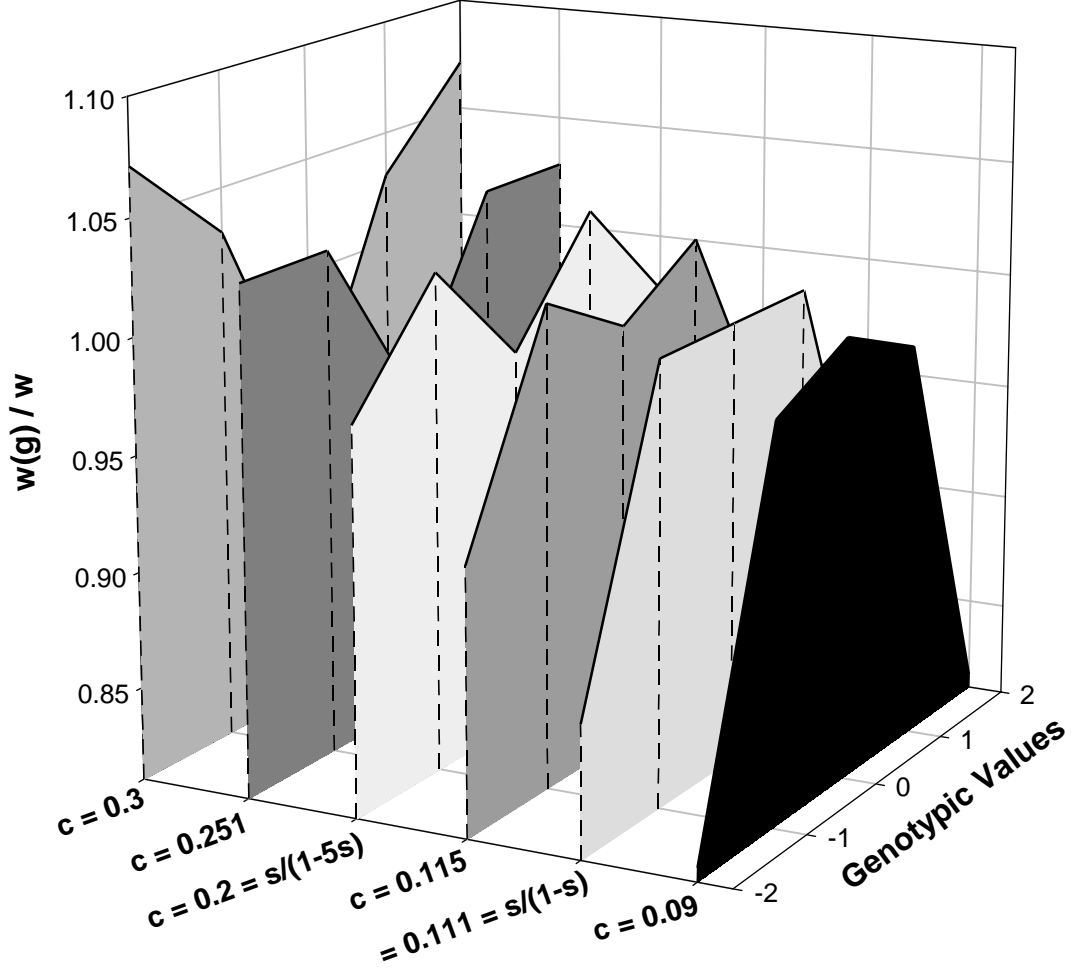
Figure 2: Genotypic fitnesses, $w(g)/\bar{w}$, at equilibrium for $s = 0.05$ and $r = 0.5$. The cases shown, beginning with $c = 0.09$, correspond to (3.9a) – (3.9f).

The case r=0

This case requires separate treatment because it is degenerate, i.e., there exists a line of stable equilibria. From (3.1), we infer immediately that any plane $p_2/p_3 = $ const. is invariant, and the proof of Lemma A.5 informs us that all trajectories converge to the plane $p_1 = p_4$. The dynamics on the resulting line is given by

$$\bar{w}(p_1' - p_1) = p_1(1 - 2p_1)[c(1 - s - 16sp_1) - s], \tag{3.10}$$

which is independent of p_2/p_3. Therefore, all trajectories with initial condition $p_2(0)/p_3(0) = \kappa$ converge to the equilibrium given by

$$\hat{p}_1 = \hat{p}_4 = \begin{cases} 0 \,, & \text{if } c \leq \frac{s}{1-s} \,, \\ \frac{c(1-s)-s}{16cs} \,, & \text{if } \frac{s}{1-s} < c < \frac{s}{1-9s} \,, \\ \frac{1}{2} \,, & \text{if } c \geq \frac{s}{1-9s} \text{ (and } s < \frac{1}{9}) \,, \end{cases} \tag{3.11a}$$

$$\hat{p}_2 = \kappa\hat{p}_3 = \frac{1 - 2\hat{p}_1}{1 + \kappa} \,. \tag{3.11b}$$
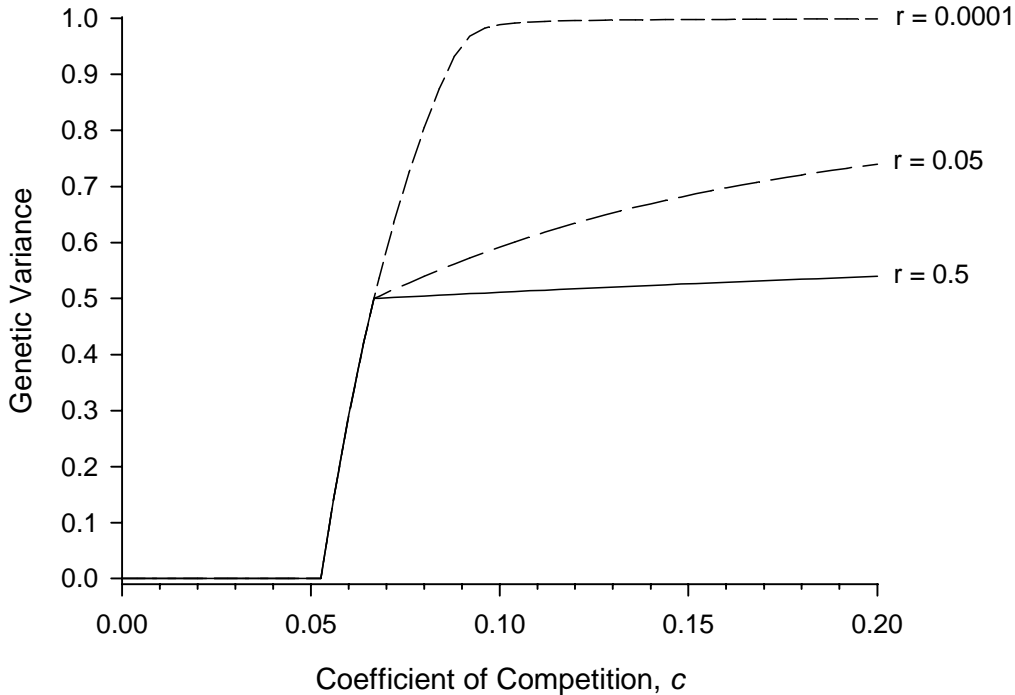
Figure 3: Additive genetic variance at equilibrium relative to the maximum possible variance of $2\gamma^2$ as a function of c for three different values of the recombination rate r. The selection coefficient is $s = 0.05$. Because this relative variance equals $2\hat{p}_1$, the figure also displays the position of the symmetric equilibrium and its linkage disequilibrium ($\hat{D} = \hat{p}_1 - \frac{1}{4}$) if $c \geq s/(1 - 5s)$.

Obviously, we have $\hat{p}_1 < \frac{1}{4}$ if and only if $c < s/(1 - 5s)$. It may also be noted that the coordinate $\hat{p}_1$ coincides with the corresponding coordinate of the pair of interior equilibria with $D = 0$ that exists if $r > 0$, cf. (3.5a).

4 Unequal Effects and Loose Linkage

For unequal effects, stabilizing selection alone can maintain stable interior polymorphisms, provided the loci are sufficiently tightly linked. If the effects are very similar, then linkage must be almost complete. However, if the effects are very different ($e > \frac{1}{3}$, i.e., $\gamma_1 \geq 2\gamma_2$), then even for freely recombining loci does stabilizing selection alone maintain stable single-locus polymorphisms (cf. Gavrilets and Hastings 1993, and Bürger 2000, Chap. VI.2). Here we shall investigate the interaction of competition and stabilizing selection for unlinked loci with different effects. The case of linked loci seems to be much more complicated and may be treated in a subsequent publication.

It is evident from Table 2.2 that the case of unequal effects ($e > 0$) leads to much more nasty expressions than the case of equal effects, thus making a complete analysis almost impossible. However, some progress can be made. For instance, with a little help from *Mathematica* (Wolfram 1996), a linear stability analysis of the monomorphic equilibria $\hat{p}_2 = 1$ and $\hat{p}_3 = 1$ reveals that they are asymptotically stable if and only if

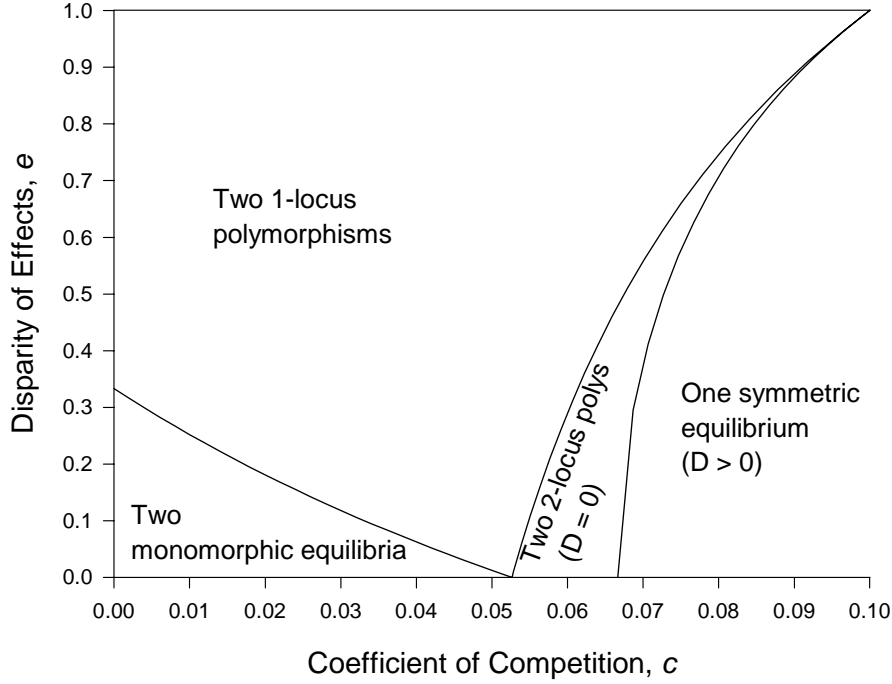$$c \leq \frac{r - 4e^2 s}{4e^2(1 - r)} \tag{4.1a}$$

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Figure 4: Regions of stability of the four classes of stable equilibria for free recombination ($r = 0.5$). The strength of stabilizing selection is $s = 0.05$.

and

$$c \leq \frac{s(1 - 3e)}{(1 + e)[1 - s(1 - e)^2]} \tag{4.1b}$$

hold. If r is large, e.g., $r = 0.5$, then validity of (4.1b) implies (4.1a). Condition (4.1b) shows that the monomorphic equilibria cannot be stable if $e > \frac{1}{3}$ or if $c > s/(1 - s)$, where the latter condition is obtained for $e = 0$. The range of c values for which the monomorphic equilibria are asymptotically stable decreases as e increases (see Figure 4). Numerical iterations of the recurrence relations suggest that each of the two monomorphic equilibria is globally attractive for half of the state space whenever it is asymptotically stable. For $e = 0$ this is proved in the Appendix.

It is also elementary to derive the conditions for existence and the positions of single-locus polymorphisms. Only the equilibria satisfying $p_1 + p_3 = 1$ or $p_2 + p_4 = 1$ can attract trajectories from the interior, i.e., only the locus with the major effect (by assumption locus A) can be stably polymorphic. The defining equation for the equilibrium at the edge $p_1 + p_3 = 1$ is

$$4cs(1 + e)^3 p_1^3 - 6cs(3 - e)(1 + e)^2 p_1^2 + 2(1 + e)[s + c + 2cs(3 + 2e - 3e^2)]p_1$$
$$+ s(1 - 3e) - c(1 + e)[1 - (1 - e)^2 s] = 0 . \tag{4.2}$$

Observe that the constant term is negative if and only if condition (4.1b) is invalid, i.e., if and only if $\hat{p}_3 = 1$ is unstable (given that r is large). In this case, (4.2) has a solution satisfying $0 < \hat{p}_1 < 1$. Indeed, since the left-hand side of (4.2) is monotone increasing on $[0, 1]$, the equilibrium is is uniquely determined. Hence, a single-locus polymorphism exists if and only if (4.1b) does not hold, i.e., if $\hat{p}_3 = 1$ is unstable. A parallel result is obtained for $p_2 + p_4 = 1$, by replacing p_1 in (4.2) by p_2.
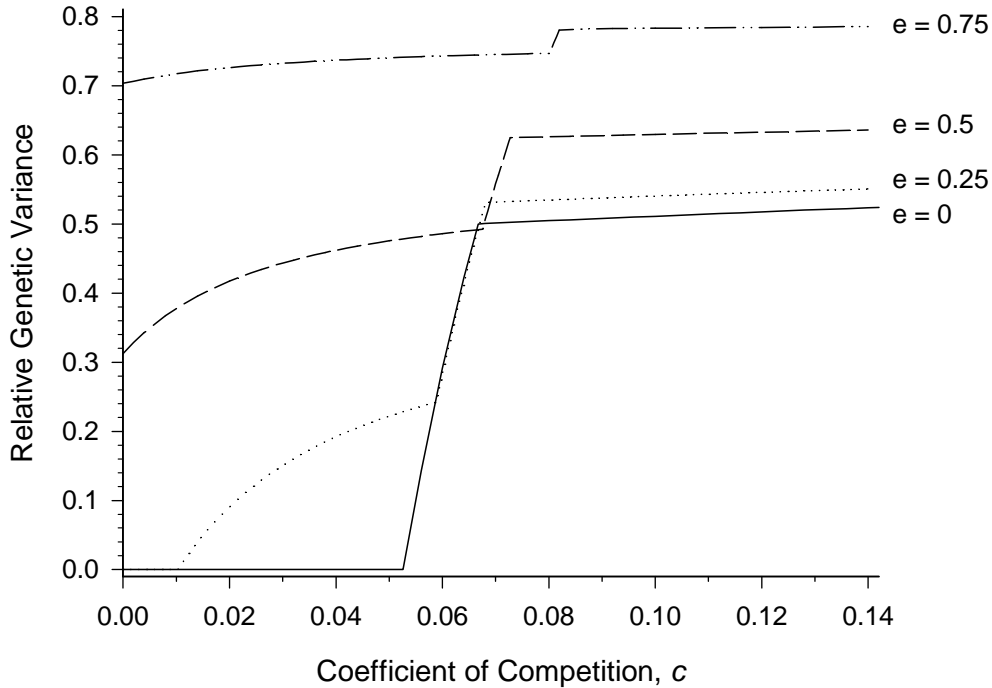
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Figure 5: Additive genetic variance at equilibrium relative to the maximum possible variance of $2\gamma^2$ as a function c for freely recombining loci ($r = 0.5$), and for various values of e (disparity of effects). Here, $e = 0$ means equal effects; further, $e = 0.25$ if $\gamma_1 = \frac{5}{3}\gamma_2$, $e = 0.5$ if $\gamma_1 = 3\gamma_2$, and $e = 0.75$ if $\gamma_1 = 7\gamma_2$. The strength of stabilizing selection is $s = 0.05$. Because this relative variance equals $2\hat{p}_1$, the figure also displays the position of the symmetric equilibrium and its linkage disequilibrium ($\hat{D} = \hat{p}_1 - \frac{1}{4}$) if c is large.

Numerical iteration of the recurrence relations and numerical solution of the equilibrium conditions shows that for a small range of (intermediate) values of c a pair of asymptotically stable interior equilibria on the Wright manifold $D = 0$ exists. They correspond to the pair of equilibria (3.5) that could be calculated explicitly in the case of equal effects. For $e > 0$, these equilibria no longer satisfy the symmetry condition $y = 0$, but still both equilibria have the same x-coordinate. Using c as the bifurcation parameter, they move into the interior of the simplex when the single-locus polymorphisms at the edges $p_1 + p_3 = 1$ and $p_2 + p_4 = 1$ become unstable (exchange of stability), and then converge to the center of the simplex. At the critical value

$$c = \frac{s}{1 - 5s(1 + e^2)} \tag{4.3}$$

(cf. Eq. 3.8) they hit the center and cease to exist. Instead, the symmetric equilibrium, $\hat{p}_1 = \hat{p}_4$ and $\hat{p}_2 = \hat{p}_3$, which always exists, becomes stable (through a pitchfork bifurcation). For all larger values of c, this symmetric equilibrium apparently is globally stable and satisfies $D > 0$. It is interesting to observe that for increasingly different effects of the loci, intraspecific competition must become stronger in order maintain a stable two-locus polymorphisms.

Numerical iteration of the recursion relations and numerical search for solutions of the equilibrium conditions suggest that no other interior equilibria exist for loose linkage, and that stability of one of these classes excludes stability of any other attractor.

The equilibrium genetic variance can be calculated from Eq. (2.9). The maximum

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possible value is attained if $x = 1$ and $y = z = 0$, and equals $2\gamma^2$. Figure 5 displays the equilibrium variance relative to this maximal value as a function of c for several values of e. The threshold like dependence on c observed for equal effects in Figure 3 still occurs, but only if the effects of the loci are similar. Otherwise, stabilizing selection alone maintains genetic variation and, hence, the contribution of competition to variation is relatively smaller. For very different effects, competition adds almost no variation. In this figure, the range of c values for which the interior equilibria with $D = 0$ exist and are stable is clearly visible by the steep increase of the variance. For c larger than (4.3), the symmetric equilibrium appears to be globally stable, and since its variance relative to the maximum possible variance is $2\hat{p}_1$, and since its linkage disequilibrium is $\hat{D} = \hat{p}_1 - \frac{1}{4}$, the right part of the figure also provides the information for the position of this equilibrium and for the linkage disequilibrium maintained. Thus, for free recombination a high amount of (positive) linkage disequilibrium is maintained only if the locus effects are very unequal and competition is sufficiently strong.

From Eq. (2.8) we observe that with unequal effects the equilibrium mean phenotype deviates from the fitness optimum, unless the population is at the symmetric equilibrium. Thus, at least for loose linkage, competition pushes the population mean towards the fitness optimum. Actually, numerical evaluation of (2.8) shows that the deviation of the mean from the optimum is a decreasing function of c, unless the population is at a monomorphic equilibrium (results not shown).

For equal effects, Figure 3 and Eqs. (3.9) show that genotypic fitnesses exhibit disruptive selection if and only if competition maintains both loci polymorphic. For unequal effects, such disruptive selection may already occur if the monomorphic equilibria are stable. Then, for values of c and e close to the boundary curve of the region in which a single-locus polymorphism is maintained (cf. Figure 4), the genotypes with genotypic values $|\gamma_2|$ (cf. Table 2.1) may have higher fitness than all other genotypes. If the single-locus polymorphisms are stable, then the genotypic values may also exhibit stabilizing or disruptive selection, depending on the combination of c and e, and either the genotypes with values $|\gamma_2|$ or with $|\gamma_1 - \gamma_2|$ may have the highest fitness. If competition maintains both loci polymorphic, then there is always disruptive selection with either the genotyes $|\gamma_1|$ or $|\gamma_1 + \gamma_2|$ having maximal fitness (results not shown).

5   Selection on Haploids

If selection acts on haploids, the same basic model as in Section 2 can be used. Since there are only four genotypes, Tables 2.1 and 2.2 become much simpler. In particular, the expressions for the marginal fitnesses and the mean fitness are greatly simplified. We leave the straightforward calculations to the interested reader. For selection on haploids, it is more convenient to assume that in the life cycle recombination occurs before selection. Then the recursion relations can be written as

$$\tilde{w}p_i' = w_i(p_i - \eta_i rD) , \tag{5.1}$$

where $\tilde{w} = \bar{w} - r(w_1 - w_2 - w_3 + w_4)D$; cf. Rutschman (1994). It turns out that, at least for equal effects of the loci, the basic equilibrium structure is exactly the same as for diploids, i.e.:

1. If $c \leq \frac{s}{1-s}$, then the equilibria $\hat{p}_2 = 1$ and $\hat{p}_3 = 1$ are asymptotically stable and attract all trajectories from the corresponding half space.

2. If $\frac{s}{1-s} < c < \frac{s}{1-\frac{3}{2}s}$, then a pair of interior equilibria with $D = 0$ is asymptotically stable. The coordinates are

$$\hat{p}_1 = \hat{p}_4 = \frac{c(1-s) - s}{2cs} \, , \tag{5.2a}$$

$$\hat{p}_2(\pm) = \frac{s - c(1-2s)}{2cs} \pm \frac{1}{2\sqrt{2}}\sqrt{\frac{s - c(1-\frac{3}{2}s)}{cs}} \, , \quad \hat{p}_3(\pm) = \hat{p}_2(\mp) \, . \tag{5.2b}$$

3. If $c \geq \frac{s}{1-\frac{3}{2}s}$, then the symmetric equilibrium is globally asymptotically stable. It is given by the unique solution of

$$16cs(1-r)p_1^3 - 8[c - s + rs(1 - \tfrac{1}{2}c)]p_1^2$$
$$+ 4[c(1 - r - s + rs) - s - r(1 - \frac{3}{2}s)]p_1 + r(1-s)(1+c) = 0 \tag{5.3}$$

that satisfies $\frac{1}{4} \leq p_1 < \frac{1}{2}$. This symmetric equilibrium exists also for smaller c, but is unstable then and satisfies $p_1 < \frac{1}{4}$.

The main difference to the diploid model is that for haploid selection the symmetric equilibrium becomes stable for smaller values of c. The proof of these results is much simpler than for diploids and omitted. For instance, by considering the Lyapunov function $(p_1'/p_4' - 1)^2$, it is not difficult to show that all trajectories converge to the plane $p_1 = p_4$. This reduces the further analysis of D' and p_2'/p_3' to a two-dimensional problem, which greatly reduces the difficulties faced in the diploid case.

6   Discussion

Previous analyses have demonstrated that intraspecific competition may be a potent force in maintaining genetic variation of traits under stabilizing selection, provided it is sufficiently strong (Slatkin 1979, Bulmer 1980, Christiansen and Loeschke 1980, Loeschke and Christiansen 1984). However, as the model of Bulmer discussed in the introduction shows (and also a single-locus model in Slatkin's article), strong competition is not necessarily sufficient to guarantee a stable polymorphic equilibrium. With the exception of the work of Loeschke and Christiansen (1984), these investigations were based either on single-locus models or on phenotypic models with a Gaussian distribution of phenotypes and a constant genetic variance. Loeschke and Christiansen studied a two-locus model similar to ours, but used the Lotka-Volterra-type functional form (1.1) as fitness function together with (1.2) for competition and a Gaussian resource function k. In the limit of weak selection, weak competition, and small allelic effects, their model and the present model should yield equivalent results. Loeschke and Christiansen (1984) restricted their attention to the case of strong competition relative to selection, i.e., in the notation of the introduction, they assumed $\sigma_k^2 > \sigma_\alpha^2$. Moreover, most of their, primarily numerical, results and their discussion are focused on the case of complete or tightly linked loci. However, they also consider scenarios when the double heterozygote is not at the resource optimum, i.e., when it deviates from the optimum fitness under stabilizing selection. In this case, Loeschke and Christiansen (1984) conclude that intraspecific competition does not play any role if the population is far from the optimum, because then directional selection prevails, whereas competition keeps the population polymorphic and its mean close to the optimum if the optimum is within the range of genotypic values.

The present analysis poses no restrictions on the relative strength of competition and stabilizing selection, or on the effects of the loci, but assumes, as most classical models of stabilizing selection, that the double heterozygote is at the fitness optimum of stabilizing selection. The main goal was to explore the interplay of the genetic parameters, recombination rate and allelic effects, with the two selective forces in maintaining genetic variation and stable polymorphisms.

Perhaps the main achievement is a complete analytical characterization of the possible equilibrium structures for the case of equal effects, but arbitary strength of competition and stabilizing selection and arbitrary recombination rates. Except for a small parameter range, global convergence results could be proved. With equal effects, the genetic variation maintained depends in a threshold-like manner on the strength of competition. If it is weak, $c \leq s/(1-s)$, then no variation is maintained at all, whereas otherwise both loci are stably polymorphic (cf. Figures 1 and 3). In terms of the original parameters, this condition on c means that no variation can be maintained if

$$\frac{\sigma_\alpha^2}{V_{\mathrm{s}}} \geq (\rho - 1)\left(1 - \frac{\gamma^2}{2V_{\mathrm{s}}}\right) ,$$

which is closely related to Bulmer's condition (1.5). However, in contrast to his model, in which the effect of the locus under consideration on the phenotypic variance is neglected, in the present model sufficiently strong competition always maintains a stable polymorphism.

This behavior extends to similar, but unequal, effects and large recombination rates. However, with such effects, a single-locus polymorphism can be stably polymorphic for intermediate values of c. The range of values c extends rapidly as the disparity of locus effects increases, and if $\gamma_1 \geq 2\gamma_2$, the pair of single-locus polymorphisms (with the major locus polymorphic) is stable for all small values of c, i.e., even in the absence of competition (the reason is single-locus overdominance); stable monomorphic equilibria do no longer exist. For strong competition, there is always one pair of stable interior equilibria with $D = 0$ that exists only for a small range of values c, otherwise the symmetric equilibrium is stable (cf. Figure 4).

Thus, in the present model, as well as in that of Loeschke and Christiansen (1984), sufficiently strong competition relative to stabilizing selection always maintains a stable symmetric two-locus polymorphism. Apparently, in our model this polymorphism is uniquely determined, globally stable, and displays positive linkage disequilibrium. In the model of Loeschke and Christiansen, up to three symmetric two-locus polymorphisms can coexist, two of which can be stable, or one can be stable and coexist with stable boundary equilibria. This occurs for strong Gaussian selection that leads to strong selection on one or both loci. This phenomenon, however, is not a consequence of competition, but a consequence of the properties of Gaussian stabilizing selection in two-locus models, and occurs also in the absence of competition (Nagylaki 1989; Gavrilets and Hastings 1994; Gimelfarb 1996; Bürger 2000, Chap. VI.2). As the properties of the two-locus model with Gaussian stabilizing selection alone have not yet been fully explored, the present analysis has been based on the quadratic optimum model. A further difference to the model of Loeschke and Christiansen (1984) is that they report numerical results about the existence and position of a pair of interior equilibria corresponding to our pair with $D = 0$ that are dependent on the recombination rate. Loeschke and Christiansen (1984) conclude that competition will in general lead to strong positive linkage disequilibrium, but they considered mainly the case of very tight linkage. Our results demonstrate that either tight linkage or very different effects are necessary to obtain high positive linkage disequilibrium.

For equal effects, the equilibrium fitnesses of the genotypic values exhibit disruptive selection if and only if competition is strong enough to maintain a two-locus polymor-

phism. Interestingly, with unequal effects, disruptive selection may be observed even if competition is not strong enough to change the equilibrium maintained by stabilizing selection alone. Hence, the conditions to observe disruptive selection are not very restrictive. This suggests that if disruptive selection is observed only rarely, then, provided the measurement methods are appropriate, strong intraspecific competition may indeed be an infrequent phenomenon.

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Appendix

Here we prove the main results of Section 3. This is done in several steps. Accordingly, the appendix is structured as follows: in the first part, we consider the dynamics on the line $\{p_1 = p_4, p_2 = p_3\}$. This will be needed subsequently. In the second part, we prove the (global) stability results for the two monomorphic equilibria that are stable if $c \leq s/(1-s)$; in the third part, we derive asymptotic stability results for the case $c > s/(1-s)$; in the fourth part, we prove global stability of the symmetric equilibrium if $c \geq s/(1-6s)$.

Throughout this appendix, we assume $r > 0$, $c \geq 0$, $0 \leq s < \frac{1}{5}$, and $\gamma_1 = \gamma_2$, i.e., $e = 0$. In Table A.1, the marginal fitnesses w_i of the four gametes and the mean fitness $\bar{w}$ are displayed. Notably, they are independent of the coordinate z. Most of the following calculations have been performed with *Mathematica* (Wolfram 1996). The statements in the proofs below can be checked easily with any decent package for symbolic computations by implementing the marginal fitnesses and the mean fitness from Table A.1, and by following the advice given in the proofs.

Table A.1. The marginal fitnesses and the mean fitness.

$$
\begin{aligned}
w_1 &= 1 - s(1 + x + 2y) + c(1 + 3x - 2y - 2y^2) \\
&\quad - cs(1 + 9x + 4y + 2x^2 - 8xy - 14y^2 + 2xy^2 + 4y^3) \\
w_2 = w_3 &= 1 - sx + c(3x - 2y^2) - cs(x + 2x^2 - 4y^2 + 2xy^2) \\
w_4 &= 1 - s(1 + x - 2y) + c(1 + 3x + 2y - 2y^2) \\
&\quad - cs(1 + 9x - 4y + 2x^2 + 8xy - 14y^2 + 2xy^2 - 4y^3) \\
\bar{w} &= 1 - 2s(x + y^2) + 4c(x - y^2) - 2cs(x + 5x^2 - 8xy^2 + 2y^4)
\end{aligned}
$$

We shall consider only trajectories for which initially (at generation $t = 0$) all four alleles are present. Thus, a statement such as "all trajectories converge to ..." is always to be understood upon this qualification. Because $r > 0$, any such trajectory will be in the interior of the simplex for all $t \geq 1$. Hence, the invariant subsets of the boundary are the lines at which one locus is monomorphic (and the vertices, of course). Since we also suppose that $w(g) > 0$ for all genotypes, no trajectory from the interior can reach the boundary within a finite number of generations. In the proofs, we shall repeatedly use this fact without further mentioning.

A.1 Dynamics on the symmetric line $\{p_1 = p_4, p_2 = p_3\}$

In this case, p_1 is sufficient to describe the population distribution ($0 \leq p_1 \leq \frac{1}{2}$). We restrict our attention to the case $c \geq s/(1 - 5s)$, because otherwise the symmetric equilibrium is unstable anyway (see next subsection). Then the recurrence relation for p_1 is computed to be

$$\bar{w}(p_1' - p_1) = 32csp_1^3 + 2[s - c(1 + 2r + 7s)]p_1^2 - [r + s - c(1 + r - s)]p_1 + \frac{r}{4}, \quad \text{(A.1)}$$

cf. (3.7). If $s, c > 0$, then this polynomial is of third degree, has a positive leading coefficient, is positive ($= \frac{1}{4}r$) at $p_1 = 0$ and negative ($= -\frac{1}{4}r(1 + 2c)$) at $p_1 = \frac{1}{2}$. Therefore, it has a unique root in the interval $(0, \frac{1}{2})$. This gives the uniquely determined equilibrium denoted by $\hat{p}_1$. The same conclusion is true if $c = 0$ or $s = 0$, when the equilibrium can be calculated explicitly.

From (A.1), p_1' can be calculated as a function of p_1, which we denote by $p_1'(p_1)$. Since $p_1'(0) = \frac{1}{4}r > 0$, $p_1'(\frac{1}{2}) < \frac{1}{2}$, and $p_1' = p_1$ if and only if $p_1 = \hat{p}_1$, all trajectories on $\{p_1 = p_4,$

$p_2 = p_3\}$ must converge to $\hat{p}_1$ without oscillation if $p_1'(p_1)$ is strictly monotone increasing. A simple calculation with *Mathematica* shows that

$$\frac{dp_1'}{dp_1} = \frac{320s^2c^2p_1^4 + A_1 - rA_2}{\bar{w}^2}, \tag{A.2}$$

where $A_2 = (1-s)(1+c) + 4c(2-5s)p_1 + 8c[3s + c(4-7s)] > 0$ and A_1 is a polynomial of degree 3. We want to show that the expression in (A.2) is positive. Since $A_2 > 0$, it is sufficient to show that $A_1 - \frac{1}{2}A_2 > 0$ for $0 \le p_1 \le \frac{1}{2}$. This is indeed the case, because we can write

$$A_1 - \tfrac{1}{2}A_2 = \tfrac{1}{2} + c(\tfrac{1}{2} + 8p_1) - s(\tfrac{1}{2} + 4p_1) - cs(\tfrac{1}{2} + 26p_1 + 36p_1^2)$$
$$+ 4c^2p_1^2(8 - 25s - 32p_1s + 8s^2 + 16p_1s^2 + 80p_1^2s^2) + 8s^2p_1^2(1 + c(5 + 8p_1)),$$

and the sum of the expressions in the first line is $\ge \frac{1}{2}$ and both expressions in the second line are ≥ 0 since $p_1 \le \frac{1}{2}$ and $c \ge s/(1-5s)$.

A.2 Stability of $\hat{p}_2 = 1$ and of $\hat{p}_3 = 1$ if $c \le s/(1-s)$

We shall prove the following result (see Sect. 3):

If (3.3) is satisfied, i.e., $c \le s/(1-s)$, then the equilibrium $\hat{p}_2 = 1$ is globally attractive for the set $p_2 > p_3$, and $\hat{p}_3 = 1$ is globally attractive for $p_2 < p_3$.

This assertion follows immediately from the following two lemmas together with the invariance of the two regions $p_2 > p_3$ and $p_2 < p_3$; cf. Eq. (3.1).

Lemma A.1 *If (3.3) holds, then $|y'| = |p_1' - p_4'| \le |p_1 - p_4| = |y|$, and equality is obtained if and only if $y = 0$, or $y = 1$ (i.e., $p_1 = 1$ or $p_4 = 1$.) Therefore, all trajectories converge to the plane $y = 0$.*

Lemma A.2 *If (3.3) holds and $y = 0$, then $|z'| = |p_2' - p_3'| > |p_2 - p_3| = |z|$, unless $x = 0$ when equality obtains.*

Proof of Lemma A.1 From the recurrence relations (2.13), we obtain

$$\bar{w}y' = \bar{w}(p_1' - p_4') = (p_1 - p_4)v_{14} = yv_{14}, \tag{A.3}$$

where

$$v_{14} = 1 - s(1+3x) + c[1 + x - 2y^2 - s(1 + 13x - 6x^2 - 14y^2 + 6xy)] > 0$$

because $0 \le s < \frac{1}{4}$, $c \ge 0$, and $0 \le y^2 \le x \le 1$. This shows that each of the regions $y > 0$ and $y < 0$ is always invariant. By (A.3), it is sufficient to investigate when

$$v_{14} - \bar{w} = -s(1 + x - 2y^2) + c(1 - 3x + 2y^2)$$
$$- cs(1 + 11x - 16x^2 - 14y^2 + 22xy^2 - 4y^4) \tag{A.4}$$

is negative. It is straightforward to check that there is no critical point satisfying $0 \le x \le 1$. (This holds for all positive c and s.) Therefore, the global maximum must lie on the boundary of the region $0 \le y^2 \le x^2 \le 1$. We investigate the three possible cases:

(i) $y = 0$. Then

$$\omega_{14} - \bar{w} = -s(1 + x) + c(1 - 3x) - cs(1 + 11x - 16x^2).$$

This function assumes the value $c(1-s) - s$ at $x = 0$ and $-2(s + c - 2cs)$ at $x = 1$ and, hence, is negative for $0 < x \leq 1$.

(ii) $y^2 = x^2$. Then

$$\omega_{14} - \bar{w} = -(1 - x)[s - c(1 - s) + 2x(s + c + cs(6 - 9x + 2x^2))] ,$$

and the term in brackets is positive if $x > 0$, because $c \leq s/(1 - s)$.

(iii) $x = 1$. Then

$$\omega_{14} - \bar{w} = -2(1 - y^2)[s + c - 2sc(1 - y^2)] ,$$

which is negative, unless $y = 1$.

This proves Lemma A.1.

Proof of Lemma A.2 Since $w_2 = w_3$, we have

$$z' = zw_2/\bar{w} ,$$

so that it is sufficient to show that $w_2 > \bar{w}$ if $y = 0$ and $x > 0$. This, however, is the case if $c \leq s/(1 - s)$, because for $y = 0$ we have

$$w_2 - \bar{w} = x[s - c(1 - s) + 8csx] > 0 .$$

A.3. Asymptotic stability of equilibria if $c > s/(1 - s)$

We shall outline the proof of the following result (see Sect. 3):
If (3.4) holds, then the pair of equilibria with $D = 0$, given by (3.5), is asymptotically stable. If (3.8) holds, then the symmetric equilibrium is asymptotically stable, otherwise it is unstable.

The eigenvalues of the pair of equilibria with $D = 0$ are given by

$$\lambda_1 = 1 - \frac{4[c(1 - s) - s](c + 3s + 5cs)}{3s^2 + 6cs(3 + s) + c^2(1 - s)(11 - 3s)} ,$$

$$\lambda_2(\pm) = 1 - \frac{2(\beta_1 \pm \sqrt{\beta_2})}{3s^2 + 6cs(3 + s) + c^2(1 - s)(11 - 3s)} ,$$

where

$$\beta_1 = [c(1 - s) - s][s - c(1 - 9s)] + 2cr(3s + c(1 - s))$$

and

$$\beta_1^2 - \beta_2 = 16cr[3s + c(1 - s)][c(1 - s) - s][s - c(1 - 5s)] .$$

Both expressions, β_1 and $\beta_1^2 - \beta_2$, are positive if (3.4) holds, hence $\lambda_2(\pm) < 1$. It can also be shown that $\lambda_2(\pm) > 0$. Finally, $\lambda_1 < 1$ if $c > s/(1 - s)$, and $\lambda_1 > 0$ holds always. This proves local asymptotic stability of this pair of equilibria.

For the symmetric equilibrium, we already know that it is asymptotically stable within the line $\{p_1 = p_4, \ p_2 = p_3\}$ if $c > s/(1 - 5s)$. Therefore, it is sufficient to consider the other two eigenvalues. These are given by

$$\lambda_1 = 1 - \frac{c(2\hat{x} - 1) + s(1 + \hat{x}) + c\hat{x}(1 - 4s\hat{x}) + cs(1 + 11\hat{x} - 12\hat{x}^2)}{1 + 2\hat{x}[c(2 - s - 5s\hat{x}) - s]} ,$$

$$\lambda_2 = 1 - \frac{\hat{x}[c(1 - s - 8s\hat{x}) - s]}{1 + 2\hat{x}[c(2 - s - 5s\hat{x}) - s]} ,$$

where $\hat{x} = 2\hat{p}_1$ denotes the position of the equilibrium. Because $\hat{x} > \frac{1}{2}$ if $c > s/(1-5s)$, it follows immediately that in this case both eigenvalues are between 0 and 1, which proves asymptotic stability. If $c < s/(1-5s)$, then $[c(1-s)-s]/(8cs) < \hat{x} < \frac{1}{2}$ (cf. Eq. 3.5a) and $\lambda_2 > 1$, whence instability follows.

A.4. Global stability of the symmetric equilibrium if $c > s/(1-6s)$

We will prove the following result (see Sect. 3):

If $s < \frac{1}{6}$ and $c \geq s/(1-6s)$, then the symmetric equilibrium given by (3.7) is globally stable.

We shall need the following lemmas:

Lemma A.3 *If $s < \frac{1}{5}$ and $c \geq s/(1-5s)$, then the region $|y| \leq \frac{1}{2}$ is positively invariant and every trajectory enters it.*

Lemma A.4 *If $s < \frac{1}{6}$ and $c \geq s/(1-6s)$, then the region $\{D \geq 0, |y| \leq \frac{1}{2}\}$ is positively invariant.*

Lemma A.5 *If $D \leq 0$, then*

$$\left(\frac{p_1'}{p_4'} - 1\right)^2 \leq \left(\frac{p_1}{p_4} - 1\right)^2 ,$$

and equality holds if and only if $p_1 = p_4$ or $p_4 = 1$.

Lemma A.6 *If $D \geq 0$, then*

$$\left(\frac{p_2'}{p_3'} - 1\right)^2 \leq \left(\frac{p_2}{p_3} - 1\right)^2 ,$$

and equality holds if and only if $p_2 = p_3$ or $D = 0$.

Lemma A.7 *If $D \geq 0$ and $p_2 = p_3$, then $|y'| \leq |y|$ and equality holds if and only if $y = 0$. Therefore, all trajectories from the planar region $\{D \geq 0, p_2 = p_3\}$ converge to the line $\{p_1 = p_4, p_2 = p_3\}$.*

Lemmas A.3–A.5 imply that every trajectory enters the region $\{D \geq 0, |y| \leq \frac{1}{2}\}$ and remains there because it is positively invariant. Lemma A.6 shows that (within this region) all trajectories converge to the plane $p_2 = p_3$, because $D = 0$ always implies $D' > 0$, unless one locus is monomorphic (see the remark below the proof of Lemma A.4). Finally, Lemma A.7 together with the result of Appendix A.1 proves the desired result, i.e., global stability of the symmetric equilibrium.

It seems to be difficult to extend this proof to $c \geq s/(1-5s)$, because if $c = s/(1-5s)$ (or if c is slightly larger), then no region of the form $\{D \geq 0, 0 < |y| \leq \alpha\}$, where $0 < \alpha \leq \frac{1}{2}$, is positively invariant. However, it can be proved that $D \geq 0$ is positively invariant in the plane $y = 0$ if $c \geq s/(1-5s)$, which implies that the symmetric equilibrium attracts all trajectories from this plane. It also seems to be difficult to derive global results in the case when (3.4) holds, because then neither $D \geq 0$ nor $D \leq 0$ is positively invariant on $y = 0$. There seems to be no simple way of proving that all trajectories converge to $y = 0$, in particular, for $c > s/(1-s)$ it is in general not true that $|y'| \leq |y|$.

Proof of Lemma A.3 First we show that if $\frac{1}{2} \leq |y| \leq x \leq 1$, then $|y'| \leq |y|$. From (A.3) we infer that it is sufficient to demonstrate that $v_{14} - \bar{w} \leq 0$; cf. (A.4). The proof of Lemma

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A.1 informs us that a global maximum can only be located on the boundary of the region $\frac{1}{2} \le |y| \le x \le 1$. Thus, we have to consider three cases:

(i) $|y| = \frac{1}{2}$. Then

$$v_{14} - \bar{w} = -\frac{1}{4}[2s(2 + 3c) + (2x - 1)(6c + 2s + cs(17 - 32x))] ,$$

which is negative because $x \ge \frac{1}{2}$ and $c > s/(1 - 5s)$.

(ii) $x = 1$. Then $v_{14} - \bar{w} = -2(1 - y^2)(s + c - 2sc(1 - y^2)) < 0$ if $y^2 < 1$.

(iii) $y^2 = x^2$. Then

$$v_{14} - \bar{w} = -(1 - x)[s(2 + 3c) + (2x - 1)(s + c + 2sc(1 - 4x + x^2))] ,$$

which is again negative for the given range of parameters.

This proves that every trajectory enters the region $|y| \le \frac{1}{2}$.

Now we show positive invariance, i.e., $|y| \le \frac{1}{2}$ implies $|y'| \le \frac{1}{2}$. Equation (A.3) informs us that we have to prove $\bar{w} - 2yv_{14} \ge 0$ if $|y| \le \frac{1}{2}$. Because of symmetry, it is sufficient to consider the case $0 \le y \le \frac{1}{2}$. It is straightforward to check that

$$\bar{w} - 2yv_{14} = 1 - 2(1 + c)(1 - s)y - 2(2c + s)y^2 + 4c(1 - 7s)y^3 - 4csy^4$$
$$+ 2[c(2 - y - s + sy(13 + 8y + 6y^2)) - s(1 - 3y)]x - 2cs(5 + 6y)x^2 .$$

Therefore, the partial derivative with respect to x is linearly decreasing in x and, as is not difficult to show, positive in $x = 1$ because $c > s/(1 - 5s)$ and $0 \le y \le \frac{1}{2}$. Therefore, $\partial(\bar{w} - 2yv_{14})/\partial x > 0$ for all $x \in [0, 1]$, whence the minimum of $\bar{w} - 2yv_{14}$ on the region $\{0 \le y \le x \le 1, y \le \frac{1}{2}\}$ must be attained on the boundary set $0 \le x = y \le \frac{1}{2}$. On this set we obtain

$$\bar{w} - 2yv_{14} = (1 - 2x)[1 + 2xc(1 - x)] + 4sx^2(1 + 4c - 6cx + 2cx^2) ,$$

which is positive if $x < \frac{1}{2}$.

The reader may note that in case (i) $v_{14} - \bar{w}$ is positive if $x < \frac{1}{2}$ and $s = 0$. Therefore, a region of the form $|y| \le a$ cannot be invariant if $a < \frac{1}{2}$. In this sense, Lemma A.3 is best possible.

Proof of Lemma A.4 From the recursion equations, we obtain easily

$$\bar{w}^2 D' = p_1 p_4(w_1 w_4 - w_2 w_3) + D(w_2 w_3 - r w_{14}\bar{w}) . \tag{A.5}$$

In order to show that for $|y| \le \frac{1}{2}$, $D \ge 0$ implies $D' \ge 0$, we have to prove that $\bar{w}^2 D' \ge 0$ if $D \ge 0$ and $|y| \le \frac{1}{2}$. Since in the following analysis only even powers of y enter, we set $q = y^2$ and recall that $0 \le q \le x^2 \le 1$ holds. For $c \ge s/(1 - 5s)$, we obtain

$$w_2 w_3 - \tfrac{1}{2}w_{14}\bar{w} = \tfrac{1}{2} + 3[c(1 - 5s) - s](x - q) + c[c(1 - 5s) - s][4(x - q)^2 + (x - 2q)^2]$$
$$+ 2s(x - q) + s^2 x^2$$
$$+ cs[(x - 2q)^2 + (x - 3q)^2 + 7(x - q) + 6x(1 - q) + (x - q^2)]$$
$$+ 2xcs(x + 2x^2 - 4q + 2xq)$$
$$+ c^2 s[4(x - q)(x - q^2) + 12(x - q)^2 + 10xq(1 - x) + 2x(1 - x)(x + 5q)]$$
$$+ c^2 s^2(x + 2x^2 - 4q + 2xq)^2 \ge 0 \tag{A.6}$$

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(check the equality with *Mathematica*; the inequality is trivial because all terms are ≥ 0 since $0 \leq q \leq x^2 \leq 1$). Therefore, if $D = 0$, we have to prove that

$$W_D = w_1 w_4 - w_2 w_3 \tag{A.7}$$

is nonnegative for $q \leq \frac{1}{4}$, whereas if $D > 0$, we have to prove that $\bar{w}^2 D' \geq 0$. To this end, we observe directly from Table A.1 that W_D depends only on x and q, but not explicitly on p_2 or p_3. (The explicit expression for W_D is complicated, and we shall not present it.) Moreover, we observe that for given p_1 and p_4 (i.e., for given x and q), D assumes its minimum if $p_2 = p_3 = \frac{1}{2}(1 - x)$, the minimum value being $D = \frac{1}{4}(2x - q - 1)$. Thus, for given x and q, D is positive for all admissible p_2 and p_3 if and only if $0 \leq q < 2x - 1$.

Therefore, in order to prove positive invariance of $D \geq 0$, it will be sufficient to show that

$$W_D > 0 \qquad \text{if} \max(0, 2x - 1) \leq q \leq \min(x^2, \tfrac{1}{4}) \tag{A.8}$$

and

$$W_I = (x^2 - q)W_D + (2x - q - 1)(w_2 w_3 - \tfrac{1}{2} w_{14}\bar{w}) \geq 0$$
$$\text{if } 0 \leq q \leq \min(2x - 1, \tfrac{1}{4}) \text{ and } \tfrac{1}{2} \leq x \leq 1, \tag{A.9}$$

where we note that $2x - 1 = \frac{1}{4}$ if $x = \frac{5}{8}$.
Step 1. Proof of (A.8). First we show that W_D has no critical point in the region defined in (A.8). Then we shall examine the boundary.

We show that the derivative of $W_D(x, q)$ in direction $(3, 4)$ is negative. Indeed, with the help of *Mathematica* we obtain

$$-\tfrac{1}{2}\left(3\tfrac{\partial W_D}{\partial x} + 4\tfrac{\partial W_D}{\partial q}\right) = 7c^2 + 4cs + 4c^2 s + 5s^2 + 58cs^2 + c^2 s^2(61 - 66q)$$
$$- 4csx(21c + 23s - 25cs)$$
$$+ 4csq(11c - 66cs + 10s + 30csx)$$
$$+ 60c^2 s^2 q^2 .$$

The second but last term is positive if $s < \frac{1}{6}$. Since $21c + 23s - 25cs$ is always positive we obtain, by omitting the last two terms and by using $q \leq \frac{1}{4}$ and $x \leq \frac{5}{8}$,

$$-\tfrac{1}{2}\left(3\tfrac{\partial W_D}{\partial x} + 4\tfrac{\partial W_D}{\partial q}\right) \geq c^2(7 - \tfrac{9}{7}2s + 107s^2) + 4cs + \tfrac{1}{2}cs^2 + 5s^2 > 0 .$$

Hence, the derivative of W_D in direction $(3, 4)$ is negative.

Therefore, W_D can attain its minimum only on one of the following subsets of the boundary: (i) $\{q = x^2, x \leq \frac{3}{8}\}$; (ii) $\{q = \frac{1}{4}, \frac{1}{2} \leq x \leq \frac{5}{8}\}$; (iii) $\{\frac{1}{2} \leq x \leq \frac{5}{8}, q = 2x - 1\}$.
(i) For $q = x^2$ we obtain

$$W_D = 2[c - s - 2cs(1 + 6x - 4x^2)] + s^2(1 + 2x - 4x^2)$$
$$+ 2cs^2(1 + 10x - 12x^2 + 8x^3 - 8x^4)$$
$$+ c^2 s^2(1 + 18x + 40x^2 - 144x^3 + 76x^4 + 24x^5 - 16x^6)$$
$$+ c^2(1 + 6x - 8x^2) - 2c^2 s(1 + 12x + 18x^2 - 60x^3 + 28x^4) .$$

It is straightforward to check that the coefficients of cs, s^2, cs^2, $c^2 s^2$, c^2, and $c^2 s$ are positive if $x \leq \frac{3}{8}$. The sum of the two terms with c^2 (in the last line) is positive if $s < \frac{1}{6}$

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(and $x \leq \frac{1}{2}$). Finally, the first term (in brackets) in the first line is positive if $x \leq \frac{3}{8}$ and $c \geq s/(1 - 6s)$. Therefore, $W_D > 0$ on this part of the boundary.

(ii) For $q = \frac{1}{4}$ we obtain

$$W_D = 2[c - 6cs - s + c^2(1 - \tfrac{23}{4}s)] + s^2(1 + 7c + \tfrac{29}{4}c^2)$$
$$- (x - \tfrac{1}{2})[4cs(6 - 11s) - 2s^2 + c^2(6 - 46s + \tfrac{131}{2}s^2)]$$
$$- 2cs(x - \tfrac{1}{2})^2(26c - 57cs - 10s) + 32c^2s^2(x - \tfrac{1}{2})^3 .$$

This is clearly positive if $x = \frac{1}{2}$, and the reader can readily convince himself that W_D is also positive at $x = \frac{5}{8}$, even if the third-order term is omitted. Since the resulting polynomial of degree two in $(x - \frac{1}{2})$ is obviously concave, W_D must be positive for $\frac{1}{2} \leq x \leq \frac{5}{8}$.

(iii) For $q = 2x - 1$, we obtain

$$W_D = (c - 5cs - s)(2 + 4c - 7cs - 2s)$$
$$- 2(x - \tfrac{1}{2})[c^2(1 - 7s)^2 + 38c^2s^2 + 4c(c - s - 6cs) + 16cs^2 + 3s^2]$$
$$- 12(x - \tfrac{1}{2})^2 cs(s + 3c - 23cs) - 144c^2s^2(x - \tfrac{1}{2})^3 . \tag{A.10}$$

This expression is monotone decreasing in x if $s < \frac{3}{23}$ and $c \geq s/(1 - 6s)$. In fact, joint consideration of the linear and quadratic terms in $(p - \frac{1}{2})$ shows that this true for all $s < \frac{1}{6}$. Setting $a = c - s - 6cs$, which is nonnegative by assumption, we obtain

$$W_D = \tfrac{1}{32}(1 - 6s)^{-2}[s^2(32 - 72s + 467s^2)$$
$$+ 2a(32 - 344s + 1067s^2 - 677s^3) + a^2(88 - 578s + 553s^2)] > 0 ,$$

as is trivial to check. This finishes the proof of (A.8).

Step 2. Proof of (A.9). We set $a = c - s - 6cs \geq 0$, $\xi = x - \frac{1}{2}$, and compute

$$\frac{\partial W_I}{\partial x} = 1 + 2s(1 + 4\xi - 3q) + \tfrac{1}{2}s^2[1 + 8(4 - 9q + 10q^2) + 4\xi(26 - 31q - 15\xi)]$$
$$+ a\big\{(5 - 9q + 16\xi) + s[\tfrac{13}{2} + 15(1 - 2q)^2 + 8q^2 + 2\xi(3\xi + 40 - 63q)]$$
$$+ s^2[28 + 3(1 - 2q)(43 - 44q - 4q^2)$$
$$+ 4\xi(105 + 8(5 + 2q)(1 - 4q) + (4 - 3\xi - 8\xi^2) + 168q\xi)]\big\}$$
$$+ a^2\big\{(8 - 31q + 28q^2) + 2\xi(20 - 37q + 24\xi)$$
$$+ s[14 + frac12(67 - 319q + 208q^2 + 24q^3) + 2\xi(113 - 149q - 54q^2)$$
$$+ \xi^2(150 - 224\xi) + 306q\xi^2]$$
$$+ s^2[4\xi(262 - 1045q) + 8\xi(290 - 237\xi - 484\xi^2 + 50\xi^3)$$
$$+ (500 - 4q(577 - 1290\xi^2 + 120\xi^3)) + 4q^2(343 - 416\xi + 36\xi^2) + 8q^3(29 - 10\xi)]\big\} ,$$

which is greater than 1 because all terms in parentheses and brackets are nonnegative on the region defined in (A.9). Therefore, W_I attains its minimum on the line $\{q = 2x - 1, \frac{1}{2} \leq x \leq \frac{5}{8}\}$. On this line, however, we have $W_I = p_1 p_4 W_D$. Since $W_D > 0$ for $q = 2x - 1$ was already proved in (A.10), the proof of (A.9) and of the lemma is finished.

Remark. From (A.5) and the above proof, it follows immediately that $D' \geq D$ if $D \leq 0$, and $D' > 0$ if $D = 0$ and $p_1 p_4 \neq 0$, provided $c > s/(1 - 6s)$. This implies that all trajectories enter $D > 0$ (with the only exception of those for which one locus is monomorphic). Lemma A.5, however, allows a slightly more general conclusion.

Proof of Lemma A.5 The recurrence relations imply

$$\frac{p_1'}{p_4'} - 1 = \left(\frac{p_1}{p_4} - 1\right)\frac{p_4 v_{14}}{p_4 w_4 - rDw_{14}} \,,$$

where v_{14} was defined below (A.3). (Note that $p_4 w_4 - rDw_{14} = p_4' > 0$ if $p_4 > 0$.) It follows immediately that

$$p_4 v_{14} - (p_4 w_4 - rDw_{14}) = rD[1 + 2c(x + y^2)] - (x^2 - y^2)[s + c + 2cs(1 - 2x + y^2)] \le 0$$

if $D \le 0$ because $y^2 \le x^2$. Therefore, $0 < p_4 v_{14}/(p_4 w_4 - rDw_{14}) < 1$ if $D \le 0$ and $y^2 < x^2$ (i.e., $p_1, p_4 < 1$), and the lemma is proved.

Proof of Lemma A.6 From the recurrence relations and because $w_2 = w_3$, or from (3.1), we obtain

$$\frac{p_2'}{p_3'} - 1 = \left(\frac{p_2}{p_3} - 1\right)\frac{p_3 w_2}{p_3 w_2 + rDw_{14}} \,.$$

Obviously, the fraction on the right-hand side is < 1 if and only if $D > 0$. This proves the lemma.

Proof of Lemma A.7 If $p_2 = p_3$, then $D = \frac{1}{4}(2x - y^2 - 1)$ and $D \ge 0$ if and only if $y^2 \le 2x - 1$. Therefore,

$$\begin{aligned}
v_{14} - \bar{w} &= c(1 - s) - s - x(3c + s + 11cs) + 16csx^2 \\
&\quad + 2y^2(c + s + 7cs - 11csx) + 4csy^4 \\
&\le -(1 - x)(c + 3s + 11cs - 12csx) < 0
\end{aligned}$$

if $0 \le x < 1$, because $y^2 \le 2x - 1$ and $c + s + 7cs - 11csx \ge c + s - 4cs \ge 0$. This proves the lemma.