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Stability analysis of the partial selfing selection model*

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Abstract. We undertake a detailed study of the one-locus two-allele partial selfing selection model. We show that a polymorphic equilibrium can exist only in the cases of overdominance and underdominance and only for a certain range of selfing rates. Furthermore, when it exists, we show that the polymorphic equilibrium is unique. The local stability of the polymorphic equilibrium is investigated and exact analytical conditions are presented. We also carry out an analysis of local stability of the fixation states and then conclude that only overdominance can maintain polymorphism in the population. When the linear local analysis is inconclusive, a quadratic analysis is performed. For some sets of selective values, we demonstrate global convergence. Finally, we compare and discuss results under the partial selfing model and the random mating model.

1. Introduction

Previous studies on the partial selfing model with selection provided conditions for the existence of a polymorphic equilibrium, without any real consideration about its stability (local or global). For example, Workman and Jain (1966) determined the values, at equilibrium, of the allelic frequencies and Wright's fixation index, for a locus with two alleles. Jain and Workman (1967) later defined a set of partial fixation indices in order to find the equilibrium genotypic frequencies for a locus with multiple alleles. Weir (1970) introduced a matrix method, based on the mean fitness of the population, that produces numerical values of these fixation indices and genotypic frequencies at equilibrium. He also determined a necessary condition for the existence of a polymorphic equilibrium. The stability of such an equilibrium was briefly considered.

Kimura and Ohta (1971) first treated the stability of the polymorphic equilibrium in the case of overdominant alleles for a locus with two alleles. They obtained

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a necessary condition on the parameters of the model for the existence of this equilibrium point and showed the uniqueness of this point when it exists. Next, assuming the existence of the polymorphic equilibrium, they examined its stability by investigating the local stability of both fixation states. But no local study of the polymorphic equilibrium itself, by considering changes in genotypic frequencies in the neighborhood of this point, was done.

Recently, Overath and Asmussen (1998) obtained some results when considering a more general model that includes apomixis which occurs with probability a (production of seeds without meiosis). Letting $a = 0$ in their equations leads to the conclusion that "... *at most one polymorphic equilibrium can exist for a given set of fitnesses and mating system parameters and that such equilibria exist only for overdominant and underdominant selection*." Also, they provided some analytical conditions for local stability of the polymorphic equilibrium, but were not able to assert the stability of this equilibrium point. They instead examined the local stability of the fixation states and the conditions that allow a protected polymorphism (PP), that is, when both fixation states are unstable. They established that "... *for overdominance a PP exists if and only if a valid internal equilibrium also exists ... for underdominance both of the boundary equilibria will always be stable whenever a polymorphic equilibrium exists and, therefore, a PP never exists under these conditions. Since two adjacent equilibria are unlikely to be both stable or both unstable, these results also suggest that (in the absence of cycling) overdominant polymorphic equilibria will be stable whenever they exist, while underdominant polymorphic equilibria will always be unstable*." In Section 4, we confirm their intuition by rigorously proving this last statement.

Assuming weak selection in the partial selfing model, Nagylaki (1997) presented a complete dynamical analysis for two alleles. Since weak selection represents a limit case of selection, we show in the Discussion section that the dynamical structure in this case can be deduced from that of the general model.

In this paper, we present the most complete analysis, up to now, on the one-locus two-allelle partial selfing selection model. In Sections 2 and 3, we examine all possible combinations of selective values and point out some exact conditions on the selfing rate under which a polymorphic equilibrium exists. Furthermore, we show that at most one polymorphic equilibrium exists in each case. In Section 4, we look at the local stability of this polymorphic equilibrium when it exists and then derive new results. In Section 5, we study local stability of both fixation states and thus complete earlier works done by Kimura and Ohta (1971). In particular, when the linear local analysis of the fixation state is inconclusive, we deduce new results by performing a quadratic analysis. In Section 6, some special cases are treated and global stability is proved. Finally, in Section 7, we summarize the results obtained in the preceding sections and compare them with those known under random mating. In this manner, we can describe the effects of selfing on a population that was previously practicing random mating. This can be the case for instance of a population subject to isolation. Table 2 of Section 7 is particularly useful in that, for a given set of selective values, one can completely determine the ultimate structure of the population for any value of the selfing rate.

2. Model

Consider a single locus with two alleles, say A_1 and A_2, in an infinite diploid population with non-overlapping generations. Each individual of the population can reproduce, either by selfing with constant probability $\beta (0 < \beta < 1)$, or by random outcrossing with the complementary probability $1 - \beta$. Let P_{11}, P_{12}, and P_{22} denote the frequencies of the genotypes A_1A_1, A_1A_2, and A_2A_2, respectively, in the population. Then the frequencies of the alleles A_1 and A_2 are

$$p = P_{11} + \tfrac{1}{2} P_{12} \quad \text{and} \quad q = P_{22} + \tfrac{1}{2} P_{12}.$$

Moreover, let the genotypes A_1A_1, A_1A_2, A_2A_2 have the corresponding selective values $w_{11}, w_{12}, w_{22} \geq 0$. Here, zygotic selection is applied through viability differences, that is, the genotypic selective parameters are proportional to the probabilities of survival from conception to maturity. It is assumed that the selective values are not all equal. Otherwise there will not be any selection. The case of a lethal homozygote ($w_{11} = 0$ or $w_{22} = 0$) and the case of a lethal heterozygote ($w_{12} = 0$) will be treated separately in Section 6. In the case of a non-lethal heterozygote ($w_{12} > 0$), we shall assume, without loss of generality, $w_{12} = 1$. Then, to simplify further the notation, it will be convenient to use the coefficients

$$a = 1 - w_{11} \quad \text{and} \quad b = 1 - w_{22}, \tag{1}$$

which cannot be both equal to 0 by assumption. There will be overdominance when $a, b > 0$, underdominance when $a, b < 0$, complete dominance when $a = 0$ or $b = 0$, and directional selection when $a > 0$ and $b < 0$ or $a < 0$ and $b > 0$. Symmetric selection will correspond to $a = b$. Note that we always have $a, b \leq 1$. The case $a = 1$ or $b = 1$ corresponds to the case of a lethal homozygote, which will be treated separately.

If P_{11}, P_{12}, and P_{22} designate the genotypic frequencies among the zygotes in the current generation at the time of conception, then the genotypic frequencies among the adults in the current generation, after selection but before mating, are

$$\begin{aligned}
P_{11}^* &= \frac{w_{11}\, P_{11}}{w_{11}\, P_{11} + P_{12} + w_{22}\, P_{22}}, \quad P_{12}^* = \frac{P_{12}}{w_{11}\, P_{11} + P_{12} + w_{22}\, P_{22}}, \\
P_{22}^* &= \frac{w_{22}\, P_{22}}{w_{11}\, P_{11} + P_{12} + w_{22}\, P_{22}}.
\end{aligned} \tag{2}$$

After mating and reproduction, the genotypic frequencies among the zygotes in the next generation are given by the equations

$$\begin{aligned}
P_{11}' &= \beta \left[P_{11}^* + \tfrac{1}{4} P_{12}^* \right] + (1 - \beta) \left[P_{11}^* + \tfrac{1}{2} P_{12}^* \right]^2, \\
P_{12}' &= \beta \left[\tfrac{1}{2} P_{12}^* \right] + 2(1 - \beta) \left[P_{11}^* + \tfrac{1}{2} P_{12}^* \right] \left[P_{22}^* + \tfrac{1}{2} P_{12}^* \right], \\
P_{22}' &= \beta \left[P_{22}^* + \tfrac{1}{4} P_{12}^* \right] + (1 - \beta) \left[P_{22}^* + \tfrac{1}{2} P_{12}^* \right]^2.
\end{aligned} \tag{3}$$

Here, we assume no fertility differences between the mating types, Mendelian segregation of genes and no gametic selection. It is useful to note that, under these assumptions, mating and reproduction do not change the allelic frequencies, that is,

$$p' = P'_{11} + \tfrac{1}{2}P'_{12} = P^*_{11} + \tfrac{1}{2}P^*_{12} = p^*,$$

and then

$$q' = 1 - p' = 1 - p^* = q^*.$$

Figure 1 below summarizes the life cycle of the population and the notation used for the genotypic and allelic frequencies. At each stage of the life cycle, the genotypic and allelic frequencies sum up to 1.

3. Equilibrium conditions

Apart from the fixation states ($P_{11} = 1$ and $P_{22} = 1$, which correspond to $q = 0$ and $p = 0$, respectively), there may exist polymorphic equilibria (at which $p, q \neq 0$). In order to determine the conditions for such equilibria, we use the fixation index F (Wright, 1951). The genotypic frequencies are written in the form

$$P_{11} = p^2 + pqF, \quad P_{12} = 2pq(1 - F), \quad P_{22} = q^2 + pqF, \tag{4}$$

where $-1 \leq F \leq 1$. The value of F varies from one generation to the next. Under the assumption $p, q \neq 0$, and using the equations (1) to (4), we have in the next generation

$$\begin{aligned} F' &= 1 - \frac{P'_{12}}{2p'q'} \\ &= \beta\left\{1 - \frac{(1-F)\left[1 - a\left(p^2 + pqF\right) - b\left(q^2 + pqF\right)\right]}{2\left[1 - a(p + qF)\right]\left[1 - b(q + pF)\right]}\right\}. \end{aligned} \tag{5}$$

At equilibrium, we must have $p' = p$. But, we have already noted that $p' = p^*$. Therefore, we have $p' = p$ if and only if

$$p^* = \frac{w_{11}P_{11} + \frac{1}{2}P_{12}}{w_{11}P_{11} + P_{12} + w_{22}P_{22}} = p,$$

which is equivalent, after algebraic manipulations using (4) and the assumption $p \neq 0, 1$, to

$$[a - (a + b)\,p]\,F = b - (a + b)\,p. \tag{6}$$

If

$$a - (a + b)\,p = 0,$$

then $p' = p \neq 0, 1$ if and only if

$$b - (a + b)\,p = 0,$$

which is compatible with the above condition if and only if $a = b$. On the other hand, if $a = b$, then we would have $F = 1$ at every polymorphic equilibrium where $p \neq \frac{1}{2}$. But then, owing to (5), we would have $F' = \beta < 1$, which contradicts equilibrium. Therefore, $\frac{1}{2}$ is the only admissible value for p at a polymorphic equilibrium in the case $a = b$. We have proved the following.

Result 1. *$\frac{a}{a+b}$ is an admissible value for p at a polymorphic equilibrium if and only if $a = b$. In this case, $\frac{1}{2}$ is the only admissible value for p at a polymorphic equilibrium.*

Let us assume $a \neq b$, and therefore

$$a - (a+b)\,p \neq 0 \quad \text{and} \quad F = \frac{b - (a+b)\,p}{a - (a+b)\,p}$$

at a polymorphic equilibrium. Then the equilibrium condition $F' = F$ with F' given by (5) becomes

$$G\,(p) = 0,$$

where

$$\begin{aligned} G\,(p) = {} & 2(a+b)(1-\beta)\,[a(1-b)+b(1-a)]\,p^2 \\ & + \{[a(1-b)+b(1-a)]\,[(3a+b)\,\beta - 2b] - 2a(a+b)(1-b)\}\,p \\ & +2ab(1-b) - \beta\,a\,[a(1-b)+b(1-a)]\,. \end{aligned} \tag{7}$$

The polynomial $G(p)$ is of the quadratic form $Ap^2 + Bp + C$ and admits two roots:

$$\hat{p}_- = \frac{-B - \sqrt{B^2 - 4AC}}{2A} \quad \text{and} \quad \hat{p}_+ = \frac{-B + \sqrt{B^2 - 4AC}}{2A},$$

where

$$\begin{aligned} A &= 2\,(a+b)\,(1-\beta)\,K, \\ B &= K\,[(3a+b)\,\beta - 2b] - 2a\,(a+b)\,(1-b)\,, \\ C &= 2ab\,(1-b) - \beta\,aK, \end{aligned} \tag{8}$$

with

$$K = a\,(1-b) + b\,(1-a)\,.$$

A priori, these two roots may correspond to polymorphic equilibria. But in order to be admissible, they must satisfy some constraints. Of course, the first one is $0 < \hat{p} < 1$, where $\hat{p}$ is a root of $G(p)$ and represents the frequency of allele A_1 at equilibrium. Then the frequency of allele A_2 at equilibrium satisfies $0 < \hat{q} = 1 - \hat{p} < 1$. The other constraints are

$$\hat{P}_{11} = \hat{p}^2 + \hat{p}\hat{q}\hat{F} \geq 0, \quad \hat{P}_{12} = 2\hat{p}\hat{q}\left(1 - \hat{F}\right) \geq 0, \quad \hat{P}_{22} = \hat{q}^2 + \hat{p}\hat{q}\hat{F} \geq 0,$$

where

$$\hat{F} = \frac{b - (a+b)\,\hat{p}}{a - (a+b)\,\hat{p}}, \tag{9}$$

which guarantee that the equilibrium genotypic frequencies are all non-negative, and then all less than or equal to one, since they sum up to one. This will be the case if and only if

$$-1 \leq \max\left(\frac{-\hat{p}}{\hat{q}}, \frac{-\hat{q}}{\hat{p}}\right) \leq \hat{F} \leq 1.$$

Therefore, $0 < \hat{p} < \frac{1}{2}$ will be admissible if and only if

$$-\frac{\hat{p}}{1-\hat{p}} \leq \frac{b-(a+b)\,\hat{p}}{a-(a+b)\,\hat{p}} \leq 1. \tag{10}$$

Workman and Jain (1966) have determined two conditions that must hold at equilibrium. It can be shown that equations (7) and (9) are in fact equivalent to these conditions.

Now, assuming

$$a-(a+b)\,\hat{p} > 0, \tag{11}$$

the right-hand side inequality in (10) will hold if and only if $a \geq b$, while we will have the left-hand side inequality in (10) if and only if $b\left(1-2\hat{p}\right) \geq 0$, that is, $b \geq 0$. Conversely, if $a \geq b \geq 0$, then $a+b > 0$, since by assumption a and b cannot be both equal to 0, and

$$\frac{a}{a+b} \geq \frac{1}{2},$$

which implies the inequality (11) under the constraint $\hat{p} < \frac{1}{2}$. Similarly, assuming

$$a-(a+b)\,\hat{p} < 0, \tag{12}$$

both inequalities in (10) are true if and only if $a \leq b \leq 0$, and this condition implies (12) under the constraint $\hat{p} < \frac{1}{2}$. The conditions for $\frac{1}{2} < \hat{p} < 1$ to be admissible are, by symmetry, $b \geq a \geq 0$ or $b \leq a \leq 0$. Finally, note that $\hat{p} = \frac{1}{2}$ would be admissible if and only if $a \geq b$ and $b \geq a$, that is, $a = b$. Therefore we have necessarily $\hat{p} \neq \frac{1}{2}$ in the case $a \neq b$. We conclude as follows.

Result 2. *A polymorphic equilibrium can exist only when a and b are of the same sign (*$a, b \geq 0$ *or* $a, b \leq 0$*) and the more frequent allele at a polymorphic equilibrium, when it exists, is necessarily the one associated with the parameter a or b closer to 0, that is, the one associated with the homozygote having the fitness closest to the heterozygote fitness. Equality of allelic frequencies at a polymorphic equilibrium is possible only in the case where the homozygotes have the same fitness (*$a = b$*).*

Note that this result on admissible allelic frequencies at a polymorphic equilibrium depends only on the fitness parameters. The proportion of selfing β is not involved. Moreover, this result excludes the possibility of a polymorphic equilibrium in the case of directional selection (a and b of opposite signs).

Now, let us look at the existence of a polymorphic equilibrium. Under the condition that a and b are of the same sign ($a, b \geq 0$ or $a, b \leq 0$) and not both equal to 0, the quadratic polynomial $G(p)$ is convex with respect to p, since the coefficient of p^2 (coefficient A in (8)) is then positive. Moreover, evaluating $G(p)$ at $p = \frac{1}{2}$ yields

$$G(\tfrac{1}{2}) = -\frac{(a-b)^2}{2} \leq 0,$$

with a strict inequality in the case $a \neq b$. Therefore the roots $\hat{p}_-$ and $\hat{p}_+$ of $G(p)$ are real and satisfy

$$\hat{p}_- \leq \tfrac{1}{2} \quad \text{and} \quad \hat{p}_+ \geq \tfrac{1}{2},$$

with strict inequalities in the case $a \neq b$. Finally, we have $\hat{p}_- > 0$ if and only if

$$G(0) = 2ab\,(1-b) - \beta\, aK > 0,$$

and $\hat{p}_+ < 1$ if and only if

$$G(1) = 2ab\,(1-a) - \beta\, bK > 0.$$

Let us look at all the cases.

- **Case of complete dominance (a = 0 or b = 0).** We have $G(0) \leq 0$ and $G(1) \leq 0$. Therefore we have $\hat{p}_- \leq 0$ and $\hat{p}_+ \geq 1$, which eliminates the possibility of a polymorphic equilibrium.
- **Case of overdominance or underdominance without symmetry.** Without loss of generality, relabelling the alleles if necessary, we may assume that the homozygote having the fitness closest to the heterozygote fitness is A_2A_2. Then we are in the case $0 < b < a$ or $a < b < 0$. In this case, we have $G(0) > 0$ if and only if

  $$\beta < \frac{2b\,(1-b)}{a\,(1-b) + b\,(1-a)} = \beta_0.$$

  This is the condition to have $0 < \hat{p}_- < \frac{1}{2}$, and therefore the existence of a polymorphic equilibrium, which is unique, with the frequency of allele A_1 given by $\hat{p}_-$ and the fixation index at equilibrium by equation (9). Note that the above condition is always satisfied when $\frac{1}{2} \leq b < a \leq 1$, since then $\beta_0 \geq 1$.
- **Case of symmetry (a = b).** At a polymorphic equilibrium, we must have $p = \frac{1}{2}$ (Result 1) and then the equilibrium condition $F' = F$ with F' given by (5) becomes

  $$aF^2 - [2 - a - \beta\,(1-a)]\,F + \beta\,(1-a) = 0,$$

  which admits a unique root F in the interval $(-1, 1)$ for $a \leq 1$ and $0 < \beta < 1$. This determines an admissible polymorphic equilibrium, which is unique. Note that $\beta_0 = 1$ in the case $a = b$.

In conclusion, we have:

Result 3. *There exists a polymorphic equilibrium only in the case of overdominance ($a, b > 0$) or underdominance ($a, b < 0$) when*

$$\beta < \frac{2b\,(1-b)}{a\,(1-b) + b\,(1-a)}, \quad \textit{if } a \leq b < 0 \textit{ or } 0 < b \leq a,$$

or

$$\beta < \frac{2a\,(1-a)}{a\,(1-b) + b\,(1-a)}, \quad \textit{if } b \leq a < 0 \textit{ or } 0 < a \leq b.$$

Moreover, a polymorphic equilibrium is unique when it exists.

Result 3 has been deduced recently by Overath and Asmussen (1998) in a model that also includes apomixis. Hence, we simply confirm the result obtained in their so-called “*standard mixed mating model without apomixis*”.

Table 1 summarizes the conditions for a unique polymorphic equilibrium to exist. In the case of symmetric selection ($a = b$), the allelic frequencies at the polymorphic equilibrium are always the same and equal to $\frac{1}{2}$ for $0 < \beta < 1$. It remains to study the change in the allelic frequencies at the polymorphic equilibrium, when it exists, in non-symmetric cases ($a \neq b$) with respect to a change in the proportion of selfing β.

At such an equilibrium, the frequency of allele A_1, denoted by $\hat{p}$, satisfies $G(\hat{p}) = 0$, where $G(p)$ is the polynomial given in (7). Taking the derivative with respect to β yields

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}\beta}G(\hat{p}) &= -2\,(a+b)\,K\hat{p}^2 + 4\,(a+b)\,(1-\beta)\,K\hat{p}\left(\frac{\mathrm{d}\hat{p}}{\mathrm{d}\beta}\right)\\ &\quad + (3a+b)\,K\hat{p} + B\left(\frac{\mathrm{d}\hat{p}}{\mathrm{d}\beta}\right) - aK = 0.\end{aligned}$$

This leads to the equation

$$\frac{\mathrm{d}\hat{p}}{\mathrm{d}\beta} = \frac{-K\left(1-2\hat{p}\right)\left[a-(a+b)\,\hat{p}\right]}{\sqrt{B^2-4AC}}.$$

This derivative of $\hat{p}$ with respect to β is negative when $a < b < 0$ or $0 < b < a$ and, by symmetry, positive when $b < a < 0$ or $0 < a < b$. Therefore we have proved the following result.

Result 4. *The frequency of the allele associated with the fittest homozygote, at the polymorphic equilibrium, when it exists, increases as β increases in the case of overdominance but decreases as β increases in the case of underdominance.*

In order to study the stability of the polymorphic equilibrium, we will consider first the cases of overdominance and underdominance without symmetry in Section 4. The special cases of dominance and symmetric selection will be studied apart in Section 6.

Table 1. Conditions for a (unique) polymorphic equilibrium to exist.

$a = b \neq 0$	$a < b < 0$ or $0 < b < a$	$b < a < 0$ or $0 < a < b$	All other cases
$\hat{p} = \frac{1}{2}$	$0 < \hat{p} < \frac{1}{2}$	$\frac{1}{2} < \hat{p} < 1$	No polym. equil.
$0 < \beta < 1$	$0 < \beta < \frac{2b(1-b)}{a(1-b)+b(1-a)}$ ($0 < \beta < 1$ in the particular case $\frac{1}{2} \leq b < a$)	$0 < \beta < \frac{2a(1-a)}{a(1-b)+b(1-a)}$ ($0 < \beta < 1$ in the particular case $\frac{1}{2} \leq a < b$)	$0 < \beta < 1$

4. Stability of polymorphic equilibria

In the preceding section, we have derived conditions for a polymorphic equilibrium to exist. In the present section, we look at conditions for local stability of such an equilibrium. In particular, Results 5 and 6 present results that, to our knowledge, have never been derived before. Suppose that a polymorphic equilibrium with $p = \hat{p}$ and $F = \hat{F}$ exists. As proposed by Weir (1970), we apply small perturbations on the values of p and F at equilibrium so that

$$\begin{aligned} p &= \hat{p} + \xi, \\ F &= \hat{F} + \eta, \end{aligned}$$

where ξ and η are small. In the next generation, using equations (2) and (4), we get

$$\begin{aligned} &p' = (\hat{p} + \xi) \\ &\times \left\{ \frac{1 - a\left[\hat{p} + \xi + (\hat{q} - \xi)\left(\hat{F} + \eta\right)\right]}{1 - a\left(\hat{p} + \xi\right)\left[\hat{p} + \xi + (\hat{q} - \xi)\left(\hat{F} + \eta\right)\right] - b\left(\hat{q} - \xi\right)\left[\hat{q} - \xi + (\hat{p} + \xi)\left(\hat{F} + \eta\right)\right]} \right\}. \end{aligned}$$

Neglecting terms in ξ^2, η^2 and $\xi\eta$, and using the identity $b\hat{q} + b\hat{p}\hat{F} = a\hat{p} + a\hat{q}\hat{F}$, derived from (6), lead to the linear approximation

$$p' \cong \hat{p} + \left[1 - \frac{\hat{p}\hat{q}(a+b)(1-\hat{F})}{1 - a(\hat{p} + \hat{q}\hat{F})}\right]\xi + \left[\frac{b\hat{p}^2\hat{q} - a\hat{p}\hat{q}^2}{1 - a(\hat{p} + \hat{q}\hat{F})}\right]\eta.$$

Similarly, from equation (5), we get after many simplifications the linear approximation

$$\begin{aligned} F' \cong \hat{F} &+ \beta \left\{ \frac{\left(1 - \hat{F}\right)^2 \left(b\hat{p} - a\hat{q}\right)}{2\left[1 - a\left(\hat{p} + \hat{q}\hat{F}\right)\right]^2} \right\} \xi \\ &+ \beta \left\{ \frac{1 - a\left(\hat{p} + \hat{q}\hat{F}\right) - \left(a\hat{q}^2 + b\hat{p}^2\right)\left(1 - \hat{F}\right)}{2\left[1 - a\left(\hat{p} + \hat{q}\hat{F}\right)\right]^2} \right\} \eta. \end{aligned}$$

Using again (6), we obtain the linear approximation

$$\begin{bmatrix} p' \\ F' \end{bmatrix} \cong \begin{bmatrix} \hat{p} \\ \hat{F} \end{bmatrix} + \mathbf{M} \begin{bmatrix} \xi \\ \eta \end{bmatrix},$$

where the entries of the matrix **M** take the form

$$\begin{aligned} m_{11} &= \frac{\hat{u}\left[1 - b - (a - b)\,\hat{p}\right]}{\hat{v}}, \quad m_{12} = \frac{-\hat{p}\left(1 - \hat{p}\right)\hat{u}^2}{\hat{v}}, \\ m_{21} &= -\frac{\beta\,(a - b)^2\,\hat{u}}{2\hat{v}^2}, \quad m_{22} = \frac{\beta}{2}\left(\frac{\hat{u}}{\hat{v}}\right)^2\left[1 - a + (a - b)\,\hat{p}\right], \end{aligned} \qquad (13)$$

with

$$\hat{u} = a - (a+b)\hat{p} \quad \text{and} \quad \hat{v} = a(1-b) - K\hat{p}.$$

It remains to analyse the eigenvalues of $\mathbf{M}$. We will consider separately the cases of overdominance and underdominance, without symmetry. The case of symmetric selection will be treated in a subsequent section.

4.1. *Case of overdominance without symmetry*

Let us assume, without loss of generality, $0 < b < a \leq 1$. In this case, a polymorphic equilibrium (with $0 < \hat{p} < \frac{1}{2}$) exists if and only if $0 < \beta < \min(\beta_0, 1)$, where

$$\beta_0 = \frac{2b\,(1-b)}{a\,(1-b) + b\,(1-a)}.$$

Let us first determine the signs of the entries m_{ij} of the matrix $\mathbf{M}$. To achieve this, we must find the signs of $\hat{u}$ and $\hat{v}$. We already know that $\hat{u} > 0$ in the case at hand (see (11) and Table 1). On the other hand, $\hat{v} > 0$ if and only if

$$\hat{p} < \frac{1}{1 + \frac{b(1-a)}{a(1-b)}}.$$

But, in the case at hand, this holds since

$$\hat{p} < \frac{1}{2} \quad \text{and} \quad 0 < \frac{b\,(1-a)}{a\,(1-b)} < 1.$$

Moreover, we have

$$1 - b - (a-b)\,\hat{p} \geq (a-b)\,\bigl(1 - \hat{p}\bigr) > 0$$

and

$$1 - a + (a-b)\,\hat{p} \geq (a-b)\,\hat{p} > 0.$$

Therefore, we have

$$m_{11} > 0, \quad m_{12} < 0, \quad m_{21} < 0, \quad m_{22} > 0.$$

Now, let us examine the eigenvalues of the matrix $\mathbf{M}$. The characteristic polynomial of $\mathbf{M}$ is

$$m(\lambda) = |\lambda\mathbf{I} - \mathbf{M}| = \lambda^2 - (m_{11} + m_{22})\lambda + m_{11}m_{22} - m_{12}m_{21}.$$

The polynomial $m(\lambda)$ is a convex parabola in λ, whose roots are distinct and real, since the discriminant $\Delta(m(\lambda))$ satisfies

$$\Delta(m(\lambda)) = (m_{11} - m_{22})^2 + 4m_{12}m_{21} > 0. \tag{14}$$

Note that these two roots are continuous with respect to β, and equal to 0 and $m_{11} > 0$ for $\beta = 0$. Moreover, $m_{11} < 1$ if and only if

$$(a^2 - b^2)\hat{p}(1 - \hat{p}) > 0,$$

which holds in the case at hand. Therefore, to show that the greatest eigenvalue of **M** in modulus is smaller than 1 in modulus, and consequently that the polymorphic equilibrium is locally stable, it suffices to show that $m(0) > 0$ and $m(1) > 0$, for $0 < \beta < \min(\beta_0, 1)$. In effect, by continuity of the roots of $m(\lambda)$, this condition implies that both roots lie in the interval (0, 1). Actually, we have

$$m(0) = \frac{\beta}{2}\left(\frac{\hat{u}}{\hat{v}}\right)^3 (1-a)\,(1-b) > 0,$$

and

$$m(1) = \frac{(a-b)\hat{p}(1-\hat{p})}{\hat{v}} H(\beta, \hat{p}), \tag{15}$$

where

$$H(\beta, p) = (a+b) - \frac{\beta K}{2}\left[\frac{a-(a+b)p}{a(1-b)-Kp}\right]^2.$$

It is shown in the Appendix that $H(\beta, \hat{p}) > 0$, and therefore that $m(1) > 0$, for $0 < \beta < \min(\beta_0, 1)$. Consequently, we have the following result.

Result 5. *In the case of overdominance without symmetry* ($0 < a < b$ *or* $0 < b < a$), *the polymorphic equilibrium is locally stable when it exists.*

4.2. *Case of underdominance without symmetry*

We assume, without loss of generality, $a < b < 0$. As before, we first look at the signs of the elements m_{ij} of the matrix **M**. To do so, we must determine the signs of $\hat{u}$ and $\hat{v}$. But $\hat{u} < 0$ owing to (12) and Table 1, while $\hat{v} < 0$ if and only if

$$\hat{p} < \frac{a(1-b)}{K},$$

where $K < 0$. But it is trivial to verify that

$$\frac{a\,(1-b)}{K} > \frac{1}{2}.$$

Since $\hat{p} < \frac{1}{2}$, we obtain that $\hat{v} < 0$. From that, it is easy to see that the elements m_{ij} of the matrix **M** satisfy

$$m_{11} > 0, \quad m_{12} > 0, \quad m_{21} > 0, \quad m_{22} > 0.$$

Moreover, we have as before $m_{11} < 1$.

Then, we look at the characteristic polynomial $m(\lambda)$ of **M**. Because equation (14) still holds in the case $a < b < 0$, we conclude that $m(\lambda)$ is a convex parabola whose roots are distinct and real. It is easy to check that (see Appendix for details)

$$m(0) > 0 \quad \text{and} \quad m(1) < 0.$$

For $0 < \beta < \min(\beta_0, 1)$, we deduce that the greatest root of $m(\lambda)$ in modulus, which corresponds to the greatest eigenvalue of **M** in modulus, is greater than 1 in modulus. Therefore, we have

Result 6. *In the case of underdominance without symmetry ($a < b < 0$ or $b < a < 0$), the polymorphic equilibrium is locally unstable when it exists.*

Note that Results 5 and 6 confirm what Overath and Asmussen (1998) had previously deduced intuitively in their study of a protected polymorphism.

5. Stability of the fixation states

We have determined so far the stability of the polymorphic equilibrium, when it exists, in the vicinity of this equilibrium point. However, outside the neighborhood of this point, this stable structure might not be preserved. Consequently, we must examine the stability of the two fixation states: if both fixation states are locally unstable, then the two alleles will be preserved in the population through subsequent generations, therefore maintaining the polymorphism in this population. To study the stability of the fixation states, we will use the same technique as for the stability analysis of the polymorphic equilibrium. We will evaluate the matrix of the linear approximations of the recursive equations (3) in the neighborhood of each fixation state. Then, we will determine if the modulus of the greatest eigenvalue of this matrix is greater or smaller than 1. In the following, we consider two cases: overdominance without symmetry and underdominance without symmetry. In Section 5.1, we confirm and complete the study previously performed by Kimura and Ohta (1971) and Overath and Asmussen (1998). Section 5.2 however provides new results, since Overath and Asmussen (1998) did not study local stability of the fixation states when no polymorphic equilibrium exists.

5.1. *Case of overdominance without symmetry*

We assume, without loss of generality, $0 < w_{11} < w_{22} < 1$. First, we develop the recursive equations near the fixation state of A_1, that is, when the genotypic frequencies are such that $P_{11} \cong 1$, $P_{12} \cong 0$ and $P_{22} \cong 0$. Using (2) and (3), one can easily obtain the linear approximation

$$\begin{bmatrix} P'_{12} \\ P'_{22} \end{bmatrix} \cong \begin{bmatrix} \frac{2-\beta}{2w_{11}} & \frac{2(1-\beta)w_{22}}{w_{11}} \\ \frac{\beta}{4w_{11}} & \frac{\beta\, w_{22}}{w_{11}} \end{bmatrix} \begin{bmatrix} P_{12} \\ P_{22} \end{bmatrix}.$$

The matrix above will be denoted by $\mathbf{L}_1$. For $0 < \beta < 1$, it is clear that all the entries of $\mathbf{L}_1$ are strictly positive. The characteristic polynomial of $\mathbf{L}_1$ is

$$m_1(\lambda) = |\lambda \mathbf{I} - \mathbf{L}_1| = \lambda^2 - \left(\frac{2\beta\, w_{22} + 2 - \beta}{2w_{11}}\right)\lambda + \frac{\beta\, w_{22}}{2w_{11}^2}. \tag{15}$$

This polynomial is a convex parabola in λ, which admits two distinct real roots since its discriminant satisfies

$$\Delta\,(m_1(\lambda)) = \frac{1}{4w_{11}^2}\{[2\beta\, w_{22} - (2-\beta)]^2 + 8\beta(1-\beta)w_{22}\} > 0. \tag{16}$$

To determine whether the greatest eigenvalue of $\mathbf{L}_1$ in absolute value is smaller or greater than 1 in absolute value, we evaluate $m_1(\lambda)$ and the derivative of $m_1(\lambda)$, which is

$$\dot{m}_1(\lambda) = 2\lambda - \left(\frac{2\beta\, w_{22} + 2 - \beta}{2w_{11}}\right),$$

at $\lambda = 0$ and $\lambda = 1$. One can trivially verify that

$$m_1(0) = \frac{\beta\, w_{22}}{2w_{11}^2} > 0 \quad \text{and} \quad \dot{m}_1(0) = -\frac{2\beta\, w_{22} + 2 - \beta}{2w_{11}} < 0. \tag{17}$$

By convexity of $m_1(\lambda)$, we deduce that both eigenvalues of $\mathbf{L}_1$ are strictly positive. We also have

$$m_1(1) = \frac{1}{2w_{11}^2}\{-2w_{11}(1 - w_{11}) + \beta[w_{11}\,(1 - w_{22}) + w_{22}(1 - w_{11})]\} \tag{18}$$

and

$$\dot{m}_1(1) = \frac{1}{2w_{11}}\left[\beta\,(1 - 2w_{22}) - 2\,(1 - 2w_{11})\right]. \tag{19}$$

For further investigation, we subdivide the general case $0 < w_{11} < w_{22} < 1$ into two cases: $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$ and $\frac{1}{2} \leq w_{11} < w_{22} < 1$. In both cases however, we will show that the greatest eigenvalue of $\mathbf{L}_1$ is greater than 1.

First, in both cases, it is clear that $m_1(1) < 0$ if and only if

$$\beta < \frac{2w_{11}\,(1 - w_{11})}{w_{11}\,(1 - w_{22}) + w_{22}\,(1 - w_{11})} = \beta_1. \tag{20}$$

Note that $\beta_1 > 0$, and $\beta_1 < 1$ if and only if $w_{11} < \frac{1}{2}$. Hence, in the case $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$, we have $0 < \beta_1 < 1$ whereas, in the case $\frac{1}{2} \leq w_{11} < w_{22} < 1$, we have that $\beta_1 \geq 1$ and consequently $m_1(1) < 0$. In the latter case, regardless of the sign of $\dot{m}_1(1)$, this suffices to assert that the greatest eigenvalue of $\mathbf{L}_1$ is greater than 1. In the former case however, we must examine the sign of $\dot{m}_1(1)$.

In the case $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$, when $\min(\frac{1}{2}, w_{22}) = w_{22}$, it is readily seen by (19) that $\dot{m}_1(1) < 0$ if and only if

$$\beta < \frac{2\,(1 - 2w_{11})}{1 - 2w_{22}} = \beta_2. \tag{21}$$

But, in this restricted case, it is easy to observe that $\beta_2 > 2$, thus leading to the conclusion that $\dot{m}_1(1) < 0$. When $w_{22} = \frac{1}{2}$ or $\min(\frac{1}{2}, w_{22}) = \frac{1}{2}$, we reach the same conclusion directly from (19). Therefore, whatever the sign of $m_1(1)$ is, we deduce that the greatest eigenvalue of $\mathbf{L}_1$ is greater than 1 in the case $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$.

Result 7. *In the case of overdominance without symmetry, the fixation of the less fit homozygote is locally unstable for* $0 < \beta < 1$.

Next, we examine the recursive equations near the fixation state of A_2, that is, when the genotypic frequencies are such that $P_{11} \cong 0$, $P_{12} \cong 0$ and $P_{22} \cong 1$. By the symmetry of equations (3), the following linear approximation is easily obtained:

$$\begin{bmatrix} P'_{11} \\ P'_{12} \end{bmatrix} \cong \begin{bmatrix} \frac{\beta\, w_{11}}{w_{22}} & \frac{\beta}{4w_{22}} \\ \frac{2(1-\beta) w_{11}}{w_{22}} & \frac{2-\beta}{2w_{22}} \end{bmatrix} \begin{bmatrix} P_{11} \\ P_{12} \end{bmatrix}.$$

The matrix $\mathbf{L}_2$ of linear approximation is formed of strictly positive entries for $0 < \beta < 1$. By interchanging w_{11} and w_{22} in (15), we find that the characteristic polynomial of $\mathbf{L}_2$ is

$$m_2(\lambda) = \lambda^2 - \left(\frac{2\beta\, w_{11} + 2 - \beta}{2w_{22}} \right) \lambda + \frac{\beta\, w_{11}}{2w_{22}^2}. \tag{22}$$

Again, the polynomial $m_2(\lambda)$ is a convex parabola in λ, which admits two distinct real roots since its discriminant is strictly positive. In a direct manner, one can verify that

$$m_2(0) > 0 \quad \text{and} \quad \dot{m}_2(0) < 0,$$

and therefore deduce, by convexity of $m_2(\lambda)$, that both eigenvalues of $\mathbf{L}_2$ are strictly positive. Also, we easily compute that

$$m_2(1) = \frac{1}{2w_{22}^2} \left\{ -2w_{22}\,(1 - w_{22}) + \beta \left[w_{11}\,(1 - w_{22}) + w_{22}\,(1 - w_{11}) \right] \right\} \tag{23}$$

and

$$\dot{m}_2(1) = \frac{1}{2w_{22}} \left[\beta\,(1 - 2w_{11}) - 2\,(1 - 2w_{22}) \right]. \tag{24}$$

At this point, we subdivide the general case $0 < w_{11} < w_{22} < 1$ into two cases: $0 < w_{11} < w_{22} \le \frac{1}{2}$ and $0 < \max(\frac{1}{2}, w_{11}) < w_{22} < 1$, since they provide different results.

From equation (23), it is trivial to verify that $m_2(1) < 0$ if and only if

$$\beta < \frac{2w_{22}\,(1 - w_{22})}{w_{11}\,(1 - w_{22}) + w_{22}\,(1 - w_{11})} = \beta_0. \tag{25}$$

In Section 3, we have outlined that $0 < \beta_2 < 1$ if and only if $w_{22} > \frac{1}{2}$. Hence, in the case $0 < w_{11} < w_{22} \le \frac{1}{2}$, we have $\beta_2 \ge 1$ and consequently $m_2(1) < 0$. Regardless of the sign of $\dot{m}_2(1)$, this suffices to ensure that the greatest eigenvalue of $\mathbf{L}_2$ is greater than 1 in this case. Note that a polymorphic equilibrium always exists in this case (see Table 1).

In the case $0 < \max(\frac{1}{2}, w_{11}) < w_{22} < 1$, it becomes necessary to look at the value of $\dot{m}_2(1)$. From equation (24), when $\max(\frac{1}{2}, w_{11}) = w_{11}$, we obtain that $\dot{m}_2(1) > 0$ if and only if

$$\beta < \frac{2\,(1 - 2w_{22})}{1 - 2w_{11}} = \beta_3. \tag{26}$$

But one can easily show that $\beta_3 > 2$, and then conclude that $\dot{m}_2(1) > 0$ in this specific case. When $w_{11} = \frac{1}{2}$ or $\max(\frac{1}{2}, w_{11}) = \frac{1}{2}$, the same conclusion arises directly from (24). Therefore, in the case $0 < \max(\frac{1}{2}, w_{11}) < w_{22} < 1$, three situations may occur with respect to condition (25):

(i) If $\beta < \beta_0$, then $m_2(1) < 0$ and consequently the greatest eigenvalue of $\mathbf{L}_2$ is greater than 1.
(ii) If $\beta > \beta_0$, then $m_2(1) > 0$ and consequently the greatest eigenvalue of $\mathbf{L}_2$ is smaller than 1.
(iii) If $\beta = \beta_0$, then $m_2(1) = 0$ and consequently the greatest eigenvalue of $\mathbf{L}_2$ is equal to 1. This situation requires a more refined analysis of the recursive equations (3). This analysis is performed in the Appendix.

Note that a polymorphic equilibrium exists if and only if $\beta < \beta_0$ (see Table 1). We summarize our conclusions in the result below.

Result 8. *In the case of overdominance without symmetry, the fixation of the fittest homozygote is locally unstable when a polymorphic equilibrium exists and locally stable otherwise,even in a degenerate case corresponding to a critical value for β.*

5.2. *Case of underdominance without symmetry*

We assume, without loss of generality, $1 < w_{22} < w_{11}$. The analysis of this case proceeds almost the same way as in the case $0 < w_{11} < w_{22} < 1$. Near the fixation state of A_1, we have deduced earlier the matrix of linear approximation $\mathbf{L}_1$ and its characteristic polynomial $m_1(\lambda)$ given by equation (15). Since (16) and (17) still hold, we infer that both eigenvalues of $\mathbf{L}_1$ are strictly positive. Next, by (18), we have that $m_1(1) > 0$ if and only if the inequality in (20) is verified, i.e. when $\beta < \beta_1$. Similarly to the case $0 < w_{11} < w_{22} < 1$, it is trivial to show that $\beta_1 > 1$, and therefore to conclude that $m_1(1) > 0$. In addition, by (19), we have that $\dot{m}_1(1) > 0$ if and only if the inequality in (21) is verified, i.e. when $\beta < \beta_2$. But, it is readily seen that $\beta_2 > 2$, which allows us to conclude that $\dot{m}_1(1) > 0$. Hence, we can assert that the greatest eigenvalue of $\mathbf{L}_1$ is smaller than 1. This leads to the result below.

Result 9. *In the case of underdominance without symmetry, the fixation of the fittest homozygote is locally stable for* $0 < \beta < 1$.

We finish this section by examining the recursive equations near the fixation state of A_2. We have previously determined the matrix of the linear approximation $\mathbf{L}_2$ and its characteristic polynomial $m_2(\lambda)$ given by (22). One can deduce that both eigenvalues of $\mathbf{L}_2$ are strictly positive. Next, by (23), we have that $m_2(1) > 0$ if and only if the inequality in (25) is verified, i.e. when $\beta < \beta_0$. In the case $w_{11} > w_{22} > 1$, we have shown that $0 < \beta_0 < 1$. Also, by (24), we have that $\dot{m}_2(1) > 0$ if and only if the inequality in (26) is verified, i.e. when $\beta < \beta_3$. Therefore, three situations may occur:

(i) If $\beta < \beta_0$, then $m_2(1) > 0$. Besides, it is easy to show that $\beta_0 < \beta_3$. Hence, we have that $\dot{m}_2(1) > 0$ and consequently that the greatest eigenvalue of $\mathbf{L}_2$ is smaller than 1.

(ii) If $\beta > \beta_0$, then $m_2(1) < 0$. Consequently, whatever the sign of $\dot{m}_2(1)$ is, the greatest eigenvalue of $\mathbf{L}_2$ is always greater than 1.

(iii) If $\beta = \beta_0$, then $m_2(1) = 0$. Consequently, the greatest eigenvalue of $\mathbf{L}_2$ is equal to 1. This represents a degenerate case which requires a more refined analysis (see Appendix).

Result 10. *In the case of underdominance without symmetry, the fixation of the less fit homozygote is locally stable when a polymorphic equilibrium exists and locally unstable otherwise, even in a degenerate case corresponding to a critical value for* β.

6. Special cases

We conclude this exhaustive study of the partial selfing selection model by considering special combinations of selective values, for which the treatment will differ from those used in the preceding sections. In fact, for some special cases, global convergence can be obtained, thus providing new interesting results.

6.1. Case of directional selection

We assume, without loss of generality, $0 < w_{11} < 1 < w_{22}$. We have shown in Section 3 that there exists no polymorphic equilibrium in this case. The only remaining equilibria are the fixation states of A_1 and A_2, respectively $p = 1$ and $p = 0$. We will show that there is global convergence to the fixation of A_2, if both alleles are initially present in the population.

We have derived earlier that $p' = p^*$. Using equations (2), it is readily verified that $p' \leq p$ if and only if

$$\left(w_{11}P_{11} + \tfrac{1}{2}P_{12}\right)\left(\tfrac{1}{2}P_{12} + P_{22}\right) \leq \left(P_{11} + \tfrac{1}{2}P_{12}\right)\left(\tfrac{1}{2}P_{12} + w_{22}P_{22}\right),$$

for $w_{11} < 1$ and $1 < w_{22}$. Moreover, if $P_{11} + \frac{1}{2}P_{12} = p \neq 0$ and $\frac{1}{2}P_{12} + P_{22} = 1 - p \neq 0$, then we have equality above if and only if $w_{11}P_{11} + \frac{1}{2}P_{12} = P_{11} + \frac{1}{2}P_{12}$ and $\frac{1}{2}P_{12} + P_{22} = \frac{1}{2}P_{12} + w_{22}P_{22}$, that is, if and only if $P_{12} = 1$, which implies that $p = \frac{1}{2}$. But, as shown in the Appendix, the state $P_{12} = 1$ cannot be an accumulation point of the iterates of the recursive equations (3) and furthermore cannot be maintained from one generation to the next. Therefore, p decreases to 0 from every state for which $p \neq 1$. We refer the reader to the Appendix for a rigorous proof.

Result 11. *In the case of directional selection, there is global convergence to the fixation of the fittest homozygote for* $0 < \beta < 1$.

6.2. Case of complete dominance

As a special case of directional selection, we consider complete dominance. We assume, without loss of generality, $w_{11} = w_{12} = 1$. After some manipulations, one can get

$$\Delta p = p' - p = \left[\frac{(1 - w_{22})(1 - P_{11} - P_{12})}{(1 - w_{22})(P_{11} + P_{12}) + w_{22}}\right] p.$$

At equilibrium, we must have $\Delta p = 0$. This equality is satisfied if and only if $p = 0$ or $P_{11} + P_{12} = 1$. The first solution corresponds to the fixation of A_2 whereas the second solution cannot be a set of accumulation points of the iterates of the recursive equations (3) except for $P_{11} = 1$, which corresponds to the fixation of A_1. The latter assertion is proved in the Appendix.

The sign of Δp is completely determined by the sign of the function

$$g(x) = \frac{(1 - w_{22})\,(1 - x)}{(1 - w_{22})\,x + w_{22}},$$

where $x = P_{11} + P_{12}$. To analyse this function, we evaluate its derivative, which is

$$\dot{g}(x) = \frac{-\,(1 - w_{22})}{[(1 - w_{22})\,x + w_{22}]^2}.$$

In the following, we distinguish two cases:

- **Case of a deleterious recessive allele ($w_{22} < 1$).** First, we have that $g(0) = (1 - w_{22})\big/w_{22} > 0$ and $g(1) = 0$. For $0 < x < 1$, the derivative of $g(x)$ is strictly negative and then $g(x)$ is strictly decreasing on this interval. This implies that Δp is strictly positive, so p increases from one generation to the next. In fact, unless $p = 0$ or $p = 1$, p increases to 1, that is, the system globally converges to the fixation of A_1.
- **Case of a deleterious dominant allele ($w_{22} > 1$).** In this case, we have that $g(0) < 0$ and $g(1) = 0$. For $0 < x < 1$, the derivative of $g(x)$ is strictly positive and then $g(x)$ is strictly increasing on this interval. This implies that Δp is strictly negative, so p decreases from one generation to the next. Unless $p = 0$ or $p = 1$, p decreases to 0, that is, the system globally converges to the fixation of A_2.

Result 12. *In the case of complete dominance, there is global convergence to the fixation of the fittest homozygote, for all* $0 < \beta < 1$.

6.3. *Case of symmetric selection*

We assume $w_{11} = w_{22} = w \neq 0, 1$. In this symmetric case, we have shown that there exists a unique polymorphic equilibrium with $\hat{p} = \hat{q} = \frac{1}{2}$. Using equations (3), it is easy to show that $P'_{11} - P'_{22} = P^*_{11} - P^*_{22}$. Therefore, we have

$$\left|P'_{11} - P'_{22}\right| = \left[\frac{w}{(w - 1)\,(P_{11} + P_{22}) + 1}\right] |P_{11} - P_{22}|\,.$$

To obtain $\left|P'_{11} - P'_{22}\right| = |P_{11} - P_{22}|$, either $P_{11} = P_{22}$ or $P_{11} \neq P_{22}$, and then

$$\frac{w}{(w - 1)\,(P_{11} + P_{22}) + 1} = 1,$$

which is possible if and only if $P_{11} + P_{22} = 1$. But this last equality can be maintained only at the fixation states ($P_{11} = 1$ for the fixation of A_1 and $P_{22} = 1$ for the fixation of A_2). Elsewhere, the states for which $P_{11} + P_{22} = 1$ cannot represent a set of accumulation points of the iterates of the recursive equations (3). This can be ascertained from Result A provided in the Appendix.

Next we examine the function

$$f(x) = \frac{w}{(w-1)\,x+1},$$

where $x = P_{11} + P_{22}$, in order to exhibit the general behavior of the system at hand. We need the derivative of $f(x)$ with respect to x, which is simply

$$\dot{f}(x) = -\frac{w\,(w-1)}{[(w-1)\,x+1]^2}.$$

In the following, we must consider the two cases $w < 1$ and $w > 1$ separately.

- **Case of symmetric overdominance ($w < 1$).** In this case, $\dot{f}(x) > 0$ for every x on the interval [0, 1], thus ensuring that the function $f(x)$ is strictly increasing on this interval. We also have that $0 < w = f(0) < f(x) < f(1) = 1$ for $0 < x < 1$. Hence, we conclude that $|P_{11} - P_{22}|$ decreases to 0, unless $P_{11} = 1$ or $P_{22} = 1$, and consequently that there is convergence to the manifold $P_{11} = P_{22}$. Next, we verify that there is convergence to the polymorphic equilibrium on the manifold $P_{11} = P_{22}$. To this end, we shall employ the transformation equation, from one generation to the next, for the frequency of the genotype A_1A_1. Letting $P_{11} = P_{22}$ in equations (3), one obtains

  $$P'_{11} = \frac{1}{4} + \frac{\beta}{2}\left(\frac{w P_{11}}{1-2\,(1-w)\,P_{11}}\right).$$

  We note that $P'_{11} = \frac{1}{4}$, when $P_{11} = 0$, and $P'_{11} = \frac{1}{4} + \frac{\beta}{4}$, when $P_{11} = \frac{1}{2}$. The derivative of P'_{11} with respect to P_{11} is such that

  $$\frac{\mathrm{d}}{\mathrm{d}P_{11}} P'_{11} = \frac{\beta}{2}\left\{\frac{w}{[1-2\,(1-w)\,P_{11}]^2}\right\} > 0,$$

  for $0 \le P_{11} \le \frac{1}{2}$. The second derivative of P'_{11} being also strictly positive, we deduce that P'_{11} is strictly increasing and convex, for $0 \le P_{11} \le \frac{1}{2}$. Therefore, the frequency P_{11} converges to the value $\hat{P}_{11}$, which satisfies $\hat{P}'_{11} = \hat{P}_{11}$ and $0 < \hat{P}_{11} < \frac{1}{2}$, and is given by

  $$\hat{P}_{11} = \frac{3 - w\,(1+\beta) - \sqrt{[3 - w\,(1+\beta)]^2 - 8\,(1-w)}}{8\,(1-w)},$$

  that is, there is convergence to the polymorphic equilibrium on the manifold $P_{11} = P_{22}$. A more rigourous proof of global convergence is presented in the Appendix.

Result 13. *In the case of symmetric overdominance, there is global convergence to the polymorphic equilibrium, for all* $0 < \beta < 1$.

- **Case of symmetric underdominance ($w > 1$).** In this case, $\dot{f}(x) < 0$ for every x on the interval [0, 1], thus ensuring that the function $f(x)$ is strictly decreasing on this interval. We also have that $w = f(0) > f(x) > f(1) = 1$, for $0 < x < 1$. Hence, we conclude that $|P_{11} - P_{22}|$ increases to 1, if $P_{11} \neq P_{22}$ initially. This implies convergence to one of the fixation states, $P_{11} = 1$ or $P_{22} = 1$. If $P_{11} > P_{22}$ initially, then the system will converge to the fixation of A_1 whereas, if $P_{11} < P_{22}$ initially, then the system will converge to the fixation of A_2, since these inequalities are always preserved afterwards. Consequently, the polymorphic equilibrium is unstable. However, there will be convergence to the polymorphic equilibrium on the manifold $P_{11} = P_{22}$, because the results previously outlined in the case $w < 1$ remain valid except that the function P'_{11} is now concave, for $0 \leq P_{11} \leq \frac{1}{2}$.

Result 14. *In the case of symmetric underdominance, the polymorphic equilibrium is unstable and both fixation states are stable, for all* $0 < \beta < 1$.

6.4. *Case of a lethal homozygote*

We assume, without loss of generality, $w_{11} = 0$. The gene A_1 is lethal when homozygote, that is, an individual who carries the genotype A_1A_1 does not survive prior to mating and reproduction, and thus does not contribute any zygote to the next generation. We shall consider the genotype frequencies of the adults from one generation to the next (for better understanding, see equations (2), (3) and Figure 1):

$$\begin{aligned}
P^{*'}_{11} &= \frac{w_{11}P'_{11}}{w_{11}P'_{11} + P'_{12} + w_{22}P'_{22}} = 0,\\
P^{*'}_{12} &= \frac{P'_{12}}{w_{11}P'_{11} + P'_{12} + w_{22}P'_{22}} = \frac{P'_{12}}{P'_{12} + w_{22}P'_{22}},\\
P^{*'}_{22} &= \frac{w_{22}P'_{22}}{w_{11}P'_{11} + P'_{12} + w_{22}P'_{22}} = \frac{w_{22}P'_{22}}{P'_{12} + w_{22}P'_{22}}.
\end{aligned}$$

Observing that $P^*_{12} = 1 - P^*_{22}$ after the very first generation, one obtains that

$$P^{*'}_{22} = \frac{w_{22}\left[1 + (2+\beta)\,P^*_{22} + (1-\beta)\,P^{*^2}_{22}\right]}{2\left(1 - P^*_{22}\right)\left[1 + (1-\beta)\,P^*_{22}\right] + w_{22}\left[1 + (2+\beta)\,P^*_{22} + (1-\beta)\,P^{*^2}_{22}\right]}. \tag{27}$$

Letting $P^{*'}_{22} = P^*_{22}$ in (27) provides a non-trivial value for P^*_{22} at equilibrium, which is given by

$$\hat{P}^*_{22} = \frac{-[2\,(1-w_{22}) - \beta\, w_{22}] + \sqrt{[2\,(1-w_{22}) - \beta\, w_{22}]^2 + 4w_{22}\,(2 - w_{22})\,(1-\beta)}}{2\,(2 - w_{22})\,(1-\beta)}.$$

This value enables us to determine the value of p at the polymorphic equilibrium (when it exists), which is simply

$$\hat{p} = \hat{P}_{11}^{*} + \tfrac{1}{2}\hat{P}_{12}^{*} = \tfrac{1}{2}\left(1 - \hat{P}_{22}^{*}\right).$$

One can verify that, when $w_{22} \leq \frac{1}{2}$, there exists a polymorphic equilibrium for all $0 < \beta < 1$, whereas when $\frac{1}{2} < w_{22} < 1$, there exists a polymorphic equilibrium if and only if $\beta < 2\,(1 - w_{22}) = \beta_0$. This is effectively the value of β_0 encountered previously, whose term w_{11} equals 0. Note that these results are consistent with Result 3.

To study the stability of the equilibrium points, we will utilize the recursive equation of P_{22}^{*}, as given in (27). Generally, the derivative of this equation, calculated at these equilibrium points, suffices to indicate the stability of such points. If the derivative is smaller than 1 in absolute value, then the equilibrium point is stable whereas if it is greater than 1, then the equilibrium point is unstable. If the derivative is equal to 1 in absolute value, we must look at the second derivative of the recursive equation at this point.

After some tedious algebraic manipulations, we find that the first derivative of equation (27) is given by

$$\begin{aligned}&\frac{\mathrm{d}}{\mathrm{d}P_{22}^{*}} P_{22}^{*'}\\ &= \frac{4w_{22}\left[1 + \beta + 2\,(1-\beta)\,P_{22}^{*} + (1-\beta)\,P_{22}^{*^2}\right]}{\left\{2\left(1 - P_{22}^{*}\right)\left[1 + (1-\beta)\,P_{22}^{*}\right] + w_{22}\left[1 + (2+\beta)\,P_{22}^{*} + (1-\beta)\,P_{22}^{*^2}\right]\right\}^2} > 0,\end{aligned}$$

for $0 \leq P_{22}^{*} \leq 1$ and $0 < \beta < 1$. Thus, $P_{22}^{*'}$ is strictly increasing as a function of P_{22}^{*} on the interval [0, 1]. Moreover, one can easily compute

$$\left.\frac{\mathrm{d}}{\mathrm{d}P_{22}^{*}} P_{22}^{*'}\right|_{P_{22}^{*}=0} = \frac{4w_{22}\,(1+\beta)}{(2 + w_{22})^2} \quad \text{and} \quad \left.\frac{\mathrm{d}}{\mathrm{d}P_{22}^{*}} P_{22}^{*'}\right|_{P_{22}^{*}=1} = \frac{2-\beta}{2w_{22}}.$$

It is easy to show that the derivative at $P_{22}^{*} = 0$ is always smaller than 1, whereas the derivative at $P_{22}^{*} = 1$ is smaller than 1 if and only if $\beta > 2(1 - w_{22}) = \beta_0$.

When $w_{22} > 1$, no polymorphic equilibrium exists. In addition, we observe that $P_{22}^{*'} = w_{22}\big/(2 + w_{22}) > 0$ at $P_{22}^{*} = 0$. Since the derivative of $P_{22}^{*'}$ evaluated at $P_{22}^{*} = 1$ is smaller than 1 for $w_{22} > 1$, we deduce that, unless $P_{22}^{*} = 1$, there is global convergence to $P_{22}^{*} = 1$ or equivalently, to the fixation of A_2. The same arguments remain valid when $w_{22} = 1$ and also when $w_{22} < 1$, but only if $\beta \geq \beta_0$, since no polymorphic equilibrium exists for these specific values of β.

However, when $\beta < \beta_0$, a polymorphic equilibrium exists. Because the derivative of $P_{22}^{*'}$ at $P_{22}^{*} = 1$ is greater than 1, the fixation of A_2 is now unstable. Also, since $P_{22}^{*'} = w_{22}\big/(2 + w_{22}) > 0$ at $P_{22}^{*} = 0$ and $P_{22}^{*'}$ is strictly increasing on [0, 1], the derivative of $P_{22}^{*'}$ calculated at $P_{22}^{*} = \hat{P}_{22}^{*}$ must be assumed smaller than 1. This enables us to assert global convergence to the polymorphic equilibrium in this case.

Result 15. *In the case of a lethal homozygote, there is global convergence to the polymorphic equilibrium, when it exists,or to the fixation of the other homozygote, when no polymorphic equilibrium exists.*

6.5. *Case of a lethal heterozygote*

This time, an individual who carries the heterozygote genotype A_1A_2 does not survive prior to mating and reproduction. Note that this case is a special case of underdominance. We assume, without loss of generality, $w_{12} = 0 < w_{22} < w_{11}$. Similarly to the previous case, we consider the genotype frequencies of the adults from one generation to the next. These frequencies are expressed as:

$$P_{11}^{*'} = \frac{w_{11} P_{11}'}{w_{11} P_{11}' + w_{22} P_{22}'}, \quad P_{12}^{*'} = 0, \quad P_{22}^{*'} = \frac{w_{22} P_{22}'}{w_{11} P_{11}' + w_{22} P_{22}'}.$$

Noting that $P_{22}^* = 1 - P_{11}^*$ after the first generation, one can write

$$P_{11}^{*'} = \frac{w_{11} P_{11}^* \left[\beta + (1-\beta)\, P_{11}^*\right]}{w_{11} P_{11}^* \left[\beta + (1-\beta)\, P_{11}^*\right] + w_{22} \left(1 - P_{11}^*\right) \left[\beta + (1-\beta) \left(1 - P_{11}^*\right)\right]}. \tag{28}$$

Letting $P_{11}^{*'} = P_{11}^*$ in (28) provides a non-trivial solution for the polymorphic equilibrium, that is, with $0 < P_{11}^* < 1$, if and only if $\beta < \beta_0 = w_{22} / w_{11}$. Thus, at the polymorphic equilibrium, we have

$$\hat{P}_{11}^* = \frac{w_{22} - \beta\, w_{11}}{(1-\beta)\,(w_{11} + w_{22})},$$

and the frequency of A_1 is given by

$$\hat{p} = \hat{P}_{11}^* + \tfrac{1}{2} \hat{P}_{12}^* = \hat{P}_{11}^* = \frac{w_{22} - \beta\, w_{11}}{(1-\beta)\,(w_{11} + w_{22})}.$$

To study the stability of the equilibrium points, we evaluate the derivative of the recursive equation of P_{11}^*, as expressed in (28). Simple calculations yield

$$\frac{\mathrm{d}}{\mathrm{d}P_{11}^*} P_{11}^{*'} = \frac{w_{11} w_{22} \left[\beta + 2\,(1-\beta)\, P_{11}^* \left(1 - P_{11}^*\right)\right]}{\left\{w_{11} P_{11}^* \left[\beta + (1-\beta)\, P_{11}^*\right] + w_{22} \left(1 - P_{11}^*\right) \left[\beta + (1-\beta) \left(1 - P_{11}^*\right)\right]\right\}^2} > 0,$$

for $0 \le P_{11}^* \le 1$ and $0 < \beta < 1$. Hence, the recursive equation (28) is strictly increasing for P_{11}^* on the interval [0, 1]. We easily compute

$$\left.\frac{\mathrm{d}}{\mathrm{d}P_{11}^*} P_{11}^{*'}\right|_{P_{11}^*=0} = \frac{\beta\, w_{11}}{w_{22}} \quad \text{and} \quad \left.\frac{\mathrm{d}}{\mathrm{d}P_{11}^*} P_{11}^{*'}\right|_{P_{11}^*=1} = \frac{\beta\, w_{22}}{w_{11}}.$$

The derivative at $P_{11}^* = 0$ is smaller than 1 if and only if $\beta < \beta_0$, whereas the derivative at $P_{11}^* = 1$ is always smaller than 1. Therefore, the fixation of A_1 is always stable.

When $\beta < \beta_0$, a polymorphic equilibrium exists and, since the derivative of $P_{11}^{*'}$ at $P_{11}^* = 0$ is smaller than 1, the fixation of A_2 is stable. Because the fixation of A_1 is always stable and $P_{11}^{*'}$ is strictly increasing on [0, 1], the derivative of $P_{11}^{*'}$ at $P_{11}^* = \hat{P}_{11}^*$ must be greater than 1 and consequently the polymorphic equilibrium is unstable. If $P_{11}^* > \hat{P}_{11}^*$ initially, then the system converges to the fixation of A_1, unless $P_{11}^* = 1$. If $P_{11}^* < \hat{P}_{11}^*$ initially, then the system converges to the fixation of A_2, unless $P_{11}^* = 0$.

When $\beta \geq \beta_0$, no polymorphic equilibrium exists. In addition, since the derivative of $P_{11}^{*'}$ at $P_{11}^* = 0$ is greater than or equal to 1 in this case, the fixation of A_2 is now unstable. Also, from the fact that $P_{11}^{*'}$ is strictly increasing on [0, 1] and that the fixation of A_1 is stable, we deduce that there must be global convergence to the fixation of A_1, unless $P_{11}^* = 0$ or $P_{11}^* = 1$.

Finally, when $w_{11} = w_{22}$, the value of $\hat{P}_{11}^*$ at the polymorphic equilibrium equals $\frac{1}{2}$. The derivative of $P_{11}^{*'}$ evaluated respectively at $P_{11}^* = 0$ and $P_{11}^* = 1$ equals β, thus ensuring that it is smaller than 1. Consequently, the fixation states are stable and the polymorphic equilibrium unstable, for $0 < \beta < 1$.

Result 16. *In the case of a lethal heterozygote, the polymorphic equilibrium is unstable, when it exists, and both fixation states are stable; otherwise, when no polymorphic equilibrium exists, there is global convergence to the fittest homozygote.*

7. Discussion

Table 2 summarizes the results derived in the present paper as well as the results for the panmictic model ($\beta = 0$), in order to perform a comparison with the partial selfing model. In this table, we assume that

$$\beta_0 = \frac{2w_{22}\left(w_{12} - w_{22}\right)}{w_{22}\left(w_{12} - w_{11}\right) + w_{11}\left(w_{12} - w_{22}\right)}, \tag{31}$$

$p^{(0)}$ designates the initial frequency of allele A_1 in the population, and $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ designates the respective frequencies of allele A_1 and A_2 at the polymorphic equilibrium under the panmictic model, where

$$\hat{p}_{\mathrm{R}} = \frac{w_{22} - w_{12}}{w_{11} - 2w_{12} + w_{22}} \quad \text{and} \quad \hat{q}_{\mathrm{R}} = 1 - \hat{p}_{\mathrm{R}} = \frac{w_{11} - w_{12}}{w_{11} - 2w_{12} + w_{22}}.$$

Under the partial selfing model, $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ designates the respective frequencies of allele A_1 and A_2 at the polymorphic equilibrium

$$\hat{p}_{\mathrm{PS}} = \frac{-B - \sqrt{B^2 - 4AC}}{2A} \quad \text{and} \quad \hat{q}_{\mathrm{PS}} = 1 - \hat{p}_{\mathrm{PS}} = \frac{2A + B + \sqrt{B^2 - 4AC}}{2A},$$

where

$$\begin{aligned} A &= 2\left(1 - \beta\right)\left(2w_{12} - w_{11} - w_{22}\right)\left[w_{22}\left(w_{12} - w_{11}\right) + w_{11}\left(w_{12} - w_{22}\right)\right], \\ B &= \left[w_{22}\left(w_{12} - w_{11}\right) + w_{11}\left(w_{12} - w_{22}\right)\right] \end{aligned}$$

Table 2. Comparative results under the panmictic model and the partial selfing model.

Selective values	Panmixia ($\beta = 0$)	Partial selfing
Overdominance $0 < w_{11} < w_{22} \leq \frac{w_{12}}{2}$	Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ Fixation of A_1 unstable Fixation of A_2 unstable	$0 < \beta < 1$ Polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ locally stable Fixation of A_1 locally unstable Fixation of A_2 locally unstable
Overdominance $0 = w_{11} < w_{22} \leq \frac{w_{12}}{2}$	Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ Fixation of A_1 unstable Fixation of A_2 unstable	$0 < \beta < 1$ Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ Fixation of A_1 unstable Fixation of A_2 unstable
Overdominance $0 < \max(w_{11}, \frac{w_{12}}{2}) < w_{22} < w_{12}$	Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ Fixation of A_1 unstable Fixation of A_2 unstable	$0 < \beta < \beta_0$ Polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ locally stable Fixation of A_1 locally unstable Fixation of A_2 locally unstable
		$\beta_0 \leq \beta < 1$ No polymorphic equilibrium Fixation of A_1 locally unstable Fixation of A_2 locally stable
Overdominance $0 = w_{11} < \frac{w_{12}}{2} < w_{22} < w_{12}$	Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ Fixation of A_1 unstable Fixation of A_2 unstable	$0 < \beta < \beta_0$ Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ Fixation of A_1 unstable Fixation of A_2 unstable
		$\beta_0 \leq \beta < 1$ No polymorphic equilibrium Fixation of A_1 unstable Global convergence to fixation of A_2
Overdominance $0 < w_{11} = w_{22} < w_{12}$	Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ Fixation of A_1 unstable Fixation of A_2 unstable	$0 < \beta < 1$ Global convergence to polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ Fixation of A_1 unstable Fixation of A_2 unstable
Underdominance $0 < w_{12} < w_{22} < w_{11}$	Polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ unstable If $p^{(0)} > \hat{p}_{\mathrm{R}}$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_{\mathrm{R}}$, then convergence to fixation of A_2	$0 < \beta < \beta_0$ Polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ locally unstable Fixation of A_1 locally stable Fixation of A_2 locally stable
		$\beta_0 \leq \beta < 1$ No polymorphic equilibrium Fixation of A_1 locally stable Fixation of A_2 locally unstable

Table 2. (continued)

Selective values	Panmixia ($\beta = 0$)	Partial selfing
Underdominance		$0 < \beta < \beta_0$
$0 = w_{12} < w_{22} < w_{11}$	Polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ unstable If $p^{(0)} > \hat{p}_{\mathrm{R}}$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_{\mathrm{R}}$, then convergence to fixation of A_2	Polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ unstable If $p^{(0)} > \hat{p}_{\mathrm{PS}}$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_{\mathrm{PS}}$, then convergence to fixation of A_2
		$\beta_0 \leq \beta < 1$ No polymorphic equilibrium Global convergence to fixation of A_1 Fixation of A_2 unstable
Underdominance		$0 < \beta < 1$
$0 \leq w_{12} < w_{11} = w_{22}$	Polymorphic equilibrium $(\hat{p}_{\mathrm{R}}, \hat{q}_{\mathrm{R}})$ unstable If $p^{(0)} > \hat{p}_{\mathrm{R}}$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_{\mathrm{R}}$, then convergence to fixation of A_2	Polymorphic equilibrium $(\hat{p}_{\mathrm{PS}}, \hat{q}_{\mathrm{PS}})$ unstable If $p^{(0)} > \hat{p}_{\mathrm{PS}}$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_{\mathrm{PS}}$, then convergence to fixation of A_2
Directional		$0 < \beta < 1$
$0 < w_{11} \leq w_{12} < w_{22}$ or	No polymorphic equilibrium	No polymorphic equilibrium
$0 < w_{11} < w_{12} \leq w_{22}$ or	Fixation of A_1 unstable	Fixation of A_1 unstable
$0 = w_{11} < w_{12} \leq w_{22}$	Global convergence to fixation of A_2	Global convergence to fixation of A_2

$$\begin{aligned}
&\times\ [(2-\beta)(w_{22}-w_{12}) - 3\beta(w_{11}-w_{12})] \\
&- 2w_{22}(w_{12}-w_{11})(2w_{12}-w_{11}-w_{22}), \\
C =\ & 2w_{22}(w_{12}-w_{11})(w_{12}-w_{22}) - \beta(w_{12}-w_{11}) \\
&\times [w_{22}(w_{12}-w_{11}) + w_{11}(w_{12}-w_{22})].
\end{aligned}$$

The comparison between the panmictic model and the partial selfing model has some interesting implications. In effect, a population under random mating at a given locus that suddenly practices partial selfing in some proportion β would undergo important changes in its genic structure and its genetic variability. This explains why our main attention will purposely be turned to those cases that guarantee the preservation of both genes A_1 and A_2 in the population.

A first look at Table 2 suggests but does not prove that polymorphism in the population can be maintained only in the overdominant case, and this in both models. For the panmictic model, there is global convergence to the polymorphic equilibrium. For the partial selfing model, however, we know only that a protected polymorphism exists, with both fixation states unstable, whenever a stable polymorphic equilibrium exists and vice versa.

On the one hand, when the heterozygote is strongly favored compared with the homozygotes ($0 < w_{11} < w_{22} \leq w_{12}/2$), referred by Overath and Asmussen (1998) as "*double overdominance*", introduction of selfing does not modify the polymorphic structure of the population even if one of the genes is lethal for a homozygote. On the other hand, when the selective values of the homozygotes tend to be closer to that of the heterozygote ($0 < \max(w_{11}, w_{12}/2) < w_{22} < w_{12}$), referred by Overath and Asmussen (1998) as "*simple overdominance*", the polymorphism is preserved under the sole condition that the proportion β of selfing is not too large ($\beta < \beta_0$). A larger proportion will break the polymorphic structure of the population. Table 2 then shows what Overath and Asmussen (1998) hypothesized as "*...when any self-fertilization occurs, simple overdominant selection may not be sufficient to maintain both alleles in the population*." In case of equality of the selective values of the homozygotes, there is global convergence to the polymorphic equilibrium, regardless of the value of β. This seems intuitively sound because of the symmetry of the recursive equations in this case.

In every other sets of selective values but the overdominant case, it appears impossible for a polymorphism to be maintained in the population. For instance, when one of the genes is completely dominant ($0 < w_{11} = w_{12} < w_{22}$ or $0 < w_{22} < w_{11} = w_{12}$), selection will determine the ultimate structure of the population. In the former case, there will be eventual extinction of the gene A_1, whereas in the latter case, there will be eventual extinction of the gene A_2. These results remain valid in both models. These features were "predictable", since the case of a gene completely dominant is a particular case of directional selection.

As deduced by Overath and Asmussen (1998), the partial selfing model has the same general equilibrium structure as the random mating model. They conclude as follows: "*... (1) at most one polymorphic equilibrium exists; (2) a polymorphic equilibrium exists only with overdominance or underdominance; (3) a stable polymorphic equilibrium exists only when selection is overdominant; and (4) a protected polymorphism, with both fixation states unstable, exists whenever a stable internal equilibrium exists and vice versa*." We rigorously proved all four results above. Furthermore, we have deduced some important qualitative features of the partial selfing model. In most cases, when the proportion β is not too large, it is essentially selection that will determine the ultimate genetic structure and, if it is possible, the preservation of the polymorphism in the population. When this proportion gets larger, no polymorphic equilibrium exists. Selfing is thus mostly responsible for compromising a possible polymorphism in the population. In fact, the partial selfing model with selection produces a struggle between two forces, selection on the one hand and selfing on the other.

Finally, it should be noted that Nagylaki (1997) has provided a complete analysis of the partial selfing model with weak selection. As expected, our results on the dynamical structure of the strong-selection model agree with those obtained under weak selection. However, Nagylaki's treatment differs greatly from ours, since his differential equation is "*... the weak-selection limit of the discrete selection model with constant inbreeding coefficient* ..." Thus, the dynamical analysis of the model is reduced to the study of a one-dimensional differential equation for the allelic frequencies. Following his notation, substituting $w_{ij} = 1 + \lambda u_{ij}$ in β_0 given in equation (31) and then letting λ tend to 0, one can show that

$$\tilde{\beta} = \frac{2\,(w_{12} - w_{22})}{(w_{12} - w_{11}) + (w_{12} - w_{22})}$$

is the limit, as λ goes to 0, of β_0. The value $\tilde{\beta}$ can be obtained from a detailed analysis of the four cases described in Nagylaki (1997). In the case of overdominance, it can be shown that β_0 monotonically decreases to $\tilde{\beta}$. This implies that strong selection is more favorable than weak selection for the preservation of a polymorphism. This can be explained by the fact that strong selection can produce a wider range of selective values than weak selection. Further, note that neither underdominance nor directional weak selection can maintain polymorphism in the population.

8. Summary

We have shown that a polymorphic equilibrium can exist only in the case of overdominance or underdominance and for a certain range of selfing rates (see Table 1). The existence of a polymorphic equilibrium in the case of directional selection is thus precluded. Moreover, a polymorphic equilibrium is unique when it exists. The results above have been first outlined by Kimura and Ohta (1971) in the case of overdominance only, and by Overath and Asmussen (1998) in their study of the partial selfing selection model with apomixis, and have been rigorously proved in the present paper. Also, the most frequent allele at a polymorphic equilibrium is the one associated with the homozygote that has the fitness closest to that of the heterozygote. Equal allelic frequencies at a polymorphic equilibrium appear only when the homozygotes have the same fitness. These new results have also been mathematically proved in this paper.

An analysis of local stability at the polymorphic equilibrium has also been conducted in this paper and has produced new results. In the case of overdominance, the polymorphic equilibrium is locally stable when it exists. In the case of underdominance, it is locally unstable when it exists. An analysis of local stability at the fixation states has confirmed results already known for the partial selfing model (Kimura and Ohta, 1971, Overath and Asmussen, 1998). We took this analysis a step further by carrying out a quadratic analysis in the degenerate case, that is, when the leading eigenvalue of the matrix of the linear approximation is equal to one, by applying a criterion due to Lessard and Karlin (1982). The local analysis outlined the fact that a protected polymorphism can only exist in the case of overdominance.

Finally, we have considered some special sets of selective values for which we can prove global convergence. In the case of directional selection and in the case of dominance, we showed that there is global convergence to the fixation of the fittest homozygote. In the case of symmetric overdominance, there is global convergence to the polymorphic equilibrium, whereas in the case of symmetric underdominance, both fixation states are stable and the polymorphic equilibrium is unstable. In the case of a lethal homozygote, there is global convergence to the polymorphic equilibrium when it exists, or to the fixation of the other homozygote when no polymorphic equilibrium exists. In the case of a lethal heterozygote, the polymorphic equilibrium is unstable when it exists and both fixation states are stable. Otherwise, when no polymorphic equilibrium exists, there is global convergence to the fixation of the fittest homozygote. These new results of global convergence represent one of our major contributions to the study of the partial selfing selection model. Some of these results about the dynamical structure of the model have also been derived by Nagylaki (1997) for weak selection. However, since weak selection is a limiting case of selection, our results on strong selection provide a wider applicability.

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Appendix

A.1. Proof of Result 5

We show that $H(\beta, \hat{p})$ is strictly positive. We have to consider separately the cases $0 < b < \min(\frac{1}{2}, a) < 1$ and $\frac{1}{2} \leq b < a < 1$. In the case $0 < b < \min(\frac{1}{2}, a) < 1$, we have exhibited (see Result 3) the condition $0 < \beta < \beta_0$ for the existence of a polymorphic equilibrium $(\hat{p}, \hat{F})$, where $0 < \hat{p} < \frac{1}{2}$. We first examine the limiting values $\beta = 0$ and $\beta = \beta_0$. When $\beta = 0$, random mating prevails in the population. Results for this model are well known in population genetics (see, e.g., Jacquard, 1974) and in particular, for $0 < b < a < 1$, it is known that there exists a unique polymorphic equilibrium with the frequency of A_1 given by $\hat{p}_{\mathrm{R}} = b\big/(a+b) < \frac{1}{2}$ (this result could have also been obtained by letting $\beta = 0$ in equation (7)). For these specific values of β and p, we have

$$H\left(0, \hat{p}_{\mathrm{R}}\right) = a + b > 0, \tag{A.1}$$

When $\beta = \beta_0$, we have (see Section 3) $\hat{p}_- = 0$, i.e. the polymorphic equilibrium degenerates to the fixation of A_2. These values of β and p yield

$$H(\beta_0, 0) = \left(\frac{1}{1-b}\right)[a(1-b) - b^2] > 0. \tag{A.2}$$

We also find that

$$H(0, 0) = a + b > 0 \tag{A.3}$$

and

$$H\left(\beta_0, \hat{p}_{\mathrm{R}}\right) = \left[\frac{a+b}{(a+b-ab)^2}\right]\left\{(a+b)\left[(a-b)(1-b) + b(1-a)\right] + a^2b^2\right\} > 0. \tag{A.4}$$

In addition, the partial derivatives with respect to β and p satisfy

$$\frac{\partial}{\partial\beta} H(\beta, p) = -\frac{K}{2}\left[\frac{a - (a+b)p}{a(1-b) - Kp}\right]^2 < 0 \tag{A.5}$$

and

$$\frac{\partial}{\partial p} H\left(\beta, p\right) = \frac{\beta\, Kab\left(a-b\right)\left[a-\left(a+b\right)p\right]}{\left[a\left(1-b\right)-Kp\right]^3} > 0,$$

for β in the open interval $(0, \beta_0)$ and p in the open interval $(0, \hat{p}_{\mathrm{R}})$. We conclude that the function $H(\beta, p)$ is strictly positive in the whole rectangle $[0, \beta_0] \times [0, \hat{p}_{\mathrm{R}}]$, since it is strictly positive at the four corners, monotonically decreasing with respect to β and monotonically increasing with respect to p.

In the case $\frac{1}{2} \leq b < a < 1$, we have shown that there exists a unique polymorphic equilibrium $(\hat{p}, \hat{F})$, where $0 < \hat{p} < \frac{1}{2}$, for all $0 < \beta < 1$. We first look at the limiting values $\beta = 0$ and $\beta = 1$. When $\beta = 0$, (A.1) remains valid. When $\beta = 1$, the population reproduces by complete selfing. The expression for $\hat{p}$ at the polymorphic equilibrium is obtained by letting $\beta = 1$ in equation (7). This expression is given by

$$\hat{p}_{\mathrm{S}} = \frac{a\left(2b-1\right)}{a\left(2b-1\right)+b\left(2a-1\right)}.$$

One can easily verify that $0 < \hat{p}_{\mathrm{S}} < \hat{p}_{\mathrm{R}} < \frac{1}{2}$. Then, we have

$$H\left(1, \hat{p}_{\mathrm{S}}\right) = a\left(2b-1\right)+b\left(2a-1\right) > 0.$$

Moreover, one can calculate and observe that

$$H(0, \hat{p}_{\mathrm{S}}) = a+b > 0 \quad \text{and} \quad H(1, \hat{p}_{\mathrm{R}}) = \left(\frac{a+b}{2}\right)\left[1+\frac{a^2b^2}{(a+b-ab)^2}\right] > 0.$$

Also, the sign of the partial derivatives of $H(\beta, p)$, given in (A.5), remains unchanged for β in the open interval $(0, 1)$ and p in the open interval $(\hat{p}_{\mathrm{S}}, \hat{p}_{\mathrm{R}})$. Hence, using arguments as above, we conclude that the function $H(\beta, p)$ is strictly positive in the whole rectangle $[0, 1] \times [\hat{p}_{\mathrm{S}}, \hat{p}_{\mathrm{R}}]$.

A.2. Proof of Result 6

We show that $m(1) < 0$ in the case $a < b < 0$. As observed in equation (15), the sign of $m(1)$ is the same as that of $H(\beta, \hat{p})$. We have determined earlier (see Result 3) the condition $0 < \beta < \beta_0$ that allows for the existence of a polymorphic equilibrium $(\hat{p}, \hat{F})$, where $0 < \hat{p} < \frac{1}{2}$. Using (A.1) to (A.4), one can trivially obtain that

$$H\left(0, 0\right) < 0, \quad H\left(0, \hat{p}_{\mathrm{R}}\right) < 0, \quad H\left(\beta_0, 0\right) < 0, \quad H\left(\beta_0, \hat{p}_{\mathrm{R}}\right) < 0.$$

It is also easy to verify that the partial derivatives of $H(\beta, p)$, given in (A.5), are both strictly positive for β in the open interval $(0, \beta_0)$ and p in the open interval $(0, \hat{p}_{\mathrm{R}})$. Therefore, we conclude that the function $H(\beta, p)$ is strictly negative in the whole rectangle $[0, \beta_0] \times [0, \hat{p}_{\mathrm{R}}]$ and consequently that $m(1) < 0$.

A.3. *Proof of Result 8*

In the degenerate case $\beta = \beta_0$, the greatest eigenvalue of $\mathbf{L}_2$ equals 1. Lessard and Karlin (1982) exhibited a general criterion for stability-instability at fixation states when the greatest eigenvalue of the matrix of the linear approximation is one. Using their notation, we let the vector $\underline{\mathbf{x}} = (x_1, x_2) = (P_{11}, P_{12})$ be such that $\underline{\mathbf{0}} = (0, 0)$ corresponds to the fixation event (F) of A_2. Let $T\underline{\mathbf{x}} = \big(U_1(\underline{\mathbf{x}}), U_2(\underline{\mathbf{x}})\big) = (P'_{11}, P'_{12})$, where T is the transformation defined by the recursive equations (3). We have that $T(\underline{\mathbf{x}}) = \underline{\mathbf{0}}$ if and only if $\underline{\mathbf{x}} = \underline{\mathbf{0}}$ and T is smooth enough in the neighborhood of $\underline{\mathbf{0}}$.

The matrix $\mathbf{L}_2$ is an irreducible aperiodic nonnegative matrix. Hence, by the theorem of Perron-Frobenius, the components of the left and right eigenvectors, $\underline{\boldsymbol{\xi}}$ and $\underline{\boldsymbol{\eta}}$, of $\mathbf{L}_2$ corresponding to the eigenvalue one are strictly positive:

$$\underline{\boldsymbol{\xi}}\mathbf{L}_2 = \underline{\boldsymbol{\xi}} = (\xi_1, \xi_2) > \underline{\mathbf{0}} \quad \text{and} \quad \mathbf{L}_2\underline{\boldsymbol{\eta}} = \underline{\boldsymbol{\eta}} = (\eta_1, \eta_2) > \underline{\mathbf{0}}.$$

Without loss of generality, we assume $\langle\langle \underline{\boldsymbol{\xi}}, \underline{\boldsymbol{\eta}} \rangle\rangle = \sum_{j=1}^{2} \xi_j \eta_j = 1$. Then we define the quantity $\mathrm{S} = \langle\langle \underline{\boldsymbol{\xi}}, \underline{\boldsymbol{\theta}} \rangle\rangle$ as the inner product of the vectors $\underline{\boldsymbol{\xi}}$ and $\underline{\boldsymbol{\theta}} = (\theta_1, \theta_2)$, where

$$\theta_i = \sum_{\lambda,\mu=1}^{2} \frac{\partial^2 U_i(\underline{\mathbf{0}})}{\partial x_\lambda \partial x_\mu} \eta_\lambda \eta_\mu, \quad \text{for} \quad i = 1, 2.$$

The general criterion for stability-instability stipulates that the fixation event F is stable if $\mathrm{S} < 0$ and unstable if $\mathrm{S} > 0$.

Now, let $b = 1 - w_{22}$, $c = 2w_{22} - 1$ and $d = w_{22} - w_{11}$. Note that $b, c, d > 0$ in the case at hand. The matrix of the linear approximation is

$$\mathbf{L}_2 = \frac{1}{K} \begin{bmatrix} 2w_{11}b & \frac{b}{2} \\ \frac{2w_{11}cd}{w_{22}} & \frac{w_{11}b + w_{22}d}{w_{22}} \end{bmatrix}.$$

The eigenvalues of $\mathbf{L}_2$ are

$$\lambda_1 = 1 > \lambda_2 = \frac{w_{11}b}{w_{22}K} > 0.$$

The left and right eigenvectors of $\mathbf{L}_2$ corresponding to the eigenvalue one are

$$\underline{\boldsymbol{\xi}} = \left(\frac{2w_{11}c}{w_{22}}, 1\right) > 0 \quad \text{and} \quad \underline{\boldsymbol{\eta}} = \left(\frac{b}{2d}, 1\right) > 0.$$

After some rather tedious calculations, we find that

$$\frac{\partial^2 U_1(\underline{\mathbf{0}})}{\partial x_1^2} = \frac{2w_{11}d}{w_{22}^2 K}\left(w_{11}c + 2w_{22}b\right),$$

$$\frac{\partial^2 U_2(\underline{\mathbf{0}})}{\partial x_1^2} = \frac{4w_{11}\left(d - w_{11}\right)cd}{w_{22}^2 K},$$

$$\begin{aligned}
\frac{\partial^2 U_1(\underline{\mathbf{0}})}{\partial x_1 \partial x_2} &= \frac{1}{w_{22}^2 K}\left[w_{11}cd - 2w_{22}b\left(w_{11}b - \tfrac{1}{4}d\right)\right],\\
\frac{\partial^2 U_2(\underline{\mathbf{0}})}{\partial x_1 \partial x_2} &= \frac{d}{w_{22}^2 K}\left[w_{22}b - c\left(3w_{11} - w_{11}c - d\right)\right],\\
\frac{\partial^2 U_1(\underline{\mathbf{0}})}{\partial x_2^2} &= \frac{1}{2w_{22}^2 K}\left(cd - 2w_{22}b^2\right),\\
\frac{\partial^2 U_2(\underline{\mathbf{0}})}{\partial\, x_2^2} &= \frac{-1}{w_{22}^2 K}\left[2w_{22}b^2 + (1+2b)\,cd\right].
\end{aligned}$$

With some algebra, one finally obtains

$$\mathrm{S} = \frac{K\left[b^2 - w_{22}\left(1 - w_{11}\right)\right]}{w_{22}^2 d\langle\langle \underline{\boldsymbol{\xi}}, \underline{\boldsymbol{\eta}}\rangle\rangle}. \tag{A.6}$$

In the case at hand, it is trivial to show that $\mathrm{S} < 0$ and consequently that the fixation of A_2 is stable.

A.4. Proof of Result 10

This proof is very similar to the above proof of Result 8. In this case, however, we have $b, d < 0$ and $c > 0$. Equation (A.6) clearly shows that $\mathrm{S} > 0$, and consequently that the fixation of A_2 is unstable.

A.5. Proof of Result 11

We first present an interesting result which will be useful in the subsequent proofs.

Let K be a compact set of $\Re^n$ and let T: $K \to K$ be a continuous function. Let $v : \Re^n \to \Re$ be a continuous function such that $v(T\underline{\mathbf{x}}) \leq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$. We define the sequence $\left\{T^n\underline{\mathbf{x}}\right\}_{n\geq 0}$ for every $\underline{\mathbf{x}} \in K$. By the compactness of K, v is bounded below and therefore the sequence $\{v(T^n\underline{\mathbf{x}})\}_{n\geq 0}$ converges, that is

$$\lim_{n\to\infty} v(T^n\underline{\mathbf{x}}) = \hat{v}.$$

Let $\hat{\underline{\mathbf{x}}}$ be an accumulation point of $\{T^n\underline{\mathbf{x}}\}_{n\geq 0}$. Then there exists a subsequence $\{T^{n_k}\underline{\mathbf{x}}\}_{k\geq 0}$ which converges to $\hat{\underline{\mathbf{x}}}$, that is

$$\lim_{k\to\infty} \{T^{n_k}\underline{\mathbf{x}}\} = \hat{\underline{\mathbf{x}}}.$$

Then, the following inequalities hold:

$$v(T^{n_{k+1}}\underline{\mathbf{x}}) \leq v(T^{n_k+1}\underline{\mathbf{x}}) \leq v(T^{n_k}\underline{\mathbf{x}}).$$

By the continuity of v,

$$\lim_{k\to\infty} v(T^{n_{k+1}}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T^{n_k}\underline{\mathbf{x}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}.$$

Also, by the continuity of v and T,

$$\lim_{k\to\infty} v(T^{n_k+1}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T \circ T^{n_k}\underline{\mathbf{x}}) = v(T\hat{\underline{\mathbf{x}}}).$$

Hence, we conclude that

$$v(T\hat{\underline{\mathbf{x}}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}.$$

More generally, for every $l \geq 1$, we obtain the following inequalities:

$$v(T^{n_{k+l}}\underline{\mathbf{x}}) \leq v(T^{n_k+l}\underline{\mathbf{x}}) \leq v(T^{n_k}\underline{\mathbf{x}}).$$

Using the same arguments as before, we obtain

$$\lim_{k\to\infty} v(T^{n_{k+l}}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T^{n_k}\underline{\mathbf{x}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}$$

and also

$$\lim_{k\to\infty} v(T^{n_k+l}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T^l \circ T^{n_k}\underline{\mathbf{x}}) = v(T^l\hat{\underline{\mathbf{x}}}).$$

Hence, for every $l \geq 1$, we conclude that

$$v(T^l\hat{\underline{\mathbf{x}}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}.$$

Result A. *Every accumulation point of* $\{T^n\underline{\mathbf{x}}\}_{n\geq 0}$ *must be invariant with respect to* v.

Note that this result remains valid for a continuous function v such that $v(T\underline{\mathbf{x}}) \geq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$.

We shall now demonstrate hereupon that the state for which $P_{12} = 1$ cannot be a point of accumulation of the iterates of the transformation T defined by the recursive equations (3) from any starting point $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$ in the case of directional selection ($0 < W_{11} < 1 < W_{22}$). Let $v(\underline{\mathbf{x}}) = p = P_{11} + \frac{1}{2}P_{12}$, for every $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$. Apply the transformation T to $\hat{\underline{\mathbf{x}}} = (0, 1, 0)$, which corresponds to $P_{12} = 1$. Trivial computations give $T\hat{\underline{\mathbf{x}}} = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ and $v(T\hat{\underline{\mathbf{x}}}) = \frac{1}{2}$. Applying once again the transformation T, one obtains that

$$v(T^2\hat{\underline{\mathbf{x}}}) = \frac{\frac{1}{4}w_{11} + \frac{1}{4}}{\frac{1}{4}w_{11} + \frac{1}{2} + \frac{1}{4}w_{22}} < \frac{1}{2}.$$

But this contradicts Result A above.

A.6. Proof of Result 12

We demonstrate that the states for which $P_{11} + P_{12} = 1$, with $P_{11} \neq 0, 1$, cannot represent a set of accumulation points of the iterates of the recursive equations (3) from any starting point $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$ in the case of complete dominance ($W_{11} = W_{12} = 1$). Let $v(\underline{\mathbf{x}}) = p = P_{11} + \frac{1}{2}P_{12}$ and $\hat{\underline{\mathbf{x}}} = (P_{11}, 1 - P_{11}, 0)$. Then, applying the transformation T to $\hat{\underline{\mathbf{x}}}$, one easily obtains $v(T\hat{\underline{\mathbf{x}}}) = P_{11} + \frac{1}{2}(1 - P_{11})$. Applying once again the transformation T, one calculates that

$$v(T^2\hat{\underline{\mathbf{x}}}) = \frac{P_{11} + \frac{1}{2}(1 - P_{11})}{1 - \frac{1}{4}(1 - w_{22})(1 - P_{11})[1 - (1 - \beta)P_{11}]} \neq v(\hat{\underline{\mathbf{x}}}),$$

thus contradicting Result A.

A.7. Proof of Results 13 and 14

First, for any value $w \neq 0, 1$, we demonstrate that the states for which $P_{11} + P_{22} = 1$, with $P_{11} \neq 0, \frac{1}{2}$ or 1, cannot represent a set of accumulation points of the iterates of the recursive equations (3) from any starting point $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$ in the case of symmetric selection ($W_{11} = W_{22} = W \neq 0$ and 1). Let $v(\underline{\mathbf{x}}) = |P_{11} - P_{22}|$ and $\hat{\underline{\mathbf{x}}} = (P_{11}, 0, 1 - P_{11})$. Applying the transformation T to $\hat{\underline{\mathbf{x}}}$, one easily obtains $v(T\hat{\underline{\mathbf{x}}}) = |2P_{11} - 1|$. Applying once again the transformation T, one can calculate that

$$v(T^2\hat{\underline{\mathbf{x}}}) = \left[\frac{w}{w + 2(1-w)(1-\beta)P_{11}(1-P_{11})}\right]|2P_{11} - 1| \neq v(\hat{\underline{\mathbf{x}}}),$$

thus contradicting Result A.

At this point, we distinguish the cases $w < 1$ and $w > 1$. In the case $w < 1$, posit again $v(\underline{\mathbf{x}}) = |P_{11} - P_{22}|$. From Section 6.3, we know that $v(T\underline{\mathbf{x}}) \leq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$. Let $\hat{v} = 0$ and $\hat{\underline{\mathbf{x}}} = (P_{11}, 1 - 2P_{11}, P_{11})$. By induction, it is easy to verify that Result A holds. The vectors $\hat{\underline{\mathbf{x}}}$ located on the manifold $P_{11} = P_{22}$ represent a set of accumulation points of the iterates of the recursive equations (3) for the case at hand.

In the case $w > 1$, with $v(\underline{\mathbf{x}}) = |P_{11} - P_{22}|$, we know by Section 6.3 that $v(T\underline{\mathbf{x}}) \geq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$. Two distinct cases must be considered:

(i) If $P_{11} > P_{22}$, then let $\hat{v} = 1$ and $\hat{\underline{\mathbf{x}}} = (1, 0, 0)$.
(ii) If $P_{11} < P_{22}$, then let $\hat{v} = 1$ and $\hat{\underline{\mathbf{x}}} = (0, 0, 1)$.

In both cases, it is trivial to verify that Result A holds.

In the case $w < 1$, we have shown that the solution of the system of recursive equations (3) converges, except from the fixation states, to the manifold $P_{11} = P_{22}$. We shall prove convergence to the polymorphic equilibrium located on this manifold. In effect, if the sequence $\left\{T^l\hat{\underline{\mathbf{x}}}\right\}_{l\geq 0}$ converges to $\hat{\underline{\mathbf{z}}}$ (here the polymorphic equilibrium) for $\hat{\underline{\mathbf{x}}}$ on the manifold $P_{11} = P_{22}$ and $\hat{\underline{\mathbf{z}}}$ is locally stable, then the sequence $\left\{T^l\underline{\mathbf{x}}\right\}_{l\geq 0}$ will converge to $\hat{\underline{\mathbf{z}}}$ for any $\underline{\mathbf{x}}$ in a certain neighborhood of $\hat{\underline{\mathbf{x}}}$ by the continuity of T. This will be the case for any $\underline{\mathbf{x}}$, taking $\hat{\underline{\mathbf{x}}}$ as an accumulation point of $\left\{T^l\underline{\mathbf{x}}\right\}_{l\geq 0}$ which must be on the manifold $P_{11} = P_{22}$. In Section 6.3, we have shown that the sequence $\left\{T^l\hat{\underline{\mathbf{x}}}\right\}_{l\geq 0}$ converges to the polymorphic equilibrium $\hat{\underline{\mathbf{z}}}$. The last step is to show that the polymorphic equilibrium is locally stable. In this purpose, we employ the method exposed in Section 4.

We develop the linear part of the recursive equations (3) in the vicinity of the polymorphic equilibrium $(\hat{p}, \hat{F})$. The matrix of the linear approximation is expressed as

$$\mathbf{M} = \begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix} = \begin{bmatrix} \frac{2w}{2-(1-w)\left(1+\hat{F}\right)} & 0 \\ 0 & \beta\left\{\frac{2w}{\left[2-(1-w)\left(1+\hat{F}\right)\right]^2}\right\} \end{bmatrix},$$

using the still valid entries given in (13) and recalling that $\hat{p} = \hat{q} = \frac{1}{2}$. Since $-1 < \hat{F} < 1$, all the entries of $\mathbf{M}$ are found positive. The characteristic polynomial of $\mathbf{M}$ simply reads as

$$m(\lambda) = (\lambda - m_{11})(\lambda - m_{22}),$$

with strictly positive eigenvalues. Note that these two eigenvalues are continuous with respect to β and equal to 0 and $m_{11} > 0$ for $\beta = 0$. Moreover, $m_{11} < 1$ if and only if $w < 1$, which always holds in the case at hand. Thus, using arguments as in the proof of Result 5, it suffices to show that $m(0) > 0$ and $m(1) > 0$, for $0 < \beta < 1$, to prove that the greatest eigenvalue of $\mathbf{M}$ is smaller than 1. We have

$$m(0) = m_{11}m_{22} > 0$$

and

$$m(1) = \frac{(1-w)\left(1-\hat{F}\right)}{\left[2-(1-w)\left(1+\hat{F}\right)\right]^3} H(\beta, \hat{F}),$$

where

$$H(\beta, F) = [2-(1-w)(1+F)]^2 - 2\beta w.$$

The sign of $m(1)$ depends upon the sign of $H(\beta, \hat{F})$. We must divide the subsequent analysis in two cases, $0 < w < \frac{1}{2}$ and $\frac{1}{2} \leq w < 1$, even though they shall lead to the same result.

Before going any further, we have to outline an essential fact that concerns the value of F at equilibrium, that is,

$$\hat{F} = 4\hat{P}_{11} - 1 = \frac{1 + w(1-\beta) - \sqrt{[3 - w(1+\beta)]^2 - 8(1-w)}}{2(1-w)}.$$

For fixed $w > 0$, the value of $\hat{F}$ increases as β increases over the interval (0, 1). This is deduced by taking the derivative of $\hat{F}$ with respect to β, expressed as

$$\frac{\mathrm{d}}{\mathrm{d}\beta}\hat{F} = \frac{w\left(1+\hat{F}\right)}{\sqrt{[3-w(1+\beta)]^2 - 8(1-w)}} > 0. \tag{A.7}$$

Let us now return to the function $H(\beta, \hat{F})$. In the case $0 < w < \frac{1}{2}$, when $\beta = 0$, the classical result asserts that $\hat{F} = 0$, since no inbreeding is generated by the panmictic model. When $\beta = 1$, the value of F at equilibrium becomes $\hat{F} = w\big/(1-w)$ (this value follows from Nagylaki, 1977). Easy computations yield

$$H(0, \hat{F}) = (1+w)^2 > 0 \quad \text{and} \quad H(1, \hat{F}) = 1 - 2w > 0.$$

Using (A.7), one can trivially verify that the derivative of $H(\beta, \hat{F})$ is such that

$$\frac{\mathrm{d}}{\mathrm{d}\beta}H(\beta, \hat{F}) = -2w - 2(1-w)\left[2-(1-w)\left(1+\hat{F}\right)\right]\left(\frac{\mathrm{d}}{\mathrm{d}\beta}\hat{F}\right) < 0. \tag{A.8}$$

The sign of this derivative ensures that $H(\beta, \hat{F}) > 0$, for all $0 < \beta < 1$. Therefore, we conclude that $m(1) > 0$ in the case $0 < w < \frac{1}{2}$.

In the case $\frac{1}{2} \leq w < 1$, when $\beta = 0$, the above conclusions remain valid. However, when $\beta = 1$, the value of F at equilibrium is $\hat{F} = 1$. Direct calculations yield

$$H(0, 1) = (1 + w)^2 > 0 \quad \text{and} \quad H(1, 1) = 2w(2w - 1) \geq 0.$$

Using (A.8), we conclude that $H(\beta, \hat{F}) > 0$, for all $0 < \beta < 1$ and consequently that $m(1) > 0$ in the case $\frac{1}{2} \leq w < 1$. Therefore, we have proved that the greatest eigenvalue of **M** is smaller than 1 and consequently that the polymorphic equilibrium $(\hat{p}, \hat{F})$ is locally stable in the case $w < 1$.

References

Crow, J.F., Kimura, M.: An introduction to population genetics theory, New York: Harper and Row, 1970

Fisher, R.A.: The genetical theory of natural selection, 2nd revised ed. New York: Dover Publications, 1958

Gantmacher, F.R.: The theory of matrices, Vol. 2. Bronx, New York: Chelsea, 1959

Hayman, B.I.: Mixed selfing and random mating when homozygotes are at a disadvantage, Heredity **7**:185–192 (1953)

Jacquard, A.: The genetic structure of populations, New York: Springer-Verlag 1974

Jain, S.K., Workman, P.L.: Generalized F-statistics and the theory of inbreeding and selection, Nature **214**:674–678 (1967)

Karlin, S.: Equilibrium behavior of population genetics models with non-random mating, J. Appl. Prob. **5**:231–313, 487–566 (1968)

Kimura, M., Ohta, T.: Theoretical aspects of population genetics, Princeton, New Jersey: Princeton University Press, 1971

Lessard, S., Karlin, S.: A criterion for stability-instability at fixation states involving an eigenvalue one with applications in population genetics, Theoretical Population Biology **22**:108–126 (1982)

Li, C.C.: First course in population genetics, Pacific Grove, California: Boxwood Press, 1976

Malécot, G.: Les mathématiques de l'hérédité, Paris: Masson, 1948

Moody, M.: Polymorphism with migration and selection, J. Math. Biology **8**:73–109 (1979)

Nagylaki, T.: Introduction to theoretical population genetics, Berlin: Springer-Verlag, 1992

Nagylaki, T.: The diffusion model for migration and selection in a plant population, J. Math. Biology **35**:409–431 (1997)

Overath, R.D., Asmussen, M.A.: Genetic diversity at a single locus under viability selection and facultative apomixis: equilibrium structure and deviations from Hardy-Weinberg frequencies, Genetics **148**:2029–2039 (1998)

Weir, B.S.: Equilibria under inbreeding and selection, Genetics **65**:371–378 (1970)

Workman, P.L., Jain, S.K.: Zygotic selection under mixed random mating and self-fertilization: theory and problems of estimation, Genetics **54**:159–171 (1966)

Wright, S.: Coefficient of inbreeding and relationship, Amer. Nat. **56**:330–338 (1922)

Wright, S.: The genetical structure of populations, Ann. Eugenics **15**:323–354 (1951)