

Evolutionary Dynamics in Frequency-Dependent Two-Phenotype Models

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General frequency-dependent selection models based on two phenotypic classes are analyzed with underlying one-locus multiallele phenotypic determination systems in diploid populations. It is proved that the mean phenotypic fitnesses tend to equality over discrete generations and genetic mutations if a phenotypic polymorphism is to be maintained. The exact conditions are examined. The present results are valid for a wide class of models whenever random groupings or assortative patterns based on phenotype and affecting fitness, linearly or not, are independent of sex, mating preferences, or kinship. They can also be applied to two-sex haploid models.

1. INTRODUCTION

Theoretical population biology models based on randomly pairwise interactions may be an important source of ideas and principles that provide some insights on intraspecific selection. When the interactions are assumed to have additive effects (incremental or decremental) on individual fitness, such models lead to linear fitness functions which is a basic form of frequency-dependence with which to deal. In haploid models the recurrence equations are usually analogous to those of standard (frequency-independent) diploid models but with fitness matrices allowed to be nonsymmetric. Such a generalization makes the dynamical analyses more delicate in multidimensional situations. The analyses of Cockerham and Burrows (1971) on a discrete time model (cf. Schutz *et al.*, 1968) and Zeeman's studies (1980, 1981) on continuous time versions have revealed complex dynamics whose exhaustive classification might be prohibitive. The latter author was motivated by the notion of evolutionary stable strategy (ESS) introduced earlier in population biology (Maynard Smith and Price, 1973; Maynard Smith, 1974; Haigh, 1975; Bishop and Cannings, 1976; see also Taylor and Jonker, 1978; Hofbauer *et al.*, 1979; and Hines, 1980a,b, 1982.

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for dynamical approaches). As a matter of fact, the hybrid concept of ESS meshing game theory and ecology with perspectives originally dealing with animal conflicts was initially defined in a framework of pairwise contests to predict the evolution and/or maintenance of behavioral traits. The notion of evolutionary stability and its meaning in view of our analytical results will be discussed in the last section of this paper. In diploid populations, further mathematical difficulties come into play due to Mendelian segregation and recombination. For models with two alleles at a single locus, direct dynamical analyses are yet feasible assuming random mating (Schutz and Usanis, 1969; Cockerham *et al.*, 1972; Maynard Smith, 1981). Note also that Matessi and Jayakar (1976a) generalizing Clarke (1972) investigated some multiallele models in an ecological context combining frequency- and density-dependent selection. In this framework, the assumption of linearity is equivalent to a first-order approximation leading to the Lotka–Volterra equations summarized in the “community matrix” introduced for interspecific selection (see e.g., Levins, 1968; MacArthur, 1970; Roughgarden, 1972).

In a more general perspective, individual selection is usually affected nonlinearly by population composition through competition for resources or cooperation for survival. Frequency-dependent selection has long been recognized to be entangled in complex relationships with viability selection (e.g., mimicry, parasitism) and/or reproduction with sexual competition and mating preferences (Fisher, 1930; Wright, 1955; Lewontin, 1958; Clarke and O’Donald, 1964; O’Donald, 1980). More recently, the development of genetical models for behavioral traits that involve formation of basic groups with/or without choice of partnership in series of encounters has led to even more intricate fitness networks (see, e.g., Boorman and Levitt, 1973, 1980; Cohen and Eshel, 1976; Matessi and Jayakar, 1976b; Axelrod and Hamilton, 1981; Eshel and Cavalli-Sforza, 1982; Karlin and Matessi, 1983). In several of these models, the interdependence between phenotypes (usually restricted to two, e.g., altruist and nonaltruist, cooperative and noncooperative, etc.) is expressed by complex fitness functions.

Population genetic models dealing with phenotypes (e.g., color and shape patterns, sex) have traditionally been based on dominance–recessivity relationships or homozygote–heterozygote schemes. With the emergence of behavioral traits, genetical zero–one determination mechanisms may not be always appropriate for they are too limited in the expression of the traits. The introduction of probabilities genotypically determined describing tendencies among a given set of phenotypic possibilities is a response toward more flexibility and generality that will be adopted in this paper. The concept of partial penetrance though different in meaning is also more in agreement with the game-theoretic approaches dealing with mixed strategies rather than pure strategies.

In this study, general frequency-dependent selection schemes based on two phenotypes segregating in large diploid populations will be analyzed assuming random mating and discrete nonoverlapping generations. The present results will be valid for a wide class of models whenever random groupings or assortative patterns based on phenotype and affecting fitness, linearly or not, are independent of sex, mating preferences, or kinship. Mendelian multiallele one-locus systems will be assumed to determine the phenotypic expression. This will make possible an investigation of the evolutionary dynamics of the population composition under genetic mutations. We refer to Uyenoyama *et al.* (1981) for a similar attempt in kin selection theory and Eshel and Feldman (1982) for a theoretical study on the evolution of the sex ratio in random mating populations. These authors dealt with necessary and sufficient conditions for initial increase of mutant alleles using heuristic covariance methods and/or standard local linear analyses. In case of departure from a previously stable equilibrium in the sex ratio evolution models, Karlin and Lessard (1983) proved that the only attainable stable equilibria exhibit a sex ratio closer to 1:1 than the original equilibrium. Note also that Eshel (1982) considered a pure (linear) game-theoretic approach for the present class of models and showed that in presence of a mixed ESS a mixture of strategies is protected.

For the class of models at hand with general fitness functions, two classes of equilibria can be distinguished: phenotypic equilibria characterized by equal phenotypic fitnesses (or phenotypic fixations) and genotypic equilibria arising from the underlying genetic systems analogous to standard viability schemes. This observation formalizes a general principle that has been put forward in the recent literature (Lloyd, 1977; Slatkin, 1978, 1979; see, e.g., Maynard Smith, 1982, for some examples of dimorphism in natural populations). Moreover, the former class generally corresponds to equilibrium surfaces for which local stability analyses fail. With linear phenotypic fitnesses independent of sex and parental type, a *global* dynamical analysis will be provided (Section 2). It will be shown that the distance between the phenotypic fitness functions is a Lyapounov function, i.e., a function monotone over time with equality only at equilibrium. It can be proved that the genetic composition of the population will always converge at a geometric rate in generic cases (Appendix). In the nonlinear case, a stability analysis is possible in the vicinity of every equilibrium (Section 3). In all the cases considered, only phenotypic equilibria have been found to be evolutionary attractive (cf. Definition 1). More precisely, two phenotypic classes segregating in a population are expected to equalize their mean fitnesses or be driven toward either fixation over successive generations through a series of random mutations if necessary. The exact conditions and domains of attraction will be examined. Finally, our results for one-sex diploid models will be applied to two-sex haploid versions (Section 4). In this

context, the above principles will hold based on the notion of reproductive value which assigns a weight to each sex inversely proportional to its mean fitness (i.e., its relative size at the mating phase). Note that such an averaging leads to nonlinear cases when different linear fitness functions are operating in the female and male populations. Our analytical results will be complemented by a discussion on the concept of ESS. In this respect, the present study offers a rigorous treatment and an extension in support of Eshel's claim (1982) that natural selection should lead to ESSs at least in one-locus random mating models.

2. BASIC MODEL OF ADDITIVE PAIRWISE INTERACTIONS
OR LINEAR MODEL

Consider an infinite diploid population in which two phenotypic classes \mathcal{C}_1 and \mathcal{C}_2 are segregating. Suppose that n alleles A_1, \dots, A_n located at a single locus are responsible for the phenotypic determination such that an offspring of genotype $A_i A_j$ expresses phenotype \mathcal{C}_1 with probability v_{ij} and \mathcal{C}_2 with the complementary probability $1 - v_{ij}$ ($i, j = 1, \dots, n$). The symmetric matrix $V = \|v_{ij}\|_{i,j=1}^n$ will be called the *phenotypic determination matrix*. In order to avoid unimportant technicalities, the following generic assumptions on V will be imposed throughout:

- (i) $0 < v_{ij} < 1$ for $i, j = 1, \dots, n$.
- (ii) Every principal submatrix of V is nonsingular.

(iii) If $\mathbf{x} = (x_1, \dots, x_n) \geq \mathbf{0}$ (i.e., $x_i \geq 0$ for $i = 1, \dots, n$) is such that $(V\mathbf{x})_i = \sum_{j=1}^n v_{ij} x_j = 1$ where $x_i > 0$, then $(V\mathbf{x})_i \neq 1$ where $x_i = 0$.

Although these assumptions are not required for the main results of this paper (namely, Propositions 1 and 2), they will simplify the exposition and afford easier understanding afterwards. Note that they are also standard for the classical one-locus multiallele viability model with V as a viability matrix. In this case, they ensure that the number of equilibria is finite and local linear analyses sufficient to investigate their stability properties. Consult, e.g., Kingman (1961a,b), Nagylaki (1977), or Karlin (1978) for a review of results on this model.

The frequency of genotype $A_i A_j$ will be denoted by $2p_{ij}$ when $i \neq j$ and p_{ii} when $i = j$. The frequency of allele A_i is then given by $p_i = \sum_{j=1}^n p_{ij}$. Assuming nonoverlapping discrete generations with random mating, the proportion of offspring in the phenotypic class \mathcal{C}_1 (\mathcal{C}_2) in the next generation is

$$w = w(\mathbf{p}) = \sum_{i,j=1}^n v_{ij} p_i p_j \tag{2.1}$$

($1 - w$, respectively), where $\mathbf{p} = (p_1, \dots, p_n)$. Then selection is assumed to act as follows: pairwise associations (one or several for each individual) or sequential encounters occur at random between the members of the population and as a result of cooperation or confrontation affect the individual expectations to participate to the next mating phase. Let f_{ij} measure the resultant fitness of an individual of phenotype \mathcal{C}_i having interacted only with individuals of phenotype \mathcal{C}_j ($i, j = 1, 2$). Let us assume $f_{ij} > 0$. The fitness matrix $F = \|f_{ij}\|_{i,j=1}^2$ may be nonsymmetric. Assuming that multiple random pairings have additive effects on individual fitness, the mean fitness of the phenotypic class \mathcal{C}_i is frequency dependent (unless $f_{i1} = f_{i2}$) and given in the linear form

$$F_i = F_i(w) = wf_{i1} + (1 - w)f_{i2}, \quad i = 1, 2. \quad (2.2)$$

These selective values transform the genotypic frequencies into

$$p'_{ij} = \frac{p_i p_j [v_{ij} F_1 + (1 - v_{ij}) F_2]}{w F_1 + (1 - w) F_2}, \quad i, j = 1, \dots, n, \quad (2.3)$$

yielding the new allelic frequencies

$$p'_i = \frac{p_i [w_i F_1 + (1 - w_i) F_2]}{w F_1 + (1 - w) F_2}, \quad i = 1, \dots, n, \quad (2.4)$$

where $w_i = w_i(\mathbf{p}) = \sum_{j=1}^n v_{ij} p_j$. Then at equilibrium we must have the relation

$$p_i (w - w_i) (F_1 - F_2) = 0, \quad i = 1, \dots, n. \quad (2.5)$$

Therefore two types of equilibrium can exist:

(I) *Phenotypic equilibrium* when $F_1(w) = F_2(w)$, i.e., both phenotypic classes have the same mean fitness. This condition only involves the phenotypic parameters of the model. Note that the equilibria $w = 0$ and $w = 1$ may also be included in this category.

(II) *Genotypic equilibrium* when $F_1(w) \neq F_2(w)$ and $p_i (w - w_i) = 0$ for $i = 1, \dots, n$, i.e., $(V\mathbf{p})_i = w(\mathbf{p})$, where $p_i > 0$. In this case the equilibrium allelic frequencies correspond exactly to those of the standard one-locus multiallele viability model with V as a viability matrix and $w(\mathbf{p})$ as a mean fitness function, i.e., for the transformation $p'_i = p_i (V\mathbf{p})_i / w(\mathbf{p})$, $i = 1, \dots, n$. Such an equilibrium is independent of the phenotypic selection taking place. Note that in case of coincidence of a genotypic equilibrium with a phenotypic equilibrium, the latter designation would prevail by definition. But this is a degenerate case that will be ignored hereafter.

Observe that the above conditions are necessary and sufficient for

equilibrium and do not depend on any special form of the phenotypic fitness functions. When these are linear functions with respect to the phenotypic frequencies as in the case at hand, the dynamics of the recurrence system is elucidated by the following result:

PROPOSITION 1. *Let F'_1 and F'_2 be the next values of the mean phenotypic fitnesses F_1 and F_2 as defined in (2.2) following transformation (2.4).*

(i) *If $(f_{11} - f_{12} - f_{21} + f_{22}) > 0$, then $|F'_1 - F'_2| \geq |F_1 - F_2|$ with equality only at the equilibria of (2.4).*

(ii) *If $(f_{11} - f_{12} - f_{21} + f_{22}) < 0$, then $|F'_1 - F'_2| \leq |F_1 - F_2|$ with equality only at the equilibria of (2.4).*

Proposition 1 means that $|F_1(w) - F_2(w)|$ is a global Lyapounov function increasing in the case of overall homogeneity advantage, i.e., $f_{11} + f_{22} > f_{12} + f_{21}$, and decreasing in the case of overall heterogeneity advantage, i.e., $f_{11} + f_{22} < f_{12} + f_{21}$. The proof is set forth in the Appendix. It will be useful for further analysis to highlight an equivalent statement.

PROPOSITION 1'. *Let w' be the next frequency of the phenotypic class \mathcal{C}_1 as defined in (2.1) following transformation (2.4). If*

$(f_{11} - f_{12} - f_{21} + f_{22}) \begin{cases} > \\ < \end{cases} 0$, then $|w' - w^| \begin{cases} \geq \\ \leq \end{cases} |w - w^*|$ where*

$$w^* = \frac{f_{22} - f_{12}}{f_{11} - f_{12} - f_{21} + f_{22}}$$

with equality only at the equilibria of (2.4).

Remark. The function $w(p)$ is actually monotone over successive generations except perhaps in the case $f_{11} < f_{21}$ and $f_{22} < f_{12}$. (See Appendix.)

The alternative version of Proposition 1 comes from the equality

$$\begin{aligned} F_1(w) - F_2(w) &= (f_{12} - f_{22}) + (f_{11} - f_{12} - f_{21} + f_{22})w \\ &= (f_{11} - f_{12} - f_{21} + f_{22})(w - w^*). \end{aligned} \tag{2.6}$$

In particular, $F_1(w) = F_2(w)$ if and only if $w = w^*$ (ignoring the degenerate case $f_{11} - f_{12} - f_{21} + f_{22} = 0$). This equation defines a level curve of the quadratic form $w(\mathbf{p})$, which can intersect the $(n - 1)$ -dimensional simplex of frequency vectors

$$\Delta = \left\{ \mathbf{p} = (p_1, \dots, p_n): p_i \geq 0, \sum_{i=1}^n p_i = 1 \right\} \tag{2.7}$$

only if the condition $0 \leq w^* \leq 1$ is satisfied. When it exists, let us denote by L^* the equilibrium manifold in Δ corresponding to w^* , i.e.,

$$L^* = \{\mathbf{p} \in \Delta: w(\mathbf{p}) = w^*\}. \quad (2.8)$$

In general, the intersection of $w(\mathbf{p}) = w^*$ with Δ may create several separated equilibrium branches of dimension $n - 2$. On the other hand, with our generic assumptions on V , the number of genotypic equilibria is necessarily finite. These are isolated points in Δ . The existence of a global Lyapounov function entails convergence of the allelic frequency vectors to these equilibrium points or to the equilibrium manifold L^* . Here convergence to L^* means convergence of $w(\mathbf{p})$ to w^* , i.e., convergence of the phenotypic frequencies. For further discussion we shall concentrate on the case $f_{11} < f_{21}$ and $f_{22} < f_{12}$, i.e., the case of overall heterogeneity advantage with $0 < w^* < 1$. The property that $|w(\mathbf{p}) - w^*|$ is a decreasing Lyapounov function in this case ensures local stability of L^* as a manifold when it occurs. This means that $w(\mathbf{p})$ will return to w^* after any small allelic perturbations from any equilibrium point of L^* . Moreover, the other locally stable equilibria, which are necessarily genotypic according to our definition, must correspond to the local minima of $|w(\mathbf{p}) - w^*|$ in Δ . We deduce:

COROLLARY 1. *Suppose $f_{11} < f_{21}$ and $f_{22} < f_{12}$.*

(i) *The phenotypic equilibrium $w(\mathbf{p}) = w^*$ is locally stable when it exists in Δ .*

(ii) *The locally stable genotypic equilibria correspond to the local maxima (minima) of $w(\mathbf{p})$ smaller (larger) than w^* .*

(iii) *The phenotypic equilibrium $w(\mathbf{p}) = w^*$ cannot coexist with any locally stable genotypic equilibrium interior to Δ .*

(iv) *Two genotypic equilibria lying on either side of w^* are separated by one and only one branch of the equilibrium manifold $w(\mathbf{p}) = w^*$. Such a situation is necessary for the existence of L^* .*

Remark. Proposition 1 does not guarantee pointwise convergence to L^* , i.e., convergence to a point of L^* from any initial frequency vector in a neighborhood of L^* . (Actually a finer inequality is required to prove this convergence of the allelic frequencies.) Moreover it can be shown that the rate of convergence is geometric in generic cases (see Appendix).

In part (ii) of Corollary 1 we recognize the basic conditions of local stability for the viability models with matrices V and $U - V$, respectively. (U designates the matrix with all entries one.) Equivalent necessary and sufficient conditions can be found in the current literature (see, e.g., Kingman, 1961b; Nagylaki, 1977; Karlin, 1978). Part (iii) is due to the fact

that $w(\mathbf{p})$ is a quadratic form and consequently a local maximum (minimum) within Δ is actually a global maximum (minimum) over all Δ . Furthermore, the restriction of $w(\mathbf{p})$ to any straight line is a quadratic form. Therefore, the last statement of Corollary 1 is immediate in generic cases where the genotypic equilibria (including those corresponding to the maxima and minima of $w(\mathbf{p})$ in Δ) do not coincide with phenotypic equilibria.

It is worth noting that a locally stable genotypic equilibrium on the boundary of Δ cannot be a priori precluded by the existence of a stable phenotypic equilibrium, and a coexistence is actually possible. This occurs for instance when $w(\mathbf{p})$ exhibits a local maximum smaller than w^* on the boundary of Δ , while its global maximum and global minimum lie on either side of w^* . In any case, an analysis of the evolutionary dynamics of the whole system under genetic mutations can be made on the basis of our results.

Suppose that the conditions of Corollary 1 are in force and let $\hat{\mathbf{p}} = (\hat{p}_1, \dots, \hat{p}_n)$ be a locally stable genotypic equilibrium involving the alleles A_1, \dots, A_n (i.e., $\hat{p}_i > 0$ for $i = 1, \dots, n$) such that $\hat{w} = w(\hat{\mathbf{p}}) < w^*$, or equivalently $F_1(\hat{w}) - F_2(\hat{w}) > 0$. Let us introduce a new allele A_{n+1} to this original equilibrium system such that the mutant marginal phenotypic frequency of \mathcal{E}_1 at $\hat{\mathbf{p}}$, namely,

$$w_{n+1}(\hat{\mathbf{p}}) = \sum_{i=1}^n v_{i,n+1} \hat{p}_i, \tag{2.9}$$

satisfies $w_{n+1}(\hat{\mathbf{p}}) > w(\hat{\mathbf{p}})$. By continuity we must have $w_{n+1}(\mathbf{p}) > w(\mathbf{p})$ and $F_1(w) - F_2(w) > 0$ in some neighborhood of $\hat{\mathbf{p}}$ in which the following relation for the frequency of A_{n+1} holds:

$$p'_{n+1} = p_{n+1} \left\{ \frac{w_{n+1}(\hat{\mathbf{p}})[F_1(w) - F_2(w)] + F_2(w)}{w(\mathbf{p})[F_1(w) - F_2(w)] + F_2(w)} \right\} > p_{n+1}. \tag{2.10}$$

This local increasing property excludes convergence to $\hat{\mathbf{p}}$ in the augmented allelic system. To the contrary, the reverse condition $w_{n+1}(\hat{\mathbf{p}}) < w(\hat{\mathbf{p}})$ would have preserved local stability for $\hat{\mathbf{p}}$. This is also precisely the condition for a stable equilibrium $\hat{\mathbf{p}}$ with $w(\hat{\mathbf{p}}) > w^*$ to become unstable under genetic mutations. To sum up, a stable boundary equilibrium $\hat{\mathbf{p}} = (\hat{p}_1, \dots, \hat{p}_n)$ becomes unstable following the introduction of a new allele A_{n+1} if and only if $w_{n+1}(\hat{\mathbf{p}})$ is in the direction of w^* with respect to $w(\hat{\mathbf{p}})$. (Compare with the conditions used by Eshel and Feldman (1982) to define EGS (evolutionary genetically stable) sex ratios.)

Whenever instability occurs in the model at hand, Proposition 1' guarantees that $w(\mathbf{p})$ will always move closer to w^* until a new equilibrium is reached. Moreover, the phenotypic equilibrium manifold $w(\mathbf{p}) = w^*$ itself

TABLE I
Evolutionary Attractive States for Model (2.4) in Terms of the Frequency of the Phenotypic Class \mathcal{C}_1 and of its Initial Value w_0

| | $w^* \leq 0^a$ | $0 < w^* < 1$ | $w^* \geq 1$ |
|---|----------------|--------------------------------------|--------------|
| $(f_{11} - f_{12} - f_{21} + f_{22}) < 0$ | 0 | w^* | 1 |
| $(f_{11} - f_{12} - f_{21} + f_{22}) > 0$ | 1 | 0 if $w_0 < w^*$ 1 if $w_0 > w^*$ | 0 |

^a $w^* = (f_{22} - f_{12}) / (f_{11} - f_{12} - f_{21} + f_{22})$.

is locally stable against any allelic mutation since Corollary 1 applies whatever the dimension of the allelic system is. Note that in this case a mutant allele need not be eliminated although its frequency will usually remain small.

The above discussion and our analytical results suggest the following definition that will be used throughout this paper.

DEFINITION 1. A phenotypic equilibrium w^* is said to be *evolutionary attractive* with domain of attraction \mathcal{D}_{w^*} if a population in a phenotypic state w in \mathcal{D}_{w^*} will evolve to w^* through a series of genetic mutations if necessary. Moreover, it is said to be *globally evolutionary attractive* if \mathcal{D}_{w^*} is the entire phenotypic space.

We are now ready to state the following general consequence of Proposition 1'.

COROLLARY 2. (i) If $f_{11} < f_{21}$ and $f_{22} < f_{12}$, then the phenotypic equilibrium $w(\mathbf{p}) = w^*$ is globally evolutionary attractive.

(ii) The phenotypic fixation $w = 0$ is (globally) evolutionary attractive if and only if $f_{11} > f_{21}$ (and $f_{22} < f_{12}$).

(iii) If $f_{11} > f_{21}$ and $f_{22} > f_{12}$, then the evolutionary attractive states $w = 0$ and $w = 1$ have domains of attraction $(0, w^*)$ and $(w^*, 1)$, respectively.

For a quick reference, hereafter, consult Table I.

3. GENERAL CASE OF NONLINEAR FREQUENCY-DEPENDENT SELECTION
BASED ON TWO PHENOTYPES

We propose to consider a generalization of the basic model allowing the phenotypic fitness functions $F_1(w)$ and $F_2(w)$ to be nonlinear positive functions of w . Such a situation may arise from a pairwise encounter model if the assumption of additivity is dropped (and replaced, e.g., by a multiplicative model which is as much—if not more—relevant in the case of successive contests jeopardizing viability). But this is a very particular interpretation of a purely formal representation that can take into account several forms of selection based on phenotype found in complex populations involving, e.g., assortative behavior in partnership or any grouping patterns independent of kinship followed by local individual interactions as well as frequency-dependence arising from mimicry or parasitism widespread in natural populations. Without the linearity assumption, the scope of application of our results will be substantially widened.

With phenotypic determination matrix V and general positive fitness functions $F_1(w)$ and $F_2(w)$ for the phenotypes \mathcal{E}_1 and \mathcal{E}_2 , respectively, where w is the frequency of \mathcal{E}_1 , the transformation equations assuming random mating are given by (2.4) which can be written in the form

$$p'_i = p_i \left\{ \frac{(V\mathbf{p})_i Q(w) + R(w)}{wQ(w) + R(w)} \right\}, \quad i = 1, \dots, n, \tag{3.1}$$

where $Q(w) = F_1(w) - F_2(w)$ and $R(w) = F_2(w)$ with $w = w(\mathbf{p}) = \sum_{i=1}^n p_i (V\mathbf{p})_i$.

For simplicity, suppose that $Q(w)$ has exactly N zeros in $[0, 1]$ denoted by w_1^*, \dots, w_N^* in this order, i.e.,

$$0 \leq w_1^* < w_2^* < \dots < w_N^* \leq 1, \tag{3.2}$$

and these zeros are simple, i.e., the derivatives satisfy

$$\frac{dQ}{dw}(w_k^*) \neq 0, \quad k = 1, \dots, N. \tag{3.3}$$

These genericity conditions on $Q(w)$ will be assumed throughout this paper. Near any phenotypic equilibrium w^* , i.e., any frequency w^* such that $Q(w^*) = 0$, a linear approximation of $F_1(w)$ and $F_2(w)$ in the form

$$F_i^*(w) = wf_{i1}^* + (1 - w)f_{i2}^*, \quad i = 1, 2, \tag{3.4}$$

yields the expression

$$\frac{dQ}{dw}(w^*) = f_{11}^* - f_{12}^* - f_{21}^* + f_{22}^* \quad \text{with} \quad w^* = \frac{f_{22}^* - f_{12}^*}{f_{11}^* - f_{12}^* - f_{21}^* + f_{22}^*} \quad (3.5)$$

(compare with (2.6)). Note that without loss of generality, we may assume $f_{ij}^* > 0$, $i, j = 1, 2$, since the fitness functions $F_1(w)$ and $F_2(w)$ can be chosen arbitrarily large. It is shown in the Appendix that near the equilibrium manifold $w(\mathbf{p}) = w^*$ the recurrence system (3.1) behaves like (2.4) with the linearized fitness functions (3.4). Moreover, the evolutionary dynamics near either phenotypic fixation state is determined by the sign of Q . The precise result is the following:

PROPOSITION 2. *The evolutionary attractive states of transformation (3.1) are the zeros of $Q(w) = F_1(w) - F_2(w)$ with negative slope and the fixation states $w = 0$ and $w = 1$ if $Q(0) < 0$ and $Q(1) > 0$, respectively.*

Since w is the frequency of \mathcal{E}_1 and $F_1(w)$ is its mean fitness compared to $F_2(w)$ for \mathcal{E}_2 , Proposition 2 is in agreement with our biological intuition of increase in frequency with superior fitness. Less obvious is its claim that an escape by alternate jumps over successive generations is never possible near a zero of Q with negative slope. As a matter of fact, this statement requires a more delicate analysis. (See Appendix.)

On the other hand, near any genotypic equilibrium $\hat{\mathbf{p}}$ with $\hat{w} = w(\hat{\mathbf{p}}) = (V\hat{\mathbf{p}})_i$ where $\hat{p}_i > 0$ and such that $Q(\hat{w}) \neq 0$, it can be checked that the local linear approximation of transformation (3.1) corresponds to that of a frequency-independent viability model with viability matrix $VQ(\hat{w}) + UR(\hat{w})$, namely,

$$p'_i = \frac{p_i [(VQ(\hat{w}) + UR(\hat{w}))\mathbf{p}]_i}{w(\mathbf{p})Q(\hat{w}) + R(\hat{w})}, \quad i = 1, \dots, n \quad (3.6)$$

(U for the matrix with all unit entries). The mean fitness for this model is $w(\mathbf{p})Q(\hat{w}) + R(\hat{w})$. Its local maxima defining the stable equilibria of (3.6) are the local maxima or minima of $w(\mathbf{p})$ accordingly as $Q(\hat{w})$ is positive or negative. We conclude:

PROPOSITION 3. *In generic cases, the stable genotypic equilibria of transformation (3.1) are the local maxima of $w(\mathbf{p})$ where $Q > 0$ and the local minima of $w(\mathbf{p})$ where $Q < 0$.*

In other words, the frequency of \mathcal{E}_1 is locally maximized whenever \mathcal{E}_1 is more advantageous, and similarly for \mathcal{E}_2 . When $Q(w)$ has three zeros or

more, stable genotypic equilibria can coexist with stable phenotypic equilibria segregating the same set of alleles. As a general rule, stable and unstable equilibria alternate.

4. APPLICATION TO TWO-SEX TWO-PHENOTYPE HAPLOID MODELS

As mentioned in the previous section, multiplicative models are natural alternatives to additive models. Also interesting is the peculiar fact that mere sex differentiation may break linearity. In this respect, the generalized system (3.1) allowing nonlinear functions will prove to be particularly relevant for two-sex haploid models. Such models may have an interest of their own in addition to enabling us to extend the principles established for one-sex diploid models to two-sex populations in which “fitness” and “sex ratio” are indissociable.

Let A_1, \dots, A_n be the haplo-types with frequencies p_1, \dots, p_n , respectively, in an infinite two-sex population with 1:1 sex ratio at conception. Assume that an A_i -type irrespective of sex exhibits a phenotype \mathcal{C}_1 with probability v_i and \mathcal{C}_2 with probability $1 - v_i$ ($i = 1, \dots, n$). Suppose that the *phenotypic determination vector* $\mathbf{v} = (v_1, \dots, v_n)$ satisfies the genericity condition $v_i \neq v_j$ for all $i \neq j$. Before selection takes place, the phenotypes \mathcal{C}_1 and \mathcal{C}_2 are present in the haploid population with frequencies $y = \sum_{i=1}^n p_i v_i$ and $1 - y$, respectively. The mean (positive) fitnesses of these two phenotypes in the male and female populations undergoing general frequency-dependent phenotypic selection will be denoted by the fitness functions $M_1(y), M_2(y)$ and $F_1(y), F_2(y)$, respectively. (The variable y will be omitted hereafter.) Following random union of gametes for the formation of diplo-types, Mendelian segregation and equal fertility in producing haplo-types, the next life cycle will start with the allelic frequencies

$$p'_i = \frac{1}{2} \left\{ \frac{p_i [v_i F_1 + (1 - v_i) F_2]}{y F_1 + (1 - y) F_2} \right\} + \frac{1}{2} \left\{ \frac{p_i [v_i M_1 + (1 - v_i) M_2]}{y M_1 + (1 - y) M_2} \right\}, \quad i = 1, \dots, n, \quad (4.1)$$

that is,

$$p'_i = (p_i/2) \{v_i S(y) + T(y)\}, \quad i = 1, \dots, n, \quad (4.2)$$

where

$$S(y) = \frac{F_1 - F_2}{F} + \frac{M_1 - M_2}{M} \quad \text{and} \quad T(y) = \frac{F_2}{F} + \frac{M_2}{M} \quad (4.3)$$

with $\bar{F} = yF_1 + (1 - y)F_2$, $\bar{M} = yM_1 + (1 - y)M_2$, and $y = y(\mathbf{p}) = \sum_{i=1}^n p_i v_i$. This recurrence system of equations is formally equivalent to (3.1) with matrix $V = \|v_i v_j\|_{i,j=1}^n$ and functions $Q(w) = S(\sqrt{w})/\sqrt{w}$ and $R(w) = T(\sqrt{w})$, where $w = y^2$. The genotypic equilibria are the genetic fixation states (i.e., $p_i = 1$ for some i), and the dynamical properties previously highlighted hold based on the functions $y = y(\mathbf{p})$ and $S = S(y)$. If we assume without loss of generality $v_1 < v_2 < \dots < v_n$, then $y(\mathbf{p})$ which is a linear function achieves its unique maximum at A_n -fixation and its unique minimum at A_1 -fixation. According to Proposition 3, the former equilibrium is stable when $S(v_n) > 0$ and the latter when $S(v_1) < 0$. Similarly, the phenotypic fixation states $y = 0$ and $y = 1$ are evolutionary attractive if they are locally more advantageous. Moreover, the polymorphic phenotypic equilibria are the zeros of $S(y)$ whose stability properties are determined as follows:

PROPOSITION 4. *The evolutionary attractive polymorphic equilibria of the two-sex two-phenotype haploid model (4.2) are the zeros from plus to minus of*

$$S(y) = \frac{F_1(y) - F_2(y)}{\bar{F}(y)} + \frac{M_1(y) - M_2(y)}{\bar{M}(y)},$$

where $F_i(y)$ and $M_i(y)$ are the fitnesses of \mathcal{C}_i ($i = 1, 2$) in the female and male populations, respectively, whose mean fitnesses are $\bar{F}(y)$ and $\bar{M}(y)$, respectively, when the frequencies of \mathcal{C}_1 and \mathcal{C}_2 are y and $1 - y$, respectively.

5. DISCUSSION

Maynard Smith (1982) made a clear distinction between an ESS or “evolutionary stable strategy” and a population in an “evolutionary stable state.” An ESS is defined as an uninvadable (possibly mixed) strategy once adopted by *all members* of a population: the population is monomorphic and any deviant strategy is selected against at least when rare. When a population composition (monomorphic or *polymorphic*) is stable against any small perturbations then the population is said to be in an evolutionary stable state.

Let us recall that if r pure strategies are possible, then a mixed strategy $\mathbf{s} = (s_1, \dots, s_r)$ is a frequency vector which assigns a probability s_j to the pure strategy j ($0 \leq s_j \leq 1$, $\sum_{j=1}^r s_j = 1$). In a game theoretic approach of pairwise contests allowing r pure strategies, an individual adopting a strategy $\tilde{\mathbf{s}} = (\tilde{s}_1, \dots, \tilde{s}_r)$ against an opponent adopting $\mathbf{s} = (s_1, \dots, s_r)$ receives a payoff in

fitness that will be denoted by $E(\tilde{\mathbf{s}}, \mathbf{s})$. In that context, a strategy $\mathbf{s}^* = (s_1^*, \dots, s_r^*)$ is called an ESS if for every alternative strategy $\mathbf{s} \neq \mathbf{s}^*$ either

$$E(\mathbf{s}^*, \mathbf{s}^*) > E(\mathbf{s}, \mathbf{s}^*)$$

or

$$(5.1)$$

$$E(\mathbf{s}^*, \mathbf{s}^*) = E(\mathbf{s}, \mathbf{s}^*) \quad \text{and} \quad E(\mathbf{s}^*, \mathbf{s}) > E(\mathbf{s}, \mathbf{s})$$

(Maynard Smith and Price, 1973). With linear games, i.e., payoff function in the form

$$E(\tilde{\mathbf{s}}, \mathbf{s}) = \sum_{i,j=1}^r \tilde{s}_i a_{ij} s_j \quad (5.2)$$

for some coefficients a_{ij} , $i, j = 1, \dots, r$, condition (5.1) is equivalent to

$$\begin{aligned} E(\mathbf{s}^*, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) &= (1 - \varepsilon) E(\mathbf{s}^*, \mathbf{s}^*) + \varepsilon E(\mathbf{s}^*, \mathbf{s}) \\ &> (1 - \varepsilon) E(\mathbf{s}, \mathbf{s}^*) + \varepsilon E(\mathbf{s}, \mathbf{s}) \\ &= E(\mathbf{s}, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) \end{aligned} \quad (5.3)$$

for every $\varepsilon > 0$ small enough, or equivalently,

$$\begin{aligned} &E(\mathbf{s}^*, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) \\ &= (1 - \varepsilon) E(\mathbf{s}^*, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) + \varepsilon E(\mathbf{s}^*, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) \\ &> (1 - \varepsilon) E(\mathbf{s}^*, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) + \varepsilon E(\mathbf{s}, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) \\ &= E((1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \mathbf{s}) \end{aligned} \quad (5.4)$$

for every $\varepsilon > 0$ small enough (cf., e.g., Hofbauer *et al.*, 1979). In a more general context of frequency-dependent selection (and after Taylor and Jonker (1978)), an ESS can be defined as an individual strategy \mathbf{s}^* such that

$$F(\mathbf{s}^*, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \tilde{\mathbf{s}}) > F(\mathbf{s}, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \tilde{\mathbf{s}}) \quad (5.5)$$

for every strategy $\tilde{\mathbf{s}} \neq \mathbf{s}^*$ and every $\varepsilon > 0$ sufficiently small, where $F(\tilde{\mathbf{s}}, (1 - \varepsilon) \mathbf{s}^* + \varepsilon \tilde{\mathbf{s}})$ represents the fitness of an \mathbf{s} strategist in a population with mean individual strategy $(1 - \varepsilon) \mathbf{s}^* + \varepsilon \tilde{\mathbf{s}}$. With two pure possible strategies (or phenotypes) \mathcal{C}_1 and \mathcal{C}_2 whose fitnesses are general functions $F_1(w)$ and $F_2(w)$, respectively, where w is the frequency of \mathcal{C}_1 in the current population, an individual adopting \mathcal{C}_1 with probability \tilde{w} and \mathcal{C}_2 with probability $1 - \tilde{w}$ has fitness

$$F(\tilde{w}, w) = \tilde{w} F_1(w) + (1 - \tilde{w}) F_2(w). \quad (5.6)$$

In this case, condition (5.5) becomes

$$F(w^*, w) - F(\tilde{w}, w) = (w^* - \tilde{w})(F_1(w) - F_2(w)) > 0, \quad (5.7)$$

where $w = (1 - \varepsilon)w^* + \varepsilon\tilde{w}$ with $\varepsilon > 0$ arbitrarily small. This entails that the ESSs are the zeros of $F_1(w) - F_2(w)$ from plus to minus, not to mention the pure strategies $w^* = 0$ and $w^* = 1$ if $F_1(0) < F_2(0)$ and $F_1(1) > F_2(1)$, respectively.

We have shown that the phenotypic equilibria corresponding to the ESSs in a general frequency-dependent selection context of mixed strategies with two components are evolutionary attractive (cf. Definition 1) over nonoverlapping discrete generations in diploid populations with individual strategy determined at a multiallelic autosomal locus subject to mutations. This extends Eshel's result (1982) that a mixture of strategies is protected in a population with an associated linear game allowing two pure strategies and having a (strictly) mixed ESS. Note that the one-side inequality (A6) in the Appendix defining locally adaptive systems was proved by Eshel but is not sufficient to conclude about convergence. Our results show that stable genotypic equilibria are possible in presence of genetically accessible ESSs even in the linear case (cf. Corollary 1). Nevertheless, genetic mutations will eventually destabilize any genotypic equilibrium and a phenotypic equilibrium corresponding to an ESS will ultimately be reached although the dynamical tendency may be temporarily stopped due to genetic constraints. It is worth noting that not only the phenotypic composition of the population will converge, but also its genotypic composition. As a matter of fact, a mixed ESS generally corresponds to a continuum of genetic polymorphisms: there is not a unique population composition of mixed strategies that can produce the phenotypic equilibrium but infinitely many. Such an equilibrium is stable as a manifold in a very strong sense since it is stable against any allelic perturbations including mutations. We may mention that it is also structurally stable meaning that small perturbations on the phenotypic parameters of the model would cause small displacements of the original equilibrium but preserve its stability properties in generic cases (i.e., with (3.2) and (3.3) in force).

The basic fact that a balance of fitnesses in dimorphic populations is established at equilibrium under the effects of frequency-dependent selection was mentioned early by Fisher (1930) in discussing the maintenance of mimetic forms. Moreover the equilibration principle is well known for the marginal allelic fitnesses in standard (frequency-independent) diploid models, and more generally in linear dynamical games, and recognized to predominate within populations over the maximization principle of the mean fitness as pointed out by Cockerham and Burrows (1971). That static principle was restated for any number of phenotypic classes in response to

frequency-dependent selection (Lloyd, 1977; Slatkin, 1978, 1979). Our dynamical analysis has specified the exact conditions on the fitness functions for actual realization and maintenance of equilibration in the case of two phenotypic classes (see (5.7) and Proposition 2). In sex-differentiated populations, we must resort to the concept of reproductive value (Fisher, 1930) to average the within-sex fitness functions in order to equalize the contributions by males and females to the next generation. Such models are intrinsically frequency-dependent and nonlinear unless the within sex fitness parameters are constant. (For this special case in haplo-diplonts, see Gregorius (1982).) As previously mentioned, the equilibration principle is subsumed in the concept of ESS. Some extensions of this concept to two-role models were proposed (Taylor, 1979; Schuster and Sigmund, 1981). Maynard Smith (1982, pp. 199–202) suggested that the mean fitnesses of the two groups should be taken into account. This is in agreement with our Proposition 4 in a more general framework of frequency-dependence for two-sex haploid populations. Weaker analytical results supporting similar principles for general two-sex models in diploid populations including parent control versions for which a global dynamical approach might be prohibitive will be published separately.

It is interesting to compare our results for discrete generations with continuous approximations. The analyses of Zeeman (1981) and Hines (1982) for haploid populations and diploid populations with additive allelic effects, respectively, revealed that the ESSs defined by (5.1) in a context of linear games allowing mixed strategies with r components are evolutionary attractive (in our terminology) in continuous time. Moreover, as pointed out by Eshel (1982) (and after Ewens, 1969), the additive case over loci in multilocus systems for our model is formally equivalent to a one-locus problem with regard to the allelic and phenotypic frequencies. Other genetic assumptions remain to be considered.

APPENDIX: PROOF OF PROPOSITION 1

For ease of exposition, the following notation will be used:

$$F = \|f_{ij}\|_{i,j=1}^2 = \begin{bmatrix} a & b \\ c & d \end{bmatrix}, \quad (a, b, c, d > 0), \quad (\text{A1a})$$

$$R = F_2 = d + (c - d)w, \quad (\text{A1b})$$

$$Q = F_1 - F_2 = (b - d) + (a - b - c + d)w. \quad (\text{A1c})$$

In this notation, transformation (2.4) on the frequency vectors $\mathbf{p} = (p_1, \dots, p_n)$ takes the form

$$p'_i = \frac{p_i(w_i Q + R)}{wQ + R}, \quad i = 1, \dots, n, \quad (\text{A2})$$

where $w_i = \sum_{j=1}^n v_{ij} p_j$ and $w = \sum_{i,j=1}^n v_{ij} p_i p_j$ with $V = \|v_{ij}\|_{i,j=1}^n$ as a phenotypic determination matrix. The next value of w is determined as follows:

$$\begin{aligned} w' &= \sum_{i,j=1}^n v_{ij} p'_i p'_j \\ &= \frac{\sum_{i,j=1}^n v_{ij} p_i p_j (w_i Q + R)(w_j Q + R)}{(wQ + R)^2} \\ &= \frac{\left[Q^2 \sum_{i,j=1}^n v_{ij} p_i p_j w_i w_j + QR \sum_{i,j=1}^n v_{ij} p_i p_j (w_i + w_j) + R^2 \sum_{i,j=1}^n v_{ij} p_i p_j \right]}{(wQ + R)^2} \\ &= \frac{Q^2 \sum_{i,j=1}^n v_{ij} p_i p_j w_i w_j + 2QR \sum_{i=1}^n p_i w_i^2 + R^2 w}{(wQ + R)^2}. \end{aligned} \quad (\text{A3})$$

Schwarz's inequality asserts that

$$\sum_{i=1}^n p_i w_i^2 \geq \left(\sum_{i=1}^n p_i w_i \right)^2 = w^2, \quad (\text{A4})$$

while Fisher's fundamental theorem of natural selection with $V = \|v_{ij}\|_{i,j=1}^n$ as a viability matrix guarantees that

$$\sum_{i,j=1}^n v_{ij} p_i p_j w_i w_j \geq w^3. \quad (\text{A5})$$

Both inequalities are strict unless $w_i = w$ where $p_i > 0$. Therefore, if $Q > 0$, we have

$$w' \geq \frac{Q^2 w^3 + 2QRw^2 + R^2 w}{(wQ + R)^2} = w \quad (\text{A6})$$

with equality only at a genotypic equilibrium of (A2). By symmetry between the two phenotypic classes (with phenotypic determination matrix $\|1 - v_{ij}\|_{i,j=1}^n$ instead of $\|v_{ij}\|_{i,j=1}^n$), the reverse inequality holds if $Q < 0$. Note that these monotonicity properties *do not require any linearity condition on Q* as a function of w . They define locally adaptive systems in Eshel's terminology (1982). They stipulate that the frequency of a phenotype increases when the phenotype is selectively favored.

Note also that the next value of Q defined by (A1c) can be expressed in the form

$$\begin{aligned}
 Q' &= (b - d) + (a - b - c + d) w' \\
 &= \frac{\left[(b - d)(w^2 Q^2 + 2wQR + R^2) + (a - b - c + d) \right. \\
 &\quad \left. \times (Q^2 \sum_{i,j=1}^n v_{ij} p_i p_j w_i w_j + 2QR \sum_{i=1}^n p_i w_i^2 + R^2 w) \right]}{(wQ + R)^2} \\
 &= Q \left\{ \frac{\left[R^2 + (b - d)(w^2 Q + 2wR) + (a - b - c + d) \right. \right. \\
 &\quad \left. \left. \times (Q \sum_{i,j=1}^n v_{ij} p_i p_j w_i w_j + 2R \sum_{i=1}^n p_i w_i^2) \right] \right\}. \quad (A7)
 \end{aligned}$$

The phenotypic equilibria of (A2) are characterized by the *identity* $Q = 0$. We are now ready to prove Proposition 1. Two cases will be distinguished:

Case (i). $(a - b - c + d) > 0$. Owing to the monotonicity property (A6) and the linear form of Q as defined by (A1c), we can conclude immediately that $Q' \geq Q$ where $Q > 0$ with equality only at a genotypic equilibrium, and symmetrically $Q' \leq Q$ where $W < 0$, i.e.,

$$|Q'| \geq |Q| \quad (A8)$$

with equality only at an equilibrium point of (A2).

Case (ii). $(a - b - c + d) < 0$. Without loss of generality, we may assume $Q > 0$. In this case, (A6) ensures $Q' \leq Q$, and it remains to show that $Q' > -Q$ to conclude that

$$|Q'| \leq |Q| \quad (A9)$$

with strict inequality at the nonequilibrium points of (A2). The fact that $0 < v_{ij} < 1$ ($i, j = 1, \dots, n$) gives the majorizations

$$\sum_{i=1}^n p_i w_i^2 \leq \sum_{i=1}^n p_i w_i = w \quad (A10)$$

and

$$\sum_{i,j=1}^n v_{ij} p_i p_j w_i w_j \leq \left(\sum_{i=1}^n p_i w_i \right)^2 = w^2. \quad (A11)$$

Hence from (A7), we have

$$Q' \geq Q \left\{ \frac{R^2 + (a - c)(w^2 Q + 2wR)}{(wQ + R)^2} \right\}, \quad (A12)$$

where Q is positive. Then it will be sufficient to show that

$$\frac{R^2 + (a-c)(w^2Q + 2wR)}{(wQ + R)^2} > -1, \quad (\text{A13})$$

or equivalently,

$$g(w) = R^2 + (a-c)(w^2Q + 2wR) + (wQ + R)^2 > 0. \quad (\text{A14})$$

But since

$$Q = (a-c) - (a-b-c+d)(1-w) \geq 0, \quad (\text{A15})$$

we have

$$\begin{aligned} g(w) &= R^2 + [Q + (a-b-c+d)(1-w)](w^2Q + 2wR) + (wQ + R)^2 \\ &= 2(wQ + R)^2 + (a-b-c+d)(1-w)(w^2Q + 2wR) \\ &\geq 2(wQ + R)^2 + 2(a-b-c+d)w(1-w)(wQ + R) \\ &= 2(wQ + R)[wQ + R + (a-b-c+d)w(1-w)] \\ &= 2(wQ + R)[(a-c)w + R] \\ &= 2(wQ + R)[aw + d(1-w)] \end{aligned} \quad (\text{A16})$$

and therefore $g(w)$ must be positive where $Q \geq 0$.

Addendum to Appendix

Suppose that $F_1(w)$ and $F_2(w)$ are nonlinear positive fitness functions. Let $Q(w) = F_1(w) - F_2(w)$ and $0 < w^* < 1$ be such that

$$Q(w^*) = 0 \quad \text{and} \quad \frac{dQ}{dw}(w^*) < 0. \quad (\text{A17})$$

Let a, b, c, d be four positive constants defined from the Taylor expansions of $F_1(w)$ and $F_2(w)$ about w^* as follows:

$$F_1(w) = b + (a-b)w + O(|w - w^*|^2), \quad (\text{A18a})$$

$$F_2(w) = d + (c-d)w + O(|w - w^*|^2). \quad (\text{A18b})$$

(A function $O(\varepsilon)$ is such that $O(\varepsilon)/\varepsilon$ is bounded for ε arbitrarily small.)
Namely,

$$\begin{aligned}
 a &= F_1(w^*) + (1 - w^*) \frac{dF_1}{dw}(w^*), \\
 b &= F_1(w^*) - w^* \frac{dF_1}{dw}(w^*), \\
 c &= F_2(w^*) + (1 - w^*) \frac{dF_2}{dw}(w^*), \\
 d &= F_2(w^*) - w^* \frac{dF_2}{dw}(w^*),
 \end{aligned}
 \tag{A19}$$

and the fitness functions $F_1(w)$ and $F_2(w)$ can be chosen sufficiently large to ensure $a, b, c, d > 0$. Furthermore

$$Q(w) = (b - d) + (a - b - c + d)w + O(|w - w^*|^2) \tag{A20}$$

with

$$(a - b - c + d) = \frac{dQ}{dw}(w^*) < 0 \quad \text{and} \quad w^* = \frac{d - b}{a - b - c + d}. \tag{A21}$$

Now assume $Q = Q(w)$ and $R = F_2(w)$ in recurrence transformation (A2). If $w < w^*$ and w is close to w^* , then a local analysis near w^* using (A6) and (A7) with inequalities (A10) and (A11) yields

$$Q(w) \left\{ \frac{R_0^2 + (a - c)(w^2 Q_0 + 2wR_0)}{(wQ_0 + R_0)^2} + O(|w - w^*|^2) \right\} \leq Q(w') \leq Q(w), \tag{A22}$$

where $Q_0 = (b - d) + (a - b - c + d)w$ and $R_0 = d + (c - d)w$ and with equality on the right side only at equilibrium. Since

$$\frac{R_0^2 + (a - c)(w^2 Q_0 + 2wR_0)}{(wQ_0 + R_0)^2} > -1, \tag{A23}$$

where $Q_0 \geq 0$, i.e., for $0 \leq w \leq w^*$ (cf. (A13)), we conclude that $-Q(w) < Q(w') \leq Q(w)$ if $w < w^*$ with $|w - w^*|$ small enough. A corresponding result holds when $w > w^*$ by virtue of symmetry. To sum up we have

$$|Q(w')| \leq |Q(w)| \tag{A24}$$

in a small neighborhood of w^* with equality only at equilibrium. (The reverse inequality can easily be deduced from (A6) if $dQ(w^*)/dw > 0$.)

Proof of Pointwise Convergence

It has been established that a phenotypic equilibrium $w = w^*$ (such that $Q(w^*) = 0$) with $dQ(w^*)/dw < 0$ is locally stable as a *manifold* in the simplex of frequency vectors Δ . We propose now to prove *pointwise* convergence, i.e., convergence of the iterates of transformation (A2) to a *point* of the equilibrium manifold from any initial allelic frequency vector in the domain of attraction of that manifold. The proof will be based on a more accurate estimate of the decay of $|Q|$ near w^* .

LEMMA A. Consider recurrence transformation (A2) and let w^* ($0 < w^* < 1$) be a zero of $Q(w)$ with $dQ(w^*)/dw < 0$. Then the successive values of Q near w^* satisfy

$$|Q'| \leq (1 - C\sigma^2) |Q|, \quad (\text{A25})$$

where C is a positive constant and $\sigma^2 = \sigma^2(\mathbf{p}) = \sum_{i=1}^n p_i (w_i - w)^2$.

Proof. Via a first-order approximation of the fitness functions near w^* if necessary (cf. Addendum to Appendix), it will be sufficient to consider the linear case for which $Q = (b - d) + (a - b - c + d)w$ with $(a - b - c + d) < 0$. Moreover, recall that if a function $f(x)$ is twice differentiable on some finite interval and the second derivative is bounded below by some constant $\alpha > 0$, then for any set of values x_1, \dots, x_n in that interval with corresponding frequencies p_1, \dots, p_n ($0 \leq p_i \leq 1$, $\sum_{i=1}^n p_i = 1$) we have the inequalities

$$\sum_{i=1}^n p_i f(x_i) \geq f\left(\sum_{i=1}^n p_i x_i\right) + \frac{\alpha}{2} \sum_{i=1}^n p_i (x_i - \mu)^2 \geq f\left(\sum_{i=1}^n p_i x_i\right), \quad (\text{A26})$$

where $\mu = \sum_{i=1}^n p_i x_i$. Indeed the Taylor expansion of $f(x)$ about μ , namely,

$$f(x) = f(\mu) + \frac{df}{dx}(\mu)(x - \mu) + \frac{1}{2} \frac{d^2f}{dx^2}(\xi)(x - \mu)^2$$

for some ξ between x and μ , leads to

$$f(x_i) \geq f(\mu) + \frac{df}{dx}(\mu)(x_i - \mu) + \frac{\alpha}{2} (x_i - \mu)^2 \quad (\text{A27})$$

which, multiplied by p_i and summed over i , yields (A26).

Successive applications of (A26) give the following inequalities in the notation of (A2):

$$\begin{aligned}
 \sum_{i,j} v_{ij} p_i w_i p_j w_j &= \sum_{i,j,k} v_{ij} v_{ik} p_i p_j p_k w_j \\
 &= \sum_{i,j,k} v_{ij} v_{ik} p_i p_j p_k \left\{ \frac{w_j + w_k}{2} \right\} \\
 &\geq \sum_{i,j,k} v_{ij} v_{ik} p_i p_j p_k \sqrt{w_j w_k} \\
 &= \sum_i p_i \left(\sum_j v_{ij} p_j \sqrt{w_j} \right)^2 \tag{A28} \\
 &\geq \left(\sum_{i,j} v_{ij} p_i p_j \sqrt{w_j} \right)^2 \\
 &= \left(\sum_j p_j w_j^{3/2} \right)^2 \quad (\text{Kingman, 1961a}) \\
 &\geq (w^{3/2} + \frac{3}{8} \sigma^2)^2 \\
 &\geq w^3 + \frac{3}{4} w^2 \sigma^2 \quad (\text{Lyubich et al., 1980}).
 \end{aligned}$$

We have also

$$\sum_i p_i w_i^2 \geq w^2 + \sigma^2. \tag{A29}$$

Therefore is $Q > 0$, the following lower bound for w' is readily deduced from (A3):

$$w' \geq w + C_1 \sigma^2 Q, \tag{A30}$$

where $C_1 = \min_{0 \leq w \leq 1} \{ (\frac{3}{4} Q w^2 + 2R) / (wQ + R)^2 \} > 0$, i.e.,

$$Q' \leq (1 - C_2 \sigma^2) Q \tag{A31}$$

with $C_2 = -(a - b - c + d) C_1 > 0$. Moreover, in view of (A12), there exists a constant $C_3 = \min_{Q > 0} \{ g(w) / (wQ + R)^2 \} > 0$ with $g(w)$ of (A14) such that

$$Q' \geq -(1 - C_3) Q \geq -(1 - C_3 \sigma^2) Q, \tag{A32}$$

where $Q > 0$. (The last inequality comes from $0 \leq \sigma^2 \leq 1$.) Then (A25) is satisfied with $C = \min\{C_2, C_3\}$ in the case $Q > 0$, and similarly when $Q < 0$ by symmetry. The proof of Lemma A is complete.

PROPOSITION A. *Let $w(\mathbf{p}) = w^*$ be a stable phenotypic equilibrium manifold for transformation (A2) (cf. Lemma A) on which $\sigma^2(\mathbf{p}) > 0$. Then pointwise convergence occurs at least in some neighborhood of $w(\mathbf{p}) = w^*$.*

Remark. Proposition A is of general validity (without any condition on

$\sigma^2(\mathbf{p})$ using the estimate $|w - w^*| = O(\sigma^{4/3})$ near every genotypic equilibrium \mathbf{p}^* (i.e., $\sigma^2(\mathbf{p}^*) = 0$) with $w(\mathbf{p}^*) = w^*$ (cf. Lyubich *et al.*, 1980).

Proof. From (A2), we have

$$p'_i - p_i = \frac{p_i(w_i - w)Q}{wQ + R}, \quad i = 1, \dots, n. \quad (\text{A33})$$

Using the norm $\|\cdot\|$ defined by $\|\mathbf{x}\| = \sum_{i=1}^n |x_i|$ for $\mathbf{x} = (x_1, \dots, x_n)$, we have

$$\|\mathbf{p}' - \mathbf{p}\| = \frac{|Q|}{wQ + R} \sum_{i=1}^n p_i |w_i - w| \leq \frac{|Q| \sigma}{wQ + R}, \quad (\text{A34})$$

where $\sigma^2 = \sigma^2(\mathbf{p}) = \sum_{i=1}^n p_i (w_i - w)^2$. In some neighborhood of $w(\mathbf{p}) = w^*$, there exists a constant $\varepsilon > 0$ such that $\sigma > \varepsilon$ by continuity of $\sigma = \sigma(\mathbf{p})$ while $|Q| \sigma^2 \leq (|Q| - |Q'|)/C$ for some constant $C > 0$ by (A25), so that

$$\frac{|Q| \sigma}{wQ + R} \leq \frac{|Q| \sigma^2}{\sigma(wQ + R)} \leq \frac{|Q| - |Q'|}{\varepsilon C(wQ + R)} \leq B \{|Q| - |Q'|\}, \quad (\text{A35})$$

where $B^{-1} = \min_{0 \leq w \leq 1} \varepsilon C(wQ + R)$. Combining (A34) and (A35) for the successive values $\mathbf{p}^{(k)}$ of \mathbf{p} with $w(\mathbf{p})$ near w^* leads to

$$\begin{aligned} \|\mathbf{p}^{(n)} - \mathbf{p}^{(m)}\| &= \left\| \sum_{k=m+1}^n (\mathbf{p}^{(k)} - \mathbf{p}^{(k-1)}) \right\| \\ &\leq \sum_{k=m+1}^n \|\mathbf{p}^{(k)} - \mathbf{p}^{(k-1)}\| \\ &\leq B \sum_{k=m+1}^n \{|Q^{(k-1)}| - |Q^{(k)}|\} \\ &= B \{|Q^{(m)}| - |Q^{(n)}|\} \\ &\leq B |Q^{(m)}|. \end{aligned}$$

Since the successive values $|Q^{(m)}|$ of $|Q|$ decrease (geometrically fast) to zero in view of Lemma A, convergence of $\mathbf{p}^{(n)}$ (at a geometric rate) ensues.

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