

THE EVOLUTION OF DISPERSAL IN A MODEL
OF MIXED SELFING AND RANDOM MATING

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Introduction

The relationship between the mating system and extent of dispersal is believed to be of central importance to the evolution of breeding systems in plants and animals (Baker, 1967; Cheney and Seyfarth, 1983). In this paper, we present a model that examines the effects of the selfing rate on the evolution of migration (used synonymously with dispersal in this paper) rates. The model is one of a class of modifier models, multi-gene models in which a selectively neutral locus influences a trait that may be of evolutionary significance, e.g. mutation rate, migration rate, or recombination rate. Here, the modified trait is the rate of migration between two demes in which the major gene controls the level of selfing. It would obviously be most appropriate to study a diploid model. This turns out to be extremely difficult in the present case so we approximate the more realistic model by a haploid one.

A correlation between the tendencies to outbreed and to disperse has been noted by botanists and zoologists. There seems to be an association between parthenogenesis and reduced dispersal in insects (Bell, 1982). Also, a correlation between the distance a seed disperses and the probability that it has been produced by out-crossing has been documented in several plant species (Holsinger, 1986). This is most evident in plants with cleistogamous and chasmogamous flowers. Seeds produced by chasmogamous (potentially out-crossed) flowers tend to disperse further than those produced by

cleistogamous (obligately self-fertilized) flowers (Cheplick and Clay, 1989; Schmitt et al., 1985). “Baker’s Law” (described in Baker, 1967) proposes an alternative relationship between the mating system and dispersal. This theory predicts that self-compatibility should be associated with long-distance dispersal so that mating could be assured when an individual migrates to a previously uncolonized site. Baker (1967) cites evidence from the breeding systems of island flora to support this theory.

Modifier theory is the study of the evolutionary dynamics of multi-locus systems where at least one locus is under selection and another (the modifier locus) is a neutral locus whose effect is to alter a trait of fundamental evolutionary importance. The goal of this type of analysis is to provide a formal population genetic basis for the evolution of the trait of interest. In these models, an increase in the frequency of the modifier allele entails a specific direction of change in the population average of the modifier trait. Migration modifier models are those where the neutral locus controls the migration rate of an individual. These models predict that the migration rate between random mating populations subject to different viability selection pressures will tend to decrease (Balkau and Feldman, 1973; Liberman and Feldman, 1989). Lower migration rates allow sub-populations to adapt to local selection pressures. The predictions of these models are in sharp contrast to those of single-locus genetic models where dispersal of offspring occurs between an infinite number of sites, each inhabited by a single adult (Hamilton

and May, 1977; Motro, 1983a,b, 1984; Frank, 1986). Analysis of these models produces non-zero optimal rates of migration.

In this model, we examine whether higher migration rates can evolve in a population in which selfing is genetically controlled. One result of non-random mating, when considered in a multi-locus context, is that linkage disequilibrium can develop even if there is no physical linkage. Earlier studies on mixed random mating and selfing in the modifier context revealed that the inclusion of non-random mating can qualitatively alter the dynamics of a system (see Holsinger and Feldman, 1983a and 1983b for examples from mutation and recombination modification). This is due to linkage disequilibrium generated by non-random mating. In the context of modification, associations may develop between the fittest genotypes at the viability locus and modifier genotypes which may be disfavored under random mating (see Uyenoyama and Bengtsson, 1989). These associations may drive the coevolutionary dynamics between traits (e.g. migration and mating behavior). In purely random mating situations, on the other hand, there seems to be an evolutionary principle of reduction that applies to modifiers of recombination, mutation and migration (Feldman and Liberman, 1986).

The model we develop in the present note allows genetic associations to develop between the level of selfing and the amount of migration. This is important because both migration and the mating system can be heritable so that the assumption that

they evolve independently may be misleading. Furthermore, our model lends theoretical context to several empirical studies which have documented the heritability of dispersal ability (Palmer and Dingle, 1989, in milkweed bugs; Harper, 1977, in agricultural plants; see Harrison, 1980 for other examples in insects) and mating tendency (Cruz-Pardilla, et al., 1989 in rye; Wyatt, 1990, in several plants; Rick, 1990, in cultivated tomato and cucurbits). Clay (1982) has shown that the degree of cleistogamy, a trait influencing both breeding tendency and dispersal ability, may be heritable.

The Model

Two large populations of haploid hermaphrodites inhabiting ecologically distinct sites are considered. The two sites are differentiated by the loss in viability of offspring produced by self-fusion of gametes (hereafter referred to as selfing). Thus, on site x , the viability of selfed offspring is $1 - s_x$ and on site y , $1 - s_y$. This assumption allows the maintenance of a polymorphism at a locus determining the rate of selfing. While we view this model as an approximation to the diploid version, inbreeding depression cannot be generated in the same way (i.e. by over-dominance or recessive lethal mutations in the homozygous state). We envision that the cost of selfing in this model results from some physiological mechanism (e.g. gametic incompatibility at another locus). The individuals are haploid for most of their life cycle, fusing for a short time in order to undergo meiosis. Selfing involves fusing of gametes from the same parent and random

mating involves fusing of gametes from individuals within a site. The adult generation dies and the offspring undergo viability selection. Migration then occurs between the two sites and the cycle repeats.

We consider a two-locus model in which the first locus determines the selfing rate and the second (neutral) locus determines the tendency of the haploid individuals to migrate to the other site. There are four genotypes with the following associated parameters:

genotype	selfing rate	migration rate	frequency
S_1M_1	α_1	m_1	x_{11} (or y_{11})
S_1M_2	α_1	m_2	x_{12} (or y_{12})
S_2M_1	α_2	m_1	x_{21} (or y_{21})
S_2M_2	α_2	m_2	x_{22} (or y_{22})

The recombination rate between the two loci is represented by r ($0 \leq r \leq 1/2$). The discounting rate is represented by δ ($0 \leq \delta \leq 1$) and has the following meaning. δ measures the effect of selfing on the composition of the pollen pool. Thus, a fraction, $1 - \delta\alpha_i$, of the pollen of individuals with selfing rate α_i enters the random mating pool (δ here is equivalent to that in Holsinger, 1986). If $\delta = 0$, then the amount of pollen available for random mating is not at all diminished by selfing in the population. This corresponds to the case where pollen:ovule ratio is virtually infinite. If $\delta = 1.0$, then

the amount of pollen available for random mating is exactly that proportion *not* used for selfing. This corresponds to the case where the pollen:ovule ratio is near 1.0. Because selfing has an associated cost (s_x or s_y), S is therefore a fitness-determining locus.

Analysis

Analysis of this model entails two steps: (1) a characterization of the polymorphic equilibrium at the mating locus, and (2) a study of the conditions for initial increase of new alleles at the migration locus. We are able to describe the fate of a second allele introduced at the migration locus by using implicit formulations of the equilibrium conditions at the first locus (without knowing the actual equilibrium values of the genotype frequencies).

Conditions for Polymorphism at the Mating Locus

The recursions describing the evolutionary dynamics of the system are shown in Appendix 1. In order to derive conditions for a polymorphism at the mating locus, we consider the case where no migration occurs between the two sites. We derive the conditions for *different* selfing alleles to be maintained at the two sites. Then, the small parameter theory of Karlin and McGregor (1972) can be applied when the migration rate, m_1 is small. Since this is a haploid model, a polymorphism cannot be maintained within a site if there is no migration between sites in the population. This suggests that a stable polymorphism can be maintained only when different S -alleles are favored on

the different sites *and* migration is non-zero.

Without loss of generality, we can assume $\alpha_1 > \alpha_2$. The condition for simultaneous fixation of allele S_2 on site 1 and allele S_1 on site 2 is

$$s_y < (1 - \delta)/2(1 - \alpha_2\delta) < (1 - \delta)/2(1 - \alpha_1\delta) < s_x \quad (1)$$

(note that these inequalities switch direction if $\alpha_2 > \alpha_1$ or if we look at the maintenance of S_1 on site 1 and S_2 on site 2).

We gain some insight into the characteristics of a polymorphism by looking at the case with no migration for the two extreme values of δ . In the $\delta = 0.0$ case, the condition for maintaining both S -alleles simplifies to $s_y < 1/2 < s_x$. This is a similar result to that seen in models for the evolution of sexual reproduction (Maynard Smith, 1978; Uyenoyama, 1984). If the cost of selfing is less than 1/2, selfing will be advantageous (as seen in other models, e.g. Feldman and Christiansen, 1984). Selfing here (and parthenogenesis in other models) has a two-fold advantage over random mating (or sexual reproduction). In the sub-population with a cost less than 1/2, high selfing rates can be maintained. If, however, the cost of selfing is greater than 1/2, its two-fold advantage will not be enough and the lower selfing rate will be favored.

The “two-fold” trade-off between the cost and advantage of selfing arises when there is no pollen discounting ($\delta = 0.0$) because in this case, selfing does not diminish the amount of pollen available for random mating. Each pollen grain can be viewed as

contributing to a self-fertilization event as well as to an out-crossing event. Therefore, selfers have intrinsically twice the fertility of out-crossers. This allows both alleles to be maintained when the cost of selfing is great enough to outweigh the fertility advantage on one of the sites and not on the other.

If, however, $\delta = 1.0$, selfing is disadvantageous in both sub-populations. Lower selfing will be favored in both sub-populations (unless $s_x = s_y = 0.0$, so that the selfing locus is neutral). In contrast to the $\delta = 0.0$ case, when $\delta = 1.0$, each pollen grain involved in selfing is, in essence, removed from the random mating pool. Thus, there is no fertility advantage to selfers and as long as $s_x, s_y > 0$, there is a viability disadvantage. Therefore, even with migration between sites, stable polymorphism will not be possible when $\delta = 1.0$.

As δ approaches 1.0, the condition for maintaining both alleles becomes more restrictive. There is some value of δ above which only one allele will exist at equilibrium. If we again assume $s_y < 1/2 < s_x$ (in order to ensure coexistence of alleles for $\delta = 0.0$), we can derive bounds on δ which allow the simultaneous maintenance of two selfing alleles in the population. The condition involves the following inequalities:

$$\begin{aligned} \delta < (1 - s_y)/(1 - 2s_y\alpha_2) & \quad s_x\alpha_1 < \frac{1}{2} \\ \delta < \{(1 - 2s_y)/(1 - 2s_y\alpha_2) \wedge (1 - 2s_x)/(1 - 2s_x\alpha_1)\} & \quad s_x\alpha_1 > \frac{1}{2} \end{aligned} \quad (2)$$

where \wedge refers to the minimum of the two expressions. The rate of pollen discounting which will allow the simultaneous maintenance of different selfing alleles at the two sites

is a function of the selection pressures at the sites (s_x, s_y) and the selfing rates produced by the alleles (α_1, α_2). When $\alpha_2 > \alpha_1$, the condition has the same form but s_x and s_y are interchanged, as are α_1 and α_2 .

Under condition (2), the small parameter theory (K & M, 1972) allows us to conclude that for small migration rates, the alleles which are favored on individual sites will be maintained in the two-population system; that is, there will be a polymorphism involving the two selfing alleles. Thus it is clear that under a fairly broad set of conditions, a stable polymorphism at the selfing locus can exist. These results are consistent with those derived in Holsinger, Feldman and Christiansen (1984) who incorporated pollen discounting into a diploid model for the evolution of selfing in a single population.

One additional point we should make is that the polymorphism achieved under condition (1) is not necessarily evolutionarily stable. That is, on either site, alleles specifying other selfing rates could invade. However, as long as $s_y < 1/2 < s_x$ and condition (2) holds, different selfing alleles (whether evolutionarily stable or not) can be maintained on the individual sites (with no migration) and within the entire population (with low migration).

Introduction of the Modifier

The second part of the analysis concerns the invasion properties at the migration

locus. Suppose \hat{x}_{11} , \hat{x}_{21} , \hat{y}_{11} , and \hat{y}_{21} are the original equilibrium frequencies (i.e. there is a polymorphic equilibrium at the S -locus and the M -locus is fixed on M_1). Using linear stability analysis, we have determined the exact conditions under which a new allele at the modifier locus (M_2) can enter a population polymorphic at the S -locus. To do this, we have made use of the equilibrium properties of the S -locus (shown in Appendix 2). A sufficient condition for invasion is shown below:

$$\frac{1}{\hat{x}_{11}\hat{x}_{21}} \frac{(\hat{w}_y - B_1)}{\hat{w}_y} \frac{(\hat{w}_y - B_2)}{\hat{w}_y} \frac{(m_2 - m_1)}{m_1} \left\{ \frac{(\hat{w}_y - B_1)}{\hat{w}_y} \frac{(\hat{w}_y - B_2)}{\hat{w}_y} \frac{(m_2 - m_1)}{m_1} \hat{y}_{11}\hat{y}_{21} - r \frac{m_2}{2} (1 - \alpha_1)(1 - \delta\alpha_2) \left(\frac{\hat{x}_{11}\hat{x}_{21}}{w_x M_x} + \frac{\hat{y}_{11}\hat{y}_{21}}{w_y M_y} \right) \right\} < 0, \quad (3)$$

where the full recursions and definitions of the terms in (3) are shown in Appendices 1 and 2. The term on the left-hand side of (3) is the value of the characteristic polynomial of the 4×4 local stability matrix, $char(\lambda)$, at $\lambda = 1.0$.

Since the matrix describing the stability of the invasion at the migration locus is non-negative, the Perron-Frobenius Theorem tells us that there is a positive, largest eigenvalue. When $char(1) < 0$, at least one eigenvalue must be greater than one. When this condition is met, the M_2 allele (producing migration rate m_2) can invade the population. Condition (3) is sufficient but not necessary to guarantee invasion since it guarantees that one eigenvalue is greater than 1.0. If there are two eigenvalues greater than one, the condition will not be satisfied. A more detailed analysis takes account of this fact.

When $r = 0$, $char(\lambda)$ is a product of two quadratic expressions ($char_1(\lambda) \cdot char_2(\lambda)$).

Where

$$char_1(1.0) = \frac{1}{\hat{x}_{11}} \left(\frac{m_2 - m_1}{m_1} \right) \left(\frac{\hat{w}_y - B_1}{\hat{w}_y} \right)^2 \hat{y}_{11}$$

and

$$char_2(1.0) = \frac{1}{\hat{x}_{21}} \left(\frac{m_2 - m_1}{m_1} \right) \left(\frac{\hat{w}_y - B_2}{\hat{w}_y} \right)^2 \hat{y}_{21}$$

so that

$$char(1.0) = \frac{\hat{y}_{11}\hat{y}_{21}}{\hat{x}_{11}\hat{x}_{21}} \left(\frac{m_2 - m_1}{m_1} \right)^2 \left(\frac{\hat{w}_y - B_1}{\hat{w}_y} \right)^2 \left(\frac{\hat{w}_y - B_2}{\hat{w}_y} \right)^2,$$

which cannot be negative. Nevertheless, since both $char_1(1.0) < 0$ and $char_2(1.0) < 0$ for $m_2 < m_1$, a sufficient condition for invasion at $r = 0$ is $m_2 < m_1$. We show in Appendix 3 that if $m_2 > m_1$, the roots of both $char_1(\lambda)$ and $char_2(\lambda)$ are less than unity. Figures 1 and 2 show $char_1(\lambda)$, $char_2(\lambda)$ (the upper graph) and their product, $char(\lambda)$, (the lower graph), all as functions of λ . When $m_2 < m_1$ (Figure 1), two eigenvalues are greater than 1.0 (one root from each quadratic expression) and two eigenvalues are less than 1.0 (the other two roots of the quadratics). If $m_2 = m_1$, the larger eigenvalue of each quadratic is unity and fixation in M_1 is neutral to invasion by M_2 . When $m_2 > m_1$ (Figure 2), all eigenvalues must be less than 1.0. This model confirms the migration-reduction principle described by Liberman and Feldman (1989) and Balkau and Feldman (1973) for models with random mating.

If $r > 0$, the analysis is somewhat more complicated but the same result holds. We examine the changes in sign of the left side of (1) as r increases. Since w_y is a weighted average of B_1 and B_2 , $(w_y - B_1)(w_y - B_2) < 0$. If $m_2 < m_1$ then two eigenvalues are both greater than 1.0 near $r = 0.0$ and the value of $char(1.0) > 0$. (3) can be rewritten as

$$char(1.0) = \frac{\hat{y}_{11}\hat{y}_{21}}{\hat{x}_{11}\hat{x}_{21}} \left(\frac{m_2 - m_1}{m_1} \right)^2 \left(\frac{\hat{w}_y - B_1}{\hat{w}_y} \right)^2 \left(\frac{\hat{w}_y - B_2}{\hat{w}_y} \right)^2 - r * (\text{positive term})$$

which decreases as r increases. Since the largest eigenvalue of the system has multiplicity one (by the Perron-Frobenius Theorem) and $char(\lambda)$ is linear in r , $char(1)$ cannot change sign twice as r increases. Therefore, while one eigenvalue may cross to the left of 1.0, the other remains greater than 1.0, thereby preventing fixation on M_1 from becoming stable (see Figure 3).

If $m_2 > m_1$, then the four eigenvalues of the $r = 0$ case are all less than 1.0. The coefficient of r in condition (3) is positive. Therefore, increases in r make $char(1)$ more positive so that no eigenvalue can exceed 1.0 (see Figure 4) and fixation in M_1 remains stable to invasion. From this analysis, we conclude that the migration-reduction principle holds in this model for any r , $0 \leq r \leq \frac{1}{2}$.

Discussion

Results from the migration modifier model we have described confirm the migration reduction principle in a case of non-random mating among haploids.

Genetically-determined selfing rates do not affect evolution at the migration locus.

There is a discrepancy between these results and those from diploid models of mutation and recombination modification (Holsinger and Feldman, 1983a and 1983b). In those models, non-random mating allows the invasion of alleles with increased rates of the modified traits which cannot occur with random mating. It is unclear whether the difference between our model and these others is an artifact of the haploid formulation of our model or whether the models are more fundamentally different in construction. If the latter were the case, a description of that difference would be an important addition to our understanding of the dynamics of modifiers.

Like the random mating migration modifier models, the results of our analysis conflict with infinite site, single-locus dispersal models (Hamilton and May, 1977; Motro, 1982a,b, 1983; Frank, 1986). Their finding of a non-zero optimal rate of dispersal is a result of the large number of offspring produced on a site who compete to replace the parent. Some individuals risk dispersal to maximize the total number of sites captured by the sibling group. Taylor (1988) generalized these results to conclude that dispersal will be more likely to evolve when the level of inbreeding is high so that the force of kin selection will be greater. Although selfing, an extreme form of inbreeding, occurs in our model, there is no local resource competition between related individuals. Thus the forces operating in the infinite-site models do not act here. Clearly the formulation of

the model, which influences the genetic structure of the population, determines whether or not dispersal can be evolutionarily stable. One does not get a complete picture by considering the effects of genetic structure on the evolution at a migration locus without accounting for the genetic associations which cause or develop from this structure.

Further, the model described above does not address the problem of finding a mate after dispersal. It would be interesting to look at the dynamics at the mating locus when the ability to outcross is a function of population density. Baker's Law predicts that we should see a positive association develop between migration rate and selfing rate when uncolonized sites may be encountered.

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APPENDIX 1

The full, two locus recursions are as follows:

$$\begin{aligned}
 T_x x'_{11} &= x_{11}^*(1 - m_1) + y_{11}^* m_1 & T_y y'_{11} &= y_{11}^*(1 - m_1) + x_{11}^* m_1 \\
 T_x x'_{12} &= x_{12}^*(1 - m_2) + y_{12}^* m_2 & T_y y'_{12} &= y_{12}^*(1 - m_2) + x_{12}^* m_2 \\
 T_x x'_{21} &= x_{21}^*(1 - m_1) + y_{21}^* m_1 & T_y y'_{21} &= y_{21}^*(1 - m_1) + x_{21}^* m_1 \\
 T_x x'_{22} &= x_{22}^*(1 - m_2) + y_{22}^* m_2 & T_y y'_{22} &= y_{22}^*(1 - m_2) + x_{22}^* m_2
 \end{aligned}$$

where

$$\begin{aligned}
 T_x &= 1 + (m_1 - m_2)(x_{12}^* + x_{22}^* - y_{12}^* - y_{22}^*) \\
 T_y &= 1 - (m_1 - m_2)(x_{12}^* + x_{22}^* - y_{12}^* - y_{22}^*),
 \end{aligned}$$

and the chromosome frequencies x_{ij}^* after mating and selection satisfy

$$\begin{aligned}
 \bar{w}_x x_{11}^* &= \frac{1}{M_x} \left\{ x_{11}^2 (1 - \alpha_1)(1 - \delta\alpha_1) + x_{11}x_{12}(1 - \alpha_1)(1 - \delta\alpha_1) \right. \\
 &\quad + \frac{1}{2} x_{11}x_{21} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \\
 &\quad + \frac{1}{2} (1 - r)x_{11}x_{22} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \\
 &\quad \left. + \frac{1}{2} r x_{21}x_{12} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right\} \\
 &\quad + \alpha_1 x_{11}(1 - s_x)
 \end{aligned}$$

$$\begin{aligned}
 \bar{w}_x x_{12}^* &= \frac{1}{M_x} \left\{ x_{12}^2 (1 - \alpha_1)(1 - \delta\alpha_1) + x_{11}x_{12}(1 - \alpha_1)(1 - \delta\alpha_1) \right. \\
 &\quad + \frac{1}{2} x_{12}x_{22} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \\
 &\quad + \frac{1}{2} (1 - r)x_{21}x_{12} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \\
 &\quad \left. + \frac{1}{2} r x_{11}x_{22} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right\} \\
 &\quad + \alpha_1 x_{12}(1 - s_x)
 \end{aligned}$$

$$\begin{aligned}
\bar{w}_x x_{21}^* &= \frac{1}{M_x} \left\{ x_{21}^2 (1 - \alpha_2)(1 - \delta\alpha_2) + \frac{1}{2} x_{11} x_{21} [(1 - \alpha_1)(1 - \delta\alpha_2) \right. \\
&\quad \left. + (1 - \alpha_2)(1 - \delta\alpha_1)] + x_{21} x_{22} (1 - \alpha_2)(1 - \delta\alpha_2) \right. \\
&\quad \left. + \frac{1}{2} (1 - r) x_{12} x_{21} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right. \\
&\quad \left. + \frac{1}{2} r x_{11} x_{22} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right\} \\
&\quad + \alpha_2 x_{21} (1 - s_x)
\end{aligned}$$

$$\begin{aligned}
\bar{w}_x x_{22}^* &= \frac{1}{M_x} \left\{ x_{22}^2 (1 - \alpha_2)(1 - \delta\alpha_2) + \frac{1}{2} x_{12} x_{22} [(1 - \alpha_1)(1 - \delta\alpha_2) \right. \\
&\quad \left. + (1 - \alpha_2)(1 - \delta\alpha_1)] + x_{21} x_{22} (1 - \alpha_2)(1 - \delta\alpha_2) \right. \\
&\quad \left. + \frac{1}{2} (1 - r) x_{11} x_{22} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right. \\
&\quad \left. + \frac{1}{2} r x_{21} x_{12} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right\} \\
&\quad + \alpha_2 x_{22} (1 - s_x),
\end{aligned}$$

where

$$M_x = 1 - \delta (\alpha_1 (x_{11} + x_{12}) + \alpha_2 (x_{21} + x_{22})),$$

$$\begin{aligned}
\bar{w}_x &= \frac{1}{M_x} \left\{ (x_{11} + x_{12})^2 (1 - \alpha_1)(1 - \delta\alpha_1) + (x_{22} + x_{21})^2 (1 - \alpha_2)(1 - \delta\alpha_2) \right. \\
&\quad \left. + \frac{1}{2} (x_{11} + x_{12})(x_{22} + x_{21}) [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right\} \\
&\quad + (1 - s_x) (\alpha_1 (x_{11} + x_{12}) + \alpha_2 (x_{21} + x_{22})).
\end{aligned}$$

The equations describing the dynamics at site 2 can be derived by substituting y_{11}^* , y_{12}^* , y_{21}^* , and y_{22}^* for x_{11}^* , x_{12}^* , x_{21}^* , and x_{22}^* , respectively, s_y for s_x , \bar{w}_y for \bar{w}_x , and M_y for M_x .

APPENDIX 2

Equilibrium conditions for the selfing locus:

$$\begin{aligned}\frac{\hat{w}_x - (1 - m_1)A_1}{\hat{w}_x} \hat{x}_{11} - \frac{m_1 B_1}{\hat{w}_y} \hat{y}_{11} &= 0 \\ \frac{\hat{w}_x - (1 - m_1)A_2}{\hat{w}_x} \hat{x}_{21} - \frac{m_1 B_2}{\hat{w}_y} \hat{y}_{21} &= 0 \\ \frac{\hat{w}_y - (1 - m_1)B_1}{\hat{w}_y} \hat{y}_{11} - \frac{m_1 A_1}{\hat{w}_x} \hat{x}_{11} &= 0 \\ \frac{\hat{w}_y - (1 - m_1)B_2}{\hat{w}_y} \hat{y}_{21} - \frac{m_1 A_2}{\hat{w}_x} \hat{x}_{21} &= 0,\end{aligned}$$

where

$$\begin{aligned}A_1 &= \frac{1}{\widehat{M}_x} \left[\hat{x}_{11}(1 - \alpha_1)(1 - \delta\alpha_1) + \frac{1}{2} \hat{x}_{21} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right] \\ &\quad + \alpha_1(1 - s_x)\end{aligned}$$

$$\begin{aligned}A_2 &= \frac{1}{\widehat{M}_x} \left[\hat{x}_{21}(1 - \alpha_2)(1 - \delta\alpha_2) + \frac{1}{2} \hat{x}_{11} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right] \\ &\quad + \alpha_2(1 - s_x)\end{aligned}$$

$$\begin{aligned}B_1 &= \frac{1}{\widehat{M}_y} \left[\hat{y}_{11}(1 - \alpha_1)(1 - \delta\alpha_1) + \frac{1}{2} \hat{y}_{21} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right] \\ &\quad + \alpha_1(1 - s_y)\end{aligned}$$

$$\begin{aligned}B_2 &= \frac{1}{\widehat{M}_y} \left[\hat{y}_{21}(1 - \alpha_2)(1 - \delta\alpha_2) + \frac{1}{2} \hat{y}_{11} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right] \\ &\quad + \alpha_2(1 - s_y).\end{aligned}$$

$$\widehat{M}_x = 1 - \delta(\alpha_1 \hat{x}_{11} + \alpha_2 \hat{x}_{21}),$$

$$\widehat{M}_y = 1 - \delta(\alpha_1 \hat{y}_{11} + \alpha_2 \hat{y}_{21}),$$

$$\begin{aligned} \hat{w}_x = \frac{1}{\widehat{M}_x} & \left\{ \hat{x}_{11}^2 (1 - \alpha_1)(1 - \delta\alpha_1) + \hat{x}_{21}^2 (1 - \alpha_2)(1 - \delta\alpha_2) \right. \\ & \left. + \frac{1}{2} \hat{x}_{11} \hat{x}_{21} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right\} + (1 - s_x)(\alpha_1 \hat{x}_{11} + \alpha_2 \hat{x}_{21}), \end{aligned}$$

$$\begin{aligned} \hat{w}_y = \frac{1}{\widehat{M}_y} & \left\{ \hat{y}_{11}^2 (1 - \alpha_1)(1 - \delta\alpha_1) + \hat{y}_{21}^2 (1 - \alpha_2)(1 - \delta\alpha_2) \right. \\ & \left. + \frac{1}{2} \hat{y}_{11} \hat{y}_{21} [(1 - \alpha_1)(1 - \delta\alpha_2) + (1 - \alpha_2)(1 - \delta\alpha_1)] \right\} + (1 - s_y)(\alpha_1 \hat{y}_{11} + \alpha_2 \hat{y}_{21}). \end{aligned}$$

APPENDIX 3

For $r = 0.0$, to show that all eigenvalues are less than 1.0 for all $m_2 > m_1$ it is sufficient to show that the eigenvalues decrease as m_2 increases. This is sufficient since we know that for $m_2 < m_1$, two of them are greater than 1.0 and at $m_2 = m_1$, two are equal to 1.0. Thus we must show $\frac{\partial \lambda_i^*}{\partial m_2} < 0$, where $\text{char}_i(\lambda_i^*) = 0$ (i.e. λ_i^* is an eigenvalue of the invasion matrix). Here, λ_i^* is a function of m_2 with $a_i = \frac{A_i}{w_x}$, and $b_i = \frac{B_i}{w_y}$ from Appendix

2. We can show $\frac{\partial \lambda_i^*}{\partial m_2} = \frac{2a_i b_i - \lambda_i^*(a_i + b_i)}{2\lambda_i^* - (1 - m_2)(a_i + b_i)}$. Solving for λ_i^* from $\text{char}_i(\lambda_i^*) = 0$ gives

$$\lambda_i^* = \frac{1}{2}(1 - m_2)(a_i + b_i) \pm \frac{1}{2}\sqrt{(1 - 2m_2)(a_i - b_i)^2 + (a_i + b_i)^2 m_2^2}. \text{ Thus,}$$

$$\frac{\partial \lambda_i^*}{\partial m_2} = \frac{2a_i b_i - \lambda_i^*(a_i + b_i)}{\pm \sqrt{(1 - 2m_2)(a_i - b_i)^2 + (a_i + b_i)^2 m_2^2}}. \text{ Here, } +\sqrt{\text{ }} \text{ refers to the larger eigenvalue and } -\sqrt{\text{ }} \text{ to}$$

the smaller one, for $\text{char}_i(\lambda_i^*)$. For $\frac{\partial \lambda_i^*}{\partial m_2} < 0$ therefore we need

$$\left| 2a_i b_i - \frac{(a_i + b_i)^2(1 - m_2)}{2} \right| < \frac{(a_i + b_i)}{2} \sqrt{(1 - 2m_2)(a_i - b_i)^2 + (a_i + b_i)^2 m_2^2}. \text{ By algebraic ma-}$$

nipulation, we can show that this condition is equivalent to $(a_i - b_i)^2 < (a_i + b_i)^2$ which must be true since a_i and b_i are real. We can use this argument to claim that $\frac{\partial \lambda_i^*}{\partial m_2} < 0$ for

both eigenvalues of $\text{char}_1(\lambda)$ and $\text{char}_2(\lambda)$.

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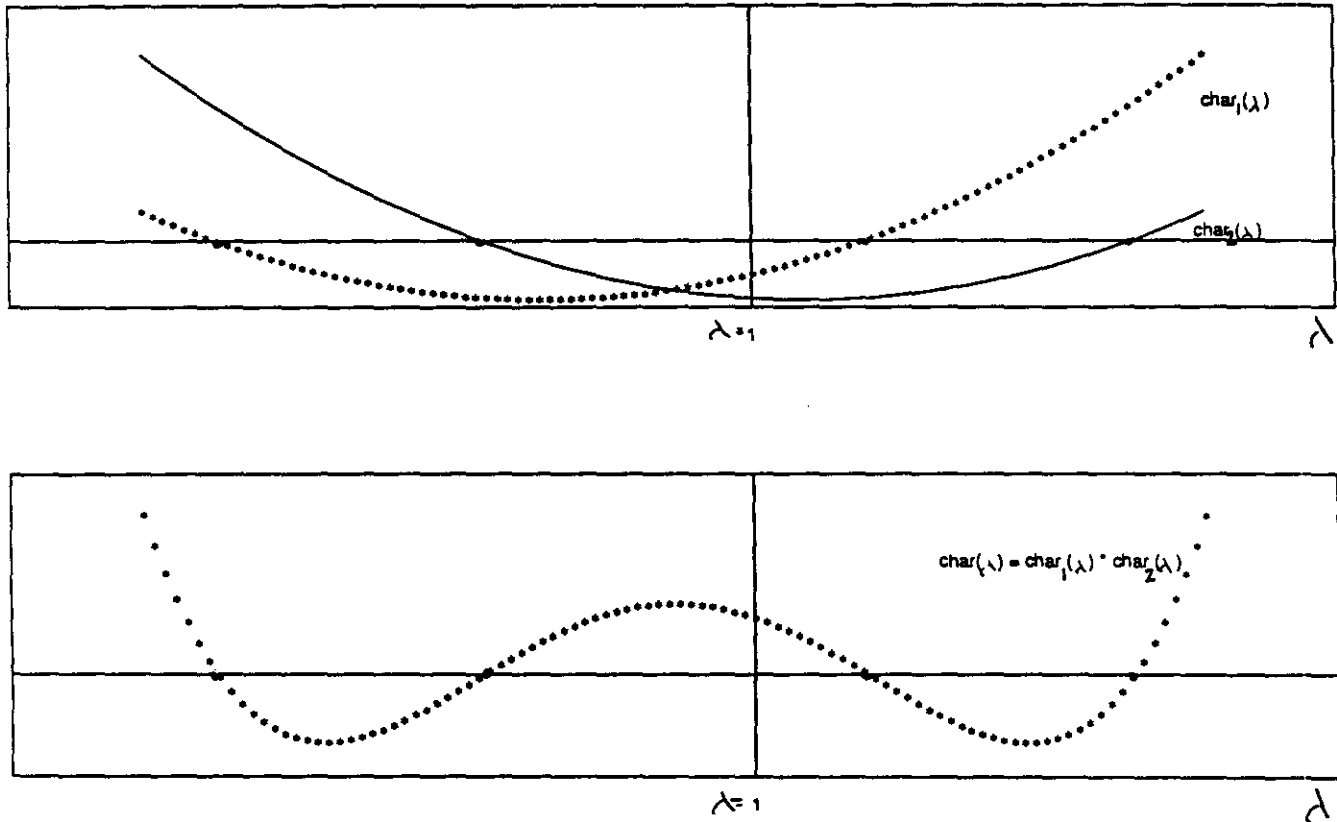


Figure 1. Graph of the characteristic polynomial as a function of λ for $m_2 < m_1$ ($r = 0.0$). When $r = 0.0$, the characteristic polynomial can be written as a product of two quadratic polynomials (top figure) or equivalently as a fourth-degree characteristic polynomial (bottom figure). Two roots of the characteristic polynomial (i.e. eigenvalues of the system) are greater than 1.0 when $m_2 < m_1$.

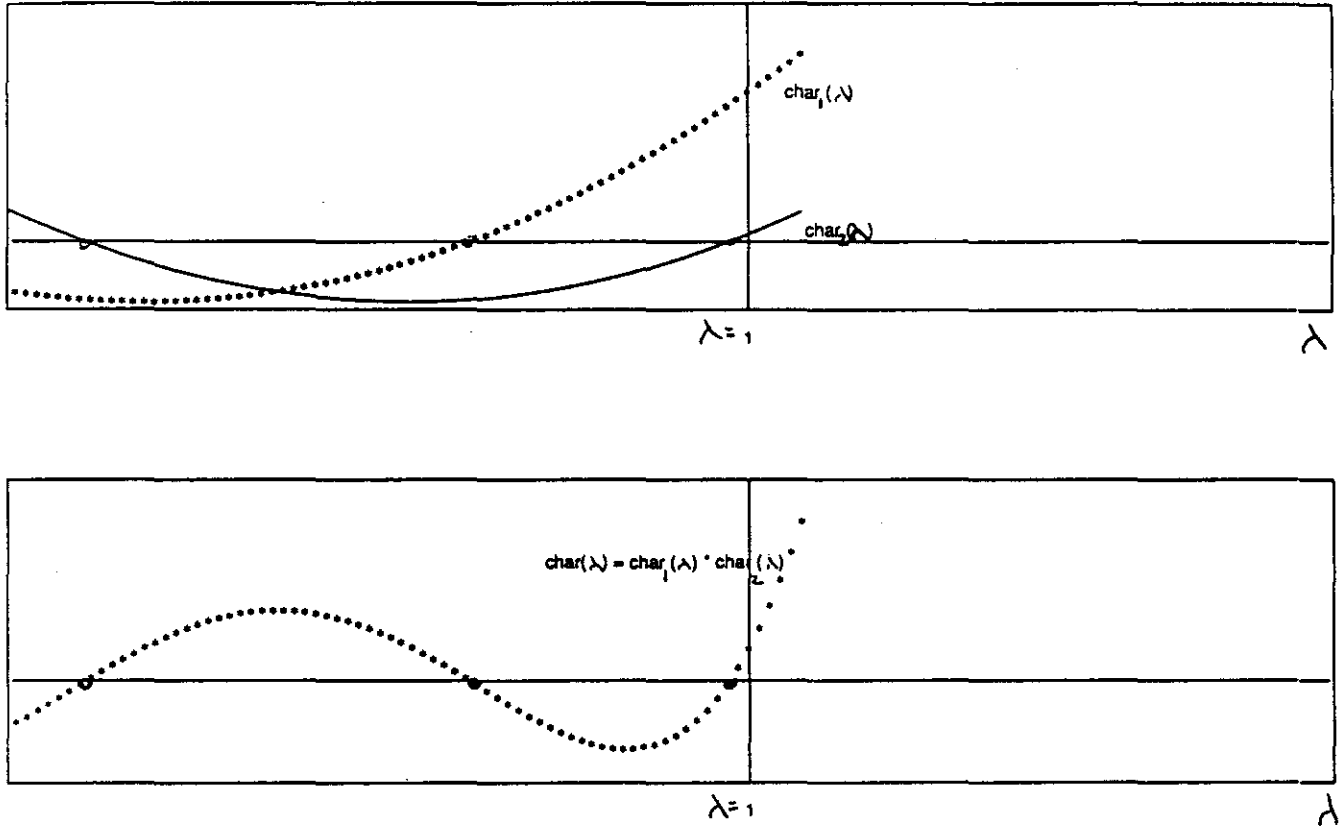


Figure 2. Graph of the characteristic polynomial as a function of λ for $m_2 > m_1$ ($r = 0.0$). As in Figure 1, the quadratic polynomials are shown above, and their product, the fourth-degree polynomial is shown below. All four eigenvalues are less than 1.0 when $m_2 > m_1$.

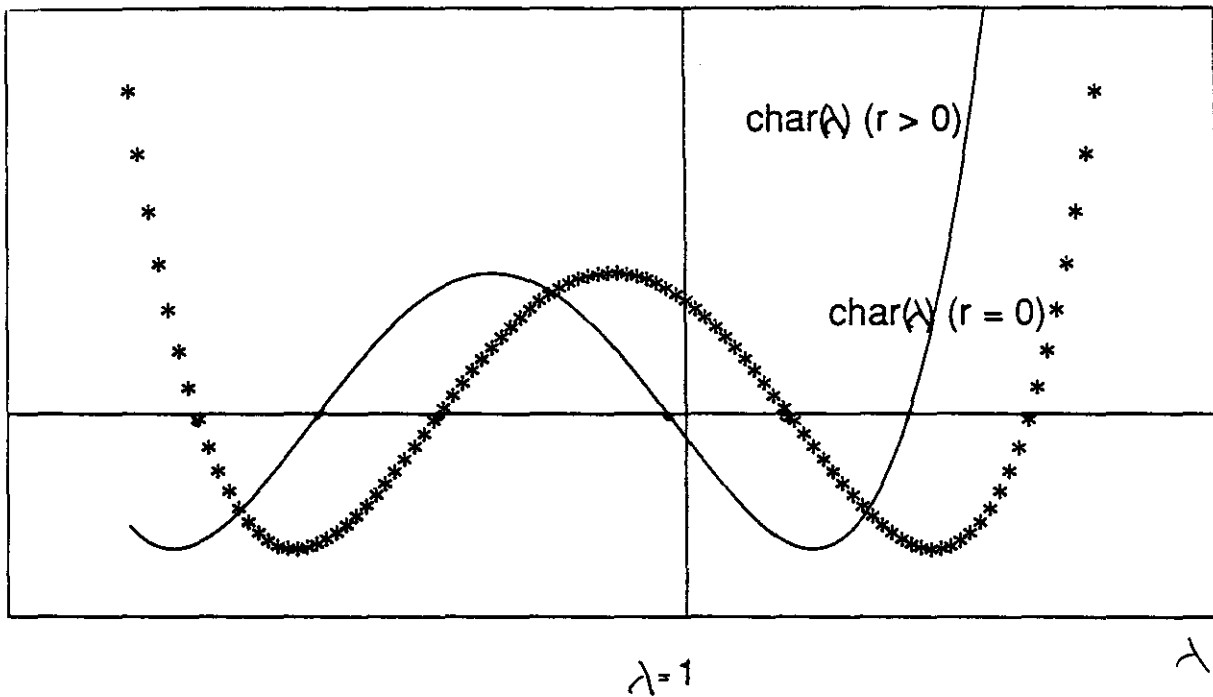


Figure 3. Graph of the characteristic polynomial as a function of the recombination rate (r) for $m_2 < m_1$. For r very small, there are two roots (i.e. eigenvalues) greater than 1.0 (as seen in Figure 1. As r increases, the polynomial shifts to the left so that one root may pass through $\lambda = 1.0$ but not both (see text).

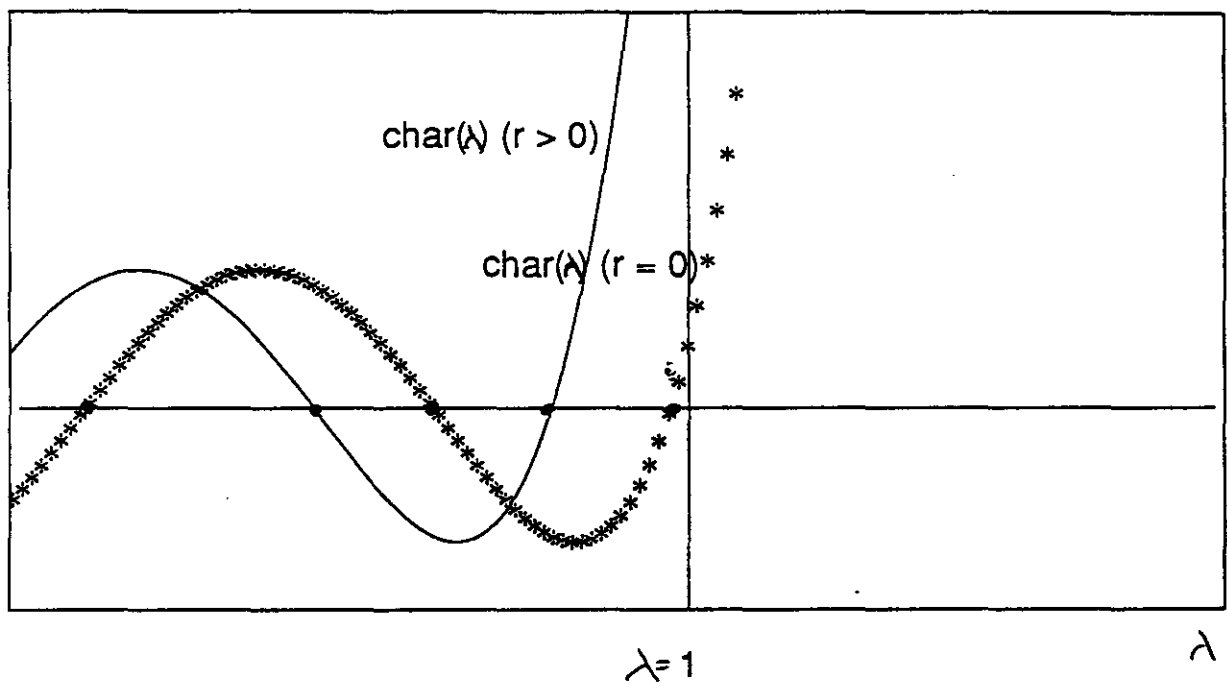


Figure 4. Graph of the characteristic polynomial as a function of the recombination rate (r) for $m_2 > m_1$. As r increases, the polynomial shifts to the left so that all eigenvalues decrease (preventing any from exceeding 1.0).