Evolving gene frequencies in a population with three possible alleles at a locus

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Abstract
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Keywords
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Evolving gene frequencies in a population with three possible alleles at a locus

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Abstract

A number of models involving reaction–diffusion equations have been developed by different authors to describe the changes in frequency of alleles in a population. Each of these models describes the case in which there are only two possible alleles at the locus in question. In the present paper, we are interested in the more realistic possibility of three alternative alleles. A system of reaction–diffusion equations can be developed to describe this situation. After transforming to the traveling wave coordinates, we introduce a nonlinear transformation which allows us to find exact solutions under certain conditions imposed on two of the parameters.

Keywords: Reaction–diffusion equations; Traveling wave solutions; Changing gene frequencies; Gene propagation

1. Introduction

To date there has been a great deal of interest in developing equations to describe the changes in the frequency of alleles in a population that has two possible alleles at the locus in question (for example [1–8]). In particular, some have studied the advance of a mutant advantageous gene through a population (for example [9,10]). Very few authors have examined situations in which there are more than two possible alleles at the locus in question, and they have mostly used stochastic models, for example [11]. In this paper, we are interested in the case in which there is a total of three possible alleles at the locus in question, resulting in six possible genotypes in the population. A system of reaction–diffusion–convection equations can be developed to describe this situation.

Many of the techniques used in the study of reaction–diffusion equations cannot easily be extended to the study of systems of equations. It is only in recent times that new methods are becoming available that enable the features of a system of equations to be analyzed. This is perhaps one of the reasons why only the simplest cases of gene invasion have been studied to date. After developing the system of reaction–diffusion equations, we find a new exact traveling wave solution using the method of Rodrigo and Mimura [12].

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Throughout this paper we assume that all genotypes have a similar death rate. Any differences in fitness and survival rates between the different phenotypes are attributed to variations in reproductive success rates. We can do this without loss of generality, since choosing a single common reproductive success rate and different death rates ultimately results in the same class of gene dispersal equations [1].

We assume that the genes at the locus in question have no influence on an individual’s mobility, allowing us to use a uniform diffusion coefficient. The ability to re-scale variables allows us to assume without loss of generality that this diffusion coefficient is one.

2. Developing the reaction–diffusion system

In order to find expressions describing the change in allelic frequencies, we first write equations describing the change in frequency of each of the genotypes. We denote the three alleles by $A_1, A_2, A_3$, and the six possible genotypes by $A_1A_1, A_1A_2, A_1A_3, A_2A_2, A_2A_3, A_3A_3$. Denoting the frequency of individuals of genotype $A_iA_j$ by $\rho_{ij}(x, t)$, the six genotype equations can then be written as

$$
\begin{align*}
\frac{\partial \rho_{11}}{\partial t} &= \frac{\partial^2 \rho_{11}}{\partial x^2} - \mu \rho_{11} + \gamma_{11} \rho_{11}^2 \rho, \\
\frac{\partial \rho_{12}}{\partial t} &= \frac{\partial^2 \rho_{12}}{\partial x^2} - \mu \rho_{12} + 2\gamma_{12} \rho_{11} \rho_{22}, \\
\frac{\partial \rho_{13}}{\partial t} &= \frac{\partial^2 \rho_{13}}{\partial x^2} - \mu \rho_{13} + 2\gamma_{13} \rho_{11}(1 - \rho_{11} - \rho_{22}), \\
\frac{\partial \rho_{22}}{\partial t} &= \frac{\partial^2 \rho_{22}}{\partial x^2} - \mu \rho_{22} + \gamma_{22} \rho_{22}^2 \rho, \\
\frac{\partial \rho_{23}}{\partial t} &= \frac{\partial^2 \rho_{23}}{\partial x^2} - \mu \rho_{23} + 2\gamma_{23} \rho_{11} \rho_{22}, \\
\frac{\partial \rho_{33}}{\partial t} &= \frac{\partial^2 \rho_{33}}{\partial x^2} - \mu \rho_{33} + \gamma_{33}(1 - \rho_{11} - \rho_{22})^2 \rho.
\end{align*}
$$

where $\rho_i$ is the frequency of allele $A_i$, which can be expressed as

$$
\rho_1 = \frac{2\rho_{11} + \rho_{12} + \rho_{13}}{2\rho}, \quad \rho_2 = \frac{\rho_{12} + 2\rho_{22} + \rho_{23}}{2\rho} \quad \text{and} \quad \rho_3 = 1 - \rho_{11} - \rho_{22}.
$$

$\rho(x, t) = \rho_{11} + \rho_{12} + \rho_{13} + \rho_{22} + \rho_{23} + \rho_{33}$ is the total population density, $\mu$ is the common death rate, and $\gamma_{ij}$ is the reproductive success rate of individuals with genotype $A_iA_j$.

Remarkably, these six equations collapse into a much smaller and simpler system describing the change in frequency of two of the alleles (shown in Appendix):

$$
\begin{align*}
\frac{\partial \rho_1}{\partial t} &= \frac{\partial^2 \rho_1}{\partial x^2} + \frac{2}{\rho} \frac{\partial \rho}{\partial x} \frac{\partial \rho_1}{\partial x} + \Phi(\rho_1, \rho_2) \\
\frac{\partial \rho_2}{\partial t} &= \frac{\partial^2 \rho_2}{\partial x^2} + \frac{2}{\rho} \frac{\partial \rho}{\partial x} \frac{\partial \rho_2}{\partial x} + \Psi(\rho_1, \rho_2),
\end{align*}
$$

as well as a trivial balance equation for $\rho_3$:

$$
\rho_3 = 1 - \rho_1 - \rho_2
$$

with

$$
\Phi(\rho_1, \rho_2) = \rho_1(\gamma_{13} - \gamma_{33}) + \rho_1^2(\gamma_{11} - 3\gamma_{13} + 2\gamma_{33}) + \rho_1^3(-\gamma_{11} + 2\gamma_{13} - \gamma_{33}) + \rho_1 \rho_2(\rho_{12} - \gamma_{13} - 2\gamma_{23} + 2\gamma_{33}) + \rho_1^2 \rho_2(2\gamma_{12} + 2\gamma_{13} + 2\gamma_{23} - 2\gamma_{33}) + \rho_1 \rho_2^2(-\gamma_{11} + 2\gamma_{13} - \gamma_{33}).
$$
\[ \Psi(p_1, p_2) = p_2(\gamma_{23} - \gamma_{33}) + p_2^2(\gamma_{22} - 3\gamma_{23} + 2\gamma_{33}) + p_3^2(-\gamma_{22} + 2\gamma_{23} - \gamma_{33}) \\
+ p_1 p_2(2\gamma_{12} - 2\gamma_{13} - \gamma_{23} + 2\gamma_{33}) + p_1 p_2^2(-2\gamma_{12} + 2\gamma_{13} + 2\gamma_{23} - 2\gamma_{33}) \\
+ p_1^2 p_2(-\gamma_{11} + 2\gamma_{13} - \gamma_{33}). \]

Eq. (3) are a system of reaction–diffusion–convection equations with cubic nonlinearities describing the changes in frequency of two of the alleles in the gene pool. The frequency of the third can be calculated once the first two are known. The convective terms in this case are due to the migratory diffusive flux of the total population. We may rigorously close the system (3) by appending a third equation for \( \rho(x,t) \), derived in the Appendix. However, in many circumstances, as discussed in Section 3, the convective terms in (3) may be neglected, thereby approximating (3) by a system of only two equations.

Eq. (3) represent the appropriate generalization of the corresponding simpler situation described in [7,8], namely that resulting from examining the change in frequency of alleles in a population that has two possible alleles at the locus in question.

So far, we have made no assumptions about dominance, or the advantage afforded by possessing a particular allele. This system of reaction–diffusion equation (3) can therefore be used to examine the advance of a recessive advantageous mutant (a similar, but more complicated, case from that of Fisher’s [9]) or simply to look at changing gene proportions in a population.

3. A new traveling wave solution

In order to analyze Eq. (3), we assume that the total population density is constant across the range (so that \( \partial \rho / \partial x = 0 \)). This assumption is common and has been made previously by a number of authors (see for example [5, 9]). This is in accord with a general expectation that a uniform environment should support an approximately uniform total population, even if the genetic makeup of that population is non-uniform. Indeed, if the total initial population density \( \rho(x,0) \) is uniformly constant, then \( \rho(x,t) \) will remain at zero, provided the birth rate \( \gamma \) does not vary with \( x \). If we initially solve an approximate closed system of two equations for \( p_1 \) and \( p_2 \) by neglecting the coupling with \( \rho \), in the convective terms, then the efficacy of that approximation can later be assessed by recalculating \( \gamma / \gamma \) according to Eq. (A.2).

A more general restriction is to set

\[ \rho(x,t) = \rho_0(t)e^{\eta(t)x}. \] (4)

Upon changing to an accelerating reference frame, \( \tilde{x} = x + 2\eta(t), \tilde{t} = t \), we are able to transform the convective terms in Eq. (3) to zero. This allows a restricted form of monotonic spatial variability in the total population density at each time. The restriction (4), while still admitting the common choice of the population density to being uniform in either space (\( \partial \rho / \partial x = 0 \) if \( \eta(t) \) is constant), or time (\( \partial \rho / \partial t = 0 \) if \( \rho_0(t) \) is constant and \( \eta(t) \) is linear), allows a slightly more general form of the total population density.

The gene frequency equations then become

\[ \frac{\partial p_1}{\partial t} = \frac{\partial^2 p_1}{\partial x^2} + \Phi(p_1, p_2) \]
\[ \frac{\partial p_2}{\partial t} = \frac{\partial^2 p_2}{\partial x^2} + \Psi(p_1, p_2). \] (5)

To look for exact traveling wave solutions, we first rewrite Eq. (5) in terms of the traveling wave coordinate \( z = x - ct \), where \( c \) is the wave speed. Setting \( p_i(x,t) = \bar{p}_i(x - ct) \) in (5) and dropping the bars for convenience, we have

\[ \frac{d^2 p_1}{dz^2} + c \frac{dp_1}{dz} + \Phi(p_1, p_2) = 0, \]
\[ \frac{d^2 p_2}{dz^2} + c \frac{dp_2}{dz} + \Psi(p_1, p_2) = 0. \] (6)

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The system of Eq. (6) has seven constant solutions, \((p_1, p_2) = (0, 0), (0, 1), (0, \alpha), (1, 0), (\beta, 0), (r_1, r_2), (s_1, s_2)\), where \(\beta, r_1, r_2, s_1, s_2\) are complicated expressions involving the \(\gamma_{ij}\), and \(\alpha\) is given below. In order to find a solution to the system of equations, we choose the boundary conditions to be
\[
(p_1, p_2)(-\infty) = (1, 0),
\]
\[
(p_1, p_2)(\infty) = (0, \alpha),
\]
where
\[
\alpha = \frac{\gamma_{23} - \gamma_{33}}{-\gamma_{22} + 2\gamma_{23} - \gamma_{33}}, \quad \text{and we require} \ 0 \leq \alpha \leq 1.
\]
This means that at \(\infty\), the gene pool for this particular locus consists of \(A_2\) and \(A_3\) alleles only. At \(-\infty\), there is a monoculture for the \(A_1\) allele. Choosing these constant solutions as boundary conditions (over the other five constant solutions) ensures that each of the three alleles is present at some time and place. Solutions can also be found by choosing the other constant solutions as boundary conditions; however, the solutions obtained are very similar to each other.

Following [12], we look for solutions that satisfy
\[
\frac{dp_1}{dz} = F(p_1), \quad p_2 = G(p_1),
\]
choosing the new independent variable to be \(p_1\). We could also have chosen \(p_2\) to be the independent variable and assumed that
\[
\frac{dp_2}{dz} = F(p_2), \quad p_1 = G(p_2).
\]
Once again, the same solutions are obtained.

Applying this transformation to Eq. (6) gives
\[
F \frac{dF}{dp_1} + cF + \Phi(p_1, G) = 0,
\]
\[
F \frac{dF}{dp_1} \frac{dG}{dp_1} + F^2 \frac{d^2G}{dp_1^2} + cF \frac{dG}{dp_1} + \Psi(p_1, G) = 0.
\]
We now assume that \(F\) and \(G\) are polynomials in \(p_1\), i.e., let
\[
F(p_1) = \sum_{n=0}^{\nu} a_n p_1^n, \quad G(p_1) = \sum_{n=0}^{\sigma} b_n p_1^n,
\]
where \(\nu, \sigma, a_n\) and \(b_n\) are constants to be determined. Substituting this into Eq. (9) gives
\[
\left(\sum_{n=0}^{\nu} a_n p_1^n\right) \left(\sum_{n=1}^{\nu} n a_n p_1^{n-1}\right) + c \sum_{n=0}^{\nu} a_n p_1^n + \Phi\left(p_1, \sum_{n=0}^{\sigma} b_n p_1^n\right) = 0,
\]
\[
\left(\sum_{n=0}^{\nu} a_n p_1^n\right) \left(\sum_{n=1}^{\sigma} n a_n p_1^{n-1}\right) \left(\sum_{n=0}^{\nu} n b_n p_1^{n-1}\right) + c \sum_{n=0}^{\nu} a_n p_1^n \left(\sum_{n=0}^{\sigma} n(n-1) b_n p_1^{n-2}\right) + \psi\left(p_1, \sum_{n=0}^{\sigma} b_n p_1^n\right) = 0.
\]
By balancing the exponents of the highest order derivative terms with the exponents of the highest order nonlinear terms, we find that \(\sigma = 1\) and \(\nu = 2\). We can then write \(F(p_1)\) and \(G(p_1)\) as
\[
F(p_1) = a_0 + a_1 p_1 + a_2 p_1^2,
\]
\[
G(p_1) = b_0 + b_1 p_1.
\]
From the boundary conditions (7), we deduce that
\[ a_0 = 0, \quad b_0 = \alpha, \]
\[ a_1 = -a_2 = a, \quad b_1 = -\alpha, \]
so that
\[ F(p_1) = a(p_1 - p_1^2), \]
\[ G(p_1) = \alpha(1 - p_1). \] (10)

Substituting these into Eq. (9) and equating the coefficients of powers of \( p_1 \) to zero, we get seven equations for \( a \) and \( c \), which can be reduced to three independent equations:
\[ \begin{align*}
  a^2 + ca + (\gamma_13 - \gamma_33) + \alpha(\gamma_12 - \gamma_13 - \gamma_23 + \gamma_33) &= 0 \\
  2a^2 + (-\gamma_11 + 2\gamma_13 - \gamma_33) + \alpha(2\gamma_12 - 2\gamma_13 - \gamma_23 + \gamma_33) &= 0 \\
  a^2 + ca + (-\gamma_12 + 2\gamma_13 + 2\gamma_23 - 3\gamma_33) + \alpha(2\gamma_12 - 2\gamma_13 + 2\gamma_22 - 5\gamma_23 + 3\gamma_33) &= 0.
\end{align*} \]

Solving these equations, we obtain expressions for the constant \( a \) and the wave speed \( c \), provided that \( \gamma_{12} = \gamma_{13} \) or \( \gamma_{22} = \gamma_{23} \). For the purposes of this investigation, we are more interested in the first case, since setting \( \gamma_{22} = \gamma_{23} \) makes \( \alpha = 1 \), so that \( p_1 = 0, \ p_2 = 1 \) and \( p_3 = 0 \) at the right boundary (i.e. \( p_3 = 0 \) at both boundaries). We therefore set
\[ \gamma_{13} = \gamma_{12}, \]
and \( a \) and \( c \) can be written as
\[ a = -\frac{1}{\sqrt{2}} \frac{\sqrt{\gamma_{11} - 2\gamma_{12} + \gamma_{33} + \alpha(\gamma_{23} - \gamma_{33})}}{\gamma_{12}}, \]
\[ c = \frac{1}{2a} \left[ (-\gamma_{11} + \gamma_{33}) + \alpha(\gamma_{23} - \gamma_{33}) \right], \]
with the restriction that \( a \) is real. (Solving the three equations gives us two values for \( a \), one positive, one negative. The negative value is chosen to satisfy the boundary conditions (7).)

Using (10), we integrate the first equation in (8) and substitute the result into the second to obtain
\[ p_1(z) = \frac{A \exp az}{1 + A \exp az}, \]
\[ p_2(z) = \frac{\alpha}{1 + A \exp az}, \]
where \( A \) is a constant. Since the solution remains valid after any shift in the coordinate system, we can choose \( z = 0 \) to be the point where \( p_1 = 1/2 \), so that a solution to the system of Eq. (6) with \( \gamma_{12} = \gamma_{13} \) is
\[ \begin{align*}
  p_1(z) &= \frac{\exp az}{1 + \exp az}, \\
  p_2(z) &= \frac{\alpha}{1 + \exp az}. \] (11)

The solution curves are shown in Fig. 1. The birth rates have been chosen so that allele \( A_1 \) is advantageous (\( \gamma_{11} = 0.5, \ \gamma_{12} = \gamma_{13} = 0.3, \ \gamma_{22} = 0.2, \ \gamma_{23} = 0.1 \) and \( \gamma_{33} = 0.25 \)). For these particular values, \( \alpha = 3/5, \ a \approx -0.1732 \) and \( c \approx 0.9815 \).

The waves are moving to the right, so the advantageous allele \( A_1 \) is shown to take over the range at the expense of the other two alleles, \( A_2 \) and \( A_3 \). This direction of wave travel is as expected, since we have chosen the values of the \( \gamma_{ij} \) so that \( A_1 \) is advantageous.

Setting \( \gamma_{12} = \gamma_{13} \) means that we are assuming that genotypes \( A_1A_2 \) and \( A_1A_3 \) have the same reproductive success rates. This means that there are now essentially five different reproductive success rates. This could occur if allele \( A_1 \) was dominant over alleles \( A_2 \) and \( A_3 \).

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3.1. Direction of wave travel

It is important to determine the direction in which the wave is traveling, since this will determine whether a gene spreads throughout the population or recedes and is lost. A “Z” shaped wave for $p_1$ (like the one in Fig. 1) must be forward-moving in order for the gene to spread through the population, so that $c > 0$. This requires that

$$(-\gamma_{11} + \gamma_{33}) + \alpha(\gamma_{23} - \gamma_{33}) < 0.$$  \hspace{1cm} (12)

This condition is easily satisfied by many different values of the $\gamma_{ij}$.

3.2. Stability of the traveling wave solution

The system of Eq. (6) has seven constant solutions, $(p_1, p_2) = (0, 0), (0, 1), (0, \alpha), (1, 0), (\beta, 0), (r_1, r_2), (s_1, s_2)$, where $\alpha$ has already been defined and $\beta, r_1, r_2, s_1, s_2$ are complicated expressions involving the $\gamma_{ij}$. The stability of these solutions can be found by considering the eigenvalue problem

$$F'(\mathbf{q})\mathbf{u} = \lambda\mathbf{u}$$  \hspace{1cm} (13)

where $F(\mathbf{p}) = (\Phi(p_1, p_2), \Psi(p_1, p_2))$ and $\mathbf{q}$ is a solution of $F(\mathbf{q}) = 0$.

The traveling wave constructed in the previous section will only be of interest if the state $(p_1, p_2, p_3) = (1, 0, 0)$ is stable, while $(p_1, p_2, p_3) = (0, \alpha, 1 - \alpha)$ is unstable and if in the absence of allele $A_1$, the state $(p_2, p_3) = (\alpha, 1 - \alpha)$ is stable. By applying linear stability analysis to Eq. (5) when $p_1 = 0$, we find that the solution $(p_2, p_3) = (\alpha, 1 - \alpha)$ is stable if

$$\alpha(\gamma_{22} - \gamma_{23}) < 0.$$  

By solving the eigenvalue problem (13) for the solution $(p_1, p_2, p_3) = (0, \alpha, 1 - \alpha)$, we find that it is unstable at least one of

$$\lambda_1 = \gamma_{13} - \gamma_{33} + \alpha(\gamma_{12} - \gamma_{13} - \gamma_{23} + \gamma_{33}) \quad \text{or}$$

$$\lambda_2 = \gamma_{23} - \gamma_{33} + \alpha(\gamma_{22} - 3\gamma_{23} + \gamma_{33})$$

is positive. By solving Eq. (13) for the solution $(p_1, p_2, p_3) = (1, 0, 0)$, we find that it is stable if

$$\lambda_3 = -\gamma_{11} - \gamma_{13} < 0, \quad \text{and} \quad \lambda_4 = -\gamma_{11} + \gamma_{12} < 0.$$  

It is possible to find a set of values for the $\gamma_{ij}$ for which the above conditions are met, and for which $0 < \alpha < 1$ and $\alpha$ is real. For example, the values used in Fig. 1 set $\alpha(\gamma_{22} - \gamma_{23}) \approx -0.187 < 0$, $\lambda_1 \approx 0.037 > 0$, $\lambda_2 \approx -0.187 < 0$, $\lambda_3 = -1 < 0$, and $\lambda_4 = -0.4 < 0$. 

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Although the stability of the scalar case has been comprehensively studied \cite{13,14}, the problem of stability for traveling wave solutions to systems of equations is not straightforward, and cannot be immediately inferred from the scalar case. The method usually used for the scalar case becomes so complicated for systems that it can only be used in a limited number of cases.

A more comprehensive investigation of the stability of a restricted class of systems of reaction–diffusion equations is given by Volpert and Volpert \cite{15}. However it remains a challenge to extend the existing theorems of stability analysis so that they apply to these more general systems of reaction–diffusion equations. This would have ramifications for the theoretical foundations of the subject and for the many and varied practical applications of such systems.

4. Spatial variation of species birth rate

In Section 3, we made the assumption that the total population density remains constant across the range. This is a common assumption, which is also motivated physically by the expectation that a uniform environment should support an approximately uniform total population density. If the initial total population density is constant, then it will remain so, provided that the total birth rate (as given by (A.2)) is constant across the range. After solving the equations by neglecting the coupling with $\rho_x$ through the convective terms, we now examine the total birth rate to ensure that it is in fact negligible.

Fig. 2 shows the small variation in the quantity $\gamma_x/\gamma$. The magnitude of the term $\gamma_x/\gamma$ is small in comparison to the other terms in Eq. (3), which are of order 1.

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Appendix. Collapse of six genotype equations into two independent equations

Using the product rule to differentiate the expression for $p_1$ in (2) with respect to time, we obtain the expression

$$\frac{\partial p_1}{\partial t} = \frac{1}{2\rho} \left[ 2 \frac{\partial \rho_{11}}{\partial t} + \frac{\partial \rho_{12}}{\partial t} + \frac{\partial \rho_{13}}{\partial t} - 2p_1 \frac{\partial \rho}{\partial t} \right].$$

Substituting the derivative of the expression for $\rho$ and the six genotype Eq. (1), and noticing that

$$\frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{12}}{\partial x^2} + \frac{\partial^2 \rho_{13}}{\partial x^2} + \frac{\partial^2 \rho_{22}}{\partial x^2} + \frac{\partial^2 \rho_{23}}{\partial x^2} + \frac{\partial^2 \rho_{33}}{\partial x^2} = \frac{\partial^2 \rho}{\partial x^2}$$

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we have
\[
\frac{\partial p_1}{\partial t} = \frac{1}{2\rho} \left[ 2 \frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{12}}{\partial x^2} + \frac{\partial^2 \rho_{13}}{\partial x^2} - 2p_1 \frac{\partial^2 \rho}{\partial x^2} + \mu(2p_1\rho - (2\rho_{11} + \rho_{12} + \rho_{13})) \\
+ \rho(2\gamma_{11}p_1^2 + 2\gamma_{12}p_1p_2 + 2\gamma_{13}p_1(1 - p_1 - p_2) - 2\gamma_{11}p_1^3 - 4\gamma_{12}p_1p_2^2 - 4\gamma_{13}p_2(1 - p_1 - p_2) \\
- 2\gamma_{22}p_1p_2^2 - 4\gamma_{23}p_1p_2(1 - p_1 - p_2) - 2\gamma_{33}p_1(1 - p_1 - p_2)^2 \right].
\] (A.1)

Rearranging the expression for \( p_1 \) (2), we notice that \( 2\rho_{11} + \rho_{12} + \rho_{13} = 2p_1\rho \), and differentiating twice with respect to \( x \), we have
\[
2 \frac{\partial^2 \rho_{11}}{\partial x^2} + \frac{\partial^2 \rho_{12}}{\partial x^2} + \frac{\partial^2 \rho_{13}}{\partial x^2} = 2\rho \frac{\partial^2 \rho_1}{\partial x^2} + 2p_1 \frac{\partial^2 \rho}{\partial x^2} + 4\frac{\partial^2 \rho}{\partial x^2} \frac{\partial^2 \rho_1}{\partial x^2}
\]
so that Eq. (A.1) reduces to Eq. (3)_1. A similar method can be used to derive Eq. (3)_2.

We may rigorously close the system of Eq. (3) by appending a third equation for the total population density \( \rho(x, t) \). By simple addition of the component population equation (1), this equation is
\[
\frac{\partial \rho}{\partial t} = \frac{\partial^2 \rho}{\partial x^2} - \mu \rho + \gamma(x, t)\rho,
\]
where
\[
\gamma(x, t) = \gamma_{11}p_1^2 + 2\gamma_{12}p_1p_2 + 2\gamma_{13}p_1(1 - p_1 - p_2) + \gamma_{22}p_2^2 + 2\gamma_{23}p_2(1 - p_1 - p_2) + \gamma_{33}(1 - p_1 - p_2)^2.
\] (A.2)

References


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