

Results on asymptotic behaviour for discrete, two-patch metapopulations with density-dependent selection

JAMES F. SELGRADE^{†*} and JAMES H. ROBERDS^{‡||}

[†]Department of Mathematics, North Carolina State University, Box 8205, Raleigh, NC 27695-8205, USA

[‡]USDA Forest Service, Southern Research Station, Southern Institute of Forest Genetics, Saucier, MS 39574, USA

(Received 20 July 2004; in final form 3 November 2004)

Dedicated to Jim Cushing on the occasion of his 62nd birthday

A 4-dimensional system of nonlinear difference equations tracking allele frequencies and population sizes for a two-patch metapopulation model is studied. This system describes intergenerational changes brought about by density-dependent selection within patches and moderated by the effects of migration between patches. To determine conditions which result in similar behaviour at the level of local populations, we introduce the concept of symmetric equilibrium and relate it to properties of allelic and genotypic fitness. We present examples of metapopulation stability, instability and bistability, as well as an example showing that differentially greater migration into a stable patch results in metapopulation stability. Finally, we illustrate a Naimark-Sacker bifurcation giving a globally asymptotically stable invariant curve for the 4-dimensional model.

Keywords: Metapopulation; Equilibrium; Attractor; Discrete population model

AMS 2000 Mathematics Subject Classification: 92D25; 39A11

1. Introduction

There is much current interest in the dynamical behaviour of populations organized as metapopulations. From the viewpoint of population biology, a metapopulation is a collection of local populations that act with at least partial independence. Considered broadly, the metapopulation concept encompasses population extinction and colonization events as well as interaction among established populations whose persistence over long time intervals is not an issue. The model and analysis described in this paper are developed to study behaviour in metapopulations of the latter type. For this case, populations are not considered as separate units functioning in isolation, but are viewed as interacting entities, connected through migration.

Much of the analysis of metapopulation dynamics has concentrated on ecological aspects with demographic behaviour being a major focus. However, it has become clear that metapopulation structure can also influence patterns of variation among and within populations at the gene and genotypic level and is involved in shaping genetic population dynamics (Hanski and Gilpin [1]).

*Corresponding author. Tel.: +1-919-515-8589. Email: selgrade@math.ncsu.edu.

||Email: jroberds@fs.fed.us

For this reason, the need to study models that incorporate both genetic and ecological components has been recognized (Hastings and Harrison [2]) as a means of obtaining a more complete understanding of evolutionary processes involved in producing population structure in nature.

Here we introduce a 4-dimensional system of difference equations that describe gene frequency and population size intergenerational transitions for a two-patch metapopulation model. We present some initial results from mathematical analysis of this system. In this treatment, the local populations are connected through interpopulation migration and local density-dependent selection. Hanski [3] pointed out that the two population model can be useful for studying the effects of migration on local population dynamics; it offers the advantage of mathematical tractability. Our purpose with mathematical analysis of our more complex system of equations is to study the interacting effects of migration and density-dependent selection on local allele frequency and population size dynamics.

In sections 2 and 3 we describe the system of equations for this model, and we discuss the state space for this system and then develop equilibrium equations. To determine circumstances where the local populations have similar asymptotic behaviours, we introduce the notion of symmetric equilibrium in section 4. With this type of equilibrium both local populations have the same allele frequencies and proportional population sizes. Theorems 1 and 2 relate the concept of symmetric equilibrium to properties of allelic and genotypic fitness of the local populations. A family of examples is presented where genotypes of one local population exhibit heterozygote superiority but genotypes of the other local population exhibit heterozygote inferiority, and the 4-dimensional metapopulation exhibits stability, instability or bistability. Also, we show by example that differentially greater migration into a stable patch tends to stabilize the metapopulation. In section 5 we discuss a Naimark-Sacker bifurcation [4, 5], which results in a globally asymptotically stable invariant curve that cannot occur in the density-dependent selection model without migration [6, 7].

2. Model equations

First, we introduce a model from ecological genetics that accounts for the effects of selection on the allele frequency and the population density of a single population (see Roughgarden [6] or Selgrade and Namkoong [7]). Let x denote population size or density of a diploid population with two alleles, A and a , at an autosomal locus and let p denote the frequency of the A allele prior to selection, where $0 \leq p \leq 1$. Hence, the population consists of individuals having one of three genotypes, AA , Aa or aa . The genotypes have nonnegative per capita growth rate functions (fitnesses), $f_{AA}(p, x)$, $f_{Aa}(p, x)$ and $f_{aa}(p, x)$, which reflect the effects of natural selection and which are decreasing functions of x because of crowding. Allele fitnesses f_A and f_a are defined by $f_A(p, x) \equiv pf_{AA}(p, x) + (1 - p)f_{Aa}(p, x)$ and $f_a(p, x) \equiv pf_{Aa}(p, x) + (1 - p)f_{aa}(p, x)$. Accordingly, the population mean fitness f is given by $f(p, x) \equiv pf_A(p, x) + (1 - p)f_a(p, x)$. Assuming random mating, the following system of difference equations describes the changes in allele frequency and population size that take place from one generation to the next:

$$p' = \frac{pxf_A(p, x)}{xf(p, x)}, \quad x' = xf(p, x). \quad (2.1)$$

Here p' and x' denote allele frequency and population size in the next generation.

The simplest generalization of this model, that includes the effects of migration and selection on allele frequency is the one-island or continent-island model in which a single population receives immigrants from a large nearby population. Even if the migrating population is of constant allele frequency, Roberds and Selgrade [8, 9] show that interesting dynamics can occur, including period-doubling and Naimark-Sacker bifurcations [4, 5]. To allow migration where the migrating population has varying allele frequency, we consider a two-island metapopulation where p_i and x_i denote allele frequency and population size on the i -th island or patch, for $i = 1, 2$. In each generation following selection, individuals emigrate at a constant rate m_i from the i -th patch to the other patch. After migration, random mating is assumed to take place within each patch, yielding Hardy-Weinberg proportions in the population of zygotes that form the next generation. For $i, j = A, a$, we let $f_{ij}(p_1, x_1)$ denote the genotype fitnesses of the local population in the first patch and $g_{ij}(p_2, x_2)$ denote the genotype fitnesses of the local population in the second patch. The fitnesses f_A, f_a, f, g_A, g_a and g are defined accordingly. With these assumptions, the following 4-dimensional system describes the allele frequencies and population sizes in the next generation:

$$\begin{aligned} p'_1 &= \frac{(1 - m_1)p_1x_1f_A + m_2p_2x_2g_A}{(1 - m_1)x_1f + m_2x_2g}, & x'_1 &= (1 - m_1)x_1f + m_2x_2g, \\ p'_2 &= \frac{(1 - m_2)p_2x_2g_A + m_1p_1x_1f_A}{(1 - m_2)x_2g + m_1x_1f}, & x'_2 &= (1 - m_2)x_2g + m_1x_1f. \end{aligned} \quad (2.2)$$

Note that the fixation planes $\{p_1 = 0 = p_2\}$ and $\{p_1 = 1 = p_2\}$, where one allele is absent, are invariant under the map (2.2). However, the planes $\{p_1 = 0, p_2 = 1\}$ and $\{p_1 = 1, p_2 = 0\}$ are not invariant. On the fixation planes, the model reduces to a two-patch metapopulation model without genetic variation.

3. Equilibria

The phase space for our system is the 4-dimensional region in Euclidean space given by

$$\mathcal{R} \equiv \{(p_1, p_2, x_1, x_2) : 0 \leq p_i \leq 1, 0 \leq x_i, i = 1, 2\}.$$

Two boundary planes of \mathcal{R} , $\{p_1 = 0 = p_2\}$ and $\{p_1 = 1 = p_2\}$, represent allele fixation and are invariant. When $m_1 = m_2 = 0$ the system (2.2) decouples and the 4-dimensional dynamical behaviour is determined by the behaviour on the (p_i, x_i) -planes where equation (2.1) holds.

From equation (2.2), we see that an equilibrium E in the interior of \mathcal{R} must satisfy the following 4-dimensional system:

$$\begin{aligned} x_1 &= (1 - m_1)x_1f + m_2x_2g, \\ x_2 &= (1 - m_2)x_2g + m_1x_1f, \\ p_1x_1 &= (1 - m_1)p_1x_1f_A + m_2p_2x_2g_A, \\ p_2x_2 &= (1 - m_2)p_2x_2g_A + m_1p_1x_1f_A. \end{aligned} \quad (3.1)$$

By adding the first and second equations in (3.1) and adding the third and fourth equations we get

$$\begin{aligned}x_1(1 - f) + x_2(1 - g) &= 0 \\p_1x_1(1 - f_A) + p_2x_2(1 - g_A) &= 0\end{aligned}\tag{3.2}$$

Hence, at $E = (\bar{p}_1, \bar{p}_2, \bar{x}_1, \bar{x}_2)$, the terms $1 - f(\bar{p}_1, \bar{x}_1)$ and $1 - g(\bar{p}_2, \bar{x}_2)$ must have opposite signs or both be zero. The analogous statement must hold for the allele fitnesses f_A and g_A . If all these terms are zero then in the next section we will see that E has some symmetry properties.

4. Symmetric equilibria

Habitat differences between patches may result in dissimilar behaviour at the level of the local populations. However, it is useful to know the circumstances that permit local populations to have similar asymptotic behaviours. For this reason, we introduce the term ‘‘symmetric equilibrium’’ which describes an equilibrium with coordinates satisfying the following conditions:

$$\text{(sym) } p = p_1 = p_2 \text{ and } m_1x_1 = m_2x_2.$$

In studying symmetric equilibria, certain relationships between fitnesses at equilibrium and migration rates are important:

- (a) $f_A(p_1, x_1) = f_a(p_1, x_1) = g_A(p_2, x_2) = g_a(p_2, x_2) = 1$,
- (b) $m_1 + m_2 = 1$ and
- (c) $f_A(p_1, x_1) = f_a(p_1, x_1)$ and $g_A(p_2, x_2) = g_a(p_2, x_2)$.

The following result illustrates the various implications of these conditions.

THEOREM 1 *Let $E = (\bar{p}_1, \bar{p}_2, \bar{x}_1, \bar{x}_2)$ be an equilibrium in the interior of \mathcal{R} . If E satisfies (sym) then E satisfies either (a) or (b). Conversely, if E satisfies either (a) or (b) then E satisfies (sym). If E satisfies (c) then $\bar{p}_1 = \bar{p}_2$.*

Proof Assume that E satisfies (sym). Substitute $m_1\bar{x}_1$ for $m_2\bar{x}_2$ in the first equation of (3.1) and cancel x_1 to obtain

$$1 = (1 - m_1)f(\bar{p}, \bar{x}_1) + m_1g(\bar{p}, \bar{x}_2),\tag{4.1}$$

Substitute $m_2\bar{x}_2$ for $m_1\bar{x}_1$ in the second equation of (3.1) and cancel x_2 to obtain

$$1 = (1 - m_2)g(\bar{p}, \bar{x}_2) + m_2f(\bar{p}, \bar{x}_1),\tag{4.2}$$

Subtracting equation (4.2) from equation (4.1) gives

$$0 = (1 - m_1 - m_2)[f(\bar{p}, \bar{x}_1) - g(\bar{p}, \bar{x}_2)],$$

from which we conclude that either $m_1 + m_2 = 1$ or that $f(\bar{p}, \bar{x}_1) = g(\bar{p}, \bar{x}_2) = 1$ using equation (3.2). A similar argument starting with the third and fourth equations of (3.1) shows

that either $m_1 + m_2 = 1$ or that $f_A(\bar{p}, \bar{x}_1) = g_A(\bar{p}, \bar{x}_2) = 1$. Finally the definitions of f and g in terms of f_A, f_a, g_A and g_a imply that E satisfies either (a) or (b).

Assuming that E satisfies (a), from the definition of mean fitness we conclude that $f(\bar{p}_1, \bar{x}_1) = 1$ and $g(\bar{p}_2, \bar{x}_2) = 1$. Then the first or second equation of (3.1) gives $m_1\bar{x}_1 = m_2\bar{x}_2$. And the third or fourth equation of (3.1) gives $\bar{p}_1 = \bar{p}_2$.

Given that E satisfies (b), we use the first two equations in (3.1) to conclude that $m_1\bar{x}_1 = m_2\bar{x}_2$ and the third and fourth equations to see that $\bar{p}_1 = \bar{p}_2$. For instance, substitute m_2 for $1 - m_2$ in the first equation and m_1 for $1 - m_2$ in the second equation. Then, in both the equations, isolate the term $\bar{x}_1 f(\bar{p}_1, \bar{x}_1) + \bar{x}_2 g(\bar{p}_2, \bar{x}_2)$ to obtain

$$\frac{\bar{x}_1}{m_2} = \bar{x}_1 f(\bar{p}_1, \bar{x}_1) + \bar{x}_2 g(\bar{p}_2, \bar{x}_2) = \frac{\bar{x}_2}{m_1}$$

This gives $m_1\bar{x}_1 = m_2\bar{x}_2$.

If E satisfies (c) then observe that $f_A = f_a = f$ and $g_A = g_a = g$ at E . Multiply the first equation in (3.1) by \bar{p}_1 and subtract the third equation to conclude that $\bar{p}_1 = \bar{p}_2$. \square

Our definition of symmetric equilibrium asserts that within each patch the allele frequencies are the same and the population sizes are proportional via the migration rates. In light of (a) where both mean fitnesses equal 1, this proportionality gives that the total number of migrants between patches are equal at equilibrium. The only other possibility is a rather stringent restriction on the migration parameters, i.e. $m_1 + m_2 = 1$. In addition, the relation that $m_1\bar{x}_1 = m_2\bar{x}_2$ has useful algebraic consequences which we explore below. Condition (c) is weaker than (a) and permits an equilibrium where the mean fitnesses of the local populations are not equal (see the example in section 4.3). Moreover, condition (c) implies genetic similarity but not necessarily demographic similarity.

Inequality relationships between genotype fitnesses may be obtained at an equilibrium $E = (\bar{p}, \bar{p}, \bar{x}_1, \bar{x}_2)$. For E satisfying (c), we rewrite the equation $f_A = f_a$ in terms of genotype fitnesses to obtain

$$\bar{p}(f_{AA}(\bar{p}, \bar{x}_1) - f_{Aa}(\bar{p}, \bar{x}_1)) + (1 - \bar{p})(f_{Aa}(\bar{p}, \bar{x}_1) - f_{aa}(\bar{p}, \bar{x}_1)) = 0 \text{ for } 0 < \bar{p} < 1, \quad (4.3)$$

which implies that heterozygote fitness is either superior, inferior or equal to that of the homozygotes. The definition of mean fitness in terms of allele fitnesses gives $f_A = f_a = f$ at E , so $f(\bar{p}, \bar{x}_1) = \bar{p}f_{AA}(\bar{p}, \bar{x}_1) + (1 - \bar{p})f_{Aa}(\bar{p}, \bar{x}_1) - \bar{p}f_{Aa}(\bar{p}, \bar{x}_1) + (1 - \bar{p})f_{aa}(\bar{p}, \bar{x}_1)$ may be rewritten as

$$\begin{aligned} 0 &= \bar{p}(f_{AA}(\bar{p}, \bar{x}_1) - f(\bar{p}, \bar{x}_1)) + (1 - \bar{p})(f_{Aa}(\bar{p}, \bar{x}_1) - f(\bar{p}, \bar{x}_1)) \\ 0 &= \bar{p}(f_{Aa}(\bar{p}, \bar{x}_1) - f(\bar{p}, \bar{x}_1)) + (1 - \bar{p})(f_{aa}(\bar{p}, \bar{x}_1) - f(\bar{p}, \bar{x}_1)). \end{aligned} \quad (4.4)$$

From equation (4.4) we conclude that $f(\bar{p}, \bar{x}_1)$ lies between, or is equal to, the fitnesses for the heterozygote and the homozygotes. Hence, one of the following three conditions holds at E :

- (1) $f_{Aa}(\bar{p}, \bar{x}_1) > f(\bar{p}, \bar{x}_1) > f_{AA}(\bar{p}, \bar{x}_1), f_{aa}(\bar{p}, \bar{x}_1)$, (heterozygote superiority);
- (2) $f_{Aa}(\bar{p}, \bar{x}_1) < f(\bar{p}, \bar{x}_1) < f_{AA}(\bar{p}, \bar{x}_1), f_{aa}(\bar{p}, \bar{x}_1)$, (heterozygote inferiority); or
- (3) $f_{Aa}(\bar{p}, \bar{x}_1) = f_{AA}(\bar{p}, \bar{x}_1) = f_{aa}(\bar{p}, \bar{x}_1) = f(\bar{p}, \bar{x}_1)$, (neutrality).

Because $g_A(\bar{p}, \bar{x}_2) = g_a(\bar{p}, \bar{x}_2)$, the analogous inequalities hold for the genotype fitnesses of the population with size x_2 . Such conditions are reminiscent of the behaviour at an

equilibrium of the classical model of density-dependent selection in a single population without migration, e.g. see Roughgarden [6] or Selgrade and Namkoong [7]. However, at a symmetric equilibrium in this metapopulation model, one local population may exhibit heterozygote superiority and the other local population, heterozygote inferiority.

Using the equations $f_A(\bar{p}, \bar{x}_1) = f(\bar{p}, \bar{x}_1)$ and $f_a(\bar{p}, \bar{x}_1) = f(\bar{p}, \bar{x}_1)$ which follow from (c), we solve for \bar{p} in terms of genotype fitnesses and equate results to get

$$p = \frac{f(\bar{p}, \bar{x}_1) - f_{Aa}(\bar{p}, \bar{x}_1)}{f_{AA}(\bar{p}, \bar{x}_1) - f_{Aa}(\bar{p}, \bar{x}_1)} = \frac{f(\bar{p}, \bar{x}_1) - f_{aa}(\bar{p}, \bar{x}_1)}{f_{Aa}(\bar{p}, \bar{x}_1) - f_{aa}(\bar{p}, \bar{x}_1)}. \tag{4.5}$$

From the right equation in (4.5), we obtain

$$f(\bar{p}, \bar{x}_1) = \frac{f_{Aa}(\bar{p}, \bar{x}_1)^2 - f_{AA}(\bar{p}, \bar{x}_1)f_{aa}(\bar{p}, \bar{x}_1)}{2f_{Aa}(\bar{p}, \bar{x}_1) - f_{AA}(\bar{p}, \bar{x}_1) - f_{aa}(\bar{p}, \bar{x}_1)} \tag{4.6}$$

We multiply equation (4.6) by 2 and show that the resulting right side is larger than $f_{Aa}(\bar{x}_1)$ in the case of heterozygote superiority. With this and (i), we obtain upper and lower bounds for the heterozygote at E , i.e. $f < f_{Aa} < 2f$. For heterozygote inferiority, from (ii) we have $0 < f_{Aa} < f$. The analogous inequalities hold for the fitnesses of the x_2 population. This discussion establishes the following result:

THEOREM 2 *Let $E = (\bar{p}, \bar{p}, \bar{x}_1, \bar{x}_2)$ be an equilibrium in the interior of \mathcal{R} and assume that E satisfies (c). Then at equilibrium, the x_1 population has genotype fitnesses that exhibit either heterozygote superiority (i) with $f(\bar{p}, \bar{x}_1) < f_{Aa}(\bar{p}, \bar{x}_1) < 2f(\bar{p}, \bar{x}_1)$, or heterozygote inferiority (ii) with $0 < f_{Aa}(\bar{p}, \bar{x}_1) < f(\bar{p}, \bar{x}_1)$ or neutrality (iii) with $f_{Aa}(\bar{p}, \bar{x}_1) = f(\bar{p}, \bar{x}_1)$. Also, the x_2 population exhibits either heterozygote superiority with $g(\bar{p}, \bar{x}_2) < g_{Aa}(\bar{p}, \bar{x}_2) < 2g(\bar{p}, \bar{x}_2)$, or heterozygote inferiority with $0 < g_{Aa}(\bar{p}, \bar{x}_2) < g(\bar{p}, \bar{x}_1)$ or neutrality with $g_{Aa}(\bar{p}, \bar{x}_2) = g(\bar{p}, \bar{x}_2)$.*

4.1 Stability analysis

Henceforth, we assume that all genotype fitnesses depend only on population size and not on allele frequency. This is commonly referred to as *density-dependent selection* and it follows that $\partial f_{ij} / \partial p_1 = 0 = \partial g_{ij} / \partial p_2$ for all $i, j = A, a$. At an interior equilibrium $E = (\bar{p}, \bar{p}, \bar{x}_1, \bar{x}_2)$ satisfying (c), let the Jacobian matrix of the right side of equation (2.2) be represented by

$$D(E) = \begin{bmatrix} B_1 & B_2 \\ B_3 & B_4 \end{bmatrix}. \tag{4.7}$$

where each B_i is a 2×2 submatrix. A computation shows that each entry in B_3 contains either the factor $\partial f / \partial p_1$ or the factor $\partial g / \partial p_2$ and

$$\frac{\partial f}{\partial p_1} = 2(f_A - f_a) \text{ and } \frac{\partial g}{\partial p_2} = 2(g_A - g_a). \tag{4.8}$$

Hence, because of condition (c), the partial derivatives in equation (4.8) are zero at equilibrium so all entries of B_3 are zero. Thus the stability of E is determined by the eigenvalues of B_1 and B_4 . According to the Jury conditions [10], a 2×2 matrix B has

eigenvalues inside the unit circle if and only if

$$|\operatorname{tr} B| < 1 + \det B < 2. \quad (4.9)$$

For $D(E)$ we have

$$B_1 = \begin{bmatrix} (1 - m_1) \left[f_A + \bar{p} \left(\frac{\partial f_A}{\partial p_1} - \frac{\partial f}{\partial p_1} \right) \right] & m_2 \bar{x}_2 \left[g_A + \bar{p} \left(\frac{\partial g_A}{\partial p_2} - \frac{\partial g}{\partial p_2} \right) \right] / \bar{x}_1 \\ m_1 \bar{x}_1 \left[f_A + \bar{p} \left(\frac{\partial f_A}{\partial p_1} - \frac{\partial f}{\partial p_1} \right) \right] / \bar{x}_2 & (1 - m_2) \left[g_A + \bar{p} \left(\frac{\partial g_A}{\partial p_2} - \frac{\partial g}{\partial p_2} \right) \right] \end{bmatrix} \quad (4.10)$$

and

$$B_4 = \begin{bmatrix} (1 - m_1) \left[f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right] & m_2 \left[g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right] \\ m_1 \left[f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right] & (1 - m_2) \left[g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right] \end{bmatrix}. \quad (4.11)$$

Note that B_1 contains primarily genetic information about allele frequency and genotype fitnesses and B_4 contains primarily demographic information.

Using equation (4.5) and the analogous equation for the fitnesses of the x_2 population, we write the matrix B_1 in terms of the mean and heterozygote fitnesses as

$$B_1 = \begin{bmatrix} (1 - m_1)(2f - f_{Aa}) & m_2 \bar{x}_2 (2g - g_{Aa}) / \bar{x}_1 \\ m_1 \bar{x}_1 (2f - f_{Aa}) / \bar{x}_2 & (1 - m_2)(2g - g_{Aa}) \end{bmatrix} \quad (4.12)$$

and determine that the determinant and trace of B_1 are given by

$$\begin{aligned} \det B_1 &= (2f - f_{Aa})(2g - g_{Aa})(1 - m_1 - m_2) \\ \operatorname{tr} B_1 &= (1 - m_1)(2f - f_{Aa}) + (1 - m_2)(2g - g_{Aa}). \end{aligned} \quad (4.13)$$

From Theorem 2, we know that heterozygote fitnesses are less than two times the mean fitnesses. Thus B_1 is a positive matrix and so the spectral radius is the eigenvalue of largest norm (Perron's Theorem [11]). Generally it is difficult to determine if this eigenvalue is less than one. However, if (a) holds then the mean and allele fitnesses equal 1 and computations show that the inequality $\operatorname{tr} B_1 < 1 + \det B_1$ is equivalent to either of the following inequalities:

$$0 < (f_{Aa} - 1)(g_{Aa} - 1) + m_1(g_{Aa} - 1)(2 - f_{Aa}) + m_2(f_{Aa} - 1)(2 - g_{Aa}) \quad (4.14a)$$

or

$$m_1(1 - g_{Aa}) + m_2(1 - f_{Aa}) < (1 - m_1 - m_2)(1 - g_{Aa})(1 - f_{Aa}). \quad (4.14b)$$

When both populations exhibit heterozygote superiority at equilibrium then each term on the right in inequality (4.14a) is positive so $\operatorname{tr} B_1 < 1 + \det B_1$. Moreover, since $-1 \leq 1 - m_1 - m_2 \leq 1$, we have $\det B_1 < 1$. Thus the Jury conditions are satisfied and both eigenvalues of B_1 are inside the unit circle. If both populations exhibit fitness neutrality at equilibrium then the right side of inequality (4.14a) is zero. Hence, $\operatorname{tr} B_1 = 1 + \det B_1$ and writing this equation in terms of the eigenvalues of B_1 implies that at least one eigenvalue is equal to 1. Thus, an equilibrium with neutral fitnesses is degenerate. Finally, assume that both populations exhibit heterozygote inferiority at equilibrium. If $m_1 + m_2 \geq 1$ then the left side of inequality (4.14b) is positive and the right side is not. So $\operatorname{tr} B_1 > 1 + \det B_1$ and this

equilibrium is unstable. If $m_1 + m_2 < 1$ and inequality (4.14b) is satisfied, a tedious computation shows that $\text{tr } B_1 > 2$. We conclude that this type of equilibrium is unstable.

For the matrix B_4 , from equation (4.11) it follows that

$$\begin{aligned} \det B_4 &= (1 - m_1 - m_2) \left(f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right) \left(g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right) \\ \text{tr } B_4 &= (1 - m_1) \left(f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right) + (1 - m_2) \left(g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right). \end{aligned} \tag{4.15}$$

Unlike B_1 , the eigenvalues of B_4 may be complex because the discriminant, $(\text{tr } B_4)^2 - 4\det B_4$, may be negative. The next result contains necessary conditions for complex eigenvalues.

PROPOSITION 1 *Assume that the interior equilibrium E satisfies (c). If the eigenvalues of B_4 are complex then*

$$1 < m_1 + m_2 \text{ and } \left(f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right) \left(g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right) < 0.$$

Proof From equation (4.15) write out the discriminant and note that

$$1 - m_1 - m_2 = (1 - m_1)(1 - m_2) - m_1 m_2.$$

Rewrite the discriminant in the form

$$\begin{aligned} &\left[(1 - m_1) \left(f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right) - (1 - m_2) \left(g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right) \right]^2 \\ &+ 4m_1 m_2 \left(f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right) \left(g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right). \end{aligned}$$

Observe that since the discriminant must be negative, we need

$$\left(f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right) \left(g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right) < 0.$$

And since $\det B_4 > 0$ then equation (4.15) implies that $1 - m_1 - m_2 < 0$. □

The Jury conditions may be used to obtain necessary and sufficient conditions for stable eigenvalues for B_4 but no general conclusions follow from the complicated formulas that result.

4.2 Example with heterozygote superiority and heterozygote inferiority

Here we present a family of examples where the genotypes of the x_1 population exhibit heterozygote superiority and the genotypes of the x_2 population exhibit heterozygote inferiority but the 4-dimensional metapopulation may exhibit stability, instability or bistability. For the x_1 population, assume that $f_{Aa}(x) > f_{AA}(x) = f_{aa}(x)$ for all $x > 0$. Thus the x_1 population has heterozygote superiority and homozygote equality. For the x_2 population, reverse the definitions of the fitnesses by letting $g_{AA}(x) = g_{aa}(x) = f_{Aa}(x)$ and $g_{Aa}(x) = f_{AA}(x)$. Hence the x_2 population has heterozygote inferiority and homozygote

equality. To guarantee that equilibria exist, assume that $f_{ij}(0) > 1$ and $f_{ij}(x)$ decreases to zero ($f'_{ij}(x) < 0$) as $x \rightarrow \infty$, for $i, j = A, a$. This is a standard crowding assumption used for many per capita transition functions. Let \bar{x} be the unique solution to

$$1 = (f_{AA}(x) + f_{Aa}(x))/2. \quad (4.16)$$

For $i = 1, 2$, if both $m_i = 0$ then equilibria occur at $(p_i, x_i) = (0.5, \bar{x})$ in the interior of the (p_i, x_i) -planes. Referring again to Roughgarden [6] or Selgrade and Namkoong [7], it can be seen that one eigenvalue of the equilibrium $(0.5, \bar{x})$ is

$$\lambda = 1 + \bar{x}(f'_{AA}(\bar{x}) + f'_{Aa}(\bar{x}))/2. \quad (4.17)$$

This eigenvalue is in the stable range if we assume

$$-4 < \bar{x}(f'_{AA}(\bar{x}) + f'_{Aa}(\bar{x})). \quad (4.18)$$

The inequality (4.18) asserts that fitnesses do not decrease too rapidly at equilibrium and has been a standard assumption since Roughgarden [12] in 1976. Because of heterozygote superiority and inequality (4.18), the equilibrium $(p_1, x_1) = (0.5, \bar{x})$ is locally asymptotically stable in the (p_1, x_1) -plane. With heterozygote inferiority and inequality (4.18), $(p_2, x_2) = (0.5, \bar{x})$ is a saddle point in the (p_2, x_2) -plane.

For the metapopulation model with $m_i \neq 0$, the portion of the plane in \mathcal{R} given by $\mathcal{P} = \{(p_1, p_2, x_1, x_2) \in \mathcal{R} : p_1 = p_2 = 0.5\}$ is invariant because on this plane $f = f_A = g = g_A = (f_{AA} + f_{Aa})/2$. On \mathcal{P} , equation (2.2) reduces to the 2-dimensional metapopulation system

$$\begin{aligned} x'_1 &= (1 - m_1)x_1(f_{AA}(x_1) + f_{Aa}(x_1))/2 + m_2x_2(f_{AA}(x_2) + f_{Aa}(x_2))/2, \\ x'_2 &= (1 - m_2)x_2(f_{AA}(x_2) + f_{Aa}(x_2))/2 + m_1x_1(f_{AA}(x_1) + f_{Aa}(x_1))/2. \end{aligned} \quad (4.19)$$

The origin $(0,0)$ in \mathcal{P} is always an unstable equilibrium of equation (4.19) because the derivative of equation (4.19) at $(0,0)$ is a positive matrix with dominant eigenvalue $(f_{AA}(0) + f_{Aa}(0))/2 > 1$. If $m = m_1 = m_2 \neq 0$ then there is a symmetric equilibrium E_m in the interior of \mathcal{P} where $p_1 = p_2 = 0.5$ and $x_1 = x_2 = \bar{x}$. The coordinates of E_m are independent of m but its stability as an equilibrium of equation (2.2) depends on m . The eigenvalues of E_m with respect to \mathcal{P} are given by λ of equation (4.17) and $(1 - 2m)\lambda$. Thus E_m is a locally stable equilibrium of equation (4.19) if equation (4.18) is satisfied. Note that when $m_1 = m_2$ (which we will assume for the remainder of this example), the line $\{(p_1, p_2, x_1, x_2) \in \mathcal{R} : p_1 = p_2 = 0.5, x_1 = x_2\}$ is invariant and contains the unstable manifold of $(0,0)$ in \mathcal{P} . However, the map of equation (4.19) is not monotone so its dynamical behaviour can be quite general.

To determine the stability of E_m in the 4-dimensional space \mathcal{R} , we study the matrices B_1 and B_4 in equation (4.7). From equation (4.13) we conclude that $\text{tr } B_1 = 2(1 - m)$ and $\det B_1 = (1 - 2m)f_{AA}(\bar{x})f_{Aa}(\bar{x})$ using the fact that $f_{AA}(\bar{x}) + f_{Aa}(\bar{x}) = 2$ (see equation (4.16)). The inequality $\text{tr } B_1 < 1 + \det B_1 < 2$ is equivalent to

$$0 < (2m - 1)(1 - f_{AA}(\bar{x})f_{Aa}(\bar{x})) < 2m. \quad (4.20)$$

For equation (4.20) to be satisfied there are two cases to be considered. If $1 - f_{AA}(\bar{x})f_{Aa}(\bar{x}) > 0$ then the left inequality in equation (4.20) is satisfied if and only if $m > 0.5$. Observing that

$$0 < 1 - f_{AA}(\bar{x})f_{Aa}(\bar{x}) = 1 - (2 - f_{Aa}(\bar{x}))f_{Aa}(\bar{x}) < 1,$$

we conclude that

$$(2m - 1)(1 - f_{AA}(\bar{x})f_{Aa}(\bar{x})) < 2m - 1 < 2m.$$

If $1 - f_{AA}(\bar{x})f_{Aa}(\bar{x}) < 0$ then the left inequality in (4.20) is satisfied if and only if $m < 0.5$. The right inequality in (4.20) is equivalent to

$$f_{AA}(\bar{x})f_{Aa}(\bar{x}) - 1 < 2mf_{AA}(\bar{x})f_{Aa}(\bar{x}).$$

Hence, inequality in (4.20) is satisfied if and only if m satisfies the following inequality:

$$\frac{f_{AA}(\bar{x})f_{Aa}(\bar{x}) - 1}{2f_{AA}(\bar{x})f_{Aa}(\bar{x})} < m < \frac{1}{2}. \tag{4.21}$$

If $m = 0.5$ then $\det B_1 = 0$ and $\text{tr } B_1 = 1$ so the eigenvalues of B_1 are 0 and 1.

From equation (4.11), we compute

$$\det B_4 = (1 - 2m)[1 + \bar{x}(f'_{AA}(\bar{x}) + f'_{Aa}(\bar{x}))/2]^2, \tag{4.22a}$$

and

$$\text{tr } B_4 = (1 - m)[2 + \bar{x}(f'_{AA}(\bar{x}) + f'_{Aa}(\bar{x}))]. \tag{4.22b}$$

Inequality (4.18) implies that $\det B_4 < 1$. To guarantee that $|\text{tr } B_4| < 1$ we assume the following inequality which is similar to Inequality (4.18) but slightly stronger:

$$-1 < 2 + \bar{x}(f'_{AA}(\bar{x}) + f'_{Aa}(\bar{x})) < 1. \tag{4.23}$$

With inequality (4.23), the eigenvalues of B_4 are inside the unit circle for all $m < 1$. The stability properties of E_m are summarized in the following result.

THEOREM 3 *Suppose that the genotype fitnesses satisfy $f_{Aa} = g_{AA} = g_{aa} > f_{AA} = f_{aa} = g_{Aa}$ for all $x > 0$. Assume that $f_{ij}(0) > 1$ and $f_{ij}(x) \searrow 0$ as $x \rightarrow \infty$, that $m = m_1 = m_2$ and that inequality (4.23) holds. Then the eigenvalues of the equilibrium $E_m = (0.5, 0.5, \bar{x}, \bar{x})$ are inside the unit circle if and only if*

- (1) $1 - f_{AA}(\bar{x})f_{Aa}(\bar{x}) > 0$ and $m > 0.5$ or
- (2) $1 - f_{AA}(\bar{x})f_{Aa}(\bar{x}) < 0$ and

$$\frac{f_{AA}(\bar{x})f_{Aa}(\bar{x}) - 1}{2f_{AA}(\bar{x})f_{Aa}(\bar{x})} < m < 0.5.$$

If $m = 0.5$ then there is a line segment of degenerate (eigenvalue 1), symmetric equilibria given by $\mathcal{L} = \{(p_1, p_2, \bar{x}, \bar{x}) \in \mathcal{R} : p_1 = p_2\}$.

For both cases (i) and (ii), E_m loses stability at $m = 0.5$ as E_m passes through a line segment of degenerate equilibria. Such bifurcations from lines of degenerate equilibria have been observed in other models from population genetics, e.g. see Munoz and Selgrade [13] or Selgrade [14]. One way in which this bifurcation occurs may be seen in the following specific example satisfying the hypotheses of Theorem 3.

Take the genotype fitnesses to be decreasing exponential functions of the form:

$$\begin{aligned} f_{AA}(x_1) = f_{aa}(x_1) &= e^{1-x_1}, \quad f_{Aa}(x) = e^{1-0.5x_1}, \\ g_{AA}(x_2) = g_{aa}(x_2) &= e^{1-0.5x_2}, \quad g_{Aa}(x_2) = e^{1-x_2}. \end{aligned} \quad (4.24)$$

With the fitnesses of equation (4.24), $\bar{x} \approx 1.4151$ is the unique solution to equation (4.16) so $E_m \approx (0.5, 0.5, 1.4151, 1.4151)$. Compute that

$$2 + \bar{x}(f'_{AA}(\bar{x}) + f'_{Aa}(\bar{x})) \approx 0.11774$$

so inequality (4.23) holds. Note that $1 - f_{AA}(\bar{x})f_{Aa}(\bar{x}) = 1 - e^{2-1.5\bar{x}} \approx 0.1154$, hence case (i) of Theorem 3 applies. Thus E_m is locally asymptotically stable if $m > 0.5$ and unstable if $m < 0.5$.

In fact, from numerical studies, $E_m = (0.5, 0.5, \bar{x}, \bar{x})$ appears to be globally asymptotically stable if $m > 0.5$. E_m loses stability as m decreases through 0.5 because one eigenvalue of B_1 increases through 1. Thus, for larger migration rates ($m > 0.5$), each local population asymptotically approaches the same density value \bar{x} and the same allele frequency $p_1 = p_2 = 0.5$, where both alleles are present in equal numbers. So the local populations are behaving alike, both demographically and genetically. For two-population metapopulation models without genetic variation, Hanski [3], Gyllenberg *et al.* [15] and others have observed that complex dynamical behaviour for the local populations may become somewhat stable and synchronous as migration rates increase.

For $m < 0.5$ our example exhibits bistable behaviour. For instance, if $m = 0.45$ then there are three interior equilibria—one unstable symmetric equilibrium $E_m \approx (0.5, 0.5, 1.4151, 1.4151)$ and two stable nonsymmetric equilibria (figure 1)

$$E_A \approx (0.95013, 0.95622, 1.3916, 1.4718) \text{ and}$$

$$E_a \approx (0.04988, 0.04378, 1.3916, 1.4718).$$

E_m has a 3-dimensional stable manifold (the plane \mathcal{P} is a subset of this stable manifold) which separates the domains of attraction of E_A and E_a . Asymptotically, each local population behaves similarly, but that behaviour depends on initial conditions. Specifically, each population approaches an equilibrium where population sizes are close to one another and the A allele frequencies are large at E_A or the a allele frequencies are large at E_a . Notice that the population sizes at E_A and E_a are identical but the allele frequencies are very different. Thus, the bistable behaviour reveals genetic but not demographic differences.

Although decreasing m through 0.5 results in the stable equilibrium E_m being replaced by the three equilibria E_m , E_A and E_a , this bifurcation at $m = 0.5$ is not a pitchfork bifurcation because E_A and E_a are never close to E_m . At $m = 0.5$, the line segment of degenerate equilibria \mathcal{L} extends from the point $(0, 0, \bar{x}, \bar{x})$ to the point $(1, 1, \bar{x}, \bar{x})$ in the plane $\{(p_1, p_2, x_1, x_2) \in \mathcal{R} : x_1 = x_2 = \bar{x}\}$. As m decreases below 0.5, the equilibria of \mathcal{L} disappears and are replaced by E_m at the midpoint of \mathcal{L} and E_A and E_a near the ends of \mathcal{L} . For $m < 0.5$, solutions to equation (2.2) rapidly collapse to the line segment \mathcal{L} and then move along \mathcal{L} toward E_A and E_a as depicted in figure 1(a). Thus population sizes x_1 and x_2 rapidly converge to equilibrium values but allele frequencies converge on a slower time scale (see figure 1(b)).

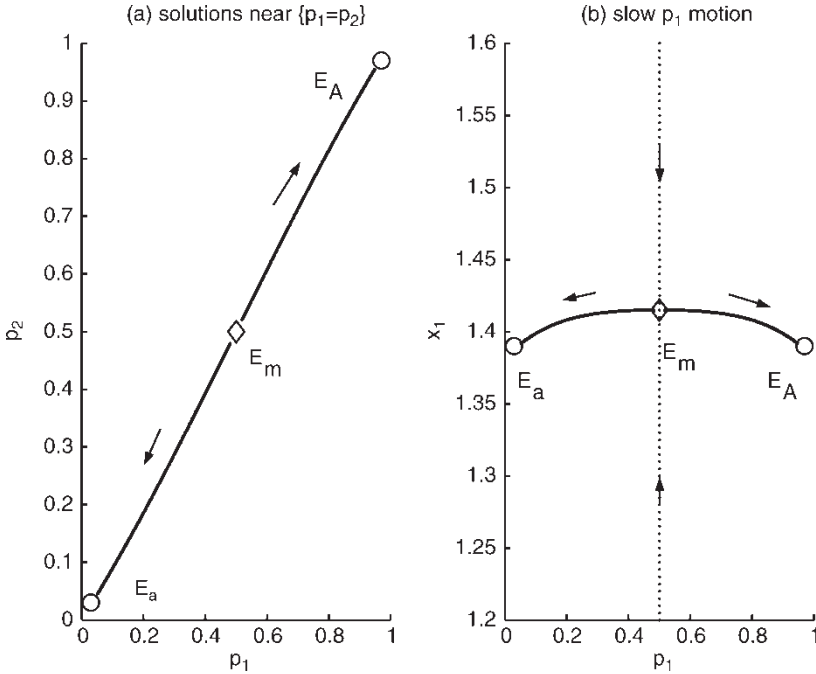


Figure 1. Solutions to equation (2.2) for fitnesses equation (4.24) with $m = 0.45$ are projected into (p_1, p_2) -plane and (p_1, x_1) -plane illustrating slow evolution of allele frequency toward stable equilibria E_A and E_a . Arrows indicate direction of iteration. In (b) the line $\{p_1 = 0.5\}$ represents the projection of the stable manifold of E_m .

4.3 Example satisfying condition (b), i.e. $m_1 + m_2 = 1$

Here we consider another example with fitnesses given by equation (4.24) but assume that $m_1 \neq m_2$. This example illustrates how migration which is larger into the patch exhibiting heterozygote superiority (stability) than out of that patch results in a stable metapopulation.

We seek symmetric equilibria with $p_1 = p_2 = 0.5$. Because of the form of the fitnesses in equation (4.24), if $p_1 = p_2 = 0.5$ then $f_A = f_a = f$ and $g_A = g_a = g$ although these fitnesses may not be equal to 1 at equilibrium. Hence (b) holds, i.e. $m_1 + m_2 = 1$. To find the x_T -coordinates of an equilibrium consider the decreasing function $h(x) = e^{1-x} + e^{1-0.5x}$ defined in terms of genotype fitnesses equation (4.24). Impose the condition $m_1 x_1 = m_2 x_2$ and observe that solving equation (3.1) for x_1 is equivalent to finding the unique positive solution \bar{x}_1 to

$$2 = m_2 h(x_1) + m_1 h(m_1 x_1 / m_2), \tag{4.25}$$

which exists since $h(0) > 2$ and $h(x)$ decreases to 0 as x increases. With $\bar{x}_2 = m_1 \bar{x}_1 / m_2$, equation (3.1) is satisfied because $m_1 + m_2 = 1$. Hence, we may assert the existence of a symmetric equilibrium in the interior of \mathcal{R} which depends on m_2 with the following result:

PROPOSITION 2 *Suppose genotype fitnesses are given by equation (4.24) and assume condition (b), i.e. that $m_1 + m_2 = 1$. Then equation (2.2) has a symmetric equilibrium $E_{m_2} = (0.5, 0.5, \bar{x}_1, \bar{x}_2)$ satisfying (sym) where \bar{x}_1 is the unique positive solution to equation (4.25).*

To determine the stability of E_{m_2} we analyse the matrix $D(E_{m_2})$ in equation (4.7). Since $f_A = f_a$ and $g_A = g_a$ at E_{m_2} , equation (4.8) implies B_3 is zero. At E_{m_2} we see that

$$B_1 = \begin{bmatrix} (1 - m_1)f_{AA}(\bar{x}_1) & m_1f_{Aa}(\bar{x}_2) \\ m_2f_{AA}(\bar{x}_1) & (1 - m_2)f_{Aa}(\bar{x}_2) \end{bmatrix} \quad (4.26)$$

and

$$B_4 = \begin{bmatrix} (1 - m_1)[h(\bar{x}_1) + \bar{x}_1h'(\bar{x}_1)]/2 & m_2[h(\bar{x}_2) + \bar{x}_2h'(\bar{x}_2)]/2 \\ m_1[h(\bar{x}_1) + \bar{x}_1h'(\bar{x}_1)]/2 & (1 - m_2)[h(\bar{x}_2) + \bar{x}_2h'(\bar{x}_2)]/2 \end{bmatrix}. \quad (4.27)$$

Note that $\det B_1 = \det B_4 = 0$, so E_{m_2} has two zero eigenvalues. The other two eigenvalues are $\text{tr } B_1$ and $\text{tr } B_4$ given by

$$\begin{aligned} \text{tr } B_1 &= m_2f_{AA}(\bar{x}_1) + m_1f_{Aa}(\bar{x}_2), \\ \text{tr } B_4 &= 1 + 0.5[m_2\bar{x}_1h'(\bar{x}_1) + m_1\bar{x}_2h'(\bar{x}_2)]. \end{aligned} \quad (4.28)$$

For parameter values of interest here $\text{tr } B_4$ is always in the stable range but $\text{tr } B_1$ may be in the stable or unstable range. In fact, numerical examples indicate that E_{m_2} is globally stable if $m_2 > 0.5 > m_1$ and unstable if $m_2 < 0.5 < m_1$. When $m_2 > m_1$, there is more migration into the stable (p_1, x_1) -patch where the local population exhibits stability than out of that patch and this migration pattern results in a stable metapopulation. If $m_1 > m_2$ then the interior equilibrium is unstable and there are two stable boundary equilibria, one in each fixation plane (see figure 3). E_{m_2} loses stability when $m_2 = m_1 = 0.5$ where $\text{tr } B_1 = 1$. This parameter set was discussed in section 4.2 since $E_{m_2} = (0.5, 0.5, 1.4151, 1.4151)$ is on the line of degenerate equilibria for $m = m_2 = m_1 = 0.5$.

For $m_2 > 0.5 > m_1$, we show that E_{m_2} is stable by showing that as m_2 increases through 0.5 then the $\text{tr } B_1$ decreases through 1. This is done by differentiating the function for $\text{tr } B_1$ in equation (4.28) with respect to m_2 at $m_2 = 0.5$ remembering that $m_1 = 1 - m_2$, $\bar{x}_2 = m_1\bar{x}_1/m_2$, and \bar{x}_1 varies with m_2 . The dependence of \bar{x}_1 on m_2 may be determined by differentiating equation (4.25) implicitly to obtain at $m_2 = 0.5$

$$\frac{d\bar{x}_1}{dm_2} = 2\bar{x}_1 \approx 2.83. \quad (4.29)$$

Figure 2 depicts the curve of points satisfying equation (4.25) near $(m_2, x_2) = (0.5, 1.4151)$, which clearly has a slope of approximately 3 at $m_2 = 0.5$.

A tedious computation using equation (4.29) shows that the derivative of $\text{tr } B_1$ in equation (4.28) with respect to m_2 at $m_2 = 0.5$ and $\bar{x}_1 = 1.4151$ is approximately -0.6659 . So an increase in m_2 of 0.05 should result in a decrease of approximately 0.0333 in $\text{tr } B_1$. This decrease is consistent with numerical simulations. For example, if $m_2 = 0.55$ and $m_1 = 0.45$ the symmetric equilibrium $E_{m_2} = (0.5, 0.5, 1.5492, 1.2676)$ is stable and its largest eigenvalue is $\text{tr } B_1 \approx 0.9666$. If $m_2 = 0.45$ and $m_1 = 0.55$ the symmetric equilibrium $E_{m_2} = (0.5, 0.5, 1.2676, 1.5492)$ is unstable and its largest eigenvalue is $\text{tr } B_1 \approx 1.0334$. In this case, solutions are asymptotic to two stable boundary equilibria, $E_1 = (1, 1, 1.312, 1.6035)$ and $E_0 = (0, 0, 1.312, 1.6035)$, see figure 3.

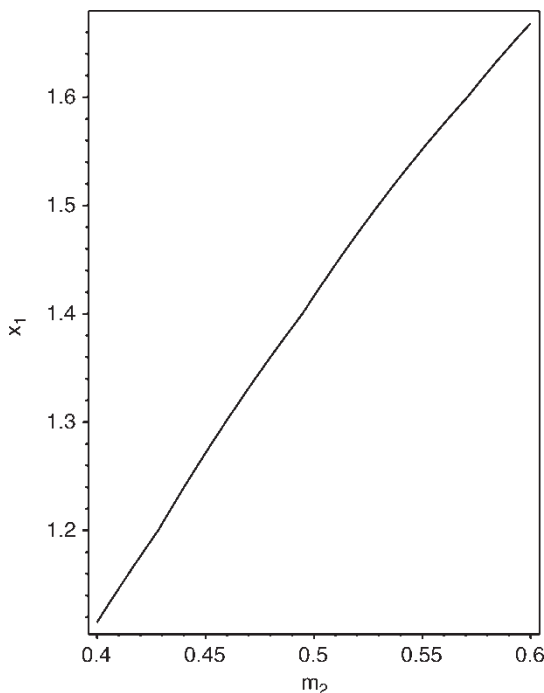


Figure 2. Curve satisfying equation (4.25) near $(m_2, x_1) = (0.5, 1.4151)$.

5. Attracting invariant curves with large migration

As observed for the example in section 4.2, a large migration rate may result in a globally stable equilibrium. However, according to Proposition 1, large migration rates ($m_1 + m_2 > 1$) are necessary for an equilibrium satisfying (c) to have complex eigenvalues. A common way to obtain an attracting invariant curve in this situation is through a Naimark-Sacker bifurcation [4, 5]. With this bifurcation an equilibrium becomes unstable because its complex eigenvalues move outside the unit circle as a parameter is varied.

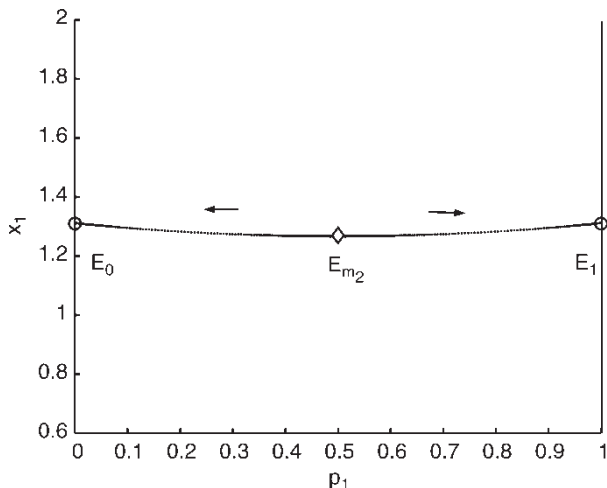


Figure 3. Solutions are projected into 2-dimensional (p_1, x_1) -space for fitnesses (4.24), $m_1 = 0.55$ and $m_2 = 0.45$. Equilibria E_0 and E_1 are stable and E_{m_2} is unstable.

We present an example where the fitnesses for the x_1 population exhibit heterozygote superiority and the fitnesses for the x_2 population exhibit neutrality. Then we show that a Naimark-Sacker bifurcation occurs as the migration rate m_2 increases. Take the genotype fitnesses to be decreasing exponential functions of the form (see figure 4):

$$\begin{aligned}
 f_{AA}(x_1) = f_{aa}(x_1) = e^{2-0.5x_1}, \quad f_{Aa}(x) = e^{2-0.15x_1} \quad \text{and} \\
 g_{AA}(x_2) = g_{aa}(x_2) = g_{Aa}(x_2) = e^{1-0.9x_2}.
 \end{aligned}
 \tag{5.1}$$

Since all genotype fitnesses for the x_2 population are the same, the x_2 population has no genetic variation, i.e. $g(x_2) = g_{ij}(x_2)$ for all $i, j = A, a$. Clearly,

$$f_{Aa}(x) > f_{ii}(x) > g(x) \text{ for all } x > 0.$$

Since $g_A = g_a$ and $f_A(0.5, x_1) = f_a(0.5, x_1)$, condition (c) is satisfied at an equilibrium where $\bar{p}_1 = 0.5$. The fact that f_{Aa} is large and slowly decreasing (see figure 4) in comparison with the other fitnesses, which suggests that it might be possible to have an equilibrium with a negative fitness product corresponding to the condition given in Proposition 1 because

$$\left(f + \bar{x}_1 \frac{\partial f}{\partial x_1} \right) > 0 > \left(g + \bar{x}_2 \frac{\partial g}{\partial x_2} \right). \tag{5.2}$$

Numerical experiments indicate that equation (2.2) with fitnesses given by equation (5.1) has a family of asymptotically stable, nonsymmetric equilibria $E_{m_2} = (0.5, 0.5, \bar{x}_1, \bar{x}_2)$ for $m_1 = 0.93$ and $m_2 < 0.9$. Because $f_{AA} = f_{aa}$ and $\bar{p} = 0.5$, (c) is satisfied and the derivatives in equation (4.8) are zero. Hence, the submatrix B_3 in $D(E_{m_2})$ is zero and the eigenvalues of E_{m_2} are those of B_1 and B_4 . Fixing $m_1 = 0.93$ and using equation (4.12), we find that

$$B_1 = \begin{bmatrix} 0.07f_{AA}(\bar{x}_1) & m_2\bar{x}_2g(\bar{x}_2)/\bar{x}_1 \\ 0.93\bar{x}_1f_{AA}(\bar{x}_1)/\bar{x}_2 & (1 - m_2)g(\bar{x}_2) \end{bmatrix}, \tag{5.3}$$

which has real eigenvalues inside the unit circle for m_2 near 0.9. The eigenvalues of B_4 are complex and move from inside to outside the unit circle as m_2 increases through 0.901.

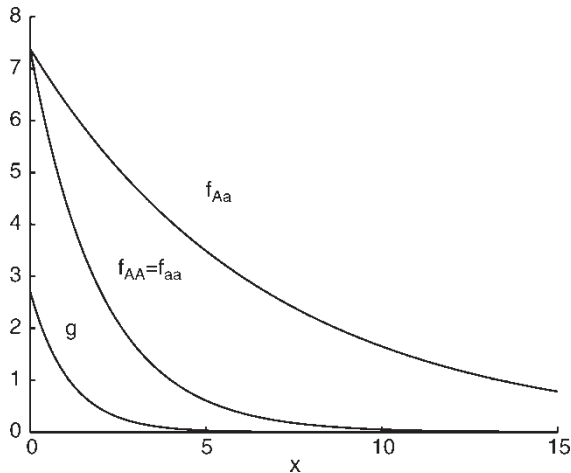


Figure 4. Genotype fitnesses equation (5.1).

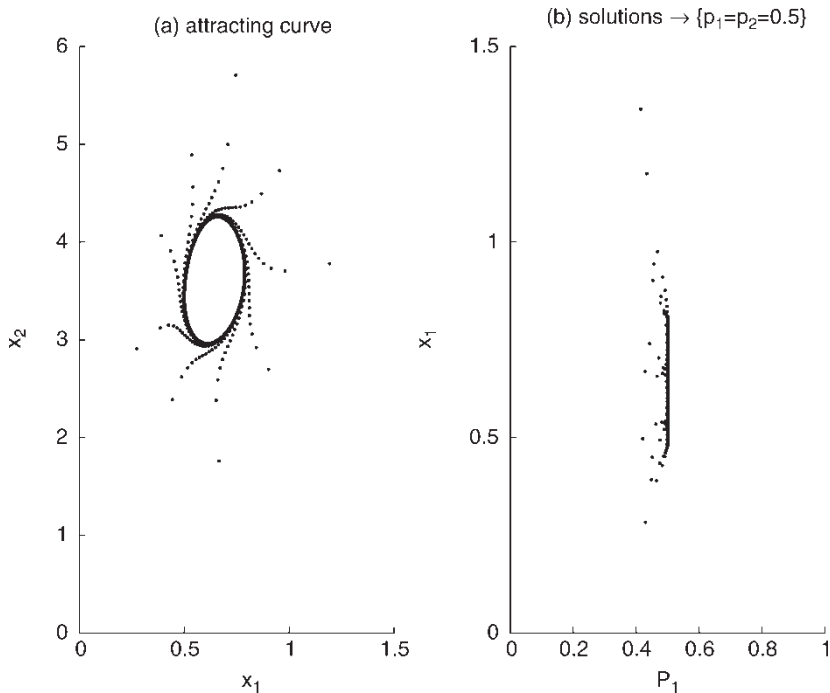


Figure 5. Two views of the attracting invariant curve are given for fitnesses (5.1) and $m_1 = m_2 = 0.93$. (a) shows attraction to the curve within the invariant plane \mathcal{P} and (b) shows attraction to \mathcal{P} .

The values for \bar{x}_1 , \bar{x}_2 and m_2 at bifurcation are found by solving simultaneously the equation

$$\det B_4 = 1$$

along with the first two equations of equation (3.1). The values obtained are $\bar{x}_1 \approx 0.6209$, $\bar{x}_2 \approx 3.5468$ and $m_2 \approx 0.901$. The eigenvalues of the equilibrium $E_{0.901} = (0.5, 0.5, 0.6209, 3.5468)$ are -0.5403 , 0.9305 and $0.1601 \pm 0.9870i$. A Naimark-Sacker bifurcation occurs at $m_2 \approx 0.901$ resulting in a locally stable invariant curve. Since $f = f_A$ and $g = g_A$, the plane $\mathcal{P} = \{(p_1, p_2, x_1, x_2) \in \mathcal{R} : p_1 = p_2 = 0.5\}$ is invariant and B_4 is the derivative matrix for equation (2.2) restricted to \mathcal{P} . Hence, the Naimark-Sacker bifurcation occurs for equation (2.2) restricted to \mathcal{P} and Pscr contains the attracting invariant curve. On this attractor the population sizes vary but the allele frequencies remain fixed at 0.5. For values of $m_2 > 0.901$, numerical results show that the metapopulation model has a globally asymptotically stable invariant curve as depicted in figure 5 when $m_2 = 0.93 = m_1$.

6. Conclusion and future directions

Here we study a 4-dimensional system of nonlinear difference equations (2.2) which models a two-patch metapopulation under the influence of density-dependent selection. To determine conditions, which result in similar behaviour in the local populations, we introduce the concept of symmetric equilibrium. The stability of a symmetric equilibrium is analyzed by considering two 2×2 matrices, one containing primarily genetic information and the other containing primarily demographic information. The genetic matrix is positive so it has only real eigenvalues but, in contrast, the demographic matrix may have complex eigenvalues.

In section 4.2, we present a family of examples where the genotypes of one local population exhibit heterozygote superiority in fitness (stability) and the genotypes of the other local population exhibit heterozygote inferiority (instability) but the 4-dimensional metapopulation can exhibit stability, instability or bistability. The bifurcation we observe from stable equilibrium to two stable equilibria is not a pitchfork bifurcation. At bifurcation, there is a line segment of degenerate equilibria which is replaced by two stable equilibria located at opposite ends of the segment and a saddle point as the migration parameter decreases. A theoretical investigation of this bifurcation will be attempted in the future.

The example of section 4.3 explores the effects of different migration rates on metapopulation stability. For this example, if the immigration rate for the stable patch exhibiting heterozygote superiority is greater than its emigration rate, then the metapopulation has a stable equilibrium. If the reverse is true then an unstable equilibrium results. These results demonstrate that migration patterns can critically affect metapopulation dynamics and, through such effects, impinge on levels of genetic polymorphism and population size outcomes. Studying the effects of different migration rates on metapopulation dynamics in a more general setting will be the topic of future work.

In section 5, we illustrate a Naimark-Sacker bifurcation that occurs as a migration parameter varies. This bifurcation results in a globally asymptotically stable invariant curve. Such behaviour cannot occur in the selection model equation (2.1) without migration. Additional studies will focus on the existence of other nonequilibrium attractors. A period-doubling cascade resulting in a strange attractor [9] has been demonstrated for a one-patch model with selection and immigration. Similar behaviour is expected for metapopulation models.

Acknowledgements

Research partially supported by the USDA-Forest Service, Southern Research Station, Southern Institute of Forest Genetics, Saucier, MS.

References

- [1] Hanski, I. and Gilpin, M.E., 1997, *Metapopulation Biology: Ecology, Genetics, and Evolution* (San Diego: Academic Press).
- [2] Hastings, A. and Harrison, S., 1994, Metapopulation dynamics and genetics, *Annual Review of Ecology and Systematics*, **25**, 167–188.
- [3] Hanski, I., 1999, *Metapopulation Ecology* (New York: Oxford University Press).
- [4] Naimark, J., 1967, Motions close to doubly asymptotic motions, *Soviet Math. Dokl.*, **8**, 228–231.
- [5] Sacker, R.J., 1964, On invariant surfaces and bifurcation of periodic solutions of ordinary differential equations. New York University, IMM-NYU **333**.
- [6] Roughgarden, J., 1979, *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (New York: MacMillan).
- [7] Selgrade, J.F. and Namkoong, G., 1992, Dynamical behavior for population genetics models of differential and difference equations with nonmonotone fitness, *Journal of Mathematical Biology*, **30**, 815–826.
- [8] Roberds, J.H. and Selgrade, F., 2000, Dynamical analysis of density-dependent selection in a discrete one-island migration model, *Mathematical Biosciences*, **164**, 1–15.
- [9] Selgrade J.F. and Roberds J.H., 2005, Equilibrium and nonequilibrium attractors for a discrete, selection-migration model, *Canadian Appl. Math. Quarterly*, **11**, 195–211.
- [10] Edelstein-Kesket, L., 1988, *Mathematical Models in Biology* (New York: Random House).
- [11] Gantmacher, J.R., 1964, *The Theory of Matrices*, Vol.II (New York: Chelsea).
- [12] Roughgarden, J., 1976, Resource partitioning among competing species, a coevolutionary approach, *Theoretical Population Biology*, **9**, 388–424.

- [13] Munoz, E. and Selgrade, F., 1989, Asymptotic behavior for a competitive model with genetic variation, *SIAM Journal of Applied Mathematics*, **49**, 1768–1778.
- [14] Selgrade, J.F., 1990, Limits of heteroclinic orbits in a competitive model with genetic variation, *Rocky Mountain Journal of Mathematics*, **20**, 1133–1155.
- [15] Gyllenberg, M., Söderbacka, G. and Ericsson, S., 1993, Does migration stabilize local population dynamics? Analysis of a discrete metapopulation model, *Mathematical Biosciences*, **118**, 25–49.