



Global stability in diallelic migration–selection models

Josef Hofbauer^a, Linlin Su^{b,*}^a Department of Mathematics, University of Vienna, Oskar-Morgenstern-Platz 1, 1090 Vienna, Austria^b South University of Science and Technology of China, 1088 Xueyuan Ave, Nanshan District, Shenzhen, Guangdong Province, 518055, PR China

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ABSTRACT

For diallelic migration–selection models in continuous time with arbitrary migration in either discrete or continuous space, a sufficient condition for the existence of a globally asymptotically stable equilibrium is established. As a special case, this condition includes concavity of the mean selection coefficient.

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1. Introduction

We consider a gene at a single locus with two alleles A_1 and A_2 . We posit weak selection and use a continuous-time approximation. The genetic structure of the population is measured by the relative frequencies p and $1 - p$ of A_1 and A_2 , respectively. Unless they are close to extinction, populations are usually distributed in space. They occupy a habitat within which they undergo selection and migration. Therefore, it is desirable to study the evolution of gene frequencies under different migration–selection schemes. For recent general reviews of this subject, consult Bürger [4], Lou et al. [21], and Nagylaki and Lou [28].

Let r_{ij} ($= r_{ji}$) for $i, j = 1, 2$ designate the selection coefficient (sometimes called Malthusian fitness) of the genotype $A_i A_j$ (among which $A_1 A_1$ and $A_2 A_2$ are called homozygotes, and $A_1 A_2$ heterozygote). Then the selection coefficient of allele A_i is

$$r_i = r_{i1}p + r_{i2}(1 - p), \quad (1.1)$$

* Corresponding author.

E-mail addresses: josef.hofbauer@univie.ac.at (J. Hofbauer), su.ll@sustc.edu.cn (L. Su).

and the mean selection coefficient of the population is

$$\begin{aligned}\bar{r} &= r_1 p + r_2(1 - p) \\ &= r_{11} p^2 + 2r_{12} p(1 - p) + r_{22}(1 - p)^2.\end{aligned}\tag{1.2}$$

Under selection the frequency of A_1 changes according to

$$\dot{p} = p(r_1 - \bar{r}) = p(1 - p)s(p),\tag{1.3}$$

where

$$s(p) = r_{12} - r_{22} + (r_{11} + r_{22} - 2r_{12})p.\tag{1.4}$$

If every r_{ij} is frequency independent, then from (1.2) and (1.4) we see that the mean selection coefficient \bar{r} is a concave function of p if and only if

$$r_{11} + r_{22} - 2r_{12} \leq 0, \quad \text{i.e.,} \quad s'(p) \leq 0.\tag{1.5}$$

The inequality (1.5) includes the following cases:

- (A) $r_{12} = \frac{1}{2}(r_{11} + r_{22})$: the alleles A_1 and A_2 contribute additively to the fitness of the genotypes, this is called *no dominance*; s is independent of p .
- (B) $r_{12} > r_{11}, r_{22}$: the heterozygote is fitter than both homozygotes, this is called *overdominance*.
- (C) $r_{12} = \max\{r_{11}, r_{22}\}$ and $r_{11} \neq r_{22}$: the heterozygote behaves the same as the fitter of the homozygotes, the fitter allele is *completely dominant*.
- (D) $\frac{1}{2}(r_{11} + r_{22}) < r_{12} < \max\{r_{11}, r_{22}\}$: the fitness of the heterozygote is between those of the homozygotes and closer to the fitter of them, the fitter allele is *partially dominant*.

In cases (A), (C), and (D), the selection function $p(1 - p)s(p)$ does not change sign for $p \in (0, 1)$, and therefore *selection is directional*. This is not the case for (B).

The main purpose of this paper is to establish a sufficient condition for the existence of a globally asymptotically stable equilibrium. In particular, this condition includes concavity of the mean selection coefficient. In fact, following Fleming [10] and Hess and Weinberger [15], for both discrete demes and continuous space, we investigate a more general situation: we replace $p(1 - p)$ in (1.3) by a general function $f(p)$ that satisfies

$$f \in C^1[0, 1], \quad f(0) = f(1) = 0, \quad f(p) > 0 \quad \text{in } (0, 1),\tag{1.6a}$$

$$f' \text{ is strictly decreasing, i.e., } f \text{ is strictly concave on } [0, 1].\tag{1.6b}$$

We prove also that under certain conditions, a sufficiently high ratio of the strength of selection to that of migration leads to a stable equilibrium where both alleles coexist everywhere in space.

We treat the discrete-space model (2.1) in Section 2; in Theorem 2.3 we establish global asymptotic stability. For the case of discrete time, Eyland [8] analyzed two demes with no dominance under a weak-selection, weak-migration assumption; Campbell [5], based on Karlin and Campbell [17], sketched a proof for global asymptotic stability under the assumption of submultiplicative fitnesses, which corresponds to the concavity of the mean selection coefficient in continuous time. Since the continuous-time model is a limiting case of the discrete-time model, one expects strong similarity between their properties; our results and the above literature confirm this. Proposition 2.7 and Remarks 2.6, 2.8, and 2.9 demonstrate that if

the concavity of the mean selection coefficient is violated in one of the demes, then there can be more than one stable equilibrium.

Section 3 is devoted to the continuous-space model (3.1). Global asymptotic stability is established in Theorem 3.8. For (3.1), assuming (1.6) and s nonincreasing in p , Hess and Weinberger [15, Th. 1] investigated global asymptotic stability for the Laplacian (i.e., migration is homogeneous and isotropic). Using a different method, we extend their result to general uniformly elliptic operators, which describes arbitrary migration. The special case that s is independent of p was studied by Henry [13] and Hess [14] for the Laplacian and by Lou and Nagylaki [19] for general uniformly elliptic operators. Remark 3.11 discusses complete dominance for continuous space, which also provides an example that if the mean selection coefficient is not everywhere concave, then more than one stable equilibrium can coexist.

In Section 4, we summarize our results, discuss the biological and mathematical connections between the two models (2.1) and (3.1), and mention some open problems.

2. Migration among finitely many demes

We consider a population with two alleles A_1 and A_2 at a single locus, distributed over a finite number, say K , demes. We denote the respective selection coefficients of A_1A_1 , A_1A_2 , and A_2A_2 by a_k , 0, and b_k in deme k . This is not a restriction, because the function $s(p)$ in (1.4) depends only on the differences $r_{11} - r_{12}$ and $r_{22} - r_{12}$.

Let p_k designate the frequency of allele A_1 in deme k , and set $p = (p_1, p_2, \dots, p_K) \in [0, 1]^K$. Then the migration–selection model in continuous time (see [4, Sect. 6], [27, Sect. 2]) is given by

$$\dot{p}_k = \sum_{\ell} \mu_{k\ell} p_{\ell} + f_k(p_k), \quad (2.1)$$

where

$$f_k(p_k) = p_k(1 - p_k) [-b_k + (a_k + b_k)p_k]. \quad (2.2)$$

The $K \times K$ backward migration rate matrix $M = (\mu_{k\ell})$ is *quasi-positive*, i.e., $\mu_{k\ell} \geq 0$ for every $k \neq \ell$. Its row sums are 0, i.e., $M\mathbf{1} = \mathbf{0}$, where $\mathbf{0}, \mathbf{1} \in \mathbb{R}^K$ denote the vectors of zeros and ones.

The *spectral bound* $\sigma(A)$ or *stability modulus* of a matrix A is defined as the maximum real part of the eigenvalues, see [1] and [34, p. 60]. The Perron–Frobenius theorem implies that for a quasi-positive matrix A , $\sigma(A)$ is an eigenvalue.

Notation. For a vector $v \in \mathbb{R}^K$ we write $v \geq \mathbf{0}$ or $v \in \mathbb{R}_+^K$ if for every i , we have $v_i \geq 0$; and $v > \mathbf{0}$ if for every i , we have $v_i > 0$; and $v \gneq \mathbf{0}$ if $v \geq \mathbf{0}$ and $v \neq \mathbf{0}$.

We call $\mathbf{0}$ and $\mathbf{1}$ the trivial equilibria of (2.1), states in $[0, 1]^K \setminus \{\mathbf{0}, \mathbf{1}\}$ nontrivial, and points in the open cube $(0, 1)^K$ interior. If the migration matrix M is irreducible, then every nontrivial equilibrium of (2.1) is interior.

Since M is quasi-positive and f_k depends only on p_k for every k , the migration–selection model (2.1) is a quasimonotone, or cooperative, system of ODEs and defines a *monotone* semiflow on $[0, 1]^K$ (see [34]): For any two solutions $p(t), q(t)$ of (2.1),

$$p(0) \leq q(0) \quad \Rightarrow \quad p(t) \leq q(t) \quad \text{for } t > 0. \quad (2.3)$$

If M is irreducible, then (2.1) generates a *strongly monotone* (or *strongly order preserving* [14]) semiflow (see [34, p. 56]):

$$p(0) \leq q(0) \quad \Rightarrow \quad p(t) < q(t) \quad \text{for } t > 0. \quad (2.4)$$

In this paper, we shall concentrate on the case where $a_k + b_k \leq 0$ holds in every deme k . According to (1.5), this is equivalent to the concavity of the mean selection coefficient in each deme.

More generally than (2.2), we allow the selection function to be of the form

$$f_k(p_k) = p_k(1 - p_k)s_k(p_k), \quad \text{where } s'_k(p) \leq 0 \text{ for every } k, \quad (2.5)$$

or, even more generally,

$$f_k(p_k) = f(p_k)s_k(p_k), \quad \text{where } f \text{ satisfies (1.6) and } s'_k(p) \leq 0 \text{ for every } k. \quad (2.6)$$

The following degenerate situation requires separate treatment: There exists a constant c in $[0, 1]$ such that

$$s_k(c) = s'_k(c) = 0 \quad \text{for every } k. \quad (2.7)$$

It means that the spatially constant state $p = c\mathbf{1}$ is an equilibrium of (2.1) with principal eigenvalue 0.

Remark 2.1. For (2.2) the condition (2.7) leads to the extreme special case $a_k = b_k = 0$ for every k , and therefore $f_k \equiv 0$, i.e., no selection; there exists a line of equilibria $\{p = c\mathbf{1} : c \in [0, 1]\}$. If the migration matrix M is irreducible, then these are the only equilibria.

The following lemma and its proof are related to Theorem 6 in [16] on the dispersal of a single species among K demes.

Lemma 2.2. *Posit (2.1) and (2.6). Assume that there exists no $c \in (0, 1)$ that satisfies (2.7), and that the migration matrix M is irreducible. If \hat{p} is an interior equilibrium, then it is linearly stable; i.e., every eigenvalue of the Jacobian of (2.1) at \hat{p} has a negative real part.*

Proof. From (2.1), (2.6), and $M\mathbf{1} = \mathbf{0}$ we have, at an equilibrium $p = \hat{p}$,

$$f_k(p_k) = f(p_k)s_k(p_k) = - \sum_{\ell} \mu_{k\ell} p_{\ell} = \sum_{\ell: \ell \neq k} \mu_{k\ell} (p_k - p_{\ell}). \quad (2.8)$$

The Jacobian matrix J at p has entries

$$J_{k\ell} = f'_k(p_k)\delta_{k\ell} + \mu_{k\ell}, \quad (2.9)$$

where $\delta_{k\ell}$ denotes the Kronecker delta. Then (2.9), (2.8), and $M\mathbf{1} = \mathbf{0}$ imply that for each k ,

$$\begin{aligned} \sum_{\ell} J_{k\ell} f(p_{\ell}) &= f'_k(p_k) f(p_k) + \sum_{\ell} \mu_{k\ell} f(p_{\ell}) \\ &= [f(p_k) s'_k(p_k) + f'(p_k) s_k(p_k)] f(p_k) + \sum_{\ell} \mu_{k\ell} f(p_{\ell}) \\ &= s'_k(p_k) [f(p_k)]^2 + f'(p_k) [- \sum_{\ell} \mu_{k\ell} p_{\ell}] + \sum_{\ell} \mu_{k\ell} f(p_{\ell}) \\ &= s'_k(p_k) [f(p_k)]^2 - \sum_{\ell: \ell \neq k} \mu_{k\ell} [f'(p_k)(p_{\ell} - p_k) - f(p_{\ell}) + f(p_k)] \leq 0. \end{aligned} \quad (2.10)$$

The term in the last bracket is nonnegative because of the strict concavity of f , and it is zero only if $p_{\ell} = p_k$. Suppose equality holds in (2.10) for every k . Then, since p is interior, we have $s'_k(p_k) = 0$ for

every k . Furthermore, for every k, ℓ with $\mu_{k\ell} > 0$, we get $p_k = p_\ell$; hence the irreducibility of M implies $p_1 = \dots = p_K$. From (2.8) we conclude that $s_k(p_k) = 0$ for every k . This implies the degenerate situation (2.7), which is excluded by our assumption.

Hence, there is a positive vector $v > \mathbf{0}$ such that $Jv \not\leq \mathbf{0}$. Since the Jacobian matrix J is quasi-positive, this implies that every eigenvalue of J has a negative real part. See, e.g., [3, 6.2.7. Th.] or [16, Lemma 1]. Indeed, let $u > \mathbf{0}$ be a left principal eigenvector of J , i.e., $u^\top J = \sigma(J)u^\top$. Then $0 > u^\top Jv = \sigma(J)u^\top v$ and hence $\sigma(J) < 0$. \square

Theorem 2.3. *Assume that (2.1) and (2.2) hold. Suppose the mean selection coefficient is concave in each deme, i.e., $a_k + b_k \leq 0$ for all k , there is selection in at least one deme, i.e., $a_k \neq 0$ or $b_k \neq 0$ for some k , and M is irreducible. Then (2.1) has a globally asymptotically stable equilibrium.¹*

Proof. The Jacobian matrices of (2.1)–(2.2) at the trivial equilibria $\mathbf{0}$ and $\mathbf{1}$ are given by $J_0 = M - \text{diag}(b_k)$ and $J_1 = M - \text{diag}(a_k)$. By [1,6,7], the spectral bound $\sigma(A)$ of a quasi-positive matrix A is a convex function of its diagonal terms. Hence

$$\frac{1}{2} [\sigma(J_0) + \sigma(J_1)] \geq \sigma\left(\frac{1}{2} [J_0 + J_1]\right) = \sigma\left(M - \frac{1}{2} \text{diag}(a_k + b_k)\right) \geq \sigma(M) = 0. \quad (2.11)$$

The second inequality in (2.11) is due to the fact that, for irreducible A , $\sigma(A)$ is a strictly increasing function of each entry of A [3, Cor. 2.1.5 on p. 27], and equality holds only if $a_k + b_k = 0$ for all k . Since M is irreducible, equality in the first estimate holds only if $a - b$ is a multiple of $\mathbf{1}$, see [7, Th. 1]. Hence equality in (2.11) holds if and only if $a = -b = d\mathbf{1}$ for some $d \in \mathbb{R}$.

The situation $\sigma(J_0) = \sigma(J_1) = 0$ happens only if $a_k = b_k = 0$ for all k , which is excluded by our assumption. (Cf. Remark 2.1.)

This leaves us with the following three cases:

- (i) $\sigma(J_0) > 0, \sigma(J_1) > 0$.

Then both $\mathbf{0}$ and $\mathbf{1}$ are unstable. Hence, orbits that start from positive initial conditions εv , where ε is close to 0 and v designates a positive eigenvector of J_0 , increase by monotonicity and converge to a positive equilibrium p , see [34, pp. 43–44, 62]. Orbits that start from $\mathbf{1} - \varepsilon \tilde{v}$, where $\varepsilon > 0$ is small and \tilde{v} is a positive eigenvector of J_1 , decrease and converge to a positive equilibrium q . Monotonicity of the flow (2.3) implies $p \leq q$. If $p = q$, this interior equilibrium is globally asymptotically stable. Otherwise, by Lemma 2.2, both equilibria p and q are linearly (and hence asymptotically) stable. By (a continuous time version of) Theorem 6.1 in [14], monotonicity of the flow implies the existence of an unstable equilibrium in between. This contradicts Lemma 2.2.

- (ii) $\sigma(J_0) \leq 0, \sigma(J_1) > 0$.

Then $\mathbf{1}$ is unstable and orbits that start from initial conditions $\mathbf{1} - \varepsilon \tilde{v}$ (as above) will decrease by monotonicity and converge to an equilibrium q . If $q = \mathbf{0}$, then $\mathbf{0}$ is globally asymptotically stable. Otherwise, $q_k > 0$ for all k , and by Lemma 2.2, q is linearly stable. If $\sigma(J_0) < 0$, then as in (i), there is an unstable equilibrium between $\mathbf{0}$ and q , which contradicts Lemma 2.2. If $\sigma(J_0) = 0$, then replace b_k by $b_k + \delta$ and a_k by $a_k - \delta$ (for all k) for any small $\delta > 0$. In this perturbed system, $\sigma(J_0) = -\delta < 0$, so that $\mathbf{0}$ is linearly stable. Since $\sigma(J_1) > 0$, the other trivial equilibrium $\mathbf{1}$ is still unstable. Since, for $\delta = 0$, q is linearly stable

¹ By this we mean a stable equilibrium which attracts all solutions except possibly the trivial states $\mathbf{0}, \mathbf{1}$.

and hence regular, the implicit function theorem provides a (linearly stable) equilibrium q_δ near q for small $\delta > 0$. Thus, we obtain the same contradiction for this perturbed system as before.

(iii) $\sigma(J_0) > 0$, $\sigma(J_1) \leq 0$.

This case is analogous to (ii). \square

Remark 2.4. Theorem 2.3 can be generalized to (2.6). If there is exactly one c such that (2.7) holds, the result of Theorem 2.3 still holds. If there are more than one c that satisfy (2.7), then the set of such c forms an interval $[c_1, c_2]$, and there is no selection for $p \in [c_1, c_2]$. The corresponding line segment of equilibria is globally asymptotically stable (as a set), and each equilibrium in this set is stable.

Remark 2.5. The *global attractor* (in the sense of Hale [12]) of a semiflow is given by $\mathcal{A} = \bigcap_{t>0} S^t(X)$, where $X = [0, 1]^K$ is the state space and $S^t : X \rightarrow X$ is the time t map. \mathcal{A} equals the union of all complete orbits in X : If $p_0 \notin \mathcal{A}$, then there is no solution $p(t)$ in X defined for all $t \in \mathbb{R}$ with $p(0) = p_0$. \mathcal{A} is a connected, compact invariant set. It contains all equilibria, in particular $\mathbf{0}$ and $\mathbf{1}$, and their unstable manifolds in X . Under our general assumption (2.6), it follows that the global attractor is one-dimensional. It is a monotone arc that connects the trivial equilibria $\mathbf{0}$ and $\mathbf{1}$. In the trivial case of no selection, it is the line segment of equilibria. In case (i) of the proof of Theorem 2.3, it consists of the three equilibria and the two connecting orbits from the unstable manifolds of the trivial equilibria. In cases (ii) and (iii), the global attractor consists of the two trivial equilibria and a single connecting orbit.

Remark 2.6. Concavity of the mean selection coefficient is crucial for global stability. If there is underdominance (heterozygote disadvantage, i.e., $r_{12} < r_{11}, r_{22}$) in at least one deme, then one expects multiple stable equilibria. More precisely, if there is underdominance in L of K demes, then for weak migration and strong selection, there are 2^L stable equilibria, see [4,28].

The following result shows that even for directional selection, the concavity of the mean selection coefficient is critical for global stability.

Proposition 2.7. Consider (2.1)–(2.2) with opposite directional selection in two demes:

$$a_1 > 0 > b_1, \quad a_1 + b_1 > 0, \quad a_2 < 0 < b_2, \quad a_2 + b_2 = 0; \quad (2.12)$$

i.e., the mean selection coefficient is strictly convex in the first deme, and there is no dominance (linear mean selection coefficient) in the second deme. Then there exist migration rates μ_{12} and μ_{21} such that both trivial equilibria $\mathbf{0}$ and $\mathbf{1}$ are asymptotically stable.

Proof. In the case of two demes, the system (2.1)–(2.2) simplifies to

$$\begin{aligned} \dot{p}_1 &= m_1(p_2 - p_1) + p_1(1 - p_1)[-b_1 + (a_1 + b_1)p_1], \\ \dot{p}_2 &= m_2(p_1 - p_2) + p_2(1 - p_2)[-b_2 + (a_2 + b_2)p_1], \end{aligned} \quad (2.13)$$

where $m_1 = \mu_{12}$ and $m_2 = \mu_{21}$ remain to be specified. The assumption $a_2 + b_2 = 0$ simplifies the second equation to

$$\dot{p}_2 = m_2(p_1 - p_2) - b_2 p_2(1 - p_2).$$

The Jacobian matrices of (2.13) at the trivial equilibria $\mathbf{0}$ and $\mathbf{1}$ are given by

$$J_0 = \begin{pmatrix} -m_1 - b_1 & m_1 \\ m_2 & -m_2 - b_2 \end{pmatrix}, \quad J_1 = \begin{pmatrix} -m_1 - a_1 & m_1 \\ m_2 & -m_2 - a_2 \end{pmatrix}.$$

Assume (2.12) and choose

$$m_1 = \frac{a_1^2 - 2a_1b_1 - b_1^2}{a_1 + b_1} > 0, \quad m_2 = \frac{b_2(3a_1 + b_1)}{a_1 + b_1} > 0.$$

Then each Jacobian matrix has positive determinant and one negative diagonal entry. This with the quasi-positivity shows that both trivial states $\mathbf{0}$ and $\mathbf{1}$ are linearly stable. \square

Remark 2.8. Suppose that $a_1 > 0 > b_1$, $a_1 + b_1 > 0$ and $a_2 < 0 < b_2$, $a_2 + b_2 < 0$, i.e., opposite directional selection with the mean selection coefficient strictly convex in the first deme and strictly concave in the second deme. Then we can find migration rates to make both trivial states asymptotically stable, provided $b_1a_2 < b_2a_1$ (roughly speaking, the convexity in the first deme is stronger than the concavity in the second deme).

Remark 2.9. Consider the limiting case $a_1 > 0 = b_1$ and $a_2 < 0 = b_2$ of the situation discussed in Remark 2.8, i.e., A_2 completely dominates A_1 in both demes. Then the mean selection coefficient is still convex in the first deme and concave in the second. This case has been fully analyzed in [26]: Both global convergence and two stable equilibria may occur.

An important question is when the globally stable equilibrium guaranteed by Theorem 2.3 is interior, i.e., when the two alleles coexist in every deme. We investigate this problem by introducing an additional parameter in (2.1), the strength of selection λ (relative to migration):

$$\dot{p}_k = \sum_{\ell} \mu_{k\ell} p_{\ell} + \lambda f_k(p_k). \quad (2.14)$$

We show that, except in a certain trivial case, sufficiently large λ will lead to coexistence of the two alleles. This trivial exception occurs if there is directional selection in the same direction in every deme, i.e., $a_k > 0 > b_k$ for every k (or $a_k < 0 < b_k$ for every k): allele A_2 (or A_1) dies out and $\mathbf{1}$ (resp. $\mathbf{0}$) is globally asymptotically stable. This is a special case of [27, Th. 3.5].

We restrict the analysis again to the classical selection function (2.2), although it works for the more general one (2.6).

Theorem 2.10. Suppose that (2.2) and (2.14) and the following assumptions hold:

- (B1) for every k , $a_k + b_k \leq 0$ (i.e., the mean selection coefficient is concave in each deme);
- (B2) there exist demes k and ℓ (not necessarily different) where $a_k < 0$ and $b_{\ell} < 0$;
- (B3) the migration matrix M is irreducible, with left principal eigenvector $u > \mathbf{0}$.

Then there are three possibilities:

- (I) If $\sum u_k a_k \leq 0$ and $\sum u_k b_k \leq 0$ (average overdominance), then for every $\lambda > 0$, there is a globally asymptotically stable interior equilibrium.
- (II) If $\sum u_k a_k < 0$ and $\sum u_k b_k > 0$, then there exists $\lambda_0 > 0$ such that for $\lambda \in (0, \lambda_0]$, the equilibrium $\mathbf{0}$ is globally asymptotically stable; for $\lambda > \lambda_0$, there exists a globally asymptotically stable interior equilibrium.

- (III) If $\sum u_k a_k > 0$ and $\sum u_k b_k < 0$, then there exists $\lambda_1 > 0$ such that for $\lambda \in (0, \lambda_1]$, the equilibrium $\mathbf{1}$ is globally asymptotically stable; for $\lambda > \lambda_1$, there exists a globally asymptotically stable interior equilibrium.

Proof. The Jacobian matrices of (2.14) at the trivial equilibria $\mathbf{0}$ and $\mathbf{1}$ are given by $J_0 = M - \lambda \operatorname{diag}(b_k)$ and $J_1 = M - \lambda \operatorname{diag}(a_k)$. By [1,6,7], the spectral bounds $\sigma(J_0)$ and $\sigma(J_1)$ are strictly convex functions of λ unless $b = b_1 \mathbf{1}$ or $a = a_1 \mathbf{1}$, when $\sigma(J_0) = -\lambda b_1$ or $\sigma(J_1) = -\lambda a_1$, respectively. Furthermore, for $\lambda = 0$, we have $\sigma(J_0) = \sigma(J_1) = \sigma(M) = 0$; for large λ , we have $\sigma(J_0) \approx \lambda \max(-b_k)$ and $\sigma(J_1) \approx \lambda \max(-a_k)$; by assumption (B2), both tend to ∞ as $\lambda \rightarrow \infty$.

Using standard perturbation theory of simple eigenvalues, one can easily compute the partial derivative of the principal eigenvalues $\sigma(J_0)$ and $\sigma(J_1)$ with respect to λ at $\lambda = 0$. They are given by

$$\sigma'(J_0) = -\sum u_k b_k \quad \text{and} \quad \sigma'(J_1) = -\sum u_k a_k, \quad (2.15)$$

where $u > \mathbf{0}$ is the left eigenvector of M , normalized by $\sum_k u_k = 1$.

Hence, if $\sigma'(J_0) > 0$, then the fact that $\sigma(J_0) = 0$ for $\lambda = 0$ and the convexity of $\sigma(J_0)$ in λ imply that $\sigma(J_0) > 0$ for every $\lambda > 0$. If $\sigma'(J_0) = 0$, we infer from (2.15), $u > \mathbf{0}$, and (B2) that b is not a multiple of $\mathbf{1}$, and therefore, $\sigma(J_0)$ is strictly convex in λ and we again obtain $\sigma(J_0) > 0$ for every $\lambda > 0$. If $\sigma'(J_0) < 0$, then the fact that $\sigma(J_0) = 0$ for $\lambda = 0$, the convexity of $\sigma(J_0)$ in λ , and the fact that $\sigma(J_0) \rightarrow \infty$ as $\lambda \rightarrow \infty$ imply that there exists a unique $\lambda_0 \in (0, \infty)$ such that $\sigma(J_0) < 0$ if $0 < \lambda < \lambda_0$, and $\sigma(J_0) > 0$ if $\lambda > \lambda_0$. The spectral bound $\sigma(J_1)$ has similar properties.

Assumption (B1) and (2.15) inform us

$$\sigma'(J_0) + \sigma'(J_1) = -\sum u_k (a_k + b_k) \geq 0, \quad (2.16)$$

which leads to the three cases in this theorem.

- (I) If both $\sigma'(J_0) \geq 0$ and $\sigma'(J_1) \geq 0$, then for every $\lambda > 0$, we have $\sigma(J_0) > 0$ and $\sigma(J_1) > 0$. Thus, case (i) of the proof of Theorem 2.3 applies.
- (II) If $\sigma'(J_0) < 0$ and $\sigma'(J_1) > 0$, then there is a unique $\lambda_0 > 0$ at which $\sigma(J_0) = 0$, and for every $\lambda > 0$, we have $\sigma(J_1) > 0$. Therefore, for every $\lambda \in (0, \lambda_0]$, case (ii) of the proof of Theorem 2.3 applies, whereas for every $\lambda > \lambda_0$, it is again case (i).
- (III) Finally, $\sigma'(J_0) > 0$ and $\sigma'(J_1) < 0$ lead to cases (iii) and (i) similarly as in (II). \square

Remark 2.11. In the cases (II) and (III) of Theorem 2.10, a transcritical bifurcation occurs at λ_0 and λ_1 , respectively. This bifurcation is forward, or supercritical: The trivial equilibrium is asymptotically stable at the critical value of the parameter λ , and the bifurcating interior equilibrium is asymptotically stable whenever it exists.

Remark 2.12. If assumption (B1) in Theorem 2.10 is weakened to *for every k , $a_k < 0$ or $b_k < 0$ (i.e., there is no deme with underdominance)* and (B2) and (B3) remain the same, then there exists $\lambda_0 \geq 0$ such that for every $\lambda > \lambda_0$, the system (2.14) has a globally asymptotically stable interior equilibrium. This is proven as follows: The instability of the trivial equilibria follows from the first paragraph of the proof of Theorem 2.10, and the uniqueness (and hence global stability) of the interior equilibrium follows from the weak-migration analysis in [4,28].

If there is underdominance in L of K demes, then for large λ , there are 2^L stable equilibria; see again the weak-migration analysis in [4,28].

3. The diffusion limit

We study a continuous habitat Ω , which is an open, connected, bounded set in \mathbb{R}^n with smooth boundary $\partial\Omega$. Let $p(x, t)$ signify the frequency of allele A_1 at position x at time t . Then the classical migration–selection model in continuous space and time leads to the following parabolic problem; see Nagylaki [23–25] and Fife [9]:

$$p_t = Lp + \lambda s(x, p)f(p) \quad \text{in } \Omega \times (0, \infty), \quad (3.1a)$$

$$Bp = 0 \quad \text{on } \partial\Omega \times (0, \infty), \quad (3.1b)$$

$$0 \leq p(x, 0) \leq 1 \quad \text{in } \bar{\Omega}, \quad (3.1c)$$

where

$$Lp = \sum_{i,j=1}^n V_{ij}(x)p_{x_i x_j} + \sum_{i=1}^n b_i(x)p_{x_i}, \quad (3.2)$$

$$Bp = \nu^T V \nabla p. \quad (3.3)$$

Here, L describes migration, in which the matrix $V(x) = (V_{ij}(x))$ is symmetric, positive definite and every V_{ij} , b_i belongs to $C^\theta(\bar{\Omega})$ ($0 < \theta < 1$).

In (3.3), the vector ν is the unit outward normal to $\partial\Omega$ and ∇p signifies the gradient of p . Therefore, since V is positive definite, the boundary operator B is of Neumann co-normal type. Then (3.1b) means that no individuals cross the boundary.

The term $\lambda s(x, p)f(p)$ designates viability selection, where the constant $\lambda > 0$ is the ratio of the selection intensity to the migration rate. We assume that $f(p)$ and $s(x, p)$ are sufficiently smooth, say, f is C^2 and s is continuous, C^θ in x , and C^1 in p . Motivated by (1.3) and (1.5), we make the following assumptions for this section:

$$f(p) \text{ satisfies (1.6), and } \frac{\partial s}{\partial p}(x, p) \leq 0 \quad \text{for every } x \in \Omega, p \in [0, 1]; \quad (3.4)$$

cf. (2.6). If the selection coefficients are frequency independent, then the assumption $\frac{\partial s}{\partial p}(x, p) \leq 0$ means that at every position x , the mean selection coefficient is concave in p ; see (1.5).

By (1.6), problem (3.1) always admits two trivial equilibria $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$. To avoid triviality, we assume that both alleles are initially present in the population, i.e.,

$$0 < \int_{\Omega} p(x, 0) dx < 1. \quad (3.5)$$

Then problem (3.1) has a unique classical solution $p(x, t)$ that exists for all positive time, and $0 < p(x, t) < 1$ for every $x \in \bar{\Omega}$ and $t > 0$ [11,30]. In particular, any nontrivial equilibrium satisfies $0 < \hat{p}(x) < 1$ for every $x \in \bar{\Omega}$.

As in the discrete-deme case, the main goal here is to investigate the behavior of $p(x, t)$ as $t \rightarrow \infty$. Hess and Weinberger [15, Th. 1] have studied global asymptotic stability for problem (3.1) under the assumption (3.4) for $L = \Delta$ (the Laplacian) and asserted that the results hold also for any L in divergence form, which restricts the migration pattern (cf. [19, Sect. 4]). We extend their results to general uniform elliptic operators (3.2), which allows arbitrary migration. The idea of proof is the same as in Theorem 2.3, which is completely different from Hess and Weinberger's. We first prove a result analogous to Lemma 2.2. To this end, we introduce the following operators as in [19,32,33].

Let L_0 be the operator induced by L and B with domain

$$D(L_0) = \{u \in C^{2+\theta}(\bar{\Omega}) : Bu = 0 \text{ on } \partial\Omega\}, \quad (3.6)$$

where $\theta \in (0, 1)$. Let L_1 be the closure of L_0 in $C(\bar{\Omega})$. It is easy to see that $(-L_1 + I)^{-1}1 = 1$, where I is the identity map from $C(\bar{\Omega})$ to itself and 1 is the function identically equal to 1 in $\bar{\Omega}$. Since $(-L_1 + I)^{-1}$ is compact and strictly positive in $C(\bar{\Omega})$, the Krein–Rutman Theorem [14,18] implies that the spectral radius of $(-L_1 + I)^{-1}$ is 1 , which is also a simple eigenvalue of its adjoint operator

$$[(-L_1 + I)^{-1}]^* : [C(\bar{\Omega})]^* \rightarrow [C(\bar{\Omega})]^* \quad (3.7)$$

with a positive eigenfunction $\Psi^* \in [C(\bar{\Omega})]^*$. Hence, $L_1^*\Psi^* = 0$. Furthermore, Ψ^* can be identified with a function in $L^q(\Omega)$ for some $q > 1$; therefore,

$$\langle \Psi^*, u \rangle := \Psi^*(u) = \int_{\Omega} \Psi^* u \, dx \quad \text{for every } u \in C(\bar{\Omega}). \quad (3.8)$$

(See [33] for more details.)

The equilibrium problem of (3.1) is

$$L\hat{p} + \lambda s(x, \hat{p})f(\hat{p}) = 0 \quad \text{in } \Omega, \quad (3.9a)$$

$$B\hat{p} = 0 \quad \text{on } \partial\Omega, \quad (3.9b)$$

whose corresponding linearized stability problem reads

$$\hat{L}\phi + \mu\phi = 0 \quad \text{in } \Omega, \quad (3.10a)$$

$$B\phi = 0 \quad \text{on } \partial\Omega, \quad (3.10b)$$

where

$$\hat{L} := L + \lambda s(x, \hat{p})f'(\hat{p}) + \lambda \frac{\partial s}{\partial p}(x, \hat{p})f(\hat{p}). \quad (3.11)$$

Again by the Krein–Rutman Theorem, the operator \hat{L} admits a principal eigenvalue μ_1 , which is simple with a positive eigenfunction $\hat{\phi} \in C(\bar{\Omega})$. We say an equilibrium \hat{p} is *linearly stable* if $\mu_1 > 0$ and *linearly unstable* if $\mu_1 < 0$.

We shall treat the following degenerate case separately at the end of this section: There exists a constant c in $[0, 1]$ such that

$$s(x, c) = \frac{\partial s}{\partial p}(x, c) = 0 \quad \text{for every } x \in \bar{\Omega}. \quad (3.12)$$

From (3.9)–(3.11) we infer that (3.12) means that $\hat{p} \equiv c$ is an equilibrium with zero principal eigenvalue.

Lemma 3.1. *Suppose that (3.4) holds and there exists no c that satisfies (3.12). Then any nontrivial equilibrium $\hat{p}(x)$ of (3.1) is linearly stable.*

Proof. By the Krein–Rutman Theorem, μ_1 is also a simple eigenvalue of the adjoint operator \hat{L}^* on $[C(\bar{\Omega})]^*$ with a positive eigenfunction $\hat{\Psi}^* \in [C(\bar{\Omega})]^*$, namely,

$$\widehat{L}^* \widehat{\Psi}^* + \mu_1 \widehat{\Psi}^* = 0. \quad (3.13)$$

It is easy to derive that

$$L[f(\hat{p})] = f'(\hat{p})L\hat{p} + f''(\hat{p})(\nabla\hat{p})^T V \nabla\hat{p}. \quad (3.14)$$

From (1.6) we infer that $f''(p) \leq 0$ and $f''(p) \not\equiv 0$ on any subinterval of $[0, 1]$. Hence, from (3.4), (3.9a), (3.11), (3.14), the fact that $0 < \hat{p}(x) < 1$, and the exclusion of (3.12), we obtain

$$\begin{aligned} \widehat{L}[f(\hat{p})] &= f'(\hat{p})L\hat{p} + f''(\hat{p})(\nabla\hat{p})^T V \nabla\hat{p} + \lambda s(x, \hat{p})f'(\hat{p})f(\hat{p}) + \lambda \frac{\partial s}{\partial p}(x, \hat{p})f^2(\hat{p}) \\ &= f'(\hat{p})[L\hat{p} + \lambda s(x, \hat{p})f(\hat{p})] + f''(\hat{p})(\nabla\hat{p})^T V \nabla\hat{p} + \lambda \frac{\partial s}{\partial p}(x, \hat{p})f^2(\hat{p}) \\ &= f''(\hat{p})(\nabla\hat{p})^T V \nabla\hat{p} + \lambda \frac{\partial s}{\partial p}(x, \hat{p})f^2(\hat{p}) \leq 0. \end{aligned} \quad (3.15)$$

It follows from (1.6), (3.8) (which also holds for $\widehat{\Psi}^*$), (3.13), (3.15), the positivity of $\widehat{\Psi}^*$, and the continuity of $\widehat{L}[f(\hat{p})]$ that

$$-\mu_1 \langle \widehat{\Psi}^*, f(\hat{p}) \rangle = \langle \widehat{L}^* \widehat{\Psi}^*, f(\hat{p}) \rangle = \langle \widehat{\Psi}^*, \widehat{L}[f(\hat{p})] \rangle < 0, \quad (3.16)$$

whence $\mu_1 > 0$. \square

Remark 3.2. In the above proof, to deduce $\mu_1 > 0$, an alternative to the last step (3.16) is to apply Theorem 2.4 in [2], since (3.15) and $B[f(\hat{p})] = f'(\hat{p})B\hat{p} = 0$ imply that $f(\hat{p})$ is a positive strict supersolution of the problem $(-\widehat{L}, B, \Omega)$.

Remark 3.3. Lemma 3.1 extends the results of Henry [13, Lemma 10.1.5], Hess [14, Lemma 0.2], and Lou and Nagylaki [19, Lemma 2.2], where $s(x, \cdot) \equiv g(x)$.

Next, we study the stability of the trivial equilibria $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$; we use the properties of the following eigenvalue problem, established by Senn [32, eqs. 1.9 and 1.10].

Lemma 3.4. For each fixed $\lambda > 0$, let $\gamma(\lambda)$ represent the principal eigenvalue of the linear eigenvalue problem:

$$L\varphi + \lambda m(x)\varphi + \gamma(\lambda)\varphi = 0 \quad \text{in } \Omega, \quad (3.17a)$$

$$B\varphi = 0 \quad \text{on } \partial\Omega, \quad (3.17b)$$

where L and B are defined in (3.2) and (3.3), respectively, and $m \in C(\bar{\Omega})$. The following conclusions hold.

- (i) If $\int_{\Omega} m \Psi^* dx \geq 0$, then $\gamma(\lambda) < 0$ for every $\lambda > 0$.
- (ii) If $\int_{\Omega} m \Psi^* dx < 0$ and $m(x)$ changes sign in Ω , then there exists a unique $\lambda_1(m) \in (0, \infty)$ such that

$$\begin{aligned} \gamma(\lambda) &> 0 && \text{for } 0 < \lambda < \lambda_1(m), \\ \gamma(\lambda_1(m)) &= 0, \\ \gamma(\lambda) &< 0 && \text{for } \lambda > \lambda_1(m). \end{aligned} \quad (3.18)$$

Remark 3.5. If $m(x) \leq 0$ in Ω , then the following simple calculations show that $\gamma(\lambda) > 0$ for every $\lambda > 0$: From (3.17a) and the equation $L_1^* \Psi^* = 0$ we have

$$\begin{aligned} 0 &= \langle \Psi^*, L\varphi + \lambda m(x)\varphi + \gamma(\lambda)\varphi \rangle \\ &= \langle L_1^* \Psi^*, \varphi \rangle + \lambda \langle \Psi^*, m(x)\varphi \rangle + \gamma(\lambda) \langle \Psi^*, \varphi \rangle \\ &= \lambda \langle \Psi^*, m(x)\varphi \rangle + \gamma(\lambda) \langle \Psi^*, \varphi \rangle, \end{aligned} \quad (3.19)$$

whence the facts $\Psi^* > 0$, $\varphi > 0$, and $m \leq 0$ imply $\gamma(\lambda) > 0$ for every $\lambda > 0$. Alternatively, since the constant function 1 is a positive strict supersolution of the problem $(-L - \lambda m, B, \Omega)$, we have $\gamma(\lambda) > 0$ [2, Th. 2.4].

Therefore, in this case we set $\lambda_1(m) = \infty$, and the condition that $m(x)$ changes sign in Lemma 3.4(ii) can be relaxed to $m \not\equiv 0$.

For notational brevity, we define

$$s_0(x) = s(x, 0), \quad s_1(x) = s(x, 1) \quad \text{for every } x \in \bar{\Omega}. \quad (3.20)$$

We shall demonstrate that the stability of the trivial equilibria 0 and 1 is determined by the sign of $\int_{\Omega} s_0 \Psi^* dx$ and $\int_{\Omega} s_1 \Psi^* dx$, respectively. From (3.4) and the inequality $\Psi^* > 0$, we infer that

$$\int_{\Omega} s_0 \Psi^* dx \geq \int_{\Omega} s_1 \Psi^* dx, \quad (3.21)$$

whence three cases may occur:

$$\int_{\Omega} s_0 \Psi^* dx \geq 0 \geq \int_{\Omega} s_1 \Psi^* dx, \quad (3.22a)$$

$$0 > \int_{\Omega} s_0 \Psi^* dx \geq \int_{\Omega} s_1 \Psi^* dx, \quad (3.22b)$$

$$\int_{\Omega} s_0 \Psi^* dx \geq \int_{\Omega} s_1 \Psi^* dx > 0. \quad (3.22c)$$

Lemma 3.6. Suppose that (3.4) holds, there exists no c that satisfies (3.12), and $s_0 \not\equiv 0$ and $s_1 \not\equiv 0$. Then the trivial equilibria $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$ of (3.1) have the following properties.

- (i) If (3.22a) holds, then both $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$ are linearly unstable for every $\lambda > 0$.
- (ii) If (3.22b) holds, then $\hat{p} \equiv 0$ is linearly stable for every $\lambda \in (0, \lambda_1(s_0 f'(0)))$ and linearly unstable for every $\lambda > \lambda_1(s_0 f'(0))$; $\hat{p} \equiv 1$ is linearly unstable for every $\lambda > 0$.
- (iii) If (3.22c) holds, then $\hat{p} \equiv 1$ is linearly stable for every $\lambda \in (0, \lambda_1(s_1 f'(1)))$ and linearly unstable for every $\lambda > \lambda_1(s_1 f'(1))$; $\hat{p} \equiv 0$ is linearly unstable for every $\lambda > 0$.

Proof. From (3.10), (3.11), and (3.20) we infer that the corresponding linearized stability problems for $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$ are

$$L\phi + \lambda s_0(x)f'(0)\phi + \mu\phi = 0 \quad \text{in } \Omega, \quad (3.23a)$$

$$B\phi = 0 \quad \text{on } \partial\Omega, \quad (3.23b)$$

and

$$L\phi + \lambda s_1(x)f'(1)\phi + \mu\phi = 0 \quad \text{in } \Omega, \quad (3.24a)$$

$$B\phi = 0 \quad \text{on } \partial\Omega, \quad (3.24b)$$

respectively. Note that (1.6) implies that $f'(0) > 0 > f'(1)$. Therefore, Lemma 3.6 follows directly from Lemma 3.4, Remark 3.5, and the assumptions that $s_i \neq 0$ for $i = 0, 1$. \square

To investigate the global dynamics of (3.1), we apply the theory of order-preserving dynamical systems [14]. The same method was used in studying the global dynamics of a population genetics model with partial panmixia in [22]. For completeness, we elaborate the method here.

Let $S(t, p_0) = p(x, t; p_0)$, where $p(x, t; p_0)$ is the unique solution of (3.1) with initial data p_0 . Then S defines a semiflow on

$$U := \{p \in C(\bar{\Omega}) : 0 \leq p \leq 1\}$$

with domain $D(S) = [0, \infty) \times U$. Suppose that $p_1, p_2 \in U$ and $p_1 \leq p_2$. Then the maximum principle [30] implies that $S(t, p_1) < S(t, p_2)$ for every $t > 0$ and every $x \in \bar{\Omega}$, namely, S is *strongly order preserving*.

It is clear that \hat{p} is a fixed point of S if and only if it is an equilibrium of (3.1). A function $u(x) \in U$ is called a *subequilibrium* of S if $u \leq S(t, u)$ for every $t > 0$, and *strict subequilibrium* if it is a subequilibrium, but not a fixed point. Similarly, *(strict) superequilibria* are defined by reversing the inequality.

Since S is strongly order preserving, if u is a strict subequilibrium, then $p(x, t; u)$ is strictly increasing in t , and

$$\hat{p}_u := \lim_{t \rightarrow \infty} p(x, t; u) \quad (3.25)$$

is the minimal equilibrium of S that satisfies $\hat{p} \geq u$; furthermore, \hat{p}_u is stable from below. Similarly, if v is a strict superequilibrium, then $p(x, t; v)$ is strictly decreasing in t and

$$\hat{p}_v := \lim_{t \rightarrow \infty} p(x, t; v) \quad (3.26)$$

is the maximal equilibrium of S that satisfies $\hat{p} \leq v$; \hat{p}_v is stable from above.

Before we finally prove the global convergence of (3.1), we show that (3.1) cannot admit more than one stable equilibrium.

Lemma 3.7. *The same assumptions as in Lemma 3.6 imply that (3.1) has at most one stable equilibrium.*

Proof. We argue by contradiction. Suppose that (3.1) has two distinct stable equilibria \hat{p}_1 and \hat{p}_2 in U . We may assume that they are ordered. Otherwise, we consider $u := \max\{\hat{p}_1, \hat{p}_2\}$ and $v := \min\{\hat{p}_1, \hat{p}_2\}$. It is easy to check that u and v are strict subequilibrium and superequilibrium, respectively. Then we replace \hat{p}_1 and \hat{p}_2 by \hat{p}_u and \hat{p}_v (defined in (3.25) and (3.26)), respectively. Therefore, without loss of generality, we may assume $\hat{p}_1 \leq \hat{p}_2$.

We infer from Lemma 3.6 that the two trivial equilibria cannot be simultaneously stable. Hence, at least one of \hat{p}_1 and \hat{p}_2 is nontrivial and therefore, by Lemma 3.1 and the implicit function theorem, isolated. Let

$$\hat{U} := \{p \in C(\bar{\Omega}) : \hat{p}_1 \leq p \leq \hat{p}_2\}.$$

By parabolic regularity, $S(t, \hat{U})$ is relatively compact for each $t > 0$. Thus, the continuous-time version of Theorem 6.1 in [14] implies that there exists an unstable equilibrium in \hat{U} , which contradicts Lemma 3.1. \square

Theorem 3.8. Suppose that (3.4) holds and there exists no c that satisfies (3.12). Then (3.1) has a unique stable equilibrium \hat{p}^* , and for all initial values that satisfy (3.5), the solution $p(x, t) \rightarrow \hat{p}^*(x)$ uniformly in x as $t \rightarrow \infty$. The equilibrium \hat{p}^* is either identically equal to 0 or 1 or is nontrivial; if (3.1) admits a nontrivial equilibrium, it is \hat{p}^* . More precisely, we have

- (i) If (3.22a) holds, then \hat{p}^* is nontrivial for every $\lambda > 0$.
- (ii) If (3.22b) holds and $s_0(x) > 0$ for some $x \in \bar{\Omega}$, then $\hat{p}^* \equiv 0$ for every $\lambda \in (0, \lambda_1(s_0 f'(0))]$, and \hat{p}^* is nontrivial for every $\lambda > \lambda_1(s_0 f'(0))$; if $s_0(x) \leq 0$ for every $x \in \bar{\Omega}$, then $\hat{p}^* \equiv 0$ for every $\lambda > 0$.
- (iii) If (3.22c) holds and $s_1(x) < 0$ for some $x \in \bar{\Omega}$, then $\hat{p}^* \equiv 1$ for every $\lambda \in (0, \lambda_1(s_1 f'(1))]$, and \hat{p}^* is nontrivial for every $\lambda > \lambda_1(s_1 f'(1))$; if $s_1(x) \geq 0$ for every $x \in \bar{\Omega}$, then $\hat{p}^* \equiv 1$ for every $\lambda > 0$.

Proof. Under the assumption (3.4), only one of the three cases in (3.22) can occur. The case (3.22a) is the simplest one, and (3.22b) and (3.22c) are similar. Therefore, we present only the proof of part (ii). Note that (3.22b) implies that $s_i \not\equiv 0$ for $i = 0, 1$.

We first assume $s_0(x) > 0$ for some $x \in \bar{\Omega}$. Then we infer from Lemmas 3.4(ii) and 3.6(ii) that $\lambda_1(s_0 f'(0)) \in (0, \infty)$ and the dynamics of (3.1) varies according to the relative relation between λ and $\lambda_1(s_0 f'(0))$.

(a) $0 < \lambda < \lambda_1(s_0 f'(0))$.

In this case $\hat{p} \equiv 0$ is linearly stable and $\hat{p} \equiv 1$ is linearly unstable. Hence, by Lemmas 3.1 and 3.7, $\hat{p} \equiv 0$ is the unique stable equilibrium of (3.1) and there is no nontrivial equilibrium.

To see that $\hat{p} \equiv 0$ is globally asymptotically stable, we consider the principal eigenvalue $\mu_1^{(1)}$ and the corresponding positive eigenfunction ϕ_1 of (3.24). We infer from the linear instability of $\hat{p} \equiv 1$ that $\mu_1^{(1)} < 0$. Let $\varepsilon > 0$ be a small number and consider the function $1 - \varepsilon\phi_1$:

$$\begin{aligned} & L(1 - \varepsilon\phi_1) + \lambda s(x, 1 - \varepsilon\phi_1)f(1 - \varepsilon\phi_1) \\ &= -\varepsilon L\phi_1 + \lambda \left\{ s(x, 1)f(1) + \left[\frac{\partial s}{\partial p}(x, 1)f(1) + s(x, 1)f'(1) \right] (-\varepsilon\phi_1) + o(\varepsilon\phi_1) \right\} \\ &= -\varepsilon L\phi_1 - \lambda s_1(x)f'(1)\varepsilon\phi_1 + o(\varepsilon\phi_1) \\ &= \mu_1^{(1)}\varepsilon\phi_1 + o(\varepsilon\phi_1) < 0 \end{aligned} \tag{3.27}$$

for sufficiently small $\varepsilon > 0$. The inequality (3.27) implies that $p(x, t; 1 - \varepsilon\phi_1)$ is strictly decreasing in t [31], and therefore, $1 - \varepsilon\phi_1$ is a strict superequilibrium. Since there exists no equilibrium between $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$, we must have

$$p(x, t; 1 - \varepsilon\phi_1) \rightarrow 0 \text{ as } t \rightarrow \infty \text{ for every } x \in \bar{\Omega}. \tag{3.28}$$

Now let $p_0 \in U$ be any initial value that satisfies (3.5). Since S is strongly order preserving, there exist some time $t_1 > 0$ and some sufficiently small $\varepsilon > 0$ such that

$$p_1(x) := p(x, t_1; p_0) \leq 1 - \varepsilon\phi_1(x) \text{ for every } x \in \bar{\Omega}. \tag{3.29}$$

Hence, (3.28) and (3.29) give

$$\limsup_{t \rightarrow \infty} p(x, t; p_0) = \limsup_{t \rightarrow \infty} p(x, t; p_1) \leq \lim_{t \rightarrow \infty} p(x, t; 1 - \varepsilon\phi_1) = 0 \text{ for every } x \in \bar{\Omega}. \tag{3.30}$$

Since $p(x, t; p_0) \geq 0$, we infer from (3.30) that $\lim_{t \rightarrow \infty} p(x, t; p_0) = 0$ for every $x \in \bar{\Omega}$.

(b) $\lambda = \lambda_1(s_0 f'(0))$.

We shall first show by contradiction that (3.1) has no nontrivial equilibrium. Suppose that \hat{p}_1 is a nontrivial equilibrium. Then by Lemma 3.1 and the implicit function theorem, for λ sufficiently close to $\lambda_1(s_0 f'(0))$, there is a connected branch of nontrivial equilibria of (3.1) given by $\hat{p}(\lambda)$ with $\hat{p}(\lambda_1(s_0 f'(0))) = \hat{p}_1$. However, we have shown in (a) that for $\lambda < \lambda_1(s_0 f'(0))$, problem (3.1) has no nontrivial equilibrium. This contradiction demonstrates that when $\lambda = \lambda_1(s_0 f'(0))$, problem (3.1) has no nontrivial equilibrium. Therefore, since $\hat{p} \equiv 1$ is linearly unstable, the same argument as in (a) yields again that $\lim_{t \rightarrow \infty} p(x, t; p_0) = 0$ for every $x \in \bar{\Omega}$.

(c) $\lambda > \lambda_1(s_0 f'(0))$.

In this case both $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$ are linearly unstable. As in (a), the linear instability of $\hat{p} \equiv 1$ implies that $1 - \varepsilon \phi_1$ is a strict superequilibrium, where $\phi_1 > 0$ is the principal eigenfunction of (3.24) and $\varepsilon > 0$ is sufficiently small.

Similarly, the linear instability of $\hat{p} \equiv 0$ yields a strict subequilibrium close to it. Let $\mu_1^{(0)}$ and $\tilde{\phi}_1$ be the principal eigenvalue and the corresponding positive eigenfunction of (3.23), respectively. The linear instability of $\hat{p} \equiv 0$ informs us that $\mu_1^{(0)} < 0$. Let $\delta > 0$ be a small number and consider the function $\delta \tilde{\phi}_1$:

$$\begin{aligned} & L(\delta \tilde{\phi}_1) + \lambda s(x, \delta \tilde{\phi}_1) f(\delta \tilde{\phi}_1) \\ &= \delta L \tilde{\phi}_1 + \lambda \left\{ s(x, 0) f(0) + \left[\frac{\partial s}{\partial p}(x, 0) f(0) + s(x, 0) f'(0) \right] (\delta \tilde{\phi}_1) + o(\delta \tilde{\phi}_1) \right\} \\ &= \delta L \tilde{\phi}_1 + \lambda s_0(x) f'(0) \delta \tilde{\phi}_1 + o(\delta \tilde{\phi}_1) \\ &= -\mu_1^{(0)} \delta \tilde{\phi}_1 + o(\delta \tilde{\phi}_1) > 0 \end{aligned} \quad (3.31)$$

for sufficiently small $\delta > 0$. The inequality (3.31) implies that $p(x, t; \delta \tilde{\phi}_1)$ is strictly increasing in t [31], and therefore, $\delta \tilde{\phi}_1$ is a strict subequilibrium.

Hence, for sufficiently small ε and δ such that $\delta \tilde{\phi}_1 < 1 - \varepsilon \phi_1$, we have

$$0 < \delta \tilde{\phi}_1(x) < \lim_{t \rightarrow \infty} p(x, t; \delta \tilde{\phi}_1) \leq \lim_{t \rightarrow \infty} p(x, t; 1 - \varepsilon \phi_1) < 1 - \varepsilon \phi_1(x) < 1 \quad \text{for every } x \in \bar{\Omega}. \quad (3.32)$$

Then we infer from (3.32) and Lemmas 3.1 and 3.7 that

$$\lim_{t \rightarrow \infty} p(x, t; \delta \tilde{\phi}_1) = \lim_{t \rightarrow \infty} p(x, t; 1 - \varepsilon \phi_1) := \hat{p}^*(x) \in (0, 1) \quad \text{for every } x \in \bar{\Omega}, \quad (3.33)$$

where \hat{p}^* must be the unique nontrivial equilibrium of (3.1).

Now let $p_0 \in U$ be any initial value that satisfies (3.5). Since S is strongly order preserving, there exist some $t_2 > 0$ and sufficiently small ε and δ such that

$$\delta \tilde{\phi}_1(x) \leq p_2(x) := p(x, t_2; p_0) \leq 1 - \varepsilon \phi_1(x) \quad \text{for every } x \in \bar{\Omega}. \quad (3.34)$$

From (3.33) and (3.34) we obtain

$$\hat{p}^*(x) = \lim_{t \rightarrow \infty} p(x, t; \delta \tilde{\phi}_1) \leq \lim_{t \rightarrow \infty} p(x, t; p_2) = \lim_{t \rightarrow \infty} p(x, t; p_0) \leq \lim_{t \rightarrow \infty} p(x, t; 1 - \varepsilon \phi_1) = \hat{p}^*(x), \quad (3.35)$$

which yields $\lim_{t \rightarrow \infty} p(x, t; p_0) = \hat{p}^*(x)$ for every $x \in \bar{\Omega}$.

In the case $s_0(x) \leq 0$ for every $x \in \bar{\Omega}$, since (3.22b) implies $s_0 \not\equiv 0$, Remark 3.5 informs us that $\lambda_1(s_0 f'(0)) = \infty$; therefore, only (a) may occur. Thus, for every $\lambda > 0$, we have $\lim_{t \rightarrow \infty} p(x, t; p_0) = 0$ for every $x \in \bar{\Omega}$.

Therefore, we have proved pointwise convergence for part (ii), whence uniform convergence follows from parabolic regularity and the Arzela–Ascoli Lemma. (See the argument around (2.17) in [19].) Thus, we have completed the proof of part (ii). \square

Remark 3.9. Theorem 3.8 extends the global asymptotic stability results of Henry [13, Th. 10.1.6], Hess [14, Th. 0.1], and Lou and Nagylaki [19, Th. 2.1], where $s(x, \cdot) \equiv g(x)$.

Remark 3.10. Recently, Nagylaki has developed new migration–selection models with partial panmixia (cf. [22] and the references therein), which have an additional nonlocal term $B(\bar{p} - p)$ in the linear operator L defined in (3.2). Here $B \geq 0$ is the scaled panmictic rate and \bar{p} is the average of p over Ω with respect to a given population density $\rho(x)$ (> 0), i.e.,

$$\int_{\Omega} \rho(x) \, dx = 1, \quad \bar{p}(t) = \int_{\Omega} \rho(x) p(x, t) \, dx. \quad (3.36)$$

Assuming (1.6) and $s(x, \cdot) \equiv g(x)$, global asymptotic stability was established in [22]. We observe that it can be extended to the general $s(x, p)$ as in Theorem 3.8. To this end, we need only to show that (3.15) still holds for the new operator. In fact, the term $B(\bar{p} - p)$ yields the following additional term in the left-hand side of the inequality in (3.15):

$$B \left[f'(\hat{p})(\hat{p} - \bar{\hat{p}}) + \overline{f(\hat{p})} - f(\hat{p}) \right], \quad (3.37)$$

which is negative in $\bar{\Omega}$ by the concavity of $f(p)$ and Jensen’s inequality (see [22, eq. 3.6]). In particular, this gives an alternative proof of Lemma 3.1 in [22].

Remark 3.11. If the selection coefficients are frequency independent and the allele A_2 is completely dominant to A_1 everywhere, namely, $r_{11} = g(x)$, $r_{12} = r_{22} = 0$, then by (1.2) the mean selection coefficient \bar{r} is convex where $g(x) > 0$ and concave where $g(x) < 0$. It is proved in [20,29] that in this case, the problem (3.1) may have more than one interior equilibrium, at least one of which is stable and one is unstable.

On one hand, this shows that concavity of the mean selection coefficient everywhere is crucial for global stability.

On the other hand, in this case of complete dominance, the nonlinear term in (3.1a) is of the form $\lambda g(x) p^2(1 - p)$. Therefore, we may choose $s(x, \cdot) \equiv g(x)$. However, then $f(p) = p^2(1 - p)$ is not concave in $(0, 1)$. This shows that the concavity of $f(p)$ is also important for the uniqueness of the interior equilibrium and the global convergence.

We close this section with the degenerate case (3.12). By dint of (3.4), there are two possibilities:

- (C1) There exists a unique $c_0 \in [0, 1]$ such that (3.12) holds.
- (C2) There exists an interval $[c_1, c_2]$ of c such that (3.12) holds, where $0 \leq c_1 < c_2 \leq 1$.

Theorem 3.12. The assumption (3.4) implies the following.

- (i) If (C1) holds, then every solution of (3.1) with initial value p_0 that satisfies (3.5) converges to c_0 uniformly in x as $t \rightarrow \infty$.

- (ii) If (C2) holds, then every solution of (3.1) with initial value p_0 that satisfies (3.5) converges to some $c^* \in [c_1, c_2]$ uniformly in x as $t \rightarrow \infty$. Furthermore, if $p_0(x) \in [0, c_1]$ for every $x \in \Omega$, then $c^* = c_1$; if $p_0(x) \in [c_1, c_2]$ for every $x \in \Omega$, then $c^* = \int_{\Omega} p_0 \Psi^* dx / \int_{\Omega} \Psi^* dx$; if $p_0(x) \in [c_2, 1]$ for every $x \in \Omega$, then $c^* = c_2$.

Proof. We prove only part (ii) for $0 < c_1 < c_2 < 1$ here because, with minor modifications, the cases that $c_1 = 0$ or $c_2 = 1$, and $c_1 = c_2 = c_0$ (i.e., part (i)) can be established similarly. From (C2) and (3.4), we have

$$s(x, c) \begin{cases} \geq 0 & \text{if } 0 \leq c < c_1, \\ = 0 & \text{if } c_1 \leq c \leq c_2, \\ \leq 0 & \text{if } c_2 < c \leq 1. \end{cases} \quad (3.38)$$

First, we observe that $\hat{p} \equiv c$ for any $c \in [c_1, c_2]$ is a stable equilibrium of (3.1). This is clear if $c \in (c_1, c_2)$, and obviously c_1 is stable from above and c_2 from below. In light of (3.1), (3.4), and (3.38), any constant $c \in (0, c_1)$ is a strict subequilibrium and any constant $c \in (c_2, 1)$ is a strict superequilibrium, which implies that c_1 is stable from below and c_2 from above, respectively. Therefore, both c_1 and c_2 are stable.

Second, we show that (3.1) has no nontrivial equilibria other than the constant ones $\hat{p} \equiv c$, where $c \in [c_1, c_2]$. We argue by contradiction. Suppose \hat{p} such that $\hat{p} \not\equiv c$ for any $c \in [c_1, c_2]$ is a nontrivial equilibrium. Then Lemma 3.1 shows that \hat{p} is linearly stable. Applying the proof of Lemma 3.7 to $\hat{p}_1 = \hat{p}$ and $\hat{p}_2 = c$ for some $c \in [c_1, c_2]$ yields the same contradiction.

Third, (3.1), (3.4), and (3.38) inform us that both the trivial equilibria $\hat{p} \equiv 0$ and $\hat{p} \equiv 1$ are linearly unstable, and therefore for sufficiently small δ and ε , $\delta\tilde{\phi}_1$ and $1 - \varepsilon\phi_1$ (as in the proof of Theorem 3.8) are strict subequilibrium and superequilibrium, respectively. Then by the above arguments, it follows from Theorem 9.2 in [14] (we take $E = C(\bar{\Omega})$ with L^∞ -norm, the semiflow S as in the proof of Lemma 3.6, and $a = \delta\tilde{\phi}_1$ and $b = 1 - \varepsilon\phi_1$) that every solution of (3.1) with initial value p_0 that satisfies (3.5) converges to some $c^* \in [c_1, c_2]$ uniformly in x as $t \rightarrow \infty$.

Finally, we deduce from the monotonicity property of (3.1) that if $p_0(x) \in [0, c_1]$ for every $x \in \Omega$ and (3.5) holds, then $c^* = c_1$; and if $p_0(x) \in [c_2, 1]$ for every $x \in \Omega$ and (3.5) holds, then $c^* = c_2$. Now, if $p_0(x) \in [c_1, c_2]$ for every $x \in \Omega$, then again the monotonicity property implies that $p(x, t) \in [c_1, c_2]$ for every $x \in \Omega$ and every $t > 0$, whence from (3.1), (3.8), and (3.38) we have

$$\begin{aligned} \frac{d}{dt} \int_{\Omega} \Psi^* p(x, t) dx &= \langle \Psi^*, \frac{\partial p}{\partial t} \rangle \\ &= \langle \Psi^*, Lp + \lambda s(x, p)f(p) \rangle \\ &= \langle L_1^* \Psi^*, p \rangle + \lambda \langle \Psi^*, s(x, p)f(p) \rangle \\ &= 0. \end{aligned} \quad (3.39)$$

Thus, $\int_{\Omega} \Psi^* p(x, t) dx$ is preserved and therefore, $c^* = \int_{\Omega} p_0 \Psi^* dx / \int_{\Omega} \Psi^* dx$. \square

4. Discussion

Here, we summarize our main results, make some comments on related literature, and mention some open problems.

In this paper, we demonstrated global asymptotic stability for the ODE system (2.1) and the PDE problem (3.1). The key conditions are (2.6) and (3.4), respectively, each of which includes the concavity of the mean selection coefficient. From the mathematical point of view, both (2.1) and (3.1) generate a strongly order-preserving semiflow and therefore lead to many similar results, i.e., Lemma 2.2, Theorems 2.3 and 2.10,

and Remark 2.4 versus Lemma 3.1, Theorem 3.8, and Theorem 3.12. The biological interpretation of this similarity is that the continuous-space model (3.1) is the diffusion limit of the discrete-space model (2.1).

Hale [12] gives a good survey of scalar parabolic equations; in particular, he covers diallelic models with non-concave selection-coefficient functions and multiple stable equilibria.

Open Problems

1. Consider K demes, all with directional selection, but with the mean selection coefficient convex in some demes and concave in the others. Characterize the selection coefficients such that for every choice of the migration matrix, there is a globally asymptotically stable equilibrium. We ask the same question for the continuous-space model.
2. Do the global stability results extend to more than two alleles? This is not clear at all, because the present analysis of the diallelic case depends critically on monotone dynamics.

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