Evolution of a semilinear parabolic system for migration and selection without dominance

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Abstract

The semilinear parabolic system that describes the evolution of the gene frequencies in the diffusion approximation for migration and selection at a multiallelic locus without dominance is investigated. The population occupies a finite habitat of arbitrary dimensionality and shape (i.e., a bounded, open domain in $\mathbb{R}^d$). The selection coefficients depend on position; the drift and diffusion coefficients may depend on position. The primary focus of this paper is the dependence of the evolution of the gene frequencies on $\lambda$, the strength of selection relative to that of migration. It is proved that if migration is sufficiently strong (i.e., $\lambda$ is sufficiently small) and the migration operator is in divergence form, then the allele with the greatest spatially averaged selection coefficient is ultimately fixed. The stability of each vertex (i.e., an equilibrium with exactly one allele present) is completely specified. The stability of each edge equilibrium (i.e., one with exactly two alleles present) is fully described when either (i) migration is sufficiently weak (i.e., $\lambda$ is sufficiently large) or (ii) the equilibrium has just appeared as $\lambda$ increases. The existence of unexpected, complex phenomena is established: even if there are only three alleles and migration is homogeneous and isotropic (corresponding to the Laplacian), (i) as $\lambda$ increases, arbitrarily many changes of stability of the edge equilibria and corresponding appearance of an internal equilibrium can occur and (ii) the conditions for protection or loss of an allele can both depend nonmonotonically on $\lambda$. Neither of these phenomena can occur in the diallelic case.

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1. Introduction

This is the third paper in a series exploring the semilinear parabolic system that describes the evolution of the gene frequencies in the diffusion approximation for migration and selection at a multiallelic locus.

In the first paper [20], we delineated this approximation, outlined its biological background and significance (including a review of the literature), and began its analysis. For two alleles (the scalar case), we extended Henry’s [10, pp. 314–319] global analysis from homogeneous, isotropic migration (corresponding to the Laplacian $\nabla^2$) to arbitrary migration (corresponding to an arbitrary elliptic operator $L$). For multiple alleles (corresponding to a parabolic system), we gave sufficient conditions for the global loss of an allele that is nowhere the fittest. In the natural, important special case without dominance, we established sufficient conditions for the existence of a globally attracting equilibrium with only one or two extreme alleles present, determined when this attractor is a vertex (corresponding to fixation of one of the two alleles) or edge (corresponding to a diallelic polymorphism), and fully specified the stability of all the vertex and edge equilibria when these sufficient conditions hold.

In the second paper [21], we greatly generalized the sufficient conditions in [20] for global loss of an allele and presented more explicit sufficient conditions for the case of weak migration. We offered sufficient conditions for the protection of an allele from loss and for the existence of an internal equilibrium, and determined the zero-migration limit of any internal equilibrium. We simplified our results in several special cases, including no dominance. For the strong-migration limit, we sketched a formal argument to support the approximation of the partial differential equations by the kinetic system (i.e., pure selection with the spatially averaged selection coefficients), and we conjectured that if the latter has a global attractor $p^*$, then the full system has a global attractor that is approximated by $p^*$.

The primary focus of this paper is the dependence of the evolution of the gene frequencies on $\lambda$, the strength of selection relative to that of migration, when there is no dominance. In Section 2, we prove that if migration is sufficiently strong (i.e., $\lambda$ is sufficiently small) and $L$ is in divergence form, then the allele with the greatest spatially averaged selection coefficient is ultimately fixed. Furthermore, for arbitrary migration, we fully specify the stability of each vertex. Section 3 is devoted to a complete description of the stability of each edge equilibrium for arbitrary $L$ when either (i) migration is sufficiently weak (i.e., $\lambda$ is sufficiently large) or (ii) the equilibrium has just appeared as $\lambda$ increases. Sections 4 and 5 reveal the existence of unexpected, complex phenomena: even if there are only three alleles and migration is homogeneous and isotropic (i.e., $L = \nabla^2$), (i) as $\lambda$ increases, arbitrarily many changes of stability of the edge equilibria and corresponding appearances of an internal equilibrium can occur and (ii) the conditions for protection or loss of an allele can both depend nonmonotonically on $\lambda$. By Theorem 2.1 of [20], neither of these phenomena can occur in the diallelic case. In Section 6, we briefly re-capitulate the main results established here and in [20,21], with particular attention to the case without dominance, and we mention some unsolved problems. In Appendix A, we show how to construct a function of type $G$, used crucially in Section 4. Appendix B comprises slight corrections of Theorems 3.1 in [20] and 1.1 in [21].

Karlin [14,15], Lyubich [22, Sections 9.1–9.4], Nagylaki [28, Sections 4.1–4.3], and Bürger [1, Section 1.9] review the theory of selection at a single locus in a panmictic population; see also Nagylaki and Lou [32]. In this paper, we posit the absence of dominance. This assumption is natural, common, and exactly or approximately correct for many loci in many species. It
greatly simplifies the theory by reducing the nonlinearity from cubic to quadratic. With random mating and no dominance, the fittest allele is ultimately fixed. Nonetheless, we shall see that when migration and spatial variation in the fitnesses are incorporated, the multiallelic system (unlike the diallelic one [3,8,10]) exhibits rich, complex evolutionary dynamics.

There are two approaches to including genotype-independent migration and deriving a diffusion approximation. In the first approach, one starts with the continuous approximation of the exact, discrete selection model for the gene frequencies and adds a diffusion term (modelled by $\nabla^2$) to incorporate migration [7,9,19]. Although this formulation yields the correct diffusion approximation for homogeneous, isotropic migration, it is biologically and mathematically unconvincing. There are two distinct difficulties: (i) it is densities, not frequencies, that diffuse, and (ii) even without migration, continuous models deviate from Hardy–Weinberg proportions [28, Section 4.10].

By writing diffusion equations for densities instead of frequencies, the first difficulty is easily overcome. Intuitive imposition of Hardy–Weinberg proportions led to the correct diallelic diffusion approximation with arbitrary, space-dependent mean-displacement vector and covariance matrix [23]. This model has been widely investigated [6,24,25,33,34]. At this intuitive level of analysis, the generalization to multiple alleles is immediate and gives the model investigated here and in [20,21].

The problem of deviations from Hardy–Weinberg proportions in continuous models is more serious. For two alleles, Fife [5, Chapter 2] presented a formal asymptotic derivation of the model in [23]. Extending his treatment to multiple alleles, separate sexes, X-linked loci, and plants with pollen and seed dispersion would be quite difficult and has not been accomplished.

Starting with the exact, discrete migration–selection model for the gene frequencies circumvents the above obstacles and permits the above important biological applications [27,29,30]. In this model, generations are discrete and nonoverlapping. The monoecious population is subdivided into panmictic colonies at the points of a lattice in $d$ dimensions; these colonies exchange migrants independently of genotype. Selection acts solely through viability differences: we posit that all genotypes have the same fertility. We neglect mutation and random genetic drift. The continuous approximation follows from the assumptions that both selection and migration are weak and the latter satisfies the standard assumptions for a diffusion process.

We denote position in the finite habitat $\Omega$ (a bounded, open domain in $\mathbb{R}^d$) by the vector $x = (x_1, \ldots, x_d)$ and measure time, $t$, in generations. The population density at $x$ is $\rho(x)$. Let $M_\alpha(x)$ and $V_{\alpha\beta}(x)$ designate the mean displacement in direction $x_\alpha$ and the covariance of the displacements in directions $x_\alpha$ and $x_\beta$ per generation; these drift and diffusion coefficients form the vector $M(x)$ and the symmetric, positive definite matrix $V(x)$. We consider a single locus with alleles $A_i$, where $i \in N \equiv \{1, 2, \ldots, n\}$. Note that $i$ and $j$ refer to alleles, whereas $\alpha$ and $\beta$ refer to spatial components.

Let $p_i(x, t)$ signify the (relative) frequency of $A_i$ at position $x$ at time $t$. For every $x \in \overline{\Omega}$ and $t \geq 0$, the vector $p(x, t)$ must satisfy

$$p(x, t) \in \Delta \equiv \left\{ p \in \mathbb{R}^n : p_i \geq 0 \forall i, \sum_{j=1}^{n} p_j = 1 \right\}. \quad (1.1)$$
To avoid the trivial case of essentially absent alleles, we suppose
\[ \int_{\Omega} p_i(x, 0) \, dx > 0 \quad (1.2) \]
for every \( i \in \mathbb{N} \).

We assume that both frequency dependence and dominance are absent. Therefore, the (scaled) selection coefficient of the genotype \( A_iA_j \) is \( s_i(x) + s_j(x) \), where \( s_i(x) \) represents the selection coefficient of \( A_i \). The mean allelic selection coefficient reads
\[ \bar{s}(x, p) = \sum_{i=1}^{n} s_i(x) p_i, \quad (1.3) \]
and the contribution of selection is
\[ S_i(x, p) \equiv \lambda p_i (s_i - \bar{s}), \quad (1.4) \]
where \( \lambda \) denotes the selection intensity (which we factored out in [21] but not in [20]). If time is scaled so that the migration rates are of order one, then \( \lambda \) becomes the ratio of the strength of selection to that of migration. In that case, weak, intermediate, and strong migration relative to selection correspond respectively to large, intermediate, and small values of \( \lambda \) compared with 1. Note that \( S_i \) is quadratic in \( p \).

We define the divergence of an arbitrary symmetric matrix \( W(x) \) as the vector with components \((\alpha = 1, 2, \ldots, d)\)
\[ (\nabla \cdot W)_\alpha = \sum_{\beta=1}^{d} W_{\alpha\beta,x_\beta}, \quad (1.5) \]
where the subscript \( x_\beta \) indicates partial differentiation. We introduce the vector
\[ b(x) = \rho^{-1} \nabla \cdot (\rho V) - M \quad (1.6) \]
and the operators \( L \) and \( B \) defined by
\[ L u = \frac{1}{2} \sum_{\alpha, \beta=1}^{d} V_{\alpha\beta} u_{x_\alpha x_\beta} + b \cdot \nabla u, \quad (1.7a) \]
\[ B u = \nu \cdot V \nabla u, \quad (1.7b) \]
where \( \nu \) denotes the unit outward normal vector on the boundary \( \partial \Omega \).

The gene frequencies \( p(x, t) \) satisfy the semilinear parabolic system [23,27,29]
\[ p_{i,t} = L p_i + S_i(x, p) \quad \text{in} \ \Omega \times (0, \infty), \quad (1.8a) \]
\[ B p_i = 0 \quad \text{on} \ \partial \Omega \times (0, \infty), \quad (1.8b) \]
\[ p(x, 0) \in \Delta \quad \text{in} \ \overline{\Omega} \quad (1.8c) \]
for every \( i \in N \). Here, \( L \) describes migration and (1.8b) specifies that no individuals cross the boundary. We are given \( \rho(x), M(x), V(x), \lambda, s_i(x), \) and \( p(x,0) \); we seek the asymptotic behavior of \( p(x,t) \) at \( t \to \infty \).

Throughout this paper, we assume that \( \rho(x), M_{\alpha}(x), V_{\alpha\beta}(x), \) and \( s_i(x) \) are all Hölder-continuous functions and each \( p_i(x,0) \) is a continuous function. We also assume that \( \partial \Omega \in C^2 \).

By the maximum principle [35, Chapter 3] and the standard existence theory of evolution equations, the problem (1.8) has a unique classical solution \( p(x,t) \) that exists for all time, \( p_i \in C(\overline{\Omega} \times [0,\infty)) \cap C^{2,1}(\overline{\Omega} \times (0,\infty)) \), and \( 0 < p_i(x,t) < 1 \) for every \( i \in N, \) every \( x \in \overline{\Omega} \), and \( t > 0 \). Therefore, without loss of generality, we posit that \( 0 < p_i(x,0) < 1 \) for every \( i \in N \) and every \( x \in \overline{\Omega} \). This problem makes sense, i.e., (1.1) holds [20].

We have proved some of our results only for special cases of (1.7).

If (1.7) can be simplified to
\[
Lu = \frac{1}{2} \nabla \cdot (V \nabla u), \quad Bu = v \cdot V \nabla u,
\]
we say that \( L \) is in divergence form. This applies if the population density \( \rho(x) \) is constant and (i) \( M \equiv 0 \) and \( V(x) \) is constant, (ii) migration is conservative (i.e., it does not change the population density [26]), or (iii) migration is symmetric (i.e., the underlying discrete migration pattern is described by a symmetric forward migration matrix [27]) [21].

If migration is homogeneous and isotropic, we can reduce (1.7) to
\[
Lu = \nabla^2 u, \quad Bu = u_v.
\]

We proceed to describe the main results of this paper, which are proved in Sections 2 to 5.

Section 2 treats strong migration and the stability of vertices. Its first principal result is that in the strong-migration limit, the allele with the greatest average selection coefficient is ultimately fixed. We define
\[
\sigma_i = \frac{1}{|\Omega|} \int_{\Omega} s_i(x) \, dx
\]
and \( N^* = \{2, \ldots, n\} \), and with suitable labelling of the alleles, make the generic assumption
\[
\sigma_1 > \sigma_1^* = \max_{i \in N^*} \sigma_i.
\]

We have

**Theorem 1.1.** If (1.9) and (1.12) hold and \( \lambda \) is sufficiently small, then \( p_1(x,t) \to 1 \) uniformly in \( x \) as \( t \to \infty \).

**Remark 1.2.** Theorem 1.1 is an immediate consequence of the much more general Theorem 2.1, in which divergence form (1.9) is posited but the nonlinearity is arbitrary.

**Remark 1.3.** Of course, Theorem 1.1 (applied to both the full system and its subsystems) implies that for sufficiently small \( \lambda \), vertex 1, i.e., \( (1, 0, \ldots, 0) \), is the only equilibrium in \( \Delta \) with \( A_1 \) present, and that every equilibrium on \( \partial \Delta \) with \( A_1 \) absent is unstable. We can improve this result
by strengthening (1.12) to the generic assumption that $\sigma_i \neq \sigma_j$ unless $i = j$. Labelling the alleles so that $\sigma_1 > \sigma_2 > \cdots > \sigma_n$ and applying Theorem 1.1 to the subsystems without $A_1$, then without $A_1$ and $A_2$, etc., we conclude that for sufficiently small $\lambda$, the vertices are the only equilibria.

**Example 1.4.** Here, we illustrate the application of Theorem 1.1 and some of the results in [20, 21] and highlight the dependence of the dynamics on $\lambda$. We consider three alleles ($n = 3$) in one dimension ($d = 1$), translate and scale $x$ so that $\Omega = (-1, 1)$, and posit (1.10). We choose

$$s_1(x) = \begin{cases} 1 & \text{if } -1 \leq x \leq 0, \\ (c-x)/c & \text{if } 0 < x < c, \\ 0 & \text{if } c \leq x \leq 1, \end{cases} \tag{1.13a}$$

$$s_2(x) = s_1(-x), \quad s_3(x) = a, \tag{1.13b}$$

where $0 \leq a < 1$ and $0 < c < 1$. We take $c > 0$ only to make $s_1(x)$ and $s_2(x)$ continuous. The conceptual basis of this example is the very simple, fully analyzed discrete Example 3.10 in [31]; the connection is especially close in the limit $c \to 0$.

According to (1.13), $A_1$ and $A_2$ are the extreme alleles and $A_3$ is the intermediate allele. An easy application of [20, Theorem 3.2] demonstrates that if $a \leq 1/2$, then $p(x,t) \to \hat{p}(x) = (q(x), 1-q(x), 0)$ uniformly in $x$ as $t \to \infty$, where $q(x)$ is the unique solution of the scalar problem

$$q'' + \lambda [s_1(x) - s_2(x)]q(1-q) = 0 \quad \text{in } (-1, 1), \tag{1.14a}$$

$$q'(-1) = q'(1) = 0, \tag{1.14b}$$

$$0 < q(x) < 1 \quad \text{in } (-1, 1). \tag{1.14c}$$

When comparing this result with Example 3.10 of [31], observe that $q(-x) = 1 - q(x)$, whence $q(0) = 1/2$.

Since $s_3(x) < \max[s_1(x), s_2(x)]$ for every $x \in [-1, 1]$, [21, Corollary 4.7] implies that for sufficiently large $\lambda$, $p_3(x,t) \to 0$ uniformly in $x$ as $t \to \infty$. Then [20, Theorem 2.1] shows that $p(x,t) \to \hat{p}(x)$ as $t \to \infty$.

From (1.11) and (1.13) we obtain

$$\sigma_1 = \sigma_2 = \frac{1}{2} \left( 1 + \frac{c}{2} \right), \quad \sigma_3 = a. \tag{1.15}$$

If $a > (1 + c/2)/2$ and $\lambda$ is sufficiently small, Theorem 1.1 shows that $p_3(x,t) \to 1$ uniformly in $x$ as $t \to \infty$. Therefore, if $a > (1 + c/2)/2$, then $A_3$ is ultimately fixed for sufficiently small $\lambda$, whereas it is ultimately lost for sufficiently large $\lambda$.

Next, for arbitrary migration, we specify the stability of the vertices. Let $\psi$ be a positive eigenfunction such that $L_1^* \psi = 0$, where $L_1^*$ denotes the adjoint of the closure of $L$ and $B$ (see [20, Sections 2.1 and 4.1] for details and examples). We normalize $\psi(x)$ so that

$$\int_{\Omega} \psi(x) \, dx = 1 \tag{1.16}$$
and generalize (1.11) to
\[ \sigma_i = \int_{\Omega} s_i(x) \psi(x) \, dx. \quad (1.17) \]

In Section 2.2, we define the eigenvalues \( \lambda_i^* \). Our second main result is

**Theorem 1.5.** Suppose that (1.12) holds and \( s_i(x) \neq s_j(x) \) for every \( i \in N \) and every \( j \in N \) such that \( i \neq j \). Then

(a) every vertex other than vertex 1 is unstable;
(b) vertex 1 is asymptotically stable if \( \lambda < \lambda_1^* \); it is unstable if \( \lambda > \lambda_1^* \).

Section 3 concerns the next level of analysis, the examination of the stability of the edge equilibria for arbitrary \( L \). Henceforth, we posit that

(A1) \( s_i(x) - s_j(x) \) changes sign in \( \Omega \) for every \( i \) and \( j \) such that \( 1 \leq i < j \leq n \).

Let \( \theta_{ij}(x) \) denote the unique solution of the problem \((1 \leq i < j \leq n)\)
\[ L \theta_{ij} + \lambda (s_i - s_j) \theta_{ij} (1 - \theta_{ij}) = 0 \quad \text{in } \Omega, \quad (1.18a) \]
\[ B \theta_{ij} \big|_{\partial \Omega} = 0, \quad 0 < \theta_{ij} < 1 \quad \text{in } \Omega. \quad (1.18b) \]

By [20, Theorem 2.1], there exists \( \lambda_{ij} \geq 0 \) such that (1.18) has a unique solution for every \( \lambda > \lambda_{ij} \). Then the equilibrium \( p^{(ij)}(x) \) of (1.8) on the \( ij \)-edge of \( \Delta \) is given by
\[ p^{(ij)}_k = \begin{cases} \theta_{ij} & \text{if } k = i, \\ 1 - \theta_{ij} & \text{if } k = j, \\ 0 & \text{if } k \neq i, j. \end{cases} \quad (1.19) \]

Note that (A1) is necessary for the existence of \( p^{(ij)} \).

Set
\[ s^{(ij)} = \max_{k \in N, k \neq i, j} s_k(x), \quad \tilde{s}^{(ij)}(x) = \max \left[ s_i(x), s_j(x) \right]. \quad (1.20) \]

For weak migration, we have

**Theorem 1.6.** Suppose that (A1) holds and \( \lambda \) is sufficiently large. The equilibrium \( p^{(ij)}(x) \) is

(a) asymptotically stable if \( s^{(ij)}(x) < \tilde{s}^{(ij)}(x) \) for every \( x \in \overline{\Omega} \);
(b) it is unstable if there exists \( x^{(ij)} \in \overline{\Omega} \) such that \( s^{(ij)}(x^{(ij)}) > \tilde{s}^{(ij)}(x^{(ij)}) \).

The stability condition in Theorem 1.6 means that, for every \( x \in \overline{\Omega} \), each allele absent at the edge equilibrium must be less fit than the fitter one of the two alleles present. In a discrete-time,
discrete-space model, the analogue of Theorem 1.6 follows directly from Karlin and McGregor’s [16,17] method of small parameters.

The next result determines the stability of each edge equilibrium immediately after its appearance as $\lambda$ increases.

**Theorem 1.7.** Suppose that (1.12) and (A1) hold.

(a) There exists $\delta_1 > 0$ such that $p^{(ij)}$ is unstable if $2 \leq i < j \leq n$ and $\lambda_{ij} < \lambda < \lambda_{ij} + \delta_1$.

(b) Suppose further that $\lambda_{1k} < \min_{l \notin k} \lambda_{1l}$ for some $k \in N^*$. Then there exists $\delta_2 > 0$ such that $p^{(1k)}$ is asymptotically stable if $\lambda_{1k} < \lambda < \lambda_{1k} + \delta_2$, and $p^{(1l)}$ is unstable if $l \neq k$ and $\lambda_{1l} < \lambda < \lambda_{1l} + \delta_2$.

Thus, under the assumptions (1.12) and (A1), as $\lambda$ increases, the only edge equilibrium that is stable immediately after its emergence is the one that materializes first among the edge equilibria that involve the allele with the highest average fitness.

In Sections 4 and 5, we demonstrate that even if there are only three alleles and migration is homogeneous and isotropic, for intermediate values of $\lambda$, surprisingly complex dynamics can occur. We choose $s_2(x)$ arbitrarily and set

$$s_1(x) = s_2(x) + \epsilon g(x), \quad s_3(x) = s_2(x) + h(x), \quad (1.21)$$

where $\epsilon > 0$ is sufficiently small. The first result of Section 4 is

**Proposition 1.8.** Suppose that $n = 3$, assumptions (1.10) and (1.21) hold, $g(x)$ changes sign in $\Omega$, $\int_{\Omega} g(x) \, dx \neq 0$, and $h(x) > 0$ somewhere in $\Omega$. Then for sufficiently small $\epsilon$, whenever the 12-edge equilibrium exists, it is unstable.

It is clear from (1.21) and follows at once from (4.4) in Section 4 that there exists $\tilde{\lambda} > 0$ such that the 12-edge equilibrium exists if and only if $\lambda > \tilde{\lambda}/\epsilon$.

We now assume that

(A2) $g(x)$ and $h(x)$ change sign in $\Omega$.

There exists $\lambda^* \geq 0$ such that for $\lambda > \lambda^*$, the problem

$$\nabla^2 \theta + \lambda h(x) \theta (1 - \theta) = 0 \quad \text{in } \Omega,$$  
$$\theta_{\nu}|_{\partial \Omega} = 0, \quad 0 < \theta < 1 \quad \text{in } \Omega \quad (1.22a)$$

has a unique solution [10]. Observe that $(0, 1 - \theta, \theta) = p^{(23)}$, the 23-edge equilibrium. Let

$$\sigma = \frac{1}{|\Omega|} \int_{\Omega} h(x) \, dx. \quad (1.23)$$

If $\sigma < 0$, we set $\theta \equiv 0$ for $0 < \lambda \leq \lambda^*$; if $\sigma = 0$, then $\lambda^* = 0$; if $\sigma > 0$, we set $\theta \equiv 1$ for $0 < \lambda \leq \lambda^*$. 


Hence, for every $\lambda > 0$, we can define

$$G(\lambda) = \int_{\Omega} g(x) \left[1 - \theta(x, \lambda)\right]^2 \, dx.$$  \hspace{1cm} (1.24)

We posit that

(A3) there exist distinct numbers $\lambda_1 < \lambda_2 < \cdots < \lambda_l$ such that $G(\lambda_i) = 0$ and $G'(\lambda_i) \neq 0$ for $i = 1, \ldots, l$, and $G(\lambda) \neq 0$ for $\lambda \notin \{\lambda_1, \ldots, \lambda_l\}$.

In Appendix A, we demonstrate how to construct a function of type $G$. The principal result of Section 4 is

**Theorem 1.9.** Suppose that $n = 3$ and (1.10), (1.21), (A2), and (A3) hold. Then for every $\Lambda > \lambda_l$, there exists a sufficiently small $\epsilon_0 = \epsilon_0(\Lambda) > 0$ such that for every $\epsilon \in (0, \epsilon_0)$, there exist $\{\lambda^\epsilon_i, \lambda_i, \epsilon\}_{1 \leq i \leq l}$ such that $\lim_{\epsilon \to 0} \lambda^\epsilon_i = \lim_{\epsilon \to 0} \lambda_i, \epsilon = \lambda_i$ and for $0 < \lambda \leq \Lambda$, the following conclusions hold.

(a) The 23-edge equilibrium changes stability at exactly $\lambda = \lambda^\epsilon_1, \ldots, \lambda^\epsilon_l$, and the 13-edge equilibrium changes stability at exactly $\lambda = \lambda_1, \epsilon, \ldots, \lambda_l, \epsilon$.

(b) An internal equilibrium exists if $\lambda \in \bigcup_{j=1}^l (\min(\lambda_j^\epsilon, \lambda_i, \epsilon), \max(\lambda_j^\epsilon, \lambda_i, \epsilon))$.

(c) There exist functions $g(x)$ for which the internal equilibrium is asymptotically stable, and other functions $g(x)$ for which it is unstable.

Thus, as $\lambda$ increases, either a branch of internal equilibria bifurcates from the 23-edge equilibrium, thereby changing the stability of that equilibrium, and meets the 13-edge equilibrium, thereby changing the stability of that equilibrium, or the internal equilibrium bifurcates from the 13-edge and meets the 23-edge, with the corresponding changes in stability. So, the 23- and 13-edge equilibria repeatedly exchange stabilities.

In Section 5, we establish that the conditions for protection or loss of an allele can both depend nonmonotonically on $\lambda$. Our result on protection is

**Theorem 1.10.** Suppose that $n = 3$, (1.10) holds, and $s_2(x) - s_3(x)$ changes sign in $\Omega$, and $\sigma_2 > \sigma_3$. Then there exists $s_1(x)$ such that, even though $\sigma_2 > \sigma_1$ and $s_2(x) > \tilde{s}^{(13)}(\tilde{x})$ for some $\tilde{x} \in \Omega$, the 13-edge equilibrium exists and is asymptotically stable for some ranges of $\lambda$.

**Remark 1.11.** In Theorem 1.10, since $\sigma_2 > \max(\sigma_1, \sigma_3)$, Theorem 1.1 shows that for sufficiently small $\lambda$, not only is $A_2$ protected from loss, but it is ultimately fixed. Since $s_2(\tilde{x}) > \tilde{s}^{(13)}(\tilde{x})$ [21, Corollary 4.9] informs us that $A_2$ is protected for sufficiently large $\lambda$. Since asymptotic stability of the 13-edge equilibrium for some intermediate ranges of $\lambda$ implies that $A_2$ is not protected, we conclude that the condition for protection is not monotone in $\lambda$.

For loss, we have

**Theorem 1.12.** Suppose that $n = 3$ and (1.10) holds. Given any $s_2(x)$, there exist $s_1(x)$ and $s_3(x)$ such that, even though $\sigma_2 < \min(\sigma_1, \sigma_3)$ and $s_2(x) < \tilde{s}^{(13)}(x)$ for every $x \in \Omega$, for some ranges of $\lambda$,
(a) the 13-edge equilibrium exists and is unstable;
(b) for every solution of (1.8) and arbitrary initial data,
\[ \limsup_{t \to \infty} \int_\Omega p_2(x, t) \, dx > 0. \]  

(1.25)

Remark 1.13. Assume that \( \sigma_2 < \sigma_1 < \sigma_3 \). Then Theorem 1.1 reveals that for sufficiently small \( \lambda \), \( A_3 \) is ultimately fixed, so \( A_2 \) is ultimately lost. Furthermore, since \( s_2(x) < \tilde{s}^{(13)}(x) \) for every \( x \in \Omega \), from [21, Corollary 4.7] we infer that for sufficiently large \( \lambda \), \( A_2 \) is ultimately lost. By part (b) of Theorem 1.12, for some intermediate \( \lambda \), the allele \( A_2 \) can not be lost. Therefore, the condition for loss is not monotone in \( \lambda \).

2. Strong migration and stability of vertices

In this section, we focus on strong migration and the stability of vertices. The main goal is to establish Theorems 1.1 and 1.5.

2.1. Strong migration

In this subsection, we consider the semilinear parabolic system

\[ p_{i,t} - Lp_i = \lambda T_i(x, p) \quad \text{in} \quad \Omega \times (0, \infty), \]
\[ Bp_i = 0 \quad \text{on} \quad \partial \Omega \times (0, \infty), \]
\[ p(x, 0) \in \text{int} \Delta, \]

(2.1a) (2.1b) (2.1c)

where \( i \in \mathbb{N}, \lambda > 0, T_i(x, p) \) is Hölder continuous in \( x \) and Lipschitz in \( p \) but otherwise arbitrary, and (1.9) holds. Moreover, we assume that \( p \in \text{int} \Delta \) for \( t > 0 \) and \( x \in \Omega \).

Set \( D = 1/\lambda, \tau = \lambda t, \) and \( q_i(x, \tau) = p_i(x, t) \). Then for \( i \in \mathbb{N}, q_i \) satisfies

\[ q_{i,\tau} - DLq_i = T_i(x, q) \quad \text{in} \quad \Omega \times (0, \infty), \]
\[ Bq_i = 0 \quad \text{on} \quad \partial \Omega \times (0, \infty), \]
\[ q(x, 0) \in \text{int} \Delta. \]

(2.2a) (2.2b) (2.2c)

Now consider the spatially averaged system

\[ \frac{dq_i^*}{d\tau} = \overline{T}_i(q^*) \equiv \frac{1}{|\Omega|} \int_\Omega T_i(x, q^*) \, dx, \quad \tau > 0, \]
\[ q^*(0) \in \text{int} \Delta, \]

(2.3a) (2.3b)

where \( i \in \mathbb{N} \). We posit that

(A4) the system (2.3) has a globally asymptotically stable equilibrium \( \hat{q}^* \), i.e., \( \hat{q}^* \) is linearly stable and \( \lim_{\tau \to \infty} q^*(\tau) = \hat{q}^* \) for every \( q^*(0) \) that satisfies (2.3b).
Theorem 2.1. Suppose that (1.9) and (A4) hold. Then for sufficiently large D, the system (2.2) has a globally asymptotically stable equilibrium \( \hat{q}(x) \) such that \( \hat{q}(x) \to \hat{q}^* \) uniformly as \( D \to \infty \).

Remark 2.2. Theorem 1.1 is an immediate consequence of Theorem 2.1. If \( T_i(x, p) \) is independent of \( x \) for every \( i \in \mathbb{N} \), Theorem 2.1 follows from a result of Conway, Hoff, and Smoller [4]. Since we are unable to locate a proof of Theorem 2.1 in the literature, we include a proof here that follows closely that of Conway et al. For a local result with explicit space dependence, see Carvalho and Hale [2].

We first exhibit the connection between \( q_i(x, \tau) \) and
\[
\bar{q}_i(\tau) \equiv \frac{1}{|\Omega|} \int_{\Omega} q_i(x, \tau) \, dx. \tag{2.4}
\]

Lemma 2.3. For every \( r > d \) and sufficiently large \( D \), there exist constants \( C_1 \) and \( C_2 \), independent of \( D \) and \( \tau \), such that
\[
\left\| q_i(\cdot, \tau) - \bar{q}_i(\tau) \right\|_{L^\infty(\Omega)} \leq C_1 \left( D^{-2/r} + e^{-C_2 D \tau} \right) \tag{2.5}
\]
for every \( \tau \geq 0 \) and every \( i \in \mathbb{N} \).

Proof. For \( \tau > 0 \), set
\[
E(\tau) = \frac{1}{2} \sum_i \int_{\Omega} (\nabla q_i) \cdot V \nabla q_i \, dx. \tag{2.6}
\]

Claim. There exist positive constants \( C_3 \) and \( C_4 \) such that for \( \tau \geq 0 \) and sufficiently large \( D \),
\[
E(\tau) \leq C_3 \left( D^{-2} + e^{-C_4 D \tau} \right). \tag{2.7}
\]

To establish this assertion, we first integrate by parts and use (2.2a):
\[
\frac{dE}{d\tau} = \sum_i \int_{\Omega} (\nabla q_{i, \tau}) \cdot V \nabla q_i \, dx = -2 \sum_i \left[ D \int_{\Omega} (Lq_i)^2 \, dx + \int_{\Omega} (Lq_i) T_i(x, q) \, dx \right]. \tag{2.8}
\]

To proceed, we need the following result. Let \( 0 = \tilde{\lambda}_0 < \tilde{\lambda}_1 \leq \tilde{\lambda}_2 \leq \cdots \) denote the eigenvalues of the scalar problem
\[
L\varphi + \lambda \varphi = 0 \quad \text{in} \ \Omega, \quad \varphi = 0 \quad \text{on} \ \partial \Omega. \tag{2.9}
\]
Then for any \( w \in C^2(\Omega) \cap C^1(\overline{\Omega}) \) with \( Bw|_{\partial \Omega} = 0 \), we have
\[
\int_{\Omega} (Lw)^2 \, dx \geq \frac{1}{2} \lambda_1 \int_{\Omega} (\nabla w) \cdot V \nabla w \, dx. \tag{2.10}
\]

The proof of (2.10) is similar to that of [4, Lemma A.1]; therefore, we omit it.
From (2.10) and (2.6) we see that $-2D\tilde{\lambda}_1E$ is an upper bound on the first term in (2.8). Recalling (1.9) and integrating the second term in (2.8) by parts yields

$$\frac{dE}{d\tau} \leq -2D\tilde{\lambda}_1E + C_5 \sum_i \int_\Omega (|\nabla q_i| + |\nabla q_i|^2) \, dx. \quad (2.11)$$

Since $V$ is positive definite, the last term in (2.11) is bounded by a multiple of $E$, and Hölder’s inequality shows that the second term is bounded by a multiple of $E^{1/2}$. Consequently, for sufficiently large $D$, we have

$$\frac{dE}{d\tau} \leq -D\tilde{\lambda}_1E + C_6E^{1/2}. \quad (2.12)$$

Solving (2.12) gives

$$E(\tau) \leq C_7\left(D^{-2} + e^{-\tilde{\lambda}_1D\tau}\right) \quad (2.13)$$

for every $\tau \geq 0$ and sufficiently large $D$, which establishes (2.7).

Since $V$ is positive definite, inequality (2.13) implies that

$$\|\nabla q_i\|_{L^2(\Omega)} \leq C_8\left(D^{-1} + e^{-\tilde{\lambda}_1D\tau}\right) \quad (2.14)$$

for every $\tau \geq 0$ and sufficiently large $D$. Therefore, the Poincaré inequality (Lemma A.2 of [4]) yields

$$\|q_i - \bar{q}_i\|_{L^2(\Omega)} \leq C_9\left(D^{-1} + e^{-\tilde{\lambda}_1D\tau}\right) \quad (2.15)$$

for sufficiently large $D$. Using the arguments in [4, pp. 14–15] and invoking (2.14), (2.15), and standard regularity theory for parabolic operators lead to (2.5). The requirement on $r$ ($r > d$) comes from the Sobolev embedding theorem. We refer to [4] for the remaining details. □

Next, we estimate the difference between $\bar{q}_i$ and solutions of the system ($i \in N$)

$$\frac{d\bar{q}_i}{d\tau} = \bar{T}_i(\bar{q}), \quad \tau > 0, \quad (2.16a)$$

$$\bar{q}_i(0) = \bar{q}_i(0), \quad (2.16b)$$

which is a special case of (2.3).

**Lemma 2.4.** As $D \to \infty$, $\bar{q}_i(\tau) \to q_i(\tau)$ uniformly for $\tau$ in any compact subset of $[0, \infty)$.

**Proof.** We first show that if $D$ is sufficiently large, then $\bar{q}_i$ satisfies

$$\frac{d\bar{q}_i}{d\tau} = \bar{T}_i(\bar{q}) + g_i(\tau), \quad (2.17)$$

where
\[ \left| g_i(\tau) \right| \leq C_{10} \left( D^{-1} + e^{-\frac{1}{2} \tilde{\omega}_1 D \tau} \right) \quad (2.18) \]

for every \( \tau > 0 \), every \( D > 0 \), and every \( i \in \mathbb{N} \).

To establish this assertion, we first note from (2.2), (1.9), and (2.15) that
\[
\frac{d \tilde{q}_i}{d\tau} = \frac{1}{|\Omega|} \int_{\Omega} \frac{\partial q_i}{\partial \tau} \, dx = \tilde{T}_i(q) = \tilde{T}_i(\tilde{q}) + g_i(\tau),
\quad (2.19)
\]
where
\[
\left| g_i(\tau) \right| = \frac{1}{|\Omega|} \left| \int_{\Omega} \left[ T_i(x, q) - T_i(x, \tilde{q}) \right] \, dx \right| \leq C_{11} \sum_j \| q_j - \tilde{q}_j \|_{L^2(\Omega)}
\]
\[
\leq C_{10} \left( D^{-1} + e^{-\frac{1}{2} \tilde{\omega}_1 D \tau} \right) \quad (2.20)
\]
for sufficiently large \( D \), every \( \tau \geq 0 \), and every \( i \in \mathbb{N} \).

Set \( F(\tau) = \left( \frac{1}{2} \right) \sum_i (\tilde{q}_i - \tilde{q}_i)^2 \). From (2.16b) we observe that \( F(0) = 0 \), and for sufficiently large \( D \), from (2.19), (2.16a), and (2.20) we derive
\[
\frac{dF}{d\tau} \leq C_{12} F(\tau) + C_{13} \left( D^{-2} + e^{-\frac{1}{2} \tilde{\omega}_1 D \tau} \right), \quad (2.21)
\]
from which it follows easily that as \( D \to \infty \), \( F(\tau) \to 0 \) uniformly for \( \tau \) in any compact subset of \([0, \infty)\). This proves Lemma 2.4. \( \square \)

From Lemmas 2.3 and 2.4, we have

**Corollary 2.5.** For every \( i \in \mathbb{N} \), as \( D \to \infty \), \( q_i(x, \tau) \to \tilde{q}_i(\tau) \) uniformly for every \( x \in \overline{\Omega} \) and \( \tau \) in any compact subset of \((0, \infty)\).

We are now ready for

**Proof of Theorem 2.1.** We first show that there exist sufficiently large \( D_1 \) and sufficiently small \( a > 0 \) such that if \( D \geq D_1 \), then (2.2) has a unique equilibrium \( \hat{q}(x) \) in \( B_a(\hat{q}^*) \cap \Delta \), where \( B_a(\hat{q}^*) \) is the ball in \( \mathbb{R}^d \) of radius \( a \) and centered at \( \hat{q}^* \). We consider three cases:

(a) If \( \hat{q}^* \in \text{int} \Delta \), then the existence and uniqueness of \( \hat{q}(x) \) follow from the linear stability of \( \hat{q}^* \) and the implicit function theorem, and \( \hat{q}(x) \to \hat{q}^* \) uniformly in \( x \) as \( D \to \infty \).

(b) If \( \hat{q}^* \) is in the interior of some face \( \Delta^* \) of \( \Delta \), then again by the implicit function theorem, the equilibrium \( \hat{q} \) lies in the interior of \( \Delta^* \), and \( \hat{q}(x) \to \hat{q}^* \) uniformly in \( x \) as \( D \to \infty \).

(c) If \( \hat{q}^* \) is one of the vertices, then \( \hat{q}(x) \equiv \hat{q}^* \) for sufficiently large \( D \). In fact, up to now it suffices to assume the nondegeneracy of \( \hat{q}^* \).

Since \( \hat{q}(x) \to \hat{q}^* \) uniformly, there exist \( D_2 > D_1 \) and \( \gamma > 0 \) such that for \( D \geq D_2 \), the equilibrium \( \hat{q} \) is linearly stable; moreover, for any eigenvalue \( \mu \) of the linearized eigenvalue problem at \( \hat{q}(x) \), we have \( \text{Re} \mu \geq \gamma \), i.e., \( \text{Re} \mu \) is uniformly bounded away from zero. Since the linear
stability of $\hat{q}$ implies its asymptotic stability, there exists $\delta^* > 0$, which depends on $\gamma$ but is independent of $D$ for large $D$, such that if $\|p(\cdot, 0) - \hat{q}(\cdot)\|_{L^\infty(\Omega)} \leq \delta^*$, then $\lim_{\tau \to \infty} q(x, \tau) = \hat{q}(x)$ uniformly for $x \in \bar{\Omega}$.

By choosing $D$ larger if necessary, we can ensure that $\|\hat{q}(\cdot) - \hat{q}^*\|_{L^\infty(\Omega)} \leq \delta^*/4$. By assumption (A4), $\hat{q}(\tau) \to \hat{q}^*$ as $\tau \to \infty$. Consequently, there exists a sufficiently large $\tau^*$ such that $|\hat{q}(\tau) - \hat{q}^*| \leq \delta^*/4$ for every $\tau \geq \tau^*$. In particular, we have $\|\hat{q}(\cdot) - \hat{q}(\cdot)^*\|_{L^\infty(\Omega)} \leq \delta^*/2$. By Corollary 2.5, $q(x, \tau) \to \hat{q}(\tau)$ uniformly for $x \in \bar{\Omega}$ and $\tau \in [\tau^*/2, \tau^*]$. Therefore, by choosing $D$ larger if necessary, we may assume that $|q(x, \tau) - q(\tau^*)| \leq \delta^*/4 < \delta^*$, which together with asymptotic stability of $\hat{q}$ implies that $q(x, \tau) \to \hat{q}(x)$ uniformly in $x$ as $\tau \to \infty$. Therefore, $\hat{q}$ is globally asymptotically stable if $D$ is sufficiently large. □

2.2. Stability of vertices

To start the proof of Theorem 1.5, for any continuous function $m(x) \neq 0$ and arbitrary $L$, consider the linear eigenvalue problem

$$-Lu = \lambda m(x)u \quad \text{in } \Omega, \quad Bu|_{\partial \Omega} = 0. \quad (2.22)$$

If $m$ is positive somewhere in $\bar{\Omega}$ and $\int_{\Omega} m \psi \, dx < 0$, then (2.22) has a unique positive eigenvalue $\lambda_0(m)$ with a positive eigenfunction. If $\int_{\Omega} m \psi \, dx \geq 0$, then (2.22) does not have a positive eigenvalue with a positive eigenfunction; in this case, we define $\lambda_0(m) = 0$. If $m(x) \leq 0$ for every $x \in \bar{\Omega}$, then (2.22) does not have a positive eigenvalue, and we define $\lambda_0(m) = \infty$ [37].

Linearizing (1.8) at vertex $j \in N$ yields the independent problems

$$p_{i,t} = Lp_i + \lambda_{mij}(x)p_i \quad \text{in } \Omega \times (0, \infty), \quad (2.23a)$$

$$Bp_i = 0 \quad \text{on } \partial \Omega \times (0, \infty), \quad (2.23b)$$

where $m_{ij}(x) = s_i(x) - s_j(x)$ and $i \in N_j \equiv \{k \in N: k \neq j\}$. We assume that $s_i(x) \neq s_j(x)$ for every $j \in N$ and every $i \in N_j$. Hence, (i) if $\sigma_i < \sigma_j$ and $s_i > s_j$ somewhere in $\bar{\Omega}$, then $0 < \lambda_0(m_{ij}) < \infty$; (ii) if $\sigma_i \geq \sigma_j$, then $\lambda_0(m_{ij}) = 0$; (iii) if $s_i(x) \leq s_j(x)$ for every $x \in \bar{\Omega}$, then $\lambda_0(m_{ij}) = \infty$.

For every $j \in N$, we set

$$\sigma_j^* = \max_{i \in N_j} \sigma_i, \quad \lambda_j^* = \min_{i \in N_j} \lambda_0(m_{ij}). \quad (2.24)$$

We conclude that (i) if $\sigma_j > \sigma_j^*$ and $s_i > s_j$ somewhere in $\bar{\Omega}$ for every $i \in N_j$, then $0 < \lambda_j^* < \infty$; (ii) if $\sigma_j \leq \sigma_j^*$ (which holds if $s_j(x) \geq s_j(x)$ for every $x \in \bar{\Omega}$ for some $i \in N_j$), then $\lambda_j^* = 0$; (iii) if $s_i(x) \leq s_j(x)$ for every $x \in \bar{\Omega}$ and every $i \in N_j$ (which implies that $\sigma_j > \sigma_j^*$), then $\lambda_j^* = \infty$.

This discussion and Theorem 2.1 of [20] establish that vertex $j$ is asymptotically stable if $\lambda < \lambda_j^*$, and that it is unstable if $\lambda > \lambda_j^*$. Thus, the stability of vertex $j$ depends on $\lambda$ in case (i), and vertex $j$ is unstable in case (ii) and asymptotically stable in case (iii).

Now we can easily complete the proof. From (1.12) we obtain $\sigma_1 > \sigma_j$, whence (2.24) yields $\sigma_j < \sigma_j^*$ for every $j \in N^*$. Therefore, case (ii) applies, which proves part (a). Part (b) is merely the special case $j = 1$. □
3. Stability of the edge equilibria

In this section, we study the stability of each edge equilibrium for arbitrary \( L \) when either (i) \( \lambda \) is sufficiently large or (ii) the equilibrium has just appeared as \( \lambda \) increases. Our main goal is to establish Theorems 1.6 and 1.7.

3.1. Proof of Theorem 1.6

Let \( \mu_1^\delta \) denote the principal eigenvalue of the linear problem
\[
-\delta L \varphi + m_\delta(x) \varphi = \mu \varphi \quad \text{in } \Omega, \quad B \varphi|_{\partial \Omega} = 0,
\]
where \( \delta > 0 \) is a constant and \( m_\delta \) is a Hölder-continuous function in \( \overline{\Omega} \). Lemma 3.1 is known for \( L = \nabla^2 \) [13].

**Lemma 3.1.** Suppose that \( m_\delta(x) \to m(x) \) uniformly in \( x \) as \( \delta \to 0 \). Then
\[
\lim_{\delta \to 0} \mu_1^\delta = \min_{x \in \Omega} m(x) \equiv m^*.
\]

**Proof.** By the comparison principle for principal eigenvalues, we have \( \mu_1^\delta \geq m^* \), whence \( \liminf_{\delta \to 0} \mu_1^\delta \geq m^* \). Therefore, it suffices to show that \( \limsup_{\delta \to 0} \mu_1^\delta \leq m^* \). To this end, we argue by contradiction. If the contrary holds, there exists \( \epsilon^* > 0 \) such that \( \limsup_{\delta \to 0} \mu_1^\delta \geq m^* + \epsilon^* \). Passing to a sequence if necessary, we may assume that there exists \( \delta^* > 0 \) such that \( \delta < \delta^* \). By the continuity of \( m(x) \), there exist \( x^* \in \Omega \) and \( a > 0 \) such that \( m^* \geq m(x) - \epsilon^*/4 \) for every \( x \in B_a(x^*) \subset \Omega \). Hence, \( \mu_1^\delta \geq m(x) + \epsilon^*/4 \) for \( 0 < \delta < \delta^* \) and every \( x \in B_a(x^*) \). Since \( m_\delta \to m \) uniformly, there exists \( \tilde{\delta} < \delta^* \) such that if \( 0 < \delta < \tilde{\delta} \), then \( m(x) \geq m_\delta(x) - \epsilon^*/8 \) for every \( x \in B_a(x^*) \). Therefore, we have
\[
\mu_1^\delta \geq m_\delta(x) + \frac{\epsilon^*}{8},
\]
for \( 0 < \delta < \tilde{\delta} \) and every \( x \in B_a(x^*) \).

Let \( \varphi_\delta > 0 \) denote a positive eigenfunction corresponding to \( \mu_1^\delta \). By (3.1) and (3.3), \( \varphi_\delta \) satisfies
\[
-L \varphi_\delta = \mu_1^\delta - \frac{m_\delta}{\delta} \varphi_\delta \geq \frac{\epsilon^*}{8\delta} \varphi_\delta
\]
in \( B_a(x^*) \), provided that \( \delta < \tilde{\delta} \).

Let \( \mu \) be the principal eigenvalue of the linear problem
\[
-L \varphi = \mu \varphi \quad \text{in } B_a(x^*), \quad \varphi|_{\partial B_a(x^*)} = 0,
\]
and let \( \varphi \) be the corresponding eigenfunction normalized so that \( \sup_{B_a(x^*)} \varphi = 1 \). It is well known that \( \mu > 0 \). Set \( \bar{\varphi}(x) = \varphi_\delta(x)/\inf_{B_a(x^*)} \varphi_\delta(x) \). Then \( \bar{\varphi} \) and \( \varphi \) satisfy \( \bar{\varphi} \geq 1 \geq \varphi \), and they are,
respectively, a supersolution and a subsolution of the problem
\[-L\Phi = \frac{\epsilon^*}{8\delta} \Phi \quad \text{in} \ B_\delta(x^*), \quad \Phi|_{\partial B_\delta(x^*)} = 0. \quad (3.6)\]
provided that \(\delta < \min\{\delta, \epsilon^*/(8\delta)\}\). By the supersolution–subsolution method, the problem (3.6) has a positive solution between \(\varphi\) and \(\bar{\varphi}\), which implies that \(\mu = \epsilon^*/(8\delta)\). Since \(\mu\) is independent of \(\delta\), we have a contradiction, and this completes the proof of Lemma 3.1. \(\Box\)

Recall (1.20) and, as in Section 2.2, set
\[m_{ij}(x) = s_i(x) - s_j(x). \quad (3.7)\]

**Lemma 3.2.** If (A1) holds, then as \(\lambda \to \infty\), the solution of (1.18) satisfies 
\[s_j(x) + m_{ij}(x)\theta_{ij}(x) \to \tilde{s}^{(ij)}(x) \quad (3.8)\]
uniformly for \(x \in \Omega\).

**Proof.** Given any \(\eta > 0\), we consider three different cases.

(a) For every \(x\) such that \(|m_{ij}(x)| \leq \eta\), we have
\[|s_j + m_{ij}\theta_{ij} - \tilde{s}^{(ij)}| \leq 2|m_{ij}| \leq 2\eta. \quad (3.9)\]

(b) For every \(x \in E_{1,\eta} \equiv \{x \in \Omega : m_{ij}(x) > \eta\}\), since \(\theta_{ij} \to 1\) uniformly in \(E_{1,\eta}\) as \(\lambda \to \infty\), for sufficiently large \(\lambda\) we have
\[|s_j + m_{ij}\theta_{ij} - \tilde{s}^{(ij)}| = m_{ij}(1 - \theta_{ij}) \leq \eta. \quad (3.10)\]

(c) The argument is similar for \(x \in E_{2,\eta} \equiv \{x \in \Omega : m_{ij}(x) < -\eta\}\), where \(\theta_{ij} \to 0\) uniformly as \(\lambda \to \infty\). This completes the proof. \(\Box\)

**Proof of Theorem 1.6.** Linearizing (1.8) at the equilibrium \(p^{(ij)}(x)\) defined in (1.19), we see that the stability of \(p^{(ij)}\) is determined by the eigenvalue problem
\[
L\varphi_k + \lambda \varphi_k (m_{kj} - m_{ij}\theta_{ij}) = -\mu \varphi_k \quad \text{in} \ \Omega, \quad k \neq i, \quad (3.11a)
\]
\[
L\varphi_i + \lambda \varphi_i m_{ij}(1 - 2\theta_{ij}) - \lambda \theta_{ij} \sum_{l \neq i,j} \varphi_l m_{lj} = -\mu \varphi_i \quad \text{in} \ \Omega, \quad (3.11b)
\]
\[
B\varphi_k = 0 \quad \text{on} \ \partial \Omega, \quad (3.11c)
\]
where \(k \in N_j = \{l \in N : l \neq j\}\).

To prove part (a), we argue by contradiction. Suppose that (3.11) has an eigenvalue \(\mu\) with \(\text{Re} \mu \leq 0\). By Lemma 3.2, we have \(m_{kj} - m_{ij}\theta_{ij} \to s_k - \tilde{s}^{(ij)}\) uniformly in \(\Omega\) for every \(k \in N\).

By the assumption in part (a), \(s_k - \tilde{s}^{(ij)} < 0\) in \(\Omega\) for every \(k \neq i, j\). Hence, for sufficiently large \(\lambda\), we obtain \(m_{kj} - m_{ij}\theta_{ij} < 0\) in \(\Omega\). Since \(\text{Re} \mu \leq 0\), by the comparison principle of
eigenvalues we see that if $\lambda$ is sufficiently large, then $\phi_k \equiv 0$ for every $k \neq i, j$. Therefore, $\phi_i$ satisfies

$$L\phi_i + \lambda \phi_i m_{ij}(1 - 2\theta_{ij}) = -\mu \phi_i \quad \text{in } \Omega, \quad B\phi_i|_{\partial\Omega} = 0.$$  \hspace{1cm} (3.12)

By [20, Theorem 2.1], we have also $\phi_i \equiv 0$, which is a contradiction. This proves part (a).

We proceed to part (b). By the assumption, there exists some $l \neq i, j$ such that $s_l - \bar{s}(ij)$ is positive somewhere, i.e., $\min_{\Omega}(\bar{s}(ij) - s_l) < 0$. Lemma 3.2 informs us that $m_{jl} + m_{ij}\theta_{ij} \to \bar{s}(ij) - s_l$ uniformly in $\Omega$ as $\lambda \to \infty$. Therefore, by Lemma 3.1, the smallest eigenvalue $\mu_1$ of the linear problem

$$L\phi_l + \lambda \phi_l (m_{ij} - m_{ij}\theta_{ij}) = -\mu \phi_l \quad \text{in } \Omega, \quad B\phi_l|_{\partial\Omega} = 0 \hspace{1cm} (3.13)$$

satisfies $\mu_1/\lambda \to \min_{\Omega}(\bar{s}(ij) - s_l) < 0$ as $\lambda \to \infty$. Hence, for sufficiently large $\lambda$, we have $\mu_1 < 0$.

We claim that $\mu_1$ is an eigenvalue of (3.11). If so, then $p^{(ij)}$ is unstable, and therefore the proof of Theorem 1.6 is complete.

To establish this assertion, set $\mu = \mu_1$ and $\phi_k \equiv 0$ for $k \in N$ and $k \neq i, j, l$ in (3.11). Then (3.13) shows that (3.11a) is satisfied, and (3.11b) reduces to

$$(\tilde{L} + \mu_1)\phi_i = \lambda \theta_{ij} m_{ij}\phi_l \quad \text{in } \Omega, \quad B\phi_i|_{\partial\Omega} = 0, \hspace{1cm} (3.14)$$

where $\tilde{L} = L + \lambda m_{ij}(1 - 2\theta_{ij})$. By [20, Theorem 2.1], all the eigenvalues of $\tilde{L}$ have negative real parts. For sufficiently large $\lambda$, since $\mu_1 < 0$, we see that all the eigenvalues of $\tilde{L} + \mu_1$ have negative real parts. Therefore, $\tilde{L} + \mu_1$ has an inverse and (3.14) has a unique solution. Consequently, for every sufficiently large $\lambda$, (3.11) has a nontrivial solution for $\mu = \mu_1$. This implies that $\mu_1$ is an eigenvalue of (3.11), which completes the proof of Theorem 1.6. \hspace{1cm} □

**Remark 3.3.** Under the assumption of part (a), by [21, Corollary 4.7], for every $k \neq i, j$, we have $p_k(x, t) \to 0$ uniformly in $x$ as $t \to \infty$. Hence, by the same argument as in the proof of [20, Theorem 3.1], we have $p(x, t) \to p^{(ij)}(x)$ uniformly as $t \to \infty$. Therefore, under the assumption of part (a), $p^{(ij)}$ is globally asymptotically stable for sufficiently large $\lambda$.

### 3.2. Proof of Theorem 1.7

For part (a), we demonstrate that for every pair $(i, j)$ such that $2 \leq i < j \leq n$, if $\lambda_{ij} < \lambda < \lambda_{ij} + \delta_1$, then the smallest eigenvalue $\mu_1(\lambda)$ of the linear problem

$$L\varphi + \lambda \varphi(m_{ij} - m_{ij}\theta_{ij}) = -\mu \varphi \quad \text{in } \Omega, \quad B\varphi|_{\partial\Omega} = 0 \hspace{1cm} (3.15)$$

is negative. The rest of the proof is similar to that of part (b) of Theorem 1.6; i.e., $\mu_1 < 0$ is an eigenvalue of (3.11), which implies the instability of $p^{(ij)}$ for every $i$ and $j$ such that $2 \leq i < j \leq n$.

Recalling (1.17), from Theorem 2.1 of [20] we see that if $\sigma_i > \sigma_j$, the branch of solutions of (1.18) bifurcates from the constant equilibrium $1$ at $\lambda = \lambda_{ij}$; if $\sigma_i < \sigma_j$, the branch of solutions of (1.18) bifurcates from the other constant equilibrium, i.e., $0$, at $\lambda = \lambda_{ij}$. The case $\sigma_i = \sigma_j$ is slightly different. If $\lambda = 0$, (1.18) has a continuum of constant solutions given by $C = \{s: 0 <$
Since 1/2 is the unique critical point of the nonlinearity of (1.18a), i.e., \( \theta_{ij}(1 - \theta_{ij}) \), one can show that if \( \sigma_i = \sigma_j \) and (A1) holds, the branch of solutions of (1.18) bifurcates from 1/2 \( \in C \) at \( \lambda = 0 \). Hence, we have

\[
\lim_{\lambda \to \lambda_{ij}^-} \theta_{ij}(x) = \begin{cases} 
1 & \text{if } \sigma_i > \sigma_j, \\
\frac{1}{2} & \text{if } \sigma_i = \sigma_j, \\
0 & \text{if } \sigma_i < \sigma_j
\end{cases}
\]  (3.16)

uniformly in \( x \). Therefore, we obtain

\[
\lim_{\lambda \to \lambda_{ij}^-} \int_{\Omega} (m_{1j} - m_{ij}\theta_{ij}) \psi \, dx = \sigma_1 - \max(\sigma_i, \sigma_j) > 0,
\]  (3.17)

where the last inequality follows from (1.12). By [20, Theorem 2.1], this implies that \( \mu_1(\lambda_{ij}) < 0 \). By the continuity of \( \mu_1(\lambda) \), we have \( \mu_1(\lambda) < 0 \) for \( \lambda \) close to but greater than \( \lambda_{ij} \), which proves part (a).

For part (b), without loss of generality, we may assume that \( k = n \), i.e., \( \lambda_{1n} < \lambda_{1l} \) for every \( l \) such that \( 2 \leq l \leq n - 1 \). We first study the stability of \( p^{(1n)} \), for which (3.11) yields the linear eigenvalue problem

\[
L\varphi + \lambda m_{1n}(1 - 2\theta_{1n})\varphi - \lambda \theta_{1n} \sum_{l=2}^{n-1} m_{ln}\varphi_l = -\mu \varphi \text{ in } \Omega,
\]  (3.18a)

\[
L\varphi_j + \lambda (m_{jn} - m_{1n}\theta_{1n})\varphi_j = -\mu \varphi_j \text{ in } \Omega, \quad 2 \leq j \leq n - 1,
\]  (3.18b)

\[
B\varphi_j = 0 \text{ on } \partial \Omega, \quad 1 \leq j \leq n - 1.
\]  (3.18c)

Claim. There exists \( \delta > 0 \) such that if \( \lambda_{1n} < \lambda < \lambda_{1n} + \delta \), then the smallest eigenvalue \( \mu_j^* \) of the linear problem

\[
L\varphi_j + \lambda (m_{jn} - m_{1n}\theta_{1n})\varphi_j = -\mu \varphi_j \text{ in } \Omega,
\]  (3.19)

is positive for every \( j \) such that \( 2 \leq j \leq n - 1 \).

To prove this assertion, observe first that \( \sigma_1 > \sigma_n \), so \( \theta_{1n} \to 1 \) uniformly as \( \lambda \to \lambda_{1n} \). Therefore, as \( \lambda \to \lambda_{1n} \), we obtain \( \mu_j^* \to \tilde{\mu}_j \) and \( \varphi_j \to \tilde{\varphi}_j \), where \( \tilde{\varphi}_j > 0 \) and

\[
L\tilde{\varphi}_j - \lambda_{1n}m_{1j}\tilde{\varphi}_j = -\tilde{\mu}_j \tilde{\varphi}_j \text{ in } \Omega,
\]  (3.20)

\[
B\tilde{\varphi}_j = 0.
\]  (3.20)

Let \( \mu_1 = \mu_1(\lambda) \) denote the principal eigenvalue of the problem

\[
L\Phi - \lambda m_{1j}\Phi = -\mu \Phi \text{ in } \Omega,
\]  (3.21)

Since \( \mu_1(0) = \mu_1(\lambda_{1j}) = 0 \) and \( \mu_1(\lambda) \) is a concave function of \( \lambda \), we have \( \mu_1(\lambda) > 0 \) for \( \lambda \in (0, \lambda_{1j}) \) (see [11] and [20, Section 3.4]). Since \( \lambda_{1n} \in (0, \lambda_{1j}) \), we get \( \tilde{\mu}_j = \mu_1(\lambda_{1n}) > 0 \). Hence, there exists \( \delta_j^* > 0 \) such that if \( \lambda \in (\lambda_{1n}, \lambda_{1n} + \delta_j^*) \), then \( \mu_j^*(\lambda) > 0 \). Setting \( \delta = \min_{2 \leq j \leq n - 1} \delta_j^* \) establishes our assertion.
To prove that \( p(1_{n}) \) is linearly stable, we argue by contradiction. If it is not, suppose that (3.18) has an eigenvalue \( \mu \) with \( \text{Re} \mu \leq 0 \). Since \( \mu^{j}_{1}(\lambda) > 0 \) for every \( j \) such that \( 2 \leq j \leq n - 1 \) and every \( \lambda \in (\lambda_{1n}, \lambda_{1n} + \delta) \), we see that \( \varphi_{j} \equiv 0 \) in (3.18) for every \( j \) such that \( 2 \leq j \leq n - 1 \). Consequently, \( \varphi_{1} \) satisfies

\[
L\varphi_{1} + \lambda m_{1n}(1 - 2\theta_{1n})\varphi_{1} = -\mu \varphi_{1} \quad \text{in } \Omega, \quad B\varphi_{1}|_{\partial\Omega} = 0. \tag{3.22}
\]

By [20, Theorem 2.1], all the eigenvalues of \( L + \lambda m_{1n}(1 - 2\theta_{1n}) \) have negative real parts. Together with \( \text{Re} \mu \leq 0 \), this implies that \( \varphi_{1} \equiv 0 \), and this contradiction shows that \( p(1_{n}) \) is linearly stable.

Finally, we demonstrate that for every \( l \) such that \( 2 \leq l \leq n - 1 \), the equilibrium \( p(1_{l}) \) is unstable if \( \lambda \) is close to but greater than \( \lambda_{1l} \). To this end, it suffices to show that the smallest eigenvalue \( \tilde{\mu}(\lambda) \) of the problem

\[
L\varphi - \lambda (m_{ln} + m_{1l}\theta_{1l})\varphi = -\mu \varphi \quad \text{in } \Omega, \quad B\varphi|_{\partial\Omega} = 0 \tag{3.23}
\]

is negative for \( \lambda \) close to but greater than \( \lambda_{1l} \). Then instability of \( p(1_{l}) \) follows as in the proof of part (b) of Theorem 1.6.

Since \( \sigma_{1} > \sigma_{l} \), therefore \( \theta_{1l} \rightarrow 1 \) uniformly as \( \lambda \rightarrow \lambda_{1l}^{+} \). Hence, \( \varphi \rightarrow \tilde{\varphi} \) and \( \hat{\mu} \rightarrow \tilde{\mu} \), where \( \tilde{\varphi} \) and \( \tilde{\mu} \) satisfy

\[
L\tilde{\varphi} - \lambda_{1l}m_{1n}\tilde{\varphi} = -\tilde{\mu}\tilde{\varphi} \quad \text{in } \Omega, \quad B\tilde{\varphi}|_{\partial\Omega} = 0. \tag{3.24}
\]

Let \( \tilde{\mu}_{1}(\lambda) \) denote the principal eigenvalue of the problem

\[
L\Phi - \lambda m_{1n}\Phi = -\mu \Phi \quad \text{in } \Omega, \quad B\Phi|_{\partial\Omega} = 0. \tag{3.25}
\]

Since \( \tilde{\mu}_{1}(0) = \tilde{\mu}_{1}(\lambda_{1n}) = 0 \) and \( \tilde{\mu}_{1} \) is a concave function of \( \lambda \), we have \( \tilde{\mu}_{1}(\lambda) < 0 \) for \( \lambda > \lambda_{1n} \) (see [11] and [20, Section 3.4]). Since \( \lambda_{1n} < \lambda_{1l} \), we obtain \( \tilde{\mu}_{1}(\lambda_{1l}) < 0 \). Therefore, for \( \lambda \) close to but greater than \( \lambda_{1l} \), the equilibrium \( p(1_{l}) \) is unstable. This completes the proof of Theorem 1.7. \( \Box \)

4. Three alleles

In this section, we examine (1.8) with \( n = 3 \), i.e., three alleles, under the assumption that migration is homogeneous and isotropic, i.e., (1.10) holds. Furthermore, we posit (1.21) and suppose that \( g(x) \) changes sign in \( \Omega \); in Theorem 1.9, so does \( h(x) \), i.e., (A2) holds. By (1.10), (1.21), and the fact that \( p_{3} = 1 - p_{1} - p_{2} \), the equilibria of (1.8) satisfy

\[
\nabla^{2}p_{1} + \lambda p_{1}[eg - h + (h - eg)p_{1} + hp_{2}] = 0 \quad \text{in } \Omega, \tag{4.1a}
\]
\[
\nabla^{2}p_{2} + \lambda p_{2}[-h + (h - eg)p_{1} + hp_{2}] = 0 \quad \text{in } \Omega, \tag{4.1b}
\]
\[
p_{1,v} = p_{2,v} = 0 \quad \text{on } \partial\Omega. \tag{4.1c}
\]

Define

\[
\Delta_{1} \equiv \{(p_{1}, p_{2}) : p_{1} \geq 0, p_{2} \geq 0, p_{1} + p_{2} \leq 1\}. \tag{4.2}
\]
First, we briefly illustrate the one-to-one correspondence between equilibria of (1.8) in $\Delta$ and solutions of (4.1) in $\Delta_1$. Of course, the vertex equilibria of (1.8) correspond to $(p_1, p_2) = (0, 0), (1, 0), \text{and} (0, 1)$. Now consider the edge equilibria. By (1.18) and (1.22), since $h(x)$ changes sign, the 23-edge equilibrium of (1.8) is given by $(0, 1 - \theta, \theta)$ and corresponds to $(p_1, p_2) = (0, 1 - \theta)$, which exists for every $\lambda > \lambda_{23} (= \lambda^*)$. It will be convenient to put $\zeta = 1 - \theta$.

From (1.18), (1.21), and (A2) we see that $\theta_{13}(x, \lambda, \epsilon)$ satisfies

$$
\nabla^2 \theta_{13} + \lambda(\epsilon g - h) \theta_{13}(1 - \theta_{13}) = 0 \quad \text{in} \, \Omega, \quad 0 < \theta_{13} < 1, \quad \theta_{13,\nu}|_{\partial\Omega} = 0, \quad (4.3)
$$

which exists for every $\lambda > \lambda_{13}$. The 13-edge equilibrium of (1.8) corresponds to the solution $(p_1, p_2) = (\theta_{13}, 0)$ of (4.1). Note that $\lambda_{13} \to \lambda^*$ as $\epsilon \to 0$.

Finally, (1.18) and (1.21) imply that $\theta_{12}$ satisfies

$$
\nabla^2 \theta_{12} + \lambda \epsilon g \theta_{12}(1 - \theta_{12}) = 0 \quad \text{in} \, \Omega, \quad 0 < \theta_{12} < 1, \quad \theta_{12,\nu}|_{\partial\Omega} = 0. \quad (4.4)
$$

Since $g(x)$ changes sign, there exists $\tilde{\lambda} \geq 0$ such that (4.4) has a unique solution for every $\lambda > \tilde{\lambda}/\epsilon$. Hence, the 12-edge equilibrium corresponds to $(p_1, p_2) = (\theta_{12}, 1 - \theta_{12})$.

In this section, we study the stability of the edge equilibria and the existence and stability of solutions of (4.1) in int $\Delta_1$. In Section 4.1, by investigating the stability of the three edge equilibria, we prove Proposition 1.8 and part (a) of Theorem 1.9. In Section 4.2, we use local bifurcation analysis of solutions of (4.1) to establish their existence in int $\Delta_1$ and prove part (b) of Theorem 1.9. We explore the stability of these internal solutions and prove part (c) of Theorem 1.9 in Section 4.3.

4.1. Stability of edge equilibria

In this subsection, we investigate the stability of all edge equilibria and establish Proposition 1.8 and part (a) of Theorem 1.9. For the 12-edge equilibrium, we present

**Proof of Proposition 1.8.** Recall that the 12-edge equilibrium is $(\theta_{12}, 1 - \theta_{12}, 0)$, where $\theta_{12}$ is the unique solution of (4.4). Since the 12-edge equilibrium is asymptotically stable with respect to perturbations within the 12-edge, we can investigate its stability by linearizing the equation satisfied by $p_3$. Thus, we find that its stability is determined by the sign of the principal eigenvalue $\mu_1^*$ of the problem

$$
\nabla^2 \varphi + \lambda(h - \epsilon g \theta_{12}) \varphi = -\mu \varphi \quad \text{in} \, \Omega, \quad \varphi|_{\partial\Omega} = 0. \quad (4.5)
$$

The variational characterization of $\mu_1^*$ is

$$
\frac{\mu_1^*}{\lambda} = \inf_{\varphi \neq 0, \varphi \in C^1(\Omega)} \frac{\int_{\Omega} \left[ \frac{1}{\lambda} |\nabla \varphi|^2 - (h - \epsilon g \theta_{12}) \varphi^2 \right] dx}{\int_{\Omega} \varphi^2 dx}. \quad (4.6)
$$

Choose a test function $\varphi$ as follows: $\varphi > 0, \varphi \neq 0$, supp $\varphi \subset \{ x \in \Omega : h(x) > 0 \}$. Hence, $\int_{\Omega} h \varphi^2 dx > 0$. Since $\int_{\Omega} g \, dx \neq 0$, we have $\tilde{\lambda} > 0$, and $\theta_{12}$ exists if and only if $\lambda > \tilde{\lambda}/\epsilon$. Then
for \( \lambda > \tilde{\lambda}/\epsilon \) we have

\[
\int_{\Omega} \left[ \frac{1}{\lambda} |\nabla \varphi|^2 - (h - \epsilon g\theta_{12})\varphi^2 \right] dx \leq -\int_{\Omega} h\varphi^2 dx + \epsilon \int_{\Omega} \left[ \frac{1}{\lambda} |\nabla \varphi|^2 + \|g\|_{\infty}\varphi^2 \right] dx < 0, \tag{4.7}
\]

provided that \( \epsilon \) is sufficiently small. This implies that, for sufficiently small \( \epsilon \), whenever the 12-edge equilibrium exists, it is unstable, which proves Proposition 1.8. \( \square \)

**Lemma 4.1.** Suppose that the assumptions in Theorem 1.9 hold. For every \( \Lambda > 0 \), there exists \( \epsilon_1 > 0 \) such that if \( \epsilon < \epsilon_1 \), there exist \( \{\lambda_i^\epsilon\}_{1 \leq i \leq l} \) such that \( \lim_{\epsilon \to 0} \lambda_i^\epsilon = \lambda_i \) and for \( 0 < \lambda \leq \Lambda \), the 23-edge equilibrium changes stability at exactly \( \lambda = \lambda_1^\epsilon, \ldots, \lambda_l^\epsilon \).

**Proof.** From (4.1a) we see that the stability of 23-edge equilibrium is determined by the sign of the principal eigenvalue \( \mu_1 = \mu_1(\epsilon, \lambda) \) of the problem

\[
\nabla^2 \varphi + \lambda (\epsilon g - h\theta) \varphi = -\mu \varphi \quad \text{in} \quad \Omega, \quad \varphi |_{\partial \Omega} = 0. \tag{4.8}
\]

Denote the eigenfunction corresponding to \( \mu_1 \) by \( \varphi_\epsilon \). We may assume that \( \varphi_\epsilon > 0, \|\varphi_\epsilon\|_2 = 1, \) and

\[
\nabla^2 \varphi_\epsilon + \lambda (\epsilon g - h\theta) \varphi_\epsilon = -\mu_1 \varphi_\epsilon \quad \text{in} \quad \Omega, \quad \varphi_\epsilon |_{\partial \Omega} = 0. \tag{4.9}
\]

Multiplying (4.9) by \( \zeta \) and integrating in \( \Omega \), we obtain

\[
\int_{\Omega} \zeta \left[ \nabla^2 \varphi_\epsilon - \lambda h\theta \varphi_\epsilon \right] dx + \lambda \epsilon \int_{\Omega} g\zeta \varphi_\epsilon dx = -\mu_1 \int_{\Omega} \zeta \varphi_\epsilon dx. \tag{4.10}
\]

By (1.22), the first integral on the left side of (4.10) vanishes:

\[
\int_{\Omega} \zeta \left[ \nabla^2 \varphi_\epsilon - \lambda h\theta \varphi_\epsilon \right] dx = -\int_{\Omega} \varphi_\epsilon \left[ \nabla^2 \theta + \lambda h\theta (1 - \theta) \right] dx = 0. \tag{4.11}
\]

Hence, from (4.10) and (4.11) we get

\[
\lambda \epsilon \int_{\Omega} g\zeta \varphi_\epsilon dx = -\mu_1 \int_{\Omega} \zeta \varphi_\epsilon dx. \tag{4.12}
\]

Therefore, the sign of \( \mu_1 \) is minus that of

\[
F(\epsilon, \lambda) \equiv \int_{\Omega} g(x)\zeta(x, \lambda)\varphi_\epsilon(x, \lambda) dx, \tag{4.13}
\]

where \( \epsilon \ll 1 \) and \( \lambda \in (0, \Lambda] \).
We first show that as \( \epsilon \to 0 \), \( F(\epsilon, \lambda) \to G(\lambda)/\|\zeta\|_2 \) uniformly for \( \lambda \leq \Lambda \). Since \( \zeta \) satisfies (4.8) with \( \epsilon = 0 \) and \( \mu = 0 \), we see that \( \mu_1 \to 0 \) as \( \epsilon \to 0 \). By standard elliptic regularity and the Sobolev embedding theorem, we have \( \varphi_\epsilon \to \bar{\varphi} \) in \( C^2(\overline{\Omega}) \), where \( \bar{\varphi} \) satisfies
\[
\nabla^2 \bar{\varphi} - \lambda h \theta \bar{\varphi} = 0, \quad \bar{\varphi} > 0 \quad \text{in } \Omega, \quad \|\bar{\varphi}\|_2 = 1, \quad \bar{\varphi}_\nu|_{\partial \Omega} = 0. \quad (4.14)
\]
Hence, \( \bar{\varphi} = \zeta/\|\zeta\|_2 \), and (1.24) and (4.13) imply that \( F(\epsilon, \lambda) \to G(\lambda)/\|\zeta(\cdot, \lambda)\|_2 \) uniformly for \( \lambda \) in any compact set. In particular, for every \( i \) such that \( 1 \leq i \leq l \), we have
\[
F(0, \lambda_i) = 0. \quad (4.15)
\]
Since \( F_\lambda(0, \lambda) = G'(\lambda)/\|\bar{\varphi}\|_2 + G(\lambda)(\|\zeta\|_2^2)^{-1} \lambda_\cdot \), we find
\[
F_\lambda(0, \lambda_i) = \frac{G'(\lambda_i)}{\|\zeta(\cdot, \lambda_i)\|_2} \neq 0 \quad (4.17)
\]
for every \( i \) such that \( 1 \leq i \leq l \). By the implicit function theorem and a compactness argument, for every \( \Lambda > 0 \), there exists \( \epsilon_1 > 0 \) such that if \( \epsilon < \epsilon_1 \), there exists \( \{\lambda^\epsilon_i\}_{1 \leq i \leq l} \) with \( \lim_{\epsilon \to 0} \lambda^\epsilon_i = \lambda_i \) such that (i) \( F(\epsilon, \lambda^\epsilon_i) = 0 \), (ii) \( F(\epsilon, \lambda) = 0 \) for \( \lambda \leq \Lambda \) if and only if \( \lambda = \lambda^\epsilon_i \) for some \( i \in \{1, \ldots, l\} \), and (iii) \( F_\lambda(\epsilon, \lambda^\epsilon_i) \neq 0 \). This implies that for every sufficiently small \( \epsilon \), \( F(\epsilon, \lambda) \) changes sign at exactly \( \lambda = \lambda^\epsilon_i \) for \( 1 \leq i \leq l \). From (4.12) and (4.13), we see that \( \mu_1 \) also changes sign at exactly \( \lambda = \lambda^\epsilon_i \), which completes the proof of Lemma 4.1.

For the stability of the 13-edge equilibrium \( (\theta_{13}, 0, 1 - \theta_{13}) \), we can similarly establish

**Lemma 4.2.** Suppose that the assumptions in Theorem 1.9 hold. For every \( \Lambda > 0 \), there exists \( \epsilon_2 > 0 \) such that if \( \epsilon < \epsilon_2 \), there exist \( \{\lambda_{i, \epsilon}\}_{1 \leq i \leq l} \) such that \( \lim_{\epsilon \to 0} \lambda_{i, \epsilon} = \lambda_i \) and for \( 0 < \lambda \leq \Lambda \), the 13-edge equilibrium changes stability at exactly \( \lambda = \lambda_{1, \epsilon}, \ldots, \lambda_{l, \epsilon} \).

Part (a) of Theorem 1.9 follows immediately from Lemmas 4.1 and 4.2.

### 4.2. Existence of an internal equilibrium

Here, we apply local bifurcation analysis of solutions of (4.1) to establish their existence in \( \text{int} \Delta_1 \) and prove part (b) of Theorem 1.9.

When \( \epsilon = 0 \), (4.1) reduces to
\[
\nabla^2 p_1 - \lambda h p_1 (1 - p_1 - p_2) = 0 \quad \text{in } \Omega, \quad (4.18a)
\]
\[
\nabla^2 p_2 - \lambda h p_2 (1 - p_1 - p_2) = 0 \quad \text{in } \Omega, \quad (4.18b)
\]
\[
p_{1, \nu} = p_{2, \nu} = 0 \quad \text{on } \partial \Omega. \quad (4.18c)
\]
Adding (4.18a) and (4.18b), we find that \( p_1 + p_2 \) satisfies
\[
\nabla^2 (p_1 + p_2) - \lambda h (p_1 + p_2)[1 - (p_1 + p_2)] = 0 \quad \text{in } \Omega, \quad (p_1 + p_2)_\nu|_{\partial \Omega} = 0. \quad (4.19)
\]
If \((p_1, p_2) \in \text{int}\Delta_1\), we have \(p_1 + p_2 = 1 - \theta = \zeta\), where \(\theta(x, \lambda)\) is the unique solution of (1.22). Together with (4.18), this implies that \((p_1, p_2) = (s\zeta, (1 - s)\zeta)\) for some constant \(s \in (0, 1)\). Hence, for every \(\lambda > \lambda^*\), the solutions of (4.18) in \text{int}\Delta_1 can be parametrized by the smooth curve \(\Gamma^{\lambda}\), where

\[
\Gamma^{\lambda} = \{(s\zeta, (1 - s)\zeta): s \in (0, 1)\}.
\]  

(4.20)

In this subsection, given any \(\tilde{\lambda} > 0\), we seek a triple \((p_1, p_2, \lambda)\) that satisfies (4.1) and is close to the curve \(\Gamma^{\tilde{\lambda}} \times \{\tilde{\lambda}\}\) for sufficiently small \(\epsilon > 0\). For \(r > d\), set

\[
X = \{(y, z) \in W^{2,r}(\Omega) \times W^{2,r}(\Omega): y_\nu|_{\partial\Omega} = z_\nu|_{\partial\Omega} = 0\},
\]  

(4.21a)

\[
Y = L^r(\Omega) \times L^r(\Omega),
\]  

(4.21b)

\[
X_1 = \text{Span}\{((\zeta, -\zeta)^T,\}
\]  

(4.21c)

\[
X_2 = \{(y, z) \in X: \int_{\Omega} (y - z)\zeta(x, \tilde{\lambda}) dx = 0\}.
\]  

(4.21d)

We suppress the dependence of \((p_1, p_2)\) and \((y, z)\) on \(x\). The main result of this subsection is

**Theorem 4.3.** There exist a neighborhood \(U\) of \(\Gamma^{\tilde{\lambda}} \times \{\tilde{\lambda}\} \subset X \times (0, \infty)\) and \(\epsilon_0 > 0\) such that the following holds.

(a) If \(G(\tilde{\lambda}) \neq 0\), then for \(\epsilon \in (0, \epsilon_0)\), the problem (4.1) has no solutions in \(U \cap \Delta_1\).

(b) If \(G(\tilde{\lambda}) = 0\) and \(G'(\tilde{\lambda}) \neq 0\), then for \(\epsilon \in (0, \epsilon_0)\), the set of solutions of (4.1) in \(U\) consists of the 13-edge and 23-edge equilibria and of the set \(\Gamma_\epsilon \cap U\), where \(\Gamma_\epsilon\) is a smooth curve in \(X \times (0, \infty)\) given by

\[
\Gamma_\epsilon = \{(p_1(\epsilon, s), p_2(\epsilon, s), \lambda(\epsilon, s)): -\epsilon_0 < s < 1 + \epsilon_0\}.
\]  

(4.22)

Here, \(p_1(\epsilon, s), p_2(\epsilon, s),\) and \(\lambda(\epsilon, s)\) are smooth functions in \([0, \epsilon_0) \times (-\epsilon_0, 1 + \epsilon_0)\) that satisfy

\[
(p_1(0, s), p_2(0, s), \lambda(0, s)) = (s\zeta(\cdot, \tilde{\lambda}), (1 - s)\zeta(\cdot, \tilde{\lambda}), \tilde{\lambda}),
\]  

(4.23a)

\[
(p_1(\epsilon, 0), p_2(\epsilon, 0)) = (0, \zeta(\cdot, \lambda(\epsilon, 0))),
\]  

(4.23b)

\[
(p_1(\epsilon, 1), p_2(\epsilon, 1)) = (\theta_{13}(\cdot, \lambda(\epsilon, 1), \epsilon), 0).
\]  

(4.23c)

In other words, a branch of internal solutions of (4.1) bifurcates from the 23-edge equilibrium at \(\lambda = \lambda(\epsilon, 0)\) and meets the 13-edge equilibrium at \(\lambda = \lambda(\epsilon, 1)\).

**Proof.** We seek solutions of (4.1) in the form

\[
(p_1, p_2) = (s\zeta(\cdot, \lambda), (1 - s)\zeta(\cdot, \lambda)) + (y, z).
\]  

(4.24)

where \(s \in R\), and \((y, z) \in X_2\) is in a neighborhood of \((0, 0)\).
For some small constant $\delta > 0$, define the map $H : X \times (-\delta, \delta) \times (-\delta, 1 + \delta) \times (\tilde{\lambda} - \delta, \tilde{\lambda} + \delta) \to Y$ by

$$H(y, z, \epsilon, s, \lambda) = \begin{pmatrix}
\frac{1}{\lambda} \nabla^2 y + h[s\zeta(y + z) - y(1 - \zeta - y - z)] \\
+ \epsilon g(s\zeta + y)(1 - s\zeta - y) \\
\frac{1}{\lambda} \nabla^2 z + h[(1 - s)\zeta(y + z) - (1 - \zeta)z + z(y + z)] \\
- \epsilon g(s\zeta + y)[(1 - s)\zeta + z]
\end{pmatrix}. \quad (4.25)$$

Substituting (4.24) into (4.1) and invoking (1.22) demonstrates that (4.24) with $(y, z) \in X_2$ satisfies (4.1) if and only if $H(y, z, \epsilon, s, \lambda) = (0, 0)^T$.

For every pair $(s, \lambda)$, define the linearized operator $K(s, \lambda) : X \to Y$ by

$$K(s, \lambda) = D_{y, z}H(0, 0, 0, s, \lambda). \quad (4.26)$$

From (4.25) we immediately infer that $K(s, \lambda)$ is given by

$$K \begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix}
\frac{1}{\lambda} \nabla^2 \varphi + sh(1 - \theta)(\varphi + \psi) - h\theta \varphi \\
\frac{1}{\lambda} \nabla^2 \psi + (1 - s)h(1 - \theta)(\varphi + \psi) - h\theta \psi
\end{pmatrix}. \quad (4.27)$$

If $K(s, \lambda)(\varphi, \psi)^T = (0, 0)^T$, then $\varphi + \psi$ satisfies

$$\frac{1}{\lambda} \nabla^2 (\varphi + \psi) + h(1 - 2\theta)(\varphi + \psi) = 0 \quad \text{in} \ \Omega, \quad (\varphi + \psi)_\nu|_{\partial\Omega} = 0. \quad (4.28)$$

By [20, Theorem 2.1], $\theta$ is asymptotically stable, so we have $\varphi + \psi \equiv 0$. Substituting this into the equation of $\varphi$, we obtain

$$\nabla^2 \varphi - \lambda h\theta \varphi = 0 \quad \text{in} \ \Omega, \quad \varphi_\nu|_{\partial\Omega} = 0. \quad (4.29)$$

Now (1.22) reveals that $\varphi$ is a scalar multiple of $1 - \theta = \zeta$, which implies that the kernel of $K$ is $X_1$.

Define the projection operator $P : Y \to X_1$ by

$$P \begin{pmatrix} y \\ z \end{pmatrix} = \frac{1}{J(\lambda)} \int_\Omega \zeta[(1 - s)y - sz] \, dx \begin{pmatrix} \zeta \\ -\zeta \end{pmatrix}, \quad (4.30a)$$

where

$$J(\lambda) = \int_\Omega \zeta^2 \, dx. \quad (4.30b)$$

Appealing to (4.30), (4.27), and (1.22) establishes that

$$P^2 = P, \quad PK = 0. \quad (4.31)$$

Following the Lyapunov–Schmidt procedure, we consider the system...
where \((y, z) \in X_2\). We choose \(\delta\) smaller if necessary such that for every \(s \in [0, 1]\) and every \(\lambda \in (\lambda - \delta, \lambda + \delta)\), we have \(\text{Ker}(K(s, \lambda)) \cap X_2 = \{0\}\), which implies that \(K(s, \lambda)\) is an isomorphism from \(X_2\) to \(\text{Range}(K(s, \lambda))\). Hence, we can apply the implicit function theorem to solve (4.32b) so that the following holds. There exist \(\delta^* > 0\), a neighborhood \(U_1\) of \((0, 0)\) in \(X_2\), and two smooth functions (in which we suppress \(x\)) \(y_1(\epsilon, s, \lambda)\) and \(z_1(\epsilon, s, \lambda): (-\delta^*, \delta^*) \times (-\delta^*, 1 + \delta^*) \times (\lambda - \delta^*, \lambda + \delta^*) \to X_2\) such that (i) \(y_1(0, s, \lambda) = z_1(0, s, \lambda) = 0\) and (ii) \((y, z, \epsilon, s, \lambda) \in U_1 \times (-\delta^*, \delta^*) \times (\lambda - \delta^*, \lambda + \delta^*)\) satisfies \(H(y, \epsilon, s, \lambda, \lambda) = 0\) if and only if \(y = y_1(\epsilon, s, \lambda), z = z_1(\epsilon, s, \lambda)\), and \((\epsilon, s, \lambda)\) solves

\[
P(s, \lambda)H(y_1(\epsilon, s, \lambda), z_1(\epsilon, s, \lambda), \epsilon, s, \lambda) = 0. \tag{4.33}
\]

By (4.30), there exists a smooth scalar function \(\xi(\epsilon, s, \lambda)\) such that

\[
\begin{pmatrix} \xi(\epsilon, s, \lambda) \\ -\xi(\epsilon, s, \lambda) \end{pmatrix} = P(s, \lambda)H\left(y_1(\epsilon, s, \lambda), z_1(\epsilon, s, \lambda), \epsilon, s, \lambda\right). \tag{4.34}
\]

Hence, in order to solve (4.33), it suffices to solve \(\xi(\epsilon, s, \lambda) = 0\). We first establish some properties of \(\xi(\epsilon, s, \lambda)\). Since \(y_1(0, s, \lambda) = z_1(0, s, \lambda) = 0\) and \(H(0, 0, 0, s, \lambda) \equiv 0\), we have

\[
\xi(0, s, \lambda) \equiv 0. \tag{4.35}
\]

Since \((0, \xi(x, \lambda))\) satisfies (4.1), therefore (4.24) yields \(y_1(\epsilon, 0, \lambda) = z_1(\epsilon, 0, \lambda) = 0\). Observing that \(H(0, 0, \epsilon, 0, \lambda) = 0\), we find

\[
\xi(\epsilon, 0, \lambda) \equiv 0. \tag{4.36}
\]

For the 13-edge equilibrium, there exist functions \(s^* = s^*(\epsilon, \lambda): (-\delta^*, \delta^*) \times (\lambda - \delta^*, \lambda + \delta^*) \to R^1\) and \((y_2(\epsilon, \lambda), z_2(\epsilon, \lambda)): (-\delta^*, \delta^*) \times (\lambda - \delta^*, \lambda + \delta^*) \to X_2\) (in which we suppress \(x\)) such that

\[
\begin{pmatrix} \theta_{13}(\epsilon, \lambda, 0) = (s^* \xi, (1 - s^*) \xi) + (y_2(\epsilon, \lambda), z_2(\epsilon, \lambda)) \end{pmatrix}, \tag{4.37}
\]

where \(s^*(0, \lambda) = 1, y_2(0, \lambda) = z_2(0, \lambda) = 0\), and \(H(y_2, z_2, \epsilon, s^*, \lambda) = 0\). Note that \(y_1(\epsilon, s^*(\epsilon, \lambda), \lambda) = y_2(\epsilon, \lambda)\) and \(z_1(\epsilon, s^*(\epsilon, \lambda), \lambda) = z_2(\epsilon, \lambda)\).

Therefore, we have

\[
\xi(s^*(\epsilon, \lambda), \lambda) \equiv 0. \tag{4.38}
\]

It follows from (4.35), (4.36), and (4.38) that \(\xi(\epsilon, s, \lambda)\) can be expressed as

\[
\xi(\epsilon, s, \lambda) = \epsilon s [s^*(\epsilon, \lambda) - s]\xi_1(\epsilon, s, \lambda), \tag{4.39}
\]
in which \( \xi_1 \) designates a smooth function. Thus, solving \( \xi(\epsilon, s, \lambda) = 0 \) reduces to solving \( \xi_1(\epsilon, s, \lambda) = 0 \).

Differentiating both sides of (4.34) with respect to \( \epsilon \) at \( \epsilon = 0 \) and recalling the fact that \( y_1(0, s, \lambda) = z_1(0, s, \lambda) = 0 \) lead to

\[
\xi_\epsilon(0, s, \lambda) \left( \begin{array}{c} \xi(\cdot, \lambda) \\ -\xi(\cdot, \lambda) \end{array} \right) = P(s, \lambda) K(s, \lambda) \left( \begin{array}{c} y_{1,\epsilon}(0, s, \lambda) \\ z_{1,\epsilon}(0, s, \lambda) \end{array} \right) + P(s, \lambda) H_\epsilon(0, 0, 0, s, \lambda) = P(s, \lambda) H_\epsilon(0, 0, 0, s, \lambda),
\]

(4.40)

where the second equality follows from (4.31). From (4.25) we at once obtain

\[
H_\epsilon(0, 0, 0, s, \lambda) = \left( \begin{array}{c} s g \xi(1 - s \xi) \\ -s(1 - s) g \xi^2 \end{array} \right).
\]

(4.41)

From (4.30), (4.41), and (1.24) we easily find

\[
P(s, \lambda) H_\epsilon(0, 0, 0, s, \lambda) = \frac{s(1 - s) G(\lambda)}{J(\lambda)} \left( \begin{array}{c} \xi \\ -\xi \end{array} \right),
\]

(4.42)

whence (4.40) gives

\[
\xi_\epsilon(0, s, \lambda) = s(1 - s) G(\lambda)/J(\lambda).
\]

(4.43)

Differentiating (4.39) at \( \epsilon = 0 \) and recalling that \( s^*(0, \lambda) = 1 \), we get

\[
\xi_\epsilon(0, s, \lambda) = s(1 - s) \xi_1(0, s, \lambda),
\]

(4.44)

whence (4.43) yields

\[
\xi_1(0, s, \lambda) = G(\lambda)/J(\lambda).
\]

(4.45)

If \( G(\tilde{\lambda}) \neq 0 \), choosing \( \delta^* \) smaller if necessary, we see that the equation \( \xi_1(\epsilon, s, \lambda) = 0 \) has no solution in the domain \((-\delta^*, \delta^*) \times (-\delta^*, 1 + \delta^*) \times (\tilde{\lambda} - \delta^*, \tilde{\lambda} + \delta^*)\). This proves part (a).

For the case \( G(\tilde{\lambda}) = 0 \), from (4.45) we have \( \xi_1(0, s, \tilde{\lambda}) = 0 \). If \( G'(\tilde{\lambda}) \neq 0 \), then (4.45) gives

\[
\xi_{1,\lambda}(0, s, \tilde{\lambda}) = G'(\tilde{\lambda})/J(\tilde{\lambda}) \neq 0.
\]

(4.46)

Therefore, by the implicit function theorem, there exists \( \delta^{**} > 0 \) such that all solutions of \( \xi_1(\epsilon, s, \lambda) = 0 \) in the neighborhood \((-\delta^{**}, \delta^{**}) \times (-\delta^{**}, 1 + \delta^{**}) \times (\tilde{\lambda} - \delta^{**}, \tilde{\lambda} + \delta^{**})\) are given by

\[
\lambda = \hat{\lambda}(\epsilon, s), \quad \epsilon \in (-\delta^{**}, \delta^{**}), \quad s \in (-\delta^{**}, 1 + \delta^{**}),
\]

(4.47)

where \( \hat{\lambda}(\epsilon, s) \) is a smooth function that satisfies \( \hat{\lambda}(0, s) = \tilde{\lambda} \). Hence, for sufficiently small \( \epsilon \), the solutions of \( \xi(\epsilon, s, \lambda) = 0 \) for \( \epsilon \in (-\delta^{**}, \delta^{**}), \ s \in (-\delta^{**}, 1 + \delta^{**}), \) and \( \lambda \in (\tilde{\lambda} - \delta^{**}, \tilde{\lambda} + \delta^{**}) \)
are given by the curves

\[ C_1 = \{(\epsilon, 0, \lambda)\}, \quad C_2 = \{(\epsilon, s^*(\epsilon, \lambda), \lambda)\}, \quad C_3 = \{(\epsilon, s, \hat{\lambda}(\epsilon, s))\}. \]  \hspace{1cm} (4.48)

Clearly, \( C_1 \) and \( C_3 \) intersect at the point \((\epsilon, 0, \hat{\lambda}(\epsilon, 0))\), which corresponds to the 23-edge equilibrium. The curves \( C_2 \) and \( C_3 \) intersect where \( s = s^*(\epsilon, \lambda) \) and \( \lambda = \hat{\lambda}(\epsilon, s) \), i.e.,

\[ s = s^*(\epsilon, \hat{\lambda}(\epsilon, s)). \]  \hspace{1cm} (4.49)

Since \( s^*(0, \lambda) \equiv 1 \), therefore, by the implicit function theorem, (4.49) has a unique solution \( s = \hat{s}(\epsilon) \) for every sufficiently small \( \epsilon \), and \( \hat{s}(\epsilon) \to 1 \) as \( \epsilon \to 0 \). Hence, the intersection of \( C_2 \) and \( C_3 \) is given by \((\epsilon, \hat{s}(\epsilon), \hat{\lambda}(\epsilon, \hat{s}(\epsilon)))\), and this point corresponds to the 13-edge equilibrium.

Set \( \hat{s} = \hat{s}(\epsilon) \) and define

\[ p_1(\epsilon, s) = \hat{s}\xi(\epsilon, \hat{s}) + y_1, \quad p_2(\epsilon, s) = (1 - \hat{s})\xi(\epsilon, \hat{s}) + z_1, \quad \lambda(\epsilon, s) = \hat{\lambda}(\epsilon, \hat{s}). \]  \hspace{1cm} (4.50)

Recalling the properties of \( \hat{\lambda}, \hat{s}, y_1, \) and \( z_1 \) and using (4.37), we see that (4.50) implies (4.23). This establishes part (b) and completes the proof of Theorem 4.3. \( \square \)

**Proof of part (b) of Theorem 1.9.** By part (b) of Theorem 4.3, near every \( \lambda_i \), since \( G(\lambda_i) = 0 \) and \( G'(\lambda_i) \neq 0 \), a branch of internal solutions of (4.1) bifurcates from the 23-edge equilibrium at \( \lambda = \lambda(\epsilon, 0) \) and meets the 13-edge equilibrium at \( \lambda = \lambda(\epsilon, 1) \). In particular, this implies that the 23-edge equilibrium is degenerate at \( \lambda = \lambda(\epsilon, 0) \). By Lemma 4.1, close to \( \lambda = \lambda_i \), the 23-edge equilibrium is degenerate only at \( \lambda = \lambda_i^\epsilon \). Hence, the only possibility is that \( \lambda(\epsilon, 0) = \lambda_i^\epsilon \).

Similarly, \( \lambda(\epsilon, 1) = \lambda_i \). By Theorem 4.3, the problem (4.1) has an internal solution for every \( \lambda \in (\min(\lambda(\epsilon, 0), \lambda(\epsilon, 1)), \max(\lambda(\epsilon, 0), \lambda(\epsilon, 1))) \). This proves part (b) of Theorem 1.9. \( \square \)

### 4.3. Stability of internal equilibria

In this subsection, we investigate the stability of the solutions \((p_1, p_2)\) of (4.1) on \( \Gamma_\epsilon \cap U \) for sufficiently small \( \epsilon \) and \( s \in (0, 1) \) and prove part (c) of Theorem 1.9. To this end, it suffices to consider the linear eigenvalue problem

\[ \nabla^2 \varphi_1 + \lambda\left[ \epsilon g - h + 2(h - \epsilon g)p_1 + hp_2 \right] \varphi_1 + \lambda h p_1 \varphi_2 = \mu \varphi_1 \quad \text{in } \Omega, \]  \hspace{1cm} (4.51a)

\[ \nabla^2 \varphi_2 + \lambda(h - \epsilon g)p_2 \varphi_1 + \lambda\left[ -h + (h - \epsilon g)p_1 + 2hp_2 \right] \varphi_2 = \mu \varphi_2 \quad \text{in } \Omega, \]  \hspace{1cm} (4.51b)

\[ \varphi_{1,v}|_{\partial \Omega} = \varphi_{2,v}|_{\partial \Omega} = 0. \]  \hspace{1cm} (4.51c)

As we saw below (4.19), when \( \epsilon = 0 \) we have \((p_1, p_2) = (s \xi, (1 - s) \xi)\) for some \( s \in (0, 1) \), so (4.51) reduces to

\[ \nabla^2 \varphi_1 + \lambda h[-1 + (1 + s)\xi] \varphi_1 + \lambda h s \xi \varphi_2 = \mu \varphi_1 \quad \text{in } \Omega, \]  \hspace{1cm} (4.52a)

\[ \nabla^2 \varphi_2 + \lambda h(1 - s)\xi \varphi_1 + \lambda h[-1 + (2 - s)\xi] \varphi_2 = \mu \varphi_2 \quad \text{in } \Omega, \]  \hspace{1cm} (4.52b)

\[ \varphi_{1,v}|_{\partial \Omega} = \varphi_{2,v}|_{\partial \Omega} = 0. \]  \hspace{1cm} (4.52c)
Adding (4.52a) and (4.52b), we see that \( \varphi_1 + \varphi_2 \) satisfies
\[
\nabla^2 (\varphi_1 + \varphi_2) + \lambda h (1 - 2\theta) (\varphi_1 + \varphi_2) = \mu (\varphi_1 + \varphi_2) \quad \text{in} \quad \Omega, \quad (\varphi_1 + \varphi_2)_\nu|_{\partial \Omega} = 0. \tag{4.53}
\]

By [20, Theorem 2.1], we see that either \( \varphi_1 + \varphi_2 \equiv 0 \) or \( \mu \) is real and negative; i.e., either \( \varphi_1 + \varphi_2 \equiv 0 \) or every eigenvalue of (4.52) is real and negative. When \( \varphi_1 + \varphi_2 \equiv 0 \), from (4.52a) we obtain
\[
\nabla^2 \varphi_1 - \lambda h \theta \varphi_1 = \mu \varphi_1 \quad \text{in} \quad \Omega, \quad \varphi_1, \nu|_{\partial \Omega} = 0. \tag{4.54}
\]

Now, (1.22) reveals that 0 is the largest eigenvalue of (4.54), and that the corresponding eigenfunction can be chosen as \( 1 - \theta \). Hence, 0 is a simple eigenvalue of the reduced system (4.52), with corresponding eigenfunction \( (\zeta, -\zeta) \) (a fact we shall use later), and every other eigenvalue is real and negative. Therefore, by spectral perturbation theory [18], for sufficiently small \( \epsilon \), the problem (4.51) has a unique eigenvalue \( \mu_0(\epsilon, s) \) such that \( \lim_{\epsilon \to 0} \mu_0(\epsilon, s) = 0 \), and all the other eigenvalues of (4.51) have negative real parts that are uniformly bounded away from zero for every \( s \in [0, 1] \) and every small \( \epsilon \). Thus, to determine the stability of solutions \( (p_1, p_2) \) of (4.1) on \( \Gamma_\epsilon \cap \text{int} \Delta_1 \) for small \( \epsilon \), it suffices to find the sign of \( \mu_0(\epsilon, s) \).

Theorem 4.3 informs us that it suffices to consider those \( \tilde{\lambda} \) that satisfy \( G(\tilde{\lambda}) = 0 \). Throughout the rest of this subsection, we shall assume that \( G(\tilde{\lambda}) = 0 \), and for the sake of simplicity, we abbreviate \( \theta(x, \tilde{\lambda}) \) as \( \theta \). Set \( H = L^2(\Omega) \). Denote the linear subspace of \( H \) spanned by \( 1 - \theta = \zeta \) by \( \Theta \) and let \( \Theta^\perp \) be its orthogonal complement. Define
\[
\mathcal{L}_1 = \nabla^2 + \tilde{\lambda} h (1 - 2\theta), \tag{4.55a}
\]
\[
\mathcal{L}_2 = \nabla^2 - \tilde{\lambda} h \theta. \tag{4.55b}
\]

The stability of \( \theta \) implies that the largest eigenvalue of \( \mathcal{L}_1 \) is negative. Hence, \( \mathcal{L}_1 \) is invertible, and we denote its inverse by \( \mathcal{L}_1^{-1} \). By contrast, as we showed below (4.54), \( \mathcal{L}_2 \) is not invertible, and \( \ker(\mathcal{L}_2) = \Theta \). We define \( \mathcal{L}_2^{-1} \) on \( \Theta^\perp \) by setting \( \mathcal{L}_2^{-1} \varphi = \psi \) if and only if \( \mathcal{L}_2 \psi = \varphi \) and \( \varphi, \psi \in \Theta^\perp \). The first main result of this subsection is

**Proposition 4.4.** For \( s \in (0, 1) \) and \( 0 < \epsilon \ll 1 \), the eigenvalue \( \mu_0(\epsilon, s) \) is given by
\[
\mu_0(\epsilon, s) = \frac{2s(1-s)\tilde{\lambda}^2 \epsilon^2}{J(\tilde{\lambda})} \left\{ \int_\Omega g \xi \left[ \mathcal{L}_2^{-1}(g\xi) - \mathcal{L}_1^{-1}(g\theta \xi) \right] dx + C_1(\epsilon, s) \epsilon \right\}, \tag{4.56}
\]

where \( J \) is defined in (4.30b) and \( C_1(\epsilon, s) \) denotes some constant that is uniformly bounded for \( s \in (0, 1) \) and \( |\epsilon| \ll 1 \).

We first establish two simple but useful lemmas.

**Lemma 4.5.** Every solution \( (p_1, p_2) \) of (4.1) satisfies
\[
\int_\Omega gp_1 p_2 dx = 0. \tag{4.57}
\]
**Proof.** Multiplying (4.1a) by \( p_2 \), (4.1b) by \( p_1 \), and subtracting, we find

\[ p_2 \nabla^2 p_1 - p_1 \nabla^2 p_2 + \lambda \epsilon g p_1 p_2 = 0. \tag{4.58} \]

Integrating (4.58) in \( \Omega \) and invoking (4.1c) yields (4.57). \( \square \)

**Lemma 4.6.** The eigenvalue \( \mu_0(\epsilon, s) \) is given by

\[ \mu_0(\epsilon, s) = \frac{\lambda \epsilon \int \Omega g(\varphi_1 p_2 + \varphi_2 p_1) \, dx}{\int \Omega (\varphi_1 p_2 - \varphi_2 p_1) \, dx}. \tag{4.59} \]

**Proof.** Multiplying (4.51a) by \( p_2 \), (4.51b) by \( p_1 \), and subtracting, we get

\[ \mu_0(\epsilon, s)(\varphi_1 p_2 - \varphi_2 p_1) = (p_2 \nabla^2 \varphi_1 - p_1 \nabla^2 \varphi_2) + \lambda p_2 \varphi_1 [\epsilon g - h + (h - \epsilon g)p_1 + hp_2] \]
\[ - \lambda p_1 \varphi_2 [-h + (h - \epsilon g)p_1 + hp_2]. \tag{4.60} \]

Integrating (4.60) in \( \Omega \) and appealing to (4.1), we obtain

\[ \mu_0(\epsilon, s) \int \Omega (\varphi_1 p_2 - \varphi_2 p_1) \, dx = \int \Omega \{ \nabla^2 p_2 + \lambda p_2 [-h + (h - \epsilon g)p_1 + hp_2] + \lambda \epsilon g p_2 \} \, dx \]
\[ - \int \Omega \{ \nabla^2 p_1 + \lambda p_1 [\epsilon g - h + (h - \epsilon g)p_1 + hp_2] - \lambda \epsilon g p_1 \} \, dx \]
\[ = \lambda \epsilon \int \Omega g(\varphi_1 p_2 + \varphi_2 p_1) \, dx. \tag{4.61} \]

This completes the proof of Lemma 4.6. \( \square \)

By Theorem 4.3, \( p_1 \), \( p_2 \), and \( \lambda \) can be expanded as

\[ p_1 = s \zeta + \epsilon p_1^* + O(\epsilon^2), \tag{4.62a} \]
\[ p_2 = (1 - s) \zeta + \epsilon p_2^* + O(\epsilon^2), \tag{4.62b} \]
\[ \lambda = \tilde{\lambda} + \epsilon \lambda_0^* + O(\epsilon^2), \tag{4.62c} \]

in which the functions \( p_1^* = p_1^*(x, s) \), \( p_2^* = p_2^*(x, s) \), and \( \lambda_0^* = \lambda_0^*(s) \) are to be determined. Set

\[ A(x, s) = \lambda_0^* \mathcal{L}_1^{-1}(h \theta \zeta), \tag{4.63a} \]
\[ B(x) = \tilde{\lambda} \mathcal{L}_1^{-1}(g \theta \zeta), \tag{4.63b} \]
\[ C(x) = \tilde{\lambda} \mathcal{L}_2^{-1}(g \zeta). \tag{4.63c} \]
Lemma 4.7. For every \( s \in (0, 1) \),

\[
    p_1^* = s \left[ A - sB - (1 - s)C \right], \quad (4.64a)
\]
\[
    p_2^* = (1 - s)\left[ A - sB + sC \right]. \quad (4.64b)
\]

**Proof.** Substituting (4.62) into (4.1) leads to

\[
    \nabla^2 p_1^* + \tilde{\lambda}\left[-h\theta p_1^* + sh\zeta(p_1^* + p_2^*) + sg\zeta(1 - s\zeta)\right] - \lambda_0^*sh\theta\zeta = 0, \quad (4.65a)
\]
\[
    \nabla^2 p_2^* + \tilde{\lambda}\left[-h\theta p_2^* + (1 - s)h\zeta(p_1^* + p_2^*) - s(1 - s)g\zeta^2\right] - \lambda_0^*(1 - s)h\theta\zeta = 0. \quad (4.65b)
\]

Adding (4.65a) and (4.65b), we have

\[
    \nabla^2 (p_1^* + p_2^*) + \tilde{\lambda}h(1 - 2\theta)(p_1^* + p_2^*) + \tilde{\lambda}sg\theta\zeta - \lambda_0^*h\theta\zeta = 0. \quad (4.66)
\]

From (4.66), (4.55a), and (4.63a, b) we obtain

\[
    p_1^* + p_2^* = A - sB. \quad (4.67)
\]

Substituting (4.67) into (4.65a) and using (4.55b) yield

\[
    \mathcal{L}_2 p_1^* + \tilde{\lambda} s\zeta \left[h(A - sB) + g(1 - s\zeta)\right] - \lambda_0^*sh\theta\zeta = 0. \quad (4.68)
\]

Now, (4.63a), (4.63b), and (4.55) inform us that \( A \) and \( B \) satisfy

\[
    \tilde{\lambda}h\zeta A = -\mathcal{L}_2 A + \lambda_0^*h\theta\zeta, \quad (4.69a)
\]
\[
    \tilde{\lambda}h\zeta B = -\mathcal{L}_2 B + \tilde{\lambda}g\theta\zeta. \quad (4.69b)
\]

Inserting (4.69) into (4.68) gives

\[
    \mathcal{L}_2[p_1^* - s(A - sB)] + \tilde{\lambda}s(1 - s)g\zeta = 0; \quad (4.70)
\]

by (4.63c), this is equivalent to (4.64a). Finally, substituting (4.64a) into (4.67) gives (4.64b). \( \square \)

Next, we expand \( \varphi_1 \) and \( \varphi_2 \). Below (4.54), we showed that when \( \epsilon = 0 \), we can choose \((\varphi_1, \varphi_2) = (\zeta, -\zeta)\). Hence, \( \varphi_1 \) and \( \varphi_2 \) can be expressed as

\[
    \varphi_1 = \zeta + \epsilon\varphi_1^* + O(\epsilon^2), \quad (4.71a)
\]
\[
    \varphi_2 = -\zeta + \epsilon\varphi_2^* + O(\epsilon^2). \quad (4.71b)
\]

To find \( \varphi_1^* \) and \( \varphi_2^* \), we first establish
Lemma 4.8. For sufficiently small $\epsilon$ and every $s \in (0, 1),$

$$\mu_0(\epsilon, s) = \frac{\tilde{\lambda} \epsilon^2}{J(\tilde{\lambda})} \int \Omega g\xi [p_2^* - p_1^* + (1 - s)p_1^* + s\varphi_2^*] \, dx + O(\epsilon^3). \quad (4.72)$$

Proof. By (4.62) and (4.71) we get

$$\int_\Omega (\varphi_1 p_2 - \varphi_2 p_1) \, dx = J + O(\epsilon). \quad (4.73)$$

From (4.62), (4.71), (1.24), and the fact that $G(\tilde{\lambda}) = 0$, we directly obtain

$$\int_\Omega g(\varphi_1 p_2 + \varphi_2 p_1) \, dx = \epsilon \int_\Omega g\xi [p_2^* - p_1^* + (1 - s)p_1^* + s\varphi_2^*] \, dx + O(\epsilon^2). \quad (4.74)$$

Lemma 4.6, (4.73), and (4.74) immediately prove Lemma 4.8. \qed

For $\varphi_1^*$ and $\varphi_2^*$ we have

Lemma 4.9. For every $s \in (0, 1),$

$$\varphi_1^* = A - 2sB + (2s - 1)C, \quad (4.75a)$$
$$\varphi_2^* = -A + (2s - 1)(B - C). \quad (4.75b)$$

Proof. By Lemma 4.8, we have $\mu_0(\epsilon, s) = O(\epsilon^2)$. Therefore, substituting (4.62) and (4.71) into (4.51), we find

$$\nabla^2 \varphi_1^* + \tilde{\lambda} \left[ h\xi (s\xi - \theta) \varphi_1^* + s\xi \varphi_2^* + \xi (p_1^* + p_2^*) \right] + g\xi (1 - 2s\xi) - \lambda_0^* h\theta \xi = 0, \quad (4.76a)$$
$$\nabla^2 \varphi_2^* + \tilde{\lambda} \left[ h\xi (1 - s) \varphi_1^* + ((1 - s)\xi - \theta) \varphi_2^* - \xi (p_1^* + p_2^*) \right] + (2s - 1)g\xi^2 + \lambda_0^* h\theta \xi = 0. \quad (4.76b)$$

Adding (4.76a) and (4.76b) yields

$$\nabla^2 (\varphi_1^* + \varphi_2^*) + \tilde{\lambda} (1 - 2\theta) (\varphi_1^* + \varphi_2^*) + \tilde{\lambda} g\theta \xi = 0. \quad (4.77)$$

From (4.77), (4.63b), and (4.55a) we get $\varphi_1^* + \varphi_2^* = -B$. Substituting this, (4.67), and (4.55b) into (4.76a), we derive

$$L_2 \varphi_1^* + \tilde{\lambda} \xi [h(A - 2sB) + g(1 - 2s\xi)] - \lambda_0^* h\theta \xi = 0. \quad (4.78)$$

Inserting (4.69) into (4.78) gives

$$L_2 (\varphi_1^* - A + 2sB) + (1 - 2s)\tilde{\lambda} g\xi = 0. \quad (4.79)$$

By (4.63c), this implies (4.75a); since $\varphi_2^* = -\varphi_1^* - B$, therefore (4.75a) yields (4.75b). \qed
The following result illustrates the connection among the functions $A$, $B$, and $C$.

**Lemma 4.10.** For every $s \in (0, 1)$,
\[
\int_{\Omega} g \xi A \, dx = \int_{\Omega} g \xi \left[ sB - \left( s - \frac{1}{2} \right) C \right] \, dx. \tag{4.80}
\]

**Proof.** Substituting (4.62) into (4.57) and recalling that $G(\tilde{\lambda}) = 0$, we find
\[
\int_{\Omega} g \xi \left[ (1 - s)p_1^* + sp_2^* \right] \, dx = 0. \tag{4.81}
\]
Inserting (4.64) into (4.81) leads to
\[
\int_{\Omega} g \xi \left[ A - sB + \left( s - \frac{1}{2} \right) C \right] \, dx = 0, \tag{4.82}
\]
which implies (4.80). \hfill \Box

**Proof of Proposition 4.4.** Employing (4.64) and (4.75) and then (4.80), we infer
\[
\int_{\Omega} g \xi \left[ p_2^* - p_1^* + (1 - s)\varphi_1^* + s\varphi_2^* \right] \, dx = 2s(1 - s)\int_{\Omega} g \xi (C - B) \, dx. \tag{4.83}
\]
Substituting (4.83) and (4.63) into (4.72) proves Proposition 4.4. \hfill \Box

By Proposition 4.4 and the self-adjointness of $L_1^{-1}$, the stability of the solutions of (4.1) is determined by the sign of
\[
I(g) = \int_{\Omega} g \xi \left( L_2^{-1} - \theta L_1^{-1} \right)(g \xi) \, dx. \tag{4.84}
\]
Recalling (1.24), we conclude that part (c) of Theorem 1.9 follows from

**Proposition 4.11.** There exist functions $g_1$ and $g_2$ such that $I(g_1) > 0$, $I(g_2) < 0$, and
\[
\int_{\Omega} g_1 \xi^2 \, dx = \int_{\Omega} g_2 \xi^2 \, dx = 0.
\]

**Proof.** Define the operator $T$ by $T = L_2^{-1} - \theta L_1^{-1}$.

**Claim.** The kernel of $T$ is
\[
\text{Ker}(T) = \text{Span} \left\{ L_2 \left( \frac{\theta^2}{\xi} \right) \right\} = \text{Span} \left\{ L_1 \left( \frac{\theta}{\xi} \right) \right\}. \tag{4.85}
\]
To establish our assertion, let $\varphi$ satisfy $T \varphi = 0$. Set $\psi = \mathcal{L}_2^{-1} \varphi = \theta \mathcal{L}_1^{-1} \varphi$. Then (4.55) shows that $\psi$ satisfies

$$
\nabla^2 \psi - \tilde{\lambda} h \theta \psi = \varphi, \quad (4.86a)
$$

$$
\nabla^2 \frac{\psi}{\theta} + \tilde{\lambda} h (1 - 2\theta) \frac{\psi}{\theta} = \varphi. \quad (4.86b)
$$

Subtracting (4.86a) from (4.86b), we find

$$
\nabla^2 \chi + \tilde{\lambda} h \xi \chi = 0 \quad \text{in } \Omega, \quad \chi \nu|_{\partial \Omega} = 0, \quad (4.87)
$$

where $\chi = \psi/\theta - \psi = \xi \psi/\theta$. Recalling (1.22), we see that $\theta$ solves the same problem as $\chi$. Therefore, $\chi$ is a scalar multiple of $\theta$, i.e., $\psi$ is a multiple of $\theta^2/\xi$, which implies that $\varphi$ is a scalar multiple of $\mathcal{L}_2(\theta^2/\xi) = \mathcal{L}_1(\theta/\xi)$. This proves (4.85).

Next, we show that $T^\dagger(\mathcal{L}_2(\theta^2/\xi))$ and $\xi$ are linearly independent, where $T^\dagger$ signifies the adjoint of $T$. To this end, we argue by contradiction. Clearly, $T^\dagger = \mathcal{L}_2^{-1} - \mathcal{L}_1^{-1} \theta$. Suppose that there exists a constant $c_1 \neq 0$ such that

$$
T^\dagger \left( \mathcal{L}_2 \left( \frac{\theta^2}{\xi} \right) \right) = c_1 \xi. \quad (4.88)
$$

Since (1.22) reveals that $\mathcal{L}_2 \xi = 0$, we have

$$
\mathcal{L}_2^{-1} \mathcal{L}_2 \left( \frac{\theta^2}{\xi} \right) = \frac{\theta^2}{\xi} - c_2 \xi \quad (4.89)
$$

for some constant $c_2$. Hence, we see that (4.88) is equivalent to

$$
\frac{\theta^2}{\xi} - \mathcal{L}_1^{-1} \left[ \theta \mathcal{L}_2 \left( \frac{\theta^2}{\xi} \right) \right] = c_3 \xi, \quad (4.90)
$$

where $c_3 = c_1 + c_2$. Applying $\mathcal{L}_1$ to (4.90) and recalling that $\mathcal{L}_2(\theta^2/\xi) = \mathcal{L}_1(\theta/\xi)$, we obtain

$$
\mathcal{L}_1 \left( \frac{\theta^2}{\xi} \right) - \theta \mathcal{L}_1 \left( \frac{\theta}{\xi} \right) = c_3 \mathcal{L}_1 \xi. \quad (4.91)
$$

By (4.55) and direct calculation we get

$$
\mathcal{L}_1 \left( \frac{\theta^2}{\xi} \right) - \theta \mathcal{L}_1 \left( \frac{\theta}{\xi} \right) = \nabla^2 \left( \frac{\theta}{\xi} \right) - \theta \nabla^2 \left( \frac{\theta}{\xi} \right) = \frac{\theta}{\xi} \nabla^2 \theta + 2(\nabla \theta) \cdot \nabla \left( \frac{\theta}{\xi} \right) = \frac{\xi}{\theta} \nabla \cdot \left( \frac{\theta^2}{\xi^2} \nabla \theta \right). \quad (4.92)
$$

Comparing (4.92) with (4.91) yields

$$
\nabla \cdot \left( \frac{\theta^2}{\xi^2} \nabla \theta \right) = \frac{c_3 \theta}{\xi} \mathcal{L}_1 \xi. \quad (4.93)
$$
From (1.22) and (4.55a) we infer
\[ \mathcal{L}_1 \zeta = \tilde{\lambda} h \zeta^2 = -\frac{\xi}{\theta} \nabla^2 \theta. \]  
(4.94)

Substituting (4.94) into (4.93), we deduce
\[ \nabla \cdot \left[ \left( \frac{\theta^2}{\zeta^2} + c_3 \right) \nabla \theta \right] = 0. \]  
(4.95)

Multiplying (4.95) by \( F(\theta) \), where \( F \) satisfies \( F'(\theta) = \frac{\theta^2}{\zeta^2} + c_3 \), and integrating in \( \Omega \), we find
\[ \int_\Omega \left( \frac{\theta^2}{\zeta^2} + c_3 \right)^2 |\nabla \theta|^2 \, dx = 0. \]  
(4.96)

Therefore, \( \theta \) must be equal to some positive constant, which contradicts (1.22).

We are now ready to complete the proof of Proposition 4.11. Since \( \zeta \) and \( T^\dagger(\mathcal{L}_2(\theta^2/\zeta)) \) are linearly independent, we can find \( \tilde{\phi} \) such that
\[ \int_\Omega \tilde{\phi} \zeta \, dx = 0, \quad \int_\Omega \tilde{\phi} T^\dagger \left( \mathcal{L}_2 \left( \frac{\theta^2}{\zeta} \right) \right) \, dx > 0. \]  
(4.97)

Let \( \delta \) satisfy \( 0 < |\delta| \ll 1 \) and set
\[ g^\delta = \frac{1}{\zeta} \left[ \mathcal{L}_2 \left( \frac{\theta^2}{\zeta} \right) + \delta \tilde{\phi} \right]. \]  
(4.98)

From the first equation in (4.97) and the facts that \( \mathcal{L}_2^\dagger = \mathcal{L}_2 \) and \( \mathcal{L}_2 \zeta = 0 \) we see that \( \int_\Omega g^\delta \zeta^2 \, dx = 0 \) for every \( \delta \). Using (4.84), (4.98), and (4.85) gives
\[ I(g^\delta) = \int_\Omega \left[ \mathcal{L}_2 \left( \frac{\theta^2}{\zeta} \right) + \delta \tilde{\phi} \right] T \left[ \mathcal{L}_2 \left( \frac{\theta^2}{\zeta} \right) + \delta \tilde{\phi} \right] \, dx \]
\[ = \delta \int_\Omega \left[ \mathcal{L}_2 \left( \frac{\theta^2}{\zeta} \right) + \delta \tilde{\phi} \right] T \tilde{\phi} \, dx \]
\[ = \delta \left[ \int_\Omega \tilde{\phi} T^\dagger \mathcal{L}_2 \left( \frac{\theta^2}{\zeta} \right) \, dx + O(\delta) \right]. \]  
(4.99)

Hence, \( I(g^\delta) > 0 \) for \( 0 < \delta \ll 1 \), and \( I(g^\delta) < 0 \) for \( -1 \ll \delta < 0 \). This completes the proof of Proposition 4.11. \( \Box \)

**Remark 4.12.** Recall the definition of \( I(g) \) in (4.84) and, in addition to the assumptions in Theorem 1.9, suppose that \( I(g) \neq 0 \). Then we can further show that for \( 0 < \lambda < \Lambda \), the problem (1.8) has a unique internal equilibrium if \( \lambda \in \bigcup_{i=1}^l (\min(\lambda_i^\epsilon, \lambda_i), \max(\lambda_i^\epsilon, \lambda_i)) \), and has no
internal equilibrium otherwise. Moreover, it is asymptotically stable if $I(g) < 0$, and is unstable if $I(g) > 0$.

5. Nonmonotonicity of the conditions for protection or loss

In this section, we demonstrate the nonmonotonicity of the conditions for protection or loss of an allele by establishing pertinent stability properties of the edge equilibria. We assume throughout that (1.10), (1.21), and (A2) hold. Our main goal is to establish Theorems 1.10 and 1.12 by constructing suitable functions $g(x)$ and $h(x)$. We first present

Proof of Theorem 1.10. We choose functions $g$ and $h$ that satisfy

\[
\begin{align*}
\int_{\Omega} g(x) \, dx < 0, & \quad \int_{\Omega} h(x) \, dx < 0, \quad (5.1a) \\
\{x \in \Omega: g(x) < 0\} \cap \{x \in \Omega: h(x) < 0\} \neq \emptyset, & \quad (5.1b) \\
\int_{\{x \in \Omega: h(x) \leq 0\}} g(x) \, dx > 0. & \quad (5.1c)
\end{align*}
\]

By (1.11), (1.21), and (5.1a), we have $\sigma_2 > \max(\sigma_1, \sigma_3)$, and it follows from (1.20), (1.21), and (5.1b) that $s_2(\tilde{x}) > \tilde{s}^{(13)}(\tilde{x})$ for some $\tilde{x} \in \Omega$. Also, (5.1a) and (5.1c) imply that both $g$ and $h$ change sign, i.e., (A2) holds.

Under assumption (5.1), we study the stability of the 13-edge equilibrium, i.e., $(\theta_{13}, 0, 0)$, where $\theta_{13}$ is the unique solution of (4.3). By (5.1a) we see that there exists a positive constant $\lambda^*_\epsilon$ such that $\theta_{13}$ exists if and only if $\lambda > \lambda^*_\epsilon$. Furthermore, (4.3), (1.22), and (5.1a) inform us that $\lambda^*_\epsilon \to \lambda^* > 0$ and $\theta_{13} \to 1 - \theta = \zeta$ as $\epsilon \to 0$.

The stability of the 13-edge equilibrium is determined by the sign of the principal eigenvalue $\mu_1$ of the linear problem

\[
\nabla^2 \varphi - \lambda \left[ \epsilon g \theta_{13} + h(1 - \theta_{13}) \right] \varphi = -\mu \varphi \quad \text{in} \quad \Omega, \quad \varphi|_{\partial \Omega} = 0.
\]

Set $E = \{\phi \in W^{1,2}: \int_{\Omega} g \theta_{13}^2 \phi^2 \, dx < 0\}$ and define

\[
\tilde{\mu}_\epsilon = \inf_{\phi \in E} \frac{\int_{\Omega} \theta_{13}^2 |\nabla \phi|^2 \, dx}{\int_{\Omega} g \theta_{13}^2 \phi^2 \, dx}.
\]

Claim. If $\tilde{\mu}_\epsilon > \lambda \epsilon$, then $\mu_1 > 0$.

To prove this assertion, we argue by contradiction. Suppose that $\mu_1 \leq 0$. Let $\varphi_1$ denote the positive eigenfunction corresponding to $\mu_1$ with $\sup \varphi_1 = 1$, and set $\varphi_1 = \theta_{13} \psi$. From (5.2) and (4.3) we easily find

\[
\theta_{13} \nabla^2 \psi + 2(\nabla \theta_{13}) \cdot \nabla \psi - \lambda \epsilon g \theta_{13} \psi = -\mu_1 \theta_{13} \psi \quad \text{in} \quad \Omega, \quad \psi|_{\partial \Omega} = 0.
\]
Multiplying (5.4) by $\theta_{13}$, we obtain
\[ \nabla \cdot (\theta_{13}^2 \nabla \psi) - \lambda \epsilon g \theta_{13}^2 \psi = -\mu_1 \theta_{13}^2 \psi \quad \text{in } \Omega, \quad \psi_{v} \big|_{\partial \Omega} = 0. \tag{5.5} \]

Since $\mu_1 \leq 0$, multiplying (5.5) by $\psi$ and integrating it in $\Omega$ yields
\[ \int_{\Omega} \theta_{13}^2 |\nabla \psi|^2 \, dx + \lambda \epsilon \int_{\Omega} g \theta_{13}^2 \psi^2 \, dx \leq 0. \tag{5.6} \]

Now, (5.4) shows that $\psi$ is not a constant function, so the first integral in (5.6) is positive. Hence, $\int_{\Omega} g \theta_{13}^2 \psi^2 \, dx < 0$, i.e., $\psi \in E$, and we may choose $\psi$ as the test function in (5.3). From (5.3) and (5.6) we get
\[ \tilde{\mu}_{\epsilon} \leq \frac{\int_{\Omega} \theta_{13}^2 |\nabla \psi|^2 \, dx}{\int_{\Omega} g \theta_{13}^2 \psi^2 \, dx} \leq \lambda \epsilon, \tag{5.7} \]

which contradicts our assumption that $\tilde{\mu}_{\epsilon} > \lambda \epsilon$, thereby completing the proof of our assertion.

Next, we show that there exist constants $\epsilon^*, \lambda$, and $\bar{\lambda}$ such that $\epsilon^* > 0$, $\bar{\lambda} > 0$, and $\tilde{\mu}_{\epsilon} > \lambda \epsilon$ for every $\epsilon < \epsilon^*$ and $\lambda \in [\bar{\lambda}, \bar{\lambda}]$. By the preceding assertion, this will imply that $\mu_1 > 0$ for $\epsilon < \epsilon^*$ and $\lambda \in [\bar{\lambda}, \bar{\lambda}]$, and thus complete the proof of Theorem 1.10.

Since $\lim_{\lambda \to \infty} \theta_{13} \to \zeta$ as $\epsilon \to 0$, we see that $\tilde{\mu}_{\epsilon} \to \tilde{\mu}$ uniformly for $\lambda \in [\bar{\lambda}, \bar{\lambda}]$ as $\epsilon \to 0$. We infer that $\tilde{\mu}_{\epsilon} \geq \delta/2$ for sufficiently small $\epsilon$ and $\lambda \in [\bar{\lambda}, \bar{\lambda}]$. Choosing $\epsilon$ smaller if necessary, we have $\tilde{\mu}_{\epsilon} > \lambda \epsilon$ for sufficiently small $\epsilon$ and $\lambda \in [\bar{\lambda}, \bar{\lambda}]$, which implies asymptotic stability of the 13-edge equilibrium for sufficiently small $\epsilon$ and $\lambda \in [\bar{\lambda}, \bar{\lambda}]$. This completes the proof of Theorem 1.10.
Proof of Theorem 1.12. We choose functions $g$ and $h$ that satisfy

\begin{align}
\int_\Omega g \, dx &> 0, \quad \int_\Omega h \, dx > 0, \\
\max\{g(x), h(x)\} &> 0 \quad \forall x \in \overline{\Omega}, \\
\int_{\{x \in \Omega: h(x) \leq 0\}} g \, dx &< 0.
\end{align}

(5.11a) (5.11b) (5.11c)

It follows from (1.11), (1.21), and (5.11a) that $\sigma_2 < \min(\sigma_1, \sigma_3)$, and from (1.20), (1.21), and (5.11b) that $s_2(x) < \bar{s}^{(13)}(x)$ for every $x \in \overline{\Omega}$. Furthermore, (5.11a) and (5.11c) reveal that both $g$ and $h$ change sign, i.e., (A2) again holds.

As in the proof of Theorem 1.10, the stability of the 13-edge equilibrium is determined by the sign of the principal eigenvalue of (5.2). Again, let $\varphi_1$ designate the eigenfunction corresponding to $\mu_1$ and set $\varphi_1 = \theta_{13} \psi$. Clearly, (5.5) still holds. Dividing (5.5) by $\psi$ and integrating, we obtain

$$
\mu_1 \int_\Omega \theta_{13}^2 \, dx = - \int_\Omega \frac{\theta_{13}^2 |\nabla \psi|^2}{\psi^2} \, dx + \lambda \epsilon \int_\Omega g \theta_{13}^2 \, dx \leq \lambda \epsilon \int_\Omega g \theta_{13}^2 \, dx.
$$

(5.12)

Instead of (5.8), now (5.11c) yields

$$
\lim_{\lambda \to \infty} G(\lambda) = \int_{\{x \in \Omega: h(x) \leq 0\}} g \, dx < 0.
$$

(5.13)

Hence, there exist positive constants $\delta$, $\lambda_1$, and $\lambda_2$ such that $\lambda_1 < \lambda_2$ and $G(\lambda) \leq -\delta$ for every $\lambda \in [\lambda_1, \lambda_2]$. Since $\theta_{13} \to \xi$ uniformly for $\lambda \in [\lambda_1, \lambda_2]$ as $\epsilon \to 0$, therefore, for sufficiently small $\epsilon$, we have

$$
\int_\Omega g \theta_{13}^2 \, dx \leq -\frac{\delta}{2} \quad \text{for } \lambda \in [\lambda_1, \lambda_2].
$$

Then (5.12) implies that $\mu_1 < 0$ for sufficiently small $\epsilon$ and every $\lambda \in [\lambda_1, \lambda_2]$. This proves part (a) of Theorem 1.12.

To prove part (b), we argue by contradiction. Suppose that

$$
\int_\Omega p_2(x, t) \, dx \to 0 \quad \text{as } t \to \infty.
$$

We first show that $p_2(x, t) \to 0$ uniformly in $x$ as $t \to \infty$. If $p_2(x, t) \not\to 0$, then there exist some positive constant $\eta$ and sequences $\{x_k\}_{k=1}^\infty$ and $\{t_k\}_{k=1}^\infty$ such that $p_2(x_k, t_k) \geq \eta$. Without loss of generality, we may assume that $t_k \to \infty$ and $x_k \to \bar{x}$ for some $\bar{x} \in \overline{\Omega}$. Since

$$
\sup_{t \geq 1} \|p_2(\cdot, t)\|_{C^{1,1}(\overline{\Omega})} < \infty
$$

we have
for every \( r \in (0, 1) \) [36], therefore, passing to a subsequence if necessary, from the Arzelà–Ascoli Lemma we get \( p_2(x, t_k) \to \tilde{p}_2(x) \) uniformly in \( x \) for some smooth function \( \tilde{p}_2 \) as \( k \to \infty \). Consequently, we have \( \tilde{p}_2 \geq 0 \) in \( \Omega \), \( \tilde{p}_2(\tilde{x}) \geq \eta \), and \( \int_\Omega \tilde{p}_2(x) \, dx = 0 \), which is a contradiction.

We conclude that \( \| p_2(\cdot, t) \|_{L^\infty(\Omega)} \to 0 \) as \( t \to \infty \). Invoking [20, Lemma 2.5] and following exactly the proof of [20, Theorem 2.1], we see that for any solution of (1.8), we have \( p_{\lambda} \) for every \( \lambda > 0 \), we obtain

\[
\int_\Omega \nabla \varphi_x \cdot \nabla x_1 (\epsilon g p_1 + h p_3) = -\mu_1 \varphi_1 + \lambda \varphi_1 \left[ \epsilon g (\theta_{13} - p_1) + h (1 - \theta_{13} - p_3) \right] \\
\quad \geq -\mu_1 \varphi_1 - \tau \lambda \varphi_1 \left( \epsilon g \| \| + \| h \| \right) \\
\quad \geq -\frac{\mu_1}{2} \varphi_1 > 0.
\]

(5.14)

From (1.8a), (1.4), and (1.21) we derive

\[
p_{2,t} = \nabla^2 p_2 - \lambda p_2 (\epsilon g p_1 + h p_3).
\]

(5.15)

Choose \( \kappa > 0 \) so small that \( p_2(x, T) \geq \kappa \varphi_1 \). By the comparison principle, we have \( p_2(x, t) \geq \kappa \varphi_1 \) for every \( x \in \Omega \) and \( t \geq T \). However, this contradicts our assumption that \( \int_\Omega p_2(x, t) \, dx \to 0 \), which completes the proof of part (b).

6. Discussion

In this brief section, we summarize the main results established in [20,21] and this paper for migration and selection, with particular attention to the case without dominance, and we mention some unsolved problems. In the standard frequency-independent situation, the nonlinearity is generally cubic. The biologically natural and important assumption that dominance is absent reduces the nonlinearity to a quadratic. This simplification and closely related discrete models [31] strongly suggest that selection without dominance should be the easiest to investigate. Nonetheless, the multiallelic behavior turns out to be rich and complex.

The diallelic case without dominance is fully understood. Theorem 2.1 in [20] extends Henry’s [10] global analysis from homogeneous, isotropic migration to arbitrary migration. A special case of this theorem shows that, in the absence of dominance, there is always a globally asymptotically stable equilibrium and determines when it corresponds to loss, fixation, or polymorphism.

This series of papers focuses on the much more difficult multiallelic case. Although our results provide considerable evolutionary insight, our analysis is far from complete.

Some of our results concern the global loss of an allele. Theorem 3.1 in [20] and its generalization [21, Theorem 1.1], provide sufficient conditions for global elimination. For weak migration (i.e., large selection–migration ratio \( \lambda \)), [21, Theorem 1.3] gives more explicit sufficient conditions. Corollaries 4.6 and 4.7 in [21] explicitly specialize these theorems to the case without dominance. In this case, [20, Theorems 3.2 and 3.3] offer sufficient conditions for global loss of every intermediate allele and determine the limit of the gene frequencies as \( t \to \infty \) (fixation of one of the extreme alleles or a diallelic polymorphism).
For a general sufficient condition that protects an allele from loss (i.e., ensures its persistence), see [21, Theorem 1.4]. In the absence of dominance, this condition reduces to the simpler one in [21, Corollary 4.9].

In [21, Theorems 1.8 and 1.9], we presented general sufficient conditions for existence of an internal equilibrium and determined its zero-migration ($\lambda \to \infty$) limit. When there is no dominance, these theorems simplify to [21, Corollary 4.10].

This paper is devoted to the case without dominance, with primary focus on the dependence of the evolution of the gene frequencies on $\lambda$. Theorem 1.1 demonstrates that if migration is sufficiently strong (i.e., $\lambda$ is sufficiently small) and the migration operator is in divergence form, then the allele with the greatest spatially averaged selection coefficient is ultimately fixed. Theorem 1.5 specifies the stability of each vertex for arbitrary $\lambda$. Theorems 1.6 and 1.7 fully describe the stability of each edge equilibrium when either (i) migration is sufficiently weak or (ii) the equilibrium has just appeared as $\lambda$ increases.

The remaining results demonstrate the existence of complex, unexpected phenomena in a particular triallelic model with homogeneous, isotropic migration. Theorem 1.9 shows that, as $\lambda$ increases, arbitrarily many changes of stability of the edge equilibria and corresponding appearance of an internal equilibrium can occur. Theorems 1.10 and 1.12 imply that, in contrast with the diallelic case, the conditions for protection or loss of an allele can depend nonmonotonically on $\lambda$.

Although selection in the absence of dominance should be the most tractable situation, many important open problems remain. As explained in [21, Remark 1.7], the sufficient conditions for protection of an allele in [21, Theorem 1.4 and Corollary 4.9] are quite strong. Can they be weakened? Since these conditions are an essential ingredient of Theorems 1.8 and 1.9 and Corollary 4.10 in [21], the same question applies to them.

The formal argument in [21, Section 5.1] strongly suggests that Theorem 1.1 in this paper holds for arbitrary migration. It is highly desirable to prove this conjecture.

Determination of the stability of the edge equilibria for arbitrary $\lambda$ would subsume Theorems 1.6 and 1.7. For three alleles, does instability of an edge equilibrium imply protection of the allele absent at that equilibrium? Even in a special case, Theorem 1.12 proves only that allele can not be lost.

Of course, the greatest challenge is to find necessary and sufficient conditions for the existence, uniqueness, and stability of internal equilibria, prove convergence of the gene frequencies (if true), and delineate the basins of attraction. Comparison of Corollary 4.9 with Corollary 4.7 in [21] indicates that for sufficiently large $\lambda$, the sufficient condition for protection in Corollary 4.9 is almost necessary, and this implies that so is the sufficient condition for existence of an internal equilibrium in [21, Corollary 4.10]. Nonetheless, even for three alleles, uniqueness and stability of internal equilibria are undetermined.

Appendix A. Construction of the function $G$

Here, we show how to construct the function $G$ with multiple nondegenerate zeros that was used in Theorem 1.9.

**Proposition A.** If $h$ changes sign, then for generic $g \in C(\Omega)$, the function $G$ satisfies $G'(\lambda) \neq 0$ whenever $G(\lambda) = 0$.

The proof of Proposition A is almost identical to that of part (i) of [12, Proposition 1.3].
**Proposition B.** If $h$ changes sign, then for every $k \geq 1$, there exists a function $g$ such that $G$ has at least $k$ nondegenerate zeros.

**Proof.** We define $\gamma(x, \lambda) = [1 - \theta(x, \lambda)]^2$. First, we

**Claim.** For every $k \geq 1$, there exist numbers $\Lambda_1 < \cdots < \Lambda_k$ such that the functions $\gamma(x, \Lambda_1), \ldots, \gamma(x, \Lambda_k)$ are linearly independent.

If this assertion holds, we can choose $\hat{g}(x)$ as a linear combination of the functions $\gamma(x, \Lambda_1), \ldots, \gamma(x, \Lambda_k)$ such that

$$\int_{\Omega} \hat{g}(x) \gamma(x, \Lambda_i) dx \cdot \int_{\Omega} \hat{g}(x) \gamma(x, \Lambda_{i+1}) dx < 0 \quad (A.1)$$

for every $i$ such that $1 \leq i \leq k - 1$. Then for any function $g$ in a sufficiently small neighborhood of $\hat{g}$, the corresponding $G$ has at least one zero $\lambda_i \in (\Lambda_i, \Lambda_{i+1})$ for every $i$ such that $1 \leq i \leq k - 1$. By Proposition A, we can choose $g$ in this neighborhood such that every $\lambda_i$ is a nondegenerate zero of $G$. Hence, Proposition B follows from our assertion.

We prove the assertion by induction on $k$. The case $k = 1$ holds automatically for every $\Lambda_1 > \lambda^*$. Suppose that the assertion holds for $k$. We show that there exists a sufficiently large $\Lambda_{k+1}$ such that for every $\lambda \geq \Lambda_{k+1}$, the functions $\gamma(x, \Lambda_1), \ldots, \gamma(x, \Lambda_k)$, and $\gamma(x, \lambda)$ are linearly independent. We argue by contradiction. If not, we may assume that there exists some sequence $\{\Lambda_{k+1,j}\}_{j=1}^{\infty}$ such that $\lim_{j \to \infty} \Lambda_{k+1,j} = \infty$, and $\gamma(x, \Lambda_1), \ldots, \gamma(x, \Lambda_k)$, and $\gamma(x, \Lambda_{k+1,j})$ are linearly dependent. Hence, for every $j \geq 1$, there exist constants $\{C_{j,i}\}_{i=1}^{k+1}$ such that

$$\sum_{i=1}^{k+1} |C_{j,i}| = 1, \quad (A.2a)$$

$$\sum_{i=1}^{k} C_{j,i} \gamma(x, \Lambda_i) + C_{j,k+1} \gamma(x, \Lambda_{k+1,j}) = 0 \quad (A.2b)$$

for every $x \in \Omega$.

Passing to a subsequence if necessary, we may assume that $C_{j,i} \to C_i$ as $j \to \infty$ for $1 \leq i \leq k + 1$. Since $\theta(x, \Lambda_{k+1,j}) \to \chi_{\{x \in \Omega: h(x) > 0\}}$ a.e. in $\Omega$ as $j \to \infty$, passing to the limit in (A.2b) yields

$$\sum_{i=1}^{k} C_i \gamma(x, \Lambda_i) + C_{k+1} \chi_{\{x \in \Omega: h(x) \leq 0\}} = 0 \quad (A.3)$$

for $x \in \Omega$. Since $\chi_{\{x \in \Omega: h(x) \leq 0\}}$ is discontinuous in $\Omega$ and the other functions in (A.3) are all smooth, we see that $C_{k+1} = 0$. Therefore, (A.2a) gives

$$\sum_{i=1}^{k} |C_i| = 1, \quad (A.4)$$
and the last term is absent in (A.3). Thus, \( \gamma(x, A_1), \ldots, \gamma(x, A_k) \) are linearly dependent, which contradicts our assumption and completes the proof of Proposition B.

**Appendix B. Correction of some previous results on loss of an allele**

The assumptions on which our previous general results on loss of a particular allele \( A_i \) are based must be slightly strengthened to take into account the possible elimination of certain other alleles.

Consider first assumption (A1) in [20], the foundation of Theorem 3.1 in [20]. We define

\[
N_i^* = \begin{cases} 
  \{i, n\} & \text{if } \gamma_i = 0, \\
  \{1, i, n\} & \text{if } \gamma_i \in (0, 1), \\
  \{1, i\} & \text{if } \gamma_i = 1,
\end{cases} \tag{B.1}
\]

\[ \Delta_i = \{ p \in \Delta: p_j > 0 \ \forall \ j \in N_i^* \}. \tag{B.2} \]

At the end of (A1), “\( j \in N \)” must be replaced by “\( j \in N_i^* \).” With the strengthened assumption (A1), Lemmas 3.4 and 3.5 in [20] hold not only for every \( p \in \text{int} \Delta \), but rather for every \( p \in \Delta_i \). Thus, Lemma 3.4 should begin “For every \( p \in \Delta_i \), the function \( u_i \) satisfies…” and we must extend the first sentence in Lemma 3.5 to “Suppose that assumption (A1) holds and \( p \in \Delta_i \).” In the proof of Lemma 3.5, in lines 13 and 16 on p. 404, “\( j \in N \)” should be replaced by “\( j \in N_i^* \).” The proofs of Lemma 3.4 and Theorem 3.1 are unaltered.

The reason for the above changes is the following. In [20, (3.24)], we know that \( \tilde{p} \in \Delta_i \), but if \( \tilde{p}_j(x, \tilde{0}) \equiv 0 \) for some \( j \notin N_i^* \), then \( \tilde{p} \notin \text{int} \Delta \). However, in the original proof of Lemma 3.5, we assumed that \( p \in \text{int} \Delta \), which means that the original form of Lemma 3.5 may not apply to \( \tilde{p} \).

Since Theorem 1.1 in [21] generalizes Theorem 3.1 in [20], the changes in [21] are very similar to those outlined above. We replace (B.1) by

\[ N_i^* = \{i\} \cup \{ j \in N: \gamma_{ij} > 0 \} \tag{B.3} \]

and retain (B.2). At the end of (A1) in [21], “\( p \in \text{int} \Delta \)” must be replaced by “\( p \in \Delta_i \).” In (A1*), we must replace the second “\( k \in N \)” by “\( k \in N_i^* \)” and “\( p \in \text{int} \Delta \)” by “\( p \in \Delta_i \).” Lemmas 2.1 and 2.2 in [21] should be revised precisely as described above for [20, Lemmas 3.4 and 3.5], respectively. These are the only changes.

The reason for the revisions in [21] is the same as in [20]: just replace (3.24) by (2.13) and Lemma 3.5 by Lemma 2.2 in the above explanation.

**References**