ANZIAM J. **68, e15** (2026), 1–16
doi:10.1017/S1446181126100388

GLOBAL BIFURCATION AND STABILITY FOR SEMI-INFINITE CLINE

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(Received 22 October, 2025; accepted 25 March, 2026)

Abstract

We study the semi-infinite Neumann problem, which models the variation law of a cline in a semi-infinite habitat. Using the bifurcation analysis method, we find that there is a unique solution curve emanating from $(\arctan\alpha, 0)$ with $\alpha > 0$, which is strictly increasing and approaches 1 in $C[0, +\infty)$. Furthermore, we show that any cline (bifurcation solution) is stable, thereby providing a confirmed answer to a conjecture. Moreover, we also establish the stability of the trivial solution. Our conclusions are consistent with the related numerical results and biological reality.

2020 *Mathematics subject classification*: primary 34C23; secondary 34D23, 34L20, 92D10.

Keywords and phrases: bifurcation, cline, stability, conjecture, infinite habitat.

1. Introduction

A cline describes a gradual change in genotypic frequency as a function of spatial location. The existence of a cline often depends on gene selection and migration, as well as the scale of favourable habitat. Studying the generation patterns and stability of clines can provide scientific theoretical support for species protection measures and biomedical therapies.

The first mathematician to analyse migration and selection was Fisher [9]. In 1948, Haldane [11] derived a reaction-diffusion equation for the equilibrium allele frequencies at a diallelic locus subject to spatially varying selection along a single spatial dimension. This work is generally regarded as the earliest mathematical theory of clines. The study of clines became a very active research area beginning in the 1970s, when the consequences of various assumptions about spatial variation in fitness and about migration patterns were investigated (see, for example, [18–26,

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29, 32]). Meanwhile, Conley [2], Fleming [10], Fife and Peletier [7, 8] and Henry [12] developed and employed advanced mathematical methods to investigate the existence, uniqueness and stability of clinal solutions under a variety of assumptions about fitness. Since the beginning of the new century, Lou et al. [13–17, 27, 28] extended previous work in several directions by modelling migration with general elliptic operators on bounded domains in arbitrary dimensions. Recently, Su et al. [33] provided conditions for the existence and linear stability of a two-locus cline when recombination is either sufficiently weak or sufficiently strong relative to selection and diffusion. More recently, using the bifurcation analysis method, Nakashima and Tsujikawa [30] studied positive stationary solutions for a problem arising from population genetics.

Let A and a denote the alleles at the locus under consideration. In his celebrated work, Nagylaki [18] derived the following semi-infinite Neumann problem [1]:

$$\begin{cases} \dfrac{d^2p}{d\xi^2} + k^2 g(\xi)p(1-p) = 0, & \xi > 0, \\ \dfrac{dp}{d\xi} = 0 & \text{at } 0, +\infty, \end{cases} \tag{1.1}$$

where p is the gene frequency of A, $k^2 = (2sa^2)/\sigma^2$ with $k > 0$ is the combination of the selection intensity $s > 0$, advantageous habitat scale $a > 0$, migration variance $\sigma^2/2$ and $sg(\xi)$ with

$$g(\xi) = \begin{cases} 1, & 0 \le \xi \le 1, \\ -\alpha^2, & \xi > 1, \end{cases}$$

the Malthusian parameter or the selection coefficient for the genotype AA. Here, $-\alpha^2$, with $\alpha > 0$, is the ratio of the selection coefficients for $\xi > 1$ and $0 \le \xi \le 1$. Let $p_0 = p(0)$. By studying the relationship between p_0 and k, Nagylaki obtained that $k > \arctan \alpha$ is a necessary and sufficient condition for a unique solution of (1.1), which corresponds to a unique cline. Here, $\arctan \alpha := k_1$ denotes the first positive root of $\tan k = \alpha$. In fact, he only obtained the unique p_0. Obviously, p_0 can be determined by p, but the converse is not true. Therefore, it is clearly necessary to study the existence and uniqueness of p. The derivation by Nagylaki [18, (31)] assumed the boundary condition $\lim_{\xi\to+\infty} p = 0$. Here, from now on, we also assume that the solution p in (1.1) satisfies $\lim_{\xi\to+\infty} p = 0$. When the unfavourable habitat is infinite, it is reasonable for the cline to approach 0. This also indicates that when the unfavourable habitat is infinite, 1 is not in equilibrium, which is consistent with biological reality. Therefore, this assumption is both realistic and reasonable.

Furthermore, he also conjectured that the cline is stable. To the best of our knowledge, this conjecture has not yet been fully resolved. This is also the main motivation for this work. Moreover, does the cline p (rather than p_0) form a solution curve with respect to k? What is the decay rate of a cline p at infinity? What is the

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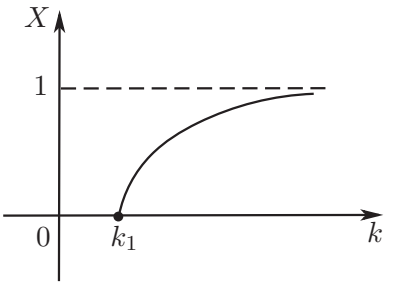


FIGURE 1. Bifurcation diagrams of Theorem 1.1.

stability of the trivial solution $p = 0$? We will provide satisfactory answers to these questions here.

Define

$$X = \left\{ p \in C[0, +\infty) \mid p'(0) = 0, \lim_{\xi \to +\infty} \frac{p e^{\alpha k_1 \xi/\sqrt{3}}}{\xi} = 0 \right\}$$

endowed with the norm $\|p\| = \sup_{\xi \in [0,+\infty)} |p(\xi)|$, which is clearly a Banach space. Let $X^+ = \{p \in X \mid p \geq 0\}$ with the deduced norm of X, and P^+ be the set of functions in X^+ which are positive in $[0, +\infty)$. Also, set $K^+ = (0, +\infty) \times P^+$ under the product topology.

The first main result of this work is the following theorem.

THEOREM 1.1. *The pair* $(\arctan \alpha, 0)$ *is a bifurcation point of problem* (1.1) *and the associated bifurcation curve* $C \subseteq (K^+ \cup \{(\arctan \alpha, 0)\})$ *is unbounded, approaching* 1 *as* $k \to +\infty$. *Moreover, for* $k \leq \arctan \alpha$, *problem* (1.1) *has only the trivial solution* $p = 0$; *while for* $k > \arctan \alpha$, *there is a unique solution* p *with* $0 < p \leq 1$. *In addition, for each* $(k, p) \in C$, p *exponentially decays to* 0 *at infinity.*

Our conclusions indicate that $k > \arctan \alpha$ is a necessary and sufficient condition for the existence and uniqueness of a solution p, rather than merely p_0 as in [18]. Moreover, we also obtain a bifurcation curve (see Figure 1) and the decay rate of the cline p at $+\infty$.

Figure 1 illustrates that a branch of positive solutions bifurcates from the trivial solution at the critical value $k_1 = \arctan \alpha$. The solution branch exists exclusively for $k > k_1$ and converges to 1 as $k \to +\infty$.

Regarding stability, we have the following result.

THEOREM 1.2. *For any* $k > \arctan \alpha$, *the cline* p *is (asymptotically linearly) stable. For the trivial solution* $p = 0$, *it is (asymptotically linearly) stable for all* $k < \arctan \alpha$ *and unstable for each* $k > \arctan \alpha$.

Our conclusion about the cline is consistent with Nagylaki's expectation. It is also consistent with Slatkin's numerical work [32]. Moreover, we also obtain the stability of the trivial solution $p = 0$. From a genetic perspective, stability indicates the dominance

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of selection. The expression for k shows that stronger selection and a larger favourable habitat both promote the survival of the cline. This is consistent with biological reality. The stability of the cline further suggests that such a genetic pattern, once established, can persist under small perturbations. These conclusions provide a theoretical basis for predicting species distribution limits and for designing conservation strategies in fragmented environments.

The combination of an unbounded domain and a sign-changing weight function g poses substantial challenges for the analysis of this problem. Due to the unboundedness of the interval, it is often difficult to obtain the compactness of related operators using the compact embedding theorem (on bounded domain) or the Arzelà–Ascoli theorem. Of course, if the weight function has a good decay rate at infinity, it is also possible to get compactness. However, the weight function g here not only changes sign, but also lacks decay. We need to develop some new tricks to achieve our goals. Here, we find that the cline is exponentially decaying at infinity. Using this property, we can define a suitable work space X and obtain the compactness of the related operator. Thus, classical bifurcation theory can be used to study this problem.

Since the weight function g is sign-changing, it is difficult to directly use the conventional linearization method or stable exchange theory [3, 4]. This may be the reason why Nagylaki's stability conjecture has not been fully resolved so far. Noting $g \neq 0$, we here overcome the difficulties caused by the sign change of g by simultaneously dividing the equation by g and then linearizing it. Furthermore, due to the sign change of the weight function g, the Rayleigh quotient for the first eigenvalue of the linearization problem may not necessarily exist, resulting in an indefinite sign of its corresponding eigenfunctions. We use the monotonicity of the cline and the piecewise constant nature of g to prove that the Rayleigh quotient for the first eigenvalue of the linearization problems does indeed exist. Furthermore, it is proven that the first eigenvalue of the linearization problem is the principal eigenvalue. Using this conclusion, the sign of the first eigenvalue of the linearization problem can be determined and the expected stability conclusion can be obtained from its sign.

Note that Nakashima et al. [25–28, 30] studied indefinite diffusion problems on bounded domains with continuous and sign-changing weight functions. The present work considers a semi-infinite habitat with a piecewise-constant sign-changing weight, proving uniqueness and stability of the cline. Moreover, the nonlinear term they considered is bistable, that is, $u^2(1-u)$. While, we consider a logistic nonlinear term here, our conclusions complement those important results.

The rest of this paper is arranged as follows. In Section 2, we first study the spectrum of the linearization problem. Then, through an auxiliary problem, we prove that the cline satisfies $0 < p \leq 1$. Furthermore, we obtain the decay behaviour of p at infinity. Section 3 establishes the global bifurcation structure and proves the uniqueness of the solution, completing the proof of Theorem 1.1. In Section 4, we complete the proof of Theorem 1.2 by a complete stability analysis for both the trivial and nontrivial solutions. Finally, Section 5 concludes the paper.

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2. Preliminary

We first study the spectrum of the linearization problem. It is not difficult to verify that the linearization problem of (1.1) at equilibrium point 0 is

$$\begin{cases} \dfrac{d^2p}{d\xi^2} + k^2 g(\xi)p = 0, & \xi > 0, \\ \dfrac{dp}{d\xi} = 0 & \text{at } 0, +\infty. \end{cases} \tag{2.1}$$

By simple calculation, we can obtain

$$p(\xi) = \begin{cases} A\cos(k\xi), & 0 \le \xi \le 1, \\ Be^{-\alpha k\xi}, & \xi > 1. \end{cases}$$

Since p and p' are continuous at $\xi = 1$, we find that $\alpha = \tan k$. Thus, problem (2.1) only has a sequence of positive eigenvalues k_i such that

$$(i-1)\pi < k_i < \frac{\pi}{2} + (i-1)\pi \quad \text{with } i \ge 1.$$

Furthermore, the corresponding eigenfunction is generated by

$$p_i(\xi) = \begin{cases} \cos(k_i\xi), & 0 \le \xi \le 1, \\ \cos(k_i)e^{\alpha k_i(1-\xi)}, & \xi > 1. \end{cases}$$

According to the range of k_i, we see that $\cos(k_i) \neq 0$ and, hence, $p_i(\xi)$ does not change sign for $\xi > 1$. Using the range of k_i again, we can see that $\cos(k_i\xi)$ has exactly $i-1$ simple zeros in $(0, 1)$. In particular, p_1 is positive. For $i \ge 2$, we can calculate the zeros of p_i as $\pi/(2k_i)$, $(3\pi)/(2k_i)$, …, $((2i-3)\pi)/(2k_i)$.

In summary, we have the following conclusion regarding the spectrum of problem (2.1).

PROPOSITION 2.1. *Problem* (2.1) *only has a sequence of positive eigenvalues* k_i *such that*

$$(i-1)\pi < k_i < \frac{\pi}{2} + (i-1)\pi, \quad i \ge 1.$$

The eigenfunction p_i *corresponding* k_i *has exactly* $i-1$ *simple zeros* $\pi/(2k_i)$, $(3\pi)/(2k_i)$, …, $((2i-3)\pi)/(2k_i)$ *in* $(0, 1)$. *In particular,* p_1 *is positive.*

From Proposition 2.1, we can see $k_1 < \pi/2$ and $k_2 > \pi$. It follows that $k_2 - k_1 > \pi/2$, which holds in all parameter regimes. This explicit spectral gap estimate shows that k_1 corresponds to the smallest admissible eigenvalue.

Since eigenfunction p_i decays exponentially to 0 at infinity, we have reason to believe that the nontrivial solution of problem (1.1) also decays exponentially to 0 at infinity. To show this, we first study the range of solutions to problem (1.1). Define

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$$f(s) = \begin{cases} 0 & \text{if } s < 0, \\ s(1-s) & \text{if } 0 \le s \le 1, \\ 0 & \text{if } s > 1 \end{cases}$$

and consider the following auxiliary problem:

$$\begin{cases} \dfrac{d^2p}{d\xi^2} + k^2 g(\xi) f(p) = 0, & \xi > 0, \\ \dfrac{dp}{d\xi} = 0 & \text{at } 0, +\infty. \end{cases} \tag{2.2}$$

Then, we have the following lemma.

LEMMA 2.2. *For any nonconstant solution p of problem* (2.2)*, one has that* $0 \le p \le 1$ *and, hence, it is also the solution of problem* (1.1)*.*

PROOF. We only prove $p \le 1$, because the proof for $p \ge 0$ is similar. If p is always greater than 1, one sees that $p'' \equiv 0$. Combining this with the boundary conditions implies that p is constant, which corresponds to a trivial solution. Therefore, there exists at least one point such that $p = 1$. From the definition of g and f, we can derive that p is decreasing. We use ξ_0 to denote the first zero of $p(\xi) = 1$. We suppose by contradiction that $p(0) = \sup p > 1$. It follows that $p(\xi) > 1$ for all $\xi < \xi_0$. Using the definition of f again, we get $p = a\xi + b$ in $[0, \xi_0)$. In view of the boundary condition $p'(0) = 0$, we have $p = b$ in $[0, \xi_0)$. Since $p(\xi_0) = 1$, we derive that $b = 1$. Thus, we obtain $p \equiv 1$ in $[0, \xi_0]$, which is a contradiction. This completes the proof. □

By Lemma 2.2, we only need to study the existence and uniqueness of nontrivial solutions for the auxiliary problem (2.2). We further *claim* that $0 < p \le 1$ for every nonconstant solution p of problem (2.2). To prove this, we first establish the following existence and uniqueness result.

LEMMA 2.3. *If nonconstant function p satisfies problem* (2.2) *and it has a double zero, then* $p \equiv 0$*.*

PROOF. Let p be such a function and ξ_* be a double zero. It follows that

$$p = -k^2 \int_{\xi_*}^{\xi} \int_{\xi_*}^{s} g(\tau) f(p)\, d\tau\, ds.$$

If $\xi \in [0, \xi_*]$, in view of Lemma 2.2, we have

$$\begin{aligned} |p(\xi)| &\le k^2 \int_{\xi_*}^{\xi} \int_{\xi_*}^{s} |g(\tau) f(p)|\, d\tau\, ds \\ &\le k^2 \max\{1, \alpha^2\} \int_{\xi_*}^{\xi} \int_{\xi_*}^{s} p\, d\tau\, ds \end{aligned}$$

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$$\leq k^2 \max\{1, \alpha^2\} \int_{\xi_*}^{\xi} \int_{\xi_*}^{\xi} p \, d\tau \, ds$$
$$\leq k^2 \max\{1, \alpha^2\} (\xi_* - \xi) \int_{\xi}^{\xi_*} p \, d\tau$$
$$\leq k^2 \max\{1, \alpha^2\} \xi_* \int_{\xi}^{\xi_*} p \, ds.$$

By the Gronwall–Bellman inequality [5, Lemma 2.2], we obtain that $p \equiv 0$ on $[0, \xi_*]$.

However, when $\xi \in [\xi_*, b]$ for any fixed $b > \xi_*$, we have

$$|p(\xi)| \leq k^2 \max\{1, \alpha^2\} (b - \xi_*) \int_{\xi_*}^{\xi} p \, ds.$$

It follows from the modified version of the Gronwall–Bellman inequality [5, Lemma 2.1] that $p \equiv 0$ on $[\xi_*, b]$. The arbitrariness of b implies $p \equiv 0$ on $[\xi_*, +\infty)$. □

If p is a nonconstant solution of problem (2.2), one has that $0 \leq p \leq 1$ via Lemma 2.2. If p has a zero ξ_1, since it is decreasing, $p(\xi) \equiv 0$ for $\xi \geq \xi_1$. By Lemma 2.3, we conclude that $p(\xi) \equiv 0$, which is impossible. In conclusion, we obtain the following lemma.

LEMMA 2.4. *For any nonconstant solution p of problem (2.2), one has that $0 < p \leq 1$ and, hence, it is also the solution of problem (1.1).*

From Lemma 2.4, we see that $p_0 \in (0, 1]$. Further, if p_0 is unique, Lemmas 2.2, 2.3 and 2.4 imply that the solution p with $p(0) = p_0$ of problem (1.1) is also unique. It should be pointed out that here, we use the auxiliary problem (2.2) to prove $p_0 \in (0, 1]$, rather than assuming it as in [18].

Now, we return to the decay rate of a nonconstant solution p of problem (2.2) at $+\infty$. We have known that $0 < p \leq 1$. Further, we have the following result.

PROPOSITION 2.5. *Let p be a nonconstant solution of (2.2). Then, for $\xi > 1$, we have*

$$\widetilde{p}_1 e^{-\alpha k(\xi-1)} < p \leq \widetilde{p}_1 e^{-\alpha k(\xi-1)/\sqrt{3}},$$

where $\widetilde{p}_1 = p(1)$.

PROOF. Since p satisfies $\lim_{\xi \to +\infty} p(\xi) = 0$, from [18, (31)], we know that

$$\alpha k(\xi - 1) = \int_{p}^{\widetilde{p}_1} \frac{1}{s(1 - 2s/3)^{1/2}} \, ds.$$

Since $0 < p \leq 1$, we find that

$$\ln \frac{\widetilde{p}_1}{p} = \int_{p}^{\widetilde{p}_1} \frac{1}{s} \, ds < \alpha k(\xi - 1) \leq \sqrt{3} \int_{p}^{\widetilde{p}_1} \frac{1}{s} \, ds = \sqrt{3} \ln \frac{\widetilde{p}_1}{p},$$

which further implies the desired conclusion. □

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Proposition 2.5 indicates the nontrivial solution of problem (2.2) decays exponentially to 0 at infinity if it satisfies $\lim_{\xi\to+\infty} p(\xi) = 0$. Further, we have the following result.

LEMMA 2.6. *If p is any nonconstant solution of problem (2.2) and satisfies $\lim_{\xi\to+\infty} p(\xi) = 0$, then for $\xi > 1$, we have*

$$\lim_{\xi\to+\infty} \frac{pe^{\alpha k_1 \xi/\sqrt{3}}}{\xi} = 0,$$

where k_1 is the first eigenvalue of problem (2.1).

PROOF. From Proposition 2.5, we know that $0 < p \le 1$ and

$$p \le \widetilde{p}_1 e^{-\alpha k(\xi-1)/\sqrt{3}}.$$

We *claim* that $k > k_1$. If it was $k \le k_1$, we have

$$\frac{d^2p}{d\xi^2} + k^2 g(\xi)p(1-p) = 0.$$

We also note that

$$\frac{d^2p_1}{d\xi^2} + k_1^2 g(\xi)p_1 = 0.$$

Multiplying the equation for p by p_1 and integrating by parts gives

$$\int_0^{+\infty} p'p_1' \, d\xi = \int_0^{+\infty} k^2 g p p_1 (1-p) \, d\xi. \tag{2.3}$$

We have known that p is decreasing. Proposition 2.5 implies that p is not a nonzero constant. Hence, $p' \le 0$ and $p' \not\equiv 0$. Since p_1 is strictly decreasing, we conclude that

$$\int_0^{+\infty} g p p_1 (1-p) \, d\xi > 0. \tag{2.4}$$

Furthermore, multiplying the equation for p_1 by p and integrating by parts, then subtracting (2.3) and using (2.4), we find that

$$\begin{aligned} 0 &= k^2 \int_0^{+\infty} g p p_1 (1-p) \, d\xi - \int_0^{+\infty} k_1^2 g p p_1 \, d\xi \\ &\le k_1^2 \int_0^{+\infty} g p p_1 (1-p) \, d\xi - \int_0^{+\infty} k_1^2 g p p_1 \, d\xi \\ &= -k_1^2 \int_0^{+\infty} g p^2 p_1 \, d\xi. \end{aligned} \tag{2.5}$$

However, multiplying the equation for p_1 by p^2 and integrating by parts yields

$$2\int_0^{+\infty} p p_1' p' \, d\xi = k_1^2 \int_0^{+\infty} g p^2 p_1 \, d\xi. \tag{2.6}$$

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Because $p' \le 0$, $p' \not\equiv 0$ and p_1 is strictly decreasing, we have

$$\int_0^{+\infty} pp_1'p'\,d\xi > 0.$$

Combining this with (2.6) shows that

$$\int_0^{+\infty} gp^2p_1\,d\xi > 0.$$

Now, in view of (2.5), we derive that

$$0 \le -k_1^2 \int_0^{+\infty} gp^2p_1\,d\xi < 0,$$

which is absurd.

Therefore, we have that

$$p < \widetilde{p}_1 e^{-\alpha k_1(\xi-1)/\sqrt{3}}.$$

It follows that

$$\frac{pe^{\alpha k_1\xi/\sqrt{3}}}{\xi} < \frac{\widetilde{p}_1}{\xi}e^{\alpha k_1/\sqrt{3}} \to 0$$

as $\xi \to +\infty$, which implies the desired conclusion. This completes the proof. □

Finally, we present a Rabinowitz-type global bifurcation result [5, Lemma 2.5]. Let E be a real Banach space with the norm $\|\cdot\|$, O be an open subset of $\mathbb{R}\times E$, $\mathrm{pr}_E(O)$ be the projection of O on E and $\mathrm{pr}_{\mathbb{R}}(O)$ be the projection of O on $\mathbb{R}$. Consider the following operator equation:

$$u = L(\lambda)u + H(\lambda,u) := G(\lambda,u), \tag{2.7}$$

where λ varies in $\mathrm{pr}_{\mathbb{R}}(\overline{O})$, the map $\lambda \to L(\lambda)$ is continuous, $L(\cdot) : \mathrm{pr}_E(\overline{O}) \to \mathrm{pr}_E(\overline{O})$ is an homogeneous completely continuous operator and $H : \overline{O} \to E$ is compact with $H = o(\|u\|)$ at $u = 0$ uniformly on bounded λ intervals in $\overline{O}$. Let

$$\mathscr{S} = \overline{\{(\lambda,u) \mid (\lambda,u) \text{ satisfies (2.7) and } u \not\equiv 0\}}^{\overline{O}}.$$

Recall that μ is called an eigenvalue of

$$u = L(\mu)u, \quad u \in E, \tag{2.8}$$

if there exists $\varphi \in E \setminus \{0\}$ such that $\varphi = L(\mu)\varphi$. Let Σ denote the set of real eigenvalues of (2.8). Thus, the Leray–Schauder degree [6, Section 8.3] $\deg(I - L(\lambda), B_R(0), 0)$ is well defined for arbitrary R-ball $B_R(0)$ in O and $\lambda \notin \Sigma$.

We recall the following Rabinowitz-type global bifurcation result, which can be seen as a complement or extension of the famous Rabinowitz global bifurcation theorem [31, Theorem 1.3].

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PROPOSITION 2.7. [5, Lemma 2.5] *If $\mu \in pr_{\mathbb{R}}(O) \cap \Sigma$ such that the Leray–Schauder degree* $\deg(I - L(\lambda), B_R(0))$ *changes when λ passes μ, then $\mathscr{S}$ possesses a maximal sub-continuum $C_\mu \subset \overline{O}$ such that $(\mu, 0) \in C_\mu$ and one of the following three properties is satisfied by C_μ:*

(i) *C_μ is unbounded in $\overline{O}$;*
(ii) *meets $\partial O \setminus \{(\mu, 0)\}$;*
(iii) *meets $(\overline{\mu}, 0)$, where $\overline{\mu} \in pr_{\mathbb{R}}(\overline{O}) \cap \Sigma$ with $\overline{\mu} \neq \mu$.*

3. Proof of Theorem 1.1

In view of Proposition 2.5, it is not difficult to verify that problem (2.2) can be equivalently transformed into

$$p = k^2 F(p),$$

where the map $F : X \to X$ is defined by

$$F(p) = \int_{\xi}^{+\infty} \int_{+\infty}^{s} gf(p)\, d\tau\, ds, \quad \xi \geq 0.$$

We *claim* that F is compact. Assume there is a sequence p_n that weakly converges to some p in X. Without loss of generality, we assume $p = 0$. For any $\varepsilon > 0$, since p_n decays exponentially to 0 at infinity, there exists $\gamma > 0$ such that

$$\left| \int_{\gamma}^{+\infty} \int_{+\infty}^{s} p_n\, d\xi\, ds \right| < \frac{\varepsilon}{\max\{1, \alpha^2\}}.$$

It follows that

$$\max\{1, \alpha^2\} \left| \int_{\gamma}^{+\infty} \int_{+\infty}^{s} f(p_n)\, d\xi\, ds \right| < \varepsilon.$$

When $\xi > \gamma$, we have that

$$\left| F(p_n)(\xi) \right| \leq \max\{1, \alpha^2\} \left| \int_{\gamma}^{+\infty} \int_{+\infty}^{s} f(p_n)\, d\xi\, ds \right| < \varepsilon.$$

While, for $\xi \leq \gamma$, from the definition of F, we can verify that $F(p_n) \in C^{\alpha}[0, \gamma]$ with any $\alpha \in (0, 1)$. Since the embedding $C^{\alpha}[0, \gamma] \hookrightarrow C[0, \gamma]$ is compact, $F(p_n)$ converges strongly in $C[0, \gamma]$. So, we get that $F(p_n)(\xi) \to 0$ for any $\xi \leq \gamma$ and n large enough. Therefore, we conclude that $(F(p_n))(\xi)$ converges strongly to 0 in X, which verifies the claim. Similarly, it can be proven that F is also continuous. Thus, F is completely continuous.

Similarly, we define

$$T(p) = \int_{\xi}^{+\infty} \int_{+\infty}^{s} gp\, d\tau\, ds, \quad \xi \geq 0.$$

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Reasoning as above, we can still show that $T : X \to X$ is completely continuous. So, $I - k^2T$ is a completely continuous vector field in X. Thus, the Leray–Schauder degree $\deg(I - \lambda T, B_R(0), 0)$ with $\lambda = k^2$ is well defined for an arbitrary R-ball $B_R(0)$ of X and $k \in (0, k_2) \setminus \{k_1\}$.

LEMMA 3.1. *For arbitrary $R > 0$, one has that*

$$\deg(I - k^2T, B_R(0), 0) = \begin{cases} 1 & \text{if } k \in (0, k_1), \\ -1 & \text{if } k \in (k_1, k_2). \end{cases}$$

PROOF. We only prove the case $k > k_1$ since the proof for $k < k_1$ is completely analogous. Since T is compact and linear, by [6, Theorem 8.10], we have that

$$\deg(I - k^2T, B_R(0), 0) = -1,$$

which is the desired conclusion. □

Now, we can give the proof of our main result.

PROOF OF THEOREM 1.1. In view of Lemma 2.4, problem (2.2) can be written equivalently as

$$p = k^2T(p) + H(k, p),$$

where

$$H(k, p) = -k^2 \int_{\xi}^{+\infty} \int_{+\infty}^{s} gp^2 \, d\tau \, ds.$$

For any $p \in X \setminus \{0\}$, we have that

$$\frac{p^2}{\|p\|} \le \frac{|p|}{\|p\|}|p| \le \|p\| \to 0 \quad \text{as } \|p\| \to 0. \tag{3.1}$$

Thus, $H(k, p) = o(\|p\|)$ near $p = 0$ in X uniformly on bounded intervals of k in $(0, +\infty)$.

In view of Lemma 3.1, applying Proposition 2.7 by taking $O = (0, +\infty) \times X$, we obtain that $(k_1, 0)$ is a bifurcation point of problem (2.2), and the associated bifurcation branch C in $(0, +\infty) \times X$ whose closure contains $(k_1, 0)$ satisfies at least one of the following three options: (i) unbounded; (ii) meets to the X at $k = 0$; (iii) contains a pair $(\overline{k}, 0)$, where $\overline{k}$ is an eigenvalue of problem (2.1) and $\overline{k} \neq k_1$.

For any $(k, p) \in C$ with $p \not\equiv 0$, Lemma 2.4 implies that $0 < p \le 1$ in $[0, +\infty)$. Hence, we have $C \subseteq ((0, +\infty) \times X^+ \cup \{(k_1, 0)\})$. We *claim* that case (ii) does not occur. Assume that $(k, p) \in C$ with $k \le k_1$ and $p \not\equiv 0$. Then, from the argument of Lemma 2.6, we obtain that

$$0 \le -k_1^2 \int_0^{+\infty} gp^2 p_1 \, d\xi < 0,$$

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which is a contradiction. In fact, we not only proved that the second option does not occur, but we have also proved that the branch C will not reach the left side of $k = k_1$. That is to say, when $k \le k_1$, problem (1.1) only has the trivial solution $p = 0$.

We *claim* that option (iii) is also impossible. Suppose, in contrast, there exists $(k_n, p_n) \to (\bar{k}, 0)$ as $n \to +\infty$ with $(k_n, p_n) \in C$, $p_n \not\equiv 0$ and $\bar{k}$ is another eigenvalue of problem (2.1). Let $w_n = p_n/\|p_n\|$. Then, w_n satisfies the following problem:

$$w = k_n^2 T(w) - k_n^2 \int_{\xi}^{+\infty} \int_{+\infty}^{s} g w p_n \, d\tau \, ds.$$

Reasoning as for the compactness of F, we obtain that for some convenient subsequence, $w_n \to w_0$ as $n \to +\infty$. From (3.1), we can see that $(\bar{k}, w_0)$ verifies problem (2.1) and $\|w_0\| = 1$. Since C does not reach the left side of $k = k_1$, one has that $\bar{k} > k_1$. Proposition 2.1 implies that w_0 must change its sign, which contradicts the fact that $p_n > 0$.

Therefore, the branch C is unbounded. Moreover, C cannot return to the trivial solution axis and does not reach the left side of $k = k_1$. Since $0 < p \le 1$ in $[0, +\infty)$ for any $(k, p) \in C$ with $p \not\equiv 0$, one sees that C does not exceed 1 in the X direction. Thus, it must be unbounded in the k direction. Therefore, we obtain that the necessary and sufficient condition for the existence of the cline is $k > k_1$.

We will finally discuss uniqueness and asymptotic behaviour of the cline p. We recall a function defined by Nagylaki [18],

$$T(p_0) = \int_{\eta}^{1} \frac{1}{\sqrt{(1-y)[1+y-\frac{2}{3}p_0(1+y+y^2)]}} \, dy,$$

where $\eta = \widetilde{p}_1/p_0$ with $\widetilde{p}_1 = p(1)$. Nagylaki proved that $T(p_0)$ is strictly increasing to $+\infty$ as $p_0 \to 1^-$. This implies that there is a unique p_0 for $k > k_1$. Reasoning as that of Lemma 2.3 with some obvious changes, we can further show that the uniqueness of p_0 implies the uniqueness of p. Therefore, C is actually a curve. Moreover, there is a unique cline p for each $k > k_1$. The asymptotic behaviour of $T(p_0)$ as $p_0 \to 1^-$ implies that C is always less than 1 and tends towards 1. This completes the proof of Theorem 1.1. □

4. Proof of Theorem 1.2

In this section, we prove the stability results stated in Theorem 1.2. Define the operator

$$F(k, p) = \frac{p'' + k^2 g(\xi) p(1-p)}{g(\xi)}.$$

Clearly, the equation of problem (1.1) is equivalent to $-F(k, p) = 0$. Define

$$Y = \left\{ p \in X \mid p \in C^2([0,1) \cup (1, +\infty)), \ \lim_{\xi \to 1^-} p''(\xi) \text{ and } \lim_{\xi \to 1^+} p''(\xi) \text{ exist} \right\}.$$

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It is easy to see that the trivial solution $p = 0$ belongs to Y and the unique cline p obtained in Theorem 1.1 belongs to Y.

We recall the stability property of solutions. For any $\phi \in Y$ and positive solution p of problem (1.1), by some simple computations, we can show that the linearized eigenvalue problem of (1.1) about p at the direction ϕ is

$$\begin{cases} -\phi'' - k^2 g(\xi)(1-2p)\phi = \mu g(\xi)\phi, & \xi > 0, \\ \phi'(0) = 0, & \lim_{\xi\to+\infty} \phi'(\xi) = 0. \end{cases} \tag{4.1}$$

The linear stability of a solution u of problem (1.1) can be determined by the linearized eigenvalue problem (4.1). A solution p of problem (1.1) is *stable* if all eigenvalues of problem (4.1) are positive, otherwise it is *unstable*. Define the *Morse index* $M(p)$ of a solution p of problem (1.1) to be the number of negative eigenvalues of problem (4.1). A solution p of problem (1.1) is *degenerate* if 0 is an eigenvalue of problem (4.1), otherwise it is *nondegenerate*.

Now, we can present the argument of Theorem 1.2.

PROOF OF THEOREM 1.2. We first study the stability of the nontrivial solution. Let (k_*, p_*) be a nontrivial solution of (1.1). The Fréchet derivative of F with respect to p at (k_*, p_*) is given by

$$F_p(k_*, p_*)\varphi = \frac{\varphi'' + k_*^2 g(\xi)(1-2p_*)\varphi}{g(\xi)}, \quad \varphi \in Y.$$

Let μ_1 be the first eigenvalue of the operator $-F_p(k_*, p_*)$.

We *claim* that the corresponding eigenfunction φ_1 is positive. Note that φ_1 satisfies

$$-\varphi_1'' - k_*^2 g(\xi)(1-2p_*)\varphi_1 = \mu_1 g(\xi)\varphi_1. \tag{4.2}$$

We *claim* that $\int_0^{+\infty} g(\xi)\varphi_1^2\, d\xi \neq 0$. Indeed, if it was, we obtain from (4.2) that

$$\int_0^{+\infty} \varphi_1'^2\, d\xi + 2k_*^2 \int_0^{+\infty} g(\xi)\varphi_1^2 p_*\, d\xi = 0.$$

This implies

$$\int_0^{+\infty} g(\xi)\varphi_1^2 p_*\, d\xi < 0.$$

So, we have

$$\int_0^1 \varphi_1^2 p_*\, d\xi < \alpha^2 \int_1^{+\infty} \varphi_1^2 p_*\, d\xi.$$

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Using the monotonicity of p_*, we see that

$$\begin{aligned}\alpha^2 p_*(1)\int_1^{+\infty}\varphi_1^2\,d\xi &= p_*(1)\int_0^1\varphi_1^2\,d\xi\\ &\le \int_0^1\varphi_1^2 p_*\,d\xi\\ &< \alpha^2\int_1^{+\infty}\varphi_1^2 p_*\,d\xi\\ &\le \alpha^2 p_*(1)\int_1^{+\infty}\varphi_1^2\,d\xi,\end{aligned}$$

which is a contradiction. Hence, we have the following Rayleigh quotient of μ_1:

$$\mu_1 = \inf_{u\in Y\setminus\{0\}}\frac{\int_0^{+\infty}\varphi_1'^2\,d\xi - k_*^2\int_0^{+\infty}g(\xi)(1-2p_*)\varphi_1^2\,d\xi}{\int_0^{+\infty}g(\xi)\varphi_1^2\,d\xi}.$$

It follows that $|\varphi_1|$ is also the eigenfunction corresponding to μ_1. Since φ_1 is in C^1, we further obtain that φ_1 has only one sign. Without loss of generality, we assume that φ_1 is nonnegative. If φ_1 has a zero $\xi_0 > 0$ which clearly is a double zero, by an argument similar to that of Lemma 2.3 with obvious changes, we can show that $\varphi_1 \equiv 0$, which is impossible. Thus, we conclude that φ_1 is positive.

Since k_* and p_* are a solution of (1.1), we have

$$-p_*'' - k_*^2 g(\xi)p_*(1-p_*) = 0. \tag{4.3}$$

Multiplying (4.2) by $p_*/g(\xi)$ and (4.3) by $\varphi_1/g(\xi)$, subtracting the resulting equations and integrating over $[0,+\infty)$, we obtain, after integration by parts,

$$\mu_1\int_0^{+\infty}\varphi_1 p_* d\xi = k_*^2\int_0^{+\infty}\varphi_1 p_*^2\,d\xi.$$

Since both integrands are positive, it follows that $\mu_1 > 0$. Consequently, all eigenvalues of $-F_p(k_*,p_*)$ are positive. Thus, for any $k > \arctan\alpha$, the cline p is (asymptotically linearly) stable.

Next, we investigate the stability of the trivial solution $p = 0$. Set $p(s) = 0$ and $k(s) = k_1 + s$ for $s \in \mathbb{R}$ and $s > -k_1$. The Fréchet derivative of F with respect to p at $(k(s), p(s))$ is given by

$$F_p(k(s),p(s))\varphi(s) = \frac{\varphi''(s) + k^2(s)g(\xi)\varphi(s)}{g(\xi)} \quad \text{for all } \varphi(s)\in Y.$$

We assume that the first eigenvalue of $-F_p(k(s),p(s))$ is $\mu(s)$ with the corresponding eigenfunction $\phi(s)$. Then, $\phi(s)$ satisfies

$$-\phi''(s) - k^2(s)g(\xi)\phi(s) = \mu(s)g(\xi)\phi(s). \tag{4.4}$$

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As in the above case, we still can show that $\phi(s)$ is positive. From the spectral analysis in Section 2, we recall that when $k(s) = k_1$, (4.4) has a zero eigenvalue. A direct computation shows that for $k(s) \neq k_1$, the first eigenvalue is given by

$$\mu(s) = k_1^2 - k^2(s) = \begin{cases} > 0, & s < 0, \\ < 0, & s > 0. \end{cases}$$

It follows that $p = 0$ is (asymptotically linearly) stable when $s < 0$ and unstable when $s > 0$. This completes the proof of Theorem 1.2. □

From the argument of Theorem 1.2, we know that the cline p is nondegenerate and has Morse index $M(p) = 0$. The trivial solution $p = 0$ is nondegenerate and has Morse index $M(0) = 0$ for $k < k_1$.

5. Conclusion

In this paper, we have shown that for a semi-infinite habitat with a piecewise-constant sign-changing selection coefficient, there exists a unique cline if and only if $k > \arctan \alpha$. The bifurcation branch emanating from $(k_1, 0)$ is unbounded and tends to 1 as $k \to +\infty$. Moreover, every cline on this branch is asymptotically linearly stable, while the trivial solution $p = 0$ is stable for $k < k_1$ and unstable for $k > k_1$. These results give a complete affirmative answer to Nagylaki's conjecture and provide a rigorous mathematical foundation for cline models in population genetics.

Acknowledgement

This research was supported by NNSF of China (No. 12371110).

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