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MONOTONE AND NONMONOTONE CLINES WITH PARTIAL PANMIXIA ACROSS A GEOGRAPHICAL BARRIER

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Abstract. The number of clines (i.e., nonconstant equilibria) maintained by viability selection, migration, and partial global panmixia in a step-environment with a geographical barrier is investigated. Our results extend the results of T. Nagylaki (2016, Clines with partial panmixia across a geographical barrier, Theor. Popul. Biol. 109) from the no dominance case to arbitrary dominance and to various other selection functions. Unexpectedly, besides the usual monotone clines, we discover nonmonotone clines with both equal and unequal limits at $\pm\infty$.

1. **Introduction.** The term *cline* was first coined by the English evolutionary biologist Julian Huxley in 1938, which describes a continuous gradient of gene frequencies, genotypic frequencies, or phenotypic frequencies of a species across its geographical range. Since the formation of clines is closely related to species adaptation, speciation, and the maintenance of genetic variability, the study of clines has been an important research subject in population genetics, ecology, and related fields.

In PDE models on the evolution of gene frequencies, *clines are nonconstant equilibrium solutions.* The general cline theory of regular migration-selection model can be found in a series of systematic studies by Lou and Nagylaki [8, 9, 10]; in the review papers by Nagylaki and Lou [17], Lou et al. [11], and Bürger [1]; and in recent works by Hofbauer and Su [5, 6], Nakashima [22, 23, 24], Sovrano [26], and Feltrin and Sovrano [2, 3].

The effect of long-distance migration can be approximated by partial global panmixia (global random mating), which adds an integral term in the regular migration-selection model, and makes it nonlocal [14, 15]. Further works in this direction are Lou et al. [12], Nagylaki et al. [18], Nagylaki and Zeng [20, 21], Su and Nagylaki [27], and Li et al. [7].

A geographical barrier that divides a habitat into two often occurs in nature such as a mountain chain, a river, or a railway. However, relatively little cline theory has considered this factor; see, e.g., Nagylaki [13] and the references therein. An

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obvious distinction is that clines will be discontinuous at a barrier. The spread of an advantageous allele may also be delayed by a barrier [25].

In the pioneer work [16], Nagylaki derived a new model that includes all of the above features, namely, a single-locus migration-selection model with partial panmixia in the presence of a geographical barrier. In particular, he deduced an explicit formula for the unique cline, which is monotone, under the assumptions of two alleles without dominance, a step-environment, and homogeneous and isotropic local migration on the entire line.

The purpose of this paper is to generalize Nagylaki's analysis in [16] from the no dominance case to arbitrary dominance, and to various other selection functions. In previously studied models, clines maintained by a step-environment are usually monotone [4, 27, 16]. Surprisingly, for a certain range of degree of dominance, we discover the existence of nonmonotone clines maintained by a step-environment. Our results shed some light on the interaction of these evolutionary factors on clines, especially the joint effects of degree of dominance, partial panmixia, and geographical barrier.

In Section 2, we formulate the model (1) and introduce some preliminary properties. We present our results on clines of (1) in Section 3 for the case $p_- < p_+$; the main results are Theorems 3.1, 3.4, 3.7, 3.8, 3.11, and 3.12. Section 4 is devoted to the case $p_- = p_+$; the main results are Theorems 4.1 and 4.3. In particular, the existence of nonmonotone clines is established in Theorems 3.11 and 4.3. We summarize our results and discuss open problems in Section 5.

2. The model problem and preliminary properties.

Here, we briefly recapitulate the formulation in [16, Sect. 4]. Assume that the gene under consideration is at a single-locus with two alleles A_1 and A_2. The diploid population occupies the entire line $\mathbb{R}$. Under the joint action of viability selection, local adult migration, and partial panmixia with a geographical barrier at $x = 0$, Nagylaki derived the following equation for the frequency of A_1 at equilibrium [16]:

$$p'' + g(x)f(p) + \beta(\bar{p} - p) = 0, \quad x \in \mathbb{R} \setminus \{0\}, \tag{1a}$$

$$p_\pm = p(\pm\infty), \tag{1b}$$

$$p'(\pm\infty) = 0, \tag{1c}$$

$$p'(0\pm) = \theta_\pm \delta, \tag{1d}$$

where

$$\bar{p} = \frac{1}{2}(p_- + p_+), \tag{1e}$$

$$\delta = p(0+) - p(0-). \tag{1f}$$

In (1a), $g(x)f(p)$ designates the effect of selection on allele A_1. If the fitness of genotype A_iA_j, denoted by r_{ij} for $i, j = 1, 2$, is independent of gene frequency, one may assume

$$r_{11} = g(x), \quad r_{12} = r_{21} = hg(x), \quad r_{22} = -g(x), \tag{2}$$

where the constant $h \in [-1, 1]$ is the degree of dominance. When $h = 0$, $h = -1$, and $h = 1$, there is no dominance, A_2 is completely dominant to A_1, and A_2 is recessive, respectively. Under (2), the selection function f reads

$$f(p) = p(1 - p)(1 + h - 2hp). \tag{3}$$

The spatial factor $g(x)$ specifies the direction of selection, i.e., at location x, allele A_1 (A_2) is selectively favored if $g(x) > 0$ (< 0).

In this paper, following [16], we focus on a step-environment, i.e.,

$$g(x) = \begin{cases} -\alpha & \text{if } x < 0, \\ 1 & \text{if } x > 0, \end{cases} \tag{4}$$

where the parameter $\alpha > 0$ measures the relative strength of negative selection to positive selection. Note that this step-environment applies also to a plane habitat of two types that is divided by a linear boundary, and x is the directed distance of any point from this boundary.

In general, directional selection functions satisfy

$$f \in C^1([0,1]), \quad f(0) = f(1) = 0, \quad f(p) > 0 \quad \text{in } (0,1). \tag{5}$$

In [19] and [27], the unimodality of f emerged as a crucial simplifying assumption, i.e.,

$$\exists\ \hat{p} \in (0,1) \text{ s.t. } f \text{ is strictly increasing \& decreasing in } (0,\hat{p}) \text{ \& } (\hat{p},1), \text{ resp.,} \tag{6}$$

which is applied also in this paper. In particular, the cubic f in (3) is unimodal.

The term $\beta[\bar{p} - p(x)]$ in (1a) describes the effect of long-distance migration. It means that at location x, a portion of population is replaced by the "averaged" population over the habitat due to panmixia. The parameter $\beta > 0$ is the scaled panmictic rate; a larger β means a larger portion of the population is pamictic. The term p'' represents the effect of population local migration, whose rate is scaled out.

The discontinuities of $p(x)$ and $p'(x)$ at $x = 0$ are due to a geographical barrier there. They satisfy the transmission conditions (1d,f). The parameters $\theta_\pm > 0$ are the scaled transmissivities crossing the barrier from left to right and from right to left, respectively. Smaller $\theta_\pm$ corresponds to a stronger barrier. In particular, $\theta_\pm \to 0$ and $\theta_\pm \to \infty$ show that the barrier becomes impenetrable and the barrier disappears, respectively.

The following Proposition 1 and Theorem 2.1 were proved by Nagylaki [16].

Proposition 1. ([16, Proposition 4.2]) *If* (1a,b,e), (4), *and* (5) *hold, then*
(i) $p''(\pm\infty) = 0$*;*
(ii)

$$f(p_+) = \alpha f(p_-) = \frac{1}{2}\beta(p_+ - p_-); \tag{7}$$

(iii) $0 < p_- < p_+ < 1$ *except for the trivial solutions* $p_- = p_+ = 0$ *and* $p_- = p_+ = 1$*.*

In the absence of both frequency dependence and dominance, i.e., $h = 0$ in (3), the selection function has the simplest form

$$f(p) = p(1 - p). \tag{8}$$

For every $\alpha > 0$, define the critical panmictic rate as

$$\beta_0(\alpha) = \begin{cases} \frac{2\alpha}{|\alpha - 1|} & \text{if } \alpha \neq 1, \\ \infty & \text{if } \alpha = 1. \end{cases} \tag{9}$$

Theorem 2.1. ([16, Proposition 4.6 and Th.4.8]) *Suppose that* (4) *and* (8) *hold. If* $\alpha > 0$, $\beta \in (0, \beta_0)$, *and* $\theta_\pm > 0$, *then* (1) *has a unique cline* $p(x) \in C^2(\mathbb{R} \setminus \{0\})$, *which satisfies* (i) $p_- < p(x) < p_+$ *in* $\mathbb{R}$, (ii) $p'(x) > 0$ *in* $\mathbb{R} \setminus \{0\}$, *and* (iii) $p''(x) \gtrless 0$ *if* $x \lessgtr 0$.

The existence and uniqueness in Theorem 2.1 were proved by tedious calculations that verify the sign and number of roots of many involved polynomials, relying crucially on the special form (8). In the next section, we mainly use phase-plane analysis to generalize Theorem 2.1 from (8) to a much wider class of selection functions.

3. **Clines with $p_- < p_+$.** We establish the existence, uniqueness, multiplicity, monotonicity, and non-monotonicity of clines for problem (1) with various selection functions f. According to Proposition 1(iii), the gene frequencies at $\pm\infty$ satisfy either $0 < p_- < p_+ < 1$, $p_- = p_+ = 0$, or $p_- = p_+ = 1$. In this section, we will focus on clines with $p_- < p_+$, and treat the latter two cases in Section 4. We state our results for $\alpha = 1$ and $\alpha > 1$ in Sections 3.1 and 3.2, respectively. The case $\alpha < 1$ can be converted to the case $\alpha > 1$ by considering the equation of $1 - p(-x)$; see [27, Sect.7.2.3] for more details regarding this transformation.

The following functions play important roles in our proofs.

$$F(p) := \int_0^p f(\xi)\, d\xi, \tag{10}$$

$$H^+(p,q) := \frac{1}{2}q^2 + F(p) - \frac{1}{2}\beta(p-\bar{p})^2, \tag{11}$$

$$H^-_\alpha(p,q) := \frac{1}{2}q^2 - \alpha F(p) - \frac{1}{2}\beta(p-\bar{p})^2, \tag{12}$$

and

$$\Phi_{\theta_-,\theta_+}(p,q) := (p + \tfrac{1}{\theta_-}q, \tfrac{\theta_+}{\theta_-}q). \tag{13}$$

3.1. **$\alpha = 1$.** Theorem 3.1 is the main result of this section, which generalizes Theorem 2.1 for $\alpha = 1$ from $p(1-p)$ to unimodal selection functions.

Theorem 3.1. *If $\alpha = 1$ and the assumptions (4)–(6) hold, then for every $\beta > 0$ and every $\theta_\pm > 0$, problem (1) has a unique cline $p(x) \in C^2(\mathbb{R}\setminus\{0\})$ with $0 < p_- < p_+ < 1$, which satisfies* (i) *$p_- < p(x) < p_+$ in $\mathbb{R}$,* (ii) *$p'(x) > 0$ in $\mathbb{R}\setminus\{0\}$, and* (iii) *$p''(x) \gtrless 0$ if $x \lessgtr 0$.*

To prove Theorem 3.1, we need the following two results.

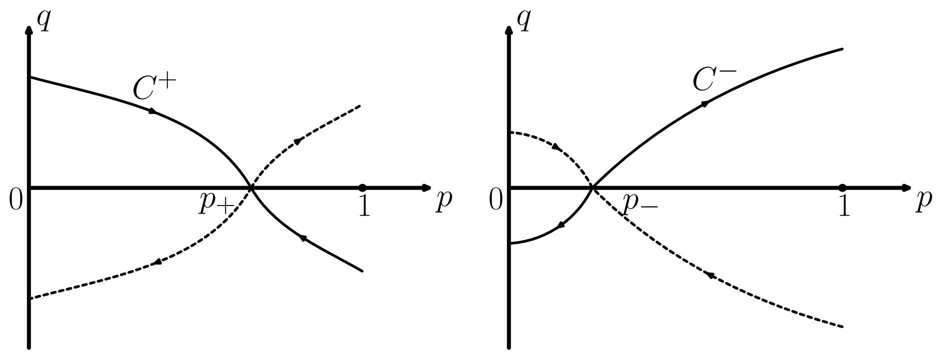
Theorem 3.2. ([27, Th.8.2]) *The assumptions $\alpha = 1$, (5), and (6) imply that for every $\beta > 0$, the system (7) has a unique solution pair $p_\pm$ with $0 < p_- < p_+ < 1$.*

Lemma 3.3. ([27, Lemma 7.9 and Fig.1]) *Under the assumptions in Theorem 3.2, for every solution pair $0 < p_- < p_+ < 1$ of (7) and the corresponding $\bar{p}$ as in (1e), it holds that*

$$f(p) - \beta(p-\bar{p}) > 0 \quad \forall\ p \in (0, p_+), \tag{14a}$$
$$f(p) - \beta(p-\bar{p}) < 0 \quad \forall\ p \in (p_+, 1), \tag{14b}$$
$$\alpha f(p) + \beta(p-\bar{p}) < 0 \quad \forall\ p \in (0, p_-), \tag{14c}$$
$$\alpha f(p) + \beta(p-\bar{p}) > 0 \quad \forall\ p \in (p_-, 1). \tag{14d}$$

Proof of Theorem 3.1. For every $\beta > 0$, let $p_\pm$ be as in Theorem 3.2. Let $q = p'$. For $x > 0$, by (4), we write (1a) as the equivalent system

$$\begin{cases} p' = q, \\ q' = -f(p) + \beta(p-\bar{p}), \quad x > 0, \end{cases} \tag{15}$$



(A) Graph of C^+. (B) Graph of C^-.

FIGURE 1

which is Hamiltonian with energy function $H^+(p,q)$ as in (11). From (11) and (14a,b) we have the following observations.

(a) H^+ is an even function of q.

(b)

$$\frac{\partial H^+}{\partial q}(p,q) = q \lesseqgtr 0 \text{ for } q \lesseqgtr 0. \tag{16}$$

(c)

$$\frac{\partial H^+}{\partial p}(p,q) = f(p) - \beta(p-\bar{p}) \begin{cases} > 0 & \forall\, p \in (0, p_+), \\ < 0 & \forall\, p \in (p_+, 1). \end{cases} \tag{17}$$

Then one can easily draw in the pq-plane the phase portrait for system (15). Fig.1(A) shows the solutions that lie in the level $H^+(p_+,0)$. In light of the boundary conditions (1b,c), the solid arcs tending to $(p_+,0)$ as $x \to \infty$, as indicated by the arrow heads, are of special interest. They are labeled by C^+ in Fig.1(A).

For $x < 0$, by (4), we write (1a) equivalently as

$$\begin{cases} p' = q, \\ q' = \alpha f(p) + \beta(p-\bar{p}), \quad x < 0, \end{cases} \tag{18}$$

which is Hamiltonian with energy function $H_1^-(p,q)$ as in (12) for $\alpha = 1$. From (12) and (14c,d) we have the following observations.

(d) H_1^- is an even function of q.

(e)

$$\frac{\partial H_1^-}{\partial q}(p,q) = q \lesseqgtr 0 \text{ for } q \lesseqgtr 0. \tag{19}$$

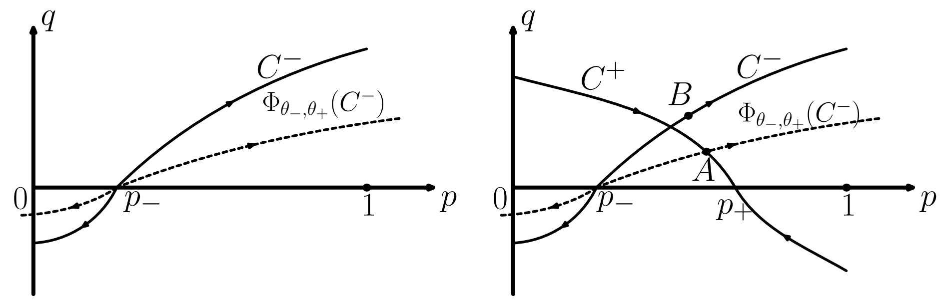
(f)

$$\frac{\partial H_1^-}{\partial p}(p,q) = -f(p) - \beta(p-\bar{p}) \begin{cases} > 0 & \forall\, p \in (0, p_-), \\ < 0 & \forall\, p \in (p_-, 1). \end{cases} \tag{20}$$

Then one can easily draw in the pq-plane the phase portrait for system (18). Fig.1(B) shows the solutions that lie in the level $H_1^-(p_-,0)$. In light of the boundary conditions (1b,c), the solid arcs emanating from $(p_-,0)$ as $x \to -\infty$, as indicated by the arrow heads, are of special interest. They are labeled by C^- in Fig. 1(B).

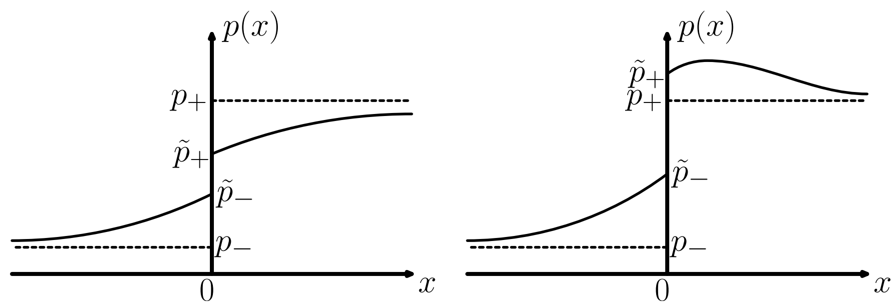
To meet the transmission conditions (1d,f), we utilize the map Φ_{θ_-,θ_+} in (13). Write $\tilde{p}_\pm = p(0\pm)$ and $\tilde{q}_\pm = q(0\pm)$. Then (1d,f) are equivalent to

$$(\tilde{p}_+, \tilde{q}_+) = \Phi_{\theta_-,\theta_+}(\tilde{p}_-, \tilde{q}_-). \tag{21}$$



(A) C^- and $\Phi_{\theta_-,\theta_+}(C^-)$. (B) C^+, C^-, and $\Phi_{\theta_-,\theta_+}(C^-)$.

FIGURE 2



(A) Monotone cline. (B) Nonmonotone cline.

FIGURE 3

From (13) we see that $\Phi_{\theta_-,\theta_+}(p_-, 0) = (p_-, 0)$; Φ_{θ_-,θ_+} maps points on C^- one-to-one to points on $\Phi_{\theta_-,\theta_+}(C^-)$, the dashed curves in Fig. 2(A), which keeps the monotonicity of C^-.

Now superimposing C^+ and the phase portraits in Fig. 2(A), one obtains a unique point of intersection of C^+ with $\Phi_{\theta_-,\theta_+}(C^-)$, denoted by A. Let B be the unique preimage of A under Φ_{θ_-,θ_+}. Thus, we obtain a unique cline $p(x)$ of (1) that connects the p_- and p_+ at infinity, which corresponds to the path

$$\text{from } (p_-, 0) \text{ to } B \text{ along } C^-, \text{ from } B \text{ jumping to } A, \text{ from } A \text{ to } (p_+, 0) \text{ along } C^+.$$

Finally, observe that $p' = q > 0$ on this path, $p'' = q' > 0$ until point B (corresponding to $x < 0$), and $p'' = q' < 0$ after point A (corresponding to $x > 0$). These demonstrate Theorem 3.1(i)-(iii). □

We draw a typical cline $p(x)$ guaranteed by Theorem 3.1 in Fig. 3(A), in which $\tilde{p}_\pm$ are the p-coordinate of points B and A in Fig. 2(B), respectively.

Remark 1. For $\alpha = 1$, Theorem 3.1 generalizes Theorem 2.1 from (8) to general unimodal f. In particular, it applies to the cubic (3) for $h \in [-1, 1]$.

3.2. $\alpha > 1$**.** In this section, we focus on unimodal f with a maximum value achieved at $\hat{p}$, which is either concave down on the left of $\hat{p}$ or has one point of inflection there.

Define

$$\beta_* = \frac{2\alpha}{\alpha - 1}[f'(0)]. \tag{22}$$

Note that the β_0 in (9) agrees with β_* when $\alpha > 1$ and $f(p) = p(1-p)$.

Theorem 3.4. *Suppose that $\alpha > 1$, the assumptions (4)–(6) and $f(p) \in C^2([0,\hat{p}])$ hold. If*

$$f''(p) < 0 \quad in\ (0,\hat{p}), \tag{23}$$

then for every $\beta \in (0,\beta_*)$ and every $\theta_\pm > 0$, problem (1) has a unique cline with $0 < p_- < p_+ < 1$, which is strictly increasing; no cline with $0 < p_- < p_+ < 1$ exists if $\beta \geq \beta_*$.

To prove Theorem 3.4, we need the following two results in [27].

Theorem 3.5. ([27, Th.8.3(i)]) *The assumptions $\alpha > 1$, (5), (6), and $f(p) \in C^2([0,\hat{p}])$ with (23) imply that system (7) has a unique solution pair $p_\pm$ with $0 < p_- < p_+ < 1$ for every $\beta \in (0,\beta_*)$ and only trivial solutions for every $\beta \geq \beta_*$.*

Lemma 3.6. ([27, Lemma 7.12 and Fig.2]) *Under the assumptions in Theorem 3.5, for every nontrivial solution pair $p_\pm$ of (7) and the corresponding $\bar{p}$ as in (1e), the inequalities in (14) hold.*

(Notice that the assumptions on f in Theorem 3.5 imply (7.40) in [27, Lemma 7.12].)

Proof of Theorem 3.4. The proof is exactly the same as the one of Theorem 3.1 with minor modifications, i.e., replacing H_1^- by H_α^- and applying Theorem 3.5 and Lemma 3.6 instead of Theorem 3.2 and Lemma 3.3. □

Remark 2. Theorem 3.4 applies to the cubic (3) if and only if $h \in [-1/3, 1]$.

Condition (23) says that f is concave down on the left of its maximum $\hat{p}$. Next, we discuss the case that f has one inflection point on the left of $\hat{p}$, i.e., there exists $\check{p} \in (0,\hat{p})$ such that

$$f''(p) > 0 \quad \text{in } [0,\check{p}) \quad \text{and} \quad f''(p) < 0 \quad \text{in } (\check{p},\hat{p}). \tag{24}$$

In this case, as explained in Remark 3, the phase portrait of (18) remains the same as in Fig. 1(B). However, we will see that the phase portrait of (15) can be much more complicated than in Fig. 1(A) as shown in Figs. 4(B), 5(B), and 7.

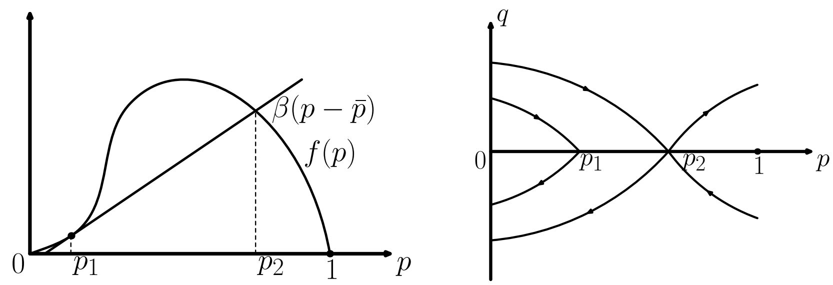
Remark 3. For $\alpha > 1$ and unimodal f with maximum value achieved at $\hat{p}$, the proof of Lemma 7.12 (especially, Cases 1 and 3) in [27] shows that p_- is the unique zero of $[\alpha f(p) + \beta(p - \bar{p})]$ in $(0,1)$, which implies that (14c,d) hold. Then the arguments for $x < 0$ in the proof of Theorem 3.1 apply, and the phase portrait of system (18) is as in Fig. 1(B).

Remark 4. For $\alpha > 1$ and unimodal f that satisfies (24), the graph of $f(p)$ and the line

$$L(p) := \beta(p - \bar{p}) \tag{25}$$

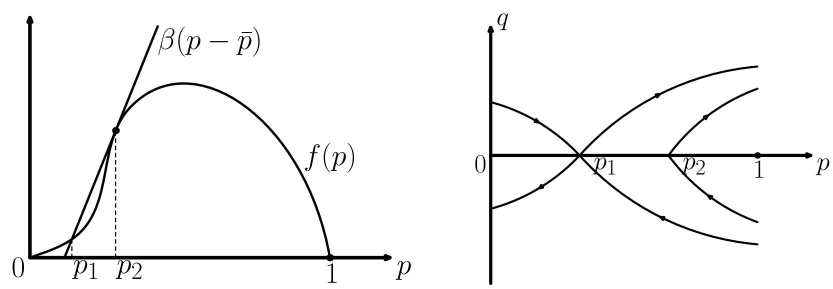
may have up to $m = 3$ intersection points in $(0,1)$. First, we consider $m = 1, 2$.
(i) $m = 1$: The unique intersection point has to be p_+ and it is clear that (14a,b) hold from the geometry of f and L. Then the arguments for $x > 0$ in the proof of Theorem 3.1 apply, and the corresponding phase portrait of system (15) is as in Fig. 1(A).
(ii) $m = 2$: We order the two intersection points as p_1 and p_2 with $p_1 < p_2$; then $p_1 < \check{p} < p_2$ and L is tangent to f at either p_1 or p_2. Figs. 4 and 5 show L and f with the corresponding phase portraits of system (15) for the tangent point being p_1 and p_2, respectively. There are four possibilities.

(a) Fig. 4 with $p_+ = p_1$: The orbit tending to p_+ in Fig. 4(B) is qualitatively the same as in Fig. 1(A).
(b) Fig. 4 with $p_+ = p_2$: Same as (a).
(c) Fig. 5 with $p_+ = p_1$: Same as (a).
(d) Fig. 5 with $p_+ = p_2$: The orbit tending to p_+ in Fig. 5(B) is below $q = 0$, which has no point of intersection with $\Phi_{\theta_-,\theta_+}(C^-)$ (see Fig. 2(B)); thus no cline exists.



(A) (B)

Figure 4. A sketch of the situation in Remark 4(ii); where (A) shows that the straight line $\beta(p-\bar{p})$ is tangent to the graph of $f(p)$ at p_1, and (B) shows the corresponding phase portraits of (15).



(A) (B)

Figure 5. Same as Fig. 4 except that the straight line $\beta(p-\bar{p})$ is tangent to the graph of $f(p)$ at p_2.

In light of Remarks 3 and 4, the same arguments as in Theorem 3.1 immediately yield the following Theorems 3.7 and 3.8.

Theorem 3.7. *Suppose that* (4)–(6) *and* (24) *hold. Assume* $\alpha > 1$, $\beta > 0$, $p_\pm$ *is a nontrivial solution pair of* (7) *and determines* $\bar{p}$ *as in* (1e), *and the function* $[f(p) - \beta(p-\bar{p})]$ *has a unique zero in* $(0,1)$. *Then for every* $\theta_\pm > 0$, *problem* (1) *has a unique solution, which is strictly increasing.*

Theorem 3.8. *Suppose that* (4)–(6) *and* (24) *hold. Assume* $\alpha > 1$, $\beta > 0$, $p_\pm$ *is a nontrivial solution pair of* (7) *and determines* $\bar{p}$ *as in* (1e), *and the function* $[f(p) - \beta(p-\bar{p})]$ *has exactly two zeros* $p_1 < p_2$ *in* $(0,1)$.
(i) *In every case of Remark* 4(iia,b,c), *for every* $\theta_\pm > 0$, *problem* (1) *has a unique solution, which is strictly increasing.*
(ii) *If Remark* 4(iid) *applies, then for any* $\theta_\pm > 0$, *problem* (1) *has no solution.*

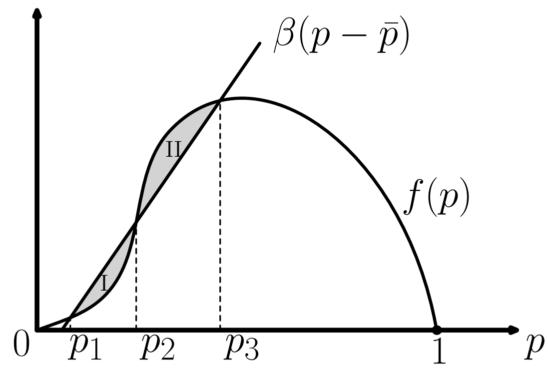


FIGURE 6. Graph of $f(p)$ and the straight line $\beta(p-\bar{p})$ if $m=3$.

Second, we discuss the case that the function $[f(p)-\beta(p-\bar{p})]$ has $m=3$ zeros in $(0,1)$ as shown in Fig. 6.

Remark 5. Since a concave up/down function can have at most two points of intersection with a straight line, if f satisfies (5), (6), and (24) such that $[f(p)-\beta(p-\bar{p})]$ has three zeros $p_1<p_2<p_3$, then $p_1\in(0,\check{p})$ and $p_3\in(\check{p},1)$.

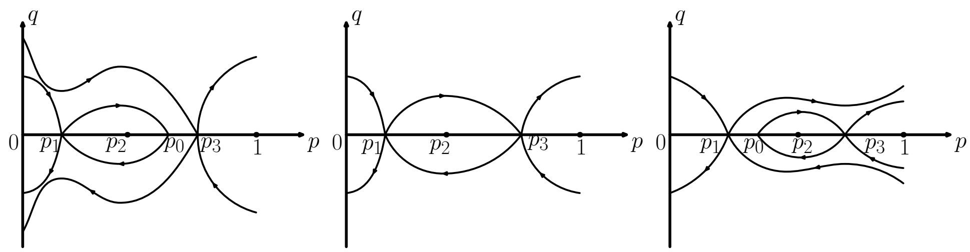
Lemma 3.9. *Suppose that f satisfies (5) and (6), and that for some fixed $\beta>0$ and $\bar{p}\in(0,1)$, the function $[f(p)-\beta(p-\bar{p})]$ has exactly three zeros p_1, p_2, and p_3 with $0<p_1<p_2<p_3<1$. Let I and II be the area surrounded by the graph of $f(p)$ and the straight line $\beta(p-\bar{p})$ for p in (p_1,p_2) and (p_2,p_3), respectively, as shown in Fig. 6. Then the following conclusions hold:*
(i) $I<II \iff H^+(p_1,0)<H^+(p_3,0)$,
(ii) $I=II \iff H^+(p_1,0)=H^+(p_3,0)$,
(iii) $I>II \iff H^+(p_1,0)>H^+(p_3,0)$,
where H^+ is as in (11).

Proof. The proof is straightforward by (10) and (11):

$$\begin{aligned} I-II &= -\int_{p_1}^{p_2}[f(\xi)-\beta(\xi-\bar{p})]d\xi-\int_{p_2}^{p_3}[f(\xi)-\beta(\xi-\bar{p})]d\xi \\ &= \int_0^{p_1}[f(\xi)-\beta(\xi-\bar{p})]d\xi-\int_0^{p_3}[f(\xi)-\beta(\xi-\bar{p})]d\xi \\ &= H^+(p_1,0)-H^+(p_3,0), \end{aligned}$$

from which (i)–(iii) follow. ∎

Lemma 3.10. *Assume that the assumptions in Lemma 3.9 hold.*
(i) *If $I<II$, then the phase portrait of (15) is as in Fig. 7(A); there exists a homoclinic orbit connecting the equilibrium $(p_1,0)$ with itself.*
(ii) *If $I=II$, then the phase portrait of (15) is as in Fig. 7(B); there exist heteroclinic orbits connecting the equilibria $(p_1,0)$ and $(p_3,0)$.*
(iii) *If $I>II$, then the phase portrait of (15) is as in Fig. 7(C); there exists a homoclinic orbit connecting the equilibrium $(p_3,0)$ with itself.*



(A) $I < II$. (B) $I = II$. (C) $I > II$.

FIGURE 7. Phase portraits of (15) in Lemma 3.10 with $I < II$, $I = II$, and $I > II$, respectively; where I and II stand for the areas enclosed by the graphs of $L(p)$ and $f(p)$ as shown in Fig. 6.

Proof. Observations (a) and (b) in the proof of Theorem 3.1 still hold, and observation (c) becomes

$$\frac{\partial H^+}{\partial p}(p,q) = f(p) - \beta(p-\bar{p}) \begin{cases} > 0 & \forall\ p \in (0,p_1) \cup (p_2,p_3), \\ < 0 & \forall\ p \in (p_1,p_2) \cup (p_3,1). \end{cases} \tag{26}$$

Then according to the relation between $H^+(p_1,0)$ and $H^+(p_3,0)$, or the equivalent relation between I and II, in each case, one can easily draw in the pq-plane the solution portraits that lie in these two levels for system (15). Note that the point $(p_0,0)$ in Figs. 7(A,C) is not an equilibrium. □

Following Fig. 7, we now discuss the cases $p_+ = p_i$ for $i = 1,2,3$, respectively.

1. $p_+ = p_1$**.**

We first consider the case (A) $I < II$ in Fig. 7. In fact, this is the only case that may produce nonmonotone clines with $p_- < p_+$. We make the following assumption.

(**H1**) Suppose that the assumptions in Lemma 3.9, $I < II$, $p_+ = p_1$ and $p_- = 2\bar{p} - p_+ > 0$ hold.

Theorem 3.11. *Suppose that* (H1) *holds and* $\alpha > 1$ *such that* $\alpha f(p_-) = f(p_+)$. *Then*
(i) *for every* $\theta_\pm > 0$, *problem* (1) *has a unique monotone cline;*
(ii) *for every* $\theta_- > 0$, *there exists* $\theta_* > 0$ *such that problem* (1) *has zero and at least two nonmonotone clines for* $\theta_+ > \theta_*$ *and* $\theta_+ < \theta_*$, *respectively.*

Proof. In light of Lemma 3.10, under assumption (H1), the phase portraits of (15) are as in Fig. 7(A) with $p_1 = p_+$. We denote the curve with energy $H^+(p_+,0)$ by C^+ and decompose it into

$$\begin{aligned} &\{C_{1,\pm}\} \cup \{C_{2,\pm}\} \\ &= \{(p,q) \in C^+ |\ q \gtrless 0, 0 < p < p_+\} \cup \{(p,q) \in C^+ |\ q \gtrless 0, p_+ < p < p_0\}. \end{aligned} \tag{27}$$

Recall Remark 3, for every $\theta_\pm > 0$, the phase portraits of (18) and the image $\Phi_{\theta_-,\theta_+}(C^-)$ are as in Fig.2(A). Superimposing them with $\{C_{1,+}\}$, one obtains the unique monotone cline exactly the same way as in the proof of Theorem 3.1. This proves Part (i).

Now for each $\theta_- > 0$, in light of (13), one may raise or lower the curve $\Phi_{\theta_-,\theta_+}(C^-)$ by varying θ_+. Let θ_* be the critical value such that $\Phi_{\theta_-,\theta_+}(C^-)$ does not intersect $C_{2,+}$ if $\theta_+ > \theta_*$ and intersects $C_{2,+}$ at two or more points if $0 < \theta_+ < \theta_*$; Fig. 8 shows

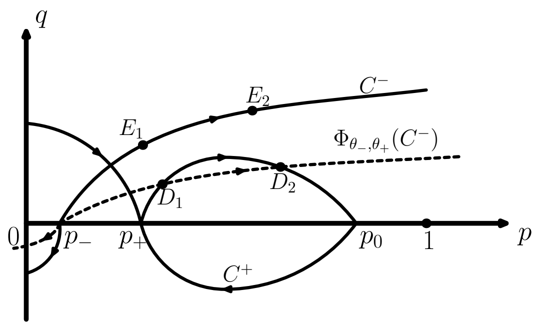


FIGURE 8. Superimposition of the phase portrait C^- of (18) and its image under Φ_{θ_-,θ_+} with the phase portraits of (15).

two intersection points D_1 and D_2 for example. For each such point of intersection D_i, we denote its unique preimage via Φ_{θ_-,θ_+} by E_i, then the corresponding cline $p(x)$ of (1) has the path

$$(p_-,0) \to E \text{ along } C^-,\ E_i \text{ jumping to } D_i,\ D_i \to (p_0,0) \text{ along } C_{2,+},$$
$$(p_0,0) \text{ to } (p_+,0) \text{ along } C_{2,-}.$$

Moreover, $p'(x) > 0$ until $p(x)$ reaches its maximum value p_0, and $p'(x) < 0$ afterwards. This completes the proof of Part (ii). □

A typical cline in Theorem 3.11(i) is qualitatively the same as in Fig. 3(A). We exhibit a typical nonmonotone cline in Theorem 3.11(ii) in Fig. 3(B).

Next, we consider the cases (B) $I = II$ and (C) $I > II$ in Figs. 7.

Theorem 3.12. *Suppose that (4)–(6) and (24) hold. Assume $\alpha > 1$, $\beta > 0$, $p_\pm$ is a nontrivial solution pair of (7) and determines $\bar{p}$ as in (1e), and the function $[f(p) - \beta(p - \bar{p})]$ has exactly three zeros in $(0, 1)$ as shown in Fig. 6 with $p_+ = p_1$ and $I \geq II$. Then for every $\theta_\pm > 0$, problem (1) has a unique cline, which is strictly increasing.*

Proof. From Figs. 7(B,C), we see that the phase portrait of the orbit that tends to p_+ is qualitatively the same as in Fig. 1(A), whence with Remark 3, the conclusion in Theorem 3.12 follows from the same arguments as in Theorem 3.1. □

2. $p_+ = p_2$.

Remark 6. We observe in either case of Fig. 7, that the level curve of $H^+(p_2, 0)$ contains a single point p_2. Therefore, if $p_+ = p_2$, there is no cline $p(x)$ connecting $p_\pm$ as $x \to \pm\infty$.

3. $p_+ = p_3$.

Remark 7. In either case of Fig. 7, if $p_+ = p_3$, only monotone clines may exist.
(A) $I < II$: We denote the curve with energy $H^+(p_3, 0)$ by C^+ and decompose it into

$$\begin{aligned} &\{C_{1,\pm}\} \cup \{C_{2,\pm}\} \\ &= \{(p,q) \in C^+ |\ q \gtrless 0, 0 < p < p_3\} \cup \{(p,q) \in C^+ |\ q \gtrless 0, p > p_3\}. \end{aligned} \tag{28}$$

Recall Remark 3, for every $\theta_\pm > 0$, the phase portrait of (18) and the image $\Phi_{\theta_-,\theta_+}(C^-)$ are as in Figs.1(B) and 2(A). Note that $\{C_{1,+}\}$ is not monotone now,

which may have multiple points of intersection with $\Phi_{\theta_-,\theta_+}(C^-)$, each of which will produce a monotone cline connecting $p_\pm$.
(B) $I = II$: We denote the heteroclinic orbit emanating from $(p_1, 0)$ to $(p_3, 0)$ by C^+. Now for each $\theta_- > 0$, in light of (13), one may raise or lower the curve $\Phi_{\theta_-,\theta_+}(C^-)$ by varying θ_+. Let θ_* be the critical value such that $\Phi_{\theta_-,\theta_+}(C^-)$ does not intersect C^+ if $\theta_+ > \theta_*$ and intersects C^+ at two or more points if $\theta_+ < \theta_*$. Each such point of intersection will produce a monotone cline connecting $p_\pm$.
(C) $I > II$: We denote the orbit from $(p_0, 0)$ to $(p_3, 0)$ by C^+. Then the situation is very similar to (B).

Remark 8. Here we summarize our results on clines in Theorems 3.7, 3.8, 3.11, and 3.12; and Remarks 6 and 7. Suppose that (4)–(6) and (24) hold. Assume $\alpha > 1$, $\beta > 0$, $p_\pm$ is a nontrivial solution pair of (7) and determines $\bar{p}$ as in (1e). There are three possibilities for the cline structure of (1).
(i) If the assumptions of Theorems 3.7, 3.8(i), and 3.12 apply, then for every $\theta_\pm > 0$, problem (1) has a unique cline, which is strictly increasing.
(ii) If the assumptions of Theorem 3.11 apply, then for every $\theta_\pm > 0$, problem (1) has a unique cline, which is strictly increasing; and for every $\theta_- > 0$, there exists $\theta_* > 0$ such that problem (1) has zero and at least two nonmonotone clines for $\theta_+ > \theta_*$ and $\theta_+ < \theta_*$, respectively.
(iii) If the assumptions of Theorem 3.8(ii) and Remarks 6 and 7 apply, then for every $\theta_\pm > 0$, problem (1) may have zero, one, or multiple clines, which, if they exist, must be monotone.

Lastly, we apply the above results on clines to the cubic f in (3) with $h \in [-1, -1/3)$. In this case, the cubic f satisfies (5), (6), and (24) with

$$\check{p} = \frac{1}{2} + \frac{1}{6h} \tag{29}$$

and

$$\hat{p} = \frac{1}{2} + \frac{1}{6h}(1 - \sqrt{1 + 3h^2}). \tag{30}$$

We shall find out for what values of h, the assumption (H1) may hold so that nonmonotone clines may exist.

Lemma 3.13. *Assume that f is as in (3) with $h \in [-1, -1/3)$ and that $[f(p) - \beta(p - \bar{p})]$ has three zeros $p_1 < p_2 < p_3$ in $(0, 1)$ as in Fig. 6. Then $I \lesseqqgtr II$ if and only if $p_2 \lesseqqgtr \check{p}$.*

Proof. We first show that if $p_2 = \check{p}$, then $I = II$. Define the line

$$L(p) := \beta(p - \bar{p}) = f(\check{p}) + \beta(p - \check{p}), \tag{31}$$

in which the "=" is due to the fact that $p_2 = \check{p}$ is a zero of $[f(p) - \beta(p - \bar{p})]$. Since $\check{p}$ is the unique critical point of the quadratic polynomial $f'(p)$, we see that

$$f'(p) = f'(2\check{p} - p). \tag{32}$$

Let $\phi(p) = f(p) - L(p)$, then (31) and (32) show that

$$\phi(\check{p}) = 0, \quad \phi'(p) = f'(p) - \beta = f'(2\check{p} - p) - \beta = \phi'(2\check{p} - p). \tag{33}$$

We conclude from (33) that $\phi(p)$ is an odd function about $p = \check{p}$, which with $\phi(p_1) = \phi(p_3) = 0$ reveals that $p_1 + p_3 = 2\check{p}$ and $I = II$.

Next, suppose that $p_2 < \check{p}$. We denote the strict line that passes through $(p_1, 0)$ and $(\check{p}, f(\check{p}))$ by $L_1(p)$, and the two areas enclosed by L_1 and f by I' and II'.

Then $I' = II'$ as above and it is clear that $I < I' = II' < II$ from the geometry of L, L_1, and f. If $p_2 > \check{p}$, we see that $I > II$ similarly. Thus, Lemma 3.13 is demonstrated. $\square$

Remark 9. From Lemmas 3.10 and 3.13 and Theorem 3.11, we conclude that for the cubic (3) with $h \in [-1, -1/3)$:
(i) If a straight line $\beta(p - \bar{p})$ with $\beta > 0$ and $\bar{p} \in (0, 1)$ intersects with the graph of $f(p)$ at p_1, p_2, and p_3 such that $0 < p_1 < p_2 < \check{p} < p_3 < 1$, then system (15) has a homoclinic orbit as in Fig. 7(A).
(ii) If, in addition, $2\bar{p} - p_1 > 0$, then we take $p_+ = p_1$, $p_- = 2\bar{p} - p_1$, and $\alpha = f(p_+)/f(p_-)$.
(iii) If the conditions in (i) and (ii) hold, then for suitable $\theta_\pm > 0$, system (1) has nonmonotone solutions.
(iv) For every $p_1 \in (0, \check{p})$, let $\bar{p}(p_1)$ be the p-intercept of the line that passes through $(p_1, f(p_1))$ and $(\check{p}, f(\check{p}))$. If

(H2) there exists some $p_1 \in (0, \check{p})$ such that $2\bar{p}(p_1) - p_1 > 0$,

then we can choose this p_1, and take p_2 slightly smaller than $\check{p}$ such that the line that passes through $(p_1, f(p_1))$ and $(p_2, f(p_2))$ satisfies the above (i) and (ii). It is clear that (H2) is also a necessary condition such that (i) and (ii) hold.

Lemma 3.14. *Assume that f is as in* (3) *with $h \in [-1, -1/3)$. Then* (H2) *holds if and only if $h < -(5 + \sqrt{17})/12$.*

Proof. For every $p_1 \in (0, \check{p})$, by the definition of $\bar{p}(p_1)$ in Remark 9(iv), we obtain

$$\bar{p}(p_1) = p_1 - \frac{p_1 - \check{p}}{f(p_1) - f(\check{p})} f(p_1). \tag{34}$$

Let $w(p_1) := 2\bar{p}(p_1) - p_1$; from (3) and (34) we see that

$$w(p_1) = p_1 - 2\frac{p_1 - \check{p}}{f(p_1) - f(\check{p})} f(p_1) = \frac{p_1(p_1 - \check{p})}{f(p_1) - f(\check{p})} \psi(p_1), \tag{35}$$

where

$$\psi(p_1) = -2hp_1^2 + (4h + \frac{4}{3})p_1 - \frac{18h^2 + 15h + 1}{9h}. \tag{36}$$

Since f is monotone for $p_1 \in (0, \check{p})$, we see from (35) that $w(p_1) > 0$ is equivalent to $\psi(p_1) > 0$. Observe that for every $h \in [-1, -1/3)$, the quadratic polynomial ψ is concave up and

$$\psi(\check{p}) = -\frac{1}{2}h + \frac{1}{18h} - \frac{2}{3} < 0.$$

Then there exists $p_1 \in (0, \check{p})$ such that $\psi(p_1) > 0$ if and only if

$$\psi(0) = -\frac{18h^2 + 15h + 1}{9h} > 0,$$

which means $h < -(5 + \sqrt{17})/12$. $\square$

Lemma 3.15. *Assume that f is as in* (3) *with $h \in [-1, -1/3)$. For every $\alpha > 1$ and every $\beta > 0$, if* (1e) *and* (7) *hold with $0 < p_- < p_+ < 1$, then the following cases cannot happen.*
(i) *The function $[f(p) - \beta(p - \bar{p})]$ has two zeros as in Fig.* 5(A) *with $p_+ = p_2$, i.e., Case* (iid) *in Remark 4.*

(ii) *The function* $[f(p) - \beta(p - \bar{p})]$ *has three zeros as in Fig.* 6 *with* $p_+ = p_2$.
(iii) *The function* $[f(p) - \beta(p - \bar{p})]$ *has three zeros as in Fig.* 6 *with* $p_+ = p_3$.

Proof. For each case, we argue by contradiction.

Suppose rather that (i) happens. Consider the straight line passing through $(\check{p}, f(\check{p}))$ with slope $f'(\check{p})$, the p-intercept of which is

$$\tilde{p} = \check{p} - \frac{f(\check{p})}{f'(\check{p})}. \tag{37}$$

From Remark 4(ii) and Fig. 5(A), we inform that $p_+ = p_2 > \check{p}$ and $\beta = f'(p_2) < f'(\check{p})$, which imply $\bar{p} < \tilde{p}$. Thus, from (1e), (3), (37), and $f'(\check{p}) > 0$ we have

$$p_- = 2\bar{p} - p_+ < 2\tilde{p} - \check{p} = \check{p} - \frac{2f(\check{p})}{f'(\check{p})} = \frac{\check{p}[2h\check{p}^2 - (1+h)]}{f'(\check{p})} < 0 \tag{38}$$

for every $h \in [-1, -1/3)$, which contradicts $p_- > 0$ and demonstrates that (i) cannot happen.

Suppose rather that (ii) happens. If $p_+ = p_2 \geq \check{p}$, from Remark 5 we see that $p_1 < \check{p}$. Then the same calculations as in (i) would lead to the contradiction $p_- \leq 0$. If $p_+ = p_2 < \check{p}$, we consider the straight line passing through $(p_2, f(p_2))$ with slope $f'(p_2)$, the p-intercept of which is

$$p_* = p_2 - \frac{f(p_2)}{f'(p_2)}. \tag{39}$$

Since f is concave up on $(0, \check{p})$, the slope β of the secant line through $(p_1, f(p_1))$ and $(p_2, f(p_2))$ satisfies $\beta < f'(p_2)$, and thus $\bar{p} < p_*$. Therefore, from (1e), (3), (39), and $f'(p_2) > 0$ we have

$$p_- = 2\bar{p} - p_+ < 2p_* - p_2 = p_2 - \frac{2f(p_2)}{f'(p_2)} = \frac{p_2[2hp_2^2 - (h+1)]}{f'(p_2)} < 0 \tag{40}$$

for every $h \in [-1, -1/3)$, which contradicts $p_- > 0$. Thus, in either case, (ii) cannot happen.

Suppose that (iii) happens. Then as in (i) we consider the straight line passing through $(\check{p}, f(\check{p}))$ with slope $f'(\check{p})$, the p-intercept of which is the $\tilde{p}$ given by (37). In light of Remark 5, we see that $p_1 < \check{p}$ and $p_+ = p_3 > \check{p}$. Since f' achieves its maximum at $p = \check{p}$ in $(0, 1)$, we see that $\beta < f'(\check{p})$; otherwise, $\beta \geq f'(\check{p})$ would imply that $\beta(p - \bar{p}) > f(p)$ for $p \in (p_1, 1)$, which contradicts our assumption that $[f(p) - \beta(p - \bar{p})]$ has two more zeros p_2, p_3 in $(p_1, 1)$. Hence, $\beta < f'(\check{p})$ and consequently, the corresponding p-intercepts satisfy $\bar{p} < \tilde{p}$. Then the same calculations as in (38) lead to the contradiction $p_- < 0$. Thus, (iii) cannot happen. □

The following theorem in [27] describes multiplicity of nontrivial solutions of (7), in which the β_* is as in (22).

Theorem 3.16. ([27, Th.8.3(ii)]) *Assume that* f *is as in* (3) *with* $h \in [-1, -1/3)$, *then for every* $\alpha > 1$, *there exists* $\tilde{\beta}$ $(> \beta_*)$ *such that for every* β *in* $(\tilde{\beta}, \infty)$, *in* $(0, \beta_*] \cup \{\tilde{\beta}\}$, *and in* $(\beta_*, \tilde{\beta})$, *the system* (7) *has exactly zero, one, and two solutions, respectively. In particular, if* $h = -1$, *then* $\beta_* = 0$, *and hence for every* β *in* $(\tilde{\beta}, \infty)$, *in* $\{\tilde{\beta}\}$, *and in* $(0, \tilde{\beta})$, *system* (7) *has exactly zero, one, and two nontrivial solutions, respectively.*

Now we come to the following results on clines for the cubic (3) with $h \in [-1, -1/3)$.

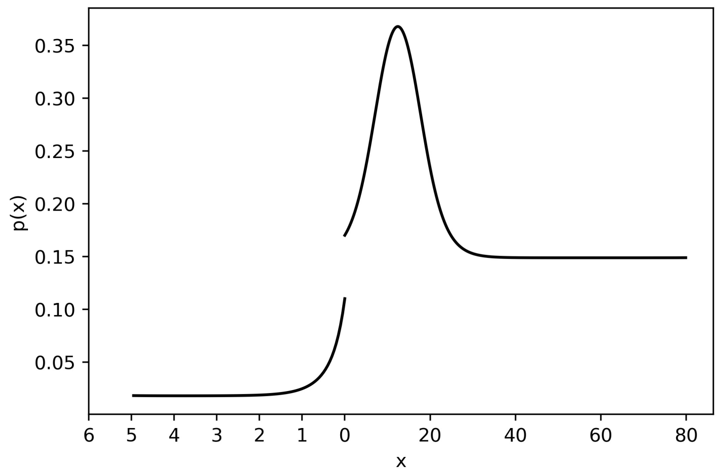


FIGURE 9. Nonmonotone cline with $f(u) = 2u^2(1-u)$.

Theorem 3.17. *Assume that f is as in (3) with $h \in [-(5+\sqrt{17})/12, -1/3)$. Then for every $\alpha > 1$, there exists $\tilde{\beta}$ $(> \beta_*)$ such that for every β in $(\tilde{\beta}, \infty)$, in $(0, \beta_*] \cup \{\tilde{\beta}\}$, and in $(\beta_*, \tilde{\beta})$, and for every $\theta_\pm > 0$, problem (1) has exactly zero, one, and two clines with $0 < p_- < p_+ < 1$, respectively. Moreover, every cline is strictly increasing.*

Proof. For every $\alpha > 1$, $\beta > 0$, Theorem 3.16 gives the exact number of $p_\pm$ that satisfies (7) and $0 < p_- < p_+ < 1$. For each such pair of $p_\pm$ and the corresponding $\bar{p}$ as in (1e), Remark 8 lists all the possible cline structure of (1). For f as in (3) with $h \in [-(5+\sqrt{17})/12, -1/3)$, Cases (ii) in Remark 8 cannot happen by Remark 9 and Lemma 3.14. Cases (iii) in Remark 8 is excluded by Lemma 3.15. This leaves only Case (i) in Remark 8, i.e., the existence of a unique monotone cline for every $\theta_\pm > 0$. $\square$

Theorem 3.18. *Assume that f is as in (3) with $h \in [-1, -(5+\sqrt{17})/12)$. Then for every $\alpha > 1$, there exists $\tilde{\beta}$ $(> \beta_*)$ such that for every β in $(\tilde{\beta}, \infty)$, in $(0, \beta_*] \cup \{\tilde{\beta}\}$, and in $(\beta_*, \tilde{\beta})$, and for every $\theta_\pm > 0$, problem (1) has exactly zero, one, and two strictly increasing clines, respectively. Moreover, there exist $\alpha > 1$ and $\beta > 0$, such that for every $\theta_- > 0$, there exists $\theta_* > 0$ and problem (1) has zero and at least two nonmonotone clines with $0 < p_- < p_+ < 1$ for $\theta_+ > \theta_*$ and $\theta_+ < \theta_*$, respectively.*

Proof. The proof of this theorem is similar to the one of Theorem 3.17, except that for $h \in [-1, -(5+\sqrt{17})/12)$, there exist $\alpha > 1$, $\beta > 0$, $p_\pm$, and $\bar{p}$ such that Case (ii) in Remark 8 happens by Remark 9 and Lemma 3.14. Once this happens, the existence of nonmonotone clines in addition to a unique monotone one follows from Theorem 3.11. $\square$

We close this section with the following numerical example of a nonmonotone cline of (1).

Example 1. Fig. 9 shows a numerically solved nonmonotone solution of (1) for the complete dominance case $f(u) = 2u^2(1-u)$ (i.e., $h = -1$ in (3)) with $\alpha = 59.44$,

$\beta = \frac{311}{540}$, $\theta_- = 5.23437$, and $\theta_+ = 0.111373$; the corresponding $p_- \approx 0.017$ and $p_+ \approx 0.148$.

First, $\bar{p} = 1/12$, β, $p_\pm$, and α are determined in turn such that assumption (H1) in Theorem 3.11 and $\alpha f(p_-) = f(p_+)$ hold. Second, we choose $((p(0+), q(0+))$ and $((p(0-), q(0-))$ with energy $H^+(p_+, 0)$ and $H^-_\alpha(p_-, 0)$, respectively, and determine the corresponding $\theta_\pm$ according to (1e,f). Lastly, we solve the first order ODE system (15) forward with initial value $(p(0+), q(0+))$ for $x > 0$, and solve system (18) backward with initial value $(p(0-), q(0-))$ for $x < 0$, using the Symplectic Partitioned Runge-Kutta Method in Mathematica.

4. **Clines with $p_- = p_+$.**

By Proposition 1, it is possible that $p_- = p_+ = 0$ or $p_- = p_+ = 1$. The previous studies show that under a step-environment with partial panmixia, they would imply that $p(x) \equiv 0$ or $p(x) \equiv 1$, respectively; see [27] (without a barrier) and [16] (with the presence of a barrier). Here, under certain conditions, we discover the existence of nonmonotone clines of (1) with $p_- = p_+ = 0$ or $p_- = p_+ = 1$.

We focus on unimodal selection functions f described by (6) that satisfy either (23) or (24) as in Section 3. We first consider nonmonotone clines of (1) with $p_- = p_+ = 0$.

Theorem 4.1. *Assume that $\alpha > 0$ and that (4)–(6) hold. Then in each of the following cases, for every $\theta_\pm > 0$, problem (1) has no cline with $p_- = p_+ = 0$.*
(i) *f satisfies (23) and $\beta > 0$.*
(ii) *f satisfies (24) and $\beta \in (0, \beta_1] \cup [\beta_2, \infty)$, where $\beta_1 = f'(0)$ and β_2 is the unique slope such that the line $\beta_2 p$ is tangent to the graph of $f(p)$.*

Proof. We use the phase-plane analysis again. The phase portrait for $x < 0$ is similar to the one in Fig. 1(B) with p_- being the origin now. We observe that under the conditions in either (i) or (ii), the line βp may have at most one point of intersection with the graph of $f(p)$ besides the origin, which determines the phase portrait for $x > 0$ in a simple way. Consequently, in either case, the trivial solution $p(x) \equiv 0$ is the only solution with $p(\pm\infty) = 0$. We omit the details here, since the method is essentially the same as the proof of Theorem 3.1. □

Remark 10. If f satisfies (5), (6), and (24), then by the definition of β_1 and β_2 in Theorem 4.1(ii), we see that for every $\beta \in (\beta_1, \beta_2)$, the line βp and the graph of $f(p)$ have two points of intersection besides the origin. The situation is exactly the same as in Fig. 6 with p_- being the origin now. I and II stand for the two areas bounded by the line βp and the graph of $f(p)$ as in Fig. 6. It is clear that there exists a unique $\tilde{\beta} \in (\beta_1, \beta_2)$ such that $I \lesseqgtr II$ if and only $\beta \lesseqgtr \tilde{\beta}$. Similarly to Lemma 3.10, we have the following lemma.

Lemma 4.2. *Assume that f satisfies (5), (6), and (24).*
(i) *If $\beta \in (\beta_1, \tilde{\beta})$, then the phase portrait of (15) with $\bar{p} = 0$ is as in Fig. 7(A) with p_1 being the origin; there exists a homoclinic orbit joining the equilibrium $(p_1, 0)$ and itself.*
(ii) *If $\beta = \tilde{\beta}$, then the phase portrait of (15) with $\bar{p} = 0$ is as in Fig. 7(B) with p_1 being the origin; there exist heteroclinic orbits connecting the equilibria $(p_1, 0)$ and $(p_3, 0)$.*
(iii) *If $\beta \in (\tilde{\beta}, \beta_2)$, then the phase portrait of (15) with $\bar{p} = 0$ is as in Fig. 7(C) with p_1 being the origin; there exists a homoclinic orbit joining the equilibrium $(p_3, 0)$ and itself.*

Theorem 4.3. *Assume that $\alpha > 0$ and that (4)–(6) and (24) hold.*
(i) *If $\beta \in (\beta_1, \tilde{\beta})$, then for every $\theta_- > 0$, there exists $\theta_* > 0$ such that problem (1) has zero and at least two nonmonotone clines with $p_- = p_+ = 0$ for $\theta_+ > \theta_*$ and $\theta_+ < \theta_*$, respectively.* (ii) *If $\beta \in [\tilde{\beta}, \beta_2)$, then for every $\theta_\pm > 0$, problem (1) has no cline with $p_- = p_+ = 0$.*

The proof of Theorems 4.3(i) and 4.3(ii) is essentially the same as the proof of Theorems 3.11 and 3.12, respectively, and hence is omitted here.

Remark 11. We can obtain the corresponding theory on clines with $p_- = p_+ = 1$ from the above results for $p_- = p_+ = 0$ via the transformation $1 - p(-x)$ introduced at the beginning of Section 3. The similar assumptions as (23) and (24) should be made on f in $(\hat{p}, 1)$ instead of in $(0, \hat{p})$.

Now we apply the above results to the cubic (3).

Theorem 4.4. *Assume that $\alpha > 0$ and that (3) and (4) hold.*
(i) *If $h \in [-1/3, 1]$, then for every $\beta > 0$ and every $\theta_\pm > 0$, problem (1) has no cline with $p_- = p_+ = 0$.*
(ii) *If $h \in [-1, -1/3)$, then there exists $\tilde{\beta} > \beta_1$ such that* (a) *for every $\beta \in (0, \beta_1] \cup [\tilde{\beta}, \infty)$ and every $\theta_\pm > 0$, problem (1) has no cline with $p_- = p_+ = 0$; and* (b) *for every $\beta \in (\beta_1, \tilde{\beta})$ and every $\theta_- > 0$, there exists $\theta_* > 0$ such that problem (1) has zero and at least two nonmonotone clines with $p_- = p_+ = 0$ for $\theta_+ > \theta_*$ and $\theta_+ < \theta_*$, respectively, where $\beta_1 = 1 + h$.*

Proof. By (3) and straightforward calculations, we infer that f satisfies (23) and (24), provided $h \in [-1/3, 1]$ and $h \in [-1, -1/3)$, respectively. We note that $f'(0) = 1 + h$. Then Theorem 4.4(i) follows from Theorem 4.1(i); Theorem 4.4(iia) follows from Theorems 4.1(ii) and 4.3(ii); Theorem 4.4(iib) follows from Theorem 4.3(i). □

Theorem 4.5. *Assume that $\alpha > 0$ and that (3) and (4) hold.*
(i) *If $h \in [-1, 1/3]$, then for every $\beta > 0$ and every $\theta_\pm > 0$, problem (1) has no cline with $p_- = p_+ = 1$.*
(ii) *If $h \in (1/3, 1]$, then there exists $\tilde{\tilde{\beta}} > \tilde{\beta}_1$ such that* (a) *for every $\beta \in (0, \tilde{\beta}_1] \cup [\tilde{\tilde{\beta}}, \infty)$ and every $\theta_\pm > 0$, problem (1) has no cline with $p_- = p_+ = 1$; and* (b) *for every $\beta \in (\tilde{\beta}_1, \tilde{\tilde{\beta}})$ and every $\theta_+ > 0$, there exists $\tilde{\theta}_* > 0$ such that problem (1) has zero and at least two nonmonotone clines with $p_- = p_+ = 1$ for $\theta_- > \tilde{\theta}_*$ and $\theta_- < \tilde{\theta}_*$, respectively, where $\tilde{\beta}_1 = 1 - h$.*

Proof. Remark 11, Theorem 4.4, and the fact $f'(1) = h - 1$ imply Theorem 4.5 directly. □

5. Discussion.

In this paper, we investigated the cline model (1) in an unbounded linear habitat. The crucial assumptions are step-environment $g(x)$ and unimodal selection $f(p)$.

In previous models on clines maintained by a step-environment and a unimodal selection function, clines are all monotone; see [4] (without partial panmixia and a barrier), [27] (with partial panmixia), and [16] (with partial panmixia and a barrier). As a consequence there exists no cline $p(x)$ with $p_- = p_+$, where $p_\pm = p(\pm\infty)$. Our results differ dramatically from the previous ones: we discover nonmonotone clines with $p_- < p_+$ (Theorem 3.11(ii)) and with $p_- = p_+$ (Theorem 4.3(i)).

Our general theorems extend the analysis of Nagylaki [16] for model (1) from the no dominance case $f(u) = u(1 - u)$ to unimodal f for $\alpha = 1$ (Theorem 3.1); to unimodal f which is concave on the left of its maximum for $\alpha > 1$ (Theorem 3.4); and to unimodal f which has only one point of inflection on the left of its maximum for $\alpha > 1$ (theorems summarized in Remark 8). The results on clines for $\alpha < 1$ can be obtained from the results for $\alpha > 1$ through the transformation $1 - p(-x)$.

In particular, we obtain the complete cline structure for the biological important cubic f in (3): The configuration of clines with $p_- < p_+$ is established in Remark 1 for $\alpha = 1$, and in Remark 2 and Theorems 3.17 and 3.18 for $\alpha > 1$, respectively. The configuration of clines for $\alpha > 0$ with $p_- = p_+ = 0$ and 1 is established in Theorems 4.4 and 4.5, respectively.

Now we posit some unsolved problems.

First, the frequencies $p(0\pm)$ at the barrier are important characteristics of a cline $p(x)$. Therefore, it is desirable to do the approximations at the barrier in various limiting cases of the parameters α, β, and $\theta_\pm$ for the selection functions that we investigated in this paper as in [16, Sect. 4.3] for $f(u) = u(1-u)$.

Second, it will be much more challenging to study the stability of the clines with respect to the corresponding time-dependent model.

Lastly, if we allow more points of inflection on the left of $\hat{p}$ instead of only one as in (24), how complex will the cline structure be? Another generalization is $g(x)$ having two steps or being a continuous monotone function instead of a single step as in (4).

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