
Article:

Nagylaki, T. and Zeng, K. (2016) Clines with partial panmixia across a geographical barrier in an environmental pocket. Theoretical Population Biology, 110. pp. 1-11. ISSN 0040-5809

https://doi.org/10.1016/j.tpb.2016.03.003

CLINES WITH PARTIAL PANMIXIA ACROSS A GEOGRAPHICAL BARRIER IN AN ENVIRONMENTAL POCKET

Thomas Nagylaki*

Department of Ecology and Evolution
The University of Chicago
1101 East 57th Street
Chicago, Illinois 60637, USA

Kai Zeng

Department of Animal and Plant Sciences
University of Sheffield
Alfred Denny Building, Western Bank
Sheffield S10 2TN, UK

Keywords: Geographical structure, Spatial structure, Population structure, Migration, Long-distance migration, Selection

*Corresponding author.

E-mail address: nagylaki@uchicago.edu (T. Nagylaki), k.zeng@sheffield.ac.uk (K. Zeng).

ABSTRACT

In a geographically structured population, partial global panmixia can be regarded as the limiting case of long-distance migration. On the entire line with homogeneous, isotropic migration, an environmental pocket is bounded by a geographical barrier, which need not be symmetric. For slow evolution, a continuous approximation of the exact, discrete model for the gene frequency $p(x)$ at a diallelic locus at equilibrium, where x denotes position and the barrier is at $x = \pm a$, is formulated and investigated. This model incorporates viability selection, local adult migration, adult partial panmixia, and the barrier. The gene frequency and its derivatives are discontinuous at the barrier unless the latter is symmetric, in which case only $p(x)$ is discontinuous. A cline exists only if the scaled rate of partial panmixia $\beta < 1$; several qualitative results also are proved. Formulas that determine $p(x)$ in a step-environment when dominance is absent are derived. The maximal gene frequency in the cline satisfies $p(0) < 1 - \beta$. A cline exists if and only if $0 \leq \beta < 1$ and the radius a of the pocket exceeds the minimal radius a^*, for which a simple, explicit formula is deduced. Given numerical solutions for $p(0)$ and $p(a\pm)$, an explicit formula is proved for $p(x)$ in $|x| > a$; whereas in $(-a, a)$, an elliptic integral for x must be numerically inverted. The minimal radius a^{**} for maintenance of a cline in an isotropic, bidimensional pocket is also examined.

1. Introduction

At a single diallelic locus, if allele A_1 is favored only in a bounded part of the habitat and its spatially averaged selection coefficient is less than that of A_2, we say A_1 is in an environmental pocket. In this general sense, a large theoretical literature treats the existence, multiplicity, stability, and characteristics of polymorphism in an environmental pocket (see refs. in Nagylaki, 2016, hereafter abbreviated as N16). Since the introduction of partial global panmixia as an approximation for long-distance migration (Nagylaki, 2012a), it has been included in theoretical investigations. However, the general and usually qualitative insights from these analyses should be complemented by the understanding and intuition derived from the study of explicitly solvable special cases. These invariably require a step-environment.

The first explicit exploration of the gene frequency in an environmental pocket appears in Nagylaki (1975). Nagylaki (1976) includes a symmetric geographical barrier, and Nagylaki (1978) incorporates asymmetric migration without a barrier. Nagylaki et al. (2014, hereafter abbreviated as NSAD14) analyse the pocket with partial panmixia but no barrier.

As discussed in N16, geographical barriers are fairly common and are often asymmetric. In this paper, we use the theory developed in N16 to incorporate at equilibrium a general geographical barrier into the unidimensional pocket model in NSAD14.

In Section 2, we formulate our problem, for which we derive some general results in Section 3. In Sections 4 and 5, we posit a step-environment and the absence of dominance. We establish a necessary and sufficient condition for the existence of the cline $p(x)$ (Section 4) and solve for $p(x)$ (Section 5). In Section 4.2, we explore the bidimensional case. In Section 6, we discuss our results and mention some open problems.

2. Formulation

The habitat is the entire line $\mathcal{R}$; it contains the environmental pocket $(-a, a)$. At the diallelic locus under consideration, allele A_1 is beneficial inside the pocket and harmful outside it. The geographical barrier at $-a$ is the reflection of the one at a. Migration is homogeneous and symmetric; partial global panmixia at scaled rate β (cf. N16) approximates long-distance migration. Selection is directional, and we can factor its scaled contribution as $g(x)f(p)$, where x denotes position and $p(x)$ designates the frequency of A_1 at equilibrium. Each of the above evolutionary forces is weak, as is the transmissivity of the barrier. We assume that mutation and random drift are negligible and study only the equilibrium.

For directional selection, we have

$$f(0) = f(1) = 0, \qquad f(p) > 0 \quad \text{in } (0,1). \tag{2.1}$$

Remark 2.1. Suppose that (2.1) holds and $f''(p) \leq 0$ in $[0,1]$. We posit that we can extend Theorem 1.1 in Lou et al. (2013) from a compact habitat to a geographical barrier in $\mathcal{R}$. Then if a nontrivial equilibrium exists, it is unique and globally asymptotically stable, and its existence can be determined by linearization at the trivial equilibrium $p \equiv 0$. These extensions are supported by the numerical calculations in Sections 4 and 5 and, for $\beta = 0$ and no barrier, by the results of Tertikas (1988) and Brown and Tertikas (1991).

(A2.1). We assume that the extensions in Remark 2.1 hold.

For any function $h(x)$ with a limit at ±∞, we abbreviate

$$h(\pm\infty) = \lim_{x\to\pm\infty} h(x). \tag{2.2}$$

For some of our results, the following hypothesis suffices.

(A2.2). We assume that $g(x)$ is bounded, changes sign, and

$$g(\pm\infty) = -\alpha < 0 \tag{2.3}$$

for some $\alpha > 0$.

We are interested in equilibria that satisfy

$$0 \leq p(x) \leq 1 \quad \text{in } \mathcal{R}, \tag{2.4a}$$

$$p(\pm\infty) = 0. \tag{2.4b}$$

Since the proof of Lemma 2.3 in NSAD14 applies unaltered, therefore the spatially averaged gene frequency (see (2.5d) in NSAD14) is zero. Defining

$$\Omega = \mathcal{R} \backslash (\{-a\} \cup \{a\}), \tag{2.5}$$

from (4.14) in N16 we obtain the scaled equilibrium problem

$$p'' + g(x)f(p) - \beta p = 0 \quad \text{ in } \Omega, \tag{2.6a}$$

$$p'(a\pm) = \theta_{\pm}[p(a+) - p(a-)], \tag{2.6b}$$

$$p'(-a\pm) = \theta_{\mp}[p(-a+) - p(-a-)], \tag{2.6c}$$

$$p(\pm\infty) = 0, \tag{2.6d}$$

$$p'(\pm\infty) = 0, \tag{2.6e}$$

where $\theta_+ > 0$ and $\theta_- > 0$ signify the scaled transmissivities across the barrier from inside and from outside the pocket, respectively.

Remark 2.2. As observed in Remark 2.5 in NSAD14, the parameter β can include both panmixia and irreversible mutation from A_1 to A_2.

Remark 2.3. As noted in Remark 2.6 in NSAD14, since the habitat $\mathcal{R}$ is unbounded, it is more convenient to investigate the existence of the cline using the radius, a, of the pocket rather than, as for a bounded habitat, the selection-migration ratio. Therefore, as in NSAD14 and N16, we scaled so that the coefficient of $g(x)f(p)$ is one and (3.1) below holds.

3. General results

Recalling (2.1) and choosing the selection coefficient sufficiently large before rescaling, we can ensure that

$$f(p) = pF(p) \qquad \text{where } 0 < F(p) < 1 \text{ in } (0,1), \tag{3.1a}$$

$$g(x) \leq 1 \qquad \text{in } \Omega. \tag{3.1b}$$

Theorem 2.7 in NSAD14 demonstrates that, absent a barrier, the gene frequency converges to zero unless $0 \leq \beta < 1$. Here, we establish in one dimension that even with a barrier, this condition is necessary for the existence of a nontrivial equilibrium. Thus, with the scaling (2.13) in NSAD14, the necessary condition $\beta < 1$ for existence of a cline in a pocket in $\mathcal{R}$ is rather general.

Theorem 3.1. *If* (2.1), (2.6), *and* (3.1) *hold and* $\beta \geq 1$, *then* $p(x) = 0$ *in* $\mathcal{R}$.

Proof. We assume that $\beta \geq 1$ and $p(x) > 0$ in Ω and seek a contradiction. (If $p \not\equiv 0$ in Ω, then $p > 0$ in Ω.) From (2.6a) and (3.1) we get

$$0 = p'' + p[g(x)F(p) - \beta] < p'' \quad \text{in } \Omega. \tag{3.2}$$

Hence, (2.6e) and (3.2) yield

$$p'(x) > 0 \qquad \text{if } x < -a, \tag{3.3a}$$

$$p'(x) < 0 \qquad \text{if } x > a. \tag{3.3b}$$

In particular,

$$p'(-a-) > 0, \quad p'(a+) < 0, \tag{3.4}$$

whence (2.6b,c) imply

$$p'(-a+) > 0, \quad p'(a-) < 0, \tag{3.5}$$

which contradict in $(-a, a)$ the convexity established by (3.2). □

We now make two assumptions.

(A3.1). Hereafter, we posit that $0 \leq \beta < 1$, and for every $x > 0$,

$$g(-x) = g(x) \tag{3.6}$$

and $g(x)$ is either continuous and monotone decreasing or a single step.

(A3.2). We assume that, in one dimension, despite the discontinuities in (2.6b,c), Theorem 2.9 in NSAD14 holds.

Then the cline is symmetric and a decreasing function of $|x|$:

Theorem 3.2. *Suppose that* $p \not\equiv 0$*; assumption* (2.1) *holds with* $f'(p) \geq 0$ *for sufficiently small* $p > 0$*; and so do* (2.6), (A2.2), (A3.1)*, and* (A3.2)*. Then*

$$p(-x) = p(x) \qquad \text{in } \Omega_+ = (0, \infty) \backslash \{a\}, \tag{3.7a}$$

$$p'(x) < 0 \qquad \text{in } \Omega_+. \tag{3.7b}$$

The proof of Corollary 2.10 in NSAD14 requires no change, which yields

Corollary 3.3. *If* (3.6) *holds and* $g'(x)$ *exists in some neighborhood of the origin, then* $p'(0) = 0$*.*

The proof of Corollary 2.11 in NSAD14 requires only obvious changes, whence the cline is convex where A_1 is deleterious:

Corollary 3.4. *If the assumptions in Theorem* 3.2 *hold, then* $p''(x) > 0$ *for every* $x \in \Omega$ *such that* $g(x) < 0$*.*

We now posit the absence of dominance:

$$f(p) = p(1 - p). \tag{3.8}$$

Remark 3.5. Note that (3.8) satisfies (2.1), (3.1a), and $f''(p) < 0$ in $[0, 1]$. Thus, assumption (A2.1) applies to (3.8).

Next, we specialize to the step-environment

$$g(x) = \begin{cases} -\alpha & \text{if } x < -a, \\ 1 & \text{if } -a < x < a, \\ -\alpha & \text{if } x > a. \end{cases} \tag{3.9}$$

Remark 3.6. Observe that (A2.2), (A3.1), and (3.1b) apply to (3.9).

The proofs of Corollaries 2.13 and 2.15 in NSAD14 require no alteration. Hence the former, (2.6b,c), and (3.7) inform us that $p(x) < 1 - \beta$ in Ω; and the latter tells us that $p(x)$ is concave in the pocket.

Corollary 3.7. *If* $p \not\equiv 0$, (2.6), (3.8), *and* (3.9) *hold, then* $p(x) < 1 - \beta$ *in* Ω.

Corollary 3.8. *If the assumptions in Corollary* 3.7 *hold, then* $p''(x) < 0$ *in* $(-a, a)$.

Remark 3.9. If $\beta = 0$ and the barrier is impenetrable, i.e., $\theta_- = \theta_+ = 0$, then (2.6) yields the stable equilibrium

$$p(x) = \begin{cases} 0 & \text{if } |x| > a, \\ 1 & \text{if } |x| < a. \end{cases} \tag{3.10}$$

Remark 3.10. For the ratio of slopes across the barrier, from (2.6b) we obtain

$$\frac{p'(a+)}{p'(a-)} = \frac{\theta_+}{\theta_-}. \tag{3.11}$$

Thus, the ratio of the slopes equals that of the transmissivities, which is an arbitrary positive number. The slope is continuous if and only if the barrier is symmetric ($\theta_- = \theta_+$).

4. Existence of the cline

After deriving and analyzing the minimal radius a^* for maintenance of a unidimensional cline, we study the minimal radius a^{**} for an isotropic, bidimensional pocket.

4.1. One dimension

On account of (2.6), Theorems 3.1 and 3.2, and Corollary 3.3, we can assume that $0 \leq \beta < 1$ and investigate the boundary-value problem

$$p'' + g(x)p(1-p) - \beta p = 0 \qquad \text{in } \Omega_+, \tag{4.1a}$$

$$p'(a\pm) = \theta_\pm(p_+ - p_-), \tag{4.1b}$$

$$p'(0) = 0, \tag{4.1c}$$

$$p(\infty) = 0, \tag{4.1d}$$

$$p'(\infty) = 0, \tag{4.1e}$$

in which

$$p_0 = p(0), \qquad p_\pm = p(a\pm). \tag{4.2}$$

By assumption (A2.1), we can determine whether a cline exists by linearizing (4.1) at $p \equiv 0$. This procedure will lead to a lower limit on the radius a of the pocket. We obtain immediately

$$\psi'' + [g(x) - \beta]\psi = 0 \qquad \text{in } \Omega_+, \tag{4.3a}$$

$$\psi'(a\pm) = \theta_\pm[\psi(a+) - \psi(a-)], \tag{4.3b}$$

$$\psi'(0) = 0, \tag{4.3c}$$

$$\psi(\infty) = 0, \tag{4.3d}$$

$$\psi'(\infty) = 0. \tag{4.3e}$$

We set

$$\lambda = (1-\beta)^{1/2}, \qquad \mu = (\alpha + \beta)^{1/2}, \tag{4.4}$$

$$a^* = \frac{1}{\lambda}\tan^{-1}\left[\frac{\mu\theta_-}{\lambda(\mu + \theta_+)}\right]. \tag{4.5}$$

Theorem 4.1. *Suppose that* (A2.1), (A3.2), (3.8), (3.9), *and* (4.1) *hold. Then a nontrivial equilibrium exists if and only if* $0 \le \beta < 1$ *and* $a > a^*$.

Proof. By Theorem 3.1, if $\beta \ge 1$, then $p(x) = 0$ in $\mathcal{R}$. Therefore, we assume that $0 \le \beta < 1$. Invoking (3.9) and (4.2)–(4.4), we easily find

$$\psi(x) = \begin{cases} B\cos\lambda x & \text{if } 0 \le x < a, \\ Ce^{-\mu x} & \text{if } x > a, \end{cases} \tag{4.6}$$

where B and C are constants. We impose (4.3b) to deduce

$$-B\lambda\sin\lambda a = \theta_-(Ce^{-\mu a} - B\cos\lambda a),$$

$$-C\mu e^{-\mu a} = \theta_+(Ce^{-\mu a} - B\cos\lambda a),$$

whence

$$C\theta_- e^{-\mu a} = B(\theta_-\cos\lambda a - \lambda\sin\lambda a), \tag{4.7a}$$

$$B\theta_+\cos\lambda a = Ce^{-\mu a}(\theta_+ + \mu). \tag{4.7b}$$

Multiplying (4.7a) by (4.7b) yields

$$\theta_+\theta_- \cos\lambda a = (\mu + \theta_+)(\theta_- \cos\lambda a - \lambda \sin\lambda a). \tag{4.8}$$

Since $\cos\lambda a = 0$ does not satisfy (4.8), we get

$$\theta_+\theta_- = (\mu + \theta_+)(\theta_- - \lambda \tan\lambda a), \tag{4.9}$$

which leads directly to (4.5). □

Remark 4.2. If there is no transmission into the pocket ($\theta_- \to 0$), then $a^* \to 0$, as is intuitively obvious. If there is at least as much gene flow out of the pocket than into it ($\theta_- \le \theta_+$), then the barrier eases the protection of A_1:

$$a^* \le \frac{1}{\lambda}\tan^{-1}\left[\frac{\mu\theta_+}{\lambda(\mu+\theta_+)}\right] < \frac{1}{\lambda}\tan^{-1}\left(\frac{\mu}{\lambda}\right) \equiv a_1, \tag{4.10}$$

which is precisely the result without the barrier in (3.2) in NSAD14. If a symmetric barrier disappears ($\theta_- = \theta_+ = \theta \to \infty$) then $a^* \to a_1$, in agreement with biological intuition.

Remark 4.3. As a^* increases (decreases), the cline becomes harder (easier) to maintain. We rewrite (4.5) in the form

$$a^* = \frac{1}{\lambda}\tan^{-1}\left[\frac{\theta_-}{\lambda}\left(1 - \frac{\theta_+}{\mu+\theta_+}\right)\right]. \tag{4.11}$$

Scrutiny of (4.5) and (4.11) informs us that if one parameter changes with the other three fixed, then a^* increases when α, β, or θ_- increases, or θ_+ decreases. These results are intuitive because they correspond to stronger negative selection on A_1 outside the pocket, more long-distance migration, more gene flow into the pocket, and less gene flow out of the pocket, respectively.

Remark 4.4. The above monotonicity properties in α and β yield bounds on a^* as $\alpha \to 0+$ and ∞, and $\beta \to 0$ and $1-$. Putting

$$\tilde{\alpha} = \sqrt{\alpha}, \qquad \tilde{\beta} = \sqrt{\beta}, \tag{4.12}$$

we deduce

$$\frac{1}{\lambda}\tan^{-1}\left[\frac{\tilde{\beta}\theta_-}{\lambda(\tilde{\beta}+\theta_+)}\right] < a^* < \frac{1}{\lambda}\tan^{-1}\left(\frac{\theta_-}{\lambda}\right) < \frac{\pi}{2\lambda}, \tag{4.13a}$$

$$\tan^{-1}\left(\frac{\tilde{\alpha}\theta_-}{\tilde{\alpha}+\theta_+}\right) < a^* < \frac{\pi}{2\lambda} \to \infty. \tag{4.13b}$$

Remark 4.5. From (4.5) we can easily see that $a^* \sim \tilde{\alpha}\theta_-/\theta_+$ as $\alpha \to 0+$ with $\beta = 0$, and that $a^* \sim \tilde{\beta}\theta_-/\theta_+$ as $\beta \to 0+$ with $\alpha = 0$.

Remark 4.6. According to NSAD14, the minimal radius a^* depends more strongly on β than on α; this still holds when there is a barrier. Furthermore, a^* depends more strongly on θ_- than on θ_+.

In Tables 1–3, we exhibit a^* for various values of α, β, and $\theta_\pm$: in Table 1, $\theta_- = 0.2$ and $\theta_+ = 5.0$; in Table 2, $\theta_- = 5.0$ and $\theta_+ = 0.2$; in Table 3, $\alpha = 0.5$ and $\beta = 0.25$. The tables agree with the qualitative Remarks 4.3 and 4.6. Note that, as (4.13a) informs us, the minimal radius $a^* > 0$ even if $\alpha = 0$, provided that $0 < \beta < 1$ and $\theta_- > 0$. This is due to the boundary condition (4.1d), which we can interpret as contact at infinity of the habitat with a continent where A_1 is absent.

INSERT TABLES 1–3 ABOUT HERE

4.2. Two dimensions

Here, we postulate the multidimensional transition conditions (3.55) in N16 and derive the necessary and sufficient condition for maintaining an isotropic bidimensional cline. A natural application would be to amphibians in a lake or to species on an island in river.

The highly plausible general transition conditions (3.55) in N16 state that the normal derivative of the gene frequency at any point $\check{x}\pm$ in the barrier $\mathcal{B}$ is proportional to the discontinuity of the gene frequency across $\mathcal{B}$ at $\check{x}$. To prove (or disprove) this condition, one could choose coordinates at $\check{x} \in \mathcal{B}$ so that the x_1-axis is orthogonal to $\mathcal{B}$ and the other axes are in the tangent manifold at $\check{x}$. It would suffice to examine nearest-neighbor migration. Of course, in the isotropic case, the normal derivative simplifies to the derivative with respect to $r = \|x\|$.

We posit the isotropic step environment

$$g(r) = \begin{cases} 1 & \text{if } r < a, \\ -\alpha & \text{if } r > a. \end{cases} \tag{4.14}$$

Then Theorem 2.9 in NSAD14 suggests that the cline is isotropic, i.e., it is $p(r)$, and $p'(r) < 0$ in Ω_+. Furthermore, Theorem 2.7 in NSAD14 suggests that a nontrivial equilibrium exists only if $0 \leq \beta < 1$. Finally, by Corollary 2.10 in NSAD14, we have $p'(0) = 0$.

We make the above assumptions and posit the absence of dominance. Then in two dimensions, (2.16) and (2.18) in NSAD14 instruct us to replace the unidimensional problem (4.1) by

$$\frac{1}{r}(rp')' + g(r)p(1-p) - \beta p = 0 \qquad \text{in } \Omega_+, \tag{4.15a}$$

$$p'(a\pm) = \theta_\pm(p_+ - p_-), \tag{4.15b}$$

$$p'(0) = 0, \tag{4.15c}$$

$$p(\infty) = 0, \tag{4.15d}$$

$$p'(\infty) = 0. \tag{4.15e}$$

The parameters $\theta_+ > 0$ and $\theta_- > 0$ signify the scaled transmissivities across the circular barrier from inside and from outside the pocket, respectively. As in one dimension, we linearize (4.15) at $p \equiv 0$:

$$\frac{1}{r}(r\psi')' + [g(r) - \beta]\psi = 0 \qquad \text{in } \Omega_+, \tag{4.16a}$$

$$\psi'(a\pm) = \theta_\pm[\psi(a+) - \psi(a-)], \tag{4.16b}$$

$$\psi'(0) = 0, \tag{4.16c}$$

$$\psi(\infty) = 0, \tag{4.16d}$$

$$\psi'(\infty) = 0. \tag{4.16e}$$

We denote the Bessel functions of the first kind and the modified Bessel functions of second kind of arbitrary order ν by J_ν and K_ν, respectively. Let $z_0 \approx 2.405$ and $z_1 > z_0$ designate the smallest positive zeros of $J_0(z)$ and $J_1(z)$, respectively (Olver, 1964, pp. 370, 409). Recall (4.4) and set

$$\lambda\theta_+ J_1(\lambda a) K_0(\mu a) = \mu K_1(\mu a)[\theta_- J_0(\lambda a) - \lambda J_1(\lambda a)]. \tag{4.17}$$

We define

$$z = \lambda a, \qquad \gamma = \frac{\mu}{\lambda} = \sqrt{\frac{\alpha+\beta}{1-\beta}}, \qquad \mu a = \gamma z, \tag{4.18a}$$

$$a_0 = z_0/\lambda, \tag{4.18b}$$

and cast (4.17) into the form

$$\chi(z) = \gamma K_1(\gamma z)[\theta_- J_0(z) - \lambda J_1(z)] - \theta_+ J_1(z) K_0(\gamma z) = 0. \tag{4.19}$$

Theorem 4.7. *If* $0 \le \beta < 1$, *then* (4.19) *has a unique root* $z^{**} \in (0, z_0)$, *to which corresponds the minimal radius* $a^{**} = z^{**}/\lambda$.

Proof. We shall require the facts that as $z \to 0$ (Olver, 1964, pp. 360, 375),

$$J_0(z) \to 1, \qquad J_1(z) \sim \tfrac{1}{2}z, \tag{4.20a}$$

$$K_0(z) \sim -\ln z, \qquad K_1(z) \sim \frac{1}{z}. \tag{4.20b}$$

Defining

$$\rho = \frac{\lambda}{\theta_-}, \qquad \sigma = \frac{\theta_+}{\gamma\theta_-}, \tag{4.21a}$$

$$X(z) = \frac{K_1(\gamma z)}{K_0(\gamma z)}, \qquad Y(z) = \frac{J_1(z)}{J_0(z)}, \tag{4.21b}$$

$$\hat{X}(z) = \frac{X(z)}{\rho X(z) + \sigma}, \tag{4.21c}$$

we can rearrange (4.19) as

$$Z(z) = Y(z) - \hat{X}(z) = 0. \tag{4.21d}$$

As $z \to 0$, from (4.21b) and (4.20b) we see that $X(z) \to \infty$, so $\hat{X}(z) \to 1/\rho$. Furthermore, (4.21b) and (4.20a) reveal that $Y(z) \to 0$. Therefore, $Z(z) \to -1/\rho < 0$.

As $z \to z_0-$, we invoke (4.21b) and (4.20b) to infer that $X(z)$ converges to a positive constant and hence so does $\hat{X}(z)$. Appealing to (4.21b) and (4.20a) tells us that $Y(z) \to \infty$, whence $Z(z) \to \infty$.

We conclude that (4.21d) has at least one root $z^{**} \in (0, z_0)$. To prove that z^{**} is unique, note first that by Lemma 2.4 in Ismail and Muldoon (1978), the ratio $X(z)$ is a decreasing function of z in $(0, \infty)$. According to (4.21c), the ratio $\hat{X}(z)$ shares this property. Lemma 2.5 in Ismail and Muldoon (1978) informs us that $Y(z)$ is increasing in $(0, z_0)$. Consequently, from (4.21d) we observe that $Z(z)$ is monotone increasing in $(0, z_0)$, which demonstrates the uniqueness of z^{**} and completes our proof. □

Theorem 4.8. *If* (3.8), (4.14), *and* (4.15) *hold, then a cline exists if and only if* $0 \leq \beta < 1$ *and* $a > a^{**}$.

Proof. By Theorem 4.7, $a^{**} \in (0, a_0)$ exists and is unique. From (4.16) we derive (Olver, 1964, pp. 358, 374)

$$\psi(r) = \begin{cases} B_0 J_0(\lambda r) & \text{if } r < a, \\ C_0 K_0(\mu r) & \text{if } r > a, \end{cases} \tag{4.22}$$

where B_0 and C_0 are constants.

Enforcing (4.16b), we deduce

$$C_0 \mu K_0'(\mu a) = \theta_+[C_0 K_0(\mu a) - B_0 J_0(\lambda a)], \tag{4.23a}$$

$$B_0 \lambda J_0'(\lambda a) = \theta_-[C_0 K_0(\mu a) - B_0 J_0(\lambda a)]. \tag{4.23b}$$

We have (Olver, 1964, pp. 361, 376)

$$J_0'(z) = -J_1(z), \qquad K_0'(z) = -K_1(z). \tag{4.24}$$

We substitute (4.24) into (4.23) and rearrange:

$$B_0 \theta_+ J_0(\lambda a) = C_0[\theta_+ K_0(\mu a) + \mu K_1(\mu a)], \tag{4.25a}$$

$$C_0 \theta_- K_0(\mu a) = B_0[\theta_- J_0(\lambda a) - \lambda J_1(\lambda a)]. \tag{4.25b}$$

Multiplying (4.25a) by (4.25b) leads directly to (4.17), which completes our proof. □

Remark 4.9. If the barrier is symmetric and extremely weak ($\theta_+ = \theta_- \to \infty$), then it disappears and (4.17) reduces to

$$\frac{\lambda J_1(\lambda a)}{J_0(\lambda a)} = \frac{\mu K_1(\mu a)}{K_0(\mu a)},$$

which is (4.1) in NSAD14.

Remark 4.10. Recalling (4.4) and (4.12), we observe that if $\beta = 0$, then (4.17) becomes

$$\theta_+ J_1(a) K_0(\tilde{\alpha} a) = \tilde{\alpha} K_1(\tilde{\alpha} a)[\theta_- J_0(a) - J_1(a)]. \tag{4.26}$$

We now derive asymptotic formulas for the minimal radius a^{**} under the assumption that one of the parameters α, β, or $\theta_\pm$ approaches a limit of its range with the other three fixed. The characteristic equation (4.9) in NSAD14 is simpler than (4.19), and we have not established here that z^{**} is monotonic in our four parameters. Therefore, our analysis must be more elaborate than that in NSAD14, and we require the following natural convergence assumption.

(A4.1). Suppose that (4.15) holds and that z in (4.19) converges in $(0, z_0)$ as any one of $\alpha \in [0, \infty)$, $\beta \in [0, 1)$, or $\theta_\pm \in (0, \infty)$ tends to a limit of its range with the other three parameters fixed.

We note first that (4.19) does not simplify if either $\beta \to 0$ with α fixed in $(0, \infty)$, or $\alpha \to 0$ with β fixed in $(0, 1)$. Next, we rewrite (4.19) as

$$\theta_- \gamma J_0(z) K_1(\gamma z) = J_1(z)[\lambda \gamma K_1(\gamma z) + \theta_+ K_0(\gamma z)] \tag{4.27}$$

and proving the following useful lemma.

Lemma 4.11. *If ξ converges, $\xi \not\to 1$, and*

$$\epsilon/\xi^2 \sim -\ln \xi \tag{4.28a}$$

as $\epsilon \to 0+$, then

$$\xi \sim (-2\epsilon/\ln \epsilon)^{1/2}. \tag{4.28b}$$

Proof. Since $\epsilon = -\xi^2 \ln \xi$ and $\xi \not\to 1$, we infer at once that $\xi \to 0$ as $\epsilon \to 0$. We can extract from ξ the dominant behavior $\sqrt{\epsilon}$ by defining the slow variable ζ through $\xi = \sqrt{\epsilon}\zeta$. Consequently, (4.28a) becomes

$$\frac{1}{\zeta^2} \sim -\ln(\sqrt{\epsilon}\zeta) = -\tfrac{1}{2}\ln\epsilon - \ln\zeta. \tag{4.29}$$

Since ξ converges, so does ζ. If $\zeta \to \check{\zeta}$ for some $\check{\zeta} > 0$ as $\epsilon \to 0$, then the left-hand side of (4.29) converges to $1/\check{\zeta}^2$, whereas the right-hand side tends to ∞. Thus, $\zeta \to 0$, which implies that $-\ln\zeta$ is negligible with respect to $1/\zeta^2$. Therefore, we obtain

$$\zeta^2 \sim -2/\ln\epsilon, \tag{4.30}$$

whence (4.28b) follows immediately. □

Corollary 4.12. *If* (A4.1) *holds and* $\beta \to 1-$ *with* α *fixed in* $[0,\infty)$*, then*

$$a^{**} \sim z_0/\lambda. \tag{4.31}$$

Proof. From (4.4) and (4.18) we get

$$\lambda \to 0, \qquad \gamma \to \infty, \qquad \gamma\lambda = \mu \to (1+\alpha)^{1/2} \equiv \hat{\mu}. \tag{4.32}$$

There are three cases.

(a) If $\gamma z \to 0$, then (4.32) immediately implies that $z \to 0$, whence (4.19), (4.20), and (4.32) yield

$$\gamma\left(\frac{1}{\gamma z}\right)(\theta_- - \tfrac{1}{2}\lambda z) \sim -\tfrac{1}{2}\theta_+ z \ln(\gamma z). \tag{4.33}$$

Since $\lambda \to 0$ and $z \to 0$, the term $\frac{1}{2}\lambda z$ on the left-hand side of (4.33) converges to zero. From (4.33) and the fact that $\gamma \to \infty$, we find

$$\frac{2\theta_-}{\theta_+ z^2} \sim -\ln(\gamma z) < -\ln z. \tag{4.34}$$

Since $\gamma \to \infty$ and θ_+ and θ_- are constants, we see that (4.34) fails for sufficiently small z. Hence, $\gamma z \not\to 0$.

(b) If $\gamma z \to \eta$ for some $\eta \in (0, \infty)$, then again $z \to 0$. Now (4.19) and (4.20) inform us

$$\gamma K_1(\eta)(\theta_- - \tfrac{1}{2}\lambda z) \sim \tfrac{1}{2}\theta_+ z K_0(\eta), \tag{4.35}$$

whence

$$2\gamma\theta_- K_1(\eta) \sim \theta_+ z K_0(\eta). \tag{4.36}$$

However, as $\gamma \to \infty$ and $z \to 0$, the left-hand side of (4.36) diverges, whereas the right-hand side converges to zero. Therefore, this case also cannot occur.

(c) Finally, suppose that $\gamma z \to \infty$. As $w \to \infty$ (Olver, 1964, p. 378),

$$K_\nu(w) \sim \left(\frac{\pi}{2w}\right)^{1/2} e^{-w}. \tag{4.37}$$

Consequently, (4.27) and (4.32) reveal

$$\theta_- \gamma J_0(z) \sim (\hat{\mu} + \theta_+) J_1(z). \tag{4.38}$$

Since $\gamma \to \infty$ and $z \in (0, z_0)$, the right-hand side of (4.38) is bounded, whereas the left-hand side diverges unless $z \to z_0$. Recalling (4.18a) validates (4.31). $\square$

Remark 4.13. Under the assumptions in Corollary 4.12, from (4.5) and (4.31) we infer

$$a^* \sim \frac{\pi}{2\lambda} < \frac{z_0}{\lambda} \sim a^{**}. \tag{4.39}$$

Thus, as is intuitive, it is harder to maintain an allele in a bidimensional pocket than in a unidimensional one. The following remarks will reinforce this conclusion.

Corollary 4.14. *If* (A4.1) *holds and* $\beta \to 0$ *with* $\alpha = 0$, *then*

$$a^{**} \sim 2\left(-\frac{\theta_-}{\theta_+ \ln \beta}\right)^{1/2}. \tag{4.40}$$

Proof. From (4.4), (4.12), and (4.18) we see

$$\lambda \to 1, \qquad \mu \sim \tilde{\beta}, \qquad \gamma \sim \mu \sim \tilde{\beta} \to 0, \qquad \gamma z \to 0, \tag{4.41}$$

whence (4.27) and (4.20b) tell us

$$\left(\frac{\theta_-}{z}\right) J_0(z) \sim J_1(z) \left[\frac{1}{z} - \theta_+ \ln(\gamma z)\right]. \tag{4.42}$$

Again, there are three cases.

(a) If $z \to \check{z}$ for some $\check{z} \in (0, z_0)$, then (4.42) implies

$$\frac{\theta_-}{\check{z}} J_0(\check{z}) \sim J_1(\check{z}) \left[\frac{1}{\check{z}} - \theta_+ \ln(\gamma \check{z})\right], \tag{4.43}$$

which is impossible because the left-hand side of (4.43) is bounded, whereas the right-hand side diverges as $\gamma \to 0$.

(b) If $z \to z_0$, then (4.42) gives

$$\frac{1}{z_0} \sim \theta_+ \ln(\gamma z_0) \sim \theta_+ \ln \gamma, \tag{4.44}$$

which cannot hold because the left-hand side of (4.44) is positive, whereas, for $\gamma < 1$, the right-hand side is negative.

(c) We conclude that $z \to 0$. Then (4.42) and (4.20) yield

$$\frac{2\theta_-}{z^2} \sim \frac{1}{z} - \theta_+ \ln(\gamma z). \tag{4.45}$$

Since $1/z$ is negligible compared with $1/z^2$, the asymptotic equivalence (4.45) reduces to

$$\frac{2\theta_-}{\theta_+ z^2} \sim -\ln(\gamma z). \tag{4.46}$$

Setting

$$\xi = \gamma z \to 0, \qquad \epsilon = \frac{2\theta_- \gamma^2}{\theta_+} \tag{4.47}$$

simplifies (4.46) to (4.28a) and therefore yields (4.28b). From (4.28b), (4.47), (4.41), and (4.12) we derive

$$\xi \sim 2\left(-\frac{\theta_- \beta}{\theta_+ \ln \beta}\right)^{1/2}. \tag{4.48}$$

Appealing to (4.47), (4.41), (4.12), and (4.18), we deduce easily that (4.48) is equivalent to (4.40), which completes our proof. □

Remark 4.15. From Remark 4.5 and (4.40) we see that under the assumptions in Corollary 4.14

$$a^* \sim \tilde{\beta}\theta_-/\theta_+ < a^{**}. \tag{4.49}$$

Corollary 4.16. *If* (A4.1) *holds and* $\alpha \to 0$ *with* $\beta = 0$*, then*

$$a^{**} \sim 2\left(-\frac{\theta_-}{\theta_+ \ln \alpha}\right)^{1/2}. \tag{4.50}$$

Proof. From (4.4), (4.12), and (4.18) we find

$$\lambda = 1, \qquad \mu \sim \tilde{\alpha}, \qquad \gamma = \mu \sim \tilde{\alpha} \to 0, \qquad \gamma z \to 0. \tag{4.51}$$

Comparison of (4.51) with (4.41) shows at once that the proof of Corollary 4.14 applies unaltered to (4.47), but in (4.48) we must replace β by α. This substitution in (4.40) establishes (4.50). □

Remark 4.17. Remark 4.5 and (4.50) demonstrate that under the assumptions in Corollary 4.16

$$a^* \sim \tilde{\alpha}\theta_-/\theta_+ < a^{**}. \tag{4.52}$$

Corollary 4.18. *If* (A4.1) *holds and* $\alpha \to \infty$ *with* β *fixed in* $[0, 1)$*, then*

$$a^{**} \to \hat{z}/\lambda, \tag{4.53}$$

where $\hat{z}$ *is the unique root in* $(0, z_0)$ *of*

$$\theta_- J_0(z) = \lambda J_1(z). \tag{4.54}$$

Proof. Here, λ is fixed in $(0, 1]$,

$$\mu \sim \tilde{\alpha} \to \infty, \qquad \gamma \sim \tilde{\alpha}/\lambda \to \infty. \tag{4.55}$$

According to (4.32), in Corollary 4.12 the parameter $\lambda \to 0$. However, parts (a) and (b) of the proof of Corollary 4.12 hold for fixed λ. In part (c), $\gamma z \to \infty$, whence (4.55) and (4.37) reduce (4.27) to

$$\theta_- J_0(z) \sim \lambda J_1(z). \tag{4.56}$$

From (4.56) and (4.21b) we see that $\hat{z}$ satisfies

$$Y(z) = \frac{J_1(z)}{J_0(z)} = \frac{\theta_-}{\lambda} \tag{4.57}$$

in $(0, z_0)$. In the proof of Theorem 4.7, we showed that $Y(z)$ increases monotonically from 0 to ∞ as z increases from 0 to z_0. Thus, (4.57) has a unique root $\hat{z} \in (0, z_0)$. This completes the proof. □

Corollary 4.19. *If* (A4.1) *holds and* $\theta_+ \to \infty$*, then*

$$a^{**} \sim \frac{2}{\lambda}\left(\frac{\theta_-}{\theta_+ \ln \theta_+}\right)^{1/2}. \tag{4.58}$$

Proof. If $z \to \check{z}$ for some $\check{z} \in (0, z_0]$ as $\theta_+ \to \infty$, then the left-hand side of (4.27) remains bounded, whereas the right-hand side diverges. Therefore, $z \to 0$, and (4.33) and the asymptotic equivalence in (4.34) hold. The latter gives

$$\frac{2\theta_-}{\theta_+ z^2} \sim -\ln z. \tag{4.59}$$

Putting $\epsilon = 2\theta_-/\theta_+$ and invoking (4.28) lead easily to

$$z \sim 2\left(\frac{\theta_-}{\theta_+ \ln \theta_+}\right)^{1/2} \tag{4.60}$$

and hence to (4.58). □

Remark 4.20. Under the assumptions of Corollary 4.19, from (4.5) and (4.58) we obtain

$$a^* \sim \frac{\mu\theta_-}{\lambda^2\theta_+} < a^{**}. \tag{4.61}$$

Corollary 4.21. *If* $\theta_+ \to 0$ *and* (A4.1) *holds, then so does the conclusion of Corollary* 4.18.

Proof. As $\theta_+ \to 0$, from (4.19) we get (4.54), whence the proof of Corollary 4.18 applies here. $\square$

Corollary 4.22. *If* $\theta_- \to \infty$ *and* (A4.1) *holds, then so does* (4.31).

Proof. We have the usual three cases.

(a) If $z \to 0$, then from (4.33) we deduce

$$2\theta_- \sim z[\lambda - \theta_+ z \ln(\gamma z)], \tag{4.62}$$

which is impossible because the left-hand side of (4.62) diverges, whereas the right-hand side converges to zero.

(b) If $z \to \check{z}$ for some $\check{z} \in (0, z_0)$ then the left-hand side of (4.27) diverges, whereas the right-hand side is bounded. Thus, $z \not\to \check{z} \in (0, z_0)$.

(c) Parts (a) and (b) tell us that $z \to z_0$, which proves Corollary 4.22. $\square$

Remark 4.23. Under the assumptions of Corollary 4.22, from (4.5) and (4.31) we derive (4.39).

Corollary 4.24. *If* (A4.1) *holds and* $\theta_- \to 0$*, then*

$$a^{**} \sim 2\theta_-/\lambda^2. \tag{4.63}$$

Proof. If $z \to \check{z}$ for some $\check{z} \in (0, z_0]$, then the left-hand side of (4.27) converges to zero, whereas the right-hand side remains positive. Hence, $z \to 0$ and (4.62) implies

$$z \sim 2\theta_-/\lambda, \tag{4.64}$$

which establishes (4.63). $\square$

Remark 4.25. Under the assumptions of Corollary 4.24, invoking (4.5) and (4.63) demonstrates

$$a^* \sim \frac{\mu\theta_-}{\lambda^2(\mu + \theta_+)} < \frac{\theta_-}{\lambda^2} < a^{**}. \tag{4.65}$$

INSERT TABLES 4–6 ABOUT HERE

Remark 4.26. Remark 4.3 establishes that a^* increases when α, β, or θ_- increases, or θ_+ decreases. Tables 4–6 and our asymptotic results for a^{**} indicate that the same holds for a^{**}.

Remark 4.27. In Remark 4.6, we found that a^* depends more strongly on β and θ_- than on α and θ_+, respectively. Tables 4–6 suggests that this observation holds also for a^{**}.

Remark 4.28. Comparison of Tables 4, 5, and 6 with Tables 1, 2, and 3, respectively, and our asymptotic results indicate that $a^* < a^{**}$. Without the barrier, Corollary 4.12 in NSAD14 showed that the minimal radius increases with dimensionality. Thus, increasing dimensionality makes it more difficult to maintain a cline. Consult Remark 4.13 in NSAD14 for references and more discussion.

5. Solution for the unidimensional cline

We recall (4.2) and under assumptions (3.8), (3.9), $0 \leq \beta < 1$, and $a > a^*$, we first solve (4.1) for $p(x)$ in terms of acceptable gene frequencies (p_0, p_-, p_+) such that

$$0 < p_+ < p_- < p_0 < 1 - \beta = \lambda^2 \tag{5.1}$$

and then show how to calculate (p_0, p_-, p_+).

The monotonicity (3.7b) allows us to set and invert

$$u(p) = p'(x) \quad \text{ in } \Omega_+, \tag{5.2}$$

whence

$$p''(x) = [u(p)]_x = u'(p)u(p) = \tfrac{1}{2}(u^2)' \quad \text{ in } \Omega_+. \tag{5.3}$$

Consequently, (4.1a) gives

$$\tfrac{1}{2}(u^2)' + g(x)p(1-p) - \beta p = 0 \quad \text{ in } (0, p_0)\backslash[p_+, p_-]. \tag{5.4}$$

We recall (3.9) and solve separately in (p_-, p_0) and $(0, p_+)$, i.e., inside and outside the pocket, respectively.

Integrating (5.4) in (p_-, p_0), we obtain

$$\int_p^{p_0} [(u^2)' + 2q(1-q) - 2\beta q]dq = 0. \tag{5.5}$$

Using (4.1c) and (4.4) tells us at once

$$\begin{aligned} [u(p)]^2 &= \lambda^2(p_0^2 - p^2) - \tfrac{2}{3}(p_0^3 - p^3) \\ &= (p_0 - p)[\lambda^2(p_0 + p) - \tfrac{2}{3}(p_0^2 + p_0 p + p^2)] \quad \text{in } (p_-, p_0). \end{aligned} \tag{5.6}$$

In $(0, p_+)$, we have

$$\int_0^{p} [(u^2)' - 2\alpha q(1-q) - 2\beta q]dq = 0, \tag{5.7}$$

whence (4.1e) and (4.4) immediately reveal

$$[u(p)]^2 = \mu^2 p^2 - \tfrac{2}{3}\alpha p^3 = p^2(\mu^2 - \tfrac{2}{3}\alpha p) \quad \text{in } (0, p_+). \tag{5.8}$$

Remark 5.1. From (4.4), the positivity of (5.8) is obvious. By Corollary 3.7 and (3.7b), we have

$$p(x) < p_0 < 1 - \beta = \lambda^2 \quad \text{in } \Omega. \tag{5.9}$$

Hence, the bracket in (5.6) is

$$\begin{aligned} &> p_0(p_0 + p) - \tfrac{2}{3}(p_0^2 + p_0 p + p^2) \\ &= \tfrac{1}{3}(p_0^2 + p_0 p - 2p^2) \\ &> \tfrac{1}{3}(p^2 + p^2 - 2p^2) = 0 \quad \text{in } (0, p_0)\backslash[p_+, p_-]. \end{aligned} \tag{5.10}$$

From (5.6), (5.8), and (3.7b) we get

$$u(p) = -(p_0 - p)^{1/2}[\lambda^2(p_0 + p) - \tfrac{2}{3}(p_0^2 + p_0 p + p^2)]^{1/2} \qquad \text{in } (p_-, p_0), \tag{5.11a}$$

$$u(p) = -p(\mu^2 - \tfrac{2}{3}\alpha p)^{1/2} \qquad \text{in } (0, p_+). \tag{5.11b}$$

We invoke (5.11a) to deduce the elliptic integral

$$\begin{aligned} x &= \int_{p_0}^{p} \frac{dq}{u(q)} \\ &= \int_{p}^{p_0} (p_0 - q)^{-1/2} [\lambda^2 (p_0 + q) - \tfrac{2}{3}(p_0^2 + p_0 q + q^2)]^{-1/2} dq \quad \text{in } (0, a). \end{aligned} \tag{5.12}$$

By removing the singularity from the integrand in (5.12), we can simplify our results and increase the accuracy of numerical calculations. Therefore, we set $v^2 = p_0 - q$ and transform (5.12) to

$$x = 2 \int_{0}^{(p_0 - p)^{1/2}} [(\lambda^2 - \tfrac{2}{3} p_0)(2p_0 - v^2) - \tfrac{2}{3}(p_0 - v^2)^2]^{-1/2} dv \quad \text{in } (0, a). \tag{5.13}$$

Analytic inversion of (5.13) is impossible.

Similarly, (5.11b) yields

$$x - a = \int_{p}^{p_+} \frac{dq}{q(\mu^2 - \frac{2}{3}\alpha q)^{1/2}} \quad \text{in } (a, \infty). \tag{5.14}$$

Recalling (4.4), for this elementary integral we find (Gradshteyn and Ryzhik, 1965, p. 78)

$$x - a = \frac{1}{\mu} \ln \left\{ \left[\frac{(\mu^2 - \frac{2}{3}\alpha p_+)^{1/2} - \mu}{(\mu^2 - \frac{2}{3}\alpha p_+)^{1/2} + \mu} \right] \left[\frac{(\mu^2 - \frac{2}{3}\alpha p)^{1/2} + \mu}{(\mu^2 - \frac{2}{3}\alpha p)^{1/2} - \mu} \right] \right\} \quad \text{in } (a, \infty). \tag{5.15}$$

Now put

$$c = \frac{\mu + (\mu^2 - \frac{2}{3}\alpha p_+)^{1/2}}{\mu - (\mu^2 - \frac{2}{3}\alpha p_+)^{1/2}} > 1. \tag{5.16}$$

Substituting (5.16) into (5.15) and inverting the result lead to

$$p(x) = \frac{3\mu^2}{2\alpha} \left\{ 1 - \left[\frac{ce^{\mu(x-a)} - 1}{ce^{\mu(x-a)} + 1} \right]^2 \right\} \quad \text{in } (a, \infty) \text{ if } \alpha > 0. \tag{5.17a}$$

Employing (4.4), (4.12), and (5.16), we can easily take the limit of (5.17a) as $\alpha \to 0$ with fixed $\beta \in (0, 1)$:

$$p(x) = p_+ e^{-\tilde{\beta}(x-a)} \quad \text{in } (a, \infty) \text{ if } \alpha = 0. \tag{5.17b}$$

We have now proved

Theorem 5.2. *If* (A2.1), (3.9), (4.1), (5.1), $0 \leq \beta < 1$, *and* $a > a^*$ *hold and* (p_0, p_-, p_+) *are given, then* (5.17a) *and the inversion of* (5.13) *specify the unique, nontrivial equilibrium.*

To determine (p_0, p_-, p_+), we appeal to (5.11) and (5.13) and write

$$\phi_1(p_0, p_-) = u(p_-) = -(p_0 - p_-)^{1/2}[\lambda^2(p_0 + p_-) - \tfrac{2}{3}(p_0^2 + p_0 p_- + p_-^2)]^{1/2}, \tag{5.18a}$$

$$\phi_2(p_+) = u(p_+) = -p_+(\mu^2 - \tfrac{2}{3}\alpha p_+)^{1/2}, \tag{5.18b}$$

$$\phi_3(p_0, p_-) = 2\int_0^{(p_0 - p_-)^{1/2}} [(\lambda^2 - \tfrac{2}{3}p_0)(2p_0 - v^2) - \tfrac{2}{3}(p_0 - v^2)^2]^{-1/2} dv. \tag{5.18c}$$

Owing to (4.1b) and (5.18), we have

$$\phi_1(p_0, p_-) = \theta_-(p_+ - p_-), \tag{5.19a}$$

$$\phi_2(p_+) = \theta_+(p_+ - p_-), \tag{5.19b}$$

$$\phi_3(p_0, p_-) = a. \tag{5.19c}$$

From (5.19a) we see immediately

$$p_+ = p_- + \frac{1}{\theta_-}\phi_1(p_0, p_-). \tag{5.20}$$

Inserting (5.20) into (5.19b) gives

$$\theta_-\phi_2\left(p_- + \frac{1}{\theta_-}\phi_1(p_0, p_-)\right) = \theta_+\phi_1(p_0, p_-). \tag{5.21}$$

Thus, we can solve (5.19c) and (5.21) numerically for (p_0, p_-) and then compute p_+ from (5.20). We have now proved

Corollary 5.3. *If* (A2.1), (3.9), (4.1), (5.1), *and* $a > a^*$ *hold, then* (p_0, p_-) *is the unique solution of* (5.19c) *and* (5.21), *and* p_+ *is given by* (5.20).

Remark 5.4. Using (5.17), for $\alpha > 0$ we can easily derive

$$p(x) = \left(\frac{6\mu^2}{\alpha c}\right) e^{-\mu(x-a)} + O[e^{-2\mu(x-a)}] \tag{5.22}$$

as $x \to \infty$, which agrees with (5.17b) in the limit $\alpha \to 0$ with fixed $\beta \in (0, 1)$.

We now return to the solution (5.12) and express $x \in (0, a)$ in terms of $F(d, s)$, the elliptic integral of the first kind (Milne-Thomson, 1964, p. 589). We rewrite (5.12) as

$$x = \sqrt{3} \int_p^{p_0} [(p_0 - q)H(q; p_0)]^{-1/2} dq \quad \text{in } (0, a), \tag{5.23}$$

where

$$\begin{aligned} H(q; p_0) &= 3\lambda^2(p_0 + q) - 2(p_0^2 + p_0 q + q^2) \\ &= -2(q - q_+)(q - q_-), \end{aligned} \tag{5.24}$$

$$q_\pm = \tfrac{1}{4}\{3\lambda^2 - 2p_0 \pm [(3\lambda^2 - 2p_0)^2 + 8p_0(3\lambda^2 - 2p_0)]^{1/2}\}. \tag{5.25}$$

Recalling (4.4) and Corollary 3.7, we have $p_0 < \lambda^2$, which shows at once that $q_+ > 0 > q_-$.

Again invoking the fact that $p_0 < \lambda^2$, by straightforward algebra we demonstrate that $q_+ > p_0$. Consequently, we have established

$$q_+ > p_0 \geq p \geq p_- > 0 > q_- \tag{5.26}$$

in

$$x = \sqrt{\frac{3}{2}} \int_p^{p_0} [(q_+ - q)(p_0 - q)(q - q_-)]^{-1/2} dq \quad \text{in } (0, a). \tag{5.27}$$

We define

$$d = \sin^{-1}\left[\frac{(q_+ - q_-)(p_0 - p)}{(p_0 - q_-)(q_+ - p)}\right]^{1/2}, \quad s = \left(\frac{p_0 - q_-}{q_+ - q_-}\right)^{1/2}. \tag{5.28}$$

Then (5.25)–(5.28) yield (Gradshteyn and Ryzhik, 1965, p. 219)

$$x = \left(\frac{6}{q_+ - q_-}\right)^{1/2} F(d, s) \quad \text{in } (0, a). \tag{5.29}$$

We have now proved

Corollary 5.5. *The solution* (5.12) *is equivalent to* (5.29)*, where the parameters are given by* (5.25), (5.26), *and* (5.28)*.*

From (5.18c), (5.19c), (5.28), and (5.29) we infer immediately

Corollary 5.6. *The result* (5.19c) *is equivalent to*

$$a = \left(\frac{6}{q_+ - q_-}\right)^{1/2} F(d_-, s), \tag{5.30a}$$

where

$$d_- = \sin^{-1}\left[\frac{(q_+ - q_-)(p_0 - p_-)}{(p_0 - q_-)(q_+ - p_-)}\right]^{1/2}. \tag{5.30b}$$

We apply Corollary 5.3 and then Theorem 5.2 with the aid of Mathematica and NLopt to produce Figs. 1–5. In each figure, we fix four of our five parameters $(a, \alpha, \beta, \theta_\pm)$ and display the clines for three values of the fifth. The light vertical lines signify the right boundary of the environmental pocket. The clines agree with (3.7b), (3.11), Corollaries 3.3, 3.4, 3.8, and biological intuition. In Fig. 2, since $\beta = 0.1$, for $\alpha = 0$ the simple formula (5.17b) implies that $p(x) \to 0$ as $x \to \infty$ very slowly. This convergence is due to the boundary condition (4.1d) rather than selection. In accord with biological intuition, as shown in Table 1 in Nagylaki (2012a), Fig. 2 in Nagylaki (2012b), Tables 1 and 2 and Fig. 3 in NSAD14, and Tables 1 and 2 and Fig. 3 in this paper, the rate β of long-distance migration has a strong effect on the cline. As expected intuitively and from Figs. 1 and 2 in N16, in Figs. 4 and 5 we observe that inflow into the environmental pocket (proportional to θ_-) affects the gene-frequencies in the pocket more than those outside, whereas outflow from the pocket (proportional to θ_+) has the opposite effect.

INSERT FIGS. 1–5 ABOUT HERE

6. Discussion

Here, we summarize our main results and mention some open problems. We examined the existence and properties of a cline at equilibrium in an environmental pocket under the joint influence of selection without dominance; homogeneous, isotropic short- and long-distance migration;

and a geographical barrier, which in general is not symmetric. We approximated long-distance migration by partial global panmixia (Nagylaki, 2012a). Excluding the investigation in Section 4.2 of the isotropic bidimensional case, all the analyses were unidimensional. Under the assumption that all the evolutionary forces and the transmissitivites of the barrier are weak, we used a continuous approximation (N16).

As established in N16, both the gene frequency, $p(x)$, and its slope, $p'(x)$, are discontinuous at the barrier; see the scaled problem (2.6) above. Otherwise, comparing Section 3 with Section 2 in NSAD14 demonstrates that, at least at equilibrium in one dimension, the introduction of the barrier has no *qualitative* effect. Thus, the cline does not exist if the scaled panmictic rate $\beta \geq 1$ (Theorem 3.1). By Theorem 3.2, if the spatial dependence of selection is symmetric, i.e, $g(-x) = g(x)$ in $\Omega_+ = (0, \infty)\backslash\{a\}$, and if the barrier is at $\pm a$, then the cline is also symmetric and $p'(x) < 0$ in Ω_+. Furthermore, $p'(0) = 0$ (Corollary 3.3), and $p''(x) > 0$ wherever $g(x) < 0$ (Corollary 3.4). For the step-environment (3.9), Corollaries 3.7 and 3.8 reveal that $p_0 = p(0) < 1 - \beta$ and $p''(x) < 0$ in $(-a, a)$, respectively.

Sections 4 and 5 treat only the step-environment (3.9). Theorem 4.1 demonstrates that a unidimensional cline exists if and only if $0 \leq \beta < 1$ and $a > a^*$, where the minimal radius a^* is given explicitly by the simple formula (4.5). In the isotropic, bidimensional case, a^* must be replaced by a^{**}, the smallest positive root of the characteristic equation (4.17); see Theorems 4.7 and 4.8 for details. Although (4.17) cannot be solved analytically, in addition to the numerical calculations in Tables 4–6, in the corollaries at the end of Section 4 we evaluated a^{**} asymptotically. These results support the intuitive conjecture $a^* < a^{**}$, which holds if there is no barrier (NSAD14, Theorem 4.12). They indicate also that the dependence of a^* and a^{**} on β is stronger than that on the solution-coefficient ratio α. Note that if $\beta > 0$, one cannot solve even for the unidimensional minimal selection-migration ratio, whereas the derivation of (4.5) for a^* was easy.

In Section 5, we investigated the unidimensional cline $p(x)$, which depends on p_0 and $p_\pm = p(a\pm)$. These essential gene frequencies can be evaluated only numerically; Corollary 5.3 shows how. Given (p_0, p_-, p_+) that satisfy (5.1), Theorem 5.2 instructs us how to calculate $p(x)$. If

$0 \leq x < a$, we must invert numerically the elliptic integral (5.13); if $x > a$, the explicit solution is (5.17).

Let us compare the necessary and sufficient conditions for the existence of a monotone cline in $\mathcal{R} = (-\infty, \infty)$ with those for a cline in the pocket. Suppose first that

$$g(x) = \begin{cases} -\alpha & \text{if } x < 0, \\ 1 & \text{if } x > 0; \end{cases} \tag{6.1}$$

there is no dominance; and (see (4.20) in N16)

$$0 \leq \beta < \beta_0(\alpha) = \frac{2\alpha}{|\alpha - 1|} \qquad \text{if } \alpha \neq 1, \tag{6.2}$$

and $\beta_0(1) = \infty$. Then, by Theorems 4.8 and 4.11 in N16, a unique cline exists. For a unidimensional pocket with step-environment (3.9) and no dominance, Theorems 4.1 and 5.2 and Corollary 5.3 demonstrate that a unique cline exists if and only if

$$0 \leq \beta < 1 \qquad \text{and} \qquad a > a^* = \frac{1}{\lambda} \tan^{-1}\left[\frac{\mu\theta_-}{\lambda(\mu + \theta_+)}\right]. \tag{6.3}$$

Since $\beta_0 \in (0, \infty)$ in (6.2) and $\beta \in [0, 1)$ in (6.3); and since (6.3) depends on a, whereas (6.2) does not, we conclude that existence of the monotone cline does not imply existence of one in the pocket and *vice versa.*

We now turn to some open problems. Many results without a barrier were proved in NSAD14; (e.g., convergence to $p \equiv 0$ when $\beta \geq 1$ in Theorem 2.7, unidimensional isotropy and $p'(x) < 0$ in $(0, \infty)$ in Theorem 2.9); we extended only some of these to a pocket with a barrier. Similarly, if the convergence assumption in (A4.1) could be proved, then our asymptotic analysis of (4.19) would become fully comparable to that of (4.9) in NSAD14.

Uniqueness and global asymptotic stability of the cline were not proved in NSAD14; demonstrating these basic properties in our more general model is very desirable.

As discussed at the beginning of Section 4.2, the conjectured multidimensional transition conditions across the barrier, though intuitively plausible, have not been established. Once they are, they can be combined with the partial differential equation and the boundary conditions

(Nagylaki, 2012a). If the problem is anisotropic, one would be forced to use the selection-migration ratio instead of the radius.

In Corollary 4.12 and Theorem 4.16 in NSAD14, it was demonstrated for a step-environment that the minimal radius increases with dimensionality, and its dependence and that of the cline on the parameters was determined. Generalization to monotone decreasing $g(r)$ and inclusion of a barrier would be worthwhile.

Acknowledgment

We are grateful to Prof. Linlin Su for comments that improved this paper.

References

Brown, K. J., Tertikas, A., 1991. On the bifurcation of radially symmetric steady-state solutions arising in population genetics. SIAM J. Math. Anal. 22, 400–413.

Gradshteyn, I. S., Ryzhik, I. M., 1965. Table of Integrals, Series, and Products, fourth ed. Academic Press, New York.

Ismail, M. E. H., Muldoon, M. E., 1978. Monotonicity of the zeros of a cross-product of Bessel functions. SIAM J. Math. Anal. 9, 759–767.

Lou, Y., Nagylaki, T., Su, L., 2013. An integro-PDE model from population genetics. J. Differential Equations 254, 2367–2392.

Milne-Thomson, L. M., 1964. Elliptic integrals. In: Abramowitz, M., Stegun, I. A. (Eds.), Handbook of Mathematical Functions. National Bureau of Standards, Washington, DC, pp. 587–628.

Nagylaki, T., 1975. Conditions for the existence of clines. Genetics 80, 595–615.

Nagylaki, T., 1976. Clines with variable migration. Genetics 83, 867–886.

Nagylaki, T., 1978. Clines with asymmetric migration. Genetics 88, 813–827.

Nagylaki, T., 2012a. Clines with partial panmixia. Theor. Popul. Biol. 81, 45–68.

Nagylaki, T., 2012b. Clines with partial panmixia in an unbounded unidimensional habitat. Theor. Popul. Biol. 82, 22–28.

Nagylaki, T., 2016. Clines with partial panmixia across a geographical barrier. Theor. Popul. Biol. 109, 28–43.

Nagylaki, T., Su, L., Alevy, I., Dupont, T. F., 2014. Clines with partial panmixia in an environmental pocket. Theor. Popul. Biol. 95, 24–32.

Olver, F. W. J., 1964. Bessel functions of integer order. In: Abramowitz, M., Stegun, I. A. (Eds.), Handbook of Mathematical Functions. National Bureau of Standards, Washington, DC, pp. 355–433.

Tertikas, A., 1988. Existence and uniqueness of solutions for a nonlinear diffusion problem arising in population genetics. Arch. Ration. Mech. Anal. 103, 289–317.

Table 1

The unidimensional minimal radius a^* in (4.5). The parameters $\theta_- = 0.2$ and $\theta_+ = 5.0$ in (2.6) denote the scaled leftward and rightward transmissivities of the geographical barrier, respectively; and α in (3.9) and β in (2.6) designate the scaled selection coefficient outside the environmental pocket and the rate of global panmixia, respectively.

$\beta \backslash \alpha$	0	0.5	1.0	2.0	5.0
0	0	0.025	0.033	0.044	0.062
0.10	0.013	0.030	0.039	0.050	0.069
0.25	0.024	0.039	0.049	0.061	0.084
0.50	0.050	0.067	0.079	0.096	0.127
0.75	0.118	0.146	0.167	0.199	0.258
0.90	0.318	0.381	0.430	0.504	0.645

Table 2

The unidimensional minimal radius a^* in (4.5) with $\theta_- = 5.0$ and $\theta_+ = 0.2$. The parameters are described and referenced in the caption to Table 1.

$\beta\backslash\alpha$	0	0.5	1.0	2.0	5.0
0	0	1.320	1.335	1.346	1.356
0.10	1.339	1.409	1.422	1.432	1.441
0.25	1.539	1.571	1.581	1.590	1.599
0.50	1.968	1.984	1.991	1.998	2.006
0.75	2.897	2.907	2.912	2.918	2.926
0.90	4.726	4.734	4.739	4.744	4.751

Table 3

The unidimensional minimal radius a^* in (4.5) with $\alpha = \frac{1}{2}$ and $\beta = \frac{1}{4}$. The parameters are described and referenced in the caption to Table 1.

$\theta_-\backslash\theta_+$	0	0.5	1.0	2.0	5.0
0.2	0.262	0.168	0.123	0.080	0.039
0.5	0.605	0.405	0.302	0.199	0.098
1.0	0.990	0.730	0.568	0.388	0.195
2.0	1.342	1.122	0.947	0.704	0.379
5.0	1.616	1.506	1.401	1.213	0.815

Table 4

The bidimensional minimal radius a^{**} in Theorem 4.8. The parameters $\theta_- = 0.2$ and $\theta_+ = 5.0$ in (4.15) signify the scaled transmissivities across the circular barrier from inside and from outside the pocket, respectively; and α in (4.14) and β in (4.15) represent the scaled selection coefficient outside the environmental pocket and the rate of global panmixia, respectively.

$\beta\backslash\alpha$	0	0.5	1.0	2.0	5.0
0	0	0.144	0.154	0.166	0.185
0.10	0.137	0.158	0.168	0.181	0.202
0.25	0.167	0.185	0.195	0.210	0.235
0.50	0.237	0.258	0.272	0.293	0.333
0.75	0.417	0.453	0.481	0.524	0.609
0.90	0.880	0.972	1.046	1.161	1.390

Table 5

The bidimensional minimal radius a^{**} in Theorem 4.8 with $\theta_{-} = 5.0$ and $\theta_{+} = 0.2$. The parameters are described and referenced in the caption to Table 4.

$\beta\backslash\alpha$	0	0.5	1.0	2.0	5.0
0	0	2.152	2.164	2.173	2.181
0.1	2.244	2.285	2.295	2.303	2.312
0.25	2.509	2.531	2.539	2.546	2.554
0.50	3.147	3.160	3.166	3.172	3.179
0.75	4.563	4.572	4.577	4.582	4.589
0.90	7.362	7.369	7.374	7.379	7.386

Table 6

The bidimensional minimal radius a^{**} in Theorem 4.8 with $\alpha = 0.50$ and $\beta = 0.25$. The parameters are described and referenced in the caption to Table 4.

$\theta_-\backslash\theta_+$	0	0.5	1.0	2.0	5.0
0.2	0.520	0.410	0.347	0.275	0.185
0.5	1.158	0.895	0.741	0.567	0.361
1.0	1.781	1.464	1.241	0.959	0.602
2.0	2.256	2.025	1.824	1.507	0.991
5.0	2.571	2.471	2.372	2.181	1.709

Figure captions

Fig. 1. The unidimensional cline in Theorem 5.2 for scaled selection coefficient $\alpha = 0.5$, panmictic rate $\beta = 0.1$, leftward barrier transmissivity $\theta_- = 1.0$, rightward transmissivity $\theta_+ = 2.0$, and environmental pocket radii $a = 0.5$, 1.0, and 1.5. See (3.9), (3.10), and (4.1) for the exact meaning of the parameters.

Fig. 2. The unidimensional cline in Theorem 5.2 for $a = 1.5$, $\beta = 0.1$, $\theta_- = 2.0$, $\theta_+ = 1.0$, and $\alpha = 0$, 1.0, and 5.0.

Fig. 3. The unidimensional cline in Theorem 5.2 for $a = 3.0$, $\alpha = 2.0$, $\theta_- = 5.0$, $\theta_+ = 0.2$, and $\beta = 0$, 0.25, and 0.50.

Fig. 4. The unidimensional cline in Theorem 5.2 for $a = 2.00$, $\alpha = 0.50$, $\beta = 0.25$, $\theta_- = 1.00$, and $\theta_+ = 0.5$, 1.0, and 2.0.

Fig. 5. The unidimensional cline in Theorem 5.2 for $a = 2.00$, $\alpha = 0.50$, $\beta = 0.25$, $\theta_+ = 1.00$, and $\theta_- = 0.5$, 1.0, and 2.0

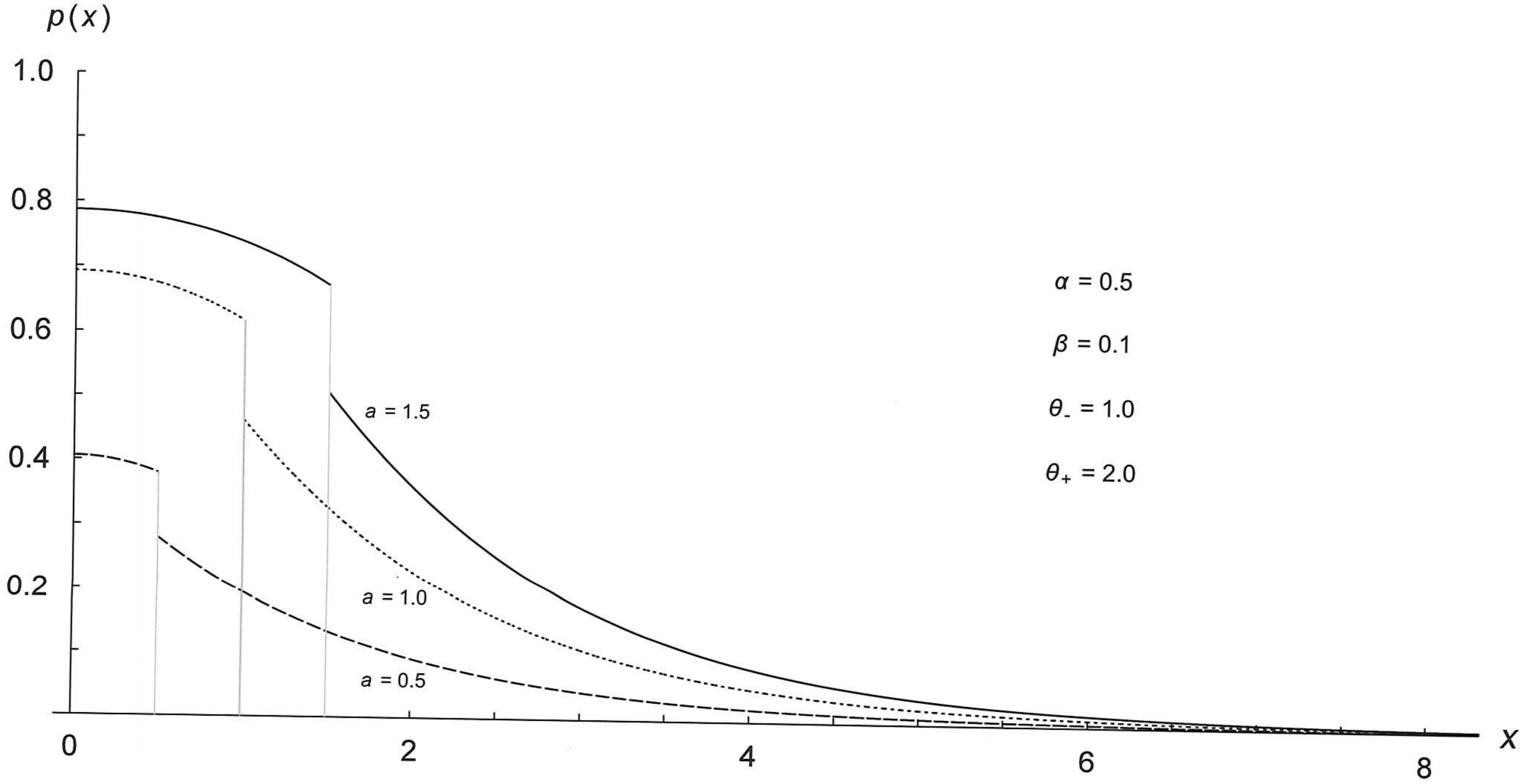

$p(x)$
1.0
0.8
0.6
0.4
0.2
0
2
4
6
8
x
$a = 1.5$
$a = 1.0$
$a = 0.5$
$\alpha = 0.5$
$\beta = 0.1$
$\theta_- = 1.0$
$\theta_+ = 2.0$

Fig. 1

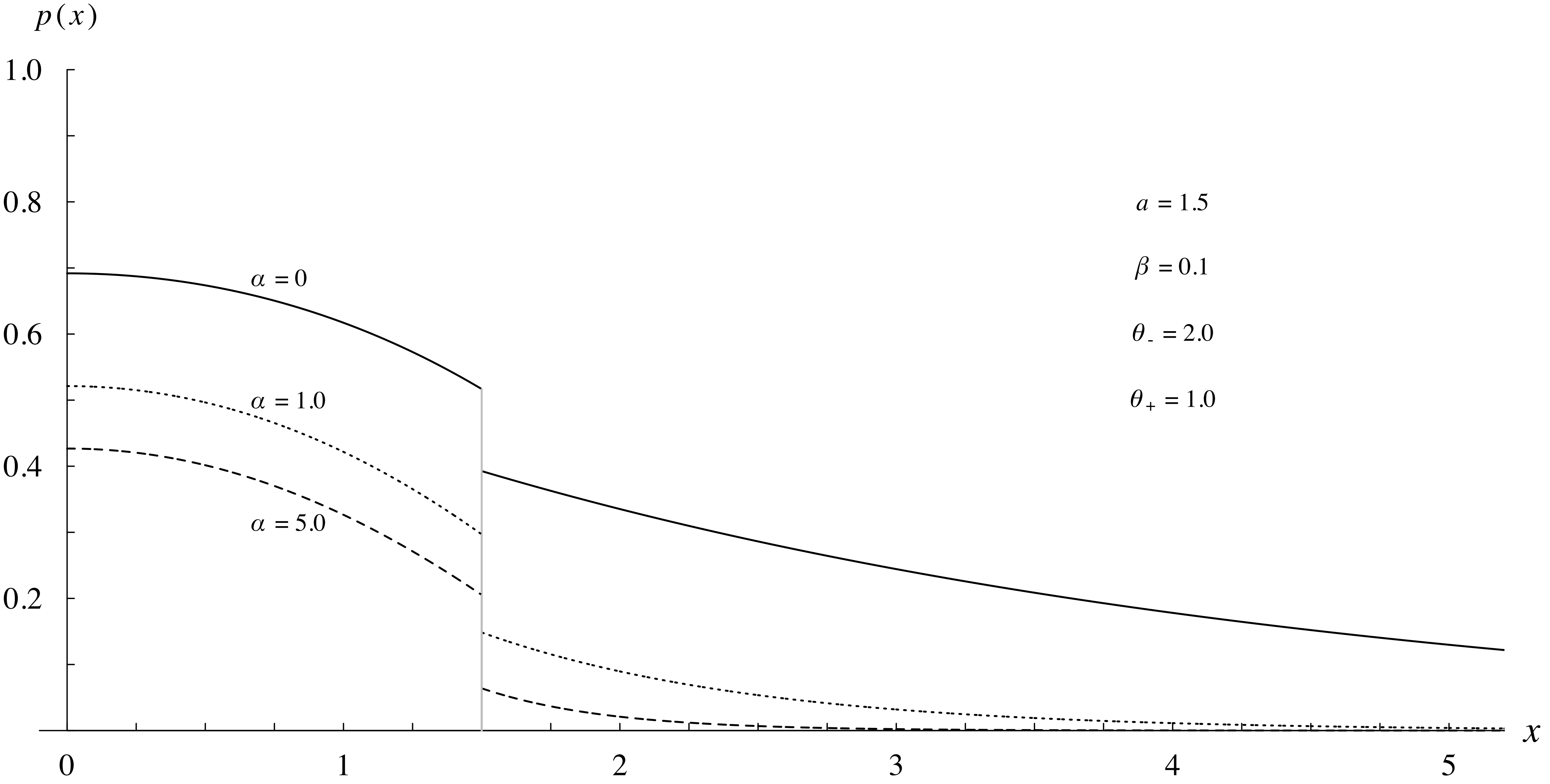
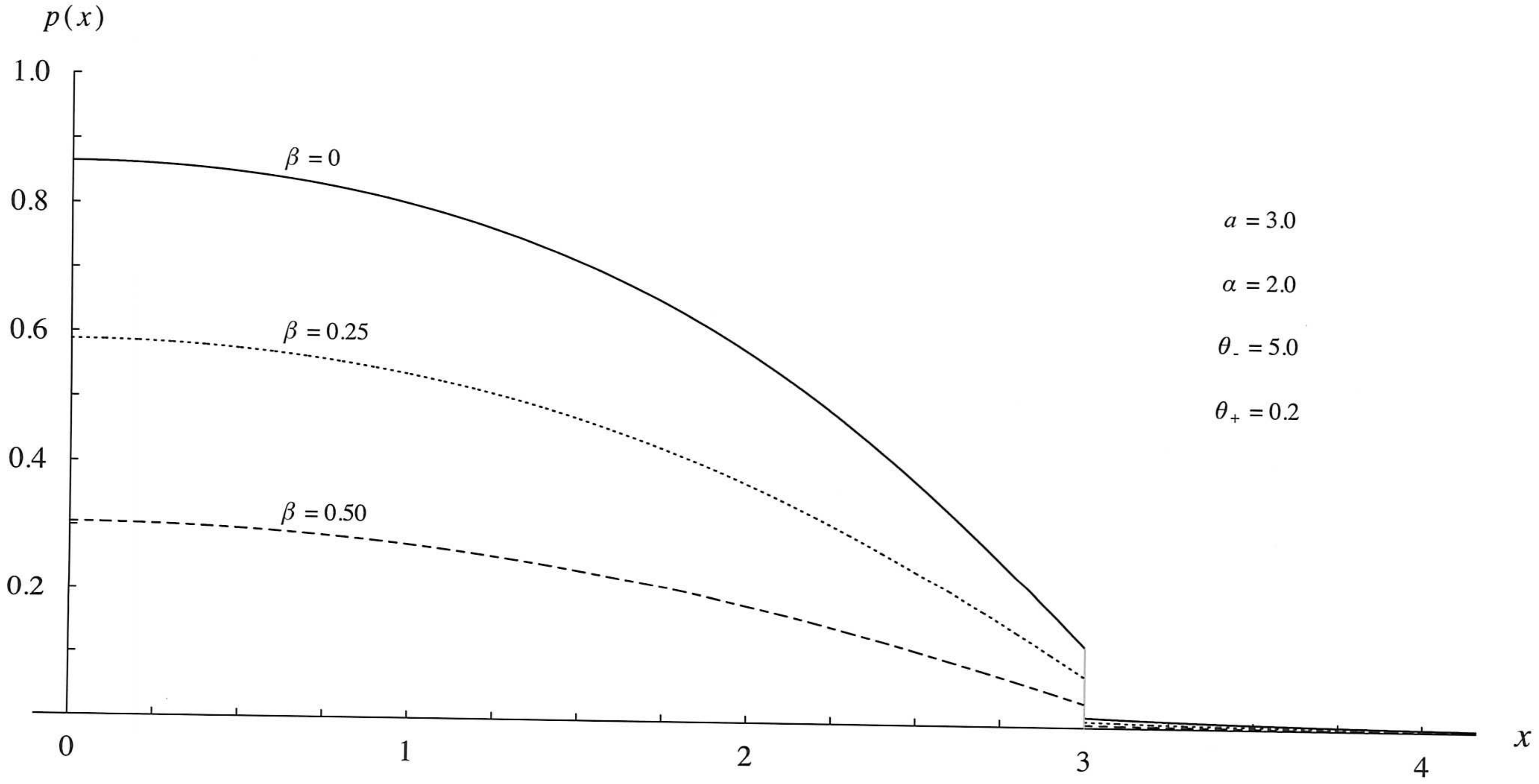

$p(x)$
1.0
0.8
0.6
0.4
0.2
0
1
2
3
4
5
x
$\alpha = 0$
$\alpha = 1.0$
$\alpha = 5.0$
$a = 1.5$
$\beta = 0.1$
$\theta_- = 2.0$
$\theta_+ = 1.0$

Fig. 2



$p(x)$
1.0
0.8
0.6
0.4
0.2
0
1
2
3
4
x
$\beta = 0$
$\beta = 0.25$
$\beta = 0.50$
$a = 3.0$
$\alpha = 2.0$
$\theta_- = 5.0$
$\theta_+ = 0.2$

Fig. 3

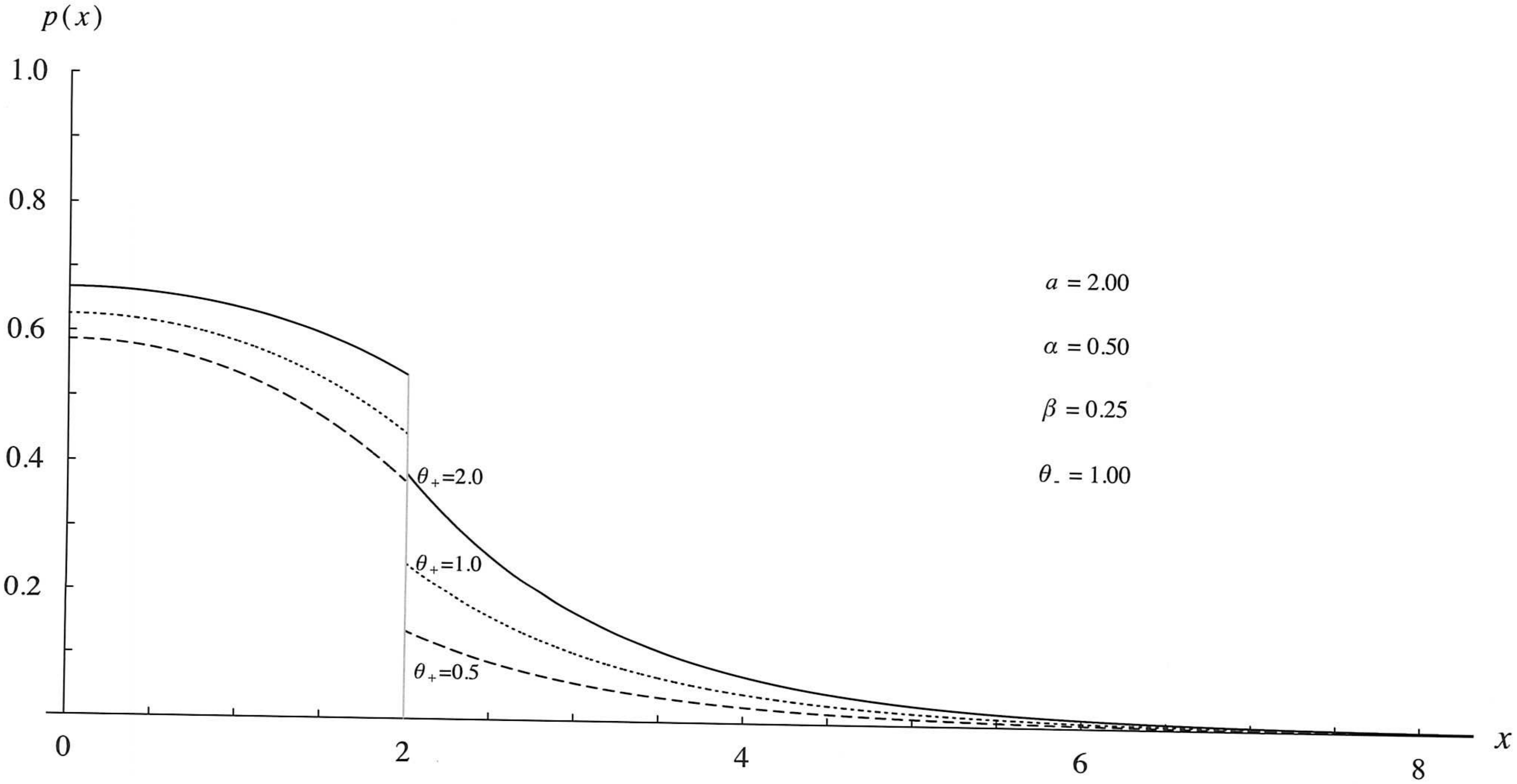
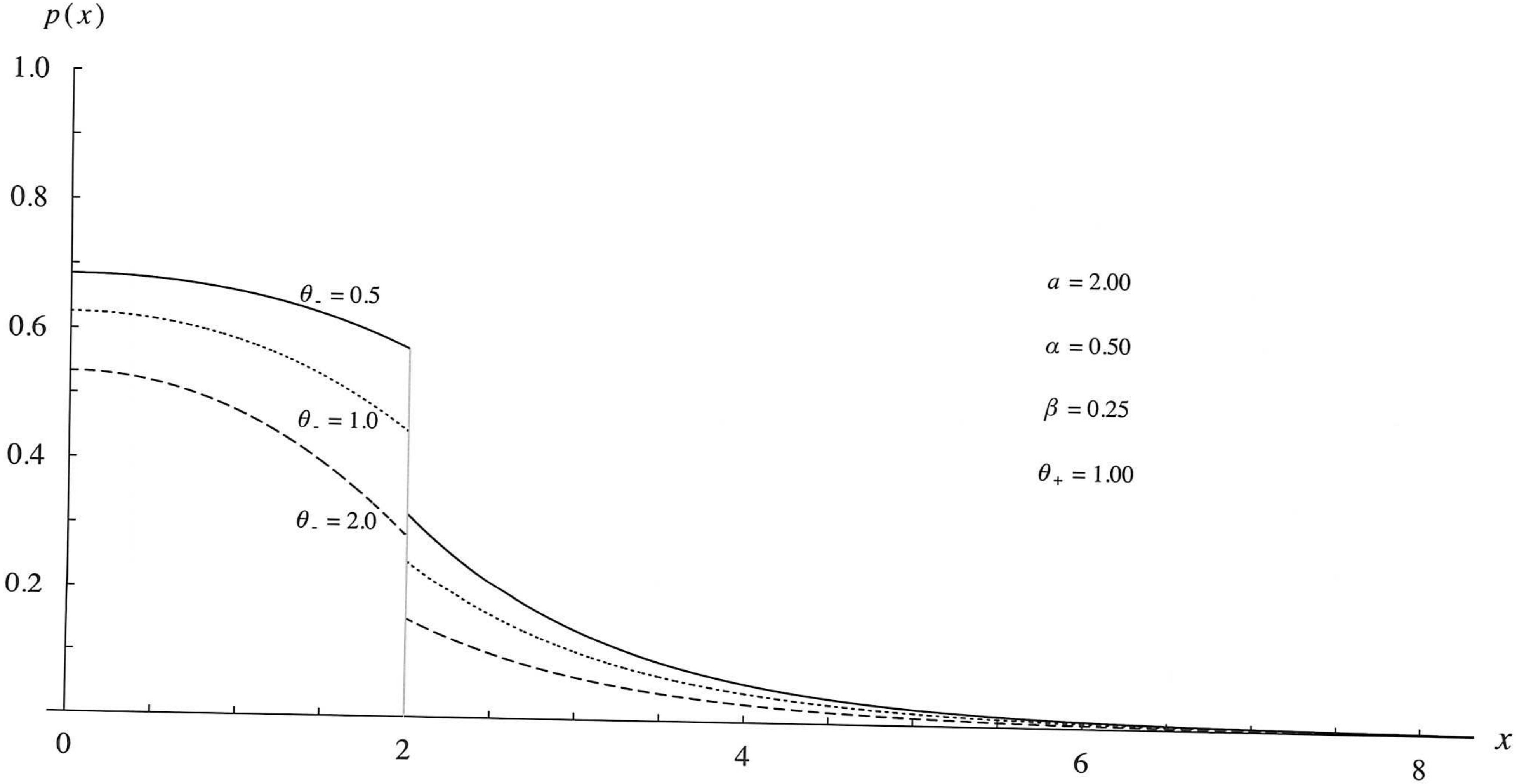

$p(x)$
1.0
0.8
0.6
0.4
0.2
0
2
4
6
8
x
θ_+=2.0
θ_+=1.0
θ_+=0.5
a = 2.00
α = 0.50
β = 0.25
θ_- = 1.00

Fig. 4



$p(x)$
1.0
0.8
0.6
0.4
0.2
0
2
4
6
8
x
$\theta_- = 0.5$
$\theta_- = 1.0$
$\theta_- = 2.0$
$a = 2.00$
$\alpha = 0.50$
$\beta = 0.25$
$\theta_+ = 1.00$

Fig. 5