

# Clines with partial panmixia in an environmental pocket



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## ABSTRACT

In geographically structured populations, global panmixia can be regarded as the limiting case of long-distance migration. The effect of incorporating partial panmixia into diallelic single-locus clines (i.e., asymptotically stable equilibria) maintained by migration and selection in an isotropic environmental pocket in  $n$  dimensions is investigated. The population density is uniform. Migration and selection are both weak; the former is homogeneous and isotropic; the latter is directional. If the scaled panmictic rate  $\beta \geq 1$ , then the allele favored in the pocket is ultimately lost. For  $\beta < 1$ , a cline is maintained if and only if the scaled radius  $a$  of the pocket exceeds a critical value  $a_n$ . For a step-environment without dominance, simple, explicit formulas are derived for  $a_1$  and  $a_3$ ; an equation with a unique solution and simple, explicit approximations are deduced for  $a_2$ . The ratio of the selection coefficients outside and inside the pocket is  $-\alpha$ . As expected intuitively, the cline becomes more difficult to maintain; i.e., the critical radius  $a_n$  increases for  $n = 1, 2, 3, \dots$  as  $\alpha, \beta$ , or  $n$  increases.

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## 1. Introduction

In a recent series of papers, the biological importance of combining short- and long-distance migration was explained, global panmixia was introduced as the limiting case of the latter, and several models were investigated (Nagylaki, 2011; 2012a,b; Lou et al. 2013b; Nagylaki and Zeng, 2014; Su and Nagylaki, in press). This work is summarized in Nagylaki and Zeng (2014). For recent general reviews of migration-selection theory, consult Nagylaki and Lou (2008), Lou et al. (2013a), and Bürger (2014).

In this article, we study this model for two alleles,  $A_1$  and  $A_2$ , in the case of an isotropic environmental pocket in  $n$  dimensions. Such pockets can be caused by changes in soil, vegetation, rainfall, and prey or predator density; by the existence of an oasis; mountain peaks or valleys; or human activity, such as cities, mines, or nature preserves (Jain and Bradshaw, 1966; Endler, 1977; Charlesworth and Charlesworth, 2010). The corresponding classical (i.e., short-distance migration) theory has been explored by Nagylaki (1975, 1976, 1978), Tertikas (1988), and Brown and Tertikas (1991). The general analysis of Lou et al. (2013b) includes

partial panmixia and could be applied to an environmental pocket in a bounded habitat.

In order to derive explicit results, we approximate the habitat as unbounded; i.e., it is  $\mathcal{R}^n$ . In the situations examined here, this common approximation should be quite accurate. Section 2 is devoted to formulating our problem and proving some general results. Section 3 concerns unidimensional pockets. In Section 4, we investigate bidimensional pockets in detail and present some results for  $n$  dimensions. We summarize our results and discuss open problems in Section 5.

## 2. Formulation and general results

We consider two alleles,  $A_1$  and  $A_2$ , at a single locus. Allele  $A_1$  is favored in an isotropic environmental pocket in  $\mathcal{R}^n$  and is deleterious outside the pocket. The population density is uniform. Migration and selection are both weak; the former is homogeneous and isotropic; the latter is directional. Global panmixia is also weak.

We begin with a general formulation for a bounded, connected, open set with a smooth boundary, the habitat  $\Omega \subset \mathcal{R}^n$ . We denote by  $P(y, t)$  the frequency of  $A_1$  at position  $y \in \Omega$  at time  $t$ . Let  $\sigma^2, s$ , and  $B$  designate the variance of local migration, selection intensity, and rate of global panmixia, respectively. We set  $\rho = \|y\|$  and

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write  $|\Omega|$  and  $\tilde{\nu}$  for the  $n$ -dimensional volume of  $\Omega$  and the outward unit normal vector on the boundary  $\partial\Omega$ , respectively. Then we have the problem (Nagylaki, 2012a)

$$P_t = \frac{\sigma^2}{2} \nabla_y^2 P + sG(y)f(P) + B(\bar{P} - P) \quad \text{in } \Omega \times (0, \infty), \quad (2.1a)$$

$$0 \leq P(y, t) \leq 1 \quad \text{in } \Omega \times [0, \infty), \quad (2.1b)$$

$$\tilde{\nu} \cdot \nabla_y P(y, t) = 0 \quad \text{on } \partial\Omega \times (0, \infty), \quad (2.1c)$$

$$\bar{P}(t) = \frac{1}{|\Omega|} \int_{\Omega} P(y, t) dy \quad \text{in } [0, \infty), \quad (2.1d)$$

where  $P_t$ ,  $\nabla_y$ ,  $\nabla_y^2$ ,  $f(P)$ ,  $G(y)$ , and  $\bar{P}(t)$  represent  $\partial P/\partial t$ , the gradient and Laplacian with respect to  $y$ , the frequency and spatial dependence of the force of selection, and the average of  $P(y, t)$  over  $\Omega$ . The common assumption that the selection term factors means that the selection coefficients have the same spatial dependence. Thus, the degree of dominance, which is determined by gene action, is space independent. We choose our coordinates so that  $0 \in \Omega$ .

Henceforth, we posit that  $f(P)$  has at least two continuous derivatives, can include frequency-dependent selection coefficients, and specifies directional selection (i.e., intermediate dominance):

$$f(0) = f(1) = 0, \quad f(P) > 0 \quad \text{in } (0, 1). \quad (2.2)$$

**Remark 2.1.** If the selection coefficients are not frequency dependent, we can write

$$f(P) = P(1 - P)(1 + h - 2hP), \quad (2.3)$$

where the constant  $h \in [-1, 1]$  represents the degree of dominance. Note that  $h = -1, 0$ , and  $1$  correspond to recessive  $A_1$ , no dominance, and recessive  $A_2$ , respectively.

**Remark 2.2.** Suppose that (2.2) holds and  $f''(P) \leq 0$  in  $[0, 1]$ . For (2.3), this condition is equivalent to  $|h| \leq \frac{1}{3}$ . (Here and below, primes indicate differentiation.) By a highly plausible extension of Theorem 1.1 in Lou et al. (2013b) from a compact habitat  $\Omega$  to  $\mathcal{R}^n$ , if a polymorphic equilibrium exists, it is unique and globally asymptotically stable (i.e., it is a cline), and its existence can be determined by linearization at the trivial equilibrium  $P = 0$ . These extensions are supported by the numerical calculations in Sections 3 and 4 and for  $\beta = 0$ , by the results of Tertikas (1988) and Brown and Tertikas (1991).

**(A2.0).** The extensions in Remark 2.2 hold.

We now extend (2.1) from  $\Omega$  to  $\mathcal{R}^n$ :

**(A2.1).** We posit throughout that  $G(y)$  is bounded, changes sign, and

$$\lim_{\rho \rightarrow \infty} G(y) = -\alpha < 0 \quad (2.4)$$

for some  $\alpha > 0$ .

Then we have

$$P_t = \frac{\sigma^2}{2} \nabla_y^2 P + sG(y)f(P) + B(\bar{P} - P) \quad \text{in } \mathcal{R}^n \times (0, \infty), \quad (2.5a)$$

$$0 \leq P(y, t) \leq 1 \quad \text{in } \mathcal{R}^n \times [0, \infty), \quad (2.5b)$$

$$\lim_{\rho \rightarrow \infty} P(y, t) = 0 \quad \text{in } [0, \infty), \quad (2.5c)$$

$$\bar{P}(t) = \lim_{R \rightarrow \infty} \frac{1}{|\Gamma_R|} \int_{\Gamma_R} P(y, t) dy \quad \text{in } [0, \infty), \quad (2.5d)$$

where  $\Gamma_R = \{y : \rho < R\}$ . In view of (2.4), the assumption (2.5c) is natural; we posit that it holds uniformly for  $t \in [0, \infty)$ .

**Lemma 2.3.** If (2.5b–d) hold, then  $\bar{P}(t) = 0$  for every  $t \geq 0$ .

**Proof.** Let  $R_0$  always satisfy  $R_0 < R$ , and rewrite (2.5d) as

$$\bar{P}(t) = \lim_{R \rightarrow \infty} (I_1 + I_2), \quad (2.6a)$$

where

$$I_1 = \frac{1}{|\Gamma_R|} \int_{\Gamma_{R_0}} P(y, t) dy, \quad (2.6b)$$

$$I_2 = \frac{1}{|\Gamma_R|} \int_{\Gamma_R \setminus \Gamma_{R_0}} P(y, t) dy. \quad (2.6c)$$

Appealing to (2.5c), we infer that for every  $\epsilon > 0$ , there exists a sufficiently large  $R_0$ , independent of  $t$ , such that if  $\|y\| \geq R_0$ , then

$$P(y, t) < \frac{\epsilon}{2}, \quad (2.7)$$

whence (2.6c) yields

$$I_2 < \frac{1}{|\Gamma_R|} \int_{\Gamma_R \setminus \Gamma_{R_0}} \frac{\epsilon}{2} dy < \frac{\epsilon}{2}. \quad (2.8)$$

From (2.5b) we see immediately that there exists a sufficiently large  $R$ , independent of  $t$ , that

$$I_1 < \left(\frac{R_0}{R}\right)^n < \frac{\epsilon}{2}. \quad (2.9)$$

Consequently, (2.8) and (2.9) give

$$I_1 + I_2 < \epsilon, \quad (2.10)$$

which demonstrates that the limit in (2.6a) is zero.  $\square$

Now Lemma 2.3 simplifies (2.5) to

$$P_t = \frac{\sigma^2}{2} \nabla_y^2 P + sG(y)f(P) - BP \quad \text{in } \mathcal{R}^n \times (0, \infty), \quad (2.11a)$$

$$0 \leq P(y, t) \leq 1 \quad \text{in } \mathcal{R}^n \times [0, \infty), \quad (2.11b)$$

$$\lim_{\rho \rightarrow \infty} P(y, t) = 0 \quad \text{in } [0, \infty). \quad (2.11c)$$

Next, we reduce the number of parameters by the scaling

$$y = \frac{\sigma x}{\sqrt{2s}}, \quad r = \|x\|, \quad t = \frac{\tau}{s}, \quad (2.12a)$$

$$B = \beta s, \quad G(y) = \check{g}(x), \quad P(y, t) = \check{p}(x, \tau). \quad (2.12b)$$

Then (2.11) becomes

$$\check{p}_\tau = \nabla^2 \check{p} + \check{g}(x)f(\check{p}) - \beta \check{p} \quad \text{in } \mathcal{R}^n \times (0, \infty), \quad (2.13a)$$

$$0 \leq \check{p}(x, \tau) \leq 1 \quad \text{in } \mathcal{R}^n \times [0, \infty), \quad (2.13b)$$

$$\lim_{r \rightarrow \infty} \check{p}(x, \tau) = 0 \quad \text{in } [0, \infty), \quad (2.13c)$$

where we have abbreviated  $\nabla_x^2$  as  $\nabla^2$ . We have now proved

**Theorem 2.4.** If (2.5) holds, then  $\check{p}(x, \tau)$  satisfies (2.13).

**Remark 2.5.** The parameter  $\beta$  in (2.13a) can be reinterpreted to include both partial panmixia and irreversible mutation from  $A_1$  to  $A_2$  (see, e.g., Nagylaki, 1992, p. 9). Then (2.13) applies to the joint action of short-distance migration (i.e., diffusion), long-distance migration, selection, and irreversible mutation.

**Remark 2.6.** With the scaling used in Nagylaki (2012a) and Lou et al. (2013b), the selection-migration ratio multiplies  $\check{g}(x)f(\check{p})$ . In this problem, as in Nagylaki (2012b), Nagylaki and Zeng (2014), and Su and Nagylaki (in press), the scaling employed here is more convenient. The critical distinction is that in the first two analyses cited, the habitat is bounded, whereas in the others, it is not.

Our next result is crucial for all that follows and enables us to restrict our investigation to  $\beta < 1$ . Recalling (2.2) and choosing  $s$  sufficiently large in (2.11a), we can ensure that the selection function and spatial dependence satisfy

$$f(\check{p}) = \check{p}F(\check{p}) \quad \text{where } 0 \leq F(\check{p}) \leq 1 \text{ in } [0, 1], \tag{2.14a}$$

$$\check{g}(x) \leq 1 \quad \text{in } \mathcal{R}^n. \tag{2.14b}$$

Note that Theorem 2.7 is independent of the dimensionality, size, and shape of the pocket.

**Theorem 2.7.** *If (2.13) and (2.14) hold and  $\beta \geq 1$ , then  $\check{p}(x, \tau) \rightarrow 0$  for every  $x \in \mathcal{R}^n$  as  $\tau \rightarrow \infty$ .*

**Proof.** From (2.13a) and (2.14) we obtain

$$\check{p}_\tau \leq \nabla^2 \check{p} + \check{p}[F(\check{p}) - \beta] \leq \nabla^2 \check{p} \quad \text{in } \mathcal{R}^n \times (0, \infty). \tag{2.15}$$

We compare (2.15) and (2.13b,c) with the heat-conduction problem

$$\hat{p}_\tau = \nabla^2 \hat{p} \quad \text{in } \mathcal{R}^n \times (0, \infty), \tag{2.16a}$$

$$\hat{p}(x, 0) = \check{p}(x, 0) \quad \text{in } \mathcal{R}^n, \tag{2.16b}$$

$$\lim_{r \rightarrow \infty} \hat{p}(x, \tau) = 0 \quad \text{in } [0, \infty). \tag{2.16c}$$

The comparison principle for parabolic equations (Pao, 1992, p. 148) tells us that  $\check{p}(x, \tau) \leq \hat{p}(x, \tau)$  in  $\mathcal{R}^n \times [0, \infty)$ . Since  $\hat{p}(x, \tau) \rightarrow 0$  for every  $x \in \mathcal{R}^n$  as  $\tau \rightarrow \infty$  (Korn and Korn, 1968, p. 518), we conclude that the same holds for  $\check{p}(x, \tau)$ , which completes the proof.  $\square$

(A2.2). Henceforth, we assume that  $\beta < 1$  and for  $r > 0$ ,  $\check{g}(x) = g(r)$  is isotropic and either continuously monotone nonincreasing or a single step, i.e., (2.27).

Furthermore, we study only the equilibria  $p^*(x)$  of (2.13), which satisfy

$$\nabla^2 p^* + g(r)f(p^*) - \beta p^* = 0 \quad \text{in } \mathcal{R}^n, \tag{2.17a}$$

$$0 \leq p^*(x) \leq 1 \quad \text{in } \mathcal{R}^n, \tag{2.17b}$$

$$\lim_{r \rightarrow \infty} p^*(x) = 0. \tag{2.17c}$$

**Remark 2.8.** For every isotropic function  $u(r)$  with two continuous derivatives, we have (Evans, 2010, pp. 21–22)

$$\nabla^2 u(x) = \frac{1}{r^{n-1}} \frac{d}{dr} \left( r^{n-1} \frac{du}{dr} \right) = u''(r) + \left( \frac{n-1}{r} \right) u'(r) \tag{2.18}$$

in  $\mathcal{R}^n$ . Of course, we are mainly interested in  $n = 1$  and  $n = 2$ . If  $n = 3$ , the form

$$\nabla^2 u = \frac{1}{r} (ru)'' \tag{2.19}$$

is often more convenient than (2.18), but then isotropy is unlikely.

We enquire first whether isotropy of  $g$  implies that of  $p^*$ , i.e., whether

$$p^*(x) = p(r). \tag{2.20}$$

To prove (2.20), we apply Theorem 2 of Li and Ni (1993). If  $g(r)$  is continuous and  $n \geq 2$ , one can verify for (2.17) that their hypotheses hold, as they do also when  $n = 1$ . However, we shall also apply the following theorem to a step-environment. We have validated this for  $n = 1$ . For  $n \geq 2$ , viewing the step-environment as the limit of continuous ones makes the following assumption entirely plausible.

(A2.3). The results of Li and Ni (1993) apply to a step-environment for  $n \geq 2$ .

**Theorem 2.9.** *Suppose that  $p^* \neq 0$ ; the assumption (2.2) holds with  $f'(p) \geq 0$  for sufficiently small  $p > 0$ ; and (A2.1)–(A2.3) and (2.17) also hold. Then so does (2.20), and  $p'(r) < 0$  in  $(0, \infty)$ .*

**Proof.** Theorem 2 of Li and Ni (1993) applies to a very general partial differential equation and therefore does not designate the center of isotropy. We now demonstrate that for (2.17), as expected, it is the origin. Our argument holds even for the step-environment.

We retain  $r = \|x\|$ , but now set

$$\rho^* = \|x - x_0\|, \quad p^*(x) = \overset{\circ}{p}(\rho^*), \quad \check{g}(x) = g(r), \tag{2.21}$$

where  $x_0$  is the center of isotropy. Then (2.17a) and (2.18) yield

$$\overset{\circ}{p}''(\rho^*) + \left( \frac{n-1}{\rho^*} \right) \overset{\circ}{p}'(\rho^*) + \check{g}(x)f(\overset{\circ}{p}(\rho^*)) - \beta \overset{\circ}{p}(\rho^*) = 0. \tag{2.22}$$

We suppose that  $x_0 \neq 0$  and derive a contradiction. From (2.22) we infer immediately that

$$\check{g}(x) = \check{g}(z) \tag{2.23}$$

whenever

$$\|x - x_0\| = \|z - x_0\|. \tag{2.24}$$

We recall that  $\check{g}(x) = g(r)$  and that  $g(r)$  is monotone nonincreasing and changes sign, which we assume occurs at  $r = a$ , i.e.,  $g(r) > 0$  if  $r < a$  and  $g(r) \leq 0$  if  $r > a$ . We draw a sphere centered at 0 with radius  $a$  and an intersecting sphere centered at  $x_0$ . Then we can choose  $x$  and  $z$  on the second sphere so that (2.24) and  $\|x\| < a < \|z\|$  both hold. However, the latter implies that  $\check{g}(x) > 0 \geq \check{g}(z)$ , which contradicts (2.23). Thus,  $x_0 = 0$ .  $\square$

Theorems 2.7 and 2.9 enable us to restrict our attention to isotropic solutions  $p(r)$  of (2.17) with  $\beta < 1$ . Our next result is quite intuitive and applies to  $p(r)$ .

**Corollary 2.10.** *If  $\check{w}(x) = w(r)$  and  $\nabla \check{w}(x)$  exists in some neighborhood  $\mathcal{N}(0)$  of the origin, then  $w'(0) = 0$ .*

**Proof.** Isotropy yields  $\check{w}(x) = \check{w}(-x)$ , whence  $\nabla \check{w}(-x) = -\nabla \check{w}(x)$  in  $\mathcal{N}(0)$ . Hence, we get  $\nabla \check{w}(0) = 0$ , which is equivalent to  $w'(0) = 0$ .  $\square$

**Corollary 2.11.** *If the assumptions in Theorem 2.9 hold, then  $p''(r) > 0$  for every  $r$  such that  $g(r) < 0$ .*

**Proof.** Invoking (2.18), we rewrite (2.17a) as

$$p'' = - \left( \frac{n-1}{r} \right) p' - g(r)f(p) + \beta p. \tag{2.25}$$

From Theorem 2.9 we have  $p'(r) < 0$  in  $(0, \infty)$ , whence (2.17b) implies that  $0 < p(r) < 1$  in  $(0, \infty)$ . Then the result follows at once from (2.25) and (2.2).  $\square$

We now suppose that there is no dominance:

$$f(p) = p(1 - p). \tag{2.26}$$

**Remark 2.12.** Since (2.26) immediately informs us that  $f''(p) < 0$  in  $[0, 1]$ , Remark 2.2 applies to (2.26).

Henceforth, we specialize our analysis to the step-environment

$$g(r) = \begin{cases} 1 & \text{if } r < a, \\ -\alpha & \text{if } r > a, \end{cases} \tag{2.27}$$

where  $\alpha > 0$  and  $a$  is the radius of the environmental pocket. Observe that (2.26) satisfies not only (2.2) but also (2.14a), and that (2.27) satisfies (2.14b), (A2.1), and (A2.2).

**Table 1**

The scaled minimal radius  $a_1$  for maintenance of a cline in a symmetric, unidimensional environmental pocket. The scaled selection coefficient  $\alpha$  and the scaled panmictic rate  $\beta$  are defined in (2.27) and (2.12b), respectively.

$\beta \setminus \alpha$	0	0.5	1.0	2.0
0	0	0.615	0.785	0.955
0.10	0.339	0.722	0.881	1.045
0.25	0.605	0.907	1.053	1.209
0.50	1.111	1.351	1.481	1.627
0.75	2.094	2.301	2.419	2.556
0.90	3.950	4.141	4.254	4.387

**Table 2**

The scaled minimal radius  $a_2$  for maintenance of a cline in an isotropic, bidimensional environmental pocket. The scaled selection coefficient  $\alpha$  and the scaled panmictic rate  $\beta$  are defined in (2.27) and (2.12b), respectively.

$\beta \setminus \alpha$	0	0.5	1.0	2.0
0	0	1.439	1.615	1.787
0.10	1.182	1.593	1.756	1.922
0.25	1.550	1.864	2.013	2.171
0.50	2.283	2.528	2.659	2.805
0.75	3.760	3.967	4.086	4.224
0.90	6.586	6.778	6.891	7.024

Although our main interest is in the effect of the change of the direction of selection (i.e.,  $\alpha > 0$ ), in Remarks 3.6 and 4.8, Corollaries 4.4 and 4.5, Tables 1 and 2, and Figs. 2 and 5, we shall also investigate  $\alpha = 0$ . These results can be viewed as limits as  $\alpha \rightarrow 0+$ , but they are also correct and intuitive for  $\alpha = 0$ . Mathematically, the stable clines for  $\alpha = 0$  follow from (2.5c), which we imposed because the entire theory developed for unbounded domains in Nagylaki (2012a,b) and Su and Nagylaki (in press) assumed (2.5c). Biologically, we can interpret these clines as due to contact at infinity of the habitat with a continent where  $A_1$  is absent. Then the zero Dirichlet condition (2.5c) leads to stable clines, as the solutions in Figs. 2 and 5 of the parabolic problem indicate.

Next, we establish an upper bound on  $p(r) \leq p(0)$ .

**Corollary 2.13.** *If (2.17), (2.26), and (2.27) hold, then  $p(0) < 1 - \beta$ .*

**Proof.** By Theorem 2.7,  $\beta < 1$ . If  $p(r) \equiv 0$ , then  $p(0) < 1 - \beta$ . If  $p(r) \not\equiv 0$ , then Theorem 2.9 shows that  $p(r)$  is maximized at the origin; therefore, (2.17a), (2.26), and (2.27) give

$$0 \geq \nabla^2 p(0) = p(0)[\beta - 1 + p(0)]. \tag{2.28}$$

Thus,  $p(0) \leq 1 - \beta$ . If  $p(0) = 1 - \beta$ , the unique solution in  $[0, a)$  of the initial-value problem (2.25) with initial conditions  $p(0) = 1 - \beta$  and  $p'(0) = 0$  (from Corollary 2.10) is  $p(r) = 1 - \beta$ , which contradicts the result in Theorem 2.9 that  $p'(r) < 0$  in  $(0, \infty)$ . Hence,  $p(0) < 1 - \beta$ .  $\square$

**Remark 2.14.** Given (2.27), Corollary 2.11 implies that  $p(r)$  is convex in  $(a, \infty)$ . In Corollary 2.15, we demonstrate that in one dimension, the cline  $p(r)$  is concave in  $[0, a)$ . However, in Corollary 4.10 we establish that, perhaps surprisingly, concavity need not hold for  $n = 2$ .

**Corollary 2.15.** *If  $n = 1$  and the assumptions in Corollary 2.13 hold, then  $p''(r) < 0$  in  $[0, a)$ .*

**Proof.** For  $r < a$ , from (2.25)–(2.27), Theorem 2.9, and Corollary 2.13 we obtain

$$p''(r) = p(r)[\beta - 1 + p(r)] < 0, \tag{2.29}$$

which validates our corollary.  $\square$

Under the assumptions in Corollary 2.13, we proceed to explore the existence of a cline. According to Remarks 2.2 and 2.12, we linearize (2.17) at  $p = 0$  and appeal to Corollary 2.10:

$$\nabla^2 \psi + g(r)\psi - \beta\psi = 0 \quad \text{in } \mathcal{R}^n, \tag{2.30a}$$

$$\psi'(0) = 0, \tag{2.30b}$$

$$\lim_{r \rightarrow \infty} \psi(r) = 0. \tag{2.30c}$$

This problem yields the critical condition for existence. Nagylaki (2012a) and Lou et al. (2013b) studied the minimal selection-migration ratio, which increases as  $\beta$  increases. Here, it will be more convenient to investigate the existence condition in the form  $a > a_n(\alpha, \beta)$ . Clearly,  $a_n$  is the required minimal radius of the environmental pocket.

**Remark 2.16.** Ismail and Muldoon (1978, hereafter abbreviated as IM) employed (2.18), (2.27), and the substitutions

$$v = \frac{1}{2}(n - 2), \quad \phi(r) = r^v \psi(r) \tag{2.31}$$

to transform (2.30a) with  $\beta = 0$  into Bessel's equation (Olver, 1964, p. 378) for  $\phi$ . Their result is easily extended to  $\beta > 0$ . However, as explained in Remark 2.8, we are primarily interested in  $n = 1$  and 2. Since elementary functions suffice for the unidimensional analysis in Section 3, we increase accessibility by postponing the use of Bessel functions until the analyses in Section 4.

### 3. One dimension

We derive the minimal radius  $a_1$  of the unidimensional environmental pocket for the existence of a cline. Define

$$\lambda = (1 - \beta)^{1/2}, \quad \mu = (\alpha + \beta)^{1/2}. \tag{3.1}$$

**Theorem 3.1.** *Suppose that  $n = 1$  and (A2.0), (2.17), (2.26), and (2.27) hold. Then a cline exists if and only if  $\beta < 1$  and*

$$a > a_1 = \frac{1}{\lambda} \tan^{-1} \left( \frac{\mu}{\lambda} \right). \tag{3.2}$$

**Proof.** From (2.30) we get

$$\psi'' + g(r)\psi - \beta\psi = 0 \quad \text{for } r > 0, \tag{3.3a}$$

$$\psi'(0) = 0, \tag{3.3b}$$

$$\lim_{r \rightarrow \infty} \psi(r) = 0. \tag{3.3c}$$

Then (3.3), (2.27), and (3.1) reveal

$$\psi(r) = \begin{cases} D_1 \cos \lambda r & \text{if } r < a, \\ E_1 e^{-\mu r} & \text{if } r > a. \end{cases} \tag{3.4}$$

Continuity of  $\psi(r)$  and  $\psi'(r)$  at  $r = a$  yields

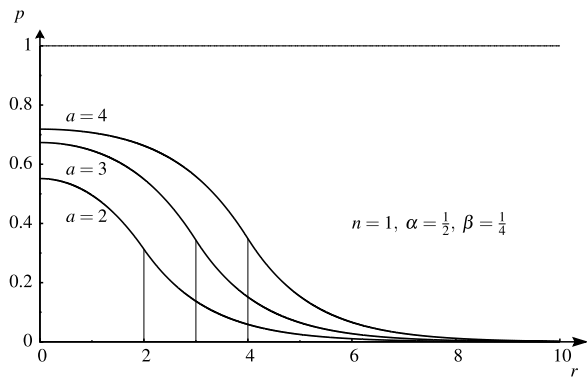
$$D_1 \cos \lambda a = E_1 e^{-\mu a}, \tag{3.5a}$$

$$-D_1 \lambda \sin \lambda a = -E_1 \mu e^{-\mu a}, \tag{3.5b}$$

whence

$$\lambda \tan \lambda a = \mu, \tag{3.6}$$

which immediately gives (3.2).  $\square$



**Fig. 1.** Isotropic unidimensional ( $n = 1$ ) clines with  $\alpha = \frac{1}{2}$ ,  $\beta = \frac{1}{4}$ , and  $a = 2, 3$ , and  $4$ . The parameters  $\alpha$  and  $\beta$  denote the scaled selection coefficient outside the environmental pocket of radius  $a$  and the scaled global panmictic rate.

**Remark 3.2.** As biological intuition suggests, we see from (3.1) and (3.2) that  $a_1(\alpha, \beta)$  increases as either  $\alpha$  increases from 0 to  $\infty$  with  $\beta$  fixed, or  $\beta$  increases from 0 to 1 with  $\alpha$  fixed. It is convenient to define

$$\hat{\alpha} = \sqrt{\alpha}, \quad \hat{\beta} = \sqrt{\beta}. \tag{3.7}$$

**Remark 3.3.** Invoking (3.1), (3.2), and Remark 3.2, for fixed  $\beta$  we find

$$\frac{1}{\lambda} \tan^{-1} \left( \frac{\hat{\beta}}{\lambda} \right) < a_1(\alpha, \beta) < \frac{\pi}{2\lambda}. \tag{3.8}$$

**Remark 3.4.** Using (3.1), (3.2), and Remark 3.2, for fixed  $\alpha$  we deduce

$$\tan^{-1} \hat{\alpha} < a_1(\alpha, \beta) < \frac{\pi}{2\lambda}. \tag{3.9}$$

**Remark 3.5.** Observe from (3.1) and (3.2) that  $a_1 \rightarrow \infty$  as  $\beta \rightarrow 1^-$ , in agreement with Theorem 2.7. Note that if we rescale and replace  $\alpha$  by  $\alpha^2$ , then the lower bound in (3.9) agrees with (38) in Nagylaki (1975).

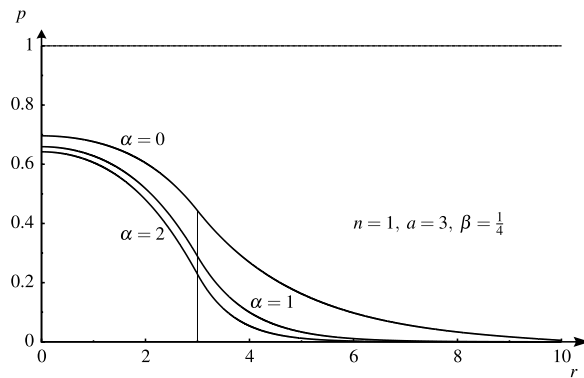
In Table 1, we exhibit  $a_1$  for various values of  $\alpha$  and  $\beta$ ; these agree with Remarks 3.2 to 3.4. According to (3.2), the critical radius  $a_1$  is bounded as  $\alpha \rightarrow \infty$  with  $\beta < 1$  fixed, whereas  $a_1 \rightarrow \infty$  as  $\beta \rightarrow 1^-$  with  $\alpha$  fixed. Therefore, we expect  $a_1$  to depend more strongly on  $\beta$  than on  $\alpha$ , in agreement with Table 1.

**Remark 3.6.** Appealing to (3.1) and (3.2), we obtain immediately that  $a_1 \sim \sqrt{\beta}$  as  $\beta \rightarrow 0$  with  $\alpha = 0$ , and  $a_1 \sim \sqrt{\alpha}$  as  $\alpha \rightarrow 0$  with  $\beta = 0$ .

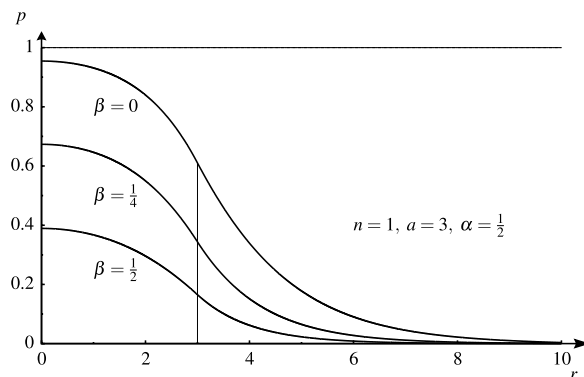
In Figs. 1–3, we present examples of unidimensional clines. We indicate the boundary of the environmental pocket by light vertical lines. The clines agree with Theorem 2.9 and Corollaries 2.10, 2.11, 2.13, and 2.15. We used the general program BuGS to solve both the elliptic problem (2.17) and the parabolic problem (2.13). In both cases, we truncated the habitat at large  $r$  with the radiation condition

$$\frac{p'(r)}{p(r)} \rightarrow \mu \tag{3.10}$$

as  $r \rightarrow \infty$ . At equilibrium, (3.10) follows at once from (3.4); in the parabolic problem, (3.10) becomes accurate as  $\tau \rightarrow \infty$ . The two computations agree in every case and support the uniqueness and global asymptotic stability discussed in Remark 2.2.



**Fig. 2.** Isotropic unidimensional clines with  $a = 3$ ,  $\beta = \frac{1}{4}$ , and  $\alpha = 0, 1$ , and  $2$ .



**Fig. 3.** Isotropic unidimensional clines with  $a = 3$ ,  $\alpha = \frac{1}{2}$ , and  $\beta = 0, \frac{1}{4}$ , and  $\frac{1}{2}$ .

### 4. Two and $n$ dimensions

Here, we investigate the minimal radius  $a_2$  of the bidimensional environmental pocket for the existence of a cline. Since  $a_2$  can not be calculated explicitly, we present the characteristic equation and a series of approximations for  $a_2$ . We deduce also the characteristic equation for  $a_n$  and the qualitative dependence of  $a_n$  on  $\alpha, \beta$ , and  $n$ . Finally, we offer a simple, explicit formula for  $a_3$ .

We denote the Bessel functions of the first kind and the modified Bessel functions of the second kind of arbitrary order  $\nu$  by  $J_\nu$  and  $K_\nu$ , respectively. Recall (3.1) and let  $a_2$  designate the smallest positive root of the equation

$$\frac{\lambda J_1(\lambda a)}{J_0(\lambda a)} = \frac{\mu K_1(\mu a)}{K_0(\mu a)}. \tag{4.1}$$

**Theorem 4.1.** Suppose that  $n = 2$  and (A2.0), (2.17), (2.26), and (2.27) hold. Then a cline exists if and only if  $\beta < 1$  and  $a > a_2$ .

**Proof.** From (2.30a) and (2.18) we obtain

$$\frac{1}{r} (r\psi')' + [g(r) - \beta]\psi = 0 \quad \text{for } r > 0. \tag{4.2}$$

Invoking (2.30b,c), we easily find (Olver, 1964, pp. 358, 374)

$$\psi(r) = \begin{cases} D_2 J_0(\lambda r) & \text{if } 0 \leq r < a, \\ E_2 K_0(\mu r) & \text{if } r > a. \end{cases} \tag{4.3}$$

Continuity of  $\psi(r)$  and  $\psi'(r)$  at  $r = a$  reveals that

$$D_2 J_0(\lambda a) = E_2 K_0(\mu a), \tag{4.4a}$$

$$\lambda D_2 J_0'(\lambda a) = \mu E_2 K_0'(\mu a), \tag{4.4b}$$



whence

$$\frac{\lambda J'_0(\lambda a)}{J_0(\lambda a)} = \frac{\mu K'_0(\mu a)}{K_0(\mu a)}. \tag{4.5}$$

Since

$$J'_0(z) = -J_1(z), \quad K'_0(z) = -K_1(z) \tag{4.6}$$

(Olver, 1964, pp. 361, 376), a glance at (4.5) establishes (4.1) and our theorem.  $\square$

Let  $z_0 \approx 2.405$  represent the smallest positive zero of  $J_0(z)$  (Olver, 1964, p. 409) and set

$$a_0^*(\lambda) = z_0/\lambda. \tag{4.7}$$

**Corollary 4.2.** *The unique root of the characteristic equation (4.1) in  $(0, a_0^*)$  is  $a_2$ .*

**Proof.** We put

$$z = \lambda a, \quad \theta = \frac{\mu}{\lambda} = \sqrt{\frac{\alpha + \beta}{1 - \beta}}, \quad \mu a = \theta z \tag{4.8}$$

and recast (4.1) as

$$\frac{J_1(z)}{J_0(z)} = \frac{\theta K_1(\theta z)}{K_0(\theta z)}. \tag{4.9}$$

Our claim now follows immediately from Theorem 3.1 in IM.  $\square$

**Remark 4.3.** If  $\beta = 0$ , we infer from (4.1), (3.1), and (3.7) that

$$\frac{J_1(a)}{J_0(a)} = \frac{\hat{\alpha} K_1(\hat{\alpha} a)}{K_0(\hat{\alpha} a)}, \tag{4.10}$$

which agrees with (71) in Nagylaki (1975) if we rescale and replace  $\alpha$  by  $\alpha^2$ .

**Corollary 4.4.** *As  $\beta \rightarrow 1-$  with fixed  $\alpha \geq 0$ ,*

$$a_2 \sim a_0^*(\lambda) = z_0/\lambda. \tag{4.11}$$

**Proof.** From (4.8) we observe that  $\theta \rightarrow \infty$  as  $\beta \rightarrow 1-$ . Theorem 3.1 in IM informs us that  $z \rightarrow z_0-$  as  $\theta \rightarrow \infty$  in (4.9). Then (4.7) and (4.8) validate (4.11).  $\square$

**Corollary 4.5.** *As  $\beta \rightarrow 0$  with  $\alpha = 0$ ,*

$$a_2 \sim 2/\sqrt{-\ln \beta}. \tag{4.12}$$

**Proof.** From (4.8) we see that

$$\theta \sim \sqrt{\beta} = \hat{\beta} \tag{4.13}$$

as  $\beta \rightarrow 0$  with  $\alpha = 0$ . Then Theorem 3.1 in IM tells us that  $z \rightarrow 0$  in (4.9).

As  $z \rightarrow 0$ ,

$$J_0(z) \rightarrow 1, \quad J_1(z) \sim \frac{1}{2}z, \tag{4.14a}$$

$$K_0(z) \sim -\ln z, \quad K_1(z) \sim 1/z \tag{4.14b}$$

(Olver, 1964, pp. 360, 375). Substituting (4.14) into (4.9) yields

$$\frac{z}{2} \sim -\frac{1}{z \ln(\hat{\beta}z)}, \tag{4.15}$$

whence

$$\frac{2}{z^2} \sim -\ln \hat{\beta} - \ln z \tag{4.16}$$

as  $z \rightarrow 0$ .

Clearly,  $-\ln z$  is negligible in comparison with  $1/z^2$  as  $z \rightarrow 0$ . Therefore, we obtain

$$\frac{2}{z^2} \sim -\frac{1}{2} \ln \beta, \tag{4.17}$$

i.e.,

$$z \sim 2/\sqrt{-\ln \beta}. \tag{4.18}$$

Since (3.1) tells us that  $\lambda \rightarrow 1$  as  $\beta \rightarrow 0$ , we conclude from (4.8) that (4.18) is equivalent to (4.12).  $\square$

**Corollary 4.6.** *As  $\alpha \rightarrow 0$  with  $\beta = 0$ ,*

$$a_2 \sim 2/\sqrt{-\ln \alpha}. \tag{4.19}$$

**Proof.** Since  $\beta = 0$ , from (3.1) and (4.8) we get

$$z = a, \quad \theta = \sqrt{\alpha} = \hat{\alpha}. \tag{4.20}$$

Thus,  $\theta \rightarrow 0$ , and (4.13) shows that the proof of Corollary 4.5 applies with  $\beta$  replaced by  $\alpha$ . Hence, (4.12) establishes (4.19).  $\square$

**Corollary 4.7.** *As  $\alpha \rightarrow \infty$  with  $\beta \in [0, 1)$  fixed,*

$$a_2 \sim a_0^*(\lambda) = z_0/\lambda. \tag{4.21}$$

**Proof.** By dint of (4.8),  $\theta \rightarrow \infty$ . Theorem 3.1 in IM and (4.9) imply that  $z \rightarrow z_0$ , whence (4.8) validates (4.21).  $\square$

**Remark 4.8.** In one dimension, from (3.1) and (3.2) we see that both  $\beta \rightarrow 1-$  (with  $\alpha \geq 0$  fixed) and  $\alpha \rightarrow \infty$  (with  $\beta < 1$  fixed) lead to the asymptotic result  $\pi/(2\lambda)$ . In two dimensions, according to Corollaries 4.4 and 4.7, the corresponding asymptotic approximations are again identical, viz.,  $z_0/\lambda$ . As we noted above (4.7),  $z_0 \approx 2.405$ ; therefore,  $z_0 > \pi/2$ , which implies that  $a_2 > a_1$  in this limit. Observe that for  $n = 2$ , as for  $n = 1$ , our asymptotic results tend to  $\infty$  as  $\beta \rightarrow 1-$ , whereas they remain bounded as  $\alpha \rightarrow \infty$ . Consequently, we expect  $a_2$  to depend more strongly on  $\beta$  than on  $\alpha$ .

**Remark 4.9.** Comparing Corollaries 4.5 and 4.6 with Remark 3.6, we note that in both of those limits, panmixia and selection against  $A_1$  vanish, and that  $a_1 \rightarrow 0$  much faster than  $a_2 \rightarrow 0$ .

**Corollary 4.10.** *Suppose that  $n = 2$ ,  $\beta < 1$ , and (2.17), (2.26), and (2.27) hold. The cline  $p(r)$  can still be convex somewhere in  $(0, a)$ .*

**Proof.** We choose  $\beta = 1-$  and  $a = a_2+$ . Then  $p(r) \ll 1$  and we can examine the linearized problem (2.30). By virtue of Corollary 4.2, positivity of  $\psi(r)$  in (4.3) requires that  $D_2 > 0$ . For  $r < a$ , from (4.3) and (4.6) we find

$$\psi'(r) = -D_2 \lambda J_1(\lambda r), \tag{4.22}$$

whence (Olver, 1964, p. 361)

$$\psi''(a_2-) = -D_2 \lambda^2 J'_1(\lambda a_2) = -D_2 \lambda^2 \left[ J_0(\lambda a_2) - \frac{J_1(\lambda a_2)}{\lambda a_2} \right]. \tag{4.23}$$

Therefore, (4.11) yields

$$\psi''(a_2-) \sim -D_2 \lambda^2 \left[ J_0(z_0) - \frac{J_1(z_0)}{z_0} \right] = \frac{D_2 \lambda^2}{z_0} J_1(z_0) > 0, \tag{4.24}$$

which demonstrates convexity at  $r = a_2-$  for  $\beta = 1-$  and  $a = a_2+$ .  $\square$

We proceed to prove for every  $n$  some biologically intuitive properties of the minimal radius of  $a_n(\alpha, \beta)$ . We recall (2.31) and (4.8) and generalize (4.9) to

$$\frac{J_{v+1}(z)}{J_v(z)} = \frac{\theta K_{v+1}(\theta z)}{K_v(\theta z)}. \tag{4.25}$$

Let  $z_v$  signify the smallest positive zero of  $J_v(z)$ .

**Theorem 4.11.** *Suppose that (A2.0), (2.17), (2.26), and (2.27) hold. Then a cline exists if and only if  $\beta < 1$  and  $a > a_n$ , where  $\lambda a_n$  is the unique root of (4.25) in  $(0, z_v)$ .*

**Proof.** Inserting (2.18) into (2.30a) gives

$$\psi'' + \left(\frac{n-1}{r}\right)\psi' + [g(r) - \beta]\psi = 0 \quad \text{for } r > 0. \tag{4.26}$$

We follow IM and substitute (2.31) into (4.26). Routine calculations lead to

$$r^2\phi'' + r\phi' + \{[g(r) - \beta]r^2 - v^2\}\phi = 0 \quad \text{for } r > 0. \tag{4.27}$$

Recalling (2.30b,c) and (3.1), we find (Olver, 1964, pp. 358, 374)

$$\phi(r) = \begin{cases} D_n J_v(\lambda r) & \text{if } 0 < r < a, \\ E_n K_v(\mu r) & \text{if } r > a. \end{cases} \tag{4.28}$$

The argument between (4.3) and (4.5) now reveals

$$\frac{\lambda J'_v(\lambda a)}{J_v(\lambda a)} = \frac{\mu K'_v(\mu a)}{K_v(\mu a)}, \tag{4.29}$$

whence (4.8) yields

$$\frac{J'_v(z)}{J_v(z)} = \frac{\theta K'_v(\theta z)}{K_v(\theta z)}. \tag{4.30}$$

Appealing to Olver (1964, pp. 361, 376), we have

$$J'_v(z) = \frac{v}{z} J_v(z) - J_{v+1}(z), \tag{4.31a}$$

$$\theta K'_v(\theta z) = \frac{v}{z} K_v(\theta z) - \theta K_{v+1}(\theta z). \tag{4.31b}$$

Substituting (4.31) into (4.30) produces (4.25).

According to (4.8) and Theorem 3.1 in IM, the unique root of (4.25) in  $(0, z_v)$  is  $\lambda a_n$ .  $\square$

**Corollary 4.12.** *The minimal radius  $a_n(\alpha, \beta)$  increases as  $n$  increases with  $\alpha$  and  $\beta$  fixed, and*

$$\frac{\partial a_n}{\partial \alpha}(\alpha, \beta) > 0, \quad \frac{\partial a_n}{\partial \beta}(\alpha, \beta) > 0. \tag{4.32}$$

**Proof.** The first assertion follows immediately from (4.25), (2.31), and Theorem 3.2 in IM. As  $\alpha$  increases with  $\beta$  fixed, from (4.8) we see that  $\theta$  increases. Then Theorem 3.1 in IM implies that  $z_v$  and hence  $a_n = z_v/\lambda$  increases. As  $\beta$  increases with  $\alpha$  fixed, from (4.8) we observe that  $\theta$  again increases, so  $z_v$  increases. By (3.1),  $\lambda$  decreases, so  $a_n = z_v/\lambda$  again increases.  $\square$

**Remark 4.13.** Although nontrivial to prove, it is biologically obvious that increasing  $\alpha$  or  $\beta$  makes maintenance of the cline more difficult, as (4.32) shows. Corollary 4.12 informs us that increasing the dimensionality  $n$  also makes maintenance of the cline more difficult. That migration becomes more effective as  $n$  increases has been noted for  $\beta = 0$  (Nagylaki, 1975; IM) and in Malécot's neutral model (Nagylaki, 1989, and references therein).

Employing (4.25), (2.31), (4.8), (3.2), and Antosiewicz (1964, pp. 437–438, 444), an interested reader can easily establish

**Corollary 4.14.** *If  $n = 3$ , the critical radius is*

$$a_3 = \frac{1}{\lambda} \left[ \pi - \tan^{-1} \left( \frac{\lambda}{\mu} \right) \right] = \frac{\pi}{2\lambda} + a_1. \tag{4.33}$$

**Remark 4.15.** Suppose that  $\beta < 1$  and (2.2), (2.17), and (2.27) hold. Explicitly displaying the dimensionality  $n$ , we write  $p(r) = p_n(r)$ . Biological intuition suggests the conjecture that if  $a > a_n$ , then

$$\frac{\partial p_n}{\partial a}(r) > 0, \quad \frac{\partial p_n}{\partial \alpha}(r) < 0, \quad \frac{\partial p_n}{\partial \beta}(r) < 0 \tag{4.34}$$

at every  $r \in [0, \infty)$ . Furthermore, for every  $n \geq 2$  and  $a > a_n$ , we expect that  $p_n(r) < p_{n-1}(r)$  for every  $r \in [0, \infty)$ .

We now establish (4.34).

**Theorem 4.16.** *If  $\beta < 1$  and (A2.0), (2.17), and (2.27) hold, then so does (4.34).*

**Proof.** We first demonstrate that  $\frac{\partial p_n}{\partial a}(r) > 0$ . For  $i = 1$  and 2, let  $a^{(1)} > a^{(2)} > a_n$  and let  $g_i(r)$  represent  $g(r)$  with  $a = a^{(i)}$ . We denote by  $p_n^{(i)}$  the corresponding solution of (2.17) with  $a = a^{(i)}$  and fixed  $\alpha$  and  $\beta$ . Then (2.27) informs us that

$$g_1(r) \geq g_2(r) \tag{4.35}$$

for every  $r \geq 0$ , where the inequality is strict for  $r \in (a^{(2)}, a^{(1)})$ . Therefore, from (2.17a), (4.35), and (2.2) we have

$$\nabla^2 p_n^{(1)} + g_2(r)f(p_n^{(1)}) - \beta p_n^{(1)} \leq \nabla^2 p_n^{(1)} + g_1(r)f(p_n^{(1)}) - \beta p_n^{(1)} = 0 \tag{4.36}$$

in  $\mathcal{R}^n$ , with strict inequality for  $r \in (a^{(2)}, a^{(1)})$ .

Thus, (4.36) and (2.17c) show that if  $g = g_2$ , then  $p_n^{(1)}$  is a strict supersolution of (2.17). From the linearization (2.30) we infer that the inequality  $a^{(2)} > a_n$  implies the instability of the trivial solution  $p = 0$ . Consequently, there must exist between 0 and  $p_n^{(1)}$  a stable solution of (2.17) with  $a = a^{(2)}$  (Sattinger, 1972); since  $p_n^{(1)}(r) \rightarrow 0$  as  $r \rightarrow \infty$ , the same holds for this solution. By the uniqueness of the cline, this equilibrium must be  $p_n^{(2)}$ , i.e.,  $0 \leq p_n^{(2)} \leq p_n^{(1)}$ . Applying the strong maximum principle (Gilbarg and Trudinger, 2001, p. 35) to  $p_n^{(1)} - p_n^{(2)}$  yields  $p_n^{(2)} < p_n^{(1)}$  in  $\mathcal{R}^n$ , which establishes that  $\frac{\partial p_n}{\partial a}(r) > 0$ .

Next, we fix  $a$  and  $\beta$ , let  $0 < \alpha_1 < \alpha_2$ , and designate the corresponding clines by  $\hat{p}_n^{(i)}$ . Again, (2.27) reveals that (4.35) holds and is strict for  $r \in (a, \infty)$ . Then the above proof applies with obvious, minor modifications. Hence,  $\frac{\partial p_n}{\partial \alpha}(r) < 0$ .

Finally, we fix  $a$  and  $\alpha$ , let  $0 < \beta_1 < \beta_2$ , and denote the corresponding clines by  $\check{p}_n^{(i)}$ . From (2.17a) we obtain

$$\nabla^2 \check{p}_n^{(1)} + g(r)f(\check{p}_n^{(1)}) - \beta_2 \check{p}_n^{(1)} < \nabla^2 \check{p}_n^{(1)} + g(r)f(\check{p}_n^{(1)}) - \beta_1 \check{p}_n^{(1)} \tag{4.37}$$

in  $\mathcal{R}^n$ . Trivial changes in the first proof demonstrate that  $\frac{\partial p_n}{\partial \beta}(r) < 0$ .  $\square$

In Table 2, we display  $a_2$  for various values of  $\alpha$  and  $\beta$ . The results agree with Remark 4.8 and Corollary 4.12.

In Figs. 4–6 we offer examples of bidimensional clines. As in one dimension, they agree with Theorem 2.9 and Corollaries 2.10, 2.11, and 2.13. Figs. 1–6 support Remark 4.15. Again as for  $n = 1$ , the elliptic and parabolic computations (using BuGS) agree and support the uniqueness and global asymptotic stability of the cline. According to (2.18), the Laplacian is singular at the origin, but

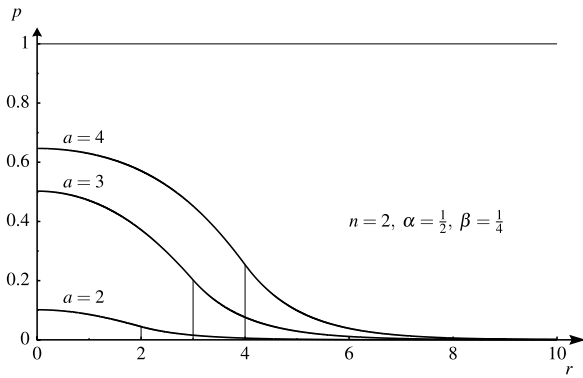


Fig. 4. Isotropic bidimensional clines with  $\alpha = \frac{1}{2}$ ,  $\beta = \frac{1}{4}$ , and  $a = 2, 3$ , and  $4$ .

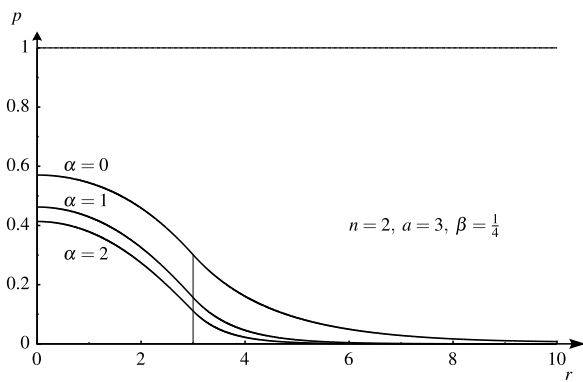


Fig. 5. Isotropic bidimensional clines with  $a = 3$ ,  $\beta = \frac{1}{4}$ , and  $\alpha = 0, 1$ , and  $2$ .

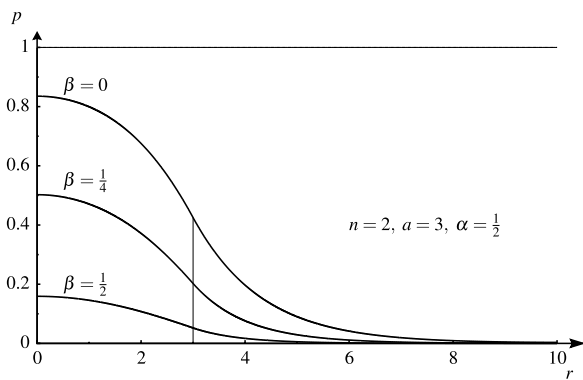


Fig. 6. Isotropic bidimensional clines with  $a = 3$ ,  $\alpha = \frac{1}{2}$ , and  $\beta = 0, \frac{1}{4}$ , and  $\frac{1}{2}$ .

Corollary 2.10 enables us to compute even close to  $r = 0$ . From (4.3), (4.6), and the fact that (Olver, 1964, p. 378)

$$K_\nu(z) \sim \left(\frac{\pi}{2z}\right)^{1/2} e^{-z} \quad (4.38)$$

as  $z \rightarrow \infty$ , we infer that we can still use (3.10) to truncate at large  $r$ .

### 5. Discussion

In this section, we recapitulate our main results and discuss some open problems.

In Section 2, we derived our environmental-pocket problem and proved some general results. By Theorem 2.4, the frequency  $\check{p}(x, \tau)$  of  $A_1$  satisfies (2.13). Lemma 2.3 shows that the spatial average of  $\check{p}(x, \tau)$  vanishes. The biological reason is that allele  $A_1$  is deleterious outside a bounded environmental pocket in  $\mathcal{R}^n$ , as (2.13c) requires.

According to (2.12b), in the original units the scaled partial-mixia parameter  $\beta = B/s$ . Theorem 2.7 establishes a remarkably simple result: under the general scaling hypotheses (2.14), if  $\beta \geq 1$ , then  $\check{p}(x, \tau) \rightarrow 0$  as  $\tau \rightarrow \infty$ . Thus, a cline can exist only if  $\beta < 1$ , which, together with equilibrium, we henceforth posit.

Theorem 2.9 states that if (2.17) holds, the spatial factor  $g(r)$  in the selection term is isotropic, and  $g'(r) \leq 0$ , then the equilibrium gene frequency satisfies  $p = p(r)$  and  $p'(r) < 0$  in  $(0, \infty)$ . These conclusions greatly simplify the analysis of (2.17). Isotropy leads to the intuitive result of Corollary 2.10, viz.,  $p'(0) = 0$ .

Convexity and concavity of the cline are more complicated than its slope. From Corollary 2.11 we have  $p''(r) > 0$  wherever  $g(r) < 0$ .

Henceforth, unless stated otherwise, we posit no dominance and the step-environment, i.e., (2.26) and (2.27), respectively. In (2.27),  $-\alpha$  denotes the ratio of the selection coefficients outside and inside the pocket. From (2.12a) we see that if  $A$  designates the radius of the pocket in the original units, then  $a = (A/\sigma)\sqrt{2s}$ .

Corollary 2.13 reveals that the cline satisfies  $p(0) < 1 - \beta$ . Corollary 2.15 informs us that in one dimension ( $n = 1$ ), we have  $p''(r) < 0$  in  $[0, a)$ . However, Corollary 4.10 shows that in two dimensions, the cline can be convex somewhere in  $(0, a)$ .

In one dimension, Theorem 3.1 provides a simple, explicit necessary and sufficient condition for the existence of the cline: the scaled radius  $a$  of the pocket must exceed the minimal radius  $a_1$ , given by (3.2). See Table 1 for values of  $a_1(\alpha, \beta)$  for various  $\alpha$  and  $\beta$ , and Figs. 1–3 for plots of  $p(r)$  for various  $a, \alpha$ , and  $\beta$ .

The two-dimensional case is more difficult. Theorem 4.1 and Corollary 4.2 characterize the minimal radius  $a_2$  such that  $a > a_2$  is necessary and sufficient for the existence of a cline. Since one can not solve (4.1) analytically for  $a_2$ , Corollaries 4.4 to 4.7 present asymptotic approximations of  $a_2$  for extreme values of  $\alpha$  and  $\beta$ . Consult Table 2 for values of  $a_2(\alpha, \beta)$  and Figs. 4–6 for graphs of  $p(r)$ .

Theorem 4.11 informs us that in  $n$  dimensions, a cline exists if and only if  $a > a_n$ , where  $a_n$  denotes the critical radius. Corollary 4.12 confirms our biological intuition that  $a_n(\alpha, \beta)$  is an increasing function of  $n, \alpha$ , and  $\beta$ ; i.e., increasing any of these parameters makes it harder to maintain the cline. Corollary 4.14 offers a simple, explicit formula for  $a_3$ .

We now turn to some open problems. Theorem 2.9 is based on Theorem 2 of Li and Ni (1993), which requires that  $g(r)$  be continuous. We overcame this technical difficulty for  $n = 1$ , but not for  $n > 1$ . Nonetheless, since the step-environment can be approximated with arbitrary accuracy by continuous functions, failure of isotropy is difficult to imagine.

The most important unsolved problem is to prove that when a cline exists, it is unique and globally asymptotically stable. This amounts to extending Theorem 1.1 in Lou et al. (2013b) from a bounded habitat to  $\mathcal{R}^n$ . It would be extremely surprising if this extension were invalid. Of course, it is desirable to study further a general decreasing  $g(r)$  and an arbitrary directional-selection factor  $f(p)$ . Anisotropic problems also would be of interest.

Finally, the monotonicities conjectured in Remark 4.15 seem biologically obvious and are supported by Theorem 4.16 and Figs. 1–6, but may be nontrivial to demonstrate.

Concerning the open problems, we cannot resist quoting an outstanding mathematician and a great theoretical physicist (personal communication to T. N.): “The obvious is the hardest to prove” (Charles C. Conley) and “More can be known than can be proved” (Richard P. Feynman).

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