

The Influence of Spatial Inhomogeneities on Neutral Models of Geographical Variation IV. Discontinuities in the Population Density and Migration Rate

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The equilibrium structure of the infinite, one-dimensional stepping-stone model with coincident discontinuities in the population density and migration rate is investigated in the diffusion approximation. The monoecious, diploid population is subdivided into an infinite linear array of equally large, panmictic colonies that exchange gametes isotropically. The population density and the migration rate have a discontinuity at the origin, but are elsewhere uniform. Generations are discrete and nonoverlapping; the analysis is restricted to a single locus without selection; every allele mutates to new alleles at the same rate. The three dimensionless parameters in the theory are $\alpha = (\rho_+/\rho_-)^2 (V_+/V_-)^{3/2}$, and $\beta_{\pm} = 4\rho_{\pm}\sqrt{2uV_{\pm}}$, where ρ_+ (ρ_-) and V_+ (V_-) designate the population density and variance of gametic dispersion per generation to the right (left) of the discontinuity, respectively, and u denotes the mutation rate. The characteristic length on the right (left) is $\sqrt{V_+/(2u)}$ ($\sqrt{V_-/(2u)}$). The probability of identity is continuous at the origin, but its partial derivatives have a discontinuity unless migration is conservative ($\rho_- V_- = \rho_+ V_+$). At least for nonconservative migration, the probability of identity (including the expected homozygosity) can be nonmonotonic even if the migration rate is uniform and the population density is monotonic. Thus, there can be a nonmonotonic genetic response in a neutral model to a monotonic environment. © 1999 Academic Press

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1. INTRODUCTION

The amount and pattern of genetic variability in neutral models of subdivided populations has been extensively investigated. This literature was reviewed in Nagylaki (1989a), and more recent studies were referenced in Nagylaki (1998). The present paper is the fourth in a series that treats the influence of spatial inhomogeneities on these models.

In the first paper of this series (Nagylaki, 1988, hereafter referred to as **I**), some biological background was presented to motivate, in particular, the study of the influence of geographical barriers and spatial variation in population density and migration rate on these models. Since the exact models that include these spatial inhomogeneities appear to be analytically intractable, approximations must be used. In the diffusion approximation, a general partial differential equation was derived for the probability of identity in a one-dimensional habitat, and transition and boundary conditions were established for a geographical barrier and for discontinuities in the population density and migration rate. The simplest boundary-value problems that involve spatial inhomogeneities were stated and briefly discussed.

In the second paper (Nagylaki and Barcion, 1988, hereafter referred to as **II**), two of the boundary-value problems formulated in **I** were used to explore the equilibrium structure of a population occupying a semi-infinite linear habitat. Boundaries that correspond to an impenetrable geographical barrier and to contact with a region of extremely high population density or dispersal rate were treated simultaneously. Qualitative properties, lower and upper bounds, the exact solution as an integral, and approximations in several important limiting cases were established for the probability of identity; numerical examples were also presented.

In the third paper (Nagylaki, Keenan, and Dupont, 1993, hereafter referred to as **III**), a boundary-value problem derived in **I** was used to treat symmetric migration across a penetrable geographical barrier in an infinite linear habitat. An exact solution for the probability of identity at equilibrium was not found, but lower and upper bounds and approximations were established, and numerical solutions were obtained.

Here, we shall use a boundary-value problem formulated in **I** to study the equilibrium structure of a population occupying an infinite linear habitat with coincident discontinuities in the population density and migration rate. In this case, the probability of identity is continuous, but its partial derivatives are not, their ratio being a simple function of the population densities and

migration rates on the two sides of the inhomogeneity. The discontinuities in the slopes exhibit the influence of variation in the population density and migration rate on the probability of identity. Our aim is to quantitate the effect of the inhomogeneity.

We shall present our results in the next section. In particular, we shall give the dimensionless parameters and characteristic lengths in the theory, state an upper bound (proved in the Appendix) on the difference between the probabilities of identity in finite and infinite habitats, and display some numerical examples. In Section 3, we shall briefly summarize and discuss our results.

2. RESULTS

The monoecious, diploid population is subdivided into an infinite linear array of equally large, panmictic colonies that exchange gametes isotropically. The population density and the migration rate have a discontinuity at the origin, but are elsewhere uniform. Generations are discrete and nonoverlapping; the analysis is restricted to a single locus without selection; every allele mutates to new alleles at the same rate u .

Let ρ_+ (ρ_-) and V_+ (V_-) designate the population density and variance of gametic dispersion per generation to the right (left) of the discontinuity, respectively. The analysis of homogeneous migration (Nagylaki, 1986) informs us that the characteristic length on the right (left) is $\sqrt{V_+/(2u)}$ ($\sqrt{V_-/(2u)}$). We define the dimensionless average position z and separation w of the points of observation x and y as

$$z = \sqrt{2u} \left(\frac{x}{\sqrt{V(x)}} + \frac{y}{\sqrt{V(y)}} \right), \quad (1)$$

$$w = \sqrt{2u} \left(\frac{x}{\sqrt{V(x)}} - \frac{y}{\sqrt{V(y)}} \right),$$

where $V(x) = V_{\pm}$ if $x \gtrless 0$. Thus, we use the natural scale at each point, which yields different scalings to the right and left of the discontinuity if $V_+ \neq V_-$. The three dimensionless parameters in the theory are (**I**)

$$\alpha = \left(\frac{\rho_+}{\rho_-} \right)^2 \left(\frac{V_+}{V_-} \right)^{3/2}, \quad \beta_{\pm} = 4\rho_{\pm} \sqrt{2uV_{\pm}}. \quad (2)$$

By symmetry under interchanging x and y , we may take $w \gtrless 0$. We denote by $f(z, w)$ the probability that at equilibrium two distinct genes chosen at random from adults just before gametogenesis, one from a colony at x

and one from a colony at y , are the same allele. In particular, $f(z, 0)$ represents the expected homozygosity at scaled coordinate z . In the diffusion approximation, $f(z, w)$ satisfies the boundary-value problem (Eq. (49) in I)

$$f_{zz} + f_{ww} - f = 0, \quad w > 0, w \neq \pm z, \quad (3a)$$

$$\beta_{\pm} f_w(z, 0+) + 1 - f(z, 0) = 0, \quad z \gtrless 0, \quad (3b)$$

$$f(z, \pm z \pm) = f(z, \pm z \mp), \quad z \gtrless 0, \quad (3c)$$

$$\begin{aligned} f_z(z, \pm z \pm) \mp f_w(z, \pm z \pm) \\ = \alpha [f_z(z, \pm z \mp) \mp f_w(z, \pm z \mp)], \quad z \gtrless 0, \end{aligned} \quad (3d)$$

$$f(z, w) \rightarrow f^{\pm}(w) \quad \text{as } z \rightarrow \pm \infty \text{ with } w \text{ fixed}, \quad (3e)$$

$$f(z, w) \rightarrow 0 \quad \text{uniformly in } z \text{ as } w \rightarrow \infty, \quad (3f)$$

where the subscripts signify partial differentiation and

$$f^{\pm}(w) = \frac{e^{-w}}{1 + \beta_{\pm}} \quad (4)$$

represents the diffusion approximation to the probability of identity with parameter β_{+} (or β_{-}) in a homogeneous habitat (Malécot, 1950, 1965; Weiss and Kimura, 1965; Nagylaki, 1976, 1986; Sawyer, 1977).

In the partial differential equation (3a), the Laplacian term ($\nabla^2 f$) and f are due to migration and mutation, respectively.

Random genetic drift enters through the boundary condition (3b). The intensity of random drift is controlled by the parameters β_{\pm} . Weak random drift (i.e., dense population, strong mutation, or rapid migration) corresponds to $\beta_{\pm} \gg 1$, whereas strong random drift (i.e., sparse population, weak mutation, or slow migration) corresponds to $\beta_{\pm} \ll 1$.

The transition conditions (3c) and (3d) mean that f is continuous when x or y crosses the inhomogeneity ($x = 0$ or $y = 0$, corresponding to $w = \pm z$), but if $\alpha \neq 1$, then the normal derivative of f has a discontinuity controlled by α . It is important to note, however, that in unscaled coordinates α in (3d) must be replaced by $(\rho_{+} V_{+})^2 / (\rho_{-} V_{-})^2$ (I), and then the normal derivative is continuous if and only if $\rho_{+} V_{+} = \rho_{-} V_{-}$. As we show in the next paragraph, this is precisely the condition that migration be conservative, i.e., that it not change the population density (Nagylaki, 1980).

To establish the last assertion, recall first that the flux of individuals is

$$J = M\rho - \frac{1}{2}(V\rho)_x, \quad (5)$$

where M denotes the mean displacement per generation (Nagylaki 1975, 1989b; Fife, 1979). If migration is conservative, then the population density is at equilibrium under migration alone (i.e., without population regulation), so $J = 0$, as proved in Appendix A from the underlying discrete model. Integrating (5) from $-\delta$ to δ , using the fact that M is bounded (actually, for isotropic migration $M = 0$), and letting $\delta \rightarrow 0$, we obtain $\rho_{+} V_{+} = \rho_{-} V_{-}$. In our model, the population density $\rho(x)$ refers to adults. Since the density of gametes before dispersion is proportional to $\rho(x)$, it is also true that the gametic density is unchanged by conservative migration, and only by conservative migration.

The asymptotic condition (3e) states that the influence of the inhomogeneity disappears as both points of observation recede from it. Finally, (3f) means that the probability of identity approaches zero as the separation of the two points tends to infinity.

We know (I) that

$$0 \leq f(z, w) \leq 1. \quad (6)$$

If the points x and y are on opposite sides of the origin ($xy < 0$, whence $|z| < w$), we have no other bounds. If they are on the same side ($xy \geq 0$, whence $|z| \geq w$), some bounds can be derived by comparison with the semi-infinite habitat (II), but these are not sufficiently tight to be useful.

We have not obtained analytic approximations to the solution of the problem (3), but have solved (3) numerically for several parameter sets. These solutions are accurate to at least 0.1%. This error is caused by discretization and habitat truncation. The following upper bound for the second component of the error is of broader interest.

As shown in Fig. 1, let Ω be a region in the upper half-plane bounded by the curve Γ and the segment Γ_0 of the z -axis that includes the origin. We denote the subsets of Γ_0 with $z \gtrless 0$ by Γ_0^{\pm} and introduce the radial coordinate

$$r = \sqrt{z^2 + w^2}. \quad (7)$$

Let D_R designate a half-disk of radius R centered at the origin such that $D_R \subset \Omega$; the semi-circular part of the boundary of D_R is Γ_R . In Appendix B, we prove that if $f^{\Omega}(z, w)$ represents the solution of (3) restricted to Ω with normal derivative zero on Γ , then

$$|f^{\Omega}(z, w) - f(z, w)| \leq U(r; R) \quad (8a)$$

in D_R , where

$$U(r; R) = I_0(r)/I_0(R) \quad (8b)$$

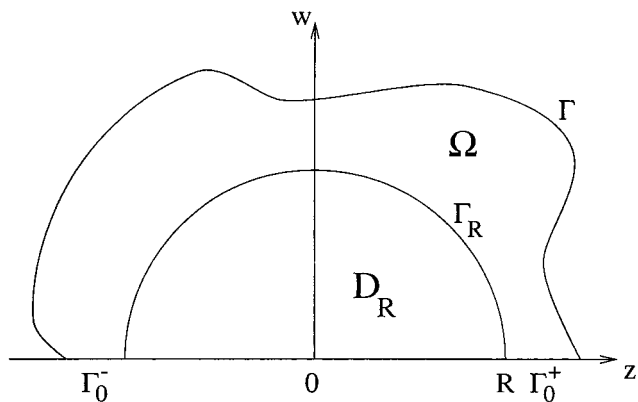


FIG. 1. Habitat truncation.

and I_0 signifies the modified Bessel function of the first kind of order zero (Olver, 1964). The function $I_0(r)$ is positive, is monotone increasing, and satisfies $I_0(0) = 1$ and

$$I_0(r) \sim \frac{e^r}{\sqrt{2\pi r}} \tag{9}$$

as $r \rightarrow \infty$ (Olver, 1964).

We seek the solution within several characteristic lengths of the origin, say in the rectangle

$$\Omega_c = \{(z, w) : |z| \leq 5, 0 \leq w \leq 5\}, \tag{10}$$

in which $r \leq r_c = 5\sqrt{2}$. Our truncated domain Ω is the rectangle with $|z| \leq 20$ and $0 \leq w \leq 20$, so we can choose $R = 20$. Therefore, an upper bound for the absolute truncation error at the origin is $1/I_0(R) \approx 2.30 \times 10^{-8}$; the greatest absolute truncation error in Ω_c cannot exceed $I_0(r_c)/I_0(R) \approx 4.13 \times 10^{-6}$.

We digress to describe an interesting biological application of the bound (8). Suppose the habitat is the line segment of scaled length L centered at the origin. Then Ω is the triangle bounded by the lines $w = 0$, $w + z = L$, and $w - z = L$, and therefore we can choose $R = L/\sqrt{2}$. We conclude that (8) is an upper bound on the effect of habitat finiteness in $r \leq R$. In particular, if r is fixed and $R \rightarrow \infty$, from (8) and (9) we obtain

$$U(r; R) \sim I_0(r) \sqrt{2\pi R} e^{-R}. \tag{11}$$

This bound should be compared with the exponential decay of the bound on the effect of a single boundary exhibited in Eq. (3.2) of II.

We now present some numerical solutions of (3). Using (2), we can express the following dimensionless parameters in terms of α and β_{\pm} :

$$\gamma = \beta_+ / \beta_-, \tag{12a}$$

$$\kappa = \rho_+ / \rho_- = \gamma^3 / \alpha, \tag{12b}$$

$$\lambda = \sqrt{V_+ / V_-} = \alpha / \gamma^2, \tag{12c}$$

$$\mu = (\rho_+ V_+) / (\rho_- V_-) = \kappa \lambda^2. \tag{12d}$$

Observe that migration is conservative if and only if $\mu = 1$.

Our first example displays the generic qualitative behavior of the solutions. We choose $\alpha = 4$, $\beta_+ = 4$, and $\beta_- = 2$, whence $\gamma = 2$, $\kappa = 2$, $\lambda = 1$, and $\mu = 2$. Since $\lambda = 1$, the scaling is the same in the entire habitat; since $\mu \neq 1$, migration is not conservative. The three-dimensional Fig. 2 exhibits the rapid decay of $f(z, w)$ with increasing scaled separation w , the weaker dependence on the scaled average position z , and the discontinuity (3d) when an observation point crosses the origin. The two-dimensional Figs. 3 to 6 exemplify these features in more detail.

Figure 3 shows $f(z, w)$ as a function of z for various fixed values of w . Note the agreement with the asymptotic condition (3e) and the discontinuities at $z = \pm w$. The most striking feature of Fig. 3 is that $f(z, w)$ is not monotonic even for $w = 0$. Since the environment is monotonic ($V_+ = V_-$ and $\rho_+ > \rho_-$), we might have expected that $f(z, w)$ would be monotonic for each fixed w , or at least that the expected homozygosity $f(z, 0)$ would be. We shall discuss this result after briefly commenting on Figs. 4 to 6.

Figure 4 depicts the roughly exponential decay of $f(z, w)$ in w for various fixed values of z . Because of our scaling, the rate of decay is approximately one. For $z = \pm 3$, there is a discontinuity at $w = 3$.

In Fig. 5, y is fixed and $x (\geq y)$ is increasing. Again, the decay of $f(z, w)$ is very roughly exponential. The discontinuity for $z - w = -3$ occurs at $x = 0$.

In Fig. 6, x is fixed and $y (\leq x)$ is decreasing. The decay of $f(z, w)$ is again very crudely exponential. The discontinuity for $z + w = 3$ occurs at $y = 0$.

Returning to the nonmonotonicity of $f(z, w)$ in z for fixed w , we first explain intuitively the qualitative behavior in Fig. 3. For simplicity, and because we present a mathematical argument below, we discuss only $f(z, 0)$. Consider first the limiting case $\rho_- = 0$. From (3d) we see at once that for $z > 0$

$$f_z(z, z-) - f_w(z, z-) = 0, \tag{13}$$

i.e., the normal derivative at the origin is zero, as for an impenetrable geographical barrier at the origin (II). The biological interpretation of this genetic equivalence is that there is no flux of individuals across the origin from

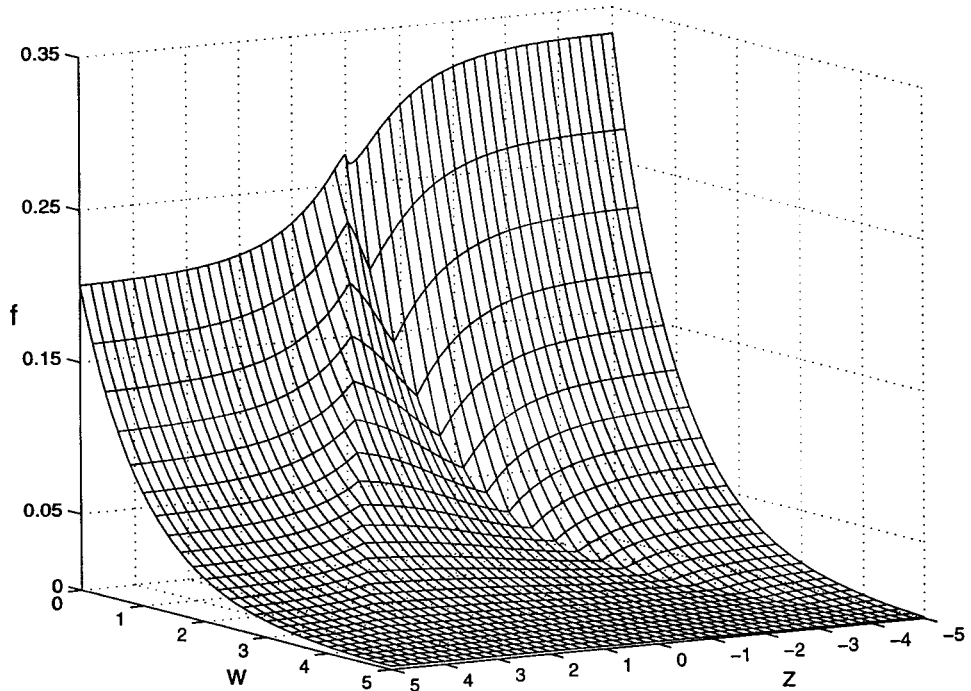


FIG. 2. The probability of identity $f(z, w)$ for $\alpha=4$, $\beta_+=4$, and $\beta_-=2$ as a function of the scaled average position z and the scaled separation w .

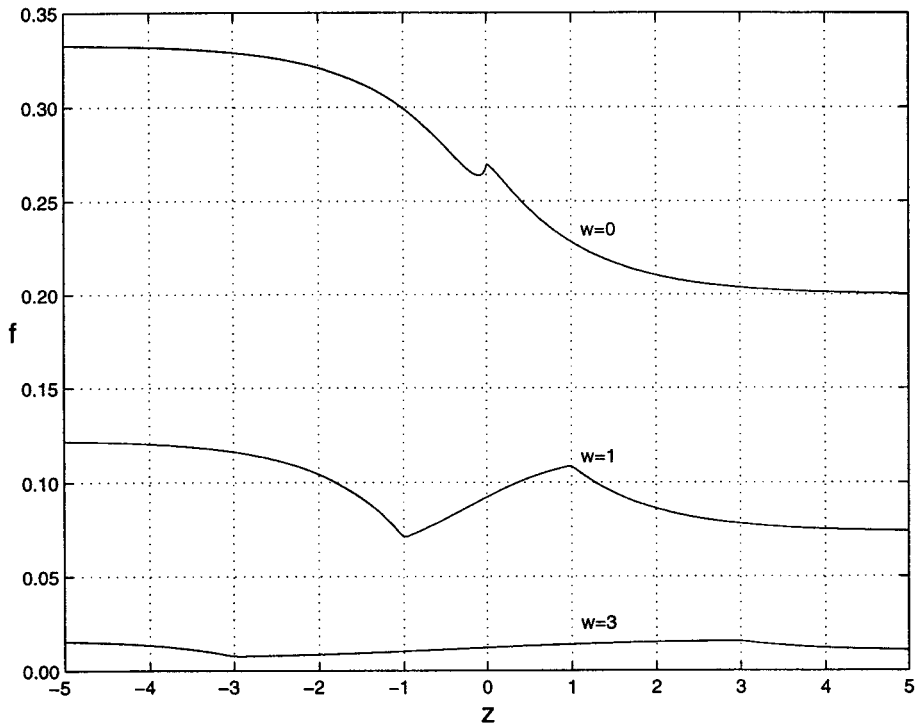


FIG. 3. The probability of identity $f(z, w)$ for $\alpha=4$, $\beta_+=4$, and $\beta_-=2$ as a function of the scaled average position z for various fixed values of the scaled separation w .

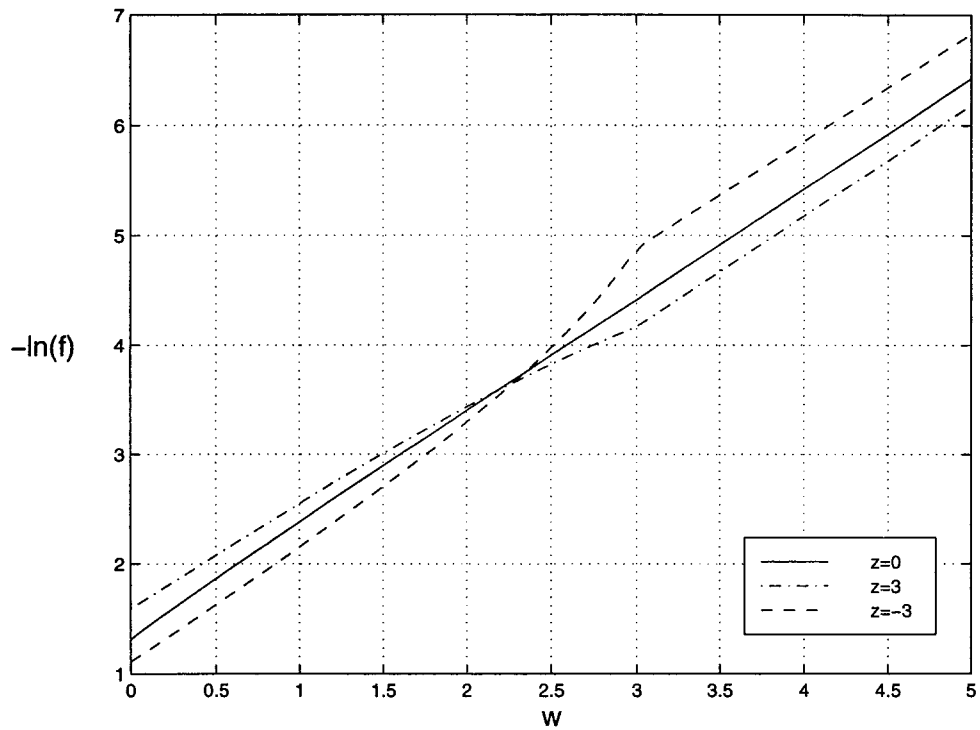


FIG. 4. The probability of identity $f(z, w)$ for $\alpha = 4$, $\beta_+ = 4$, and $\beta_- = 2$ as a function of the scaled separation w for various fixed values of the scaled average position z .

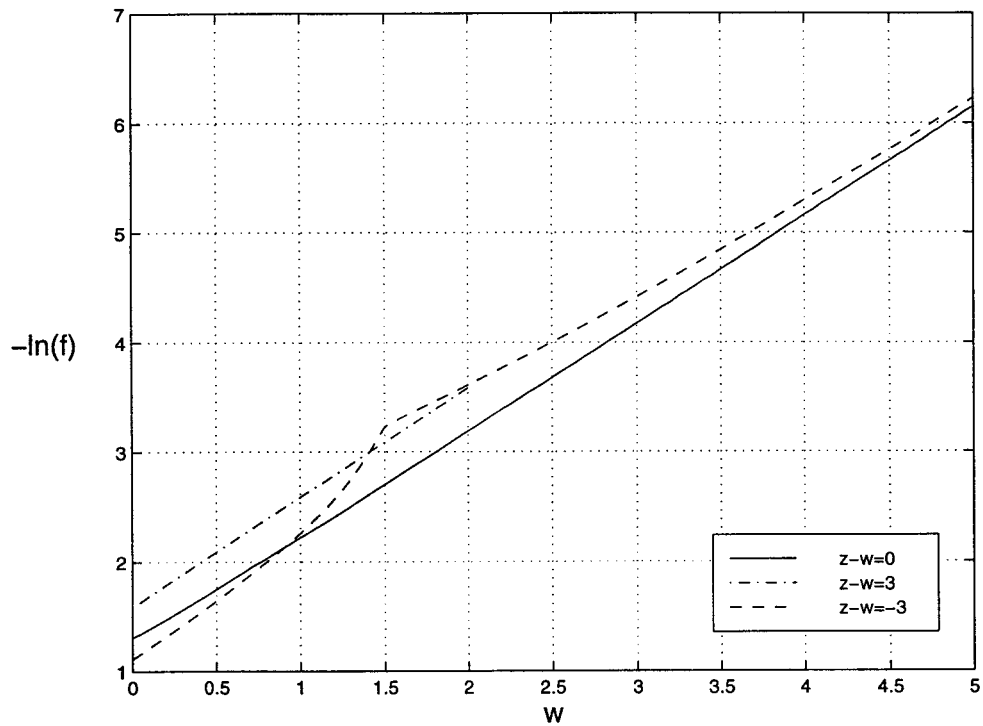


FIG. 5. The probability of identity $f(z, w)$ for $\alpha = 4$, $\beta_+ = 4$, and $\beta_- = 2$ as a function of the scaled separation w for various fixed locations of the point on the left.

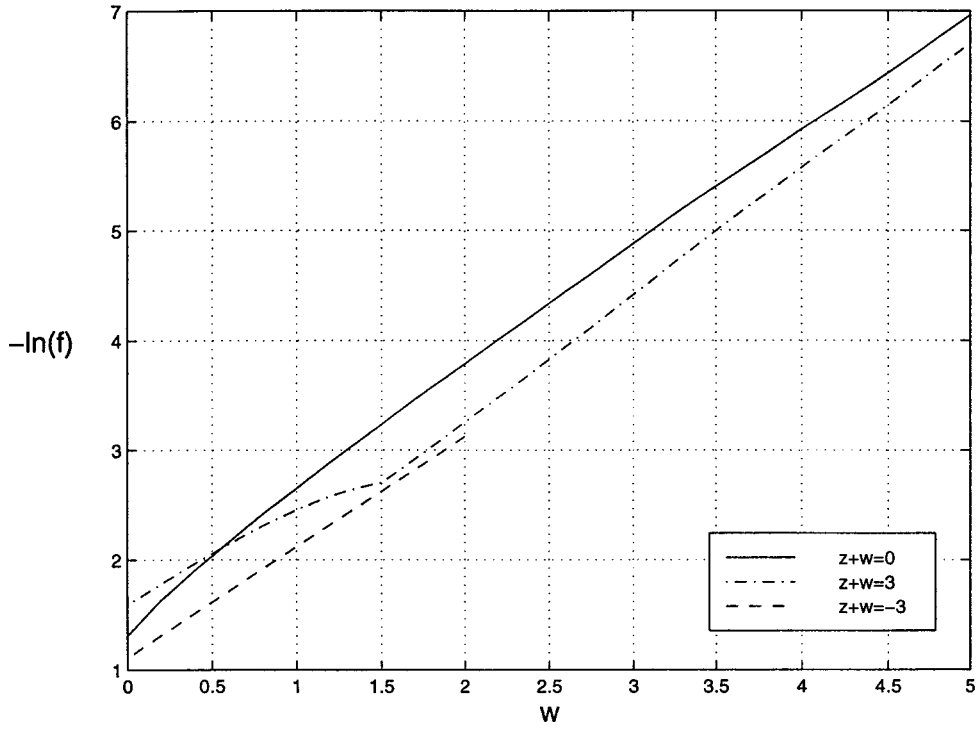


FIG. 6. The probability of identity $f(z, w)$ for $\alpha=4$, $\beta_+=4$, and $\beta_-=2$ as a function of the scaled separation w for various fixed locations of the point on the right.

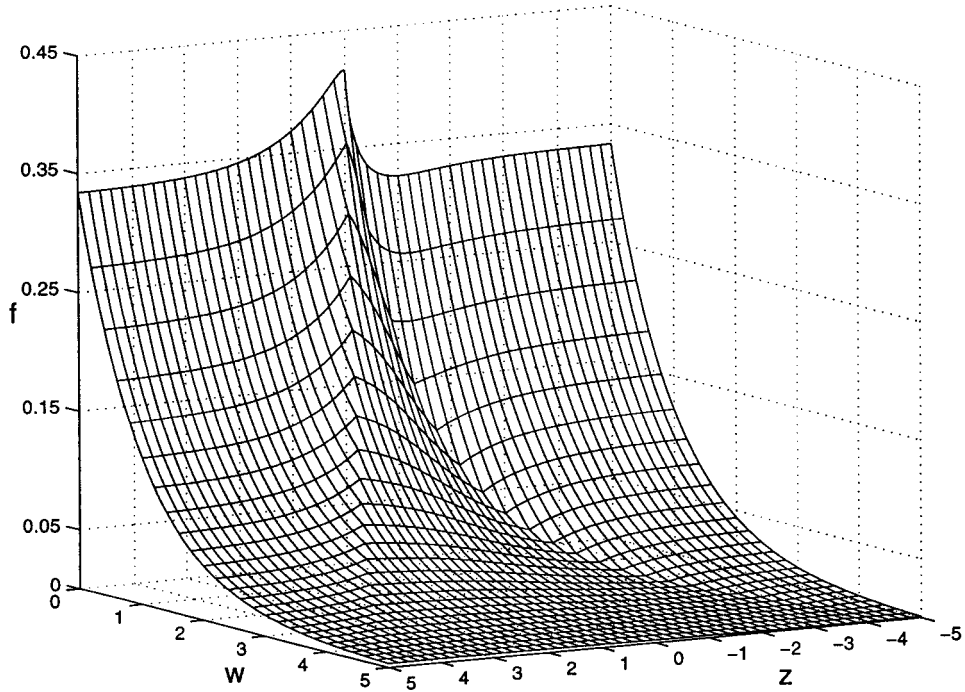


FIG. 7. The probability of identity $f(z, w)$ for $\alpha=4$ and $\beta_{\pm}=2$ as a function of the scaled average position z and the scaled separation w .

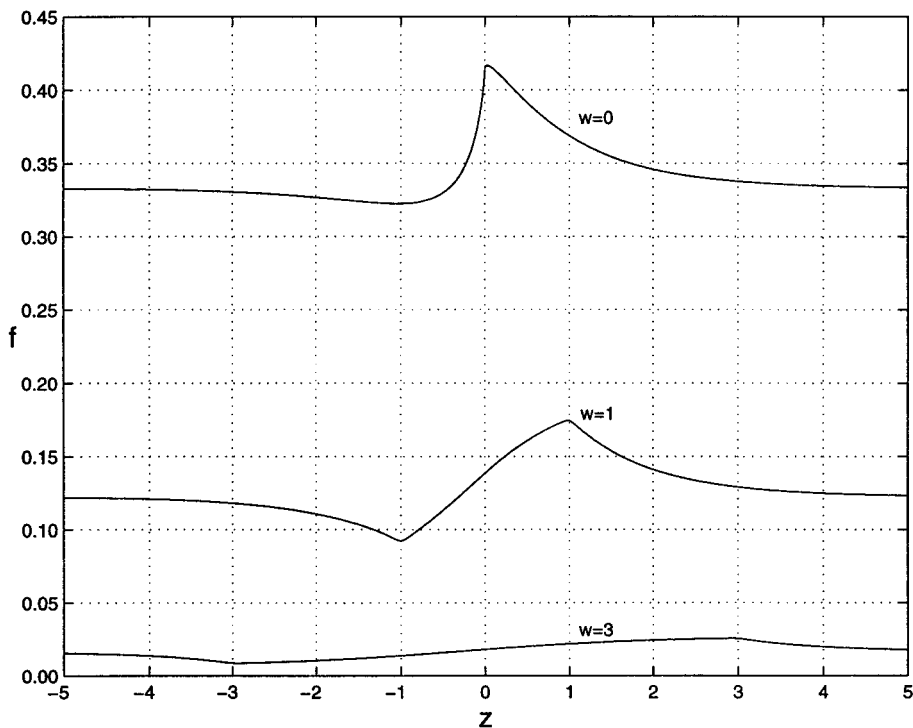


FIG. 8. The probability of identity $f(z, w)$ for $\alpha = 4$ and $\beta_{\pm} = 2$ as a function of the scaled average position z for various fixed values of the scaled average separation w .

left to right, and since the population is regulated, the loss of individuals due to flux from right to left is genetically the same as if they were reflected. An impenetrable barrier raises $f(z, 0)$, up to twofold (II).

Suppose now that $V_+ = V_-$ ($\lambda = 1$) and $\rho_+ \gg \rho_-$ ($\kappa \gg 1$) and examine $f(z, 0)$ close to the origin ($|z| \ll 1$). For $z > 0$, the above argument indicates that f is significantly increased; for $z < 0$, the influx of individuals significantly lowers f . This reasoning suggests the non-monotonic behavior in Fig. 3: decrease, increase, and decrease.

If $V_+ \neq V_-$ and $\rho_+ \neq \rho_-$, but migration is conservative ($\mu = 1$), then the above reasoning fails because there is no flux across the origin. Consequently, we might still expect monotonicity of $f(z, 0)$ and perhaps even of $f(z, w)$ for fixed w .

The following simple mathematical argument yields further insight and demonstrates that monotonicity cannot always hold. Posit that $f(z, w)$ is monotonic in z for fixed w and that $\beta_+ \geq \beta_-$. Then (3e) implies that

$$f^+(z, w) \leq f(z, w) \leq f^-(z, w). \tag{14}$$

However, if $\beta_+ = \beta_-$ ($\gamma = 1$), then (4) and (14) show that $f^+ \equiv f \equiv f^-$, which is patently false unless $\alpha = 1$. We conclude that monotonicity of $f(z, w)$ and at least one of the

inequalities in (14) must sometimes fail. This is illustrated in Figs. 7 and 8, where $\alpha = 4$ and $\beta_{\pm} = 2$. Observe in Fig. 8 that f^{\pm} is neither an upper nor a lower bound.

The above contradiction does not occur for conservative migration, because in that case (12) informs us that $\alpha = 1$ if $\gamma = \mu = 1$. Thus, monotonicity and (14) may still hold, but we have neither a proof nor a counterexample. As an example (not shown), choose $\alpha = 4$, $\beta_+ = 4$, and $\beta_- = 1$; since $\mu = 1$, migration is conservative. Then the numerical solution $f(z, w)$ of (3) is monotonic in z for each fixed w . The discontinuities (3d) in the normal derivative occur only because the length scales are different on either side of the origin. We define the new coordinates (Z, W) so that

(a) $z \leq -w$:

$$Z = \lambda^{-1}z, \quad W = \lambda^{-1}w; \tag{15a}$$

(b) $-w < z < w$:

$$\begin{aligned} Z &= \frac{1}{2}[(1 + \lambda^{-1})z + (1 - \lambda^{-1})w], \\ W &= \frac{1}{2}[(1 - \lambda^{-1})z + (1 + \lambda^{-1})w]; \end{aligned} \tag{15b}$$

(c) $z \geq w > 0$:

$$Z = z, \quad W = w. \tag{15c}$$

These have the same scaling everywhere. If we replot f using (15) with $\lambda = \frac{1}{4}$, the result is both monotonic and smooth.

If $\alpha = 1$, $\beta_+ = 4$, and $\beta_- = 2$, then migration is not conservative ($\mu = \frac{1}{2}$), but f is both smooth and monotonic. In the coordinates (15), the normal derivative is discontinuous, but f is still monotonic.

Finally, we note that for the two parameter sets (i) $\alpha = 4$, $\beta_+ = 2$, $\beta_- = 4$ and (ii) $\alpha = 8$, $\beta_+ = 2$, $\beta_- = 1$, all qualitative features were as expected from the above examples.

3. DISCUSSION

We have investigated the influence of coincident discontinuities in the population density and migration rate on the probability of identity f in a one-dimensional habitat. Figures 2 to 6 exemplify the qualitative behavior of f . The influence of the discontinuity on f can be considerable. When one of the points of observation crosses the discontinuity, f is continuous, but its corresponding partial derivative is discontinuous unless migration is conservative.

If migration is not conservative, then f may not be monotonic even if the migration rate is uniform and the population density is monotonic. Thus, there can be a nonmonotonic genetic response to a monotonic environment in a neutral model. This should be kept in mind in the interpretation of nonmonotonic observations. We have not determined whether f is always monotonic for conservative migration. If so, this would be yet another example of a simple, intuitive behavior for conservative migration that does not extend to nonconservative migration (cf. Nagylaki, 1998; and references therein).

4. APPENDIX

A. Conservative Migration

Here, we shall demonstrate that the flux (5) must vanish for conservative migration. We shall do this by deriving the partial differential equation and boundary condition satisfied by the population density under arbitrary pure migration (i.e., without population regulation). We shall find the diffusion limit of the following discrete model.

Let $N_i(t)$ denote the number of individuals in deme i ($= 0, \pm 1, \pm 2, \dots$) in generation t ($= 0, 1, 2, \dots$). Let

$\tilde{m}_{ij}(t)$ designate the probability that, in generation t , an individual in deme i migrates to deme j . Then we have

$$N'_i = \sum_j N_j \tilde{m}_{ji}, \quad (\text{A1})$$

where the prime signifies the next generation.

We scale space and time as $x = \varepsilon i$ and $\tau = \eta t$, and let $\varepsilon \rightarrow 0$ and $\eta \rightarrow 0$ so that ε^2/η remains fixed. We set $\hat{\rho}(x, \tau) = N_i(t)$ and assume that $\hat{\rho}(x, \tau) \rightarrow \rho(x, \tau)$ uniformly in x as $\eta \rightarrow 0$. For migration, we require the diffusion hypotheses

$$\lim_{\eta \rightarrow 0} \frac{\varepsilon}{\eta} \sum_{j: |j-i| < \theta/\varepsilon} (j-i) \tilde{m}_{ij} = M(x, \tau), \quad (\text{A2a})$$

$$\lim_{\eta \rightarrow 0} \frac{\varepsilon^2}{\eta} \sum_{j: |j-i| < \theta/\varepsilon} (j-i)^2 \tilde{m}_{ij} = V(x, \tau), \quad (\text{A2b})$$

$$\lim_{\eta \rightarrow 0} \frac{1}{\eta} \sum_{j: |j-i| \geq \theta/\varepsilon} \tilde{m}_{ij} = 0 \quad (\text{A2c})$$

uniformly in x for every fixed $\theta > 0$. We assume also that the partial derivatives that appear below are the uniform limits of the corresponding discrete quantities as $\eta \rightarrow 0$ and are continuous.

For a bounded function $g_i(t) = G(x, \tau)$ such that G_{xx} is continuous, we have (Nagylaki, 1989b)

$$\begin{aligned} \sum_i \tilde{m}_{ji} g_i(t) &= G(y, \tau) + \eta M(y, \tau) G_y(y, \tau) \\ &\quad + \frac{1}{2} \eta V(y, \tau) G_{yy}(y, \tau) + o(\eta) \end{aligned} \quad (\text{A3})$$

as $\eta \rightarrow 0$, where $y = \varepsilon j$. We introduce a nonnegative test function $\phi_i = \Phi(x)$ such that Φ_{xx} is continuous and that $\Phi(x)$, $\Phi_x(x)$, and $\Phi_{xx}(x)$ vanish unless $x_1 < x < x_2$. We multiply (A1) by ϕ_i and sum over i :

$$\sum_i N'_i \phi_i = \sum_{i,j} N_j \tilde{m}_{ji} \phi_i. \quad (\text{A4})$$

Invoking (A3), we can express (A4) in the form

$$\begin{aligned} \sum_i \hat{\rho}(x, \tau + \eta) \Phi(x) &= \sum_j \hat{\rho}(y, \tau) [\Phi(y) + \eta M(y, \tau) \Phi_y(y) \\ &\quad + \frac{1}{2} \eta V(y, \tau) \Phi_{yy}(y) + o(\eta)] \end{aligned} \quad (\text{A5})$$

as $\eta \rightarrow 0$, which we recast to read

$$\begin{aligned} & \sum_i \eta^{-1} [\hat{\rho}(x, \tau + \eta) - \hat{\rho}(x, \tau)] \Phi(x) \\ &= \sum_i \hat{\rho}(x, \tau) [M(x, \tau) \Phi_x(x) \\ & \quad + \frac{1}{2} V(x, \tau) \Phi_{xx}(x) + o(1)]. \end{aligned} \quad (\text{A6})$$

In the limit $\eta \rightarrow 0$, this yields

$$\begin{aligned} & \int_{x_1}^{x_2} \rho_\tau(x, \tau) \Phi(x) dx \\ &= \int_{x_1}^{x_2} \rho(x, \tau) [M(x, \tau) \Phi_x(x) + \frac{1}{2} V(x, \tau) \Phi_{xx}(x)] dx. \end{aligned} \quad (\text{A7})$$

Integrating the right-hand side of (A7) by parts and recalling the assumptions on $\Phi(x)$, we find (cf. Nagylaki, 1975, 1989b; Fife, 1979)

$$\rho_\tau = -J_x, \quad (\text{A8a})$$

where the flux is given by

$$J(x, \tau) = M(x, \tau) \rho(x, \tau) - \frac{1}{2} [V(x, \tau) \rho(x, \tau)]_x. \quad (\text{A8b})$$

We conclude that $J_x = 0$ if migration is conservative ($\rho_\tau = 0$). To see that, in fact, we must have $J(x, \tau) = 0$, we either claim that $J(x, \tau) \rightarrow 0$ as $x \rightarrow \pm\infty$ or posit that there is an impenetrable boundary, say on the left at $x = 0$. In the latter case, at $i = 0$, from (A1) we obtain

$$\eta^{-1} (N'_0 - N_0) = \eta^{-1} \left(\sum_{j=0}^{\infty} N_j \tilde{m}_{j0} - N_0 \right). \quad (\text{A9})$$

Since the right-hand side of (A9) is clearly the net flow per unit scaled time into the deme at $i = 0$, the limit $\eta \rightarrow 0$ gives

$$\rho_\tau(0, \tau) = -J(0, \tau), \quad (\text{A10})$$

whence $J(0, \tau) = 0$ if $\rho_\tau(0, \tau) = 0$ (cf. Nagylaki, 1975, 1989b; Fife, 1979).

B. Habitat Truncation

In this section, we establish the bound (8). Although our proof has many steps, the underlying intuitive idea is simple. We shall see below that our boundary-value problem can be interpreted as one for the temperature distribution in a plate, in which case increasing the boundary value or the outward normal derivative

corresponds to increasing the temperature or heat inflow on the boundary (Stakgold, 1979, pp. 2–7); clearly, this increases the temperature at each point in the plate. The mathematical proof uses the maximum principle for elliptic partial differential equations (Protter and Weinberger, 1967, pp. 64–67, 76–79).

First, we rewrite (3a)–(3d) as

$$\nabla \cdot (\psi \nabla f) - \psi f = 0, \quad w > 0, \quad (\text{B1a})$$

$$\beta_\pm f_\nu = 1 - f, \quad z \geq 0, w = 0, \quad (\text{B1b})$$

in which ν signifies the outward normal derivative and

$$\psi(z, w) = \begin{cases} \alpha, & z > w, \\ 1, & |z| < w, \\ \alpha^{-1}, & z < -w. \end{cases} \quad (\text{B2})$$

To see that (B1) is equivalent to (3), note first that (B1a) and (3a) agree. Integrating (B1a) over a square with side δ , centered at (z, z) with diagonals parallel to the axes, using the divergence theorem, and letting $\delta \rightarrow 0$, we deduce (3c) and (3d).

Next, we define the truncated solution $f^\Omega(z, w)$, restricted to Ω in Fig. 1 so that it satisfies

$$\nabla \cdot (\psi \nabla f^\Omega) - \psi f^\Omega = 0, \quad \mathbf{x} \in \Omega, \quad (\text{B3a})$$

$$\beta_\pm f^\Omega_\nu = 1 - f^\Omega, \quad \mathbf{x} \in \Gamma_0^\pm, \quad (\text{B3b})$$

$$f^\Omega_\nu = 0, \quad \mathbf{x} \in \Gamma, \quad (\text{B3c})$$

where $\mathbf{x} = (z, w)$. Applying the maximum principle to the boundary-value problems satisfied by $-f^\Omega(\mathbf{x})$ and $f^\Omega(\mathbf{x}) - 1$, we easily establish that

$$0 \leq f^\Omega(\mathbf{x}) \leq 1, \quad \mathbf{x} \in \Omega. \quad (\text{B4})$$

Note that we can interpret $f^\Omega(\mathbf{x})$ as the equilibrium temperature at \mathbf{x} in a plate Ω , with heat loss at \mathbf{x} proportional to the temperature, heat influx on Γ^\pm proportional to $1 - f^\Omega(\mathbf{x})$, and Γ insulated.

The truncation error in Ω is

$$h(\mathbf{x}) = f^\Omega(\mathbf{x}) - f(\mathbf{x}); \quad (\text{B5})$$

by (6) and (B4), this has the bound $|h(\mathbf{x})| \leq 1$ in Ω . Subtracting (B1a) and (B1b) from (B3a) and (B3b), respectively, we see that $h(\mathbf{x})$ satisfies the boundary-value problem

$$\nabla \cdot (\psi \nabla h) - \psi h = 0, \quad \mathbf{x} \in \Omega, \quad (\text{B6a})$$

$$\beta_\pm h_\nu = -h, \quad \mathbf{x} \in \Gamma_0^\pm, \quad (\text{B6b})$$

$$|h| \leq 1, \quad \mathbf{x} \in \Gamma. \quad (\text{B6c})$$

Let $\hat{h}(\mathbf{x})$ satisfy (B6a,b) and the boundary condition $\hat{h}(\mathbf{x}) = 1$ on Γ . The maximum principle informs us that $0 \leq \hat{h}(\mathbf{x}) \leq 1$ in Ω .

Now,

$$H(\mathbf{x}) \equiv h(\mathbf{x}) - \hat{h}(\mathbf{x}) \tag{B7}$$

satisfies (B6a,b) and $H(\mathbf{x}) \leq 0$ on Γ , so the maximum principle implies that $H(\mathbf{x}) \leq 0$, i.e., $h(\mathbf{x}) \leq \hat{h}(\mathbf{x})$ in Ω . But $-h(\mathbf{x})$ also satisfies (B6), and hence we have also $-h(\mathbf{x}) - \hat{h}(\mathbf{x}) \leq 0$, i.e., $h(\mathbf{x}) \geq -\hat{h}(\mathbf{x})$ in Ω . Since $\hat{h}(\mathbf{x}) \geq 0$, we have demonstrated that $|h(\mathbf{x})| \leq \hat{h}(\mathbf{x})$ in Ω .

Let $\hat{U}(\mathbf{x})$ be the solution in D_R in Fig. 1 of the boundary-value problem

$$\nabla \cdot (\psi \nabla \hat{U}) - \psi \hat{U} = 0, \quad \mathbf{x} \in D_R, \tag{B8a}$$

$$\beta_{\pm} \hat{U}_v = -\hat{U}, \quad 0 < \pm z < R, w = 0, \tag{B8b}$$

$$\hat{U} = 1, \quad \mathbf{x} \in \Gamma_R. \tag{B8c}$$

By the maximum principle, $\hat{h}(\mathbf{x}) \leq \hat{U}(\mathbf{x})$ in D_R .

Finally, we define $\tilde{U}(\mathbf{x})$ so that it satisfies

$$\nabla \cdot (\psi \nabla \tilde{U}) - \psi \tilde{U} = 0, \quad \mathbf{x} \in D_R, \tag{B9a}$$

$$\tilde{U}_v = 0, \quad -R < z < R, w = 0, \tag{B9b}$$

$$\tilde{U} = 1, \quad \mathbf{x} \in \Gamma_R. \tag{B9c}$$

Since $\hat{U}(\mathbf{x}) \geq 0$, the maximum principle reveals that $\hat{U}(\mathbf{x}) \leq \tilde{U}(\mathbf{x})$ in D_R . But the solution of (B9) is isotropic because $U(r; R) \equiv \tilde{U}(\mathbf{x})$ has normal derivative zero on $w = 0$ and $w = \pm z$. Therefore, U satisfies the simple boundary-value problem

$$\frac{1}{r} \frac{d}{dr} \left(r \frac{dU}{dr} \right) - U = 0, \quad r < R, \tag{B10a}$$

$$U(0; R) < \infty, \quad U(R; R) = 1, \tag{B10b}$$

which has the unique solution (8b) (Olver, 1964).

Thus, we have shown that

$$|h(\mathbf{x})| \leq \hat{h}(\mathbf{x}) \leq \hat{U}(\mathbf{x}) \leq U(r; R), \quad r \leq R, \tag{B11}$$

which completes our proof.

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