

Spatial Patterns in the Distributions of Polygenic Characters

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The spatial patterns in the mean and variance of a quantitative character that result from the interaction of spatially varying, optimizing selection and gene flow are considered. The model analyzed is an extension of those of Kimura (1965) and Lande (1976) for the distribution of a quantitative character maintained in a population by independent mutations. For weak selection, it is shown that there is only a small effect of gene flow on the variance of the character and that the mean value changes on a length scale that is large compared to the average dispersal distance. As in models of clines in allele frequencies, it is possible to define a "characteristic length" in terms of the average dispersal distance and strength of selection. The characteristic length is the smallest length scale environmental change to which the mean value of the character can significantly respond. It is also shown that, for weak selection, an asymmetry in dispersal can result in a significant shift in location of a cline. By considering an infinite linear cline in optimal values, it is shown that gene flow can increase the variance only when there is sufficient mixing in each generation of individuals from locations with different means. A model of selection in different niches is also considered. There is an increase in variance due to the effective weakening of the intensity of selection because of the differences in optimal values in different niches.

The implications of the different models for maintenance of genetic polymorphism are discussed. Under some conditions gene flow can produce a significant increase in heterozygosity. It is also argued that spatial variation in selection on a polygenic character can be much more effective in increasing heterozygosity than temporal variation because of the potentially greater increase in phenotypic variance. The difference between some of the results for polygenic characters from those of similar models of one and two locus systems is accounted for by the fact that for normally distributed polygenic characters, changes in the variance are effectively decoupled from changes in the mean.

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1. Introduction

In order to interpret the geographic patterns in natural populations, we must understand the consequences of the interaction between gene flow and spatially varying natural selection. Much progress has been made on the analysis of clines in the frequencies of alleles at a single locus or two linked loci maintained by gene flow and selection (Karlin & Richter-Dyn, 1976; Nagylaki, 1975, 1976; May, Endler & McMurtic, 1975; Slatkin, 1975), but there has been less analysis of the problem of clines in polygenic characters. Bulmer (1971*a,b*) has considered the problem of the effect of gene flow on a polygenic character but did not consider clinal variation, and Felsenstein (1977) has a solution for an infinite linear cline maintained by optimizing selection with a linear gradient in the optimal value of the character. In this paper, I will analyze a simple model of the expected spatial patterns in the distribution of a polygenic character that is subject to spatially varying, optimizing selection.

2. Assumptions and General Analysis

The model of spatial patterns in the distribution of a polygenic character is an extension of Lande's (1976) model of the distribution of a polygenic character in a single, panmictic, diploid, population with discrete, non-overlapping generations. The assumptions in Lande's model are:

(i) The character in an infinite population is determined additively by n linked loci.

(ii) The character is subject to density independent, optimizing selection with the selection function, $W(z)$, of the form:

$$W(z) \propto e^{-(z-z_0)^2/2w^2}, \quad (1)$$

where z is a measure of the phenotypic character, z_0 is the optimal value of the character and w^2 is a measure of the strength selection.

(iii) At each of the n loci, there is a constant rate of mutation to new alleles that have a slightly different effect on the value of the character. The mean effect of each is zero, the variance of the effects at loci i is m_i and the higher moments are assumed to be negligible. The mutation rate at locus i is μ_i .

With these assumptions, Lande (1976) is able to extend the results of Kimura (1965) for one locus to a system with an arbitrary number of loci. The underlying variables for the model are x_i the allelic effects at the i th locus, and population is completely described by $f(x_1, \dots, x_n, t) = f(x, t)$.

the joint distribution of the x_i in generation t . Lande's results for the equilibrium distribution, $f(x)$, that are of importance here are:

(a) $f(x)$ is approximately a multi-variate normal distribution with a covariance matrix C_{ij} whose elements are explicit functions of the various parameters.

(b) The expressed genetic variance and the total phenotypic variance, σ_z^2 are much smaller than w^2 when w^2 is large. From Lande (1976, equation 21c)

$$\frac{\sigma_z^2}{w^2} = O\left(\frac{1}{\sqrt{w^2}}\right) \quad (2)$$

for large w^2 .

(c) The equilibrium values for σ_z^2 and the C_{ij} do not depend on the average value of the character being at the optimum. That is, the co-variance matrix converges to its equilibrium independently of the overall mean value of the character, \bar{z} , and of the average allelic effects \bar{x}_i .

While the general problem of spatial variation in a character whose dynamics at each location are governed by Lande's model is complex, I will show that under certain conditions, some approximations can be made to reduce the general problem to one that is analytically tractable. The conditions that allow the problem to be simplified are still sufficiently general that a number of problems of biological interest can be treated. We will consider variation in only one direction and let ξ be the spatial variable. We will make the following assumptions:

(1) At each spatial location, the assumptions of Lande's model are valid and the parameters, except the optimal value of the character, $z_0(\xi)$, are the same. That is, the strengths of selection, mutation rates, environmental components of the variance and allelic effects are the same at all locations so that, in the absence of gene flow between locations, there would be the same covariance matrix at equilibrium at each location. We will denote the equilibrium C_{ij} values in the absence of gene flow by \bar{C}_{ij} .

(2) Optimizing selection at each location is weak. That is, w^2 is large enough that σ_z^2/w^2 is small.

(3) The size of the range in values of $z_0(\xi)$, the optimum at ξ is significantly smaller than w .

The results derived using these assumptions will be approximately correct when selection is weak and when the range of optima is not too large. Furthermore, the analysis leading to these results will give some indication of the behavior of the model when these assumptions are not valid.

To construct the complete model, assume that there are three separate stages in each generation: random association of the gametes, selection and production of gametes for the next generation, and gene flow caused by

gametic movement. The assumption that there is dispersal only at the gametic stage is for algebraic simplicity and is not restrictive. Also for simplicity, both maternal and paternal gametes can move but only a minor change is required if one type does not. We assume that $f(x, \xi)$ is the equilibrium joint distribution of allelic effects at ξ after the gene flow stage. We define $\tilde{f}(x, \xi)$ to be the joint distribution of allelic effects after mating and selection and $M(\xi, \xi')$ to be the probability that an individual gamete moves from location ξ' to ξ . Assuming a uniform population density and no genetic differences in dispersal tendencies, we must have:

$$f(x, \xi) = \int_{-\infty}^{\infty} M(\xi, \xi') \tilde{f}(x, \xi') d\xi', \quad (3)$$

at equilibrium where we write the limits of the integral as infinite because we are assuming that there are no boundaries to the region being considered. The effects of boundaries and partial barriers to gene flow can also be analyzed using this method.

The dispersal function, $M(\xi, \xi')$ must have certain properties, some of which depend on the assumptions about the actual dispersal patterns. First,

$$\int_{-\infty}^{\infty} M(\xi, \xi') d\xi' = 1 \quad (4)$$

for all ξ because a gamete arriving at ξ must have originated somewhere in the range. Second, if we assume the environment is homogeneous with respect to the dispersal of gametes, then $M(\xi, \xi')$ must be a function only of $(\xi - \xi')$, which we will write as $M(\xi - \xi')$. This means that there are no barriers to dispersal. The first two moments will be of importance so we define:

$$m = \int_{-\infty}^{\infty} \xi' M(\xi') d\xi', \quad (5)$$

and

$$l^2 = \int_{-\infty}^{\infty} (\xi' - m)^2 M(\xi') d\xi'. \quad (6)$$

An important special case is that of symmetric dispersal, for which $m = 0$. We assume that M has finite moments of all order and that the higher order moments are not too large. Also, we will have to assume m is much smaller than l , so we can consider populations which have only a small directional component to the gene flow.

The model is completed by the details of the steps of recombination, selection and gamete production at each location giving $\tilde{f}(x, \xi)$ as a function of $f(x, \xi)$. However, this model would be extremely difficult to solve

analytically or even numerically for more than a few loci because $f(x, \xi)$ and $\tilde{f}(x, \xi)$ are not necessarily multi-variate normal functions. In fact, when there is spatial variation in the distribution of the character, we would expect the distribution *not* to be multi-variate normal because, in each generation, distributions with different means and variances would be combined, thus destroying any simple functional form of $f(x, \xi)$. However, we will see that, when our assumptions about the selection function are satisfied, $f(x, \xi)$ is approximately multi-variate normal in x_1, \dots, x_n at each ξ and that the co-variance matrix, C_{ij} , is the same at each ξ and equal to \hat{C}_{ij} . The problem is, then, reduced to finding $\bar{z}(\xi)$, the distribution of mean values of the character, as a function of $z_0(\xi)$, the spatial pattern in the optima.

To demonstrate that the approximations leading to the solution are valid, we will show by direct substitution that the error made by using the approximate solution is small. This is a consistency method, similar to that used by Lande (1976) for a single population, and it avoids the difficult mathematical problem of uniqueness of the solution. We will simply assume, for intuitive reasons, that there is a solution of the specified form. That does not rule out the possibility of other solutions, although, in the present system, it is difficult to imagine what form they could take.

There are two features of this model that suggest the type of approximation to be used. First, in a one locus model with weak selection, allele frequencies at equilibrium change only by a small amount over a length scale of the average dispersal distance, l , regardless of the spatial pattern in selection coefficients (Slatkin, 1973; May, Endler & McMurtie, 1975). Thus, we might expect $\bar{z}(\xi)$ and $\bar{x}_i(\xi)$ to have similar properties. Second, if the average allelic effects, $\bar{x}_i(\xi)$, change slowly, then the deviation from multivariate normality due to gene flow each generation might be small.

If we multiply each side of equation (3) by x_i and integrate with respect to x_i , we get the equation:

$$\bar{x}_i(\xi) = \int_{-\infty}^{\infty} \tilde{x}_i(\xi') M(\xi - \xi') d\xi', \quad (7)$$

for $i = 1, \dots, n$, where $\tilde{x}_i(\xi)$ is the i th component of the vector of mean values of $\tilde{f}(x, \xi')$. Similarly, we multiply by $[x_i - \bar{x}_i(\xi)][x_j - \bar{x}_j(\xi)]$ for all pairs of i and j and integrate with respect to x_i and x_j to obtain:

$$C_{ij}(\xi) = \int_{-\infty}^{\infty} M(\xi - \xi') d\xi' \iint [x_i - \bar{x}_i(\xi)][x_j - \bar{x}_j(\xi)] \tilde{f}(x, \xi') dx_i dx_j. \quad (8)$$

So far we have made no approximations but the system of equations obtained in this way is not closed and we cannot evaluate the integrals in equation (8). However, we can approximate the integrals in equation (8)

when each $\bar{x}_i(\xi)$ changes by only a small amount over l , the measure of the area from which parents of any generation are drawn.

If we assume that $f(x, \xi)$ is multi-variate normal with covariance matrix $\hat{\mathbf{C}}_{ij}$, then Lande shows that after selection and mating, $\tilde{f}(x, \xi)$ is still approximately multi-variate normal with co-variance matrix $\hat{\mathbf{C}}_{ij}$ and $\tilde{x}_i(\xi)$, the i th component of the vector of mean values of $\tilde{f}(x, \xi)$ is:

$$\tilde{x}_i(\xi) = \bar{x}_i(\xi) - \alpha_i [\bar{z}(\xi) - z_0(\xi)] \quad (9)$$

(Lande, 1976, equation 15). In equation (9), α_i depends only on $\hat{\mathbf{C}}_{ij}$ and with our assumption of weak selection, $\alpha_i \ll 1$, for all i .

In equation (9) we can evaluate the integrals with respect to x_i and x_j if we replace $\tilde{f}(x, \xi')$ by $f(x, \xi)$. Since the co-variance matrices are the same, the substitution involves only the vector of mean values. We can proceed in two steps. First, if we assume that each of the $\bar{x}_i(\xi)$ vary by only a small amount as functions of ξ over a range of size l , then, from equation (9), $\tilde{x}_i(\xi)$ also varies by only a small amount over that range. Because the contributions to the integral with respect to ξ' are significantly different from zero only over a range of $\xi - \xi'$ of roughly l in size, the error made in replacing $\tilde{x}_i(\xi')$ by $\tilde{x}_i(\xi)$ in equation (9) is of the same order of magnitude as the change in $\bar{x}_i(\xi)$ or $\tilde{x}_i(\xi)$ in $(\xi - l, \xi + l)$. More precisely, if,

$$[\tilde{x}_i(\xi) - \tilde{x}_i(\xi')]^2 < \varepsilon_i (\xi - \xi')^2 / l^2, \quad (10)$$

where $\varepsilon_i \ll 1$, then the error made in the substitution is of the order of magnitude of ε_i . This can be shown by directly expanding $\tilde{f}(x, \xi')$ about ξ . The assumption that $\bar{x}_i(\xi)$ varies only slowly with ξ must be explicitly verified when the solutions are found.

Thus, the first step is the replacement of $\tilde{f}(x, \xi')$ by $\tilde{f}(x, \xi)$. The second step is the replacement of $\tilde{f}(x, \xi)$ by $f(x, \xi)$ which can be justified by using equation (9). The error made by replacing each $\tilde{x}_i(\xi)$ by $\bar{x}_i(\xi)$ is of the same order of magnitude as α_i so the error made by replacing one vector by the other is of the order of magnitude as the sum of the α 's. From Lande (1976),

$$\alpha = 2 \sum_{i=1}^n \alpha_i = \frac{h^2 \sigma_z^2}{\sigma_z^2 + w^2} \quad (11)$$

where h^2 is the heritability and, by assumption, α is small.

With the replacement of $\tilde{f}(x, \xi')$ by $f(x, \xi)$, the right hand side of equation (8) becomes $\hat{\mathbf{C}}_{ij}$. That is, the equilibrium solution for $\mathbf{C}_{ij}(\xi)$ is $\hat{\mathbf{C}}_{ij}$ with an error of the same order of magnitude as in the approximation of the integrals. We must verify that the approximation leading to this result are valid. This can be done after the $x_i(\xi)$ are found explicitly.

If we sum equation (9) over all i and multiply by two, we get:

$$\bar{z}(\xi) = \bar{z}(\xi) - \alpha[\bar{z}(\xi) - z_0(\xi)] \quad (12)$$

where α is given by equation (11). From equations (7) and (12):

$$\bar{z}(\xi) = \int_{-\infty}^{\infty} M(\xi - \xi') \{ \bar{z}(\xi') - \alpha[\bar{z}(\xi') - z_0(\xi')] \} d\xi'. \quad (13)$$

Equation (13) is a linear integral equation of a standard form that can be solved by Fourier transform methods. However, we have already assumed that $\bar{z}(\xi)$ varies slowly and we can use that assumption again to simplify the analysis. Expanding $\bar{z}(\xi')$ as a Taylor series in $(\xi - \xi')$ and evaluating the resulting integrals term by term, we get:

$$\begin{aligned} \bar{z}(\xi) = (1 - \alpha) \left[\bar{z}(\xi) + m \frac{d\bar{z}(\xi)}{d\xi} + \frac{(l^2 + m^2)}{2} \frac{d^2\bar{z}(\xi)}{d\xi^2} + \dots \right] \\ + \alpha \int_{-\infty}^{\infty} z_0(\xi') M(\xi - \xi') d\xi'. \end{aligned} \quad (14)$$

In equation (14) the terms involving the higher derivatives of $\bar{z}(\xi)$ are small because $\bar{z}(\xi)$ is assumed to be slowly varying. If we define ε to be $\sqrt{\alpha}$, then the lowest order terms in ε in equation (14) are:

$$\frac{(l^2 + m^2)}{2} \frac{d^2\bar{z}(\xi)}{d\xi^2} + m \frac{d\bar{z}(\xi)}{d\xi} - \varepsilon^2 \bar{z}(\xi) = -\varepsilon^2 \int_{-\infty}^{\infty} M(\xi - \xi') z_0(\xi') d\xi'. \quad (15)$$

It is at this point that we need the assumption that m be small and assume that it is of order ε or smaller. Otherwise, the terms in equation (15) would not be of the same order of magnitude.

The solution to equation (15) is found directly by taking Fourier transforms to be:

$$\bar{z}(\xi) = \frac{-\varepsilon^2}{2\pi} \int_{-\infty}^{\infty} z_0(\xi') d\xi' \int_{-\infty}^{\infty} \frac{M^*(k) e^{ik(\xi' - \xi)} dk}{(-l^2 k^2/2) + ikm - \varepsilon^2}, \quad (16)$$

where:

$$M^*(k) = \int_{-\infty}^{\infty} M(\xi) e^{ik\xi} d\xi \quad (17)$$

and m^2 is dropped from the k^2 term in the denominator of equation (16) (Carrier, Krook & Pearson, 1966). The second integral can be evaluated approximately because the two poles of the denominator are of order ε . To order ε , $M^*(k)$ is approximately 1 at the poles of the denominator. Thus:

$$\bar{z}(\xi) = \frac{\varepsilon^2}{\sqrt{m^2 + 2l^2\varepsilon^2}} \left\{ \int_{-\infty}^{\xi} z_0(\xi') e^{k_1(\xi' - \xi)} d\xi' + \int_{\xi}^{\infty} z_0(\xi') e^{-k_2(\xi' - \xi)} d\xi' \right\}, \quad (18)$$

where:

$$k_1 = \frac{1}{l^2} [-m + \sqrt{m^2 + 2l^2\varepsilon^2}] \quad (19)$$

and

$$k_2 = \frac{1}{l^2} [m + \sqrt{m^2 + 2l^2\varepsilon^2}]. \quad (20)$$

Equation (18) is the general solution for the equilibrium spatial distribution of mean values of the character for a population that satisfies our initial assumptions. Before discussing special cases, we must verify that the derivatives of $\bar{z}(\xi)$ and the $x_i(\xi)$ are small. First, considering $\bar{z}(\xi)$, it is easiest to obtain the magnitude of the derivatives directly from equation (16) rather than equation (19) to find,

$$\frac{d^j \bar{z}(\xi)}{d\xi^j} = -\frac{\varepsilon^2}{2\pi} \int_{-\infty}^{\infty} z_0(\xi') d\xi' \int_{-\infty}^{\infty} \frac{(-ik)^j M^*(k) e^{ik(\xi' - \xi)}}{(-l^2 k^2/2) + ikm - \varepsilon^2} dk. \quad (21)$$

Now evaluating the second integral in equation (21) to order ε ,

$$\frac{d^j \bar{z}(\xi)}{d\xi^j} = \frac{\varepsilon^2}{\sqrt{m^2 + 2l^2\varepsilon^2}} \left\{ \int_{-\infty}^{\xi} z_0(\xi') (-k_2)^j e^{k_1(\xi' - \xi)} d\xi' + \int_{\xi}^{\infty} z_0(\xi') k_1^j e^{-k_2(\xi' - \xi)} d\xi' \right\}. \quad (22)$$

If we assume arbitrarily that $m > 0$, then $k_2 > k_1$ and we can bound the right hand side of equation (22) by $k_2^j z_m$ where z_m is the maximum absolute value of $z_0(\xi)$. From equation (20), k_2 is of order ε so the j th derivative is of order ε^j , as is required. However, the assumption we used to derive the results is slightly stronger and requires that the error made in using only the first term in the Taylor series expansion of $\bar{z}(\xi')$ about ξ is of order ε for ξ' within roughly a distance l of ξ , over which range $M(\xi' - \xi)$ is significantly different from zero. For that to be the case, we need to assume in addition that $z_0(\xi)$ does not vary by too much. If the variations in $z_0(\xi)$ are small, then, the j th derivatives are of the correct order of magnitude and the error made in using only the first term is small enough that the approximation scheme is consistent. Approximately, the maximum range of $z_0(\xi)$ is much less than w , the strength of selection. If that is the bound on the range of $z_0(\xi)$, then the error made in computing the changes due to selection [equations (9) and (12)] when the first term in the Taylor series is used is still of order ε .

As in Lande's model of a panmictic population, the \bar{x}_i 's are almost completely indeterminate. The only condition they must satisfy is that twice their

sum be $\bar{z}(\xi)$. Each $x_i(\xi)$ satisfies a differential equation of the same form as equation (15) with α_i replacing ε^2 . Therefore the magnitude of the j th derivative of $x_j(\xi)$ is of order $(\alpha_i)^{j/2}$, and, even though the values of the x_i are indeterminate, their derivatives must be small, as required to make the approximation procedure work.

The above analysis verifies in a complicated way something basically simple. If the mean value of the character varies by only a small amount over the average dispersal distance, l , then the error made in assuming that the sum of multi-variate normal distributions with different mean values but the same co-variance matrix is multi-variate normal is small. This follows from the fact that the co-variance matrix after the averaging is increased by the variance and co-variance of the means and that those contributions must be small because of the length scale of variation in the means. The reason for limitation of variation of $z_0(\xi)$ is to ensure that the range of values of the $\bar{x}_i(\xi)$ that are averaged over each generation is small enough that \hat{C}_{ij} is not altered significantly. It is important to note that, in applying this result, the restriction on $z_0(\xi)$ is unnecessary. The function $\bar{z}(\xi)$ can be found from equation (18) and magnitude of the derivatives explicitly computed. In that way the validity of the approximation method can be tested and the accuracy of the solution established. This point will be illustrated in the examples.

From the form of equation (18) we can see that $\bar{z}(\xi)$ is an average of $\bar{z}_0(\xi)$ weighted by an exponential that decays over a length scale large compared to the average dispersal distance. We can define,

$$l_c = l/\varepsilon = l/\sqrt{\alpha}, \quad (23)$$

as the length scale associated with the decay of the exponential. The basic feature of this averaging is that fluctuations in $z_0(\xi)$ that occur over a length scale much less than l_c will not appear in $\bar{z}(\xi)$ while fluctuations over the same or longer length scale will. Thus l_c plays the same role in this model as the "characteristic length" defined for the one locus model (Slatkin, 1973). In this model, as in the one locus model, l_c is an estimate of the minimum length scale of variations to which a population can respond, and an estimate of the minimum distance over which the population can vary significantly.

3. Examples

To illustrate the importance of the characteristic length in determining spatial patterns, we consider a few examples. Initially, we assume $m = 0$ and $z_0(\xi) = +z_0$ for $\xi > 0$ and $-z_0$ for $\xi < 0$, representing symmetric dispersal

and a step change in environmental conditions. In that case,

$$\begin{aligned}\bar{z}(\xi) &= z_0 \{1 - \exp[-\xi\sqrt{2}/l_c]\} \quad \xi > 0, \\ &= -z_0 \{1 - \exp[+\xi\sqrt{2}/l_c]\} \quad \xi < 0,\end{aligned}\quad (24)$$

and we see that the width of the cline is approximately the characteristic length.

This model of a step change in the optimal value of the character represents an extreme type of environmental change and can be used to demonstrate the practical limitation in applying the present method. The maximum slope in the cline in $\bar{z}(\xi)$ is $z_0\sqrt{2}/l_c$ at $\xi = 0$. An estimate in the maximum variance in mean values over which averages are taken each generation is found by approximating $\bar{z}(\xi)$ in the neighborhood of zero by $z_0\sqrt{2}\xi/l_c$, squaring and integrating with respect to $M(\xi)$ to give $2z_0^2e^2$. This variance has to be small relative to σ_z^2 . That is,

$$2z_0^2e^2 \ll \sigma_z^2, \quad (25)$$

or, using equation (11) and the fact that w^2 is assumed to be large:

$$h^2 z_0^2 \ll w^2. \quad (26)$$

Thus the approximate solution can still be useful when z_0 is not too much less than w . The same condition is found by considering each of the x_i .

A closely related example is one in which the change in the optimal value is gradual. If $z_0(\xi) = -z_0$ for $\xi < -1/\beta$, $\beta\xi$ for $-z_0/\beta < \xi < z_0/\beta$ and $+z_0$ for $\xi > 1/\beta$ for any positive β , then:

$$\begin{aligned}\bar{z}(\xi) &= z_0 \left\{ 1 - \frac{\beta l_c}{\sqrt{2}} \sinh \left(\frac{\sqrt{2}}{\beta l_c} \right) \exp \left(\frac{\sqrt{2}\xi}{\beta l_c} \right) \right\} \quad \xi < -\frac{1}{\beta}, \\ \bar{z}(\xi) &= z_0 \left\{ \beta\xi - \frac{\beta l_c}{\sqrt{2}} \sinh \left(\frac{\sqrt{2}\xi}{\beta l_c} \right) \exp \left(-\frac{\sqrt{2}}{\beta l_c} \right) \right\} \quad -\frac{1}{\beta} < \xi < \frac{1}{\beta}, \\ \bar{z}(\xi) &= z_0 \left\{ 1 - \frac{\beta l_c}{\sqrt{2}} \sinh \left(\frac{\sqrt{2}}{\beta l_c} \right) \exp \left(-\frac{\sqrt{2}\xi}{\beta l_c} \right) \right\} \quad \xi > \frac{1}{\beta}.\end{aligned}\quad (27)$$

If $\beta \ll 1/l_c$, i.e. the region of the transition is much smaller than the characteristic length, then equations (27) and (24) are equal to $O(\beta l_c)$. If $\beta \gg 1/l_c$, i.e. the region of the transition is large compared to the characteristic length, then equation (27) is approximately $\beta\xi$ for small ξ to $O(e^{-1/\beta l_c})$. In this example, when $\beta \gg 1$, there is no upper bound on z_0 because the derivatives of $\bar{z}(\xi)$ are always small. The characteristic length is an estimate of the minimum size of the region in which there is a cline in the mean value of the character but if the environmental change is more gradual, then the width of the cline can be much larger. This result is analogous to

that for a similar model of a cline in allele frequencies at one locus that is analyzed by Slatkin (1973) and May, Endler & McMurtie (1975).

Because of the simple form of the integral in equation (18) it is possible to analyze a large variety of spatial patterns in selection. It is also possible to consider $z_0(\xi)$ as a stochastic function of ξ and determine the expected spatial autocorrelation of the mean values of the character at different locations. The procedure would be similar to that used by Roughgarden (1974) for spatial patterns in population densities. Although we will not carry through that analysis here, from equation (18) we can see that interaction of dispersal and selection acts as a low-pass filter for the spatial patterns in the selection with the filter width equal to roughly the characteristic length, l_c .

We can also consider the problem in which $M(\xi)$ is not a symmetric function of ξ indicating that there is some preferred direction for the dispersal. This problem is analyzed for the one locus model by May, Endler & McMurtie (1975). We consider only the step change in environmental conditions and find by evaluating equation (18):

$$\begin{aligned}\bar{z}(\xi) &= -z_0 \left[1 - \frac{2k_1}{k_1 + k_2} \exp(+k_2\xi) \right] \quad \xi < 0, \\ &= z_0 \left[1 - \frac{2k_2}{k_1 + k_2} \exp(-k_1\xi) \right] \quad \xi > 0,\end{aligned}\quad (28)$$

where k_1 and k_2 are given by equations (19) and (20). Equation (28) reduces to (24) when $m = 0$ and is continuous at $\xi = 0$ for all m . As a measure of the effect of the asymmetry in dispersal, we can find the value of ξ for which $\bar{z}(\xi) = 0$. Assuming $m > 0$ and defining that value of ξ to be ξ_0 , we find from equations (28) that:

$$\xi_0 = -\frac{l}{k_1} \ln \left[\frac{k_1 + k_2}{2k_2} \right] \quad (29)$$

which is positive. Therefore, the center of the cline can be shifted by a distance of the same order of magnitude as the characteristic length even though the first moment of $M(\xi)$ is of order ϵ . This same conclusion is reached by May, Endler & McMurtie (1975) for the one locus model.

In considering stronger optimizing selection at each location, it is no longer possible to use the same approximation methods and in general it would be necessary to carry out a complete computer analysis of the basic integral equation in order to make detailed predictions about the characteristics of the spatial patterns. However, from the above results we can speculate that stronger selection could produce steeper clines in the mean values of the character, possibly varying over the same length scale as the average dispersal distance. If that is the case, then there would be an increase in the variance

of the character at each location due to the mixing in each generation of individuals from locations that have significantly different mean values. One consequence of the increase in variance is that optimizing selection would be more effective. That in turn would tend to make any clines somewhat steeper than would be expected if the equilibrium variance in the absence of gene flow were used.

It is also possible to analyze this model when there is an infinite linear cline in the optimum. Such a model can provide no information about the response of $\bar{z}(\xi)$ to the selection since $\bar{z}(\xi)$ is determined by the translational symmetry inherent in the model, but the effect of gene flow on the total variance can be found for arbitrary slopes of $\bar{z}(\xi)$. A special case of this model, with the mutation rates set to zero, has been solved by Felsenstein (1977).

Let $z_0(\xi) = \beta\xi$ for all ξ . The only possible solution for $\bar{z}(\xi)$ is also $\beta\xi$. It is also clear that C_{ij} must be independent of ξ , but, in this case, there is no reason to assume it is \hat{C}_{ij} , the equilibrium value in the absence of gene flow. If $f(x, \xi)$ is multi-variate normal with co-variance matrix C_{ij} , then after selection and mating, $\tilde{f}(x, \xi)$ is also multi-variate normal with \tilde{C}_{ij} determined by:

$$\tilde{C}_{ij} = C_{ij} - \frac{\mathbf{R}_i \mathbf{R}_j}{w^2 + \sigma_z^2} - r_{ij} C_{ij} + u_i \delta_{ij}, \quad (30)$$

where:

$$\mathbf{R}_i = \sum_{j=1}^n C_{ij}, \quad (31)$$

r_{ij} is the recombination fraction between locus i and locus j , and u_i is the net mutational effect at the i th locus (including both mutation rates and the variance in effects) (Lande, 1975, equation 19).

If we assume $M(\xi)$ is normal with mean 0 and variance l^2 , then $f(x, \xi)$ is still multi-variate normal after the migration stage. Each of the $\bar{x}_i(\xi)$ must be linear in ξ even though their values are not determined, so the convenient property of normal functions simplifies the analysis of this special model and preserves the multi-variate normal form of f after dispersal. By direct calculation,

$$C_{ij} = \tilde{C}_{ij} + \beta^2 l^2, \quad (32)$$

and the equilibrium values of C_{ij} can be found by solving equations (30) and (32). The quantity of interest is the total variance, σ_z^2 , which is:

$$\sigma_z^2 = \sigma_e^2 + 2\gamma\sqrt{w^2 + \sigma_e^2 + \gamma^2} + 2\gamma^2, \quad (33)$$

where:

$$\gamma = \sum_{i=1}^n \sqrt{u_i + \beta^2 l^2} \quad (34)$$

and σ_e^2 is the environmental variance. Equation (33) is simply Lande's solution with each of the mutational effects augmented by $\beta^2 l^2$. From equation (33), the slope of the gradient in $z_0(\xi)$ may be sufficiently large that the mutational effects can be ignored.

The linkage disequilibrium between pairs of loci, measured by C_{ij} for $i \neq j$ is:

$$C_{ij} = \frac{\beta^2 l^2 - \sqrt{(\beta^2 l^2 + u_i)(\beta^2 l^2 + u_j)}}{r_{ij}} \quad (35)$$

so, as Felsenstein (1977) points out, gene flow tends to increase the C_{ij} , offsetting, to some extent, the tendency of the selection to reduce them. Note that in equation (35), $C_{ij} \leq 0$. If $u_i = 0$ for all i , then $C_{ij} = 0$ $i \neq j$ and the above solution reduces to Felsenstein's.

There is another model of subdivided populations in which Lande's model can be simply analyzed. If a population randomly mates but then disperses into different areas or "niches" which have different optimal values of the character and possibly different strengths of selection, then the effect of the subdivision is the modification of the selection function to take the different selection regions into account. There is no geographic structure of the population imposed by restricted dispersal abilities, and no habitat selection, so individuals are assumed to enter different niches independently of their phenotype. Density regulation occurs in the entire population, not in each niche, so this model is not analogous to that of Levene (1953).

Assume the strength of selection in each niche is the same and equal to w_n^2 . If the optimal value of the character in each niche is normally distributed with mean zero and variance σ_0^2 , then the average selection function for an individual with phenotype z is:

$$W(z) = \exp [-z^2/2(w_n^2 + \sigma_0^2)] \quad (36)$$

and the results of Lande's model can be used directly. As is intuitively clear from the specification of the model, there are two components to the strength of selection, the within-niche selection intensity and the variance in the optima.

The effect of spatial subdivision in this model is the increase in phenotypic variance. There is no restriction to weak selection and the extent of the increase in the variance depends on the relative values of the other parameters. From equations (33) and (34) with $\beta^2 l^2 = 0$, if $w_n^2 + \sigma_0^2$ is much smaller than $\sigma_e^2 + \gamma^2$, then spatial subdivision has little effect on the variance, but if $w_n^2 + \sigma_0^2$ is large, then the σ_z^2 increases roughly with σ_0 . It is not possible to relate this directly to the increased heterozygosity in the population due to spatial subdivision because this model of a phenotypic character in an

infinite population assumes essentially that the heterozygosity at each locus is one. However, if we assume that for a large finite population, the predictions are still valid and that heterozygosity increases with increasing phenotypic variance, then spatial subdivision should lead to an increased level of heterozygosity.

4. Discussion

There are two major effects of gene flow on a quantitative character, the increase in variance due to the mixing of distributions with different means and the change in the mean value due to accumulated differences in mean values. In general, these two effects interact and the analysis of even a simple model can become difficult. However, there are some model problems that are of direct biological relevance and that can be simplified because the equations for the mean and the variance can be decoupled. In such cases it is possible to find solutions that are of interest both for their application in the particular model and their implications for more general models that are too difficult to analyze in any detail.

In the first example of a cline or sequence of clines maintained by weak selection, the gradient in the mean value of the character is sufficiently small that the increase in the variance due to gene flow can be ignored. The variance at equilibrium is approximately the variance that would be found in the absence of gene flow and the spatial pattern in the mean can be found for a large class of spatial patterns in selection. The spatial pattern in the mean can be best understood in terms of the "characteristic length" associated with the average dispersal distance and the intensity of selection. The mean value of the character cannot respond to spatial changes in the optimum that occur over a length scale much less than the characteristic length. The results are analogous to those for a model of selection in clines at one and two loci (Slatkin, 1973, 1975).

In the second two examples of an infinite, linear cline and the multiple niche model, the mean value of the character is determined by the symmetry of the selection, and the variance is found by a method that is essentially an analysis of variance within and between locations. In the model of an infinite cline, the increase in variance is due to the mixing of individuals from populations with different mean values in each generation. For there to be a significant increase in variance, the variance in the means of the populations that are mixing must be comparable to the expected variance within each population in the absence of gene flow. In the multiple-niche model, the increase in variance is due to a weakening of the selection because of the differences in the optima in the different niches. For there to be a significant

increase in variance, the variance in the optima must be comparable to the strength of selection in each niche.

An important problem in population genetics theory is the understanding of the maintenance of genetic polymorphism in natural populations. The above results have some bearing on the possible role of gene flow in the maintenance of genetic variability, and the implications of these results are somewhat different from those of one and two locus models. We cannot compute the expected heterozygosity from the genetic models of Kimura (1965) and Lande (1976) because they are based on the assumption of an infinite number of alleles at each locus and effectively assume a heterozygosity of one at each locus. However, in a finite population there should be a direct relationship between the variance of the character and the heterozygosity at the loci that determine the character in the simple additive manner considered. This is demonstrated by Latter (1970) for a single locus, but it seems to be difficult to take the linkage effects that Lande (1976) has shown to be important into account in the multiple locus problem.

If we assume that an increase in variance of an additive character indicates an increase in the heterozygosity at the underlying loci, then the above result indicates that an increase in heterozygosity at those loci due to gene flow is possible only when there is mixing of populations with different mean values in each generation. When there is such mixing, gene flow can have a very large effect on variance. However, when there is only a small amount of mixing each generation, there is almost no change in the variance. Thus there is no accumulation of small effects that can lead to a significant increase in heterozygosity and, in this way, the results differ from those of one and two locus models. If we consider a one locus cline due to a step change in environmental conditions, the region in which there is a significant increase in the heterozygosity is large compared to the average dispersal distance (Slatkin, 1973, 1975). The heterozygosity in these models is completely determined by the allele frequency or frequencies that respond to the spatial pattern in selection. Since the cline in those frequencies is, in general, over a much longer length scale than the dispersal distance, there must be a significant increase in heterozygosity in the same area. For polygenic characters of the kind discussed here, the mean and variance are not necessarily coupled. For this simple cline model, the mean of the character responds to selection in the same way as the allele frequencies do in one and two locus models. However, the phenotypic variance and, thus, the heterozygosity do not have to respond because, for weak selection, they are approximately independent of the mean.

We can contrast the effects of spatial and temporal variation on the heterozygosity of loci that determine a quantitative character. Fluctuations

that occur within a generation must be averaged over with the effect that the selection for each generation will be somewhat weaker. This would produce an increase in variance in exactly the same way as in the multiple-niche model considered above. Fluctuations in the optimum from one generation to the next have no effect on the phenotypic variance of an additively based character. As Lande (1976) has shown, the variance approaches its equilibrium value independently of changes in the mean. There may be selection in favor of modifiers of the total variance as a result of such fluctuations and as analyzed in Slatkin & Lande (1976), but there is no direct effect on the variance. This is also a consequence of the decoupling of the mean and the variance for a normally distributed polygenic character. Thus, gene flow and spatially varying selection is potentially much stronger than temporal varying selection in maintaining phenotypic and genetic polymorphism.

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