

THE ISLAND MODEL WITH STOCHASTIC MIGRATION*

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ABSTRACT

The island model with stochastically variable migration rate and immigrant gene frequency is investigated. It is supposed that the migration rate and the immigrant gene frequency are independent of each other in each generation, and each of them is independently and identically distributed in every generation. The treatment is confined to a single diallelic locus without mutation. If the diploid population is infinite, selection is absent and the immigrant gene frequency is fixed, then the gene frequency on the island converges to the immigrant frequency, and the logarithm of the absolute value of its deviation from it is asymptotically normally distributed. Assuming only neutrality, the evolution of the exact mean and variance of the gene frequency are derived for an island with finite population. Selection is included in the diffusion approximation: if all evolutionary forces have comparable roles, the gene frequency will be normally distributed at all times. All results in the paper are completely explicit.

WRIGHT (1948) was the first to investigate the consequences of fluctuations in systematic evolutionary forces. KIMURA (1954), JENSEN and POLLAK (1969), OHTA (1972), OHTA and KIMURA (1972), and JENSEN (1973) subsequently explored the effects of random variation in selection intensities. GILLESPIE (1978 and references therein), HARTL and COOK (fully referenced in HARTL 1977), KARLIN and LEVIKSON (1974), KARLIN and LIBERMAN (1974, 1975), LEVIKSON and KARLIN (1975) and AVERY (1977) have provided a detailed description of the dynamics of finite and infinite populations in random environments.

If a population receives migrants at all, the rate of migration is extremely unlikely to remain constant for many generations. If the immigrants come from a panmictic population, but their number is small, the migrant gene frequency will fluctuate due to random sampling. It may also vary deterministically or stochastically if the gene frequency on the "continent" supplying the immigrants is not constant or if the immigrants originate from different regions of a geographically diverse continent. Therefore, random fluctuations in the proportion and gene frequency of migrants are of considerable evolutionary interest.

WRIGHT (1948) studied the island model (WRIGHT 1931) with randomly varying migration rate and migrant gene frequency. KIMURA (CROW and KIMURA 1956) presented a formula for the distribution of the gene frequency in an infinite population in the diffusion approximation, assuming the absence of

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selection, fixed migrant gene frequency, and random migration rate. Recently, SVED and LATTER (1977) derived a recurrence relation for the variance in gene frequency for the same process in a finite population.

For analyses of a finite number of islands with deterministic migration, consult MARUYAMA (1970) and LATTER (1973).

In Section I, we shall reconsider the problem examined by KIMURA (CROW and KIMURA 1956), and show that his probability density should be divided by 2. Then we shall discuss the more difficult case including selection. We shall find the condition for a protected polymorphism for deterministically varying migration rate and monomorphic migrants. The exact mean and variance of the frequency of a neutral allele in a finite population receiving migrants at a random rate with random gene frequency will be calculated in Section II. In the following section, we shall deduce the diffusion approximation for the distribution of the gene frequency at any time with all evolutionary forces present.

Let the alleles A_1 and A_2 segregate at the locus under consideration in a diploid panmictic population of actual size N and variance effective number N_e . A_1 and A_2 may refer, of course, to sets of selectively equivalent alleles. We denote the frequency of A_1 in generation t ($t = 0, 1, 2, \dots$) by the random variable X_t . Every generation a random fraction m_t of the population is removed and replaced by immigrants with the random gene frequency ξ_t . We assume that m_t and ξ_t are stochastically independent for each t , and $\{m_t\}$ and $\{\xi_t\}$ are sequences of independent identically distributed random variables. Although mutation could easily be included in the migration process, for simplicity of description we shall not do so.

I. FLUCTUATING MIGRATION RATE IN AN INFINITE POPULATION

We suppose that the population is infinite, there is no selection and A_1 has the fixed frequency ξ in the immigrants. Then

$$X_{t+1} = (1 - m_t)X_t + m_t\xi, \quad (1)$$

so

$$Z_t = -\ln|X_t - \xi| \quad (2)$$

satisfies

$$Z_{t+1} = Z_t + l_t, \quad (3)$$

where

$$l_t = -\ln(1 - m_t). \quad (4)$$

From (3) we have

$$Z_t = Z_0 + \sum_{\tau=0}^{t-1} l_{\tau}. \quad (5)$$

Denoting the mean and variance of l_t (both assumed to be finite) by

$$\bar{l} = E(l_t) \quad \text{and} \quad \sigma_l^2 = \text{Var}(l_t), \quad (6)$$

we obtain from (5) and (6)

$$E(Z_t) = Z_0 + \bar{l}t \quad \text{and} \quad \text{Var}(Z_t) = \sigma_l^2 t. \quad (7)$$

Thus, both the mean and the variance of Z_t increase linearly. Since $\{l_t\}$ is a sequence of independent identically distributed random variables, the Central Limit Theorem (FELLER 1971, p. 259) informs us that as $t \rightarrow \infty$, the random variable

$$W_t = (Z_t - Z_0 - \bar{l}t) (\sigma_l^2 t)^{-1/2} \quad (8)$$

is normally distributed with mean 0 and variance 1.

From (2) and (8) we infer that the gene frequency converges to that of the immigrants as $t \rightarrow \infty$, a conclusion we may draw for more general migration rates by appealing to the Law of Large Numbers in analyzing (5).

Some care must be exercised in deriving our result from the diffusion approximation. As (3) shows, the sequence $\{Z_t\}$ is monotone increasing. But a sample path of a diffusion process at z at time τ will enter both $(-\infty, z)$ and (z, ∞) with probability 1 during any time interval $\Delta\tau > 0$ starting at time τ , provided the diffusion coefficient is positive at z . To avoid this difficulty, we study $Z_t - E(Z_t)$. Let $\varepsilon \rightarrow 0$ be a small positive parameter. We fix the scaled time $T = \varepsilon t$, and set

$$U_T = \sqrt{\varepsilon} [Z_t - E(Z_t)]. \quad (9)$$

Using (3) and (9), we derive easily

$$U_{T+\varepsilon} = U_T + \sqrt{\varepsilon} k_t, \quad (10)$$

where $k_t = l_t - \bar{l}$. Therefore, as $\varepsilon \rightarrow 0$ the probability density of U_T satisfies the heat equation, and we confirm the assertion following (8).

For weak migration, (4) tells us that $\bar{l} \approx \bar{m} + (1/2)\sigma_m^2$ and $\sigma_l^2 \approx \sigma_m^2$, \bar{m} and σ_m^2 being the mean and variance of m_t . This shows that KIMURA'S (CROW and KIMURA 1956) probability density should be divided by 2.

To include the effect of selection, suppose adults migrate. Then

$$X_{t+1} = (1 - m_t) X_t^* + m_t \xi, \quad (11)$$

where X_t^* represents the frequency of A_1 after selection. The following argument, which applies equally well without selection, shows that a direct diffusion approximation of (11) is unlikely to be correct. For such an approximation, we require $\bar{m} = \varepsilon$ and $E(m_t^2) = \varepsilon v$. Hence, invoking a special case of Schwarz's inequality (FELLER 1971, p. 155), we have

$$E(m_t^2) \geq [E(m_t)]^2 / E(m_t) = \varepsilon v^2,$$

contradicting the sufficient condition

$$\lim_{\varepsilon \rightarrow 0} \varepsilon^{-1} E(m_t^2) = 0$$

for a diffusion. The reason for the failure is the non-negativity of the random variable m_t .

In view of the above difficulty, we shall examine the discrete-time equation (11). If $0 < \xi < 1$, *i.e.*, the immigrants carry both alleles, it is clear that the population remains polymorphic. Therefore, we assume that all immigrants are A_2A_2 ($\xi = 0$), and seek a sufficient condition for maintaining A_1 in the population. To avoid technicalities, we posit here that m_t varies in an arbitrary, but deterministic, manner.

If w_t is the fitness of A_1A_2 relative to that of A_2A_2 , and $u_t = w_t(1 - m_t)$, as $X_t \rightarrow 0$ (11) yields $X_{t+1} \sim u_t X_t$, whence

$$X_t \sim X_0 \prod_{\tau=0}^{t-1} u_\tau$$

We infer that A_1 is protected from loss if the geometric mean

$$u_t^* = \left(\prod_{\tau=0}^{t-1} u_\tau \right)^{1/t} > 1 \quad (12)$$

for sufficiently large t . We can rewrite (12) as

$$\ln u_t^* = \frac{1}{t} \sum_{\tau=0}^{t-1} \ln u_\tau \equiv E(\ln u_t) > 0 \quad (13)$$

for sufficiently large t .

The protection conditions for deterministically (HALDANE and JAYAKAR 1963) and randomly (KARLIN and LIBERMAN 1975) varying fitnesses without migration suggest that the last form of (13) should be valid with probability one, if the fitnesses and the migration rate are each sequences of independent identically distributed random variables.

Expressing (13) in the form

$$E(\ln w_t) > -E[\ln(1 - m_t)] \quad (14)$$

leads to some interesting biological results, all of which are based on the fact that, by Jensen's inequality (FELLER 1971, p. 153) and the concavity of $\ln x$, for any random variable $Y \geq 0$,

$$E(\ln Y) \leq \ln E(Y), \quad (15)$$

with equality if and only if $\text{Var}(Y) = 0$ [provided the left-hand side of (15) exists].

For a fixed sequence $\{m_t\}$ of migration rates, (14) and (15) establish that variation in the fitness of the heterozygote relative to that of A_2A_2 decreases the

likelihood of polymorphism compared to constant selection with the mean relative fitness. Setting $v_t = 1/w_t$, (14) becomes

$$E(\ln v_t) < E[\ln (1 - m_t)] . \quad (16)$$

Thus, variation of the fitness of A_2A_2 relative to that of A_1A_2 decreases the stringency of the condition (16) for protecting A_1 . The first situation is exemplified by variable heterozygote and constant homozygote fitnesses; the second by the reverse. It is obvious from (14) that even without migration heterozygote fitness variation makes polymorphism less likely and homozygote variability more so. Consult NAGYLAKEI (1977, pp. 68–71) for more detailed discussion.

Since

$$-E[\ln (1 - m_t)] \geq -\ln (1 - \bar{m}) \geq \bar{m} ,$$

(14) restricts the fitnesses more severely than constant migration at rate \bar{m} , and still more than no migration. Therefore, variation in the migration rate decreases the chance for a protected polymorphism.

With $w_t = 1 + s_t$, for weak selection and migration, $|s_t| \ll 1$ and $m_t \ll 1$, we obtain from (14)

$$\bar{s} - (1/2) E(s_t^2) > \bar{m} + (1/2) E(m_t^2),$$

which should be compared to the lowest order protection criterion with constant selection and migration, $s > m$ (NAGYLAKEI 1977, p. 126).

II. THE MEAN AND VARIANCE IN A FINITE POPULATION

In this section, we shall calculate the exact mean and variance of the gene frequency in a finite population. We exclude selection, but allow both the migration rate and the gene frequency in the immigrants to be random variables, as described in the last paragraph of the introduction.

Let N , X_t , and $i = 2NX_t$ be the number of adults, the frequency of A_1 , and the number of A_1 alleles at the beginning of generation t . These adults produce $N^* \gg N$ zygotes without fertility differences. Next, migration alters the allelic frequency to X_t^* . Finally, the population is reduced to N adults with gene frequency X_{t+1} , the number of A_1 alleles being $j = 2NX_{t+1}$. Random drift with variance effective population number N_e occurs at this stage.

Clearly,

$$X_t^* = (1 - m_t) X_t + m_t \xi_t . \quad (17)$$

We denote by $T_{ij}(m, \xi)$ the transition probabilities for the usual Wright-Fisher Markov chain for random drift with migration rate m and immigrant frequency ξ . If $P(m, \xi)$ represents the joint probability density of m_t and ξ_t , the transition probabilities for the Markov chain defined above read

$$R_{ij} = \int T_{ij}(m, \xi) P(m, \xi) dm d\xi = E [T_{ij}(m_t, \xi_t)] . \quad (18)$$

We shall require only the conditional means and variances

$$E(X_{t+1} | X_t, m_t, \xi_t) = X_t^* , \quad (19a)$$

$$\text{Var}(X_{t+1} | X_t, m_t, \xi_t) = X_t^*(1 - X_t^*)/(2N_e) , \quad (19b)$$

where X_t^* is given by (17).

For the mean gene frequency, (17) and (19a) give

$$\begin{aligned} \bar{X}_{t+1} &= E[E(X_{t+1} | X_t, m_t, \xi_t)] \\ &= E(X_t^*) \\ &= (1 - \bar{m}) \bar{X}_t + \bar{m} \bar{\xi} , \end{aligned} \quad (20)$$

in which $\bar{\xi} = E(\xi_t)$. In the last step we relied on the postulated stochastic independence of m_t , ξ_t , and X_t . The elementary recursion relation (20) has the solution

$$\bar{X}_t = \bar{\xi} + (x_0 - \bar{\xi})(1 - \bar{m})^t , \quad (21)$$

where $\bar{X}_0 = x_0$. As expected for a linear problem, (21) is the same as the deterministic solution with parameters \bar{m} and $\bar{\xi}$.

To compute the variance $V_t = \text{Var}(X_t)$, we employ successively (19b), (17), and the independence of m_t , ξ_t , and X_t :

$$\begin{aligned} E(X_{t+1}^2) &= E[E(X_{t+1}^2 | X_t, m_t, \xi_t)] \\ &= E\{[1 - (2N_e)^{-1}](X_t^*)^2 + (2N_e)^{-1}X_t^*\} \\ &= (2N_e)^{-1}[(1 - \bar{m})\bar{X}_t + \bar{m}\bar{\xi}] + [1 - (2N_e)^{-1}] \\ &\quad \{[(1 - \bar{m})^2 + \sigma_m^2](V_t + \bar{X}_t^2) + 2\bar{\xi}[\bar{m}(1 - \bar{m}) \\ &\quad - \sigma_m^2]\bar{X}_t + (\bar{m}^2 + \sigma_m^2)(\bar{\xi}^2 + \sigma_\xi^2)\} , \end{aligned} \quad (22)$$

in which $\sigma_\xi^2 = \text{Var}(\xi_t)$. From (20) and (22) we deduce that

$$\begin{aligned} V_{t+1} &= E(X_{t+1}^2) - \bar{X}_{t+1}^2 \\ &= \lambda V_t + [1 - (2N_e)^{-1}][\sigma_m^2(\bar{X}_t - \bar{\xi})^2 + \sigma_\xi^2(\bar{m}^2 + \sigma_m^2)] \\ &\quad + (2N_e)^{-1}[(1 - \bar{m})\bar{X}_t + \bar{m}\bar{\xi}][1 - (1 - \bar{m})\bar{X}_t - \bar{m}\bar{\xi}] , \end{aligned} \quad (23)$$

with

$$\lambda = [(1 - \bar{m})^2 + \sigma_m^2][1 - (2N_e)^{-1}] . \quad (24)$$

Substituting (21) into (24) produces the difference equation

$$\begin{aligned} V_{t+1} = & \lambda V_t + [1 - (2N_e)^{-1}] \sigma_\xi^2 (\bar{m}^2 + \sigma_m^2) + (2N_e)^{-1} \bar{\xi} (1 - \bar{\xi}) \\ & + (2N_e)^{-1} (1 - 2\bar{\xi}) (x_0 - \bar{\xi}) (1 - \bar{m})^{t+1} \\ & + \{ \sigma_m^2 - (2N_e)^{-1} [(1 - \bar{m})^2 + \sigma_m^2] \} (x_0 - \bar{\xi})^2 (1 - \bar{m})^{2t} . \end{aligned} \quad (25)$$

Assuming that the initial gene frequency is x_0 , we have $V_0 = 0$. The solution of (25) is easily derived by combining a particular solution with the general solution of the corresponding homogeneous difference equation, as explained in a general setting in NAGYLAKI (1977, p. 99). Defining

$$\hat{V} = \frac{\bar{\xi}(1 - \bar{\xi}) + \sigma_\xi^2(2N_e - 1)(\bar{m}^2 + \sigma_m^2)}{2N_e - (2N_e - 1)[(1 - \bar{m})^2 + \sigma_m^2]} , \quad (26a)$$

$$b = \frac{(1 - 2\bar{\xi})(1 - \bar{m})(x_0 - \bar{\xi})}{2N_e(1 - \bar{m}) - (2N_e - 1)[(1 - \bar{m})^2 + \sigma_m^2]} , \quad (26b)$$

$$c = -(x_0 - \bar{\xi})^2 , \quad (26c)$$

we find

$$V_t = \hat{V} - (\hat{V} + b + c)\lambda^t + b(1 - \bar{m})^t + c(1 - \bar{m})^{2t} . \quad (27)$$

If the immigrants originate from a large number of islands similar to the one under consideration, we expect $x_0 = \bar{\xi}$, whence $\bar{X}_t = \bar{\xi}$ and $V_t = \hat{V}(1 - \lambda^t)$. SVED and LATTER (1977) have derived a recurrence relation for the variance with the additional assumption that ξ_t is fixed. Their result differs from the special case of (25) with $x_0 = \bar{\xi}$ and $\sigma_\xi^2 = 0$ by small terms because in their model, in contradistinction to ours, random drift precedes migration.

Since m_t has mean \bar{m} and $0 \leq m_t \leq 1$, therefore $\sigma_m^2 \leq \bar{m}(1 - \bar{m})$, from which we easily conclude that the equilibrium variance \hat{V} , given by (26a), is positive. As anticipated, (26a) shows that variation in the immigrant gene frequency raises the equilibrium variance. For an infinite population, (26a) reduces to

$$\hat{V} = \frac{\sigma_\xi^2(\bar{m}^2 + \sigma_m^2)}{1 - (1 - \bar{m})^2 - \sigma_m^2} , \quad N_e = \infty . \quad (28)$$

A straightforward application of the inequalities $\sigma_m^2 \leq \bar{m}(1 - \bar{m})$ and $\sigma_\xi^2 \leq \bar{\xi}(1 - \bar{\xi})$ proves that (28) is less than (26a). Thus, random drift contributes to the variance, as it must. Note that with $N_e = \infty$ and $\sigma_\xi^2 = 0$, (28) tells us that $\hat{V} = 0$, *i.e.*, the gene frequency converges to $\bar{\xi}$ ($= \bar{\xi}$). A much less obvious consequence of the upper bounds on σ_m^2 and σ_ξ^2 is that variation in the migration rate increases the equilibrium variance in the gene frequency.

Since (24) implies that

$$\lambda \leq (1 - \bar{m})[1 - (2N_e)^{-1}] , \quad (29)$$

(27) informs us that the ultimate rate of convergence of the variance is $(1 - \bar{m})^t$, the same as that of the mean.

If migration is weak, $\bar{m} \ll 1$, and the effective population number is large, $N_e \gg 1$, our results simplify considerably to

$$\bar{X}_t \approx \bar{\xi} + (x_0 - \bar{\xi})e^{-\bar{m}t} , \quad (30a)$$

$$\hat{V} \approx \frac{\bar{\xi}(1 - \bar{\xi}) + 2N_e\sigma_{\xi}^2(\bar{m}^2 + \sigma_m^2)}{1 + 2N_e(2\bar{m} - \sigma_m^2)} , \quad (30b)$$

$$b \approx \frac{(1 - 2\bar{\xi})(x_0 - \bar{\xi})}{1 + 2N_e(\bar{m} - \sigma_m^2)} , \quad (30c)$$

$$V_t \approx \hat{V} - (\hat{V} + b + c) \exp \{-[2\bar{m} - \sigma_m^2 + (2N_e)^{-1}]t\} \\ + b \exp(-\bar{m}t) + c \exp(-2\bar{m}t). \quad (30d)$$

We can specialize immediately our solution to mutation and random drift in a finite population. With the substitutions $\sigma_m^2 = \sigma_{\xi}^2 = 0$, $\bar{\xi} = v/(u + v) \equiv \hat{x}$, and $\bar{m} = u + v$, where u and v are the mutation rates from A_1 to A_2 and A_2 to A_1 , respectively, (21), (24), (26), and (27) become

$$\bar{X}_t = \hat{x} + (x_0 - \hat{x})(1 - u - v)^t , \quad (31a)$$

$$\hat{V} = \frac{\hat{x}(1 - \hat{x})}{2N_e - (2N_e - 1)(1 - u - v)^2} , \quad (31b)$$

$$b = \frac{(1 - 2\hat{x})(x_0 - \hat{x})}{1 + (2N_e - 1)(u + v)} , \quad (31c)$$

$$c = -(x_0 - \hat{x})^2 , \quad (31d)$$

$$\lambda = (1 - u - v)^2[1 - (2N_e)^{-1}] , \quad (31e)$$

$$V_t = \hat{V} - (\hat{V} + b + c)\lambda^t + b(1 - u - v)^t + c(1 - u - v)^{2t} . \quad (31f)$$

For weak mutation, $u + v \ll 1$, (31b) is well approximated by WRIGHT's (1931) formula,

$$\hat{V} = \frac{\hat{x}(1 - \hat{x})}{1 + 4N_e(u + v)} .$$

For irreversible mutation from A_1 to A_2 at rate u ($v = 0$), (31) reduces to

$$\bar{X}_t = x_0(1 - u)^t, \quad (32a)$$

$$b = \frac{x_0}{1 + u(2N_e - 1)}, \quad (32b)$$

$$\lambda = (1 - u)^2[1 - (2N_e)^{-1}], \quad (32c)$$

$$V_t = (x_0^2 - b)\lambda^t + b(1 - u)^t - x_0^2(1 - u)^{2t}, \quad (32d)$$

demonstrating that the variance converges to zero as A_1 is lost. Finally, for pure random drift ($u = 0$), (32) yields WRIGHT's (1931) class results, $\bar{X}_t = x_0$ and

$$V_t = x_0(1 - x_0)[1 - (2N_e)^{-1}]^t.$$

III. THE DIFFUSION APPROXIMATION IN A FINITE POPULATION

We shall derive the distribution of the gene frequency in the diffusion approximation with selection, random drift, and migration at a random rate with random gene frequency all present. We modify the life cycle of SECTION II by including selection, and summarize the pertinent information in the formal scheme below.

$$\begin{array}{ccccccc} \text{Adult} & \longrightarrow & \text{Zygote} & \longrightarrow & \text{Adult} & \longrightarrow & \text{Adult} \longrightarrow \text{Adult} \\ & & \text{reproduction} & & \text{selection} & & \text{migration} \quad \text{regulation} \\ N, X_t & & N^*, X_t & & N^{**}, X_t^* & & N^{***}, X_t^{**} \quad N, X_{t+1} \end{array}$$

We assume that N^* , N^{**} , N^{***} all greatly exceed N . If we parametrize the constant fitnesses of A_1A_1 , A_1A_2 , and A_2A_2 by $1 + s$, $1 + hs$, and $1 - s$, so that s ($-1 \leq s \leq 1$) represents the selection intensity and h ($-\infty < h < \infty$) determines the degree of dominance, then the gene frequency after selection reads

$$X_t^* = X_t + sS(X_t) + O(s^2), \quad (33)$$

where

$$S(x) = x(1 - x)(1 + h - 2hx). \quad (34)$$

Migration changes this to

$$\begin{aligned} X_t^{**} &= X_t^* + m_t(\xi_t - X_t^*) \\ &= X_t + sS(X_t) + m_t(\xi_t - X_t) + O(s^2, sm_t). \end{aligned} \quad (35)$$

We still define our Markov chain as in (18), but T_{ij} now includes selection. The conditional mean and variance are

$$E(X_{t+1} | X_t, m_t, \xi_t) = X_t^{**}, \quad (36a)$$

$$\text{Var}(X_{t+1} | X_t, m_t, \xi_t) = X_t^{**}(1 - X_t^{**})/(2N_e), \quad (36b)$$

where X_t^{**} is given by (35).

For a diffusion limit with all evolutionary forces playing a role to apply, the various parameters must be appropriately related to each other and to intrinsic

time scale of the process. These relations may be deduced systematically from the expectation of the change and squared change in gene frequency in a generation as follows. These expectations, $M_0(x)$ and $V_0(x)$, will yield directly the drift and diffusion coefficients, $M(x)$ and $V(x)$.

From (36a) and (35) we obtain

$$\begin{aligned} M_0(x) &\equiv E(X_{t+1} - X_t \mid X_t = x) \\ &= E[E(X_{t+1} - X_t \mid m_t, \xi_t, X_t = x)] \\ &= E(X_t^{**} - X_t \mid X_t = x) \\ &= sS(x) + \bar{m}(\bar{\xi} - x) + O(s^2, s\bar{m}) . \end{aligned} \quad (37a)$$

Using (36), (35), and the fact that $\sigma_m^2 \leq \bar{m}(1 - \bar{m}) \leq \bar{m}$, we find

$$\begin{aligned} V_0(x) &\equiv E[(X_{t+1} - X_t)^2 \mid X_t = x] \\ &= E\{E[(X_{t+1} - X_t^{**})^2 + (X_t^{**} - X_t)^2 \\ &\quad + 2(X_{t+1} - X_t^{**})(X_t^{**} - X_t) \mid m_t, \xi_t, X_t = x]\} \\ &= E[X_t^{**}(1 - X_t^{**})(2N_e)^{-1} + (X_t^{**} - X_t)^2 \mid X_t = x] \\ &= x(1 - x)(2N_e)^{-1} + (\bar{m}^2 + \sigma_m^2)[\sigma_\xi^2 + (\bar{\xi} - x)^2] \\ &\quad + 2s\bar{m}(\bar{\xi} - x)S(x) + O(sN_e^{-1}, \bar{m}N_e^{-1}, s^2, s\bar{m}^2, s\sigma_m^2) . \end{aligned} \quad (37b)$$

In the diffusion limit, we require $M_0(x) \rightarrow 0$ and $V_0(x) \rightarrow 0$. Hence, (37) implies that selection and migration must be weak, $|s| \ll 1$ and $\bar{m} \ll 1$, and the effective population number large, $N_e \gg 1$. We introduce a small positive parameter ε by scaling the time as $\tau = \varepsilon t$. Then diffusion time τ of order 1 corresponds to many generations, leading us to expect predominantly gene frequencies close to $\bar{\xi}$. Therefore, we may reasonably posit the parameter scalings

$$\bar{m} = \varepsilon^\alpha, \quad s = B\varepsilon^\beta, \quad \sigma_m^2 = C\varepsilon^{2\alpha}, \quad N_e = \nu\varepsilon^{-\gamma}, \quad (38a)$$

and employ the diffusion variable

$$Y_\tau = (X_t - \bar{\xi})(D\varepsilon^\delta)^{-1} - \gamma^* . \quad (38b)$$

We shall determine $\alpha, \beta, \gamma, \delta, D$, and γ^* ; then B, C , and ν will be given in terms of s, σ_m^2, N_e , and \bar{m} by (38a). In view of the discussion above, we assume that $\alpha, \beta, \gamma, \delta, \nu$, and D are all (strictly) positive and $C \geq 0$. We suppose also that $\sigma_\xi^2 > 0$ (which implies, of course, $0 < \bar{\xi} < 1$); this essential restriction to variable immigrant gene frequency accounts for the simplicity of our results, as well as their deviation from standard random drift theory.

Since X_t is close to $\bar{\xi}$ with high probability, we expand $S(x)$ in (37) in a Taylor series near $x = \bar{\xi}$. Inserting (38) into (37a) yields

$$M_0(x) = B\varepsilon^\beta S(\bar{\xi}) - D\varepsilon^{\alpha+\delta}(\gamma + \gamma^*) + O(\varepsilon^{2\beta}, \varepsilon^{\alpha+\beta}, \varepsilon^{\beta+\delta}), \quad (39)$$

where

$$\gamma = (x - \bar{\xi})(D\varepsilon^\delta)^{-1} - \gamma^*. \quad (40)$$

The constant drift in (39) will be eliminated as $\varepsilon \rightarrow 0$ if and only if

$$\beta = \alpha + \delta \quad \text{and} \quad \gamma^* = BS(\bar{\xi})/D. \quad (41)$$

In that case (39) becomes

$$M_0(x) = -D\varepsilon^\beta \gamma + o(\varepsilon^\beta). \quad (42)$$

Observe that with the choice $\beta = \alpha + \delta$ the migration and selection terms in (39) are of the same order of magnitude.

Substituting (38) and (41) into (37b) leads to

$$V_0(x) = \varepsilon^\gamma (2\nu)^{-1} \bar{\xi}(1 - \bar{\xi}) + \varepsilon^{2\alpha} \sigma_\xi^2 (1 + C) + O(\varepsilon^{2\beta}, \varepsilon^{2\alpha+\beta}, \varepsilon^{\alpha+\gamma}, \varepsilon^{\beta+\gamma}, \varepsilon^{\gamma+\delta}). \quad (43)$$

Random drift and variation in the migrant frequency will be of the same order of magnitude if and only if

$$\gamma = 2\alpha, \quad (44)$$

which reduces (43) to

$$V_0(x) = \varepsilon^\gamma [(2\nu)^{-1} \bar{\xi}(1 - \bar{\xi}) + \sigma_\xi^2 (1 + C)] + o(\varepsilon^\gamma). \quad (45)$$

With the aid of (42) and (45), we can compute at once the drift and diffusion coefficients, $M(x)$ and $V(x)$. We have from (38b) and (42)

$$\begin{aligned} M(x) &= \lim_{\varepsilon \rightarrow 0} \varepsilon^{-1} E(Y_{\tau+\varepsilon} - Y_\tau | Y_\tau = \gamma) \\ &= \lim_{\varepsilon \rightarrow 0} (D\varepsilon^{1+\delta})^{-1} E(X_{t+1} - X_t | X_t = x) \\ &= -\gamma, \end{aligned} \quad (46)$$

provided

$$\beta = 1 + \delta. \quad (47)$$

Similarly, (38b) and (45) yield

$$\begin{aligned} V(x) &= \lim_{\varepsilon \rightarrow 0} \varepsilon^{-1} E[(Y_{\tau+\varepsilon} - Y_\tau)^2 | Y_\tau = \gamma] \\ &= \lim_{\varepsilon \rightarrow 0} (D^2 \varepsilon^{1+2\delta})^{-1} V_0(x) \\ &= 1, \end{aligned} \quad (48)$$

if and only if

$$\gamma = 1 + 2\delta \quad \text{and} \quad D = [(2\nu)^{-1} \bar{\xi}(1 - \bar{\xi}) + \sigma_\xi^2 (1 + C)]^{1/2}. \quad (49)$$

Equations (41) and (49) determine γ^* and D . Solving (41), (44), (47), and (49) gives $\alpha = 1$, $\beta = 3/2$, $\gamma = 2$, and $\delta = 1/2$. Therefore, (38) takes the form

$$\tau = \bar{m}t, \quad s = B\bar{m}^{3/2}, \quad \sigma_m^2 = C\bar{m}^2, \quad N_e = \nu/\bar{m}^2, \quad (50a)$$

$$Y_\tau = (X_t - \bar{\xi})(D\bar{m}^{1/2})^{-1} - BS(\bar{\xi})D^{-1} \quad (50b)$$

Since $\bar{m} \rightarrow 0$, (50b) shows that the range of the diffusion is $-\infty < \gamma < \infty$. Hence, (46) and (48) give the Ornstein-Uhlenbeck process with transition probability density ($Y_0 \equiv \gamma_0$)

$$\phi(\gamma_0, \gamma, \tau) = [\pi(1 - e^{2\tau})]^{-1/2} \exp \left[-\frac{(\gamma - \gamma_0 e^{-\tau})^2}{1 - e^{-2\tau}} \right] \quad (51)$$

(FELLER 1971, p. 335).

Thus, Y_τ is normally distributed with mean $\gamma_0 e^{-\tau}$ and variance $(1 - e^{-2\tau})/2$. The equilibrium distribution is Gaussian with mean 0 and variance 1/2. Consequently, the gene frequency, X_t , is normally distributed with mean

$$E(X_t) = \bar{\xi} + (x_0 - \bar{\xi})e^{-\bar{m}t} + (s/\bar{m})S(\bar{\xi})(1 - e^{-\bar{m}t}) \quad (52a)$$

and variance

$$\text{Var}(X_t) = (1/2) D^2 \bar{m} (1 - e^{-2\bar{m}t}). \quad (52b)$$

These have equilibrium values

$$E(X_\infty) = \bar{\xi} + (s/\bar{m})S(\bar{\xi}) \quad (53a)$$

and

$$\text{Var}(X_\infty) = D^2 \bar{m}/2. \quad (53b)$$

Note that in this approximation the only effect of selection is to shift the mean by the last term in (52a). Only the selective force at $x = \bar{\xi}$ enters. The effective population size and variation in the migration rate and immigrant gene frequency do not influence the mean gene frequency. Finite effective population size and variation in the migration rate and immigrant gene frequency each increase the equilibrium variance, $D^2 \bar{m}/2$, of the gene frequency, as proved exactly in SECTION II. If $\sigma_m^2 = 0$ or $N_e = \infty$, we set $C = 0$ or $\nu = \infty$, respectively, in (49).

Although we utilized the condition $\sigma_\xi^2 > 0$ in deriving our solution, the limit $\sigma_\xi^2 \rightarrow 0$, affecting only D in (49), is well behaved and quite instructive. Supposing that there is no selection ($s = 0$) and changing to the mutation interpretation above (31), we obtain FELLER's (1951; note two obvious misprints) Gaussian limit for mutation and random drift. This happens because (50a) implies $N_e \bar{m} \rightarrow \infty$, precisely Feller's assumption.

WRIGHT (1948) gave a formula for the equilibrium distribution of the gene frequency on an island with an infinite population, a fixed migration rate and no

dominance. Without selection, his result agrees exactly with the equilibrium limit (53) of ours. In the presence of selection, his distribution is not normal; if the required relations (50) are imposed on it, however, it simplifies in the diffusion limit to a normal distribution with mean and variance given by (53).

Finally, using (49) and (50), it is easy to show that in the absence of selection (52) agrees with the diffusion limit of the discrete solution (30).

SUMMARY

We investigated various cases of the island model with stochastic migration. If the population is infinite, the immigrants have a fixed gene frequency and the alleles are neutral, the gene frequency on the island converges to that of the immigrants. As exhibited in (8), the logarithm of the absolute value of the deviation of the gene frequency from the immigrant gene frequency is normally distributed for long times. If there is selection, but both migration and selection vary deterministically and all immigrants are A_2A_2 , A_1 will be protected from loss if for sufficiently long times the geometric mean of the sequence $\{w_t(1-m_t)\}$ (where w_t denotes the fitness of A_1A_2 relative to that of A_2A_2 and m_t represents the migration rate) exceeds 1. Variation in the migration rate or in the heterozygote fitness decreases the likelihood of maintaining polymorphism; variation in the fitness of A_2A_2 increases it.

We calculated exactly the mean and variance of the gene frequency in the absence of selection for a finite population with random migration rate and immigrant gene frequency. See (21) and (27) for the exact results and (30) for a useful approximation. Finiteness of the population size and variation in the migration rate and immigrant gene frequency all increase the equilibrium variance of the gene frequency. An application of these results is the solution (31) for the exact mean and variance of the gene frequency with mutation and random drift.

If all evolutionary forces have comparable roles, the gene frequency in the diffusion approximation will be normally distributed at all times, as shown by (51), with the mean and variance appearing in (52). In this approximation, only the selection pressure at the average gene frequency of the immigrants matters, and its only effect is to shift the expected gene frequency.

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