A Diffusion Approximation for Selection and Drift in a Subdivided Population

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ABSTRACT

The population-genetic consequences of population structure are of great interest and have been studied extensively. An area of particular interest is the interaction among population structure, natural selection, and genetic drift. At first glance, different results in this area give very different impressions of the effect of population subdivision on effective population size (N_e), suggesting that no single value of N_e can completely characterize a structured population. Results presented here show that a population conforming to Wright's island model of subdivision with genic selection can be related to an idealized panmictic population (a Wright-Fisher population). This equivalent panmictic population has a larger size than the actual population; *i.e.*, N_e is larger than the actual population size, as expected from many results for this type of population structure. The selection coefficient in the equivalent panmictic population, referred to here as the effective selection coefficient (s_e), is smaller than the actual selection coefficient (s). This explains how the fixation probability of a selected allele can be unaffected by population subdivision despite the fact that subdivision increases N_e, for the product $N_e s_e$ is not altered by subdivision.

THE genetic consequences of population structure—subdivision of the population or population viscosity—have been of interest to population geneticists since the beginnings of the field (Wright 1931). An obvious motivation for this interest is that most, if not all, real populations have some sort of structure. An additional, more theoretical, motivation concerns the notion of effective population size. It is not clear to what extent this measure is applicable to subdivided populations. A single effective size might be insufficient to characterize a structured population, which might not be comparable in every way to any panmictic population.

Natural selection in a structured population provides what seems like an example of the inadequacy of a single N_e as a descriptor of a population. Maruyama (1970b, 1974) showed that subdivision does not affect an allele's fixation probability under genic selection if migration does not change the overall allele frequency and selection and drift occur separately in each deme. This might seem to indicate that the effective population size (N_e) of a subdivided population is equal to its actual size for some purposes. On the other hand, various treatments of genetic drift in a subdivided population show that N_e is increased by subdivision under these same conditions: more neutral variation is maintained in a subdivided population, and genetic drift happens on a longer timescale (Wright 1939; Maruyama 1970a; Slatkin 1981, 1991; Takahata 1991; Nei and Takahata 1993).

Much theoretical work has been done on the effective size of structured populations. In addition to work on simple migration models with no selection (cited above), there have been many efforts to calculate effective size under more general conditions. Slatkin (1977) and Maruyama and Kimura (1980) studied the effects of extinction and recolonization of subpopulations. Santiago and Caballero (1995) dealt with selection under various mating systems. Nordborg (1997) explored a generalization of spatial structure in which alleles move among classes that can be defined in any way. In some of the cases analyzed, classes corresponded to coupling with different alleles at linked loci that were under selection. Whitlock and Barton (1997) considered a very general model that included extinction and recolonization and arbitrary patterns of migration among demes. Wang and Caballero (1999) review various developments in this area. It should be noted that the question of effective size is complicated by the fact that different definitions of N_e can yield very different values for a structured population (Ewens 1979; Gregorius 1991; Chesser *et al.* 1993; Caballero 1994).

Maruyama (1972a,b,c) studied the effects of selection on structured populations described by stepping-stone and spatially continuous models. He assumed recurrent mutation, which replenishes allelic diversity, and derived distributions of allele frequencies at the resulting mutation/selection/drift equilibrium. Despite several differences between the models, some of the results presented here are closely related to those of Maruyama.

The model of population structure considered here is Wright's (1931) island model. Specifically, the version in which a large number of demes ("islands") exchange migrants is considered (Wright 1940, 1969; Rannala 1996; Rousset 2001), rather than the version

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in which one or more islands receive migrants from a continental source population. Many treatments of subdivided populations, including that presented here, make the assumption that the number of subpopulations is large. Under this assumption, the population-wide allele frequency in an island model changes more slowly than the frequency within a deme, so long as selection is absent or sufficiently weak. This means that from the point of view of any particular deme, the other demes serve as a source population that has a more or less constant allelic composition over relatively long periods of time. This leads to a quasi-equilibrium in which each deme is like an island population that has been receiving migrants from an unchanging source population (Rannala 1996; Gillespie 1998, p. 101; Rousset 2001).

A diffusion approximation is given here for the combined process of genetic drift and genic selection under the island model of subdivision. This diffusion is equivalent to that describing a certain ideal (Wright-Fisher) population. The size of the equivalent Wright-Fisher population (N_e, by definition) is larger than that of the actual population. However, this equivalent population also has a smaller selection coefficient, referred to here as the effective selection coefficient s_e. The product of population size and selection coefficient is the same for the actual population and the equivalent ideal population, as required for consistency with Maruyama's (1970b) result.

MODEL AND RESULTS

Consider a population consisting of D demes, each containing N haploid individuals. Migration occurs at rate m. This means that under strict neutrality the parent of an individual would come from within the deme with probability $1 - m$ and from the population at large with probability m. With selection, the sampling of alleles from these potential parents is biased toward more fit alleles in the usual way. Two alleles are considered, and further mutation is neglected. One allele has a fitness of $1 + s$ relative to the other. The frequency of this allele in the ith deme is denoted by x_i, and $\bar{x}$ denotes the mean frequency among demes, *i.e.*, the overall frequency of the allele in the entire population.

For a diffusion approximation we need expressions for the per-generation mean and variance of the change in allele frequency as functions of that allele frequency. These are well established for populations with no structure. The mean change in a panmictic population, $M_{\Delta x}$, is given approximately by

$$M_{\Delta x} = sx(1 - x),$$

where x is the allele frequency. The variance $V_{\Delta x}$ is given approximately by $x(1 - x)/N$ for a haploid Wright-Fisher population consisting of N individuals. For other population models, the effective population size N_e takes the place of N and the variance is given approximately by

$$V_{\Delta x} = \frac{1}{N_e}x(1 - x).$$

This equation is essentially the definition of the variance effective population size (Ewens 1979, equation 3.96). For populations to which these expressions apply, both the mean and the variance are (approximately) proportional to $x(1 - x)$, and their ratio is therefore independent of x.

For our subdivided population, no single allele frequency completely describes the population. A variable of obvious interest is the overall allele frequency $\bar{x}$. However, a particular value of $\bar{x}$ can be realized in many different ways. At one extreme, all demes could have the same allele frequency ($\bar{x}$). At another, a fraction $\bar{x}$ of the demes could have allele frequency one, while the rest have frequency zero. Between these extremes lie a myriad of possibilities. Nonetheless, we can still hope to write a diffusion for $\bar{x}$. The key is that for a particular value of $\bar{x}$, and for given values of m and N, we can know roughly what distribution of within-deme allele frequencies to expect when D is large. Most importantly for the present purposes, we can write an expression for the expected value of $x_i(1 - x_i)$, where x_i is a within-deme allele frequency, as a function of $\bar{x}$.

The change in overall allele frequency $\bar{x}$ is the mean of the changes in the x_i. The variance in one of these changes is $\sim x_i(1 - x_i)/N$. The variance in the change in $\bar{x}$, the mean of the x_i, is equal to

$$\frac{1}{ND^2}\sum_i x_i(1 - x_i).$$

The average of a large number of identically distributed random variables will be close to their common expected value. Thus, for large D, the above will be close to

$$\frac{1}{ND}Ex_i(1 - x_i).$$

Two forces, migration and selection, contribute to the mean change within a deme. Strictly speaking, these forces interact in a way that depends on the order in which selection and migration occur. However, under the usual assumptions that $m \ll 1$ and $s \ll 1$, these components of change can be treated separately. The component due to migration has mean $m(\bar{x} - x_i)$. This quantity sums to zero across demes (migration does not change the overall allele frequency in this model). In a particular deme, the mean change due to selection is $\sim sx_i(1 - x_i)$. Thus the mean change in overall allele frequency is approximately

$$sEx_i(1 - x_i).$$

Thus we would have the desired expressions for both

the mean and the variance of the change in $\bar{x}$ if we had $Ex_i(1 - x_i)$ as a function of $\bar{x}$.

Imagine that the migrants received by a deme had an allele frequency $\bar{x}$ whose value was fixed for all time. Under these conditions, it is known that the allele frequency in the deme would reach an equilibrium distribution that is given approximately by the probability density

$$Ce^{2Nsx}x^{a-1}(1 - x)^{b-1}, \quad (1)$$

where $a = 2Nm\bar{x}$, $b = 2Nm(1 - \bar{x})$, and C is a normalization constant (Wright 1931).

In reality, $\bar{x}$ changes over time. However, if these changes are sufficiently slow, then a deme will be exposed to roughly the same value of $\bar{x}$ for some time and would be approximately at the equilibrium (Wright 1931). Under what conditions would the change in $\bar{x}$ be sufficiently slow?

Drift within a deme is a more rapid process than drift within the population as a whole. Within-deme drift has a characteristic time of N generations, whereas for the population as a whole this time is at least ND generations (this is the limit for high migration; subdivision makes population-wide drift even slower). Migration only speeds the approach of a deme to its equilibrium distribution. Specifically, the deviation of $Ex_i(1 - x_i)$ from its equilibrium value decreases by a factor of $(1 - 1/N)(1 - m)^2$ each generation. This follows from the recursion relation for $Ex_i(1 - x_i)$ under the constant $\bar{x}$ assumption, with the condition that $Ex_i = \bar{x}$ at the outset. Thus, absent of selection, the population will be in a state of quasi-equilibrium, with the distribution of within-deme allele frequencies given above.

Very strong selection might change $\bar{x}$ so rapidly that this quasi-equilibrium approximation does not hold. However, a simple limit on the magnitude of s guarantees that this approximation works well. The average change in $\bar{x}$ due to selection is at most $s\bar{x}(1 - \bar{x})$ per generation (population structure slows the rate below this, as will be clear from what follows), which cannot be greater in magnitude than $|s|/4$. If $|s|$ is small compared to $1/N$, little change in $\bar{x}$ will occur during the N generations that it takes for within-deme drift to occur, and the quasi-equilibrium will hold.

Under this same condition ($|Ns| \ll 1$), selection is not a strong force in determining the equilibrium distribution of within-deme allele frequencies (Equation 1). This distribution becomes approximately the same as that expected under neutrality. This is a β-distribution whose probability density function (pdf) is

$$Cx^{a-1}(1 - x)^{b-1}, \quad (2)$$

with $a = 2Nm\bar{x}$ and $b = 2Nm(1 - \bar{x})$. The same approximation was used by Dobzhansky and Wright (1941), who applied it to recessive-lethal alleles with deleterious heterozygous effects.

The assumption that $|Ns| \ll 1$, which is made in all of what follows, does not restrict us to especially weak selection. It allows that NDs, the quantity that determines fixation probabilities, can be quite large in magnitude. Indeed if $|Ns|$ is not small compared to 1, $|NDs|$ will be quite large for even moderate D. In that case, an infinite-population model would describe the population well: the more fit allele, when not initially rare, would almost certainly go to fixation via a nearly deterministic path, and an advantageous allele present in a single copy would fix with a probability of $\sim 2s$.

We can now write the expected value of $x_i(1 - x_i)$ as a function of $\bar{x}$, using knowledge of the moments of a β-distribution (Equation 2). The first moment of a β-distribution is $a/(a + b)$, and the second moment is $a(a + 1)/(a + b)(a + b + 1)$. For the β family member of interest, $a = 2Nm\bar{x}$ and $b = 2Nm(1 - \bar{x})$. Substitution and simplification yield

$$Ex_i(1 - x_i) = Ex_i - Ex_i^2 = \left(\frac{2Nm}{2Nm + 1}\right)\bar{x}(1 - \bar{x}). \quad (3)$$

Thus, the mean of the within-deme quantity $x_i(1 - x_i)$ is proportional to $\bar{x}(1 - \bar{x})$. The proportionality constant $2Nm/(2Nm + 1)$ is a familiar expression for $1 - F_{ST}$ under an island model, where F_{ST} is the fractional decrease in heterozygosity due to subdivision. The mean change in $\bar{x}$ is given approximately by

$$M_{\Delta\bar{x}} = s\left(\frac{2Nm}{2Nm + 1}\right)\bar{x}(1 - \bar{x}).$$

The variance is given approximately by

$$V_{\Delta\bar{x}} = \frac{1}{DN}\left(\frac{2Nm}{2Nm + 1}\right)\bar{x}(1 - \bar{x}),$$

which is similar to the expression used by Maruyama (1972a, Equation 4) in the context of a stepping-stone model of population structure. These are the same as the mean and variance for a panmictic Wright-Fisher population with certain parameters. The size of this equivalent panmictic population, N_e, is given by

$$N_e = DN\Big/\left(\frac{2Nm}{2Nm + 1}\right) = \left(1 + \frac{1}{2Nm}\right)DN.$$

The selection coefficient in the equivalent population, referred to here as the effective selection coefficient and denoted by s_e, is given by

$$s_e = \left(\frac{2Nm}{2Nm + 1}\right)s.$$

The product $N_e s_e$ is equal to DNs, as required for consistency with Maruyama's (1970b) conclusion that subdivision does not affect fixation probability in this model. Nonetheless, the fact that N_e is larger than the actual population size ND, and s_e is smaller than s, means that changes in allele frequency happen more slowly than

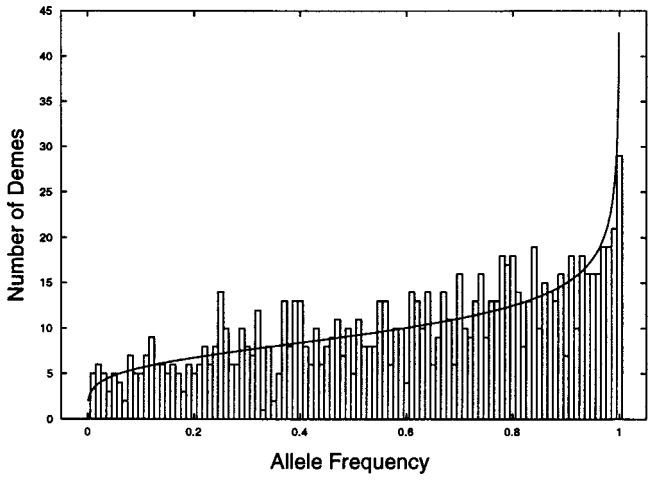

FIGURE 1.—The observed distribution of allele frequencies among demes at one time point in a simulation (bars) is compared to the theoretical β density function (curve). The parameters for the β-distribution are determined by the observed overall allele frequency $\bar{x}$ and the value of Nm in the simulation. The parameters used in the simulation were as follows: $D = 1000$, $N = 100$, $m = 0.01$, $s = 0.001$. In the generation shown, $\bar{x}$ was 0.611.

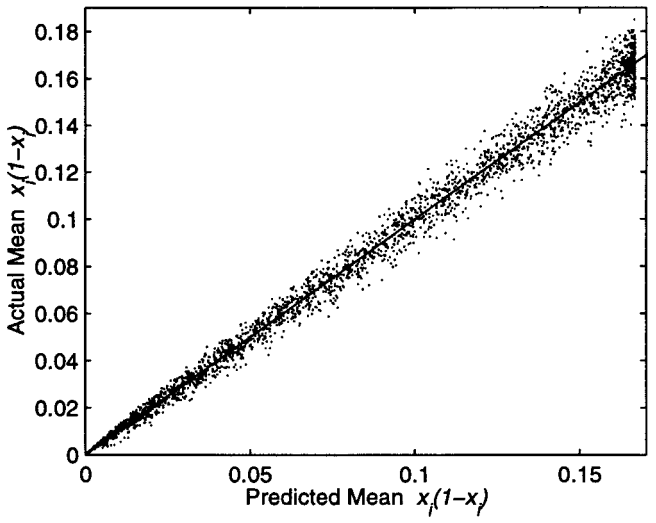

FIGURE 2.—Actual *vs.* predicted values of the mean of $x_i(1 - x_i)$. Each point represents a time point in a simulation. The points come from 100 independent simulations, each of which was assessed at intervals of 100 generations. The simulation parameters were $D = 100$, $N = 100$, $m = 0.01$, $s = 0.001$. The starting condition was $\bar{x} = \frac{1}{2}(x_i = \frac{1}{2}$ for all $i)$. The line corresponds to equality of predicted and actual values.

in a panmictic population, as established by previous investigations (SLATKIN 1981; TAKAHATA 1991).

COMPUTER SIMULATIONS

The approximations used above for the among-deme distribution of allele frequencies can be tested by comparison of the theoretical predictions to the results of computer simulations. In these simulations the state of the population is represented by an array of D integers, each corresponding to a deme. Each integer indicates the number of copies of the allele in the deme and hence ranges from 0 to N. Each generation, the value for each deme is drawn from a binomial distribution. The index parameter n of this binomial is equal to N. The probability parameter p is determined by the current allele frequency in the deme x_i, the population-wide mean allele frequency $\bar{x}$, the migration rate, and the selection coefficient. Let $\tilde{p} = (1 - m)x_i + m\bar{x}$. This would be the mean allele frequency in the ith deme in the next generation if there were no selection. With selection, we have $p = (1 + s)\tilde{p}/(1 + s\tilde{p})$.

Figure 1 shows the distribution of allele frequencies among demes in one particular generation of a simulation. The parameter values used in the simulation were $D = 1000$, $N = 100$, $m = 0.01$, and $s = 0.001$. The β density function given by Equation 2, with $\bar{x}$ equal to the actual overall allele frequency, should approximate this distribution. This function is also shown in Figure 1, and it agrees well with the observed distribution.

The only aspect of this distribution that is directly relevant to the diffusion is the mean value of the $x_i(1 - x_i)$. Figure 2 compares the observed mean of the $x_i(1 - x_i)$ to the value predicted on the basis of the observed $\bar{x}$. This predicted value is given by Equation 3. Each plotted point represents the predicted and observed values at a time point. The data come from many independent simulations, with $D = 100$, $N = 100$, $m = 0.01$, and $s = 0.001$. The observed values agree well with the predictions. This confirms that the mean of the $x_i(1 - x_i)$ is given, to a good approximation, by a function of $\bar{x}$.

Another computational test of the analytic approximation involves the evolution of the distribution of the overall allele frequency $\bar{x}$ over time. The diffusion approximation developed here relates this distribution to that describing a certain panmictic population. This can be related to a much smaller population by a scaling of time. This is convenient because it is feasible to obtain an exact numerical solution for this smaller population by repeated application of its transition matrix. This is an alternative to numerical integration of expressions given by KIMURA (1955a,b), and the result is easier to compare to a histogram because it is discrete and lacks δ-functions at the boundaries. Figure 3 compares the resulting prediction for the distribution of $\bar{x}$ to the results of many simulations after 5000 generations. The parameters were $D = 100$, $N = 100$, $m = 0.01$, and $s = 0.001$, and the initial allele frequency was $\frac{1}{2}$. The theoretical prediction is in excellent agreement with the simulation results.

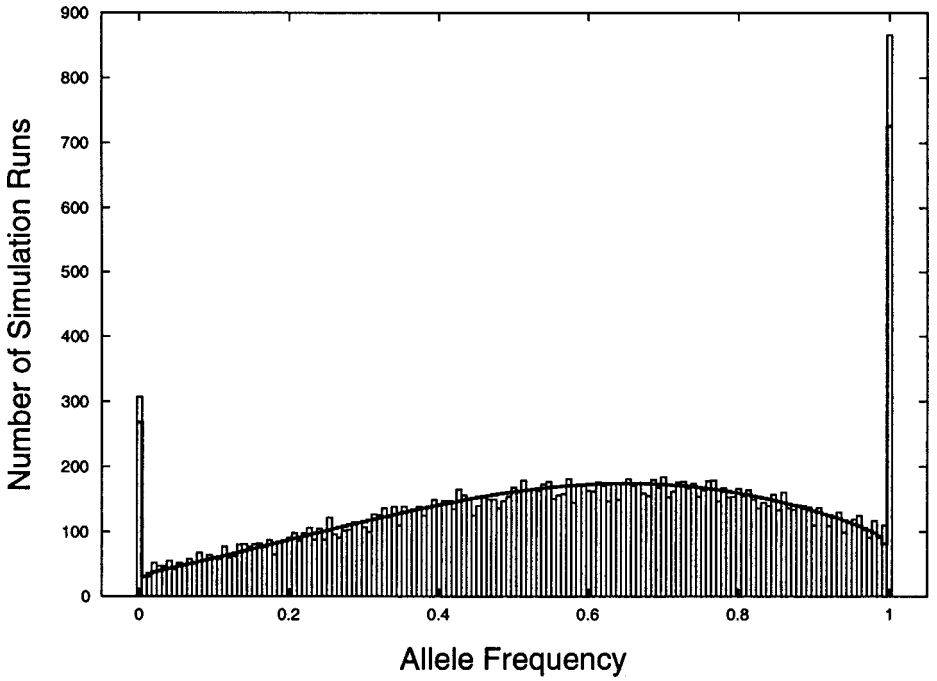

FIGURE 3.—The distribution of overall allele frequencies after 5000 generations of 20,000 independent simulation runs (bars) is compared to a theoretical prediction. In the simulations, $D = 100$, $N = 100$, $m = 0.01$, $s = 0.0001$, and the initial allele frequency is 1/2. The predicted distribution is obtained by iteration of the transition matrix for a Wright-Fisher population with $N = 150$ and $Ns = N_e s_e$, with time scaled by a factor of 100 (because $N_e = 15{,}000$).

A closely related distribution is that of the absorption time, the time until fixation or extinction of an allele. Figure 4 compares the distribution predicted on the basis of N_e and s_e to simulation results for $D = 100$, $N = 100$, $m = 0.001$, $s = 0.0001$, and an initial allele frequency of ½. Again there is excellent agreement between the prediction and the outcome of the simulations. As an additional test, the mean of these absorption times can be compared to that predicted by the diffusion approximation. Diffusion theory gives the mean absorption time in a Wright-Fisher population as a certain integral (EWENS 1979, Equations 4.22 and 5.47). Numerical evaluation of this integral, with N and s replaced by N_e and s_e, yields the desired prediction. For the parameters used in the simulations presented in Figure 4, the predicted mean absorption time is 7.76×10^4 generations. The actual mean in the simulations, 7.62×10^4 generations, is close to this. For comparison, the mean predicted in the absence of subdivision is 1.29×10^4 generations, and without selection the prediction is 8.32×10^4 generations.

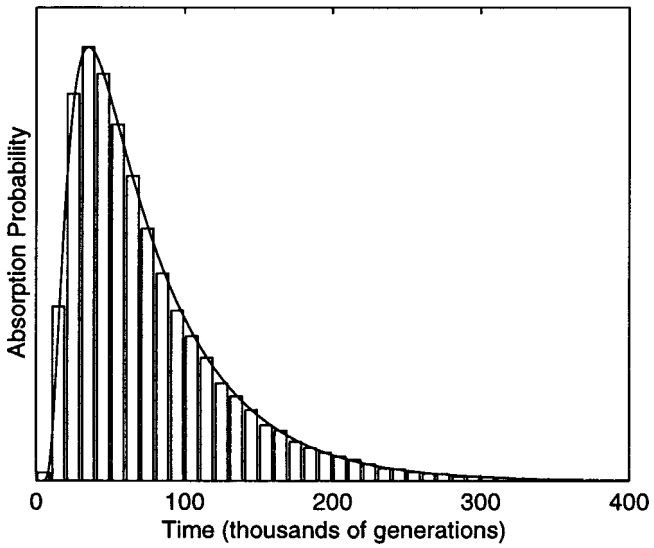

FIGURE 4.—The distribution of time until absorption (fixation or extinction) in 50,000 simulations (bars), compared to a theoretical prediction (curve). The simulation parameters were as follows: $D = 100$, $N = 100$, $m = 0.001$, $s = 0.0001$. The initial allele frequency was ½. The predicted distribution is based on iteration of the transition matrix for a Wright-Fisher population of size 1000.

Table 1 compares the observed and predicted mean absorption times for a variety of parameter values with an initial allele frequency of ½. For $D = 100$ and $N = 100$, the simulation results are in excellent agreement with the predictions. All of the observed values are slightly smaller than the predictions, but only by at most a few percent. With $D = 1000$ and a mere 10 individuals per deme, the simulation results are again close to the theoretical predictions, even with strong selection and weak migration. For smaller numbers of demes this agreement deteriorates somewhat as migration becomes weak, as expected because the predictions involve the assumption that D is large. However, even with as few as 10 demes, the observed means differ from the predictions by $<20\%$.

Table 2 shows results for alleles starting out at a single copy. For the higher migration rates the mean absorption times are in accord with the predicted values. For

TABLE 1

Predicted and observed mean absorption times for an initial allele frequency of ½

No. of demes	Deme size	Migration rate	Selection coefficient	Nm	$N_e s_e = NDs$	Predicted mean absorption time	Observed mean absorption time
$D = 100$	$N = 100$	$m = 0.1$	$s = 0.0001$	10	1	13,579	13,497 ± 69
			$s = 0.0005$	10	5	6,656	6,615 ± 24
			$s = 0.001$	10	10	3,911	3,879 ± 11
		$m = 0.01$	$s = 0.0001$	1	1	19,399	19,246 ± 98
			$s = 0.0005$	1	5	9,508	9,362 ± 35
			$s = 0.001$	1	10	5,587	5,442 ± 16
		$m = 0.001$	$s = 0.0001$	0.1	1	77,594	76,195 ± 248
			$s = 0.0005$	0.1	5	38,033	37,013 ± 140
			$s = 0.001$	0.1	10	22,347	21,168 ± 62
		$m = 0.0001$	$s = 0.0001$	0.01	1	659,553	645,863 ± 6,572
			$s = 0.0005$	0.01	5	323,283	314,510 ± 2,432
			$s = 0.001$	0.01	10	189,951	181,408 ± 773
$D = 1000$	$N = 10$	$m = 0.01$	$s = 0.001$	0.1	10	22,347	21,957 ± 89
		$m = 0.001$	$s = 0.001$	0.01	10	189,951	190,847 ± 1,700
$D = 30$	$N = 100$	$m = 0.001$	$s = 0.001$	0.1	3	16,146	15,064 ± 71
		$m = 0.0001$	$s = 0.001$	0.01	3	137,241	126,867 ± 587
$D = 10$	$N = 100$	$m = 0.1$	$s = 0.001$	10	1	1,358	1,345 ± 7
		$m = 0.01$	$s = 0.001$	1	1	1,940	1,837 ± 10
		$m = 0.001$	$s = 0.001$	0.1	1	7,759	6,728 ± 39
		$m = 0.0001$	$s = 0.001$	0.01	1	65,955	55,399 ± 329
		$m = 0.00001$	$s = 0.001$	0.001	1	647,913	571,948 ± 15,587

the lower migration rates the observed means are smaller than the predictions. This phenomenon has nothing to do with selection; it occurs even in its absence. It reflects the fact that extinction, the usual fate of an allele present in a single copy, occurs very quickly. When migration is weak, quasi-equilibrium cannot be achieved this rapidly. In the limit of very low migration, extinction almost always occurs before the allele can spread to other demes, and the time to loss is similar to that in a population of size N. A number more informative than the mean absorption time is the mean time until fixation (conditional on eventual fixation rather than on loss). Observed values of this quantity are compared to predictions in Table 2 [predicted values were calculated according to Kimura and Ohta (1969, Equation 17), with s_e substituted for s and adjustments made

TABLE 2

Predicted and observed mean absorption and fixation times for an allele present in a single copy, with $D = 100$ and $N = 100$

Migration rate	Selection coefficient	Nm	$N_e s_e = NDs$	Predicted mean absorption time	Observed mean absorption time	Predicted mean fixation time	Observed mean fixation time
$m = 0.1$	$s = 0$	10	0	21.4	20.3 ± 0.1	20,999	20,170 ± 327
	$s = 0.0001$	10	1	23.4	22.2 ± 0.4	19,931	18,847 ± 614
	$s = 0.0005$	10	5	27.2	26.9 ± 0.4	11,620	11,877 ± 138
	$s = 0.001$	10	10	28.8	27.8 ± 0.4	7,391	7,307 ± 47
$m = 0.01$	$s = 0$	1	0	30.6	25.7 ± 0.2	29,999	30,110 ± 518
	$s = 0.0001$	1	1	33.5	28.9 ± 0.2	28,473	28,397 ± 281
	$s = 0.0005$	1	5	38.9	34.2 ± 0.3	16,600	16,424 ± 85
	$s = 0.001$	1	10	41.1	35.3 ± 0.4	10,559	10,417 ± 53
$m = 0.001$	$s = 0$	0.1	0	122.5	73.2 ± 0.7	119,994	121,379 ± 2,110
	$s = 0.0001$	0.1	1	133.9	83.0 ± 1.1	113,893	114,134 ± 1,819
	$s = 0.0005$	0.1	5	155.6	105.1 ± 0.7	66,400	65,548 ± 245
	$s = 0.001$	0.1	10	164.6	112.7 ± 0.9	42,236	41,028 ± 118
$m = 0.0001$	$s = 0$	0.01	0	1,041	556 ± 19	1,019,949	1,027,879 ± 55,420.2
	$s = 0.0001$	0.01	1	1,138	608 ± 14	968,093	934,624 ± 23,741
	$s = 0.0005$	0.01	5	1,323	801 ± 20	564,400	568,132 ± 6,749
	$s = 0.001$	0.01	10	1,399	899 ± 17	359,004	352,044 ± 2,290

for haploidy]. The mean fixation times in the simulations are in excellent agreement with these predictions: the observed means are all within a few percent of the predicted values, even when migration rates are small.

In all of the simulations presented above, except where $s = 0$, $|NDs| \geq 1$ (NDs ranges from 1 to 100). Therefore selection has a significant effect on the fate of the allele in the population as a whole. Thus the simulations test the ability of the theory to account for selection; had $|NDs|$ been small, the deviation of the results from the strictly neutral case would be insignificant, and the simulations would test only whether the theory worked well under neutrality. The results demonstrate that the theoretical approximations work well in the presence of significant selection, so long as $|Ns|$ is small compared to one (Ns ranges from 0.01 to 0.1 in the simulations).

DISCUSSION

Despite the fact that the state of a subdivided population cannot be described by a single allele frequency, the trajectory of the overall allele frequency $\bar{x}$ in an island model (Wright 1931) can be described well by a one-dimensional diffusion approximation. This is the case even in the presence of selection that is strong enough to have a large influence on the probability of an allele's fixation. Furthermore, this diffusion approximation is equivalent to that for some idealized panmictic population. Thus, classical diffusion results for nonstructured populations may be applied to a structured population that conforms to the island model. Simulation results confirm the validity of these approximations.

The equivalent panmictic population has parameter values that are different from their counterparts in the island model. As is the case for many population-genetic models, the size of the hypothetical equivalent Wright-Fisher population, N_e, is different from (in this case greater than) the size of the actual population. This state of affairs is familiar in population genetics and is the reason for defining effective population size in the first place. A less familiar aspect of the present result is that the selection coefficient in the hypothetical equivalent population is different from that in the actual population. This motivates the definition, by analogy to effective population size, of the effective selection coefficient s_e. In the present case, $s_e < s$. Specifically, subdivision lowers the effective selection coefficient by the same factor by which it raises effective population size. This factor depends on the product of deme size and migration rate (Nm), which determines the extent of differentiation among the demes.

The effects of subdivision on N_e and s_e both result from the fact that the expected value of the within-deme quantity $x_i(1 - x_i)$ is smaller than the quantity $\bar{x}(1 - \bar{x})$, which would be relevant if the population were panmictic. Both the mean and the variance of the change in allele frequency are approximately proportional to the mean of $x_i(1 - x_i)$. Subdivision therefore slows down drift and selection by the same factor. While s_e is directly proportional to the mean change in allele frequency, N_e is inversely proportional to the variance, so it changes by the same factor but in the opposite direction. The quantity $N_e s_e$, which is the ratio of the mean to the variance of the change in allele frequency, is unaffected by subdivision. Therefore, as expected from the results of Maruyama (1970b, 1974), fixation probabilities are also unaffected by subdivision. However, the rate at which allele frequencies change is decreased. Because the two components of this change, selection and drift, are slowed by the same factor, the effect of subdivision on the trajectory of allele frequency is simply a dilation in time.

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