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SOME POPULATION GENETIC CONSEQUENCES OF COLONY FORMATION AND EXTINCTION: GENETIC CORRELATIONS WITHIN FOUNDING GROUPS

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Abstract.—Extinction and recolonization in an island model affects genetic differentiation among subpopulations through a combination of sampling and mixing. We investigate the balance of these forces in a general model of population founding that predicts first the genetic variance among new groups and then the effect of these new groups on the total genetic variance among all populations. We allow for a broad range of types of mixing at the time of colonization and demonstrate the significant effects on differentiation from the probability of common origin of gametes (ϕ). We further demonstrate that kin-structured founding and inbreeding within populations can have a significant effect on the genetic variance among groups and use these results to make predictions about lineal fission and fusion of populations. These results show that population structure is critically affected by non-equilibrium dynamics and that the properties of new populations, especially founding number, probability of common origin, and kin structure, are vital in our understanding of genetic variation.

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Much of theoretical population genetics is simplified by the assumption that the forces of migration, random drift, mutation, and selection have reached an equilibrium in their effects on the distribution of gene frequencies among populations. For example, at equilibrium between the forces of migration and drift, differentiation of local populations (F_{ST}) in an island model is expected to be approximately $1/(1 + 4Nm)$, where N is the local population size and m is the migration rate (Wright, 1940). Nature is not always so patient. In many species, local populations come and go on a temporal scale that does not permit the attainment of that equilibrium. In this case, the distribution of gene frequencies among populations reflects the interaction of two phases of a population's history: first, a perturbation from equilibrium caused by a founding event, followed by the progress to-

wards equilibrium; progress that is ultimately terminated by local extinction. As the extinction rate increases, this equilibration is truncated more quickly, and the founding event comes to dominate. With local extinction and recolonization, the metapopulation will display an age-structure since subpopulations can vary in the time since each was formed. Any difference in the allele frequency variance among newly founded groups relative to that among older populations can cause the genetic variance among the whole array of populations to deviate from equilibrium conditions. It is the purpose of this paper to describe a general population genetic model of founding group formation and to illustrate the effects of a broad range of colonization patterns on the neutral genetic differentiation of populations.

Wright (1940) was the first to discuss the

effect local extinction can have on population differentiation, suggesting extinction as a factor likely to increase among-population genetic variance. Yet, despite Wright's insight, relatively little formal work on population differentiation has incorporated the effects of extinction/recolonization, and less has paid explicit attention to the mode of new group formation. One useful model, developed by Slatkin (1977), mathematically considers two forms of colonization that can have very different consequences for population differentiation (Wade and McCauley, 1988). The first, the migrant pool model, describes the effects of colonization when individual colonists (gametes) are chosen at random from the entire metapopulation. In the migrant pool model, extinction can either enhance or diminish differentiation, depending on the relative size of certain parameters (Wade and McCauley, 1988). On the other hand, the propagule model, where each colonizing group is chosen at random from a single parental population, predicts that extinction never decreases differentiation (as expressed by some measure such as Wright's F_{ST}) and under most conditions enhances it, sometimes by an order of magnitude, relative to equilibrium conditions with no extinction (Wade and McCauley, 1988). Thus, the two modes of colonization have very different effects on among-population variance.

Natural populations are not limited to these extreme forms of colony formation, for a variety of reasons. In nature, propagules are not always formed from a single parent population, nor are individual gametes chosen strictly at random from all existing groups. An obvious example is gametes traveling together as diploid organisms: each of the pair of alleles within an individual shares a common site of origin, even if all of the diploid individuals in the colonizing group come from different source populations. Furthermore, not all populations in the same species are colonized in the same manner. Variance in the degree of common origin and in the number, sex ratio, and fecundity of individuals in the colonizing group should strongly affect the resulting genetic variance. Finally, we must allow for kin-structured colonization, a factor that is of some considerable importance

in many species (Hedrick and Levin, 1984; Rogers, 1987, 1988; Levin 1988), for example in the movement of whole, multi-seeded fruits or in the fission of an animal population along familial lines (Smouse et al., 1981).

In this paper we extend Slatkin's model to present a set of general equations that allow for a diversity of modes on colonization. We will examine the effect of among-population genetic variance of the probability of common origin, of the number and type of colonists, and of inbreeding and kin-structure within propagules. We will show that these variations in the manner of propagule formation can significantly change the distribution of genetic variance within a metapopulation. Further we will discuss this non-equilibrium model as a general device capable of describing many patterns of population structure. We show that population fission/fusion processes are a special case of our model and also use non-equilibrium concepts to illustrate the connections between trait group and demic structure models of group selection. We find that non-equilibrium conditions can be very different from those at equilibrium, and that the extent of that difference depends critically on the properties of the founding event.

The Model

Variance in gene frequencies among a cohort of populations changes towards an equilibrium value through sampling and migration each generation after founding. Extinction can prevent a subset of the metapopulation from reaching that equilibrium. It is therefore essential to incorporate an age structure of populations when extinction occurs. We present an infinite-island, infinite-alleles model of population structure with a population level age structure. We use a recurrence equation following Maruyama (1970) and Slatkin (1977, Model II), although we have changed the order in which sampling events and migration occur so that the system is more manageable and more compatible with Slatkin's variance component model (Model I, derived in Slatkin, 1977). We follow these models in assuming selective neutrality among alleles. Our general model allows for any age structure for the array of populations, but we consider

particularly the case in which extinction occurs with equal probability in all population age classes, a situation implicit in Slatkin (1977). Our treatment considers specifically the case when the metapopulation has reached a stable population age structure. Our measure of differentiation will be the probability of identity of two alleles chosen at random within a population. This has the fortunate properties of being equal to Wright's F_{ST} when the number of populations is large (Wade and McCauley, 1988) and equal to the within-population homozygosity when $F_{IS} = 0$; these values are often estimated in natural populations by allozyme techniques.

The probability that two alleles at the same locus selected at random from within a randomly chosen population are identical by descent, f_0 , is the weighted probability of identity averaged across all populations,

$$f_0 = \sum_{t=0}^{\infty} p^{(t)} f_0^{[t]} \quad (1)$$

where t is the age of a population, $p^{(t)}$ is the proportion of populations of age t , and $f_0^{[t]}$ is the probability of identity of 2 randomly chosen alleles in a randomly chosen population of age t . In the case of an infinite alleles, infinite island model, this weighted probability can be found from a consideration of a single recurrence equation. We now assume that migration precedes sampling by random mating or by colonization (an order similar to that in Model I in Slatkin (1977) but different from prior recurrence models including Slatkin's Model II), we find

$$f'_0 = (1 - u)^2 (p^{(0)} f_0^{[0]} + \sum_{t=1}^{\infty} p^{(t)} \cdot [1/2N + (1 - 1/2N) \cdot (1 - m)^2 f_0^{[t-1]})] \quad (2)$$

where f_0 and f'_0 are the probabilities of identity of alleles chosen within a population for two successive generations, e is the extinction rate, $f_0^{[0]}$ is the probability of identity of two alleles in a newly formed population, u is the mutation rate, m is the migration rate among populations, and N is the size of extant populations, so that $2N$ is the num-

ber of haplotypes in each population. We have followed Slatkin (1977) in assuming that newly founded populations grow immediately with random mating to size N to allow for simplicity in the further analysis. Identity by descent of alleles in the group of migrants and between migrants and residents is therefore indefinitely small. We will examine the case in which the probability of extinction is independent of the age of the population, hence $p^{(t)} = e(1 - e)^t$, where e is the extinction rate. We assume that the number of populations does not change, thus the extinction rate is the colonizing rate. When we assume that each population age class contributes to the founding of new populations proportional to its representation in the metapopulation, Equation (2) simplifies to

$$f'_0 = (1 - u)^2 [(1 - e)(1/2N + (1 - 1/2N) \cdot (1 - m)^2 f_0 + e f_0^{[0]})] \quad (3)$$

which is similar to Equation (9) of Slatkin (1977). Hence a specific age structure of populations is implicit in Slatkin's equations in his Model II. It may be noted that any other age structure would be difficult to handle analytically. Variation in age structure of populations may be dealt with by numerical techniques using modifications of Equation (2).

Genetic Variation Among New Populations

The probability of identity among the gametes of a newly founded group may be found to depend on several qualities of the founding group. We find

$$f_{0,i}^{[0]} = 1/2k_i + \phi_i(1 - 1/2k_i) \cdot (1/2N + (1 - 1/2N)f_c) \quad (4)$$

In this equation, $2k_i$ represents the number of haploid genomes in founding group i , ϕ_i is the probability that two alleles in newly formed population i come from the same parental population (the probability of common origin), and f_c is the probability that 2 alleles in the same founding group that share common origin are identical by descent. Averaging over all new subpopulations creates an effective size, k_e , equal to the harmonic mean of k_i , or $1/E(1/k)$. We follow Slatkin (1977) in assuming for simplicity that the population instantaneously achieves

size N . In the terminology of Slatkin (1977) and Wade and McCauley (1988), $\phi = 0$ describes the migrant pool; $\phi = 1$ gives the propagule pool.

The value of ϕ is determined by a variety of factors. We may describe

$$\phi_i = \frac{\sum_h (r_{h,i} - 1)r_{h,i}}{2k_i(2k_i - 1)} \quad (5)$$

where $r_{h,i}$ is the number of gametes from the h th parental population, such that the sum over h of $r_{h,i} = 2k_i$. If we hold k constant, it is simple to find the expectation for ϕ over all i founding populations,

$$\phi = \frac{E[n_c(\sigma_r^2 + r^2 - r)]}{2k(2k - 1)} \quad (6)$$

where ϕ is the weighted average over all new populations and n_c is the number of contributing subpopulations. Therefore ϕ is increased by variance in the representation of subgroups. With this formulation of ϕ , we can account for both a case where each propagule is formed in an identical manner but intermediate to the propagule pool and the migrant pool and also a case where founding groups vary in the way they are formed.

Some special cases seem worthy of mention. When alleles move only as diploid individuals, we find, with equal representation of parental populations,

$$\phi = \frac{(2k - 2)\Psi + 1}{(2k - 1)} \quad (7)$$

where Ψ is the probability of common origin of the diploid individuals. This probability of common diploid origin is obviously increased when founding individuals are females preinseminated by a male from the same parental population, or when individuals move in groups such as seeds in a fruit. One may also view population bottlenecks as a special case of colonization where all but migrants come from the same parental population: $\phi = (1 - m)^2$.

If we assume that $f_c = f_0(1 - m)^2$, that is, the probability of identical descent in alleles with common origin is the probability of identity within a population after migration, solving the recursion (3) gives us the equilibrium value of f_0 shown below (Eq. 8): when the mutation rate is small. The equilibrium here is in population turnover, not in individual populations. Equation (8) describes an equilibrium of metapopulation conditions. This equation agrees with Slatkin's (1977) Model I when $\phi = 0$ (migrant pool) or when $\phi = 1$ (propagule pool) and with Wright's rule when $e = 0$, thereby confirming Wade and McCauley's assertion that Model I and Model II of Slatkin (1977) are similar in the limit where n is large. Slatkin's Model I and our recurrence model are in fact identical because of an identical ordering of sampling events. It can be shown that f_0 is a monotonically increasing function with decreasing N , m , and k , but the direction of change in f_0 with respect to the parameters ϕ and e depends on the relative values of many of the parameters. It is useful to know the conditions under which the process of extinction and recolonization enhances differentiation relative to the traditional equilibrium conditions. We find that $f_{0(e>0)} > f_{0(e=0)}$ when

$$\phi > (1 - m)^2 \quad (9)$$

or failing that, when

$$k < \frac{N[1 - (1 - 1/2N)(1 - m)^2]}{1 - \phi} - \frac{\phi}{2(1 - \phi)} \quad (10)$$

When $m \ll 1$, this condition is approximated by

$$k < \frac{2Nm}{1 - \phi} + \frac{1}{2} \quad (10a)$$

(to the same degree of accuracy as Wright's approximation of $F_{ST} = 1/(4Nm + 1)$). It can be shown that these conditions are

$$f_0(\text{eq}) = \frac{(1 - e + e\phi(1 - 1/2k))/2N + e/2k}{1 - (1 - m)^2(1 - 1/2N)(1 - e + e\phi(1 - 1/2k))} \quad (8)$$

equivalent to the requirement that variance among newly formed populations be greater than variance among populations at equilibrium. It is also worth noting that when $\phi = 0$, condition (9) simplifies to condition (7) in Wade and McCauley (1988) for migrant pool, and when $\phi = 1$, extinction always increases differentiation for $m > 0$, just as Wade and McCauley (1988) found for propagule pool (see also Slatkin, 1977).

Inbreeding Within Populations

Kin-structured migration seems common in nature. Plant genes often move as full- or half-sib seeds in a fruit (see Levin, 1988 for review), and many socially structured animals have similar patterns of migration, particularly humans (Fix, 1978; Cheverud et al., 1978; see Hedrick and Levin (1984) for more examples). Hedrick and Levin (1984) have shown inbreeding within the propagating groups of gametes to be a significant factor increasing the fixation rate of chromosomal variants.

The effect on variance among populations of inbreeding and kin-structured founding can be analyzed generally in the present model. In relaxing the assumption that $f_c = f_0(1 - m)^2$ we notice that $(1 - f_c) = (1 - f_0)(1 - f_p)$, if f_p is the additional probability of identity within parental populations contributing to the same propagule group. To comply with our assumptions of the order of migration and sampling, f_0 in these recursions must be corrected by a term $(1 - m)^2$, leaving

$$f_c = f_p + f_0(1 - m)^2 - f_p(f_0)(1 - m)^2 \quad (11)$$

The equilibrium variance with non-zero f_p is given as shown below (Eq. 12):

Note that when $f_p > 0$, variance is increased relative to the case of $f_p = 0$. Likewise, when $f_p < 0$, variance is reduced relative to $f_p = 0$. Hence, if alleles move in ordered pairs such as diploids or in predated females, inbreeding within populations increases variance among populations through the process of colonization, while any form of

disassociative mating can reduce variance. Non-zero values of F_{IS} (the probability of identity of two alleles within the same individual) can significantly affect the level of differentiation among populations if haplotypes move in diploids. Inbreeding within populations can significantly increase inbreeding among groups at the next higher hierarchical level; in other words, inbreeding reduces the effective number of colonists. Similarly, if individuals move as families or in kin-structured groups, the similarity in genotype among relatives increases f_p and is converted into reduced variance within and increased variance among founding groups.

DISCUSSION

Nature rarely follows a simple course. Even the relatively inclusive model presented here is "a simplification and an idealization, and consequently a falsification" (Turing, 1952 p. 5). Yet several useful features emerge.

Our model of colonization generalizes the migrant pool and the propagule pool and accounts for many important properties of newly founded populations that affect differentiation of gene frequencies among populations. As we have discussed above (see also Wade, 1978; Wade and McCauley, 1988), nature rarely follows either the propagule pool or the migrant pool models strictly. When gametes move in diploids, as sperm in gravid females, as seeds in a pod or fruit, in social groups or families, or simply when movement is assortative by distance or by size of parent population, the migrant pool model does not accurately describe nature. At the same time, gametes may rarely come to a new location from a single existing population, and the propagule pool is insufficient.

The effect of the degree of common origin within propagules on population differentiation is shown in two examples in Figure 1a and b. In Figure 1a conditions (9) and (10) are always true; therefore colonization events always enhance variation among

$$f_0 = \frac{[1 - e + e\phi(1 - 1/2k)(1 - f_p)]/2N + e/2k + e\phi(1 - 1/2k)f_p}{1 - (1 - m)^2(1 - 1/2N)(1 - e + e\phi(1 - 1/2k)(1 - f_p))} \quad (12)$$

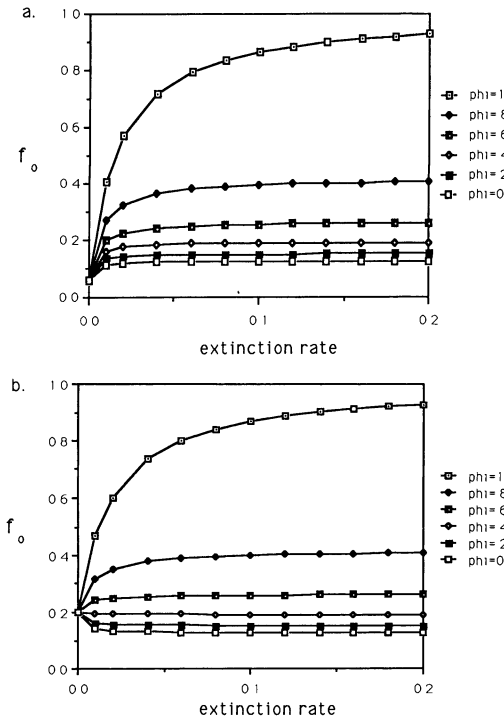


FIG. 1. The probability of identity within populations given for a range of values of the extinction rate and the probability of common origin. (a) $k = Nm = 4$; $N = 4,000$. Conditions 9 and 10 are always met; extinction always increases f_0 . (b) $k = 4Nm = 4$; $N = 1,000$. Conditions for increase are only met when $\phi > 0.43$.

populations. In Figure 1b, the conditions are met only when $\phi > 0.43$. Both examples illustrate the point that increasing ϕ increases variance in a non-linear fashion, with greatest effect as ϕ approaches unity. Population size and migration rate remain important; in fact, the interaction of these parameters is much complicated by non-equilibrium conditions. Like migration between extant populations, a small amount of mixing among parent populations in the formation of a colonizing group has disproportionate effect; the relationship between ϕ and F_{ST} is distinctly non-linear and monotonically increasing. Yet even small values of e and ϕ can significantly change F_{ST} compared to the traditional case with no extinction.

The variance among propagules is also significantly affected by other properties of the distribution of founding group types. The effective value of k is a function of the vari-

ance among new groups in number, sex ratio deviations, and variance within groups in reproductive success (Crow and Kimura, 1970; Crow and Denniston, 1988). Colonizing groups are unlikely to be uniform in size, due to differences in habitat (McCauley, 1989). If male and female colonization rates are uncorrelated, significant departures from equal sex ratios are possible, particularly in founding groups with a small number of total colonists and in species with sex-biased dispersal (McCauley, 1989).

Variance in reproductive success may be large in colonizing groups. Variance in traveling distance among colonists could generate variance in reproductive success (Roff, 1977). Variance in time of arrival will create variance in the length of the reproductive season and in access to mates, which is further increased if some males are represented only by preinsemination. The influence of variance in propagule number, sex ratio bias, and variance in reproductive success is therefore particularly great in colonizing populations; effective propagule number may be much reduced in comparison to actual founding group sizes.

Other factors are important as well. The inclusion of the f_p term, the inbreeding and kin-structuring within propagules from the same parent population, not only allows for differentiation even more extreme than in the propagule pool model of group formation, but also demonstrates that inbreeding within diploid populations affects variance among populations. If population founding events are based on kin-biased movement, variance among populations is significantly increased, an effect similar to that shown before in the case of kin-structured migration (Rogers, 1987). This type of "kin-founding" (as defined in Hedrick and Levin, 1984) has the effect of increasing the variance produced at founding. Figure 2 illustrates the effect on f_0 from f_p for a range of values of ϕ . As ϕ increases, the effect of within group inbreeding increases; so that in a system in which colonization occurred similar to propagule pool, inbreeding within founding groups can have a rather large effect, almost doubling f_0 for large values of f_p , relative to $f_p = 0$.

Our inclusion of kin-structured founding allows study of various types of population

structure. Many species have populations which undergo fission and fusion (see Fix, 1978; Ober et al., 1984 for reviews), yet no formal theory of fission/fusion population structure is available (Fix, 1978). The analysis we present begins to fill this gap: fission is formally equivalent to the extinction of one population and the recolonization of two (or more) new populations, and fusion can be represented as the founding of a new population (Long et al., 1987). Considered in this way, among group variance may be determined, accounting for the effects of variation in contribution from different parent populations, variation in new group size, and lineal versus random group fissions (which may be expressed in terms of f_c). When new populations formed by fission or fusion satisfy conditions (9) and (10), fission/fusion dynamics enhance differentiation. If fission events are not followed by fusion, then fission, particularly lineal fission, will always increase differentiation. Fusion events, on the other hand, will in all but extraordinary cases decrease variance among groups.

Our model also can help to reconcile divergent models of intra-group selection. As described by Wade (1978) and Wilson (1983), traditional models of group selection and models of kin or trait-group selection are extremes on a continuum varying in the rate at which populations are formed and break down. Evolution by group selection depends quantitatively on the existence of genetic variance among groups, which is created anew by recolonization events; models which allow new colonization are more conducive to group selection (Wade, 1978; Wilson, 1983). Our format should facilitate investigation of intermediately lasting groups in terms of individual and group selection. Wade (1985) has described the effects on social evolution of some variants in colony formation with multiple foundresses and multiple insemination. It is straightforward to include the present work in the analysis of social evolution, and thereby have a more general theory that includes kin-founding, variation in common origin, and intermediately aged populations.

The evolution of among group variance is important in many aspects of evolution-

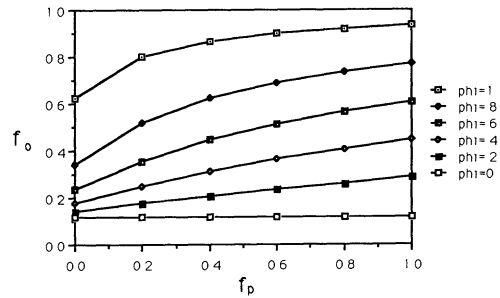


FIG. 2. The effect of non-random selection of gametes on f_0 . The values for the other parameters used here are $e = 0.1$, $k = Nm = 4$, and $N = 1,000$.

ary theory and is affected by many factors. A more complete understanding of these factors requires the inclusion of non-equilibrium, extinction/recolonization models. These models should be as informative as possible across the range of probable natural systems. We have provided a more general model of group formation and its effects on genetic variation among populations, and we have shown that the properties of founding groups are of primary importance in the determination of genetic variation. It is clear that more empirical investigations of group formation are necessary: knowing the number, sex, condition, kin structure, and, particularly, the history of colonists is essential in understanding the effect of colonization on population structure.

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