GENETIC AND PHYLOGENETIC CONSEQUENCES OF ISLAND BIOGEOGRAPHY

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Abstract.—Island biogeography theory predicts that the number of species on an island should increase with island size and decrease with island distance to the mainland. These predictions are generally well supported in comparative and experimental studies. These ecological, equilibrium predictions arise as a result of colonization and extinction processes. Because colonization and extinction are also important processes in evolution, we develop methods to test evolutionary predictions of island biogeography. We derive a population genetic model of island biogeography that incorporates island colonization, migration of individuals from the mainland, and extinction of island populations. The model provides a means of estimating the rates of migration and extinction from population genetic data. This model predicts that within an island population the distribution of genetic divergences with respect to the mainland source population should be bimodal, with much of the divergence dating to the colonization event. Across islands, this model predicts that populations on large islands should be on average more genetically divergent from mainland source populations than those on small islands. Likewise, populations on distant islands should be more divergent than those on close islands. Published observations of a larger proportion of endemic species on large and distant islands support these predictions.

Key words.—Extinction, genetic divergence, island isolation, migration, speciation.

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Equilibrium island biogeography predicts that the number of species on an island should increase with island area and decrease with island distance to the mainland source population (MacArthur and Wilson 1963, 1967). Although some of the details of the island biogeography model have been criticized (Sauer 1969; Gilbert 1980; for an overview, see Brown and Lomolino 1998), the predicted pattern has been upheld for a wide range of taxa including birds (Hamilton et al. 1964; Vuilleumier 1970; Adler 1992), insects (Darlington 1943), and plants (Preston 1962). These predictions arise from an equilibrium in the underlying dynamics of extinction and colonization of islands. These underlying dynamics have also been verified in experimental systems (Patrick 1967; Cairns et al. 1969; Simberloff and Wilson 1969; Have 1987). Populations on large islands exhibit lower extinction rates, and populations on islands far from the mainland have lower colonization rates (MacArthur and Wilson 1963, 1967). When assumptions of the island biogeography model are not met, the model can often be successfully altered to account for different assumptions (Brown and Lomolino 1998). For example, in the absence of colonization, species diversity dynamics on islands are driven by extinction, as with mammals on Great Basin mountains (Brown 1971).

In addition to being important processes in ecological time, extinction and colonization are major processes in evolutionary time and have important implications for evolution on islands. In particular, because island populations are often isolated from mainland populations, they should diverge over time (genetically and morphologically) from populations of respective mainland species due to genetic drift, changed selection pressures, or both. The magnitude and rate of this divergence might depend on extinction (how often accumulated divergence is erased by extinction), colonization (how often new island populations are established), and migration (how often new migrants from the mainland population contribute to the island gene pool). In the extreme, isolation on islands will lead to speciation between the island

and mainland (Adler 1992), speciation between islands in an archipelago (Cox 1990), or even speciation within an island (MacArthur and Wilson 1963; e.g., Hawaiian *Drosophila*).

The basic assumptions of island biogeography are that extinction and colonization rates are related to island size and distance from the mainland, respectively. Because both of these processes are difficult to measure directly, we develop a genetic framework for estimating the parameters and evaluating these assumptions. Specifically, we provide evolutionary predictions for the magnitude and nature of genetic divergence of island populations in relation to island size and distance from the mainland. Genetic divergence can be estimated in practice by comparing sequence differences between island and mainland alleles. First, we derive the expected distribution of allelic divergence times within island populations from which the time of colonization and migration rates can be estimated. To test this expectation, one could examine genetic divergences between island and mainland populations of one species across many loci. We then determine this distribution averaged across island populations from which extinction and migration rates can be estimated. This distribution could be estimated by examining divergences between island and mainland populations across many species on a single island for a small number of loci. Finally, we incorporate speciation of island populations into the model from which the timing of speciation can be estimated.

MODEL

How do populations on islands diverge genetically from mainland populations over time? More specifically, what is the proportion of sites that differ between island and mainland alleles?

Our models are based on several simplifying assumptions: (1) all colonization and immigration occurs from the mainland to the island; (2) rates of extinction, colonization, immigration, mutation, and drift are constant over time; and (3) mutations are neutral, occur according to infinite sites and
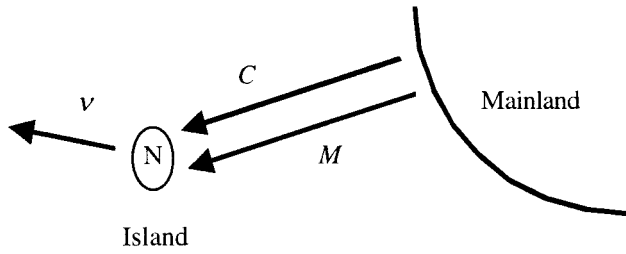
FIG. 1. Diagram illustrating the processes of colonization (*C*), immigration (*M*), fixation (related to *N*), and extinction (*v*) on islands.

alleles models (Hartl and Clark 1989), and change in frequency according to neutral expectation (Kimura 1968). These processes are illustrated in Figure 1.

The assumptions can be formalized with the following parameters: *C,* colonization rate, the rate per generation at which new island populations are formed; *v*, extinction rate per generation of island populations; *M*, rate at which immigrants enter the island population from the mainland per generation; *N,* size of the island population; $m = M/N$ (for strictly neutral alleles this is the rate per generation at which migrant alleles fix in the island population); and *k*, constant rate per generation of genetic divergence due to mutation and drift (for neutral alleles the rate of substitution of new mutants is the mutation rate; Kimura 1968).

Genetic Divergence of a Single Population

For a single island population, we are interested in the amount of genetic divergence between island and mainland alleles across all loci and how this might be influenced by population parameters (e.g., population size and island distance). We derive the expected distribution of genetic distances across loci in a single population given the processes of extinction, colonization, immigration, mutation, and drift. For a given island population in which colonization occurred at time *T* in the past (in generations), the probability density function for allelic divergence times is:

$$g(t) = \begin{cases} me^{-mt} & \text{for } 0 \leq t < T \\ e^{-mT}\delta(t - T) & \text{for } t = T \\ 0 & \text{for } t > T, \end{cases} \quad (1)$$

where δ is the Dirac delta function, which describes an ''atom'' of probability at $t = T$. The allelic divergence time is the time since arrival on the island (in generations) of the ancestor of a particular island allele currently in the population. Alleles in the current island population can be descended from alleles present in the original colonists ($t = T$) or be descended from alleles in migrant individuals who arrived on the island subsequent to colonization ($0 \leq t < T$). The fraction e^{-mT} corresponds to direct descendants of alleles that remain in the island population from the original colonization event (Fig. 2).

The mean genetic distance across all alleles for an island population of age *T* can be derived by integrating back to the time of colonization over the density function for allelic ages and multiplying by the rate of genetic divergence. This calculation must include migrant alleles that have fixed, as
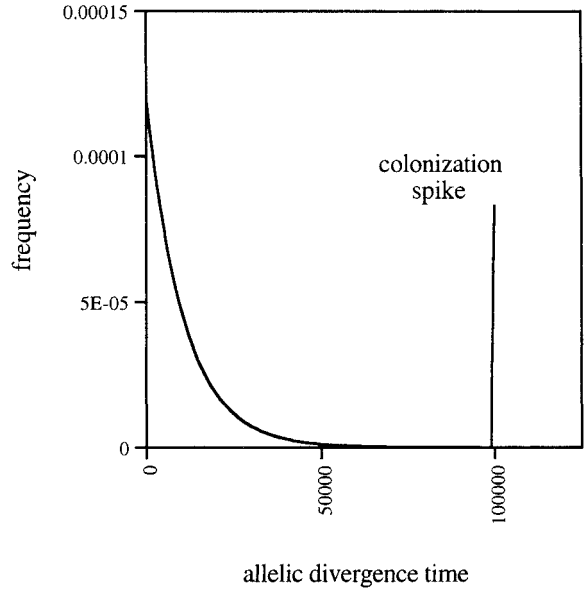

FIG. 2. Distribution of allelic divergence times across loci within an island population as indicated by equation (1). $T = 100,000$, $m = 0.00012$. The height of the colonization spike represents the density (area) at this point and is for illustration purposes.

well as descendants of original alleles at the time of colonization. The mean genetic distance is

$$\int_0^T ktg(t) \, dt = \int_0^T mkte^{-mt} \, dt + kTe^{-mT} = \frac{k}{m}(1 - e^{-mT}). \quad (2)$$

Model across Populations

Because populations of different species on the same island will have different colonization times, we want to know how genetic divergences between island and mainland alleles will be distributed across different species. Under the assumption that all species have the same extinction rate, the time from the present to past colonization (*T*) across species takes on values according to the probability density function

$$h(t) = ve^{-vT}. \quad (3)$$

The expected age of extant island populations is affected only by the extinction rate, because it is conditioned on island occupancy. If colonization rates were low, there would be fewer occupied islands (see eqs. 19a–c), but the distribution of allelic divergences would be the same.

Across species, the mean allelic divergence time is

$$\bar{g}(t) = \int_0^\infty g(t \mid T)h(T) \, dT$$

$$= \int_t^\infty me^{-mt}ve^{-vt} \, dT + \int_0^t e^{-mt}\delta(t - T)ve^{-vt} \, dT$$

$$= (m + v)e^{-(m+v)t}. \quad (4)$$

Averaging across species produces an exponential distribution (Fig. 3) without the truncation and spike at the coloni-
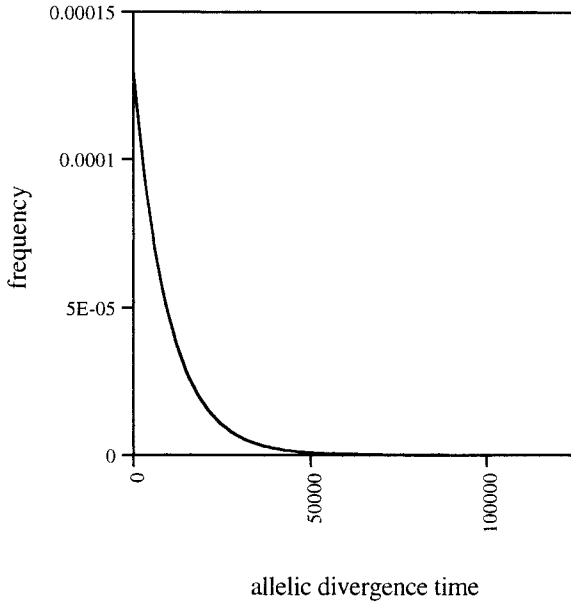
FIG. 3. Mean allelic divergence times of alleles across species on the same island. Here each population provides an estimate of the sum of the substitution rate for new migrants plus the extinction rate of island populations ($m + v$). This distribution is an exponential that now lacks the characteristic spike of alleles from colonization as within a single population. $m = 0.00012$, $v = 0.00001$.

zation event evident across genes within a single species (Fig. 2). The parameter $m + v$ can be thought of as the hazard whose rate is given by m for encountering the migration event and hazard v for encountering the extinction event, so $m + v$ is the hazard for encountering the allelic divergence event (the arrival of an ancestor to a current allele on the island). Across all species, the mean genetic divergence is

$$\int_0^\infty kt(m + v)e^{-(m+v)t} = \frac{k}{m + v}. \quad (5)$$

Not surprisingly, mean genetic divergence is larger when the mutation rate is larger, the rate of fixation of immigrant alleles is smaller and the extinction rate of populations on the island is smaller.

Island biogeography models describe how island size affects extinction rates and how the distance to the island affects colonization and immigration rates (MacArthur and Wilson 1963). The mean genetic divergence can thus be expressed in terms of island size and distance.

More specifically, let A represent the area of the island and x the distance from the mainland to the island. We suppose that population size N is proportional to the area A. Then, if extinction is inversely proportional to population size,

$$v = \frac{1}{c_2A}. \quad (6)$$

The rate at which mutant alleles fix is

$$m = \frac{M(x)}{N} = \frac{M(x)}{c_1A}. \quad (7)$$

The mean genetic divergence of a species on an island is then

$$\frac{k}{m + v} = \frac{k}{\dfrac{M(x)}{c_1A} + \dfrac{1}{c_2A}} = \frac{kA}{\dfrac{M(x)}{c_1} + \dfrac{1}{c_2}}. \quad (8)$$

Finally, we suppose the migration rate is a product of the probability of survival ($e^{-\alpha x}$) and of the probability of encountering an island ($1/x$), giving

$$M(x) = \frac{e^{-\alpha x}}{x} \quad (9)$$

(Adler and Nuernberger 1994). In general, as islands get larger, mean genetic divergence increases linearly with area because of the decrease in extinction rate and the lower substitution rate of immigrant alleles (eq. 8, Fig. 4a). Mean genetic divergence increases nonlinearly with distance because the rate of input of new alleles through immigration decreases (eq. 8, Fig. 4b).

Probability of Speciation of Island Populations and Its Effect on Genetic Divergence

Genetic isolation of populations on islands often leads to speciation. Speciation can increase observed genetic divergence by reducing or eliminating gene flow from the mainland. We include speciation in the model using the framework of Orr and Orr (1996). Under Orr and Orr's model, speciation occurs when incompatible alleles fix at two different loci. Their simplest model is based on the assumption that any pair of nonmatching loci has an equal probability of leading to instant speciation. To compute the rate of speciation, we must find $p(t)$, the probability that an allele in the island population is identical to the allele at the same locus on the mainland population at time t after colonization. The probability follows the differential equation

$$\frac{dp}{dt} = m(1 - p) - 2\mu p, \quad (10)$$

because alleles diverge at rate 2μ (mutant on either island or mainland) and come to match again at rate m (due to successful migration from the mainland). With the initial condition $p(0) = 1$, this equation has the solution

$$p(t) = \frac{m}{m + 2\mu} + \frac{2\mu}{m + 2\mu}e^{-(m+2\mu)t}. \quad (11)$$

The probability that island and mainland alleles match decays exponentially from one to $m/(m + 2\mu)$. If the migration rate is much larger than the mutation rate, the probability of identity between island and mainland alleles can be approximated by

$$p(t) \cong 1 - \frac{2\mu}{m} + \frac{2\mu}{m}e^{-mt} = 1 - \frac{2\mu}{m}(1 - e^{-mt}). \quad (12)$$

If N is small and migration is high, this approximation is reasonable. If N is large and migration is low, the approximation does not hold. However, all subsequent calculations remain possible, although the results are more complicated.

The rate of speciation is related to (1) the rate of production of new unmatched pairs of alleles on the island and mainland; (2) the probability that the two populations were still the
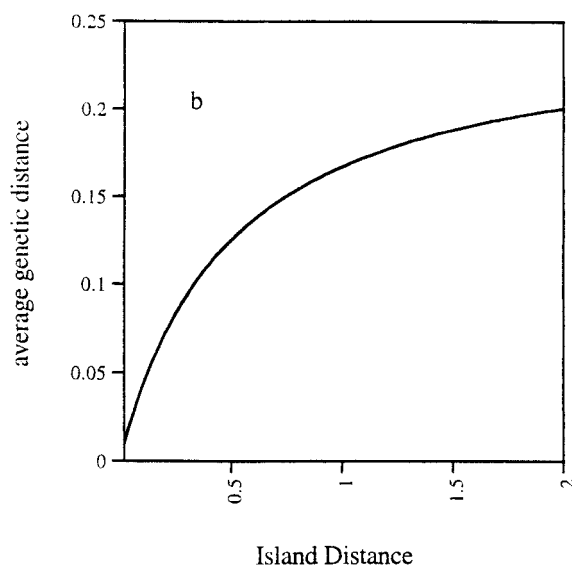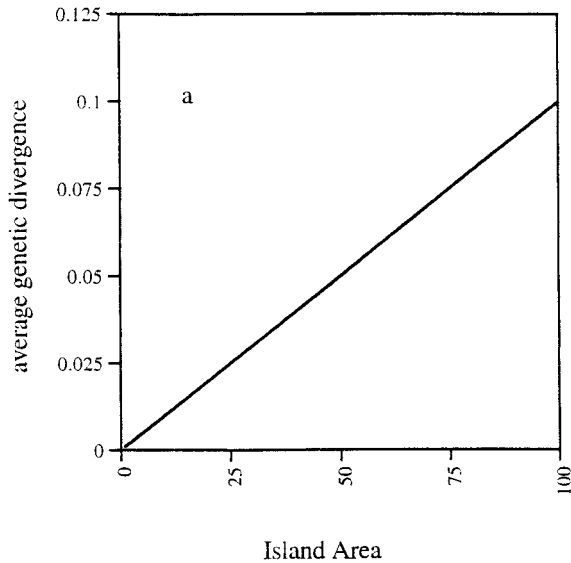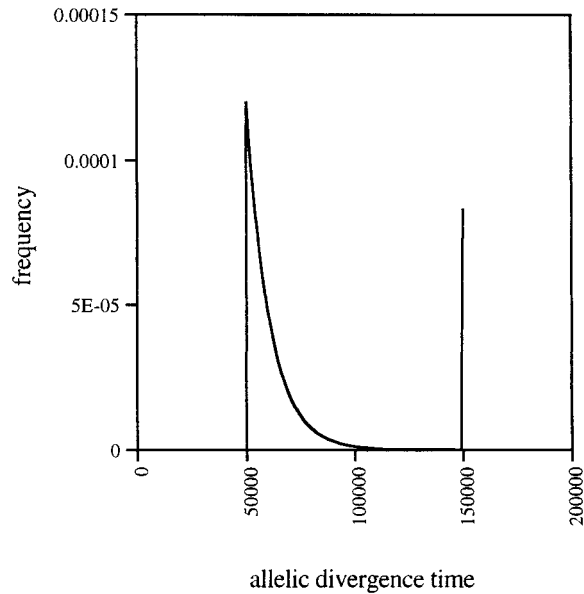
FIG. 5. Distribution of allelic divergence times across loci under the island biogeography model with speciation (from eq. 16). $T = 150,000$, $T_s = 50,000$, $m = 0.00012$. The height of the colonization spike represents the density (area) at this point and is for illustration purposes.

FIG. 4. (a) Mean genetic divergence across populations as a function of island area (distance held constant), from equation (8),

$$\frac{k}{\dfrac{M(x)}{c_1} + \dfrac{1}{c_2}} = 0.001;$$

(b) mean genetic divergence across populations as a function of island distance from mainland (area held constant), from equation (8), $kA = 0.2135$, $\alpha = c_1 = c_2 = 1$.

same species $[S(t)]$; and (3) the probability that a new unmatched pair of alleles results in speciation $[p_0]$, according to the differential equation

$$\frac{dS}{dt} = -2\mu G[1 - p(t)]GS(t)p_0, \tag{13}$$

with the initial condition $S(0) = 1$. G is the number of genes

where incompatible alleles might cause speciation. Substituting for $p(t)$, the equation becomes

$$\frac{dS}{dt} \cong -2\mu G^2 \frac{2\mu}{m}(1 - e^{-mt})p_0 S(t) = -\gamma \frac{(1 - e^{-mt})}{m} S(t), \tag{14}$$

where $\gamma = 4\mu^2 G^2 p_0$. The probability $S(t)$ that the island and mainland populations are still the same species has the solution

$$S(t) = \exp\left[-\frac{\gamma}{m}\left(t + \frac{e^{-mt} - 1}{m}\right)\right], \tag{15}$$

which is consistent with results of Orr and Orr (1996). The rate of speciation, s, is the negative of the derivative of the probability that two populations are the same species, S.

The probability density function for allelic divergence times in an island population under the speciation model is now truncated at the time of speciation, T_s, and at the time of colonization (see Fig. 5), T:

$$g(t) = \begin{cases} me^{-m(t-T_s)} & \text{for } T_s \leq t < T \\ e^{-m(T-T_s)}\delta(t - T) & \text{for } t = T \\ 0 & \text{for } t > T \text{ or } t < T_S. \end{cases} \tag{16}$$

The probability density function for allelic divergence times across species under the speciation model is

$$\int_{T=t}^{\infty} \int_{T_s=0}^{T} g(t \mid T, T_S)h(T)s(T - T_s) \, dT_s \, dT. \tag{17}$$

Equation (17) has no explicit solution and must be evaluated numerically (see Fig. 6).

To link these genetic predictions for extant species with the ecological predictions of presence and absence, we de-

termine the probability that a mainland species is (1) extinct (or never existed) on the island; (2) conspecific with the island population; and (3) distinct from a new island species. The probability $H(m, v)$ that an extant population on the island remains conspecific with the mainland population is

$$H(m, v) = \int_0^\infty v e^{-vt} S(t) \, dt, \tag{18}$$

averaging over all possible founding dates. This probability can be evaluated in relation to island area and distance (Fig. 7). The probabilities of an island population being extinct (eq. 19a), same species (eq. 19b), and different species (eq. 19c) are

$$\frac{v}{C + v}, \tag{19a}$$

$$\frac{C}{C + v} H(m, v), \quad \text{and} \tag{19b}$$

$$\frac{C}{C + v} [1 - H(m, v)]. \tag{19c}$$

Discussion

The model presented here considers a subdivision of populations such that island populations are isolated from mainland populations. The majority of research on genetics of subdivided populations has focused on the maintenance of genetic variability in the population as a whole (Slatkin 1977; Wade and McCauley 1988; McCauley 1991; Harrison and Hastings 1996; Barton and Whitlock 1997). These studies generally consider classic metapopulations consisting of many small transient populations linked by migration (Hanski and Simberloff 1997). A few studies have examined genetic dynamics in the mainland-island models addressed here. Boorman and Levitt (1973) examined the potential for group selection in a population with a mainland-island structure. Gaggiotti (1996) considered the maintenance of genetic variation in a source-sink population consisting of a mainland with several islands, but again this only evaluated the properties of the population as a whole. Other recent work has considered the probability of identity by descent in a mainland-island model (Rannala and Hartigan 1995; Rannala 1996), but where the population dynamics on the island follow a stochastic birth-death-immigration process rather than the deterministic growth and stochastic extinction considered in our genetic model of island biogeography.

Predictions

The above population genetic model of island biogeography makes several predictions concerning the nature of genetic diversification on islands. First, we predict the distribution of allelic divergence times within island populations. Given immigration of alleles from a mainland source population, allelic divergence times will follow a distribution such that some of the alleles will date to the time of colonization and the remaining allelic divergence times will show a decrease in frequency from newly arrived alleles to alleles descended from past colonists. The distribution of allelic divergence times can be estimated by comparing sequences of island alleles against those of mainland alleles. The parameters of this distribution will reflect the size of the island (which influences population size) and distance to the mainland (which influences the immigration rate). For close islands, the distribution of genetic divergences (measured in terms of substitutions) is greatly influenced by the probability of a new migrant allele fixing, which is the inverse of the population size. In this case, populations on large islands (Fig. 8a) will contain many alleles of small divergence and many alleles originating at the time of colonization. In contrast, most of the alleles on small, close islands (Fig. 8b) derive from recent immigrants, and most of the alleles from the time of colonization have been lost because of the higher fixation probability of new migrants. Genetic divergences on distant islands are more heavily influenced by the low immigration rate. For large, distant islands (Fig. 8c) the distribution of genetic divergences shows that most alleles will descend from ancestors at the time of colonization with little fixation of more recent migrants. For small, distant islands (Fig. 8d), the distribution shifts toward newly arrived immigrant alleles, which have a reasonable chance of fixation.

To evaluate these predictions, one can compare sequence divergence between island and mainland populations using sequences from many loci with roughly the same substitution rates. The accumulation of mutations provides an estimate of the allelic divergence time. The frequency histogram of number of base substitutions (or some other measure of divergence) should often show evidence of bimodality. That is, many alleles should show little divergence, few alleles should be intermediate in divergence, and many alleles should show high divergences (from ancestors at the time of colonization). Because of the Poisson nature of the mutation process, the colonization spike will be spread out such that a peak will be evident for both recent immigrants and alleles descended from those at the colonization event (Fig. 8). With some combinations of immigration and extinction rates, only one peak will be evident, either recent immigrants or descendants of original colonists (see Fig. 8). From the distribution of divergences, the time of colonization could be estimated using the most divergent alleles. In addition, the shape of the distribution provides an estimate of m, the rate of migrant allele fixation, using equation (1).

The sum of migration and extinction rates can be estimated by examining the distribution of genetic divergences (as compared to mainland populations) across species on the same island. This distribution should be exponential so that larger migration rates (inverse of island area and distance) and extinction rates (inverse of island area) should increase the fraction of alleles that are descended from recent immigrants (Fig. 3). Subtracting the estimate of migration rates derived from the within-population comparison from this estimate should provide an estimator for the extinction rate of island populations.

If we include speciation in the model (Orr and Orr 1996), such that eventually new immigrants have no probability of becoming incorporated into the gene pool, the distributions of allelic divergence times truncates at the time of speciation.
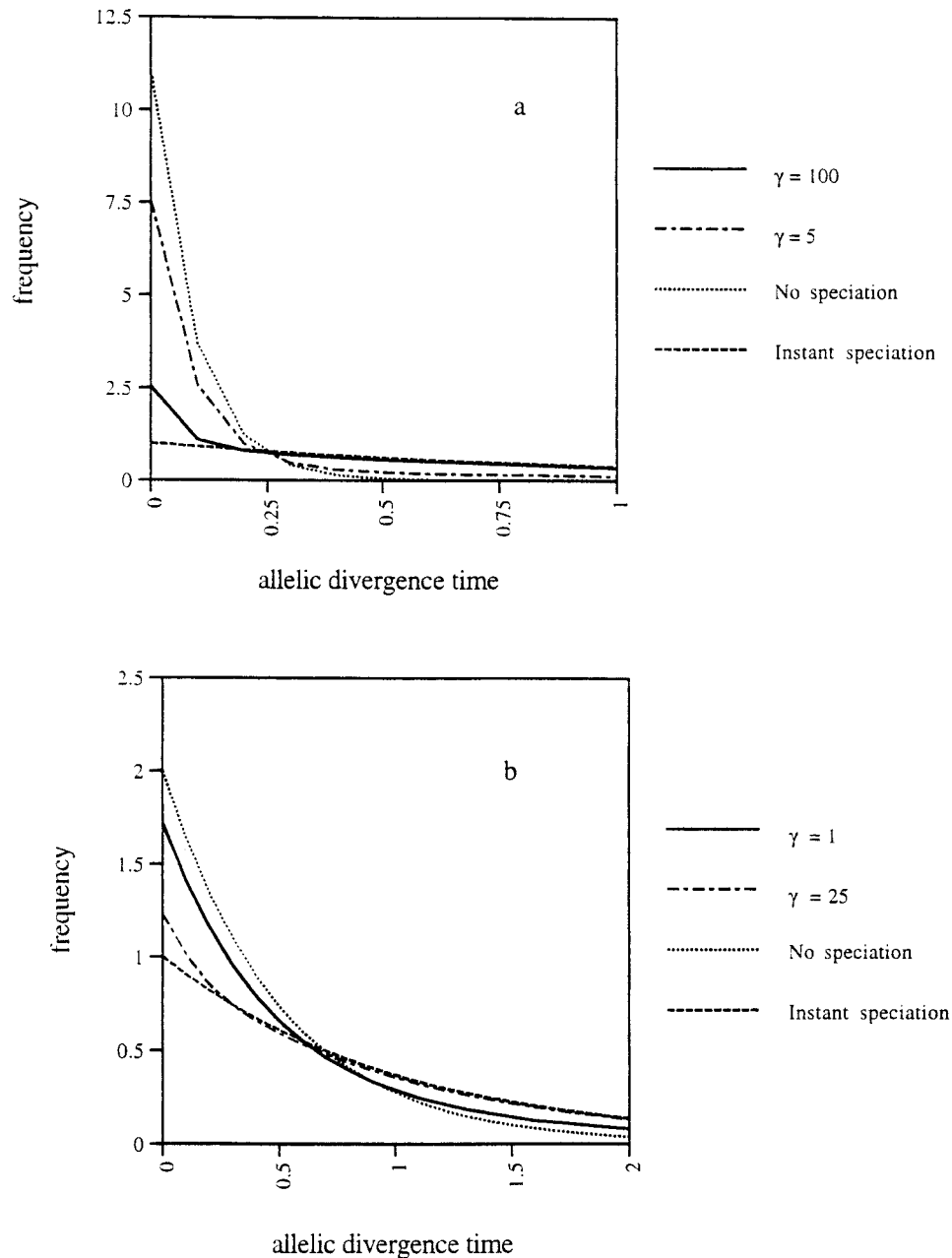
FIG. 6. Frequency distribution of allelic divergence times across species on the same island under the speciation model in terms of average time to extinction ($v = 1$). (a) $m = 10$; (b) $m = 1$. For each distribution we show different speciation constants, γ. Also shown for comparison are the no speciation (eq. 4) and the instant speciation ve^{-vt} cases.

Plots of frequency distributions of allelic divergences across loci should still contain evidence of bimodality; however, now the least divergent alleles should show an appreciable divergence (Fig. 5). Again, the shape of this distribution will depend on the substitution rate (which depends on the area and distance of the island), such that small, close island populations will likely not even exhibit speciation, whereas large, distant island populations will have speciated and still retain a large fraction of alleles descended from original colonists. Under this model, speciation becomes more likely on distant islands because of the infrequency of new migrants.

In addition to making predictions about the distribution of allelic divergences within an island population, this model also makes predictions about allelic divergences across populations on different islands. The mean allelic divergence across a set of loci is influenced by both island size (population size) and distance to mainland (immigration rates). Because populations on large islands (with larger population sizes) are less subject to extinction, populations will show longer persistence times such that allelic divergences have the potential to become much larger than on small islands. In addition, newly arriving migrant alleles have a lower probability of going to fixation in large populations. The increased persistence of alleles descended from colonists owing to low
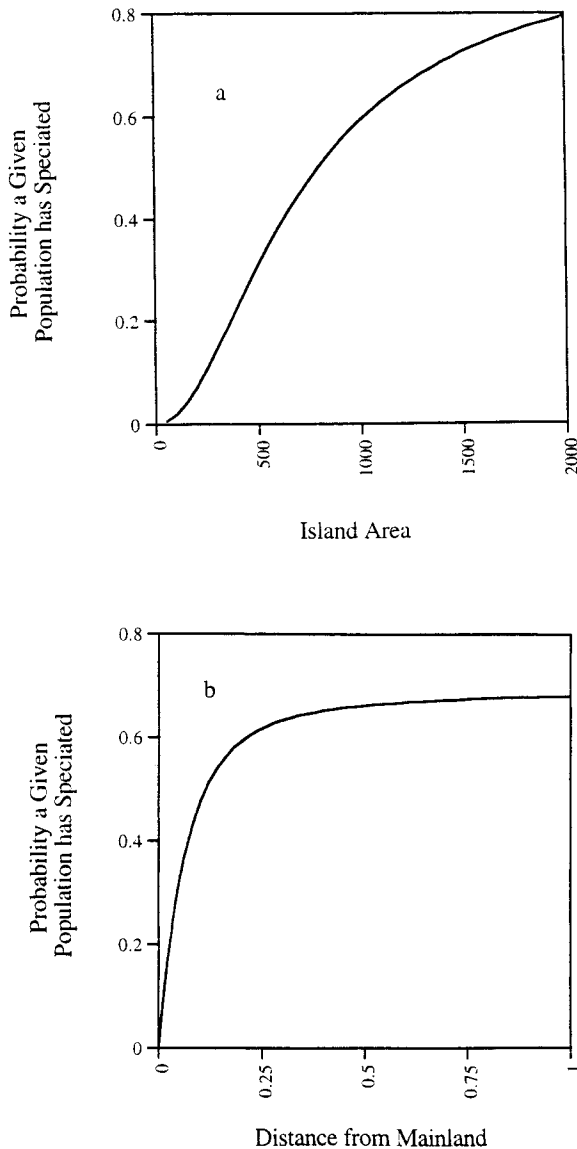
FIG. 7. The probability of speciation (from eq. 18) against (a) area, $x = 0.2$, $\gamma = 0.00001$, $\alpha = c_1 = c_2 = 1$; (b) distance, A = 1000, $\gamma = 0.00001$, $\alpha = c_1 = c_2 = 1$.

rates of both extinction and migrant allele fixation will cause the average allelic divergence to increase linearly with island size (see Fig. 4a). Island distance also has an influence on average allelic divergence. Because the immigration rate of new alleles from the mainland is higher for near islands, more divergent alleles are replaced with immigrant alleles at a higher rate than they are on distant islands. This has the effect of decreasing the average allelic divergence for close islands (Fig. 4b). These predictions could be tested by surveying populations on a wide variety of islands for the same locus (or across loci) and examining the correlation between average genetic divergence and island size and distance. The area effect should be stronger than the distance effect because the distance effect saturates at the point of no immigration.

Although extensive genetic data from island populations needed to test many of these predictions are not yet available,

estimates of divergence can be approximated by species endemism (which roughly equates with some level of morphological divergence). Under the model that incorporates speciation, we would predict that large islands should possess a larger proportion of populations described as species than should small islands (Fig. 7). In addition, distant islands should have a larger proportion of populations described as species than should close islands (Fig. 7). Mayr (1965) showed that the proportion of endemic bird species increased with the log of island size in several island groups. Adler (1992) more thoroughly examined patterns of endemism in birds of tropical Pacific islands and found that both island size and distance from the mainland were important predictors of the proportion of endemic species on islands. The results of these studies are consistent with predictions from our model. In addition to patterns of species endemism, examination of mitchondrial sequence divergences in doves (Johnson and Clayton 2000) and ducks (Johnson and Sorenson 1998) indicates that species on larger, more distant islands tend to be more divergent on average than species on smaller, close islands. However, there are not yet enough comparisons in these groups for valid statistical analysis.

Implications of Assumption Violation

Although we have assumed that colonization and extinction processes occur continuously in time, it is well known that islands vary in age (time of appearance out of the ocean). Whereas the age of the island will put an upper limit to allelic divergence times, it is unlikely to greatly affect the other predictions of the model if colonization and extinction are operating on a shorter time scale than island origins. Another possibility is that an island (or several islands in an archipelago) is formed by a rise in sea level such that populations are isolated on the island rather than being colonized through dispersal. In this case, the predictions of the model still hold, because divergence is still driven by the processes of immigration, substitution, and extinction. In this case, the time of the colonization event (T) is the island isolation event and the most divergent alleles (barring prior extinction) should date to the time of the isolating event.

We also assume that alleles change in frequency and substitute at rates according to predictions of strictly neutral models. If neutrality is violated, for example, under the nearly neutral models (Ohta 1992), then substitution rate may vary with effective population size. Under nearly neutral models, smaller island populations would be expected to possess a faster substitution rate relative to large mainland populations. This would have the effect of increasing the rate of genetic divergence on island populations. However, this elevated rate should affect all loci (of a particular type) in the same way such that the predicted distribution of allelic divergences (Fig. 2) still holds. If population size effects are large enough, however, the prediction of increased divergence on large islands might be compromised. Substitution rates in populations on large islands are expected to be lower than rates on small islands under the predictions of nearly neutral models (Ohta 1992). This could have the effect of eliminating or switching the direction of the pattern of divergence with island size under our model (Fig. 4a). An evaluation of the
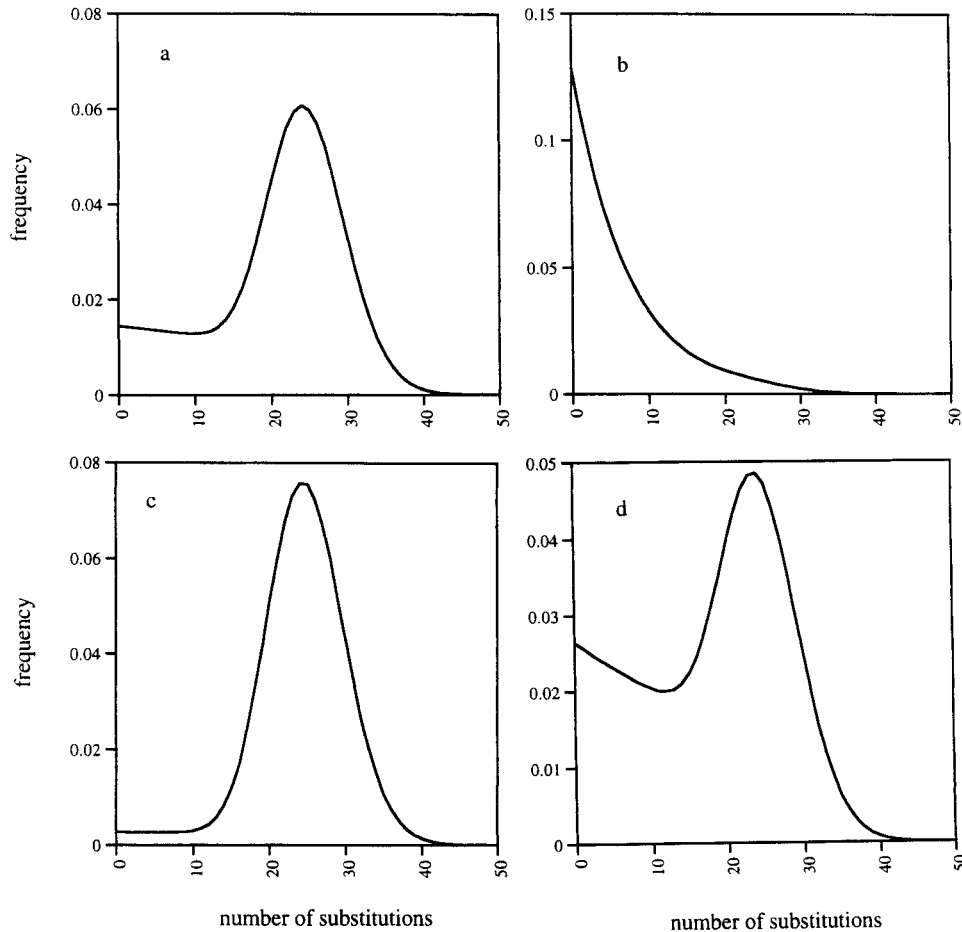
FIG. 8. Distribution of genetic divergences across loci under the island biogeography model with no speciation (from eq. 1) within a population. Equation (1) is combined with a Poisson mutation model, which results in a smoothing of the distribution. We plot the number of substitutions between island and mainland alleles across loci. Shown are populations on (a) large ($A = 1000$), close ($x = 1$); (b) small ($A = 100$), close ($x = 1$); (c) large ($A = 1000$), distant ($x = 2$); (d) small ($A = 100$), distant ($x = 2$) islands. $T = 2,500,000$, $k = 0.5 \times 10^{-5}$, $\alpha = 1$, and $c_1 = 4 \times 10^{-4}$ for each.

types of substitutions (e.g., synonymous vs. nonsynonymous) in island populations might help distinguish between nearly neutral models and our island biogeography model.

Another major assumption of our model is that colonization and migration occur only in the direction of mainland to the island. We have ignored colonization from other islands or migration back to the mainland population. However, this assumption could be tested by implementing thorough population sampling. For example, colonization from other islands (e.g., in the same archipelago) could be detected by constructing a gene phylogeny for samples from all island and mainland populations. If colonization has come from other islands, alleles from different islands should be more closely related to each other than they are to mainland alleles. Phylogenies of island taxa have the potential to reveal other interesting patterns that could be incorporated into our model, such as stepwise colonization of islands in a chain.

In comparisons across islands, we have assumed that different species are equivalent in terms of the parameters of the model. If parameters vary between taxa, our predictions could be compromised. In this case, however, variation in parameters will only add variance to the relationships of ge-

netic divergence with island size and distance and the overall trend should still be apparent, especially given a large sample of species. We suggest that across-island tests of our model use taxa with similar mutation rates, immigration rates, and effective population sizes to avoid confounding effects of variation in these parameters on genetic divergence.

We have tacitly assumed that the divergence of the mainland and island lineages occurred when the progenitor of the island allele left the mainland. Like any two alleles drawn from a population, the progenitor of the island allele and the allele destined to be the ancestor of a modern mainland allele would have already been diverging for some time. Coalescent theory gives the approximate distribution of this time (in generations) as exponential with mean equal to twice the effective population size on the mainland (Kingman 1982). Our results could be adjusted to include this time (e.g., the distribution given by eq. 4 should be convolved with the appropriate exponential distribution). However, this correction is only important in a certain region of parameter space. If the mean time since the movement of an allele from the mainland to the island ($1/[m + v]$) is much greater than the mean divergence time of two mainland alleles ($2N_e$), the cor-
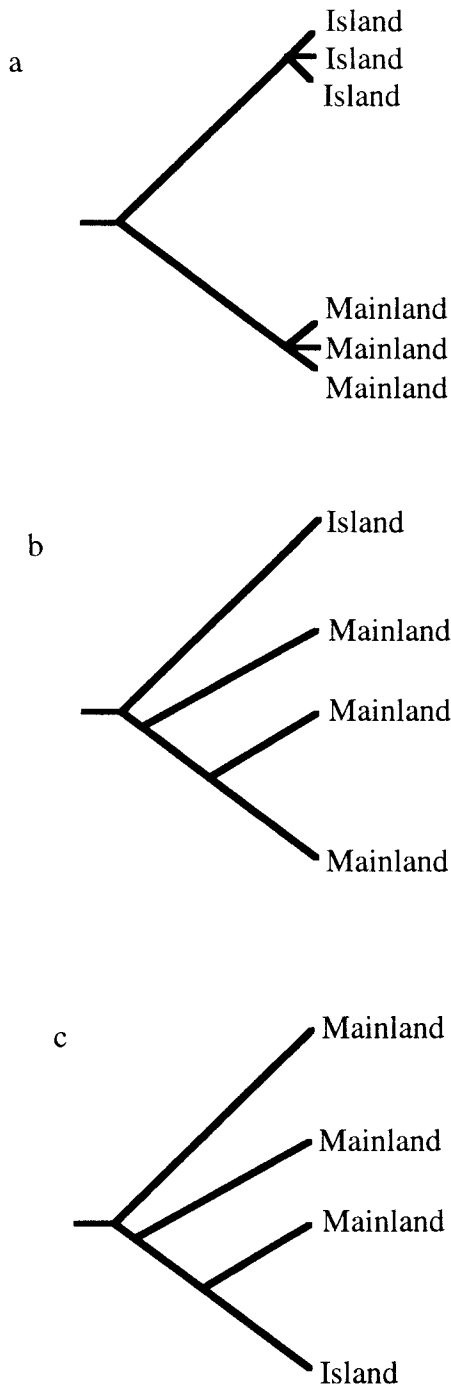
FIG. 9. Hypothetical phylogenies of island and mainland alleles. (a) Each forms a monophyletic cluster where no correction for within-mainland divergence would be necessary; (b) each is monophyletic, but large divergences within mainland indicate that a correction is needed for within-mainland divergence; (c) paraphyly of mainland alleles indicating that a correction is needed for within-mainland divergence.

rection will be small. However, if $1/(m + v)$ is small compared to $2N_e$, the island will not be significantly differentiated from the mainland. An island allele and a mainland allele would then be about as diverged as two mainland alleles. It

is only when $1/(m + v)$ and $2N_e$ are comparable that a correction is sensible.

One empirical approach to this problem is to evaluate several mainland alleles. In cases where the mainland alleles group in a tight cluster to the exclusion of island alleles, no correction would be necessary (Fig. 9a). This situation might occur if both the island and mainland populations are relatively small or a long time has passed since colonization. However, if mainland alleles show divergences approaching the distance to the island alleles (Fig. 9b) or if the island alleles fall within mainland alleles (Fig. 9c), then our method could be modified as suggested above to accommodate this added divergence. These situations might occur if the mainland population is very large, exhibits geographic structure, or a short time has passed since colonization.

Finally, if island size affects colonization, predictions from our model may be slightly different. The effect of area on colonization and migration could be added to the model. In general, increased migration with island size would lessen the effect of island area on genetic divergence because the increased migration to large islands would offset the decreased rates of extinction and substitution of new migrants. Although there is some evidence that immigration rates increase with island area, usually this will not be large enough to offset the effect of area on extinction rates (Brown and Lomolino 1998). Thus, we have not included the effect of island area on immigration in our model.

LITERATURE CITED

Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy, irregular landscapes. Theor. Popul. Biol. 45:41–75.

Adler, G. H. 1992. Endemism in birds of tropical Pacific islands. Evol. Ecol. 6:296–306.

Barton, N., and M. C. Whitlock. 1997. The evolution of metapopulations. Pp. 183–210 in I. Hanski and M. E. Gilpin, eds. Metapopulation biology. Academic Press, San Diego, CA.

Boorman, S. A., and P. R. Levitt. 1973. Group selection on the boundary of stable populations. Theor. Popul. Biol. 4:85–128.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. Am. Nat. 105:467–478.

Brown, J. H., and M. V. Lomolino. 1998. Biogeography. 2d ed. Sinauer Associates, Sunderland, MA.

Cairns, J., M. L. Dahlberg, K. L. Dickson, N. Smith, and W. T. Waller. 1969. The relationship of fresh-water protozoan communities to the MacArthur-Wilson equilibrium model. Am. Nat. 103:439–454.

Cox, G. W. 1990. Centers of speciation and ecological differentiation in the Galapagos land bird fauna. Evol. Ecol. 4:130–142.

Darlington, P. J. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. Ecol. Monogr. 13:37–61.

Gaggiotti, O. E. 1996. Population genetic models of source-sink metapopulations. Theor. Popul. Biol. 50:178–208.

Gilbert, F. S. 1980. The equilibrium theory of island biogeography: fact or fiction? J. Biogeogr. 7:209–235.

Hamilton, T. H., R. H. Barth, Jr., and I. Rubinoff. 1964. The environmental control of insular variation in bird species abundance. Proc. Natl. Acad. Sci. 52:132–140.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pp. 5–26 *in* I. Hanski and M. E. Gilpin, eds. Metapopulation biology. Academic Press, San Diego, CA.

Harrison, S., and A. Hastings. 1996. Genetic and evolutionary consequences of metapopulation structure. Trends Ecol. Evol. 11: 180–183.

Hartl, D. L., and A. G. Clark. 1989. Principles of population genetics. 2d ed. Sinauer Associates, Sunderland, MA.

Have, A. 1987. Experimental island biogeography: immigration and extinction of ciliates in microcosms. Oikos 50:218–224.

Johnson, K. P., and D. H. Clayton. 2000. Nuclear and mitochondrial genes contain similar phylogenetic signal for pigeons and doves (Aves: Columbiformes). Mol. Phylogenet. Evol. 14:141–151.

Johnson, K. P., and M. D. Sorenson. 1998. Comparing molecular evolution in two mitochondrial protein coding genes (cytochrome *b* and ND2) in dabbling ducks (Tribe:Anatini). Mol. Phylogenet. Evol. 10:82–94.

Kimura, M. 1968. Evolutionary rate at the molecular level. Nature 217:624–626.

Kingman, J. F. C. 1982. The coalescent. Stoch. Proc. Appl. 13: 235–248.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373–387.

———. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, NJ.

Mayr, E. 1965. Avifauna: turnover on islands. Science 150: 1587–1588.

McCauley, D. E. 1991. Genetic consequences of local population extinction and recolonization. Trends Ecol. Evol. 6:5–8.

Ohta, T. 1992. The nearly neutral theory of molecular evolution. Annu. Rev. Ecol. Syst. 23:263–286.

Orr, H. A., and L. H. Orr. 1996. Waiting for speciation: the effect of population subdivision on the time to speciation. Evolution 50:1742–1749.

Patrick, R. 1967. The effect of invasion rate, species pool, and size of area on the structure of the diatom community. Proc. Natl. Acad. Sci. 58:1335–1342.

Preston, F. W. 1962. The canonical distribution of commonness and rarity. Part I. Ecology 43:185–215.

Rannala, B. 1996. The sampling theory of neutral alleles in an island population of fluctuating size. Theor. Popul. Biol. 50:91–104.

Rannala, B., and J. A. Hartigan. 1995. Identity by descent in island-mainland populations. Genetics 139:429–437.

Sauer, J. 1969. Oceanic islands and biogeographic theory: a review. Geogr. Rev. 59:582–593.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278–296.

Slatkin, M. 1977. Gene flow and genetic drift in a species subject to frequent local extinctions. Theor. Popul. Biol. 12:253–262.

Vuilleumier, F. 1970. Insular biogeography in continental regions. I. The northern Andes of South America. Am. Nat. 104:373–388.

Wade, M. J., and D. E. McCauley. 1988. Extinction and colonization: their effects on the genetic differentiation of local populations. Evolution 42:995–1005.

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