

Islands, Equilibria, and Speciation

Ricklefs and Bermingham (1) demonstrated that divergence times of Lesser Antillean avifauna from sister taxa do not follow the exponential distribution predicted with constant colonization and extinction rates (2). Their explanation for this observation was a lack of equilibrium due to historical changes in colonization or extinction rates. However, they mistakenly estimated species numbers from the distribution of divergence time, and they neglected the possibility that migration and speciation could have generated the observed pattern.

Ricklefs and Bermingham have confounded the measured cumulative distributions with the time course of colonization of empty islands. Only the latter has an asymptote at the equilibrium number of species. The asymptote of the fitted exponential curve, at 30.8, differs from the total number of bird lineages on the Lesser Antilles not because the model is inadequate, but because it estimates only the number of data points, at 37. This “test” would have rejected the exponential prediction even if the data had fit an exponential distribution perfectly. The fitted constants, even in more complex models, cannot estimate absolute colonization rates, but only relative rates (e.g., the ratio of rates in a two-phase model).

The deviation from an exponential distribution is, however, supported by other tests. To explain that deviation, Ricklefs and Bermingham proposed temporal changes in extinction or colonization rates. They did not consider that island populations may receive migrants from a source population after colonization and that this process may cease when a reproductive barrier arises (speciation) (3). We used maximum likelihood to fit their data to five models: (i) the exponential distribution; (ii) variable extinction rate (two phase); (iii) a mass extinction event; (iv) migration with speciation occurring deterministically at a fixed genetic distance; and (v) migration with speciation times following an exponential distribution.

The exponential distribution can be rejected in favor of any of the other models, and the speciation and variable-rate models are all statistically indistinguishable (log likelihoods differ by much less than two). The migration-and-speciation models consistently estimate migration rates of about 140 per unit of genetic distance (about two to three fixations of migrant alleles per million years) and genetic distances for speciation in the range of 0.03 to 0.13

(support intervals include significantly lower values). This viable alternative model for the deviation from an exponential distribution deserves further consideration.

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Response: Most models of island biogeography (1) predict an exponential distribution of species ages at equilibrium. Accordingly, one can estimate colonization and extinction rates from the asymptotic accumulation of species with age. This distribution applies identically to faunal development of an empty island when colonization and extinction are linear with respect to increasing island diversity. Our concern was not with estimating the equilibrium number of species, which is a feature of the data, but rather with the fit of the species accumulation curve to an exponential distribution. Clearly, the fit is not there; our explanation for the discrepancy involved heterogeneous extinction or colonization rates, and we concluded that the system is not in equilibrium (2).

Cherry *et al.* present an important alternative to our analysis, because their model describes a nonexponential equilibrium distribution of divergence times under constant conditions. This is accomplished by creating two classes of island populations separated by a speciation divide (3). In the first class, continuing migration of alleles from continental source populations prevents differentiation until some incompati-

bility mechanism results in species formation and brings gene flow to a halt. After that point, a second class of island populations diverges at a more rapid rate, set, for example, by mutation and drift in the case of neutral alleles. Prior to speciation, divergence distances are exponentially distributed, with a mean asymptotically approaching $1/m$ (or less when extinction is a factor) as the time since initial colonization increases. The parameter m is the rate of fixation of migrant alleles in the island populations, estimated from our data by Cherry *et al.* to be 1.4 per percent mitochondrial DNA (mtDNA) sequence divergence. These populations thus accumulate at low divergence distances, compared with the larger increments in divergence between “speciated” taxa, matching the pattern observed in the Lesser Antillean avifauna.

The fits of the two models appear to be indistinguishable statistically, according to Cherry *et al.* Whether the two-class speciation model (3) provides a better explanation for the data than our heterogeneous-colonization-and-extinction model (2) can be tested by how well it predicts the geographic structure of genetic variation. Recurrent migration should result in cases in which divergence (d) from the source population increases with distance in the Lesser Antilles, with relationships ordered as [(mainland, nearer island), farther island]. Of 18 nonendemic species in our sample, only one [$d = 1.2\%$ (farther), 0.4% (nearer)] showed this pattern. Two others ($d = 0.8\%$, 0.1% ; $d = 0.9\%$, 0.9%) show multiple colonization of a single island, in one case from different sources (4). Beyond $d = 1.2\%$, genetic relationships group island populations within the Lesser Antilles rather than grouping individual island populations with the mainland source. Sympatric species of passerine birds generally differ by more than 3% mtDNA sequence divergence (5), which is consistent with the estimate by Cherry *et al.* of speciation distances between 3 and 13% divergence. Given the interval between migration events of $d = 1/1.4 = 0.7\%$ estimated by Cherry *et al.*, one would expect more evidence of multiple colonization. Along with evidence of occasional secondary expansion of taxa within the Lesser Antilles (6), observed phylogeographic patterns suggest that colonization from the mainland is episodic, with transiently high migration rates followed quickly by evolutionary independence and progressive genetic divergence. If that is true, the Johnson *et al.* model (3) would not predominate in this system. Regardless, additional work on the distribution of genetic variation in island populations and their continental sources is needed.

TECHNICAL COMMENTS

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