

Nonequilibrium Diversity Dynamics of the Lesser Antillean Avifauna

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MacArthur and Wilson's model of island diversity predicts an increase in the number of species until colonization and extinction are balanced at a long-term steady state. We appraise this model on an evolutionary time scale by molecular phylogenetic analysis of the colonization of the Lesser Antilles by small land birds. The pattern of accumulation of species with time, estimated by genetic divergence between island and source lineages, rejects a homogeneous model of colonization and extinction. Rather, our results suggest an abrupt, roughly 10-fold increase in colonization rate or a 90% mass extinction event 0.55 to 0.75 million years ago.

MacArthur and Wilson's (*I*) equilibrium theory of biogeography explains the number of species on islands as representing a balance between colonization and extinction. Accordingly, the biota of an island reaches a steady state at which the appearance of new species equals the disappearance of residents. Lack (2) argued instead that colonization was not limiting and that the ecological space on islands was filled with established populations that resisted replacement by new colonists. Both theories hold that the number of species on an island should be stable over long periods, but they differ with respect to the rate of accumulation of species and the prediction of species turnover.

Some aspects of the equilibrium theory of biogeography have been supported (3–7). However, most studies to date have addressed dynamics on ecological time scales (typically <100 years). Evolutionary time scales (> ~10⁴ years), which are applicable to the biotas of large islands and archipelagos (8–12), have been inaccessible because of the absence of detailed fossil records from islands.

Here, we use a molecular phylogenetic approach based on mitochondrial DNA (mtDNA) sequences to estimate relative colonization times of the avifauna of the Lesser Antilles. Many of these species are endemic (13), indicating that patterns of avian distribution and diversity in the archipelago are established over evolutionary time. We constructed phylogenetic hypotheses on the basis of mtDNA sequences (14) for island populations and continental sister populations or

sister taxa representing 39 lineages observed in 37 of the 65 species of land birds in the Lesser Antilles, including 30 of 38 passerine species (Passeriformes) (15). The relative time of colonization of each lineage was determined by the average genetic divergence (d_A) between Lesser Antillean populations and the closest sister population or sister species in Trinidad or Venezuela to the south or in the Greater Antilles to the north (Fig. 1).

We characterized the temporal pattern of colonization of the contemporary avifauna of the Lesser Antilles by plotting the cumulative number of species as a function of d_A between island and continental or Greater Antillean populations (Fig. 2). The resulting cumulative divergence curve shows a distinct change in slope at about 1 to 2% genetic divergence.

The simplest model for the gain and loss of taxa from an archipelago features constant colonization and extinction rates (6). Accordingly, lineages would become established in the Lesser Antilles at rate C , which is inde-

pendent of the number of lineages in the archipelago, and they would become extinct at rate M , which is independent of lineage age in the archipelago. The survival of Lesser Antillean lineages would be an exponentially declining function of time (x) since their arrival. Thus, the density distribution of extant lineages (L) with respect to time x since initial colonization of the archipelago would be

$$\frac{dL}{dx} = Ce^{-Mx} \quad (1)$$

For this model, the cumulative number of lineages at time t is the integral of the density function from $x = 0$ to t , that is

$$L(t) = \int_{x=0}^t Ce^{-Mx} = \frac{C}{M} (1 - e^{-Mt}) \quad (2)$$

This function is exponentially asymptotic to $L = C/M$, which represents the equilibrium number of lineages within the system (16).

The cumulative lineages function was fitted to the data in Fig. 2 (17) by nonlinear curve fitting (18), which estimated $C = 1701 \pm 132$ SE and $M = 55.2 \pm 5.0$ SE (Fig. 3A). Thus, the estimated equilibrium number of lineages (C/M) would be 30.8, i.e., considerably fewer than the number of extant lineages of land birds in the Lesser Antilles. Using the error mean square (MSE) as a goodness-of-fit criterion, we determined that this model fits the observed data poorly ($P = 0.995$) (19). The apparent lack of homogeneity in colonization and extinction rates of Lesser Antillean birds prompted us to explore heterogeneous models incorporating an abrupt change in these rates or an extinction event at some time in the past superimposed on homogeneous "background" rates of colonization and extinction.

A stepwise change in either colonization

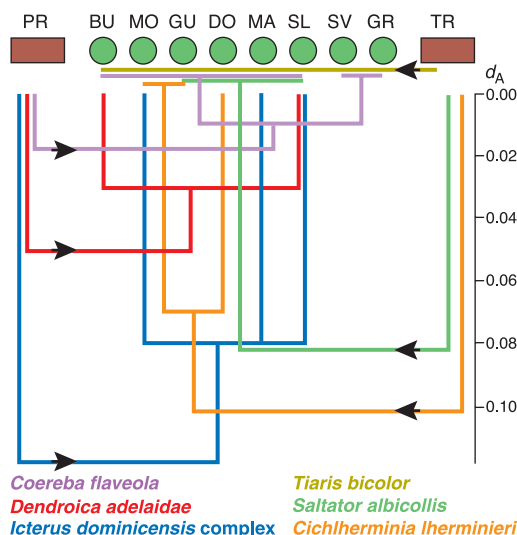


Fig. 1. Approximate phylogeographic relationships of populations of six species of passerine birds in the Lesser Antilles. The vertical scale of relative age is the mtDNA sequence divergence (d_A) between island populations and sister populations in external source areas [solid rectangles, Puerto Rico (PR) and Trinidad (TR)]. Major Lesser Antillean islands (solid circles), from north to south, are Antigua/Barbuda (BU), Montserrat (MO), Guadeloupe (GU), Dominica (DO), Martinique (MA), St. Lucia (SL), St. Vincent (SV), and Grenada (GR).

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or extinction rates would imply a similarly dramatic change in ecological conditions within the Caribbean Basin. Application of a molecular clock indicates that the change in slope of the lineage accumulation curve corresponds approximately to the onset of major Pleistocene glaciation, suggesting that climate and associated habitat change might have been a causative factor. An increase in arid, open habitat, possibly associated with drier climates during glacial periods (20) and combined with lowered sea levels and greater extent of exposed land, might have led to higher colonization rates. Climate fluctuations during the latter part of the Pleistocene could have resulted in higher extinction rates.

We constructed a model with different colonization and extinction rates before and after a break point (B) corresponding approximately to the inflection of the lineage accumulation curve in Fig. 2 (21). Comparably good fits were obtained for break-point values of genetic divergence (d_B) between 0.02 and 0.04; however, the estimated extinction rate before the break point [$M(>d_B)$] did not differ significantly from 0. We then estimated the value of $M(<d_B)$ associated with an unchanging colonization rate and $M(>d_B) = 0$. The error mean square was minimized when d_B was 0.026, at which point the estimated colonization rate (C) was 2433 ± 56 and $M(<d_B)$ was 110 ± 2 , or more than 100% per 1% sequence divergence (Fig. 3B). At such a high rate of archipelago-wide extinction one would expect frequent extinction of individual island populations. However, none of the younger lineages in the Lesser Antilles have gaps in their distributions indicative of extinct island populations. Thus, we feel that elevated archipelago-wide extinction is unlikely.

We also fitted a model with constant ex-

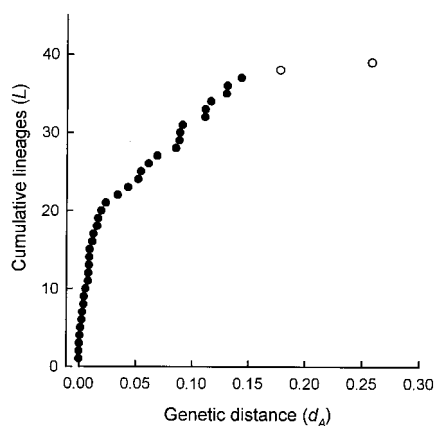


Fig. 2. Cumulative number of lineages of Lesser Antillean birds with increasing relative colonization time (genetic distance, d_A). The open symbols indicate two species for which d_A is probably overestimated owing to inadequate sampling of potential continental sister taxa. These are not included in the present analyses.

tinction rate and a change in colonization rate between $C(>d_B)$ and $C(<d_B)$ at break point B . The best fit occurred at $d_B = 0.011$, for which the estimate of M (3.8 ± 2.4) did not differ significantly from 0. With background extinction removed from the model, $d_B = 0.011$ continued to provide the best fit, for which $C(<d_B) = 1618 \pm 35$ and $C(>d_B) = 151 \pm 6$ (Fig. 3C).

As an alternative to a stepwise change in the colonization rate, we included a transient extinction event in an otherwise homogeneous colonization and extinction model. Potential causes would include a tsunami produced by a marine landslide (22) or deep-water bolide impact (23), which rarely leave superficial geological evidence (24). Hurricanes and volcanic eruptions are probably too localized to cause widespread extinction (25, 26), but loss of habitat following abrupt climate change might have a regional impact. To model an extinction event, we supposed that proportion S of existing lineages survived an event at time E . The best fit of this model to the data occurred at $d_E = 0.011$, for which $C = 1616 \pm 36$, $M = 3.8 \pm 2.5$ (not significantly different from 0), and $S = 0.120 \pm 0.020$. When background extinction

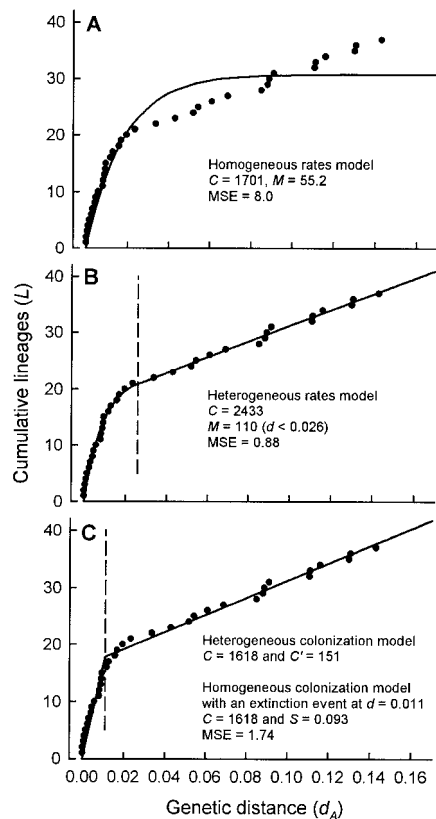


Fig. 3. (A) Best fit of a homogeneous rates model to the observed lineage accumulation curve. (B) Heterogeneous extinction rates model with a breakpoint at $d_A = 0.026$. (C) Heterogeneous colonization model or homogeneous colonization model with an extinction event ($S = 0.094$) at $d_A = 0.011$.

was deleted from the model ($M = 0$), $C = 1618 \pm 35$ and $S = 0.093 \pm 0.005$. The fit is identical to the model of step-wise increase in colonization rate (Fig. 3C) because the extinction of $1 - S$ lineages is equivalent to reducing the colonization rate to proportion S of its previous value.

Deleting background extinction (M) from the model of lineage dynamics eliminates the curvature in the lineage accumulation relation (Fig. 3B), which provided a better fit to the data for recent colonization events [i.e., $d_A < d_B$; compare Fig. 3B (MSE = 0.88) with Fig. 3C (MSE = 1.74)]. However, this curvature can be produced in the absence of background extinction by the stochasticity of nucleotide substitution combined with a change in colonization rates or a mass extinction event (Fig. 4). For a particular time of colonization (A), the number of nucleotide changes between a colonist and its source population is binomially distributed with mean knA , where k is the rate of nucleotide substitution and n is the number of nucleotides (842 for ATPase 6 and 8). We simulated the genetic divergence of 37 lineages colonizing the archipelago between the present and a point in the past equivalent to a genetic divergence ($d_A = kA$) of 0.15. In the model, the colonization rate increases in stepwise fashion by factor R at break point B . This is equivalent to a mass extinction event at time B with proportion $1/R$ of lineages surviving (27). The best fit of this stochastic substitution model was obtained for $B = 0.011$ and $R = 13$ (or $S = 0.077$) (28). For these parameters, 51% of the colonization events occurred during the more recent period ($A < B$) and the apparent colonization rates were 1705 ($A < B$) and 131 ($A > B$). As shown by the close fit to the data

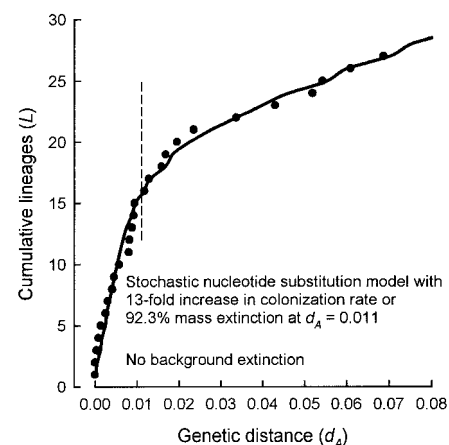


Fig. 4. Model of lineage accumulation with relative age in which genetic distance is estimated by a stochastic model of nucleotide substitution with a change in the colonization rate at $B = 0.011$. The apparent colonization rates are 1705 ($A < B$) and 131 ($A > B$). The genetic distance scale extends only to 0.08 to emphasize the fit to the more recent accumulation of lineages.

in Fig. 4, this model does not require background extinction within the archipelago.

Regardless of the cause of temporal heterogeneity, it is clear that Lesser Antillean avian biogeography has been dominated by nonequilibrium dynamics and that the number of species in the avifauna of the Lesser Antilles is, at present, far from equilibrium. The earliest extant colonists to the archipelago have d_A values on the order of 0.15, which because of the absence of significant background extinction may represent the beginning of the present avifaunal build up. Estimated times of subsequent colonization are consistent with two contrasting scenarios. One has a homogeneous colonization rate of about 1700 per unit sequence divergence (17 per 1% sequence divergence) and a transient extinction event involving more than 90% of all lineages at a relative time about $d_A = 0.011$ in the past. The other postulates a change in colonization rate from about 130 to 1700 per unit sequence divergence at about the same time. Calibrations for avian mitochondrial molecular clocks [~ 1.5 to 2% sequence divergence per million years (My)] (8, 29) place the origin of the contemporary avifauna at 7.5 to 10 million years ago (Ma) and the change in colonization rates or mass extinction event at 0.55 to 0.75 Ma. A colonization rate of 1700 is equivalent to only 26 to 34 new arrivals per My, or an average interval between arrivals of 29 to 39 thousand years.

Because there is no statistically detectable background extinction, the number of lineages in the Lesser Antilles apparently is not currently regulated by extinction around a stable number. The pool of potential colonists ultimately must limit the number of lineages in the archipelago; however, such an effect has not yet left a strong imprint on the observed lineage accumulation curve. When the number of lineages on an island approaches that of the pool of colonists in a linear model, new lineages should appear infrequently because most have already colonized the island and the lineage accumulation curve should decelerate and approach an asymptote (30). It does not. This suggests that the long-term pool of potential colonists is larger than the number of suitable taxa in the source area at any given time.

Dramatic events, possibly including mass extinction or the opening of a region to accelerated colonization, have kept the contemporary avifauna of the Lesser Antilles far from a steady state. History has left an enduring imprint on this system. MacArthur and Wilson's (1) emphasis on extinction and turnover appears not to apply to Lesser Antillean birds on an archipelago-wide basis, although extinction may be a prominent feature of individual island populations. In this case, the paucity of pre-human extinction among small land birds in the Lesser Antilles

as a whole may be due to occasional colonization phases of endemic taxa that re-establish individual island populations from within the archipelago, referred to as the taxon cycle (31, 32). Lack's idea of ecological limitation (2) also must be re-evaluated because the number of lineages in the Lesser Antillean avifauna appears to be limited by the rate of colonization and the archipelago is not close to saturation.

Clearly, one must exercise caution in applying equilibrium theories of homogeneous colonization and extinction to the numbers of species in island archipelagoes. Beyond the possible mass extinction event detected in the Lesser Antilles, there is little evidence for a "background" level of extinction. Moreover, the islands of the Lesser Antilles were nowhere near ecologically saturated with bird species (33) even before the arrival of human populations. Human-caused extinctions of birds and other animals have decimated island biotas in many parts of the world, including the West Indies (34). However, it is evident that the pre-human biotas of some of these islands were shaped by natural environmental changes or catastrophes of an even greater magnitude (35).

References and Notes

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14. Phylogenetic reconstructions were based on 842 base pairs (bp) of the partially overlapping mitochondrial ATPase 6 and ATPase 8 protein-coding genes. Relative time of colonization is estimated by Tamura-Nei genetic distances. Altogether, the analysis is based on 295 sequences from 161 island populations of 37 species of Lesser Antillean birds plus 82 sequences of Greater Antillean or continental sister taxa. For details, see *Science Online* at www.sciencemag.org/cgi/content/full/294/5546/1522/DC1.
15. Species and lineages do not match exactly because two radiations have occurred within the Lesser Antilles and several species include multiple colonization events. For additional information, see *Science Online* at www.sciencemag.org/cgi/content/full/294/5546/1522/DC1.
16. The cumulative number of lineages with progressively older colonization times is identical to the build up of lineages over time. Thus, looking back through time, $dL/dx = C - ML$, which can be rearranged and integrated to give $L(t) = C[1 - \exp(-Mt)]/M$.
17. Continental sampling for the two oldest coloniza-

tions was poor and these lineages were, therefore, deleted from analyses. Including these did not change results qualitatively. For details, see *Science Online* at www.sciencemag.org/cgi/content/full/294/5546/1522/DC1.

18. Proc NLIN (nonlinear regression) of the Statistical Analysis System (SAS), version 6.12 (SAS Institute, Cary, NC).
19. We generated data by simulating the homogeneous rates model with $C = 1701$ and $M = 55.2$. For each simulated data set, we produced 37 extant lineages by drawing colonization times at random from a uniform probability distribution between 0 and 0.15 genetic distance, followed by exponentially declining probability of survival to the present. This was repeated 1000 times. The MSE of the cumulative species-distance curve fitted to the observed data (8.0) exceeded 995 of the 1000 simulated values (mean, 2.2; median, 1.8).
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21. We modified the homogeneous model to the following expression (primed variables refer to $d_A > d_B$): cumulative number of lineages $L(d_A) = C[1 - \exp(-Md_A)]/M$ for $d_A < d_B$, and $L(d_A) = C[1 - \exp(-Md_B)]/M + \exp(-Md_B)C'[1 - \exp(M(d_A - d_B))]/M'$ for $d_A > d_B$. Models were fitted for values of d_B in 0.001 increments. For constant colonization and $M(>d_B) = 0$, the second expression becomes $L(d_A) = i[1 - \exp(-Md_B)]/M + \exp(-Md_B)C(d_A - d_B)$.
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27. Colonists were apportioned to the older ($A > B$) and more recent ($A < B$) time intervals in proportion to the product of the colonization rate and the length of the time interval. Colonization times were first randomly distributed between time intervals and then were randomly distributed within each time interval. For each colonization time (A), genetic divergence was determined at random from the binomial distribution

$$P(x|p) = \binom{n}{x} p^x (1-p)^{n-x}$$

where x is the number of nucleotide substitutions and p is equal to the expected proportion of substitutions, kA . The value of P was drawn at random from a uniform 0-1 distribution, and the equation solved for x using the RANBIN function of SAS, version 6.12 (SAS Institute, Inc., Cary, NC). The 37 divergence values were rank-ordered, and the simulation was repeated 1000 times and averaged to estimate the lineage accumulation curve with respect to genetic divergence. Goodness-of-fit (f) was calculated as the square root of the sum of the squared differences between observed and predicted divergence values.

28. The goodness-of-fit (f) was 0.0201 for these parameters. Fits to the model were only slightly less good for parameter combinations (R, B, f): 10, 0.014, 0.0224; 11, 0.013, 0.0222; 12, 0.012, 0.0209; 14, 0.010, 0.0205; and 15, 0.009, 0.0216.
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30. Constant colonization is unrealistic but there is no indication that the external species pool limits colonization rate. For further details see *Science Online* at www.sciencemag.org/cgi/content/full/294/5546/1522/DC1.
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