

Equilibrium speciation dynamics in a model adaptive radiation of island lizards

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Edited* by David B. Wake, University of California, Berkeley, CA, and approved November 5, 2010 (received for review May 30, 2010)

The relative importance of equilibrium and nonequilibrium processes in shaping patterns of species richness is one of the most fundamental questions in biodiversity studies. If equilibrium processes predominate, then ecological interactions presumably limit species diversity, potentially through diversity dependence of immigration, speciation, and extinction rates. Alternatively, species richness may be limited by the rate at which diversity arises or by the amount of time available for diversification. These latter explanations constitute nonequilibrium processes and can apply only to biotas that are unsaturated or far from diversity equilibria. Recent studies have challenged whether equilibrium models apply to biotas assembled through in situ speciation, as this process may be too slow to achieve steady-state diversities. Here we demonstrate that speciation rates in replicate Caribbean lizard radiations have undergone parallel declines to equilibrium conditions on three of four major islands. Our results suggest that feedback between total island diversity and per-capita speciation rates scales inversely with island area, with proportionately greater declines occurring on smaller islands. These results are consistent with strong ecological controls on species richness and suggest that the iconic adaptive radiation of Caribbean anoles may have reached an endpoint.

island biogeography | macroevolution | species-area relationship | ecological limits | phylogeny

Under MacArthur and Wilson's equilibrium model of island biogeography (1), a positive relationship between an island's area and its species diversity arises from a dynamic balance between the rate at which new species colonize an area and the rate at which species are lost due to extinction. For a given degree of isolation, larger islands should contain more species than smaller islands because they have lower rates of extinction and, potentially, increased rates of colonization. Although this model is clearly a simplification of processes influencing species richness (2, 3), it has nonetheless retained considerable explanatory power (2, 4, 5).

A number of recent analyses, however, suggest that nonequilibrium dynamics might prevail when speciation, as opposed to immigration, is the principal contributor to species richness (6, 7). In some systems, speciation rates may be too low relative to the age of a given island or geographic region to achieve equilibrium species numbers (6–8). In other cases, extinction pulses might occur with sufficient frequency that diversity never reaches equilibrium (9). Because speciation dominates the assembly of biotas on large islands and continents, understanding many patterns of species richness potentially requires a nonequilibrium, evolutionary theory of diversity. Such a nonequilibrium model of diversity would entail primary control of species richness by variation in net diversification rates, clade age, or time within regions (10–14).

Alternatively, species richness might be governed by a logistic growth process (15, 16), such that speciation and extinction rates reach a balance only when some island- or region-specific carrying capacity has been achieved. These models have been widely used in paleobiological studies to explain diversity dynamics at the largest temporal and spatial scales (17, 18), and some recent

studies on dated phylogenetic trees support speciation rate decline over time during evolutionary radiations, perhaps due to saturation of ecological niches with increasing species richness (19, 20). However, the evidence for equilibrium dynamics from more restricted phylogenetic and spatial scales is generally mixed, particularly for islands (7, 21–23).

The species diversity of reptiles and amphibians observed across the West Indian archipelago has been used to support both equilibrium, immigration-based and nonequilibrium, speciation-based explanations for the species-area relationship (1, 7, 24). Here, we test whether equilibrium or nonequilibrium macroevolutionary models best characterize patterns of diversification in the archipelago's most diverse lizard genus (*Anolis*). We focus on anole radiations that have occurred on the four large islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico), which resulted primarily from in situ speciation (7). Previous analyses suggested that speciation rates in Caribbean anoles reflect far-from-equilibrium dynamics, with relatively constant but island-specific diversification rates through time (7, 25). These results suggest that, at least for anoles, species richness within islands is limited by the rate at which diversity arises (e.g., the difference between the speciation rate, λ , and the extinction rate, μ) and not by ecological limits on diversification or island-specific carrying capacities (14). However, the nonequilibrium model has never been tested using methods that explicitly allow for temporal variation in rates of species diversification through time. If net diversification rates ($\lambda - \mu$) in *Anolis* follow the equilibrium model, we predict that (i) island-specific declines in diversification should occur on each of the four major islands of the Greater Antilles and (ii) rates should decline more quickly to an equilibrium on smaller islands, consistent with the hypothesis that small islands have lower carrying capacities than large islands.

Results

We used the state-dependent speciation-extinction (SSE) framework that has previously been used to study the relationship between character states and diversification rates (26–28), extended to include dynamic processes of character change, speciation, and extinction. The binary-state (BiSSE) model (27) describes the probability that a lineage in state k at some point in time will evolve into a clade identical to the observed clade, given a particular set of speciation (λ_0, λ_1), extinction (μ_0, μ_1), and character transition (q_{01}, q_{10}) parameters. By assuming that lineage dispersal between islands can be modeled as a transition between character states on a phylogenetic tree, we can use a generalization of this model to study the dynamics of diversification in Caribbean anoles. Let $D_i(t)$ be the probability that

Author contributions: D.L.R. and R.E.G. designed research, performed research, contributed new reagents/analytic tools, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1007606107/-DCSupplemental.

a lineage in state i at time t evolves into a clade identical to the observed clade, and let $E_i(t)$ be the corresponding probability of clade extinction before the present. For each character state, we obtain a pair of differential equations that describe changes in $D_i(t)$ and $E_i(t)$ through time,

$$\frac{dD_i}{dt} = -\left(\mu_{i,t} + \lambda_{i,t} + \sum_{j=1}^{j \neq i} q_{ij,t}\right) D_i(t) + \sum_{j=1}^{j \neq i} q_{ij,t} D_j(t) + 2\lambda_{i,t} E_i(t) D_i(t)$$

and

$$\frac{dE_i}{dt} = \mu_{i,t} - \left(\mu_{i,t} + \lambda_{i,t} + \sum_{j=1}^{j \neq i} q_{ij,t}\right) E_i(t) + \sum_{j=1}^{j \neq i} q_{ij,t} E_j(t) + \lambda_{i,t} E_i(t)^2,$$

where $\lambda_{i,t}$ and $\mu_{i,t}$ are the rates of speciation and extinction for the i th character state at time t , and where $q_{ij,t}$ is the rate of character change from state i to state j at time t . For n character states, computing the probability of the observed data given the model and parameters requires that we solve $2n$ ordinary differential equations that jointly describe the dynamics of speciation, extinction, and state change along each branch of a phylogenetic tree (*SI Materials and Methods*). We assume that rates of speciation, extinction, and dispersal change linearly through time, such that

$$r(\tau) = \max\left\{0, r_0\left(1 - \frac{\tau}{K}\right)\right\},$$

where r_0 is the initial rate at the root node of the complete tree ($\lambda_{i,0}$, $\mu_{i,0}$, or $q_{ij,0}$), τ is time measured from the root node, and K controls the rate of change in speciation, extinction, or dispersal through time.

We applied this framework to a phylogenetic tree for Greater Antillean *Anolis* (29) that was 88% complete at the species level (Figs. S1 and S2) and modified initial values for D_i and E_i to account for incomplete taxon sampling. Implementation of the model requires an appropriate rate matrix describing possible dispersals between islands (e.g., $q_{ij,t} = q$ for a one-rate, time-constant symmetric model). We used maximum likelihood to evaluate 12 alternative time-constant or time-varying dispersal models (*Materials and Methods*, *SI Materials and Methods*, Table S1, and Fig. S3). Models with temporal declines in the rate of dispersal between islands fit the data much better than those with time-invariant dispersal ($\Delta\text{AIC} = 19.2$ in favor of models with temporal variation in q ; Table S1). This result may also be consistent with the possibility that between-island speciation events reflect early vicariance of Antillean proto-islands, rather than among-island dispersal (30).

We then incorporated this “background” biogeographic model into a series of diversification models that allowed speciation and extinction dynamics to vary among islands. Our candidate set of models included a model with a common time-invariant speciation rate (λ) across all islands (model 1: GlobalConstant), a model with island-specific but time-invariant λ (model 2: IslandConstant), a model with “global” changes in diversification rate (model 3: GlobalVariable), and two models with island-specific linear change in λ through time (model 4: IslandVariable; and model 5: IslandVariableFull). The IslandVariableFull model has separate λ_0 and K parameters for each island, whereas IslandVariable is a reduced model with a common starting rate λ_0 at the root node of the tree. For each model of speciation described above, we considered variants with and without extinction (*Materials and Methods*).

The GlobalVariable model describes a scenario where speciation rates across the entire Greater Antillean radiation have changed with a common underlying dynamic that is independent of the island to which each lineage belongs. Including these models

enables us to distinguish island-specific dynamics from well-known biases that can lead phylogenetic studies to infer spurious declines in speciation rates through time (19, 31, 32). If apparent rapid speciation at the base of a phylogeny is an artifact of tree construction, sampling biases, and inadequate models of molecular evolution, we should observe superior fit of the GlobalVariable model. This model would also be expected to fit the data well if diversification rates have changed during the course of the anole radiation in response to a common climatic driver.

Our results strongly reject the hypothesis that island-specific but time-invariant diversification underlies patterns of anole species richness in the Greater Antilles (Table 1). The conditional probability of the two constant rate models (*Materials and Methods*) is very low ($P < 0.0001$). Rather, our results support the hypothesis that speciation rates have declined independently on each island (Fig. 1), against a background of low extinction (Table 1). The best-fit model specified independent linear declines in the rate of speciation on each island (IslandVariable; conditional probability = 0.811), and the second-best model was the IslandVariableFull model ($P = 0.184$). Together, these island-specific decline models account for 0.995 of the total probability of the data explained by the candidate set of models and do not support the hypothesis that lineage accumulation patterns in *Anolis* reflect global drivers of diversification or artifacts of tree construction. If the IslandVariableFull model is excluded, the conditional probability of the IslandVariable model is very high ($P = 0.994$). These results are robust to phylogenetic uncertainty (Fig. S4); virtually identical results are obtained under alternative biogeographic models, including a simple model with symmetric time-invariant dispersal rates between islands (Table S2). Models without extinction consistently fit the data better than the corresponding models with extinction (Table 1).

We estimated occupancy probabilities and lineage accumulation curves for each island under the best-fit diversification model (Fig. 2); these curves suggest relatively rapid accumulation of lineages on Hispaniola, Puerto Rico, and Jamaica. In conjunction with rate estimates under the best-fit model, these results imply equilibrium or near-equilibrium conditions on Puerto Rico, Hispaniola, and Jamaica; speciation rates on each island have declined to a small fraction of the inferred initial rate (Fig. 1). Only the largest island, Cuba, appears to have potential for substantial species accumulation. Our results further suggest that the rate of decline in speciation through time is negatively correlated with island area: Proportionately more rapid declines occur on smaller islands ($\rho = -0.92$, $P = 0.056$; Fig. 3), suggesting that per-lineage feedback between speciation rates and total species richness is greater on small islands. This negative correlation is robust to uncertainty in phylogenetic tree topology and branch lengths (Fig. S5).

We simulated phylogenetic trees and character state data under maximum-likelihood parameter estimates for GlobalConstant, GlobalVariable, IslandConstant, and IslandVariable models to assess whether the fitted models could reconstruct major features of the observed data. Simulated distributions of species richness under the IslandVariable model were closer to the observed data than alternative models that did not allow island-specific changes in speciation through time (Fig. 4). The GlobalVariable model underpredicts species richness on Cuba relative to the IslandVariable model and overpredicts richness on both Jamaica and Puerto Rico (Fig. 4; Table S3). Analyses of branch length distributions from simulated trees further suggest that the IslandVariable model provides a much better match to the observed data than alternative models specifying global changes in speciation rates or constant speciation through time (Fig. S6). Taken together, these results suggest that models with independent, island-specific changes in speciation rates through time provide a better absolute fit to the observed data than

Table 1. Diversification models specifying dynamic or time-invariant rates of speciation (λ) and extinction (μ) fitted to the maximum clade credibility (MCC) tree for the Greater Antillean *Anolis* radiation

Model	Description	LogL	AIC (np)	AIC_EX (np)	Δ_i
IslandConstant	Rates differ among islands but are constant through time	-40.84	93.68 (6)	101.7 (10)	0
GlobalConstant	Rates are constant through time and among lineages	-43.81	93.62 (3)	95.6 (4)	0
GlobalVariable	Linear change in rates through time; no differences between islands	-32.12	72.24 (4)	74.8 (6)	0.005
IslandVariableFull	Island-specific linear change in rates through time	-22.36	64.72 (10)	74.08 (18)	0.184
IslandVariable	Island-specific linear change in rates through time; shared r_0 (λ_0, μ_0)	-23.96	61.92 (7)	66.58 (12)	0.811

LogL and AIC give log-likelihoods and AIC scores for models formulated without extinction ($\mu = 0$), and AIC_EX gives the corresponding AIC for the models with extinction ($\mu \geq 0$). The number of parameters in each model (np) is given in parentheses after the AIC score. Δ_i : conditional probability of the i th model given the candidate set of models. Models without extinction ($\mu = 0$) fit the data better than the corresponding model with extinction in all cases.

models assuming constant rates through time or global changes in the rate of speciation.

Discussion

The extent to which biological diversity is regulated by diversity-dependent, equilibrium processes relative to diversity-independent, nonequilibrium processes is a fundamental question in evolutionary ecology. Our results provide evidence for parallel declines in speciation rates in radiations of *Anolis* lizards on the four major islands of the Greater Antilles. These results are consistent with a diversity-dependent model involving a decline in speciation rates as species richness and ecological disparity increase (5, 19, 20, 31, 33, 34), possibly reflecting a role for ecological opportunity as a driver of speciation in Caribbean anoles (35, 36). Recent work suggesting that diversification of phenotypic traits associated with ecological specialization also declined through time during the anole radiation further supports this scenario (29, 37).

Our results further suggest that three of four islands are at or near equilibrium diversity and that equilibrium diversity is

a function of island area (Fig. 3). One explanation for the higher diversity on larger islands involves the presence of multiple ecologically similar species occurring in geographic isolation; for example, both Cuba and Hispaniola harbor multiple species of montane twig and trunk-crown ecomorph anoles that are endemic to isolated mountain ranges (30). Larger islands also support more species specialized for geographically distinct macrohabitats. Hispaniola, for example, is home to eight species of allopatrically or parapatrically distributed trunk-ground anoles restricted to distinctly different forest types (e.g., montane, lowland mesic, and lowland xeric). A third aspect of increased diversity on larger islands appears to involve finer-scale partitioning of habitats available across islands of all sizes (30); sympatric anole assemblages on Cuba and Hispaniola, for example, may contain more species than the entire island-wide fauna of Jamaica (38).

Our analyses reject models that posit a shared decline in diversification rates across islands in favor of alternative models where speciation dynamics vary among subtrees assigned to dif-

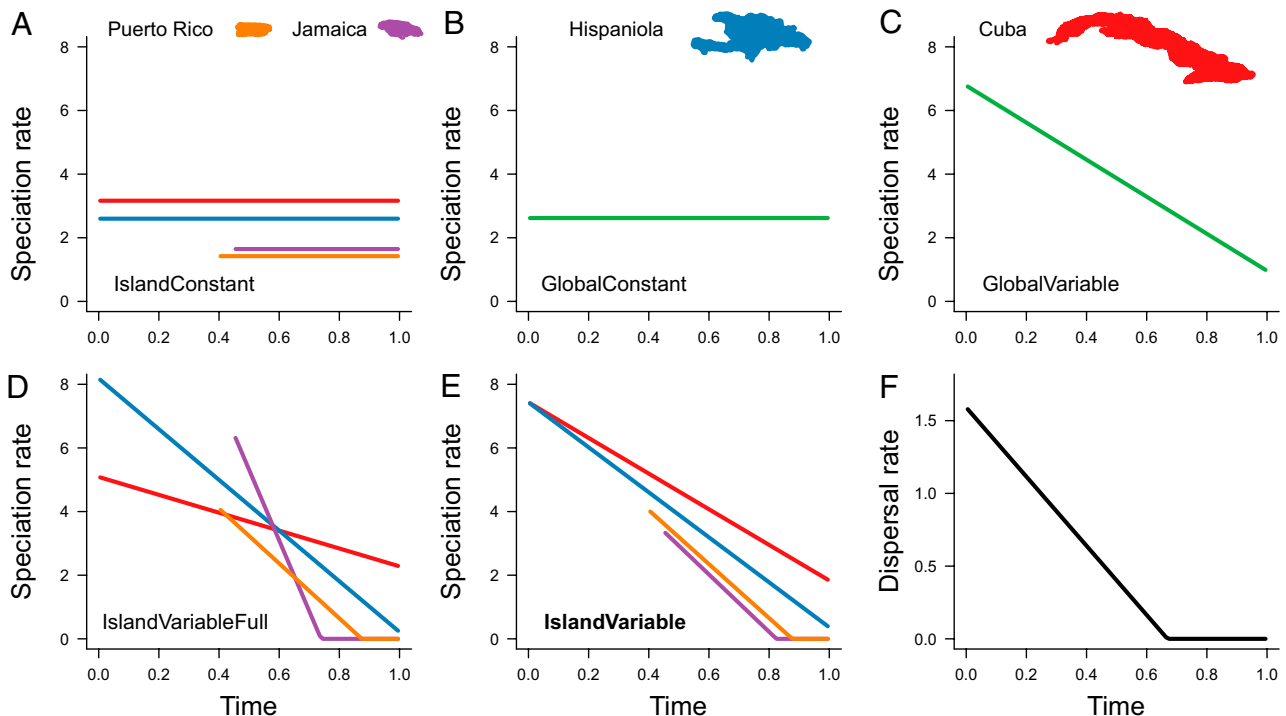


Fig. 1. (A–E) Reconstructed speciation-through-time curves under five diversification models fitted to the *Anolis* phylogeny (Fig. 2, Fig. S1). Green curves denote models without state-dependent diversification; other colors describe speciation dynamics on Cuba, Hispaniola, Jamaica, and Puerto Rico. Models are sorted (left to right, top to bottom) from lowest to highest conditional probability (Table 1). Models with island-specific changes in speciation (D and E) account for $P = 0.995$ of the total probability of the data taken across all models. The maximum-likelihood estimate of the dispersal rate between islands under the IslandVariable model is shown in F. Rates are shown in relative time units, as the tree was scaled to basal divergence of 1.0.

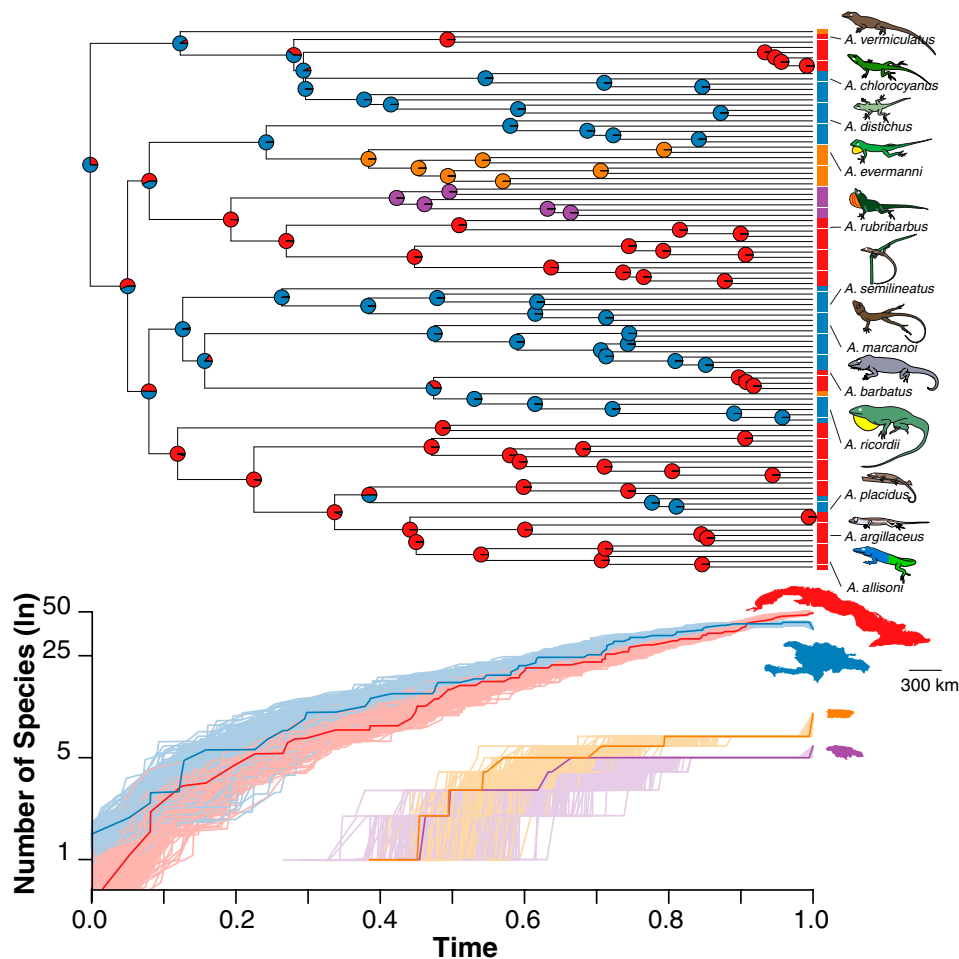


Fig. 2. *Anolis* MCC tree with reconstructed island occupancy probabilities and lineage accumulation curves for Cuba (red), Hispaniola (blue), Jamaica (purple), and Puerto Rico (orange). Occupancy probabilities on internal nodes were estimated under the overall best-fit model (IslandVariable). The MCC tree with all taxon labels is shown in Fig. S1.

ferent islands (Table 1) and add an important dimension to the interpretation of diversification patterns typically seen in molecular phylogenies (19, 20, 39, 40). A criticism of diversity-dependent speciation, as inferred from molecular phylogenies, is that this pattern might simply be an artifact of phylogeny reconstruction or taxon sampling. For example, use of inadequate models of mo-

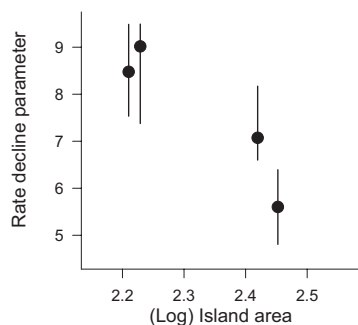


Fig. 3. Island-specific rate-decline parameters as a function of island area for (from left to right) Puerto Rico, Jamaica, Hispaniola, and Cuba. The rate-decline parameter is the slope of the relationship between speciation and time ($-\lambda_0/K$). Confidence intervals reflect uncertainty in tree reconstruction and represent the 0.025 and 0.975 percentiles of the distribution of parameter estimates taken across the posterior distribution of trees sampled with BEAST.

lecular evolution can lead to apparent slowdowns in the rate of speciation through time (32), but phylogenies affected by this bias should not have been favored by models with island-specific speciation dynamics. Likewise, if *Anolis* contains additional cryptic species diversity that has not been accommodated by our analyses, we would observe an artifactual slowdown in speciation toward the present in the full *Anolis* phylogeny. However, such incomplete sampling would require proportionately greater cryptic diversity on the smallest islands, which have undergone the most severe slowdown in speciation through time (Fig. 3). This pattern of undersampling is unlikely given the considerable attention received by Puerto Rican and Jamaican anole faunas relative to those of Cuba; despite this work, no new species have been described on either island since the 1960s, whereas new species continue to accumulate on Cuba (30).

Elucidating the role of extinction from molecular phylogenies is notoriously difficult (41–44). However, among anole lineages that left present-day descendants, extinction appears to have been negligible, and our results suggest that the decline in net diversification rates on each island has been mediated by declining speciation rates against a background of very low extinction. There is no evidence from explicit modeling of extinction rates (Table 1 and Table S2) or from visual inspection of lineage accumulation plots (Fig. 2) for substantial species turnover during the historical occupancy of each island. It is possible that many species have gone extinct, but the dominant signal is of a tendency

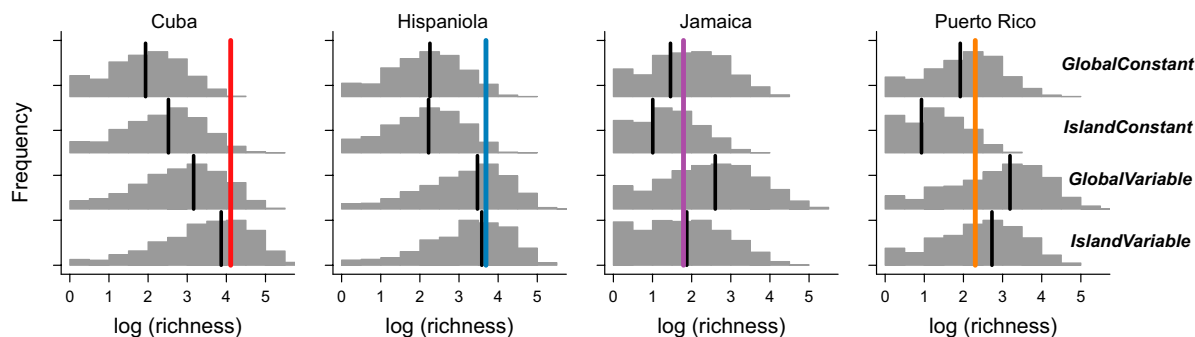


Fig. 4. Distribution of species richness for islands of the Greater Antilles predicted under (*Top to Bottom*) GlobalConstant, IslandConstant, GlobalVariable, and IslandVariable models. Colored lines denote observed species richness on each island; black lines and histograms represent mean values and distributions tabulated from 2,000 datasets simulated under maximum-likelihood parameter estimates for each model. The GlobalVariable model underpredicts species richness on Hispaniola and overpredicts richness on both Jamaica and Puerto Rico relative to the IslandVariable model.

for lineages that arose during the earliest stage of each island's radiation to persist to the present: Any subsequent extinction events have failed to leave a signature that can be inferred from molecular phylogenies. This result is consistent with previous analyses that have documented a tendency for major ecological types to have arisen early during the radiation of anoles on each island (29). Such a pattern might be expected if there are strong ecological limits on species diversity and if species tend to give rise to ecologically similar species. Even if extinction rates are high, comparatively little phylogenetic turnover within island communities would occur once diversity reached saturation, because any particular extinction event would be followed by a speciation event from an ecologically similar member of the same major lineage.

When all Caribbean *Anolis* communities are considered together (7), our results imply that communities assembled through speciation have proportionately greater equilibrium diversities than are attained when immigration is the sole source of new species. This hypothesis follows from the observation that the slope of the species–area curve for Caribbean anoles is greater for islands with appreciable in situ speciation (7) than for immigration-derived island assemblages; qualitatively similar patterns occur in Caribbean butterflies (2). This result is not simply a manifestation of the “small island effect,” whereby demographic stochasticity on smaller islands may eliminate the expected relationship between island area and species richness (2); rather, immigration-derived anole communities show a positive species–area relationship (7, 25). Further support for this pattern follows from the observation that the slope of the species–area relationship for oceanic archipelagoes is positively correlated with mean island endemicity (45). It is unclear why the scaling relationship between area and equilibrium diversity might change when speciation becomes the dominant contributor to regional diversity, but these observations suggest fundamental differences between communities assembled through speciation and immigration/dispersal.

The variation in species richness among geographic regions, such as the islands we consider here, potentially results from differences in rates of species diversification (11, 13, 46) as well as the ages of constituent clades (12, 47). With the possible exception of Cuba, our results argue against these nonequilibrium processes and suggest that anole species richness is primarily determined by island-specific limits on total diversification (14). These findings have implications for how we study the variation in species richness among geographic regions: If faunas derived principally from in situ speciation typically reach steady-state diversity, then variation in species richness must result in large part from ecological interactions (3) and not necessarily from variation in clade age and net rates of species diversification (14, 48–50).

Materials and Methods

Phylogeny Reconstruction. We analyzed ultrametric phylogenetic trees generated by Mahler et al. (29), consisting of 189 species and comprising an ~1,500-bp region of mitochondrial DNA extending from the beginning of the NADH dehydrogenase subunit 2 (ND2) gene and including five tRNAs before ending shortly after the start of the cytochrome c oxidase (COI) gene (see *SI Materials and Methods* for details). We fit all diversification models to 400 trees sampled without replacement from the set of pruned trees generated by Mahler et al.'s BEAST analyses.

Diversification Analyses and Biogeographic Model Selection. The modeling framework described here allows for an extremely large candidate set of models and poses a challenging combinatorial problem. Even with simple linear changes in parameters through time, we must potentially consider 8 speciation rates (e.g., initial and final rates for each of four islands), 8 extinction rates, and 24 dispersal rates (12 initial rates and 12 final rates). Rather than consider hundreds of possible biogeographic models, we evaluated 12 key models against a diversification background of time-constant but island-specific differences in speciation (see *SI Materials and Methods* for details; Table S1, Fig. S3). These models included a simple 1-parameter symmetric scenario with equal rates between all island pairs, a 2-parameter symmetric model with rates changing linearly through time, and a full 12-parameter asymmetric model. The best-fit model from this analysis (Table S1) was selected as a background model for all subsequent diversification analyses and allowed only the following transitions: q_{21} , q_{12} , q_{13} , and q_{24} (Cuba, 1; Hispaniola, 2; Jamaica, 3; Puerto Rico, 4). Note that dispersal parameters were estimated separately for each diversification model shown in Table 1. Virtually identical results for diversification were obtained when we considered simpler alternative biogeographic models (Table S2). We accounted for incomplete sampling by setting initial states $D_i(0)$ and $E_i(0)$ equal to f_i and $1 - f_i$, where f_i is the proportion of species on island i that have been sampled (26). For models with extinction, extinction functions through time were mirror images of those used for speciation. For example, GlobalConstant with extinction had time-invariant rates λ and μ for all lineages, and IslandVariable with extinction had a common μ_0 term and separate K terms for each island. Additional details are given in *SI Materials and Methods*.

Model Adequacy and Comparisons. We used Akaike weights to estimate the probability of each model conditional on the Akaike Information Criterion (AIC) scores observed in the candidate set of models (51). See *SI Materials and Methods* for details. To assess model adequacy, we developed a continuous-time phylogenetic tree simulation program in R to generate trees and character state data under all SSE models described here. We simulated 2,000 trees under maximum-likelihood parameter estimates for GlobalConstant, IslandConstant, GlobalVariable, and IslandVariable models and computed a series of summary statistics to assess the match between the simulated data and the *Anolis* MCC tree. We tabulated the numbers of species in each character state at the end of the simulation, to determine whether simulated patterns of species richness matched those observed in the Greater Antilles (Fig. 4). We then computed two summary statistics that described the distribution of branch lengths associated with particular island states: the mean and coefficient of variation in terminal branch lengths associated with each character state (*SI Materials and Methods*; Fig. S6). The best-fit model (IslandVariable) outperformed the other candidate models for all three summary statistics.

ACKNOWLEDGMENTS. We thank A. Agrawal, J. Huelsenbeck, I. Lovette, A. McCune, A. Phillimore, R. Ricklefs, K. Wagner, and members of the Glor lab for comments on the manuscript and/or discussion of these topics. This research was supported by US National Science Foundation Grants DEB-

0814277 and DEB-0920892, by the Fuller Evolutionary Biology Program at the Cornell Laboratory of Ornithology, by the University of Rochester, and by the Miller Institute for Basic Research in Science at University of California, Berkeley.

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