

A major shift in diversification rate helps explain macroevolutionary patterns in primate species diversity

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Primates represent one of the most species rich, wide ranging, and ecologically diverse clades of mammals. What major macroevolutionary factors have driven their diversification and contributed to the modern distribution of primate species remains widely debated. We employed phylogenetic comparative methods to examine the role of clade age and evolutionary rate heterogeneity in the modern distribution of species diversity of Primates. Primate diversification has accelerated since its origin, with decreased extinction leading to a shift to even higher evolutionary rates in the most species rich family (Cercopithecidae). Older primate clades tended to be more diverse, however a shift in evolutionary rate was necessary to adequately explain the imbalance in species diversity. Species richness was also poorly explained by geographic distribution, especially once clade age and evolutionary rate shifts were accounted for, and may relate instead to other ecological factors. The global distribution of primate species diversity appears to have been strongly impacted by heterogeneity in evolutionary rates.

KEY WORDS: BAMM, cercopithecidae, lineage diversification, mammals, phylogenetic imbalance, phylogenetic comparative methods.

Primates is one of the largest (>400 species), most ecologically diverse, socially complex, and broadly distributed orders of mammals (Lefebvre et al. 2004; Dunbar and MacDonald 2013; Fahy et al. 2013; Tran 2014). As a consequence, considerable interest has been placed in how Primates have diversified and the factors contributing to the uneven distribution of species diversity across its major clades (Fabre et al. 2009; Stadler 2011; Springer et al. 2012). Modern Primates span 16 families, which vary considerably in species richness (Figs. 1 and 2)--from the monotypic Daubentoniidae (Aye-Aye) to the diverse Cercopithecidae (Old World monkeys, >100 species). A number of studies have focused on investigating patterns of lineage diversification within Primates; these have suggested discrete speciation or extinction rate shifts in particular clades (e.g., Cercopithecidae and Galagidae, Purvis et al. 1995; Anthropoidea, Lemuriformes and Macaca, Fabre et al. 2009) or at specific times (e.g., increases in the late Miocene, slowdowns in the Pleistocene; Springer et al. 2012). Other comparative analyses have linked changes in primate lineage diversification to biogeographic or ecological factors (Gomez and Verdu 2012; Rolland et al. 2014). For example, primate diversity peaks toward the equator (Fig. S1), and a combination of increased speciation and decreased extinction has been proposed to contribute to the high species richness of Primates in the tropics (Rolland et al. 2014). This hypothesis, however, is not well supported within the largest primate family (Cercopithecidae). It has also been proposed that changes in diversification rates among Primates may be associated with changes in geographic range size, with larger geographic ranges enhancing speciation rates potentially as a result of increased allopatric speciation (Gomez and Verdu 2012). This diversification pattern is consistent with patterns of increasing range overlap as node level increases in some primate tribes (largely consistent with allopatric speciation; Barraclough 1998; Kamilar and Martin 2009). Contrastingly, some analyses have found higher species richness in



Figure 1. Species richness in primate families. Species counts are derived from the IUCN red list, with additions from recent taxonomic descriptions or revisions (see Methods). Dark gray = Strepsirrhini, light gray = Haplorhini.

species with small ranges (Eeley and Foley 1999). More complex scenarios, such as changing opportunities following extinction events (Meredith et al. 2011; Perelman et al. 2011; Springer et al. 2012), changing climatic conditions (Springer et al. 2012), or cycles of habitat contraction and expansion (Kamilar and Martin 2009; Guschanski et al. 2013), have also been proposed as driving primate diversification trends.

Overall, there remains considerable debate on the major factors influencing primate diversification and their impact on species richness. Importantly, most previous studies of primate diversification have not applied comparative methods that can simultaneously accommodate processes occurring broadly across a phylogeny (e.g., changing diversification through time) as well as discrete, clade-specific shifts in evolutionary rates. Failure to account for such a mixture of processes may bias parameter estimates, for example of clades of differing ages (Rabosky 2010, 2014; Rabosky and Glor 2010). Additionally, rarely have studies subsequently investigated the extent to which proposed diversification rate changes or shifts actually contribute to patterns of primate diversity, for example with posterior predictive approaches (Slater and Pennell 2014). These are critically needed to understand if and how historical and ecological factors have shaped heterogeneity in evolutionary rates, and the uneven species diversity observed among modern primate clades.

In the following analyses, we seek to use modern tools to address the impact of three factors that have been previously linked to the distribution of species diversity across a variety of clades (e.g., McPeek and Brown 2007; Wiens 2011; Pyron and Burbrink 2013; Morlon 2014; Rabosky 2014; Stadler et al. 2014), and that are likely to have influenced species richness and patterns of diversification in Primates: (1) time, (2) evolutionary rate heterogeneity, and (3) geographic distribution. Using a published, time-calibrated phylogeny (Springer et al. 2012), we test for diversification rate heterogeneity by applying a recently developed Bayesian Markov Chain Monte Carlo (MCMC) method that is capable of accommodating a mixture of evolutionary rate regimes, including both continuous and discrete processes. This Bayesian MCMC method also accounts for missing lineages under a conservative assumption of constant evolutionary rates (Rabosky 2014). With an evolutionary-simulation approach, we further examined whether and how changing evolutionary rates through time and within specific clades has had an impact on the unevenness in species diversity across primate families and across the evolutionary history of primates. Lastly, to investigate if changes in diversification rates among Primates are associated with changes in geographic range, we tested for relationships between species richness and geographic variables while accounting for factors such as clade age and evolutionary rate heterogeneity. Altogether, these new analyses clarify the strong influence of clade age and changes in diversification rate among the largest clade on the distribution of species diversity across Primates.

Methods primate phylogenies

We took phylogenetic relationships and divergence times from a supermatrix analysis of 69 nuclear and 10 mitochondrial genes from 367 species, with 14 fossil calibrations applied in a "MCMC tree" analysis in PAML (Yang 2007; Springer et al. 2012). Divergence time analyses in the aforementioned study used either autocorrelated or independent rates, and either hard or soft-bounded divergence time constraints, for a total of four divergence time scenarios (Springer et al. 2012). To account for uncertainty associated with the divergence times in primates, we carried out all subsequent analyses across each of the four phylogenies available from Springer et al. (2012). After eliminating synonymized taxa from the phylogenies following the International Union for Conservation of Nature's "Red List" (IUCN 2015), we retained subtrees containing a total of 340 primate species from the original set of 367 (>80% of the total primate species diversity) for lineage diversification. Phylogenies, as well as BAMM control files and R scripts for functions (see below), are provided via Dryad (DOI:10.5061/dryad.q51ph).



Figure 2. Patterns of primate diversification rates from BAMM analyses. (A) Prior and posterior distribution of diversification rate shifts from a Bayesian analysis of lineage diversification in primates; (B) Primate phylogeny with branch lengths scaled to the mean marginal odds ratio (across all four phylogenies) for a shift occurring per branch (scale bar givens the length of a 10-fold increase in the probability of a rate shift); (C) Primate phylogeny (AS) with branches colored by median diversification rate as summarized from its BAMM posterior distribution. The first and second best supported rate shifts are given as (i) and (ii) respectively. Species names follow Springer et al. (2012). Family abbreviations: Gal = Galagidae, Lor = Lorisidae, Dau = Daubentoniidae, Lem = Lemuridae, Lep = Lepilemuridae, Che = Cheirogaleidae, Ind = Indriidae, Tar = Tarsiidae, Pit = Pitheciidae, Ate = Atelidae, Ceb = Cebidae, Cal = Callitrichidae, Aot = Aotidae, Hom = Hominidae, Hyl = Hylobatidae, Cer = Cercopithecidae; (D) Diversification, speciation and extinction rates through time across the posterior distribution of BAMM analyses of the AS primate phylogeny. Lines give the median values from the posterior distribution, while shaded areas give the 95% confidence intervals.

DIVERSIFICATION ANALYSES

We employed a recently developed Bayesian approach to estimate discrete shifts in lineage diversification rates across the evolutionary history of primates. We conducted a Bayesian Analysis of Macroevolutionary Mixtures (Rabosky 2014) (bamm-project.org) using the "BAMM" software package (v. 2.5), and the R package "BAMMtools." BAMM implements reversible jump, Metropolis Coupled Markov Chain Monte Carlo, and allows for both timedependent speciation rates as well as discrete shifts in the rate and pattern of diversification. To account for incomplete taxon



Figure 3. Macroevolutionary cohorts across primates; (A) cohort matrix illustrating the cumulative posterior probability (across all four divergence time scenarios) of any two primate species belonging to the same diversification rate regime; (B) standard deviation of the posterior probabilities (for evolutionary cohorts) across the four phylogenies examined.

sampling, we determined the percentage of species sampling per genus where possible (e.g., except for polyphyletic genera, such as *Galago* and *Cercopithecus*, see Springer et al. 2012; see Supplementary Materials). We relied on IUCN taxonomic classifications (IUCN 2015), with the exception of recent taxonomic descriptions or revisions (Thinh et al. 2010; Gregorin and De Vivo 2013; Munds et al. 2013; Thiele et al. 2013; Marsh 2014; Lei et al. 2015; Li et al. 2015).

We sampled four MCMC chains of 10 million generations every 10,000 iterations, with a burn-in of 10%, for each phylogeny. We set the prior distribution of the number of shifts (as shown in Fig. 1) so that a regime with zero shifts was the most likely condition (BAMM parameter "expectedNumberofShifts" = 1). We selected phylogeny-specific diversification rate parameter priors ("lambdaInitPrior," "lambdaShiftPrior," and "muInitPrior") for each of the four phylogenies using the R function "setBAMMpriors." We calculated the effective sample size and examined trace plots for posterior distribution of (1) the likelihood of the rate regime and (2) the number of rate shifts in each regime using functions from the R package "coda." Given some recent criticisms of BAMM (Moore et al. 2016), especially in regards to the influence of the prior on the posterior distribution of rate shifts in versions prior to 2.5, we ran additional BAMM analyses on all four phylogenies using two extreme values of "expectedNumberofShifts" (0.1 and 10; Fig. S2). All three priors resulted in nearly identical posterior distributions of rate shifts (Fig. 2 and Fig. S2). Across all trees, the highest probability shift positions (see below) remained the same across priors (results not shown),

which is consistent with the results of follow-up evaluations of BAMM (Mitchell and Rabosky 2016; Rabosky et al. 2017).

The prior probability of a rate shift is proportional to the length of a branch in the phylogeny, and therefore longer branches have had greater shift opportunities (Rabosky 2014). We computed the average marginal odds ratio (branch-specific or "marginal" Bayes-factor, *sensu* Shi and Rabosky (2015) as the ratio of the posterior to prior probability of a shift occurring along each branch across all phylogenies. For each phylogeny, we also identified the number of core-shifts (defined here as those shifts with a marginal odds ratio > 10) and the frequency of each unique configuration of core-shifts using the R function "distinctShift-Configuration" (threshold = 10). We determined median speciation, extinction, and net diversification rates for each of 100 temporal slices across the posterior distribution of the BAMM analyses of each phylogeny.

MACROEVOLUTIONARY COHORTS

Macroevolutionary cohort analysis assesses whether pairs of taxa are likely to have evolved under a common inherited evolutionary rate regime (Rabosky et al. 2014a). For each sample in the posterior distribution of a BAMM analysis, each pairwise comparison (between species) is assigned a 1 if they have evolved under the same regime, and 0 if they evolved under different regimes. Summarizing across the posterior distribution of BAMM analyses, the resulting matrix (i.e., "cohort matrix"), provides the posterior probability of two species belonging to the same evolutionary regime (Rabosky et al. 2014a, 2015; Shi and Rabosky 2015). It



Figure 4. Clade age and species richness relationships in Primates. Age and species richness were analyzed using PGLS (dashed line = regression line, shaded region = 95% prediction interval), results from the AS phylogeny shown; (A) Species richness versus age in accepted primate taxonomic families; (B) Species richness vs. age using a stringent time-based criterion (stem age > h (median taxonomic family age) > crown age) to defined subclades as "families."

is important to note that longer branches are more likely to have experienced a rate shift under the BAMM model (Rabosky 2014), which may result in lower cohort matrix values for species in clades separated by older divergence times. We determined the mean cohort matrix across the four phylogenies, and determined the standard deviation of the cohort matrix pairwise values to indicate the uncertainty in cohort membership associated with divergence time variation.

AGE-SPECIES RICHNESS RELATIONSHIPS

We tested for a relationship between the crown age of primate families and their species richness using phylogenetic generalized least squares (PGLS; Grafen 1989) regressions with a Brownian Motion (BM) correlational structure, which accounts for the evolutionary nonindependence of lineages. We excluded Daubentoniidae, the monotypic family of the Aye-Aye, because its crown age could not be included and stem ages are considered less reliable for age-species richness analyses (Stadler et al. 2014). To determine the effect of incomplete lineage sampling, we contrasted species richness per family both from the number of tips in the phylogeny and previous literature counts with clade age (see BAMM methods). We log-transformed species counts per family prior to PGLS, as lineages accumulate exponentially under a pure-birth process (Rabosky et al. 2012; Bloom et al. 2014; Stadler et al. 2014; Shi and Rabosky 2015).

Stadler et al. (2014) showed that taxonomic classifications may bias age-species richness relationships toward nonsignificant or negative results. Such bias may be resolved by using a stringent phylogenetic definition of taxonomic levels. We defined "Families" using the Sibley-Ahlquist model, as those lineages whose crown age is younger than time *h* and whose stem age is older than time *h* (Sibley and Ahlquiest 1990; Stadler et al. 2014). We repeated the PGLS analysis of \log_{10} species richness (based on tips in the phylogeny) using a time-based criterion for subclades, based on *h* being equal to the median primate family crown age for each phylogeny, and after removing monotypic "families." To ensure that the results were not unique to the single chosen value of *h* for each tree, we also used values of h +5 Ma to -5 Ma, in 1 Ma steps (see Table S2).

PHYLOGENETIC IMBALANCE

Shi and Rabosky (2015) described a method for measuring timespecific phylogenetic imbalance (the extent to which lineages vary in diversity) based on the variability of species richness occurring across contemporaneous subclades. As such, we characterized phylogenetic imbalance as the variance in the log-transformed descendant species richness across all lineages present at a particular time in the phylogeny. We extended this analysis by adopting the posterior predictive methods applied to several other comparative phylogenetic analyses (Slater and Pennell 2014) to assess the significance of this metric of phylogenetic imbalance under a number of null evolutionary scenarios.

We calculated the observed phylogenetic imbalance (PI_{obs}) and the imbalance calculated from a series of 1000 simulated trees with 340 extant tips (PI_{sim}) across 100 uniformly distributed temporal slices across each phylogeny (Fig. 5). Simulated phylogenies were generated under a series of models, including a constant rate birth-death process, a time-variable birth-death process, and a time variable birth-death process with the best supported rate shift from BAMM analyses (see Results). Similar to the morphological

Model	Tree	λ_1	μ_1	\mathbf{k}_1	λ_2	μ_2	k_2
Birth-death, constant rate	AS	0.304	0.231	_	_	_	_
	AH	0.291	0.219		_		
	IS	0.486	0.435				
	IH	0.416	0.359	_	_		_
Birth-death, variable rate	AS	0.159	0.152	0.0198	—	—	
	AH	0.111	0.111	0.0183	—		
	IS	0.260	0.334	0.0178	—		
	IH	0.282	0.341	0.0103	—	—	
Discrete shift model (w/variable rates)	AS	0.174	0.187	0.0141	0.323	0.015	0.0029
	AH	0.171	0.167	0.0139	0.343	0.0174	0.0022
	IS	0.254	0.324	0.0118	0.463	0.0216	0.0024
	IH	0.281	0.355	0.0111	0.485	0.0477	0.0026

Table 1. Diversification rate parameters for Primates under three evolutionary models.

Median diversification parameter values (λ = speciation [# lineages/Ma], μ = extinction [# lineages/Ma], k = scaler, change in speciation through time). Parameters were calculated from the function "birthdeath" in the R package "ape" (constant rate) and from BAMM analyses of primate phylogenies (variable rates and discrete shift). Where multiple regimes were estimated, λ_1 , μ_1 , and k_1 give the root process and λ_2 , μ_2 , and k_2 give the cercopithecid regime values.



Figure 5. Patterns of phylogenetic imbalance through time among primates. Black, solid lines display the phylogenetic imbalance, as measured by the variance of log (descendant species richness) for each lineage present in the phylogeny (AS divergence times) at each of 100 points in time (Pl_{obs}). Gray lines show the phylogenetic imbalance for a sample of 100 simulated phylogenies (Pl_{sim}). Dashed lines show the median imbalance per time slice in the phylogeny across 1000 simulated phylogenies; (A) Primate phylogenetic imbalance compared to expectations under a constant rate model; (B) Primate phylogenetic imbalance compared to expectations under the BAMM rate shift model (faster diversification among cercopithecids and changing diversification rates through time).

disparity index (MDI) in "disparity-through-time" analyses (Slater and Pennell 2014), we quantified total phylogenetic imbalance as the area between the PI_{obs} curve (Fig. 6 dark, solid lines) and the median PI values of all simulated curves (Fig. 5, dashed lines). Henceforth, this value is referred to as the Descendant Variability Index (DVI). Positive values of DVI indicate that the number of descendant species is more unevenly distributed across contemporaneous subclades in the phylogeny than expected under a particular generating process (Shi and Rabosky 2015). The posterior predictive *P*-value was calculated as the frequency of the (1000) simulated DVI values greater than the observed DVI (Slater et al. 2010; Slater and Pennell 2014). The median values of speciation, extinction, and timedependent rate from the posterior distribution of each of the four BAMM analyses (Table 1) were used to simulate phylogenies. We used the function "tess.sim.taxa.age" from the R package "TESS" to simulate trees under constant rate and variable rate processes, based on the number of primate species (n = 340) and the root age for each phylogeny. Trees with a discrete shift were generated by simulating separate phylogenies (with proportional species numbers), which were subsequently combined at the appropriate ages using the R function "bind.tree" from the package "ape." We calculated DVI after truncating the first and last 15% of time in the phylogeny, to account for the low sampling of

Phylogeny	h (Ma)	intercept (SD)	slope (SD)	Р
Taxonomic families				
AS	NA	1.07 (0.365)	0.0114 (0.0153)	0.473
AH	NA	1.11 (0.368)	0.00862 (0.0144)	0.561
IS	NA	1.08 (0.381)	0.0120 (0.0169)	0.492
IH	NA	1.09 (0.380)	0.0108 (0.0155)	0.500
Time-based "families"				
AS	18.1	0.530 (0.255)	0.0378 (0.0132)	0.0097^{*}
AH	18.0	0.527 (0.243)	0.0366(0.0134)	0.0131*
IS	13.2	0.509 (0.295)	0.0519 (0.0165)	0.0052^{*}
IH	13.7	0.494 (0.281)	0.0497 (0.0154)	0.0042^{*}

Table 2. Clade age-species richness relationships across Primates.

Results of PGLS analysis of log (species richness) on clade age under a taxonomic definition of primate families and a stringent time-based categorization (h) of "family" (Sibley and Ahlquiest 1990; Stadler et al. 2014). *Indicates significant values (P < 0.05). The intercept is given in log(species) and the slope is given in log(species)/Ma. The cutoff age for time-based "families" is given as h in Ma before present. For taxonomic families, n = 15, for time-based "families", n = 22.

lineages early in the tree and incomplete taxon sampling toward the present, respectively (Slater et al. 2010; Shi and Rabosky 2015).

RELATIONSHIPS BETWEEN SPECIES RICHNESS AND BIOGEOGRAPHY

We obtained species distributions shapefiles from the IUCN mammal distribution database and analyzed them using functions from the R packages "sp," "rgeos," "rgdal," and "geosphere." We calculated the absolute value for the centroid latitude of each species distribution, so that these measures represented distances from the

Tree	Diversification model	DVI	\mathbf{p}_{pp}
AS	Birth-death	14.3	0.032^{*}
	Time-variable birth-death	14.8	0.076
	Cercopithecidae shift	11.4	0.118
AH	Birth-death	13.3	0.023^{*}
	Time-variable birth-death	13.6	0.012^{*}
	Cercopithecidae shift	10.6	0.126
IS	Birth-death	17.6	0.037^*
	Time-variable birth-death	18.3	0.060
	Cercopithecidae shift	17.2	0.105
IH	Birth-death	15.3	0.035^{*}
	Time-variable birth-death	15.9	0.045^{*}
	Cercopithecidae shift	16.5	0.130

Table 3. Summary of phylogenetic imbalance analyses.

DVI is the area between the observed and simulated phylogenetic imbalance curves across 100 temporal slices across the phylogeny (see Fig. 5); higher values indicate higher variance in species richness per lineage than expected. Posterior predictive *P*-values were calculated using a distribution of 1000 simulated trees with 340 tips, per primate phylogeny and diversification model.

*Indicates significant values (P < 0.05).

equator (Santana et al. 2013). We determined the total geographic range (in km² using the R function "areaPolygon," from the package "geosphere") from each shapefile and log_{10} transformed it. We measured degree of sympatry as the sum of a species' territory shared with other members of its genus (Santana et al. 2013), scaled by the total area occupied by the target species (e.g., 1 unit = a species shares 100% of its range with one congeneric, or 50% of its range with each of two congenerics, etc.). We made comparisons among congenerics because secondary sympatry is more common in older lineages (Barraclough 1998) and congenerics are more likely to be similar in morphology and ecology. This measurement did not appear to be biased by range size or species richness per genus (results not shown).

We used PGLS to investigate the impact of each of these three geographic variables on the phylogenetic distribution of primate species diversity. We determined the mean of each geographic variable for each of the time-based subclades (stem age > h >crown age, see age-species richness methods) and compared them to the log species richness for each subclade (Table 4, Fig. 6). The cercopithecid subclade appeared as an outlier in some comparisons (Fig. 6C, right) and may have undergone a major diversification rate shift (see results), so all PGLS analyses were repeated after excluding this family. Additionally, to account for the potential impact of clade age, we calculated timecorrected richness (residuals of species richness on clade age; Table 2) and tested these values against all geographic variables (Table 4).

Results lineage diversification of primates

In a Bayesian MCMC analysis of discrete evolutionary rate shifts occurring across the primate phylogeny, we found strong

		Log-species richness, all subclades $(n = 22)$	Log-species richness, without cercopithecids $(n = 21)$	Time-corrected log-richness, all subclades $(n = 22)$	Time-corrected log-richness, without cercopithecids $(n = 21)$
Latitude (absolute °)	coef.	0.0224: 0.0290	0.0200: 0.0243	0.0290: 0.0416	0.0237: 0.0390
	P-value	0.195: 0.358	0.267: 0.395	$0.0368: 0.143^{*}$	$0.0300: 0.196^{*}$
Geographic range size (log km ²)	coef	-0.124: -0.0353	-0.124: -0.0716	-0.0575: 0.0133	-0.102: 0.00304
	P-value	0.536: 0.826	0.523: 0.646	0.672: 0.986	0.425: 0.983
Sympatry (proportion of range)	coef	0.824: 0.984	0.455: 0.613	0.609: 0.633	0.191: 0.339
	<i>P</i> -value	$0.0249: 0.0385^{*}$	0.200: 0.275	0.0520: 0.0653	0.309: 0.567

Table 4. Results of PGLS analyses of primate subclade (stem age > h > crown age) log-species richness on four geographic variables.

Analyses were carried out on the full 22 polytypic subclades (see Table 2), after excluding cercopithecids (n = 1) and also using the residuals of the PGLS of log species richness on subclade age (Ma). Regression coefficients (coef.) and *P*-values are given as min: max, across 4 phylogenies. *Indicates *P* < 0.05 on at least one phylogeny.

evidence for evolutionary rate heterogeneity, with the posterior distribution differing strongly from the prior (Fig. 2A). Across the four phylogenies examined (differing in models for divergence time estimation, see methods), Bayesian Analysis of Macroevolutionary Mixtures (BAMM) most frequently reconstructed a single rate shift, followed by two rate shifts (Fig. 2A). No posterior distribution contained a regime with no rate shifts (compared to an expected frequency of 50% under the prior).

The most frequent core shift (i.e., shifts occurring above the background rate; marginal odds ratio > 10), occurred at the base of Cercopithecidae (Fig. 2C, shift i). This shift was observed across 70.7% of the cumulative posterior distribution of all four phylogenies, and was the most frequent core shift on three of four phylogenies, and the second most frequent on the remaining tree (Fig. S2). This rate shift configuration also showed the largest mean branch-specific Bayes factor (marginal odds ratio), across the primate tree (Fig. 2B). A rate shift at the base of Simiiformes was the second most frequent core shift (Fig. 2C, shift ii), occurring in 29.4% of the posterior distribution of evolutionary regimes, and the most frequently reconstructed rate shift on one tree ("AH" divergence times, and see Fig. S1). Some rate shift configurations included a core shift at the base of Platyrrhini (8.0% of the posterior distribution) or Lepilemuridae (8.4% of the posterior distribution), alongside one of the two primary rate shifts within cercopithecids or Simiiformes (Fig. S2). However, these did not occur within all four phylogenies. Once excluding non-core shifts (marginal odds ratio < 10), a model of no discrete rate shifts represented only 1.1% of rate shift configurations (Fig. S1).

All evolutionary rate regimes showed an increase in net diversification rates through time (Fig 2, Fig. S1, and Table 1). Across the highest posterior probability regime, cercopithecids exhibited an increase in net lineage diversification compared to noncercopithecids evolving under the root evolutionary regime (Fig. 2D). While cercopithecids exhibited a moderate increase in the rate of speciation (Fig. 2D), they also showed a slower acceleration of speciation through time (Table 1). Rather, the increased net diversification rate is largely attributable to a substantial decrease in the rate of extinction (6.67–13.4% of the root extinction rate across the four phylogenies; Fig. 2D).

MACROEVOLUTIONARY COHORTS

Patterns of lineage diversification in Primates were dominated by two macroevolutionary cohorts, one representing the root rate regime, and another occupied exclusively by cercopithecids (Fig. 3A). Noncercopithecid Simiiformes showed the highest phylogenetic-uncertainty associated with cohort analyses (Fig. 3B), with intermediate average posterior probabilities and an overall greater likelihood of belonging to the root regime.

AGE-SPECIES RICHNESS RELATIONSHIPS

We found no significant relationship between crown age and species richness within families, whether analyses were based on the full species sampling (Table 2; Fig. 4A), or only those lineages present in the phylogenies (*P*-values 0.62–0.70; slope values 0.00616–0.00768). Comparatively, when a stringent, time-based criterion was used to select "families" (i.e., all subclades where stem age > time h > crown age), clade age and species richness were significantly and positively correlated across all



Figure 6. Comparison of macroevolutionary cohorts and geographic distribution of 334 primate species. Variables from top to bottom are, (A) absolute latitude of the centroid of the species distribution, (B) geographic range size (area in log (km²)), (C) degree of sympatry measured as the total overlapping area of all congenerics scaled by the range size of the species. Left column: phenogram of geographic distribution variables on the AS primate phylogeny (ancestral values estimated under BM). Red node indicates the origin of Cercopithecidae, Middle column: density histogram of geographic variables within cercopithecids (blue) and other primate clades (red). Right column: log of species richness compared to the mean value of each geographic variable per time-based subclade (cercopithecid = blue, other primate clades = red).

phylogenies for h = median family crown age (Table 2; Fig. 4B). Almost all alternative values of h (h + 5Ma to h – 5 Ma before present) also showed a significant and positive relationship between richness and age, with the exception of two early values (+5Ma) where sample size was small and h was older than almost all primate families (Table S2). A time-based taxonomic criterion (h = median family crown age) preserved most simian families (all except Pitheciidae), but subdivided families in Strepsirrhini as well as Tarsiidae (Fig. 4B). This indicates a simian bias in taxonomic classification systems. Based on the stringent, time-based definitions of primate families, cercopithecids were unusually species rich for their crown age (i.e., showed very large, positive residuals across all trees, see Fig. 4B). Removal of cercopithecids from either PGLS analyses did not alter the significance of the relationships, which also remained positive (results not shown).

PHYLOGENETIC IMBALANCE

Phylogenetic imbalance, measured as the variance in species diversity among lineages through time using DVI (see methods), showed that all primate phylogenies examined were significantly more imbalanced than expected under a constant rate birth-death process (Table 3). Allowing for time-variable speciation rates (a nonshift BAMM model) increased some, but not all, P-values $(P_{pp} = 0.012 - 0.105)$. Only by including a diversification rate shift among cercopithecids did all phylogenies show nonsignificant DVI values (Table 3). Phylogenetic imbalance plots also illustrate the considerably greater similarity between the observed PI values and those simulated under a rate shift process, when compared with a simple birth-death process (Fig. 5). Observed and median simulated imbalance values were nearly identical over the posterior third of the phylogeny when a shift in diversification rate was incorporated into the null, simulated distribution (Fig. 5B, dashed vs dark lines).

SPECIES RICHNESS—GEOGRAPHIC DISTRIBUTION RELATIONSHIPS

Compared to other primates, extant cercopithecids are characterized by living at slightly lower latitudes, having slightly larger geographic ranges, and being highly sympatric with congenerics (on average). However, they overlap substantially with other primate clades in all three variables (Fig. 6, middle). After accounting for phylogenetic relatedness using PGLS, the degree of sympatry was the only variable significantly associated with subclade species richness (Table 4). However, this positive relationship was primarily driven by the high value observed in Cercopithecidae (Fig. 6C, right), and removing this outlier resulted in nonsignificant relationships across all variables. Furthermore, accounting for the higher species richness observed within older clades (Fig. 4, Table 2) also led to a nonsignificant relationship between sympatry and species richness (Table 4). Highly sympatric species within Cercopithecidae were also largely clustered within Cercopithecus and Macaca (Fig. 6C left), and subclades with high average values for sympatry tended to be older (>5 Ma). Interestingly, after accounting for the impact of clade age, more diverse clades tended to be characterized by geographic centroids located in more temperate latitudes (Table 4), but a significant relationship between latitude and species richness was only observed for two of the four phylogenies (Table 4; IS and IH).

Discussion

We investigate patterns of species richness, phylogenetic imbalance, and diversification rate heterogeneity in Primates, a species rich and ecologically diverse clade of mammals. We found that the distribution of species richness in Primates is partially explained by the relative ages of different lineages; older primate lineages tended to contain more species, at least when taxonomic groups are defined under a consistent, time-based paradigm (Fig. 4B; Table 2). However, when modern "family" level definitions are considered, age does not contribute to the species diversity of primate families (Fig. 4A; Table 2). This discrepancy in age-species richness relationships may result from bias introduced by how families are defined (e.g., to maintain a consistent amount of morphological disparity per clade) (Stadler et al. 2014). This is likely the case in Primates; we found a strong phylogenetic bias when taxonomic families were subdivided using a consistent time criterion (e.g., strepsirrhines and Tarsiidae, whereas simian families were conserved). Alternatively, age-species richness relationships may have varied through time or been obscured by the effect of extinction, as the time-based criterion we used resulted in examining a narrowed temporal range (Fig. 4). When patterns of phylogenetic imbalance across the whole primate phylogeny were examined, they differed significantly from those patterns expected under a constant rate model of speciation-extinction dynamics (Fig. 5, Table 3), suggesting that clade age is an insufficient explanation for the uneven distribution of species diversity across Primates.

Using a Bayesian MCMC analyses that specifically permitted a mixture of evolutionary rate regimes with variable and timedependent speciation and extinction rates (Rabosky 2014), we found strong support for an evolutionary rate shift among cercopithecids. Increased diversification rates were largely driven by substantially lower extinction rates within this family, with only moderate increases in speciation rate. Interestingly, some previous studies have suggested changes in diversification dynamics in cercopithecids (among other families), a pattern generally attributed to increased speciation rates (Purvis et al. 1995; Fabre et al. 2009). These studies utilized methods that detect discrete rate shifts occurring within a constant rate birth-death process, which would not have accounted for the general increase in diversification rates through time in Primates. Rather, when we incorporate both time-based and clade-based processes into our analyses, we find that a difference in extinction rates is the most important distinction between cercopithecids and other primate diversification patterns.

Cercopithecidae is the most species rich primate family and represents $\sim 30\%$ of all extant primate species (Perelman et al. 2011; Springer et al. 2012; Finstermeier et al. 2013; IUCN 2015). The position of the evolutionary rate shift detected by our analyses is consistent with the unusually high species diversity of cercopithecids relative to their age (Fig. 4). Diversification dynamics within Primates may therefore be characterized by two macroevolutionary rate regimes, one predominantly influenced by a trend of increasing diversification toward the present, and a second with more temporally stable but greatly increased diversification rates. This scenario contrasts with a previous BAMM analysis of another major mammalian clade, Chiroptera (Shi and Rabosky 2015). This study found that significant evolutionary rate heterogeneity was limited to a subclade (Stenodermatinae), that most bat lineages could be attributed to a global pattern of decelerating diversification rates, and that diversification rates and speciation rates were strongly associated. These differences between Primates and bats illustrate how major mammalian clades may be defined by very different macroevolutionary processes, even when both exhibit positive clade age--species richness relationships.

The Bayesian analysis presented here revealed a pattern of dramatically decreased extinction rates among cercopithecids. It is important to note, however, that while the BAMM analyses used herein incorporate incomplete lineage sampling, they do not include fossil taxa (Rabosky 2014; Rabosky et al. 2014b, 2015). The reliability of extinction rates estimated from molecular phylogenies, which lack fossil taxa, remains controversial (Rabosky 2010, 2015; Beaulieu and O'Meara 2015), and thus the difference in extinction rates between the two macroevolutionary regimes should be interpreted with caution. However, a considerable and disproportionate bias in the fossil record for primate lineages would be necessary to significantly alter the patterns of diversification observed here. Rather, fossil records from the palaeobiology database (https://paleobiodb.org), which is albeit a geographically and temporally biased sample, present numerous and diverse extinct prosimian species (e.g., Adapiformes and Omomyiformes), and noncercopithecid simians (Springer et al. 2012). Furthermore, previous analyses using different diversification models have also shown reduced extinction among cercopithecids compared to the background primate rate (Rolland et al. 2014).

The uneven distribution of species diversity in Primates could not be completely explained by clade age (Fig. 5, Table 3). Nevertheless, when a shift in cercopithecid diversification rates was incorporated into simulated phylogenies, we consistently found a nonsignificant difference with the observed phylogenetic imbalance of Primates, even across several divergence time scenarios (Table 3; Fig. 5). Therefore, significant rate heterogeneity across this global mammalian radiation contributes to the uneven distribution of species in modern taxa.

Geographic distribution did not explain the allocation of species diversity across primate subclades, especially once accounting for the influence of a rate shift among cercopithecids and for the impact of clade age on species richness (Table 4, Fig. 6). The lack of association between species richness and latitude in Primates is comparable to the results of recent diversification rate analyses in birds, mammals, and among several other clades (Soria-Carrasco and Castresana 2012; Rabosky et al. 2015; Sanchez-Ramirez et al. 2015; Marin and Hedges 2016; Schluter 2016). Comparatively, Rolland et al. (2014) found an association between high speciation and low extinction rates in tropical (vs temperate) species in several mammalian clades, including Primates. This may have been partly driven by diversification patterns among cercopithecids, which showed poor support (Δ AICs < 2) for differing tropical versus temperate speciation rates (Rolland et al. 2014); a latitudinal pattern across Primates may have been biased by the high evolutionary rates of the somewhat more tropical Cercopithecidae (Fig. 6A, middle). Interestingly, after accounting for the impact of clade age and a rate shift among cercopithecids, higher subclade species richness was marginally associated (significant across some but not all phylogenies; Table 4) with more temperate latitudes, opposite to predictions based on Rolland et al. (2014). The state-based speciation and extinction ("-SSE") class of diversification models (i.e., GeoSSE, BiSSE, etc.) appear to have a propensity toward elevated type I error rates (Maddison et al. 2007; Goldberg et al. 2011; Rabosky and Goldberg 2015; Beaulieu and O'Meara 2016). Such methods may be particularly weak in cases where a single subclade diversifies at a different rate from the "background" process (Rabosky and Goldberg 2015), as appears to be the case within Primates.

While larger geographic range sizes have been previously associated with increased speciation in Primates (Gomez and Verdu 2012), we found no relationship between range size and species richness (Table 4), and the distribution of range sizes in cercopithecids was very similar to that of other primate clades (Fig. 6B, middle). Lastly, while allopatric speciation has been proposed as a major mode of divergence in Primates (possibly through cycles of waxing and waning habitats; Gomez and Verdu 2012; Guschanski et al. 2013; Kamilar and Martin 2009), clades with a higher degree of sympatry were found to be more species rich on average. Nevertheless, the significance of this pattern was entirely driven by the usually high range overlap between congenerics in Cercopithecidae (Table 4; Fig. 6C, right). Overall, the geographic parameters examined here were insufficient to explain patterns of species richness across Primates. It is possible that the geographic distribution of modern species does not reflect the conditions under which speciation occurred (Barraclough 1998; Losos and Glor 2003). For example, the degree of sympatry is expected to increase with clade age even under a paradigm of solely parapatric speciation (Barraclough 1998), and the positive relationship between sympatry and species richness was weakened when age-corrected subclade values were used. However, the increased incidence of highly sympatric species among cercopithecids (Fig. 6C, middle

and right) is somewhat suggestive that ecological or social factors may have contributed to the faster rates of evolution in this highly diversifying clade. Previous work has associated the complexity of facial coloration, which may be useful to individual and species recognition, with higher sympatry and social group size in catarrhine primates (Santana et al. 2013). Thus, it is possible that the evolution of socially relevant phenotypes could have facilitated cercopithecid diversification. This hypothesis requires further exploration, especially in light of the considerable overlap in degree of sympatry between the two macroevolutionary regimes, and the broad variation in facial features and social systems in cercopithecids. Geographic data at finer resolution and addressing sympatry at the ecosystem level may also be necessary to fully address their impact on primate diversification.

It is also possible that diversification rates among Primates have been influenced by ecological or habitat opportunities. A previous analysis of the evolution of climatic niches found a greater number of diversification rate shifts among cercopithecids than any other primate clade (Duran and Pie 2015), suggesting that these shifts may be related to the presence of more variable climatic environments (e.g., montane regions, or ecosystems with monsoons). Gomez and Verdu (2012) also suggest that mutualistic ecological interactions with plants increases speciation rates, possibly through associated expansions in range size. Thus, increased lineage diversification rates may have also been enabled by traits that permitted expansion into a wider variety of habitats and climatic niches. It is important to note that the diversification rates estimated here under the BAMM framework are based on an assumption of discrete shifts in evolutionary rates. While BAMM provides a robust MCMC framework for diversification pattern estimation, some processes may be better described by changes in rates distributed over several nodes (Rabosky 2014; Burin et al. 2016). Future studies should investigate diversification rates in an explicit ecological or community context to elucidate if ecological or environmental factors (or a combination thereof) explain the extreme divergence in macroevolutionary patterns between cercopithecids and other primate clades.

The comparative analyses presented here illustrate that both age and a pattern of heterogeneous diversification rates explain the uneven distribution of modern species diversity across primate clades. While some previous studies have linked diversification patterns in Primates to biogeographical variables, we found no association between species richness and major geographic factors such as latitude, range size, or range overlap. Incorporating information about habitat, ecology, behavior, or innovations may be necessary to explain the remarkable diversity of the most species rich family of Primates. Reduced extinction rates, potentially stemming from favorable ecological conditions, appear to have facilitated the high species diversity of Old World monkeys compared to other primate clades. Primates exhibit a particularly high incidence of endangered species compared to other mammal orders (Jernvall and Wright 1998; IUCN 2015), and our analyses indicate that different clades have experienced vastly different extinction rates. The potential impact of this evolutionary history on the conservation risk of different primate clades is unknown and deserves further investigation. Further studies are also necessary to elucidate the causes of the high diversification rate (and potentially low extinction rate) of cercopithecids. This will improve our understanding of the origin of species diversity in this clade, and across the global radiation of Primates.

AUTHOR CONTRIBUTIONS

S. Santana and J. Arbour conceived of and designed the study. J. Arbour carried out and summarized the analyses. J. Arbour and S. Santana wrote the manuscript.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Fig. S1: Primate species diversity across latitude.

Fig. S2: Prior (black) and posterior (grey) distributions of rate shifts under an expected number of shifts of a) 0.1 and b) 10, across all four phylogenies. **Fig. S3:** All distinct shift configurations (shifts with marginal odds ratio > 10) found on at least 5% of samples from the posterior distribution of diversification rate shifts across Primates (rows = results of BAMM analyses on each of the four phylogenies from Springer et al 2012). **Table S1:** Effective sample size

Table S2: Analysis of clade-age species richness relationships based on stringent time-based definition of "families" on each of the four primate phylogenies.