

Molecular Phylogenetics and the Diversification of Hummingbirds

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Summary

The tempo of species diversification in large clades can reveal fundamental evolutionary mechanisms that operate on large temporal and spatial scales [1–4]. Hummingbirds have radiated into a diverse assemblage of specialized nectarivores comprising 338 species, but their evolutionary history has not, until now, been comprehensively explored. We studied hummingbird diversification by estimating a time-calibrated phylogeny for 284 hummingbird species, demonstrating that hummingbirds invaded South America by ~22 million years ago, and subsequently diversified into nine principal clades (see [5–7]). Using ancestral state reconstruction and diversification analyses, we (1) estimate the age of the crown-group hummingbird assemblage, (2) investigate the timing and patterns of lineage accumulation for hummingbirds overall and regionally, and (3) evaluate the role of Andean uplift in hummingbird speciation. Detailed analyses reveal disparate clade-specific processes that allowed for ongoing species diversification. One factor was significant variation among clades in diversification rates. For example, the nine principal clades of hummingbirds exhibit ~15-fold variation in net diversification rates, with evidence for accelerated speciation of a clade that includes the Bee, Emerald, and Mountain Gem groups of hummingbirds. A second factor was colonization of key geographic regions, which opened up new ecological niches. For example, some clades diversified in the context of the uplift of the Andes Mountains, whereas others were affected by the formation of the Panamanian land bridge. Finally, although species accumulation is slowing in all groups of hummingbirds, several major clades maintain rapid rates of diversification on par with classical examples of rapid adaptive radiation.

Results

We present a multilocus phylogenetic estimate for hummingbirds (Figure 1 and Figure S1 available online) based on

much richer sampling of hummingbird species (284 species and 436 exemplars) and loci (six genes and five loci) than any previous study (e.g., [6], which included 151 species, four genes, and three loci). Our phylogenetic estimate corroborates the general framework proposed by Bleiweiss [5] and elaborated upon by McGuire et al. [6, 7], namely that the Trochilidae consists of nine strongly supported, principal clades: Topazes, Hermits, Mangoes, Brilliants, Coquettes, *Patagona*, Mountain Gems, Bees, and Emeralds. The topology of the McGuire et al. [6] phylogenetic tree is supported here, with one major exception. Whereas the prior study concluded that Topazes (*Topaza* and *Florisuga*) are weakly supported as the sister taxon of all other hummingbirds, the present analysis places strong support (posterior probability of 1.0) for Topazes as the sister taxon of the Hermits. Prior to McGuire et al. [6, 7], hummingbirds were traditionally divided into two subfamilies: Phaethornithinae (Hermits) and Trochilinae (all other hummingbirds). The relatively basal placement of Topazes (and consequent polyphyly of the traditional concept of Trochilinae) continues to represent one of our most surprising phylogenetic discoveries for hummingbirds.

Our substitution rate-calibrated time-tree indicates that hummingbirds split from their sister group, the swifts, ~42 million years ago (\bar{x} = 42.1 mega-annum [Ma]; 95% highest posterior density [HPD] interval: 36.9–47.4 Ma; Figure S2). Our inferred divergence date is similar to the estimate obtained by the avian phylogenomics group (42.56 million years ago) using complete genome data for 48 species of birds and 18 conservatively selected fossil calibrations (E.D. Jarvis, personal communication). The age of the most-recent common ancestor of extant hummingbirds is estimated to have occurred only 22.4 million years ago (95% HPD interval: 20.3–24.7 Ma). This is a remarkably young age for this group given its large extant species diversity. These divergence dates bracket the ages of fossil stem hummingbirds recently described from the Oligocene of Europe (28–34 million years ago) [8–10]. Ancestral state reconstructions undertaken in the context of our densely sampled phylogeny unequivocally indicate that extant hummingbirds originated in South America (Figure 1), most likely in the lowlands (Figure S3). Indeed, the first six principal clades of hummingbirds (Topazes, Hermits, Mangoes, Brilliants, Coquettes, and *Patagona*) are nearly entirely composed of species restricted to South America or with ranges spanning the Isthmus of Panama (Figure 1). We infer one emigration event to the Caribbean that occurred deep within the Mango assemblage, as well as a few apparently recent range expansions into Central America by members of species complexes that still maintain most of their distributions in South America. Taken together, these results suggest that stem hummingbirds evolved in Eurasia well outside of the current New World geographic range of the family, invaded South America between ~40 and ~22 million years ago, and subsequently diversified into ~340 species, first in South America, and later in North America and the Caribbean. Ultimately, hummingbirds expanded across nearly the entirety of the Americas, from Alaska to Tierra del Fuego and throughout the Caribbean.

We explored regional hummingbird diversification using methods that visualize the accumulation of lineages within a

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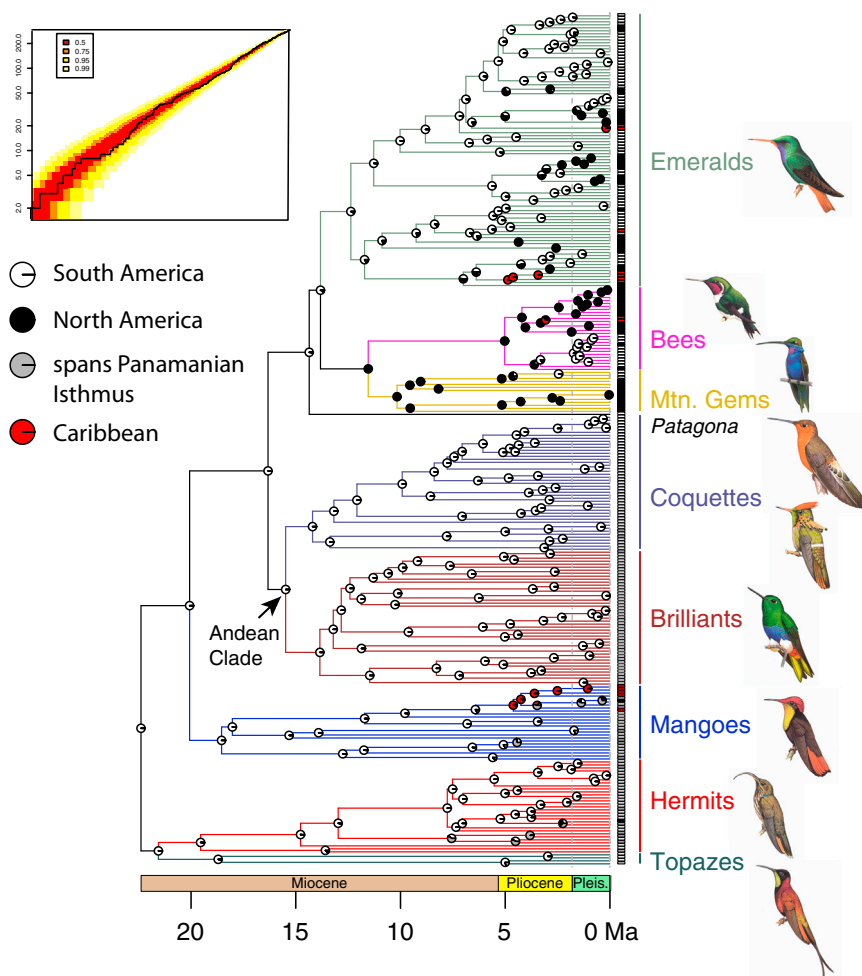


Figure 1. Time-Calibrated Phylogenetic Tree with Ancestral State Reconstructions of Primary Bioregions Inhabited by Hummingbirds

Color-coded bars at the tips of the tree indicate the contemporary distribution of the corresponding species. Color-coded pie diagrams at each node indicate the proportion of the maximum likelihood supporting alternative reconstructed character states. “Andean clade” is the informal name applied to the monophyletic assemblage composed of Coquettes and Brilliants. Bayesian posterior support values are presented in [Figure S1](#). An LTT plot for the 22.4 Ma history of hummingbirds is presented in the upper left, exhibiting a pattern of constant lineage accumulation through time. Hummingbird illustrations by Hilary Burn, Jan Wilczur, Richard Allen, Norman Arlott, and H. Douglas Pratt were obtained with permission from the Handbook of Birds of the World. See also [Figures S1–S3](#).

[12] that recovered much older divergence dates and consequently proposed many independent overwater colonizations of North America prior to Panamanian uplift. Finally, the Caribbean was invaded by hummingbirds more recently (~5 million years ago), and this assemblage has not experienced an increase similar to the South American and North American communities, despite the Caribbean fauna being composed of at least five independent origins (see [Figure 1](#)). However, the tempo of Caribbean lineage accumulation is similar to those of South and North America at comparable ages,

region of interest (see [11]). In one analysis we plotted the accumulation of lineages in South America, North America, and the Caribbean ([Figure 2A](#)), and in another the accumulation of lineages within and external to the Andes ([Figure 2B](#)). These analyses differ from standard lineage-through-time (LTT) plots, which show the accumulation of lineages within a particular clade (e.g., [Figure S4](#)). A key difference of the regional lineage accumulation plots is that they may include taxa representing several distinct clades because they not only capture diversity originating via in situ diversification, but also reflect diversity arising from independent immigration events. Lineages began to accumulate in South America about 22 million years ago ([Figure 2A](#)), at first slowly, followed by rapid cladogenesis, as is expected under an exponential process. The North American assemblage began with a single invasion from South America by the common ancestor of the Bee and Mountain Gem clades ~12 million years ago. After this invasion, species accumulation in North America proceeded slowly at first, following a similar initial trajectory as for South America, with a rapid increase during the past 5 Ma. The timing of this increase, which corresponds closely with Panamanian uplift, reflects not only in situ diversification of Mountain Gems and Bees, but also multiple independent invasions of North America by Emeralds, Coquettes, Mangoes, and Hermits and single invasions by Brilliants and Topazes, presumably all of which occurred overland via the Panamanian land bridge. This interpretation contrasts with that of a recent study of *Amazilia* hummingbirds

and so the Caribbean community may simply be too young to have experienced an increased accumulation rate.

The Andes Mountains are an epicenter of Neotropical species richness [13, 14] and are home to at least 140 species of hummingbirds [15]. This encompasses ~40% of contemporary hummingbird diversity despite the fact that the Andes represent only ~7% of the total land area of North and South America. Despite their physical magnitude, the Andes have only recently attained their extreme elevational relief, with summits above 6,000 m and a vast Central Andean Plateau averaging ~3,700 m elevation between the western and eastern cordilleras. Recent evidence suggests that the central Andean massif grew by 1.5–2.5 km during a period of exceptionally rapid uplift between ~10 and ~6 million years ago [16, 17], followed by another period of accelerated uplift in the northern Andes between ~5 and ~2 million years ago [18]. If Andean uplift has played a dominant role in the diversification of the South American biota, then much of this diversity must be quite young (i.e., originating during the past ~10 Ma).

Among hummingbirds, the Coquettes and Brilliants are sister clades that are almost entirely Andean and together contain ~30% of extant trochilid diversity ([Figure S3](#)); hence, we refer to them jointly as the Andean clade. Our time tree indicates that both the Coquettes and Brilliants had already initiated diversification before the first pulse of high Andean uplift occurred (~10 million years ago) but that the great

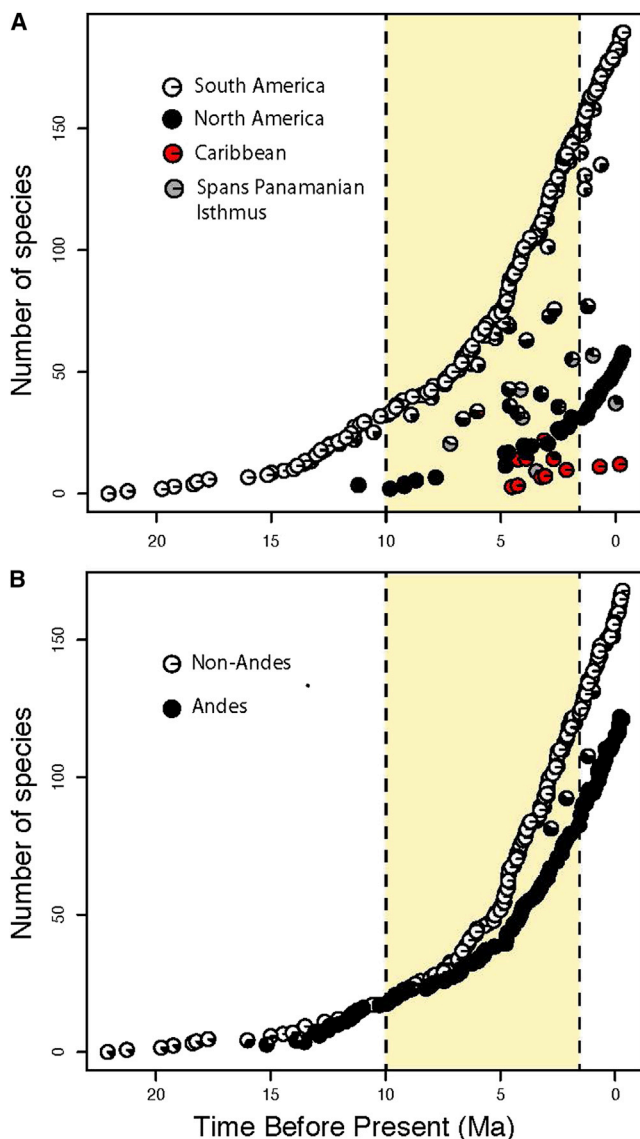


Figure 2. Hummingbird Species Accumulation Estimates over Time
(A) Primary bioregion and (B) Andean versus non-Andean occurrence are shown. Values compare historical lineage diversity estimates and relative branching times obtained from the time-calibrated phylogeny. These plots differ from standard LTT plots in that species accumulation in a region can include in situ diversification and independent invasion. Pie diagrams are color coded to reflect the proportion of the maximum likelihood supporting alternative ancestral state reconstructions of primary bioregion and Andean occurrence, respectively.

majority of their speciation took place over the last 10 Ma in the context of the rapidly rising Andes (Figures 2B and S3). Furthermore, the Andean clade has experienced a temporal decline in speciation (all species included: Monte Carlo constant rate [MCCR] gamma [19] = -2.569 , $p = 0.02$; non-Andean species excluded: MCCR gamma = -1.875 , $p = 0.03$), suggesting that lack of available ecological or geographic space may be limiting ongoing diversification for Andean clade members. Of course, the Andes are home not only to the Andean clade taxa but also to numerous Hermits, Mangoes, Bees, and Emeralds, most of which arrived or originated in the Andes only after peak uplift was well underway (Figures 2B and S3;

see also [20]). Thus, in contrast to the Andean clade, an analysis based on all Andean species (118 tip species plus 23 missing species) indicates that the Andean assemblage as a whole does not exhibit a significant signature of density-dependent diversification (MCCR gamma = -1.890 , $p = 0.08$). This suggests that even though diversification of the Andean clade is slowing, the Andes continue to provide available niche space into which hummingbirds can diversify, especially for those taxa ecologically differentiated from members of the Andean clade. The Andes do appear closer to species saturation than do non-Andean areas (MCCR gamma for 163 non-Andean species = -1.138 , $p = 0.30$), which is consistent with the higher contemporary density of hummingbirds in Andean habitats. Furthermore, non-Andean habitats are available to a wider range of hummingbird phylogenetic diversity (i.e., they exhibit phylogenetic overdispersion; see [21]), whereas high-elevation Andean habitats are dominated by the Andean clade members, many of which have compensatory adaptations necessary for reduced air density and oxygen availability at high elevation [22–24].

The large concentration of species in the Andes also points to another aspect of hummingbird biology that has clearly played a prominent role in enhancing diversification: the propensity of many species to have tiny ranges. This pattern has been noted for birds of the tropical Andes generally [25] but has not been previously quantified for hummingbirds, many of which are restricted to isolated high-elevation valleys or cordilleras. We analyzed hummingbird range-size data for species living within and outside the Andes (Andean occurrence taken from [26]). Compared to birds generally (see [27]), hummingbirds as a whole have much smaller mean range sizes (all birds: $\bar{x} = 2.82 \times 10^6$ km², hummingbirds: $\bar{x} = 0.93 \times 10^6$ km²). Furthermore, the Andean hummingbird species have significantly smaller range sizes (~ 4 -fold smaller) than do non-Andean hummingbird species ($t_{281} = 3.57$, $p = 0.0004$). This pattern suggests that characteristics of the Andes such as topographic complexity or climatic stability created opportunities for hummingbirds to finely partition geographical space.

We employed a new method [28] to model diversification because traditional LTT-based approaches are less able to account for extinction [29, 30]. Indeed, using traditional methods (MCCR gamma statistics and comparisons of rate-constant and diversity-dependent models [31]), it would appear that hummingbird diversification has been nearly constant during the past ~ 22 Ma (Figure 1, inset), and we could not reject a pure-birth diversification model with zero extinction. We therefore employed recently developed methods better able to model extinction. First, we used BAMM [28], a Bayesian framework for modeling and visualizing speciation and extinction rates that uses transdimensional (reversible-jump) Markov chain Monte Carlo (RJMCMC) to explore a vast state space of candidate diversification models and that explicitly accommodates diversification rate variation through time and among lineages. Unlike our analyses using more-traditional approaches, BAMM analyses recovered strong support for a diversity-dependent speciation process underlying the hummingbird radiation, with a net speciation rate ($\lambda = 0.25$ species/Ma) that was initially very high and has been declining ever since (but see below). The analysis also found a positive extinction rate ($\mu = 0.06$ species/my) that has been mostly stable throughout the history of hummingbirds (Figure S5). Furthermore, BAMM found strong support for heterogeneous diversification dynamics in the form of multiple

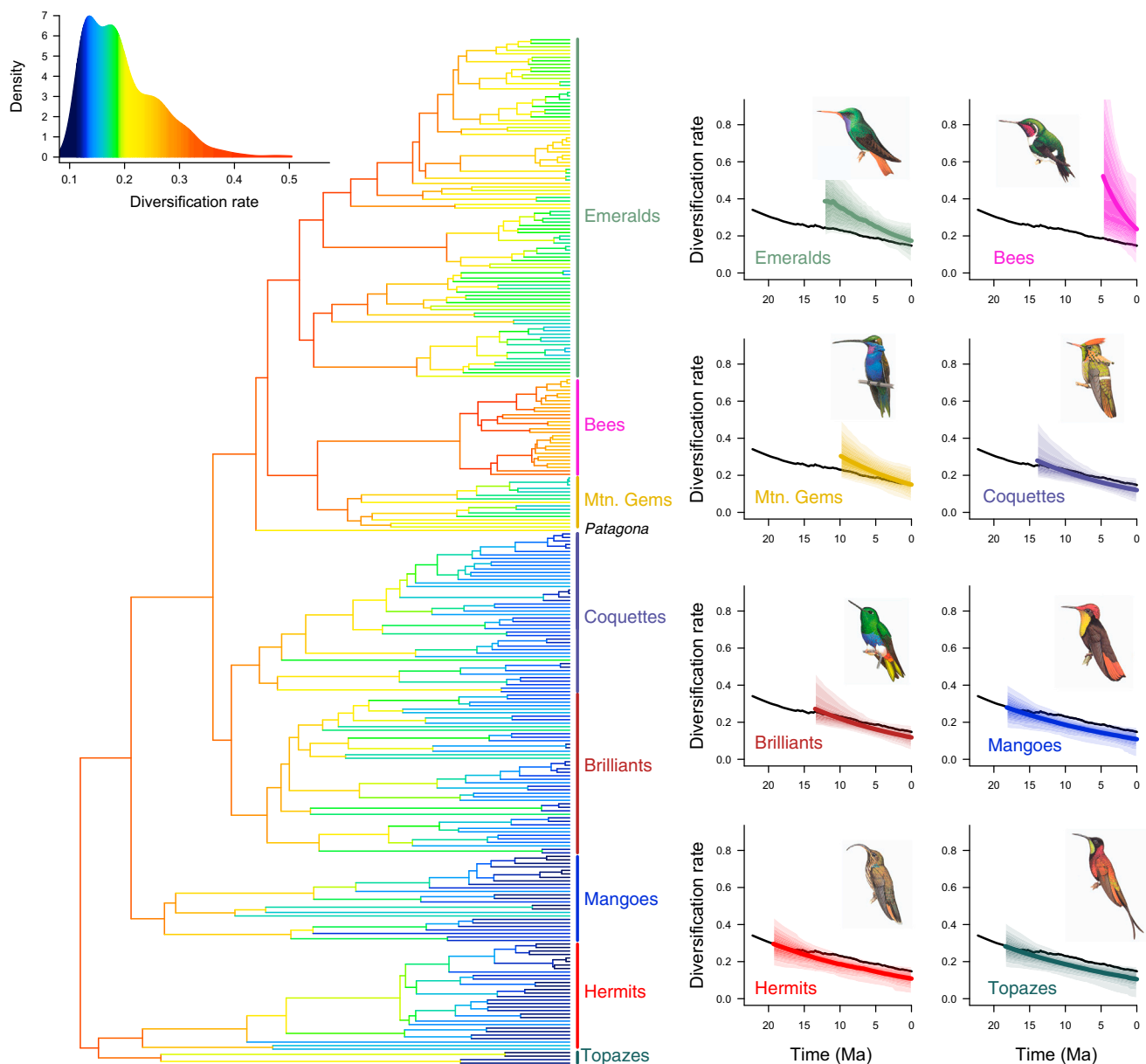


Figure 3. Diversification Rates through Time and among Lineages during the Radiation of Hummingbirds

The phylogeny shows a time-calibrated MCC tree, with branches colored by reconstructed net diversification rates. Rates on each branch are means of the marginal densities of branch-specific rates. Rate-through-time curves depict clade-specific net diversification trajectories and were computed from the joint posterior density of macroevolutionary rate parameters simulated using the reversible jump MCMC algorithm in BAMM. The black line denotes the mean diversification rate-through-time curve across all hummingbirds. Shading intensity of the colored line for each species reflects relative probability of a given diversification trajectory, with upper and lower bounds denoting the 90% Bayesian credible interval on the distribution of rates through time. Note the exceptional pulse of diversification in the Bee clade, followed by subsequent slowdown through time. Emeralds, Mountain Gems, and especially the Bees have consistently elevated net diversification rates relative to background rates for hummingbirds. See also [Figures S4](#) and [S5](#).

accelerations in the rate of diversification (posterior probability of a single rate model = 0.023; posterior probability density of 2-4 rate shifts = 0.87). The distinct diversification regimes were associated with the clade that includes Bees, Mountain Gems, and Emeralds ([Figure 3](#)), with particularly strong support for a shift in diversification dynamics associated with the Bees (cumulative posterior probability = 0.86). Following up on the BAMM analyses, we employed DDD [30] to estimate speciation, extinction, and carrying capacities for each hummingbird principal clade. DDD uses hidden Markov models to better

estimate speciation and extinction likelihoods under several constant-rate and diversity-dependent models; however, it does not account for temporal and branch-specific shifts in diversification rates as were detected with BAMM. Therefore, we restricted our use of DDD to individual analyses of the principal clades. The DDD results suggest 9-fold variation in mean speciation rates across the principal clades, ranging from 0.09 species/Ma for Topazes to 0.87 species/Ma for Bees. The carrying capacity estimates for each clade returned from these analyses ([Table S1](#)) indicate that

hummingbirds are expected to reach a speciation/extinction equilibrium at ~767 species, more than twice as many as occur today.

The above analyses provide strong support for heterogeneous diversification dynamics during the history of hummingbirds, and we propose that this was primarily driven by clade-specific species accumulation processes (Figures 3 and S4). For example, the principal hummingbird clades exhibit a nearly ~15-fold variation in net diversification rate (ranging from 0.04 species/Ma for the Topazes to 0.57 species/Ma for the Bees (see [32] for description of the metric; Figure S4). The Bees, in particular, have experienced an extraordinarily high rate of net diversification, accumulating as many or more species during their brief 5 Ma history (36 species) than have the Topazes (four species), Hermits (36 species), or Mangoes (27 species) over the past ~20 Ma.

Discussion

Our time-calibrated phylogeny sheds new light on the origin of hummingbirds. Ancestral hummingbirds split from their sister group, the swifts and treeswifts, ~42 million years ago. This divergence most likely occurred in Eurasia, given the presence of fossil stem hummingbirds from several sites in Europe during the early Oligocene, as well as the concentration of swift and treeswift phylogenetic diversity in this region [33]. Our dated phylogeny indicates a substantial temporal gap between the European hummingbird fossils (~34–28 million years ago) and the common ancestor of hummingbirds in South America (~22 million years ago). Given the absence of relevant fossils, the most parsimonious explanation is that hummingbirds reached South America by dispersal across Beringia and North America during this time interval. We propose a Beringian route because hummingbirds are metabolically constrained from undertaking extreme overwater dispersal events, suggesting that direct transatlantic dispersal was unlikely. The Beringian dispersal pathway is suspected for other Neotropical terrestrial bird groups that diversified between continents during the mid-Cenozoic (e.g., [34, 35]). This scenario requires that stem hummingbirds invaded South America from North America by overwater dispersal prior to ~22 million years ago. Overwater dispersal from North America to South America before the formation of the Central American land bridge may have become more likely in the late Oligocene as the Isthmus of Panama became a partially complete subaerial chain at this time [36, 37]. After their successful invasion of South America, hummingbirds may have gone extinct both in Eurasia and North America, only to have a more xeric-tolerant descendent species (the common ancestor of Bees and Mountain Gems) recolonize North America about 12 million years ago.

After their arrival in South America, hummingbirds radiated dramatically. The rapid rate of hummingbird diversification and the large number of constituent species can be attributed to multiple factors. First, hummingbirds evolved a specialized relationship with plants that set the stage for their dramatic radiation. The nature of this relationship has been described as “diffuse coevolution” [38] because plant species are rarely involved in one-to-one relationships with individual hummingbird species, but rather tend to be serviced by a group of hummingbird species with compatible bill sizes and shapes [39]. The partitioning of flower nectar resources allows for communities of 25 or more syntopic hummingbird species [21]. This level of “species packing” may have contributed

substantially to their overall rate of diversification. Second, a substantial proportion of hummingbird diversification has occurred in conjunction with Andean uplift, with ~140 species occurring in the Andes Mountains today. The large number of Andean hummingbird species in what amounts to a small fraction of the total land area of North and South America is linked both to high ecological diversity and corresponding species-packing in the Andes, as well as to their ability to occur as small-range endemics.

Although hummingbirds as a whole have maintained high rates of diversification (0.23 species/Ma; Figures 3 and S4), the rate is slowing, consistent with a diversity-dependent process. Diversity dependence may result from diminishing ecological opportunity, lack of geographical space for further allopatric speciation, or a combination of the two [40, 41]. An ecological explanation may underlie diversity dependence in Hermits and Topazes, which remain primarily restricted to humid, lowland forest habitats and date to ~20 million years ago but comprise only 36 and four species, respectively. In contrast, a combination of ecological and geographical constraints may explain diversity dependence in the Andean clade, given the high density of Andean clade species restricted to the Andes. In addition to diversity dependence, we have observed substantial variation in net diversification rates among clades (Figures 3 and S4). The Bees are notable in having experienced the highest rate of species accumulation among hummingbirds (0.57 species/Ma), comparable to that of rapidly evolving adaptive radiations. This is remarkable because, unlike many classical adaptive radiations [42–44], which have evolved in relative isolation, Bee hummingbirds have radiated in the context of the richest avifauna in the world and at a time when the remaining eight principal hummingbird clades were already well established. We note that much of the complexity of the hummingbird radiation described here, including extinction and diversity dependence, was not detected using traditional LTT methods. A similar inability to reject constant-rate models using traditional methods has been observed for several other radiations including cetaceans [4], furnariid ovenbirds [1], and Southeast Asian shrews [3]. Our results suggest that the methods employed here [28, 30] hold much promise for elucidating the factors affecting evolutionary radiations.

In summary, hummingbirds have diversified at a high, but decelerating, rate throughout their ~22 Ma history, driven primarily by their invasion of previously unexploited land areas such as the rising Andes, North America, and the Caribbean and by specialization on alternative habitats, flower shapes, and foraging strategies, thereby allowing for large numbers of sympatric and syntopic species. Our analyses suggest that species diversity remains on an upward trajectory, even though the rate of speciation is declining. Our findings strongly indicate that hummingbirds remain engaged in a dynamic diversification process, filling available ecological and spatial niches across North America, South America, and the Caribbean. Thus, the dramatic radiation of this unique avian lineage is far from complete.

Experimental Procedures

Taxonomic Sampling, DNA Sequence Data, and Alignment

DNA sequences representing six genes (four nuclear and two mitochondrial) were obtained for 451 individual birds, including 436 hummingbirds representing 284 species. Our sampling includes 101 of 105 currently recognized trochilid genera (lacking only three monotypic genera, *Anopetia*, *Hylophyllos*, and *Sternoclyta*, as well as the bitypic genus *Augastes*). We

included 15 outgroup species spanning four avian orders. A list of outgroup taxa, genes sequenced, and DNA sequencing procedures are detailed in the [Supplemental Experimental Procedures](#).

Phylogenetic Analysis

Our preferred time-calibrated Bayesian phylogenetic analyses were performed using BEAST v1.7.1 [45], with calibrations for divergence-dating analyses using substitution rate priors (rather than fossil calibrations; but see the [Supplemental Experimental Procedures](#)) using the rate estimates generated for Hawaiian honeycreepers [46]. Details of the phylogenetic analyses are in the [Supplemental Experimental Procedures](#).

Ancestral State Reconstructions

We performed maximum-likelihood ancestral state reconstructions of regional and Andean occurrence on our time-calibrated tree using the “re-rootingMethod” function in Phytools version 0.3-10 [47] in R version 3.01 [48]. Our analyses were on discrete characters under an equal-rates model.

Diversification Analyses

Standard LTT plots were generated in R [48] using functions implemented in Ape [49], Laser version 2.3 [31], and TreeSim version 1.9 [50]. Net diversification rates [32] were calculated using Geiger version 1.99-3 [51]. We tested alternative constant rates and diversity-dependent models using Laser and DDD [30], which were compared via simulation of a pure-birth tree to infer AIC critical values (Laser) and using Akaike Weights (DDD). We tested for shifts in diversification rate through time and among lineages using BAMM [28]. Details of the BAMM methodology are in the [Supplemental Experimental Procedures](#).

Bird Range-Size Analyses

Range maps were obtained from BirdLife International [52]. Area was calculated for the shapefiles using a NAD83 Contiguous USA Albers Equal Area projection in ArcGIS version 10.2. Average range sizes were calculated on the basis of untransformed data, but before performance of statistical tests, range sizes were calculated from the sum of the areas of all shapefiles provided for each species. Range sizes were \log_{10} transformed to improve normality and homogeneity of variances. Range sizes of Andean versus non-Andean species were compared with a two-sample t test in R.

Accession Numbers

The GenBank accession numbers for the previously unpublished sequence data reported in this paper are KJ601785–KJ603160.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, five figures, and two tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.03.016>.

Acknowledgments

We thanks R. Bowie, P. Fine, S. Rovito, members of the McGuire lab, Gavin Thomas, and two anonymous reviewers for helpful comments that improved the manuscript, L. Mahler for assistance with R scripts that made the regional lineage accumulation plots possible, and R. Etienne for help with DDD. We are grateful to our home institutions, as well as to the following collections, which provided samples: Academy of Natural Sciences, American Museum of Natural History, Field Museum of Natural History, National Museum of Natural History, University of Kansas Museum of Natural History, University of Michigan Museum of Zoology, STRI, UNAM, and the Zoological Museum Copenhagen. This research was supported by National Science Foundation grants (DEB 0330750, 0543556, and 1146491).

Received: December 14, 2013

Revised: February 12, 2014

Accepted: March 5, 2014

Published: April 3, 2014

References

- Derryberry, E.P., Claramunt, S., Derryberry, G., Chesser, R.T., Cracraft, J., Aleixo, A., Pérez-Emán, J., Remsen, J.V., Jr., and Brumfield, R.T. (2011). Lineage diversification and morphological evolution in a large-scale continental radiation: the neotropical ovenbirds and woodcreepers (aves: Furnariidae). *Evolution* 65, 2973–2986.
- Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L., Carnevale, G., and Harmon, L.J. (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl. Acad. Sci. USA* 106, 13410–13414.
- Esselstyn, J.A., Timm, R.M., and Brown, R.M. (2009). Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. *Evolution* 63, 2595–2610.
- Slater, G.J., Price, S.A., Santini, F., and Alfaro, M.E. (2010). Diversity versus disparity and the radiation of modern cetaceans. *Proc. Biol. Sci.* 277, 3097–3104.
- Bleiweiss, R., Kirsch, J.A.W., and Matheus, J.C. (1997). DNA hybridization evidence for the principal lineages of hummingbirds (Aves: Trochilidae). *Mol. Biol. Evol.* 14, 325–343.
- McGuire, J.A., Witt, C.C., Altshuler, D.L., and Remsen, J.V., Jr. (2007). Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Syst. Biol.* 56, 837–856.
- McGuire, J.A., Witt, C.C., Remsen, J.V., Jr., Dudley, R., and Altshuler, D.L. (2009). A higher-level taxonomy for hummingbirds. *J. Ornithol.* 150, 155–165.
- Mayr, G. (2004). Old World fossil record of modern-type hummingbirds. *Science* 304, 861–864.
- Mayr, G. (2007). New specimens of the early Oligocene Old World hummingbird *Eurotrochilus inexpectatus*. *J. Ornithol.* 148, 105–111.
- Bochenski, Z., and Bochenski, Z.M. (2008). An Old World hummingbird from the Oligocene: a new fossil from Polish Carpathians. *J. Ornithol.* 149, 211–216.
- Mahler, D.L., Revell, L.J., Glor, R.E., and Losos, J.B. (2010). Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution* 64, 2731–2745.
- Ornelas, J.F., González, C., Espinosa de los Monteros, A., Rodríguez-Gómez, F., and García-Feria, L.M. (2014). In and out of Mesoamerica: temporal divergence of *Amazilia* hummingbirds pre-dates the orthodox account of the completion of the Isthmus of Panama. *J. Biogeogr.* 41, 168–181.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Pennington, R.T., Lavin, M., Särkinen, T., Lewis, G.P., Klitgaard, B.B., and Hughes, C.E. (2010). Contrasting plant diversification histories within the Andean biodiversity hotspot. *Proc. Natl. Acad. Sci. USA* 107, 13783–13787.
- Parker, T.A., III, Stotz, D.F., and Fitzpatrick, J.W. (1996). A guide to the databases. In *Neotropical Birds: Ecology and Conservation*, D.F. Stotz, J.W. Fitzpatrick, T.A. Parker, III, and D.K. Moskovits, eds. (Chicago: The University of Chicago Press), pp. 118–436.
- Garzone, C.N., Hoke, G.D., Libarkin, J.C., Withers, S., MacFadden, B., Eiler, J., Ghosh, P., and Mulch, A. (2008). Rise of the Andes. *Science* 320, 1304–1307.
- Bershaw, J., Garzone, C.N., Higgins, P., MacFadden, B., Anaya, F., and Alvarenga, H. (2010). Spatial-temporal changes in Andean plateau climate and elevation from stable isotopes of mammal teeth. *Earth Planet Sci. Lett.* 289, 530–538.
- Gregory-Wodzicki, K.M. (2000). Uplift history of the central and northern Andes: a review. *Geol. Soc. Am. Bull.* 112, 1091–1105.
- Pybus, O.G., and Harvey, P.H. (2000). Testing macro-evolutionary models using incomplete molecular phylogenies. *Proc. Biol. Sci.* 267, 2267–2272.
- Bleiweiss, R. (1998). Origin of hummingbird faunas. *Biol. J. Linn. Soc. Lond.* 65, 77–97.
- Graham, C.H., Parra, J.L., Rahbek, C., and McGuire, J.A. (2009). Phylogenetic structure in tropical hummingbird communities. *Proc. Natl. Acad. Sci. USA* 106 (Suppl 2), 19673–19678.
- Altshuler, D.L., Dudley, R., and McGuire, J.A. (2004). Resolution of a paradox: hummingbird flight at high elevation does not come without a cost. *Proc. Natl. Acad. Sci. USA* 101, 17731–17736.
- Altshuler, D.L., Stiles, F.G., and Dudley, R. (2004). Of hummingbirds and helicopters: hovering costs, competitive ability, and foraging strategies. *Am. Nat.* 163, 16–25.
- Projecto-García, J., Natarajan, C., Moriyama, H., Weber, R.E., Fago, A., Cheviron, Z.A., Dudley, R., McGuire, J.A., Witt, C.C., and Storz, J.F.

- (2013). Repeated elevational transitions in hemoglobin function during the evolution of Andean hummingbirds. *Proc. Natl. Acad. Sci. USA* 110, 20669–20674.
25. Fjeldså, J., Bowie, R.C.K., and Rahbek, C. (2012). The role of mountain ranges in the diversification of birds. *Annu. Rev. Ecol. Evol. Syst.* 43, 249–265.
26. Schuchmann, K.L. (1999). Hummingbirds. In *Handbook of the Birds of the World, Volume 5*, J. del Hoyo, A. Elliott, and J. Sargatal, eds. (Barcelona: Lynx Edicions), pp. 468–680.
27. Orme, C.D.L., Davies, R.G., Olson, V.A., Thomas, G.H., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P.F., et al. (2006). Global patterns of geographic range size in birds. *PLoS Biol.* 4, e208.
28. Rabosky, D.L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE* 9, e89543.
29. Quental, T.B., and Marshall, C.R. (2010). Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol.* 25, 434–441.
30. Etienne, R.S., Haegeman, B., Stadler, T., Aze, T., Pearson, P.N., Purvis, A., and Phillimore, A.B. (2012). Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc. Biol. Sci.* 279, 1300–1309.
31. Rabosky, D.L. (2006). LASER: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evol. Bioinform. Online* 2, 273–276.
32. Magallón, S.M., and Sanderson, M.J. (2001). Absolute diversification rates in angiosperm clades. *Evolution* 55, 1762–1780.
33. Dickinson, E.C., and Remsen, J.V., Jr. (2013). The Howard and Moore Complete Checklist of the Birds of the World, *Volume 5* (Eastbourne: Aves Press).
34. Mourer-Chauviré, C. (1999). The relationships between the Lower Tertiary avifaunas of Europe and South America. *Bull. Soc. Geol. Fr.* 170, 85–90.
35. Moyle, R.G., Chesser, R.T., Prum, R.O., Schikler, P., and Cracraft, J. (1996). Phylogeny and evolutionary history of Old World suboscine birds (Aves: Eurylaimides). *Am. Mus. Novit.* 3544, 1–22.
36. Farris, D.W., Jaramillo, C., Bayona, G., Restrepo-Moreno, A., Montes, C., Cardona, A., Mora, A., Speakman, R.J., Glascock, M.D., and Valencia, V. (2011). Fracturing of the Panamanian Isthmus during initial collision with South America. *Geology* 39, 1007–1010.
37. Montes, C., Cardona, A., McFadden, R., Morón, S.E., Silva, C.A., Restrepo-Moreno, S., Ramírez, D.A., Hoyos, N., Wilson, J., Farris, D., et al. (2012). Evidence for Middle Eocene and younger land emergence in central Panama: Implications for Isthmus closure. *Geol. Soc. Am. Bull.* 124, 780–799.
38. Cotton, P.A. (1998). Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis* 140, 647–653.
39. Feinsinger, P., and Colwell, R.K. (1978). Community organization among Neotropical nectar-feeding birds. *Am. Zool.* 18, 779–795.
40. Rabosky, D.L., and Lovette, I.J. (2008). Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* 62, 1866–1875.
41. Phillimore, A.B., and Price, T.D. (2008). Density-dependent cladogenesis in birds. *PLoS Biol.* 6, e71.
42. Baldwin, B.G., and Sanderson, M.J. (1998). Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proc. Natl. Acad. Sci. USA* 95, 9402–9406.
43. Grant, P.R. (1986). *Ecology and Evolution of Darwin's Finches* (Princeton: Princeton University Press).
44. Losos, J.B. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles* (Berkeley: University of California Press).
45. Drummond, A.J., and Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* 7, 214.
46. Lerner, H.R.L., Meyer, M., James, H.F., Hofreiter, M., and Fleischer, R.C. (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Curr. Biol.* 21, 1838–1844.
47. Revell, L.J. (2012). Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3, 217–223.
48. R Development Core Team (2012). *R: A Language and Environment for Statistical Computing* (Vienna: R Foundation for Statistical Computing).
49. Paradis, E., Claude, J., and Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
50. Stadler, T. (2011). Simulating trees with a fixed number of extant species. *Syst. Biol.* 60, 676–684.
51. Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., and Challenger, W. (2008). GEIGER: investigating evolutionary radiations. *Bioinformatics* 24, 129–131.
52. Ridgely, R.S., Allnutt, T.F., Brooks, T., McNicol, D.K., Mehlman, D.W., Young, B.E., and Zook, J.R. (2012). *Digital Distribution Maps of the Birds of the Western Hemisphere, Version 5.0* (Arlington: NatureServe).