

EVOLUTION

The evolution of a tropical biodiversity hotspot

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The tropics are the source of most biodiversity yet inadequate sampling obscures answers to fundamental questions about how this diversity evolves. We leveraged samples assembled over decades of fieldwork to study diversification of the largest tropical bird radiation, the suboscine passerines. Our phylogeny, estimated using data from 2389 genomic regions in 1940 individuals of 1287 species, reveals that peak suboscine species diversity in the Neotropics is not associated with high recent speciation rates but rather with the gradual accumulation of species over time. Paradoxically, the highest speciation rates are in lineages from regions with low species diversity, which are generally cold, dry, unstable environments. Our results reveal a model in which species are forming faster in environmental extremes but have accumulated in moderate environments to form tropical biodiversity hotspots.

Most biological diversity originated in tropical regions (1, 2), but long-standing questions remain about how tropical species diversity forms and is maintained (3). Are tropical peaks in diversity a result of faster rates of evolution or greater time for species accumulation (4)? When species do form in the tropics, what is the primary driver: climatic instability (5), the narrow stratification of habitats along elevation gradients (6–8), or divergence caused by interactions among species (9, 10)? Alternatively, recent evidence suggests that speciation occurs most frequently when few other species are present (11). Might this explanation apply even in the species-rich tropics? Addressing these questions requires detailed investigation of the dynamics of speciation and species diversity through time, among lineages, and across geographic space in tropical groups. This work is particularly urgent because the same tropical regions that harbor and generate biotic diversity are under rapidly intensifying human pressure (12).

Through decades of expeditions and research in the tropics, our knowledge and sampling of tropical bird diversity are finally at a level of completeness sufficient for a

detailed investigation of tropical diversification. Global avian diversity reaches its peak in the New World tropics, and a large portion of that diversity is attributable to a single massive radiation: the suboscine passerines (class Aves, suborder Tyranni). Roughly one in three Neotropical bird species (1250 of 4192 total) is a suboscine, even though the group is only 40 to 51 million years (Ma) old (13–15). Suboscines have varied phenotypes and ecologies and are the predominant avian group in essentially all terrestrial habitats in the Neotropics, from the Andean snow line to lowland Amazonia and from cloud forests to deserts (16). However, a comprehensive species-level estimate of suboscine phylogeny has not been available, precluding our understanding of diversification in this large tropical radiation and limiting identification of the broader drivers of tropical evolution.

We assembled a large, complete phylogenomic dataset [table S1 (17)] containing 1940 samples representing 1287 of 1306 suboscine species (98.5%) sequenced at 2389 orthologous genomic regions. Our maximum-likelihood phylogenetic tree (Fig. 1) was highly resolved. Relationships across the tree were supported by markers throughout the genome, with

elevated support at sex-linked loci and high bootstrap support at most nodes. The tree topology and branch lengths were highly concordant between datasets with minimal and extensive filtering of missing data (fig. S1). A concatenated maximum-likelihood tree and a coalescent-based species tree accounting for heterogeneity in phylogenetic histories across the genome recovered highly similar relationships [figs. S2 and S3 (17)]. Time calibration of the phylogeny using existing fossil records within and outside suboscines indicates that the extant suboscine radiation began diversifying 44.5 Ma ago (range, 42.2 to 45.7 Ma ago) and individual suboscine families originated 18.7 to 36.5 Ma ago (stem ages; table S2). This time-calibrated tree provided the information needed for estimating the dynamics of suboscine diversification across time, lineages, and geography and for testing links between those dynamics and potential drivers of tropical diversity.

We found that suboscine diversification has been relatively steady since the origin of the group. Extant suboscine lineages have accumulated gradually, and our intraspecific sampling reveals continued accumulation through the present (Fig. 1). Diversification-through-time analyses did not find evidence for shifts in diversification rate over most of the history of the group [Fig. 2A (17)] aside from a drop within the past 2 Ma likely resulting from unsampled intraspecific diversity and unsorted ancestral polymorphism. Diversification models

Fig. 1. Species-level phylogeny of suboscine birds. The three infraorders are colored and the 24 families are outlined with white polygons. Smaller families are numbered as follows: (1) Philepittidae, (2) Eurylaimidae, (3) Calyptomenidae, (4) Sapayoidea, (5) Pittidae, (6) Onychorhynchidae, (7) Oxyruncidae, (8) Pipritidae, (9) Platyrinchidae, (10) Tachurisidae, (11) Melanopareiidae, (12) Conopophagidae, (13) Formicariidae, and (14) Scleruridae. Nodes that are at the crowns of families or older are annotated with circles that indicate bootstrap support (see gradient scale inset) and error bars depicting uncertainty in their ages. Above the phylogeny, a time axis and lineage-through-time (LTT) plots are depicted. The gray LTT plot depicts currently recognized species, and the black area near the top depicts the accumulation of additional lineages within currently recognized species. The inset in the bottom left is a Manhattan plot of gene tree support for the consensus topology at loci across the genome. Points are colored by chromosome (mapped to the zebra finch *Taeniopygia guttata*), alternating gray and black, and chromosomes are ordered by size (some smaller chromosomes are not labeled). Support is higher at sex-linked loci than at autosomal loci ($t = -10.3$, $P < 0.01$). Representative bird images for each family are illustrations reproduced by permission of Lynx Edicions.

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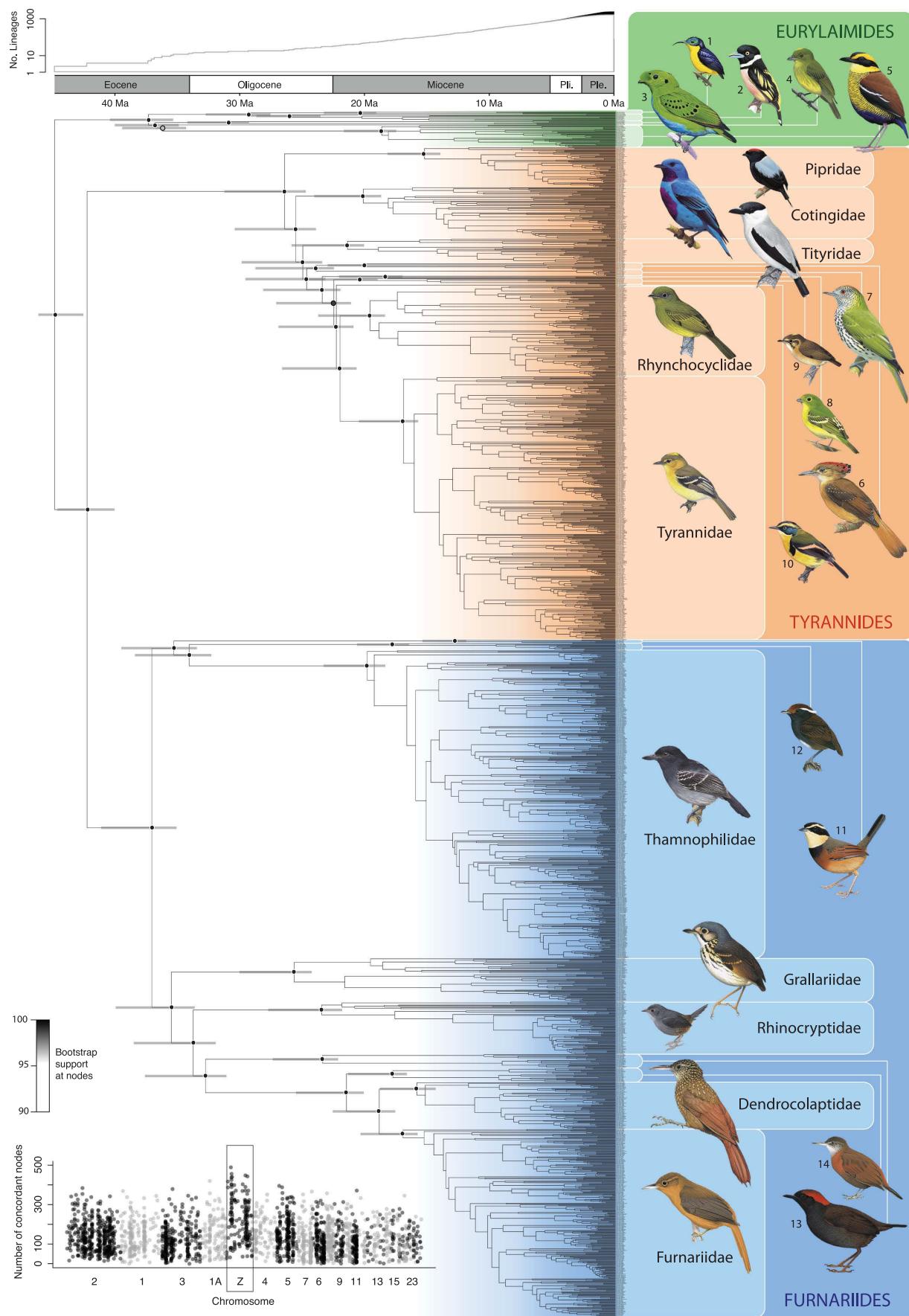
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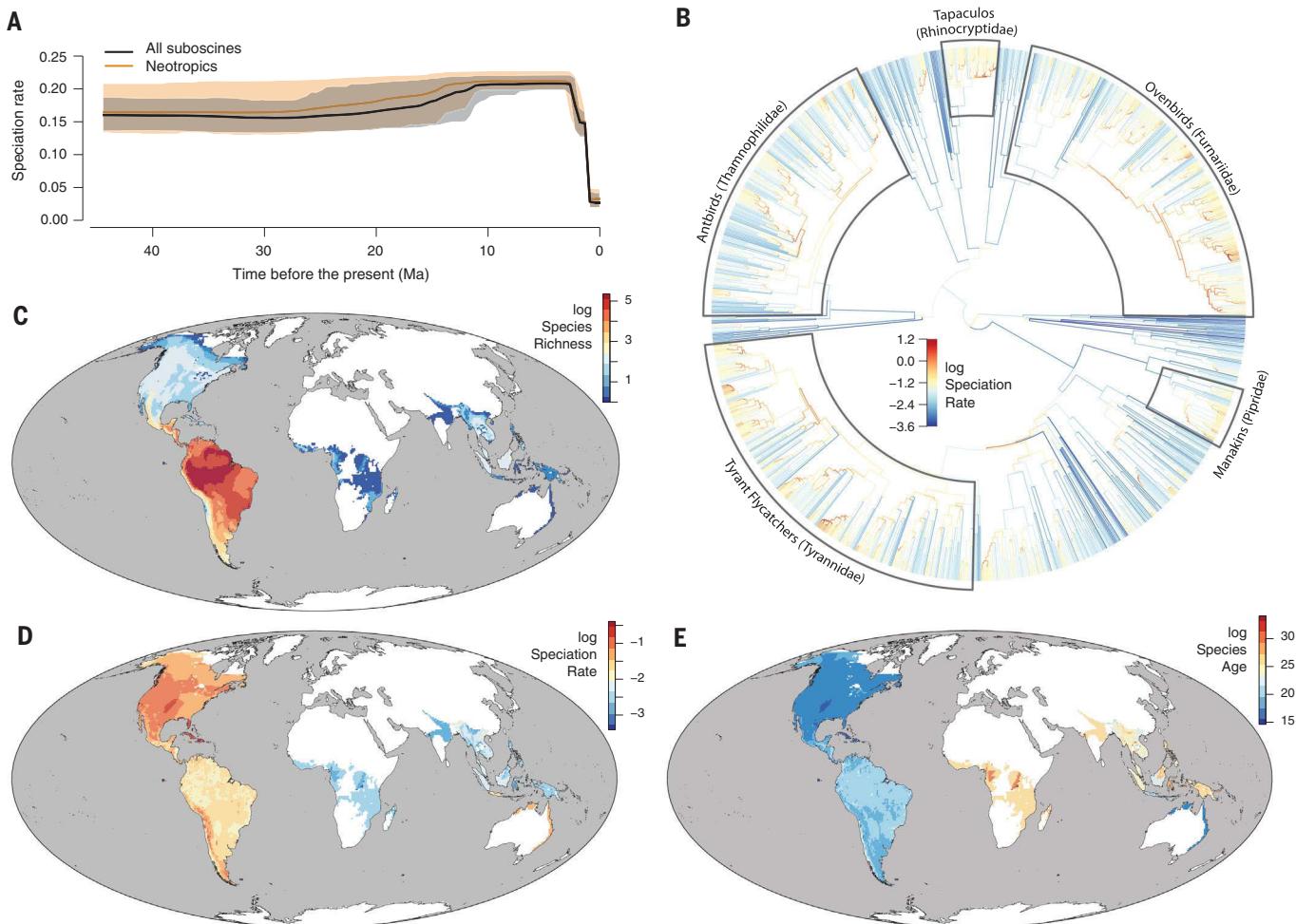


Fig. 2. Temporal, taxonomic, and geographic dynamics of suboscine diversification.

diversification. (A) Suboscine speciation is relatively stable over most of the group's history, lacking an early burst. (B) Speciation rate varies widely among lineages, and five groups are consistently inferred to exhibit shifts to elevated speciation rates relative to background rates. Branches are colored according to the equal splits speciation rates estimator (ES). Groups outlined with polygons share an elevated speciation rate relative to the background regime in the best shift configuration from Bayesian analysis of macroevolutionary mixtures (BAMM) and are supported by other models with

branch-specific diversification rates (see the supplementary text). The groups are labeled with the name of the most species-rich family contained therein. (C) Suboscine species richness is highest in the Neotropics. (D) Recent suboscine speciation rates (based on ES) do not peak in Neotropical centers of species richness. (E) Areas with high richness have moderate speciation rates and moderate diversity age, here measured using average node height. To avoid the excessive contribution of wide-ranging species to perceived spatial patterns, cell values in the maps of evolutionary statistics (D and E) represent averages weighted by the inverse of species range size.

fit to the suboscine phylogeny as a whole indicate that constant-rate models fit better than models with decreasing diversification rates through time [birth-death log likelihood = -3626.1 ; diversity-dependent log likelihood = -3658.7 ; change in corrected Akaike information criterion (ΔAIC_c) = 67.18]. Recent work has highlighted challenges associated with identifying alternative diversification histories in phylogenies of extant taxa (18), but even identifiable estimators do not show major shifts through time in suboscines (fig. S4). The steady dynamics in suboscines contrast with the pattern found in many other groups, in which an early burst of diversification is followed by a gradual slowdown (19). There are multiple potential causes for the absence of rate shifts

(20, 21). For example, tropical clades may have been less subject to bursts of speciation associated with episodic ecological opportunity, the suboscine radiation may be old enough that the signature of an early burst has eroded, or suboscines may represent an assemblage of smaller radiations with distinct dynamics that produce the overall trend [figs. S5 to S7 and tables S3 and S4 (17)].

Recent speciation rates varied >100 -fold among different evolutionary lineages of suboscine birds (Fig. 2B). We focused on estimators of speciation rates that are most influenced by recent branching events and are thus robust to assumptions about extinction, but we also compared these with other model-based estimates (17). Five groups in particular were

responsible for 77.4% of suboscine diversity and were consistently inferred to have experienced a shift to higher rates of diversification by a suite of methods [Fig. 2B (17)]. These include the lineages containing manakins (Pipridae), tyrant flycatchers (Tyrannidae), antbirds (Thamnophilidae), tapaculos (Rhinocryptidae), and ovenbirds (Furnariidae), groups that are highly distinct from one another in ecology and morphology (16). Future work, however, may reveal shared attributes that have contributed to elevated diversification across these groups.

When mapped onto geography, the Neotropical regions with the greatest suboscine species richness (Fig. 2C) do not contain lineages with the highest recent speciation

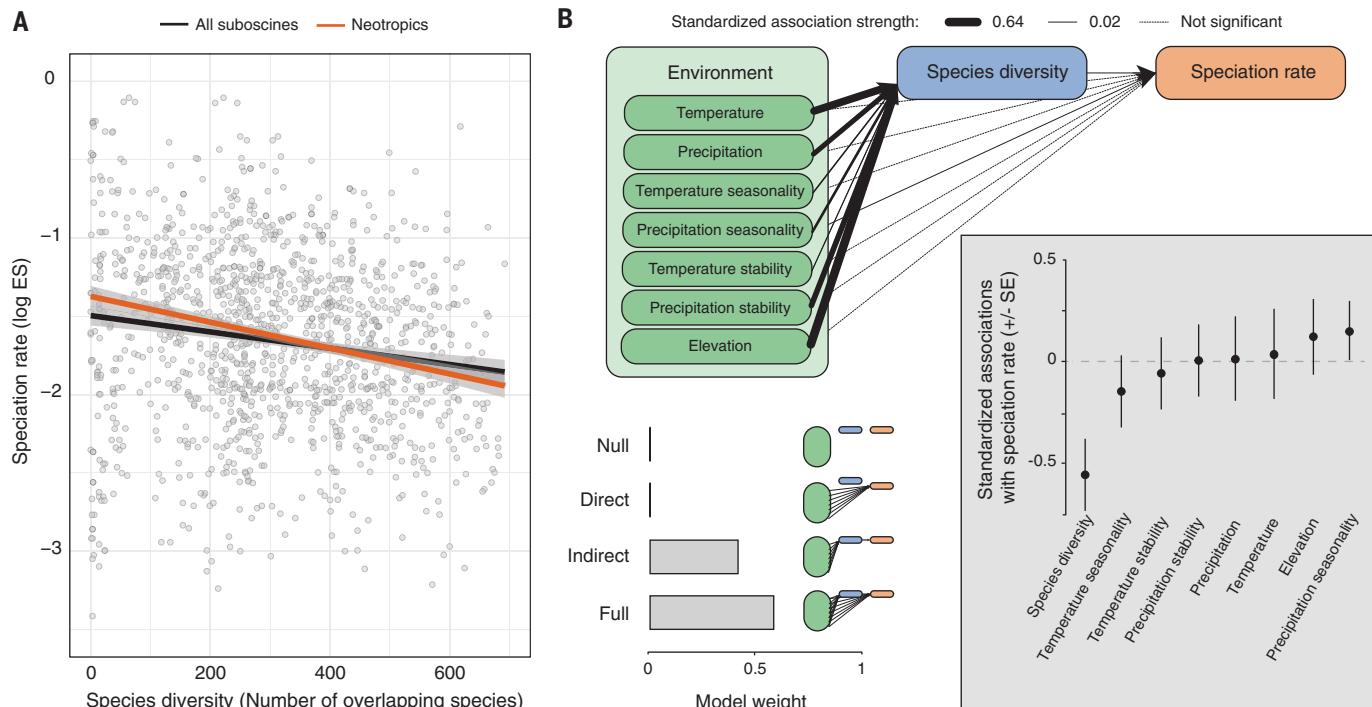


Fig. 3. Examination of the drivers of suboscine speciation rate variation reveals the role of low species diversity. (A) Plot of speciation rate (based on ES) versus species diversity for all suboscines showing that areas of high species diversity contain mostly lineages with low speciation rates. The negative speciation rate–diversity association is found both by examining all suboscines and by focusing on only those in the Neotropics. (B) The best-fitting model from phylogenetic path analysis includes strong associations

between environmental variables and species diversity and then an impact of species diversity on speciation rate. Species diversity is the variable with the greatest impact (standardized association deviating from zero) on speciation rate (based on ES). The full model slightly outperforms a model in which the environment mediates speciation rate entirely through its impact on species diversity, and substantially outperforms a model in which environment impacts speciation rate directly.

rates (Fig. 2D) but instead exhibit moderate speciation rates and harbor species diversity that is older than in surrounding areas (Fig. 2E). This result is concordant with recent latitudinal studies of diversification in widespread samples of birds, mammals, and fishes that have found speciation rates in the tropics similar to or lower than those in the Temperate Zone (22–24). The spatial patterns in speciation rate and species age that we observed were consistent with the results of biogeographic modeling of the colonization history of suboscine lineages: Old World species were contained within a single, old clade of modest diversity, and Nearctic species derived from 15 to 20 recent (all <10.8 Ma ago) colonizations of the Temperate Zone [fig. S8 (17)]. Moreover, the transition of lineages into the Neotropics has only occurred four to nine times, which indicates that colonization is not a primary driver of elevated Neotropical diversity. Although the potential evolutionary importance of time has long been recognized (25, 26), its contribution in suboscines further establishes a key role in the accumulation of tropical species. Species-rich regions in the tropics are not merely a locus of young diversity but contain diversity accumulated over a protracted evolutionary period.

We failed to find strong associations between speciation rates in the New World and environmental variables (table S5). Speciation rate was not correlated with elevation ($\rho = 0.187$; $P = 0.100$), nor did species from mountainous regions exhibit higher speciation rates than those from lowland regions ($\lambda_0 = 0.176$ species/Ma; $\lambda_1 = 0.200$; $P = 0.933$). This result is notable in light of evidence of positive associations between speciation rates and elevation in prior studies (7, 8, 27). Elevation may not be a strong and general predictor of speciation rate variation. We also found few strong associations between speciation rate and current climatic variables such as temperature, precipitation, seasonality, or average rates of climatic change since the last glacial maximum or across five time slices since the Pliocene (table S5).

A key result from our study is that the best predictor of elevated speciation rates in New World suboscines is low current standing species diversity (Fig. 3). Higher speciation rates were observed in lineages with ranges that overlapped few other suboscines ($\rho = -0.247$; $P = 0.007$; Fig. 3A) or few overall bird species ($\rho = -0.223$; $P = 0.021$). This result was robust to phylogenetic uncertainty, incomplete sampling, simulated random and nonrandom

extinction, alternative taxonomic classifications, and the effects of spatial autocorrelation in species richness estimates [table S6 (17)]. Moreover, this result was also evident using state-dependent speciation and extinction models and traditional sister clade comparisons [table S7 and figs. S9 and S10 (17)]. The negative speciation–species richness association runs counter to the idea that greater potential for species interactions promotes speciation in the tropics (8). It instead supports recent arguments that the geographic dynamics of species formation at a given time are a response to rather than a cause of broad species diversity patterns (11, 28). In this framework, new species form at higher rates in areas containing relatively few species or where there is a diversity debt relative to the environmental capacity for species.

A model including variable extinction rates suggested that areas of low diversity have experienced historically high levels of extinction (table S7), which may help explain the low levels of standing diversity in those areas today. This supports prior work suggesting that extinction may overwhelm speciation as a driver of patterns in species richness (22, 29). In suboscines, areas of low diversity were associated with environments characterized by

low temperatures and precipitation, greater seasonality in temperature and precipitation, and larger changes in climate through geologic time (table S5). These may be areas in which the contemporary habitat is younger and lineages are recent colonists from elsewhere. Areas of low species richness and high speciation rates included parts of the central and southern Andes and Patagonia, the Caribbean, and the Nearctic (Fig. 2, C and D). These are also areas found to result in low simulated species persistence under recent (i.e., the past 800,000 years) paleoclimatic models (30). We used phylogenetic path analysis to simultaneously evaluate causal connections among different environmental and biotic variables. The best model contained causal links between climatic variables and species richness and then a link between species richness and speciation rates (Fig. 3B). This result indicates that environmental variables mediate the number of species in an area, which in turn drives speciation rate variation.

By characterizing the dynamics of diversity through time, among lineages, and across space in a major tropical group, we were able to address long-standing questions about tropical evolution. We found that diversity in a tropical group has accumulated over a protracted period, and that the hotspots of species diversity in the tropics are associated with time for species accumulation rather than exceptional speciation rates in those areas. We provide evidence that the environment mediates speciation dynamics through this filter of species richness. Overall, extreme environments appear to limit diversity but provide enhanced opportunities for speciation, whereas moderate environments reduce species formation within lineages but permit diversity to accumulate.

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ACKNOWLEDGMENTS

We thank the many field workers and museum staff and administrators who made this work possible, particularly those at the Field Museum of Natural History, the Instituto Alexander von Humboldt, the Instituto de Ciencias Naturales (Universidad Nacional de Colombia), the Instituto Nacional de Pesquisas da Amazônia, the Colección Ornitológica Phelps, the Instituto de Zoología y Ecología de la Universidad Central de Venezuela, the Museu de Zoologia da Universidade de São Paulo, the Museum of Southwestern Biology (University of New Mexico), the Australian National Wildlife Collection, the Peabody Museum of Natural History (Yale University), the Burke Museum (University of Washington), the Cornell University Museum of Vertebrates, the Academy of Natural Sciences of Philadelphia (Drexel University), the Museum of Vertebrate Zoology (UC Berkeley), the Museo de la Universidad de Costa Rica, the Laboratório de Genética e Evolução Molecular de Aves (Universidade de São Paulo), the Museum of Comparative Zoology (Harvard University), the University of Michigan Museum of Zoology, the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, the

Museu Paraense Emílio Goeldi, and the Museum of Natural Science (Louisiana State University). Fieldwork support by the Ornithology Section at MZUSP, especially by V. Piacentini and F. Schunk, was important to improving taxon sampling in Brazil. D. Lane, B. Whitney, J. V. Remsen Jr., S. S. Taylor, J. E. McCormick, C. H. Oliveros, S. P. Galeano, C. Sánchez, J. S. Schenck, M. Bornschein, R. Belmonte, M. Maldonado, the Derryberry and Brumfield laboratory members, the Ornithology Section at MZUSP, and the LSUMNS vertebrate group provided additional advice with study design and assistance with sampling. F. Raposo do Amaral, G. Thom, V. Piacentini, J. Weckstein, L. Musher, G. Del-Rio, and C. Miyaki generously provided sequence data for 51 individuals. R. Beco, S. Bolívar, F. Bocalini, L. Neves, and Rapid Genomics provided support with laboratory work. The Louisiana State University High Performance Computing Center, the University of Michigan Advanced Research Computing Technology Service, and the Harvard University FAS Research Computing Group provided computational support. D. L. Rabosky and his laboratory group, S. Mirarab, S. M. Smith, J. W. Brown, N. Upham, A. Cloutier, W. Jetz, and S. Orzchowski, provided advice and assistance with analyses. J. T. Weir and three anonymous reviewers provided helpful comments on an earlier version of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. **Funding:** This work was supported by U.S. National Science Foundation grants DEB-1146265 (to R.T.B.), DEB-1146423 (to E.P.D.), DEB-1146248 (to J.C.), DEB-1146345 (to R.G.M.), DEB-1011435 (to G.A.B. and R.T.B.), IOS-1210556 (to M.G.H. and R.T.B.), DBI-1523893 (to M.G.H.), DEB-1655624 (to B.C.F. and R.T.B.), and DEB-1241066 (to J.C.); National Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant RGPIN-2018-06747 (to S.C.); São Paulo Research Foundation—FAPESP grants 2012-23852-0 (to G.A.B.) 56378-0 and 2017-23548-2 (to L.F.S.); and Brazilian Research Council (CNPq) grants 457491/2012-4 and 302291/2015-6 (to L.F.S.); 457974-2014-1 (to G.A.B and L.F.S.), and 306843/2016-1, 574008/2008-0, 563236/2010-8 and 471342/2011-4 (to A.A.).

Author contributions: E.P.D., R.T.B., J.C., L.F.S., R.T.C., A.A., F.H.S., R.G.M., and J.P.E. conceived of the study. M.G.H., G.A.B., S.C., A.M.C., G.E.D., J.B., G.F.S., J.S.M., B.C.F., and B.T.S. developed the methods and collected the data. M.G.H., G.A.B., S.C., G.E.D., and B.C.O. conducted the analyses. M.G.H., G.A.B., S.C., R.T.B., and E.P.D. wrote the paper with the assistance of S.V.E., B.C.O., B.C.F., B.T.S., J.P.E., and L.F.S. The manuscript reflects the contributions and ideas of all authors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Raw sequence data are in the NCBI Sequence Read Archive (PRJNA655842). Protocols, code, trees, and alignments are available on Zenodo (31).

SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S72
Tables S1 to S47
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MDAR Reproducibility Checklist

1 October 2019; resubmitted 1 May 2020

Accepted 29 October 2020

10.1126/science.aaaz6970

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Science 370 (6522), 1343-1348.
DOI: 10.1126/science.aaz6970

Diversity does not drive speciation

The role of the environment in the origin of new species has long been debated. Harvey *et al.* examined the evolutionary history and species diversity of suboscine birds in the tropics (see the Perspective by Morlon). Contrary to expectations that the tropics have higher rates of speciation, the authors observed that higher and more constant speciation rates occur in harsh environments relative to the tropics. Thus, for this group of birds, diversification in temperate to Arctic regions followed by the movement and retention of species in the tropics results in their higher local levels of species diversity.

Science, this issue p. 1343; see also p. 1268

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