Article

Multiple bursts of speciation in Madagascar's endangered lemurs

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Lemurs are often cited as an example of adaptive radiation, as more than 100 extant species have evolved and filled ecological niches on Madagascar. However, recent work suggests that lemurs lack a hallmark of other adaptive radiations: explosive speciation rates that decline over time. Thus, characterizing the tempo and mode of evolution in lemurs can reveal alternative ways that hyperdiverse clades arise over time, which might differ from traditional models. We explore lemur evolution using a phylogenomic dataset with broad taxonomic sampling that includes the lorisiforms of Asia and continental Africa. Our analyses reveal multiple bursts of diversification (without subsequent declines) that explain much of today's lemur diversity. We also find higher rates of speciation in Madagascar's lemurs compared to lorisiforms, and we demonstrate that the lemur clades with high diversification rates also have high rates of genomic introgression. This suggests that hybridization in these primates is not an evolutionary dead-end, but potential fuel for diversification. Considering the conservation crisis affecting strepsirrhine primates, with approximately 95% of species threatened with extinction, this study offers a perspective for explaining Madagascar's primate diversity and reveals patterns of speciation, extinction, and gene flow that will help inform future conservation decisions.

The lemurs of Madagascar (Strepsirrhini: Lemuriformes and Chiromyiformes[1]) are a fascinating case study in evolutionary biology. They are highly diverse—representing more than 15% of all living primate species—yet all members of the clade live on an island representing <1% of Earth's land area[2]. After colonizing Madagascar, lemurs evolved to fill a wide range of ecological niches, from the smallest primate species in the world—the arboreal mouse lemurs (*Microcebus*)—to recently extinct terrestrial species as large as female gorillas (*Archaeoindris*). Given their phenotypic and ecological diversity,

lemurs are often highlighted as an example of adaptive radiation[3] along with other classic examples like Darwin's finches from the Galápagos Islands[4] and cichlids from Lake Victoria[5]. However, a recent study[6] found that lemurs did not follow an expected pattern of adaptive radiation, i.e., they did not experience rapid or explosive speciation that decreased over time as niches became filled[7,8]. With this new understanding of the overall rates of lemur diversification, the stage is set to further unravel evolutionary tempo in the accumulation of Madagascar's primate diversity. Access to genomic data provides the

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opportunity to refine estimates of lemur phylogeny and branch lengths, to test more detailed models of diversification, and to ask whether previously unexplored evolutionary factors have shaped lemur diversity.

To fully understand the evolutionary dynamics of lemurs, we must properly contextualize their diversification alongside their often-neglected sister group, Lorisiformes. Lemurs and lorisiforms (collectively known as the wet-nosed primates, suborder Strepsirrhini) together form a comparative system for understanding how evolutionary dynamics in different geographical regions can produce drastically different levels of species diversity. The lorisiform primates, which occur in Asia and continental Africa, include galagos, pottos, angwantibos, and lorises, all of which are nocturnal and elusive. While they exhibit several interesting morphological adaptations−e.g., they include the only venomous primates (*Nycticebus* and *Xanthonycticebus*)−the lorisiforms are less diverse than lemurs overall, both phenotypically and in terms of species diversity[6,9]. As a result, they have been comparatively neglected in scientific literature[10]. Here, we use a phylogenomic dataset to reconstruct the evolutionary history of Strepsirrhini, providing a framework for evaluating if lemurs diversified according to the classic adaptive radiation model and whether their rates of diversification differed from those of lorisiforms. Given abiding uncertainty about phylogenetic relationships within these groups (discussed in the following section), we also consider the possibility that introgressive hybridization has introduced conflicting genealogical histories across the genome. Hybridization has been historically conceptualized as a homogenizing force in evolutionary biology that counteracts divergence[11], but a recent systematic review of adaptive radiations showed that gene flow often provides fuel for diversification as well[12]. To address this idea, we additionally test for a relationship between introgression and the rate of diversification in strepsirrhines, providing insights into a continuing question in evolutionary biology, i.e., whether hybridization impedes or promotes the formation of new species[13–15].

Results and Discussion
A phylogenomic tree of strepsirrhines
Using a phylogenomic dataset comprising 334 nuclear loci with an average length of 3339 base pairs (bp; range: 158−6985 bp; total concatenated alignment length: 1,108,850 bp), we reconstructed a phylogenetic tree of Strepsirrhini that includes 71% of all currently recognized species (50% of all lorisiform species and 79% of all lemur species per the taxonomic references in Supplementary Data 1; sample information in Supplementary Data 2). After assessing the impacts of missing data (Supplementary Figs. 1, 13–17; Supplementary Data 1; see Materials and Methods), we used two different species-tree inference approaches (SVDquartets[16,17], based on DNA sequence data, and ASTRAL[18], based on estimated gene trees). Both analyses produced a tree that was largely concordant with prior studies, with Madagascar's lemurs (infraorders Chiromyiformes and Lemuriformes) as a monophyletic group sister to all strepsirrhine species from Asia and continental Africa (infraorder Lorisiformes) and well-supported clades representing each strepsirrhine family (Fig. 1, Supplementary Figs. 2, 3).

This nuclear dataset confirms that the family Lorisidae [the 'slow-climbing' angwantibos (*Arctocebus*), pottos (*Perodicticus*), and lorises (*Loris*, *Nycticebus*, and *Xanthonycticebus*)] and the family Galagidae [the 'fast-leaping' galagos and bushbabies (*Euoticus*, *Galago*, *Galagoides*, *Otolemur*, *Paragalago*, and *Sciurocheirus*)] are reciprocally monophyletic, resolving a longstanding debate (Fig. 1)[10,19–21]. Previous genetic studies have sometimes recovered a sister relationship between galagids and angwantibos/pottos (see also our mitochondrial results below), leading some authors to conclude that traits associated with slow climbing evolved in parallel[10,22]. Although our study does not support parallel evolution, our molecular analyses do recover a

relatively short internode (Fig. 2) suggesting that adaptations to slow climbing evolved rapidly.

In lemurs, a major area of phylogenetic disagreement has been the placement of the family Indriidae [the woolly lemurs (*Avahi*), sifakas (*Propithecus*), and indri (*Indri*)]. Some studies have placed indriids as sister to the family Lemuridae [the true lemurs (*Eulemur*), bamboo lemurs (*Hapalemur* and *Prolemur*), ring-tailed lemur (*Lemur*), and ruffed lemurs (*Varecia*)[23,24]; while other studies have placed indriids as sister to the Cheirogaleidae + Lepilemuridae clade [the mouse lemurs (*Microcebus*), fork-marked lemurs (*Phaner*), dwarf lemurs (*Allocebus*, *Cheirogaleus*, and *Mirza*), and sportive lemurs (*Lepilemur*)][25–27]; and still other studies have recovered indriids as the sister group to all of these[28,29]. Our study confirms the placement of Indriidae as sister to Cheirogaleidae + Lepilemuridae, although bootstrap support for this node was 89% (Fig. 1), which was lower than any other family-level relationship on the tree and may be due to an ancient history of introgression (discussed below).

Timing of the colonization of Madagascar
We dated the strepsirrhine phylogeny using calibrations for nine nodes of the tree based on the fossil record (Fig. 2, Supplementary Data 3)[30,31]. We estimate that lemurs and lorisiforms diverged during the Paleocene or early Eocene [median 53.2 million years ago (MYA), 95% confidence interval (C.I.) = 47.8−57.6 MYA] and the crown diversifications of both groups took place during the mid to late Eocene (lemur median = 41.9 MYA, 95% C.I. = 33.9−49.7 MYA; lorisiform median = 38.7 MYA, 95% C.I. = 36.9−41.4 MYA). If we use these 95% C.I.s and assume that lemurs colonized Madagascar through a single dispersal event, then the ancestral lemur must have arrived on Madagascar sometime between 33.9 and 57.6 MYA (Fig. 2). However, to account for conflicting recommendations related to fossil placement and node priors among previous studies, we also explored how these times might vary under different fossil calibration regimes (Supplementary Data 3). Across these analyses we observed some conflicting time estimates and large C.I.s on older nodes on the tree (Supplementary Fig. 4), which resulted in a wide window for the timing of the colonization of Madagascar. If we consider the 95% C.I.s across all possible analyses, then lemurs may have colonized Madagascar any time between 27.0 and 84.5 MYA. This window is wider than the full range of possible colonization times estimated by 22 previous studies (Supplementary Data 4), providing a clear example of how sensitive these analyses can be to parameter settings and model choice.

It is worth noting that some recent studies have used mutation rates rather than fossils to calibrate the diversification of mouse lemurs (genus *Microcebus*), and these have produced younger split times than those estimated here. For example, these studies estimated the crown diversification of *Microcebus* at -1.5 MYA compared to -5 MYA in this study[32–34]. The younger ages recovered in mouse lemur studies may be due to inaccurately elevated pedigree-based mutation rate estimates. Alternatively, our fossil-calibrated tree may overestimate divergence times for young nodes given the dependence on older fossil calibrations deeper in the phylogeny[33]. There are no known lemur fossils on Madagascar that can be used for node calibration, so young lemur nodes are particularly susceptible to overestimation due to reliance on phylogenetically distant fossils. As divergence time estimation is a rapidly changing field, we are hopeful that a consensus may one day be reached using a combination of fossils and demographic modeling. Regardless of the exact timing, it is also important to note that all of these estimates for the colonization of Madagascar assume that all lemurs originated from a single dispersal event. A recent study of African fossils, potentially related to the aye-aye, suggests that Chiromyiformes and Lemuriformes may have colonized Madagascar independently[35] and we cannot rule out this possibility. If that is the case, then there is much greater uncertainty in the timing of colonization for both groups due to their long
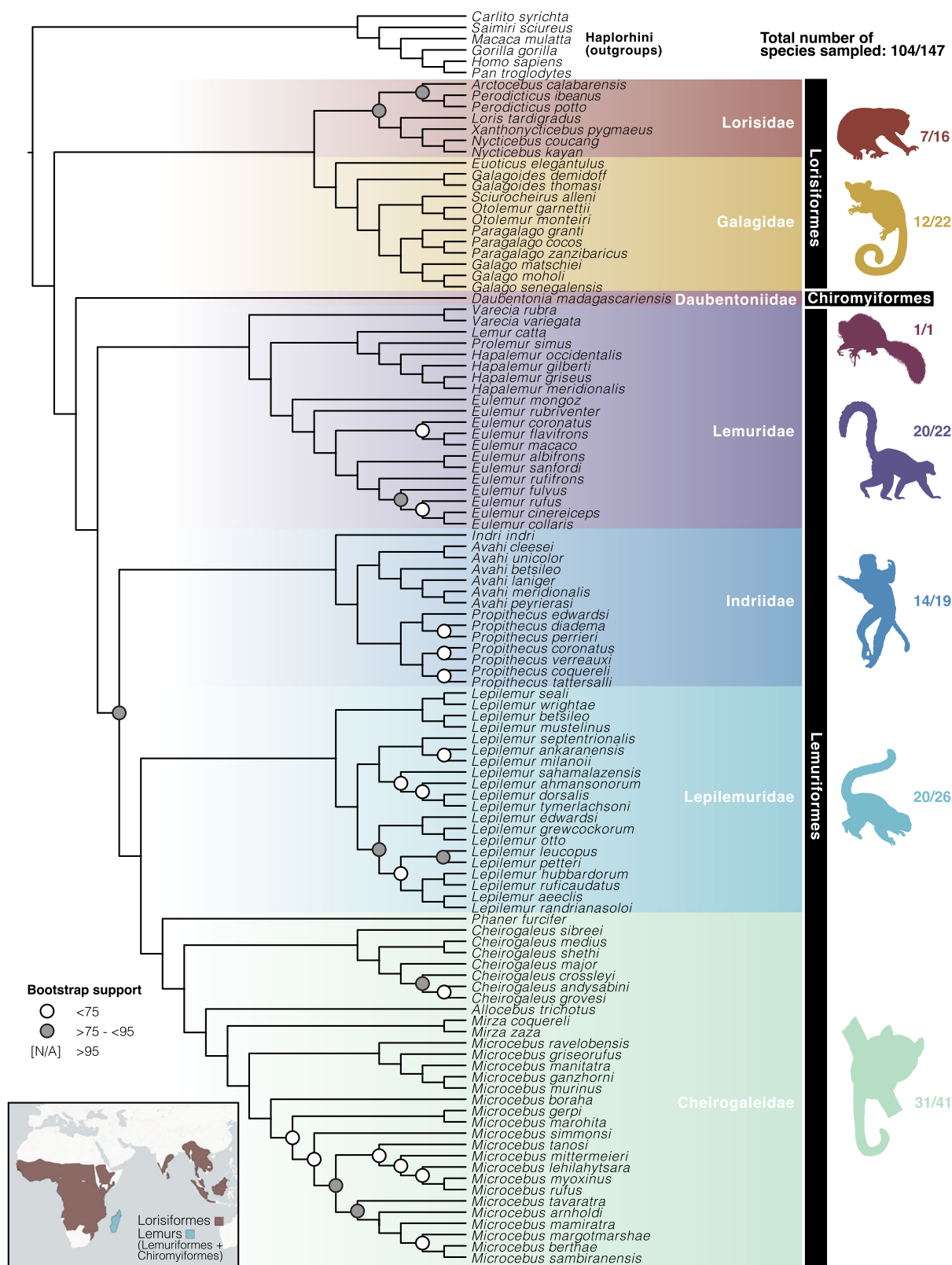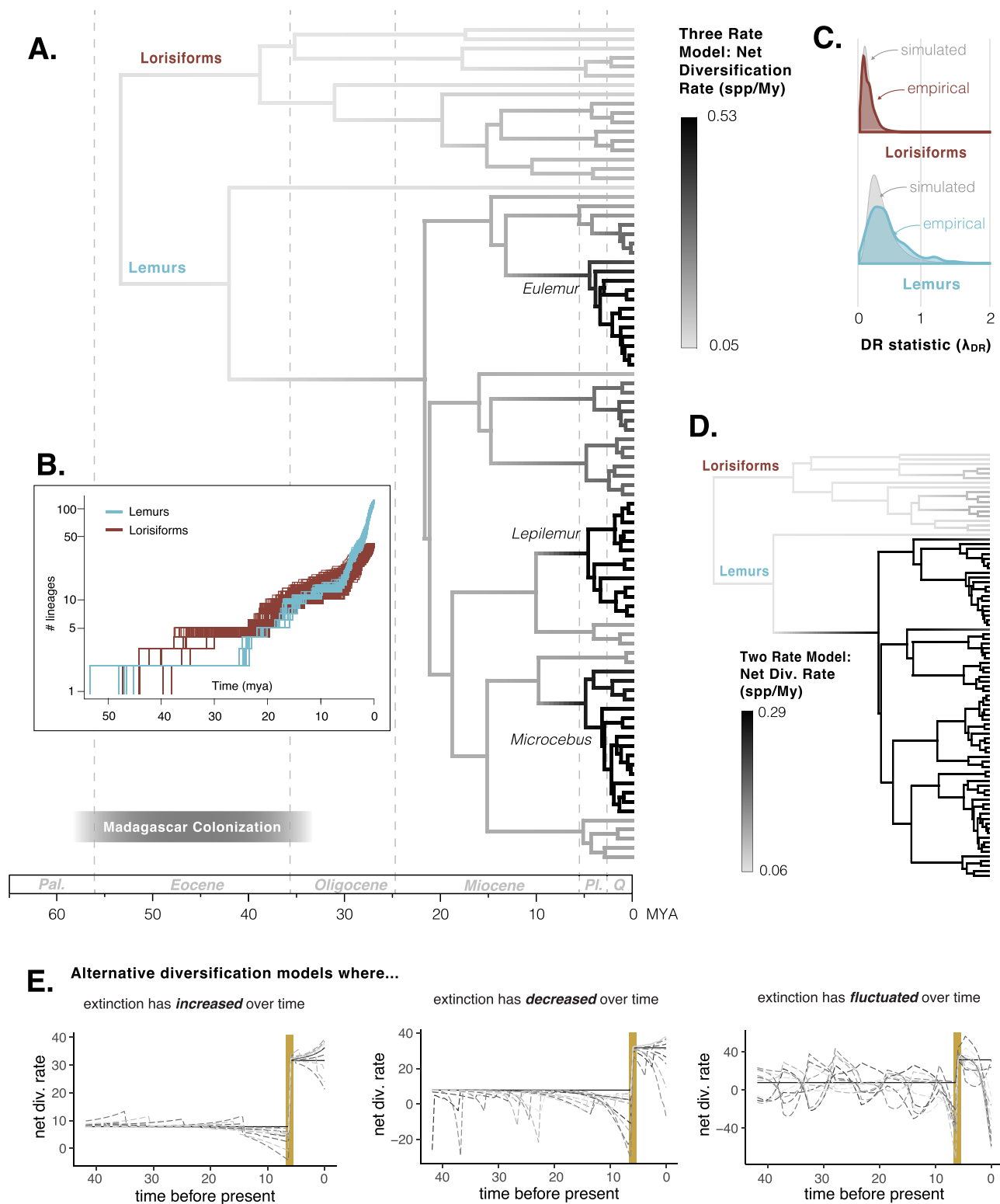
Fig. 1 | A species tree of strepsirrhine primates estimated using SVDQuartets. Node support values were estimated using 1000 bootstrap replicates. Nodes with > 95% bootstrap support are not labeled, while nodes with 75-95% support and <75% support are indicated by gray and white circles, respectively. The actual bootstrap support values for all nodes are provided in Supplementary Fig. 2. Branch lengths are not scaled. Infraordinal names are shown in black bars, and family names are shown in different colors matching the silhouette image of a representative species to the right of the tree. Silhouettes were obtained from PhyloPic.org and are public domain. The numbers next to each silhouette indicate the number of species sampled from each family as a fraction of the total number of described species in the family. Inset map shows the combined distributions of all lorisiform and lemur species in red and blue, respectively. Distribution maps were obtained from the IUCN Red List spatial database[110].

stem branches, and further resolution may not be possible at this time.

Tempo of diversification on Madagascar

Using lineages-through-time plots (Fig. 2b) and Pybus and Harvey's γ[36] (a statistic based on internode distances from our ultrametric tree), all of our time-calibrated phylogenies produced clear and significant patterns of increasing diversification rates toward the present in lemurs without a subsequent decline (median γ = 6.37, p-value <

0.0001; Supplementary Fig. 5a). These estimates of γ were still significantly greater than zero even after pruning up to 20 lemur species (median γ = 5.77, p-value < 0.0001; Supplementary Fig. 5a), suggesting that this pattern reflects increasing diversification rates toward the present rather than being an artifact of possible taxonomic inflation[37,38]. To further explore variation in diversification rates across the strepsirrhine tree, we estimated species-specific tip diversification rates (λ_{DR}; Supplementary Data 5)[39]. In lorisiforms, we recovered a distribution of λ_{DR} values that tightly mirrored the expectations under

Fig. 2 | Variation in diversification rate (DR) over time and across strepsirrhine phylogeny. A A time-calibrated phylogeny of Strepsirrhini, with branches colored according to DR (species per million years) estimated using a three-rate model in MiSSE. Full results of this analysis can be found in Supplementary Fig. 6. Dashed vertical lines distinguish geological epochs (Pal. Paleocene, Pl. Pliocene, Q. Quaternary). Fully detailed time-calibrated phylogenies showing tip labels, node confidence intervals, and outgroups are shown in Supplementary Fig. 4. Three genera with particularly high speciation rates (*Eulemur*, *Lepilemur*, and *Microcebus*) are indicated on the tree and are discussed in the text. **B** Lineages-through-time plots of lemurs (blue) and lorisiforms (red). Each line represents a distinct tree generated using six different fossil calibration sets and accounting for incomplete taxonomic sampling, which was done by stochastically adding missing taxa to the proper genus 1000 times. The complete set of 6000 trees is available on Figshare (https://doi.org/10.6084/m9.figshare.28699742). Note that the y-axis representing the number of lineages is log-transformed. **C** Variation in DR between lorisiforms and lemurs is visualized as the distribution of tip DR (λ_{DR}) values for all species within

each taxon. Darker colored distributions represent the empirical λ_{DR} values across the set of 6000 stochastically resolved trees, while light gray distributions represent simulated λ_{DR} values, in which trees of the same species richness as each Family were simulated using a rate-constant birth-death model. The empirical and simulated values shown in these plots were calculated using a custom script (TipDr_Calculation.R; see Code Availability statement)[102]. **D** MiSSE results, identical to panel A, but estimated using a two-rate model. See Supplementary Fig. 7 for the full visualization of this analysis, and Supplementary Data 6 for MiSSE model testing results. **E** Results of our CRABS analysis which estimated ten different diversification models in the congruence class (the set of speciation and extinction functions with equal likelihoods) under three different extinction treatments (left, models where extinction increased over time, center, models where extinction decreased over time, and right, models where extinction fluctuated randomly over time). Each line represents a different model in the congruence class. Across all analyses, an increase in net diversification rate was detected ~5-6 mya (indicated by a yellow vertical bar). Full details of this analysis are provided in Supplementary Fig. 8.

a pure-birth model (Fig. 2c). The empirical λ_{DR} distribution for lemurs was also similar to expectations, but included some values that were higher than expected, suggesting that diversification on certain lemur branches cannot be explained by a pure-birth model.

To visualize variation in macro-evolutionary rates of speciation among branches, we fitted a missing state speciation and extinction (MiSSE) model which estimates shifts in diversification as a function of one or more hidden states[40]. Across the six time-calibrated trees that we estimated, MiSSE selected models with either two or three hidden states (Supplementary Data 6). All of the two- and three-state models show a clear increase in diversification rate along the branch leading to Lemuriformes (all lemurs except the aye-aye) and all of the three-state models show an additional increase in diversification rate in the last ~5 million years, which is concentrated on three lemur genera: *Microcebus*, *Lepilemur*, and *Eulemur* (clades dominated by darker branches on Fig. 2a, Supplementary Figs. 6, 7). The former rate estimates (those along the branch leading to Lemuriformes) should be interpreted with some caution, as this branch is located towards the root of the tree where uncertainty is higher in the state-dependent speciation and extinction models implemented in MiSSE[40]. The estimated rates of diversification towards the tips of the tree (including the elevated rates in *Microcebus*, *Lepilemur*, and *Eulemur*) are comparatively robust.

We focused our analyses on extant species because there are no known primate fossils from Madagascar older than the Holocene. An important consequence of using time trees with only extant taxa is that —because lineages that originated recently have had less time to go extinct—there can be a bias toward increased rates of speciation closer to the present[41]. Despite concerns that absolute rates of diversification may be inaccurate in such analyses, previous research suggests that relative differences in state-dependent rates (e.g., how fast lemurs radiated relative to lorisiforms, discussed below) can still be estimated with high confidence[42]. It is still concerning, however, that time-varying diversification models suffer from non-identifiability; that is to say, an infinite number of speciation and extinction rate functions could be produced from the same phylogeny with equal likelihoods (this set of functions is known as the congruence class)[41]. To address this specific concern, we used the R package CRABS[43] to test whether trends in diversification rates remained consistent across models in the congruence class. We evaluated scenarios where extinction rates were (1) initially high but decreased over time, (2) initially low but increased over time, and (3) allowed to fluctuate randomly over time. Remarkably, all models in the congruence class consistently recovered a clear signal of a sudden increase in speciation rate around 5-6 MYA (Supplementary Fig. 8). This suggests that the signature that we recovered of a burst of speciation around the Miocene-Pliocene boundary in lemurs is robust and can be detected even from extant-only time trees[44].

Lemurs are often cited as a classic example of adaptive radiation, i.e., a clade that diversified from a single common ancestor in response

to ecological opportunity. The implied ecological opportunity for lemurs was the colonization of Madagascar, an island with presumably underutilized resources at the time of dispersal. The general model for adaptive radiation includes an early burst of rates of speciation and morphological change followed by a decline in both rates as niches become filled – a pattern that has been observed in some Malagasy taxa[45,46]. However, our analyses, as well as some previous studies[6,47], show that diversification rates in lemurs have not yet declined and may in fact still be increasing. One possible alternative characterization of lemurs is a constructive radiation, defined as a radiation that continues to expand as new opportunities are generated continually over time, either due to changing environmental conditions or due to ecological feedback constructed by the radiation itself[48]. A prediction of constructive radiations is that there may be a lag time between phenotypic disparification and taxonomic diversification[49]. Although we did not assess phenotypic rates of evolution in this study, previous work has shown that morphological disparity in lemurs did evolve quickly after colonization[6]. If we assume that all lemurs (Chiromyiformes + Lemuriformes) originated from a single colonization event 33.9–57.6 MYA, then there was a lag time of approximately 10–20 million years before taxonomic diversification rates significantly increased.

It is also important to recognize that many early writers on adaptive radiation did not include explosive speciation as a defining feature at all[50–52] and it is widely acknowledged that radiations (in the more general use of the term) may arise slowly due to a variety of biotic and abiotic factors, with different predictions for island versus continental radiations[53–55]. Island radiations often begin after an ancestor colonizes a depauperate area, with character displacement among daughter lineages being driven by competition in sympatry. However, on larger continental scales, it is more common for radiations to arise allopatrically as taxa cross geographical barriers or become isolated in habitat fragments when climatic conditions change[53]. Lemurs colonized Madagascar shortly after the Cretaceous-Paleogene extinction event, so they likely arrived on an island that was depauperate and relatively homogeneous in terms of environmental conditions[56]. However, Madagascar is large enough, old enough, and contains enough modern topological and environmental heterogeneity, that speciation has often occurred in allopatry; for example, there are many examples of lemur species boundaries shaped by river barriers, mountains, or watersheds[57–61]. Thus, while Madagascar is an insular, island system, studying Madagascar's biodiversity only through the lens of island biogeography may overlook patterns that arose through continental processes.

Recent radiations in Madagascar's lemurs

In several of the diversification analyses described above, we observed a burst of diversification in lemurs around the start of the Pliocene (~5 MYA; Fig. 2a and Supplementary Fig. 6). This pattern is particularly

evident in three genera: *Microcebus*, *Lepilemur*, and *Eulemur*. Thus, while lemurs overall might not conform to a traditional definition of adaptive radiation, these three subclades within lemurs might still offer opportunities for scientists who are interested in young, explosive radiations to directly observe ecological speciation, sexual selection, and the spread of key innovations. We suggest that the high diversification rates observed in *Microcebus*, *Lepilemur*, and *Eulemur* around the Miocene-Pliocene transition (or during the Pleistocene, if mutation-date-based divergence times from other studies are applicable[32-34]) are the result of multiple biotic and abiotic processes. In terms of biotic factors, our results (below) suggest that all three of these genera were experiencing high levels of interspecific gene flow, which might have resulted in novel combinations of alleles that were fuel for diversification. At the same time, the Miocene-Pliocene transition is associated with massive expansions of grasslands and savannas around the world (including Madagascar) as temperatures became cooler[62,63]. The forest ecosystems that had already been established on Madagascar as early as the Cretaceous would have become fragmented during this time, forcing lemur populations into allopatry and contributing to diversification. One additional abiotic factor that may have promoted high speciation rates toward the end of the Miocene is the increasing amount of topological complexity due to montane uplift[64]. The mountains of Madagascar reached their current elevations ~10 MYA[65], which could have set the stage for diversification as lemurs adapted to new elevational niches and once-contiguous populations were separated from each other. A line of evidence supporting this hypothesis is that lemur species are tightly linked to specific watersheds that were shaped by these mountains[59].

Tempo of diversification in lemurs' sister group

Our macroevolutionary rate analyses (Fig. 2a, Supplementary Figs. 6, 7) consistently support higher diversification rates in lemurs relative to their sister group, the lorisiforms. We estimated a moderate rise in diversification rate within the family Galagidae (specifically the genera *Galago* and *Paragalago*), but these were still lower overall than most lemuriform clades. These results were concordant with our analyses of λ_{DR}, which estimated median values to be more than twice as high in lemurs relative to Lorisiformes: 0.44 species per million years (My) compared to 0.15 species/My, respectively (Fig. 2c, Supplementary Data 5). Notably, some prior studies have failed to detect a strong difference in diversification rate between these two clades[44,66], or produced equivocal results across various analyses[6]. However, most studies to date have suffered from poor species-level sampling of lorisiforms, and several new species have been identified in recent years, making lorisiform taxonomy and diversification a subject of continuing discussion[10,67,68]. To explore how greater taxonomic attention could influence our estimated rates of diversification, we artificially added up to 20 tips on the lorisiform tree. Interestingly, even with 20 added species (an implausibly high increase in described diversity) lorisiforms would still not match the high rates of diversification seen in lemurs ($\gamma = 5.62$ compared to the above-estimated lemur $\gamma = 6.37$; Supplementary Fig. 5). That lemurs and lorisiforms have dramatically different rates of diversification is perhaps unsurprising given that lemurs occur singularly on an island, whereas the evolution of lorisiforms has played out over continental scales where several of the niches occupied by lemurs have been occupied by competing species not found on Madagascar (e.g., there are no diurnal lorisiforms, perhaps due to competition with catarrhine primates).

Signatures of introgression in strepsirrhines

Considering the historical difficulty in resolving the strepsirrhine phylogeny, it seems likely that a variety of biological processes, including incomplete lineage sorting (ILS) and introgression, have left signatures in the genome that deviate from the true history of speciation[69]. As a first step toward assessing whether introgression has

been present in the evolutionary history of strepsirrhines, we compared the phylogeny generated from our nuclear dataset to a mitochondrial phylogeny (Fig. 3; Supplementary Fig. 9). While we acknowledge that our nuclear dataset is more likely to reflect the true species tree compared to mitochondrial data, topological differences between these two trees can help identify candidate branches of the tree that have experienced introgression[70]. In our case we observed three topological differences between these trees (Fig. 3): (1) Indriidae was sister to all other lemuriform families in the mitochondrial phylogeny, as opposed to Cheirogaleidae + Lepilemuridae in the nuclear phylogeny; (2) the genus *Hapalemur* was sister to *Lemur* in the mitochondrial phylogeny as opposed to *Prolemur*; and (3) in the mitochondrial phylogeny the genera *Perodicticus* and *Arctocebus* formed a clade with galagids, rendering Lorisidae paraphyletic.

To explicitly test whether introgression rather than ILS caused these topological differences (labeled with gray circles in Fig. 3) we used the program QuIBL, which estimates the proportion of introgressed loci for each species triplet using gene-tree branch lengths[71]. This analysis recovered significant signatures of introgression for all three topological differences (gray arrows on Fig. 3; full results in Supplementary Fig. 10). On average, we estimated 7.9% introgressed loci for topological difference #1 (between Lemuridae and Indriidae), 0.4% for topological difference #2 (between the genera *Lemur* and *Hapalemur*), and 2.2% for topological difference #3 (between the family Galagidae and the *Perodicticus-Arctocebus* clade). This indicates that an ancient history of introgression likely contributed to topological uncertainty in these regions of the phylogeny. This analysis also identified small but significant proportions of introgressed loci in three other regions of the tree: 0.4% between *Eulemur* and two other lemur genera (*Lemur* and *Varecia*), 0.6% between *Nycticebus* and two other lorisiform genera (*Galago* and *Euoticus*), and 0.7% between lemurs and three lorisiform genera (*Euoticus, Nycticebus*, and *Xanthonycticebus*; Supplementary Fig. 10). These results suggest that introgression was prevalent during early strepsirrhine evolution, likely occurring before and after the colonization of Madagascar and/or among now-extinct lemur relatives in continental Africa.

At shallower taxonomic levels we also observed many uncertain relationships (low or moderate node support) within five lemur genera: *Eulemur*, *Propithecus*, *Lepilemur*, *Cheirogaleus*, and *Microcebus*. One possible reason for low node support could be introgression. To test this hypothesis, we estimated phylogenetic networks for each of the five genera. In all five analyses a model with at least one reticulate branch ($H = 2-5$) was highly supported (Fig. 4, Supplementary Fig. 11). These reticulations are predominantly among ancestral species. However, in two instances we recovered introgression between extant taxa (*Lepilemur tymerlachsoni/L. dorsalis* and *Microcebus lehilahytsara/ M. mittermeieri*) which are both parapatric species pairs, making hybridization highly plausible. This suggests that introgression has been prevalent in the evolutionary history of all five of these genera and has likely been an additional source of genealogical conflict beyond ILS. Another recent study also suggested that a burst of speciation (and resulting phylogenetic uncertainty) in the *Microcebus* clade is the result of an ancient introgressive hybridization event[72]. These results highlight an important consideration for phylogeneticists: if we continue to use species-tree models that only account for ILS as a source of gene tree heterogeneity across the genome, larger genomic datasets will never result in 100% node support for branches affected by a history of introgression.

Gene flow is a topic of keen interest for lemur biologists, as there are several documented active hybrid zones across Madagascar[73] and introgression appears to have been a staple of lemur evolution on recent timescales[27,74]. Our phylogenomic evidence expands our understanding of the history of hybridization in lemurs by showing that introgressive hybridization is not merely a recent phenomenon but has been a pervasive force throughout the evolutionary history of
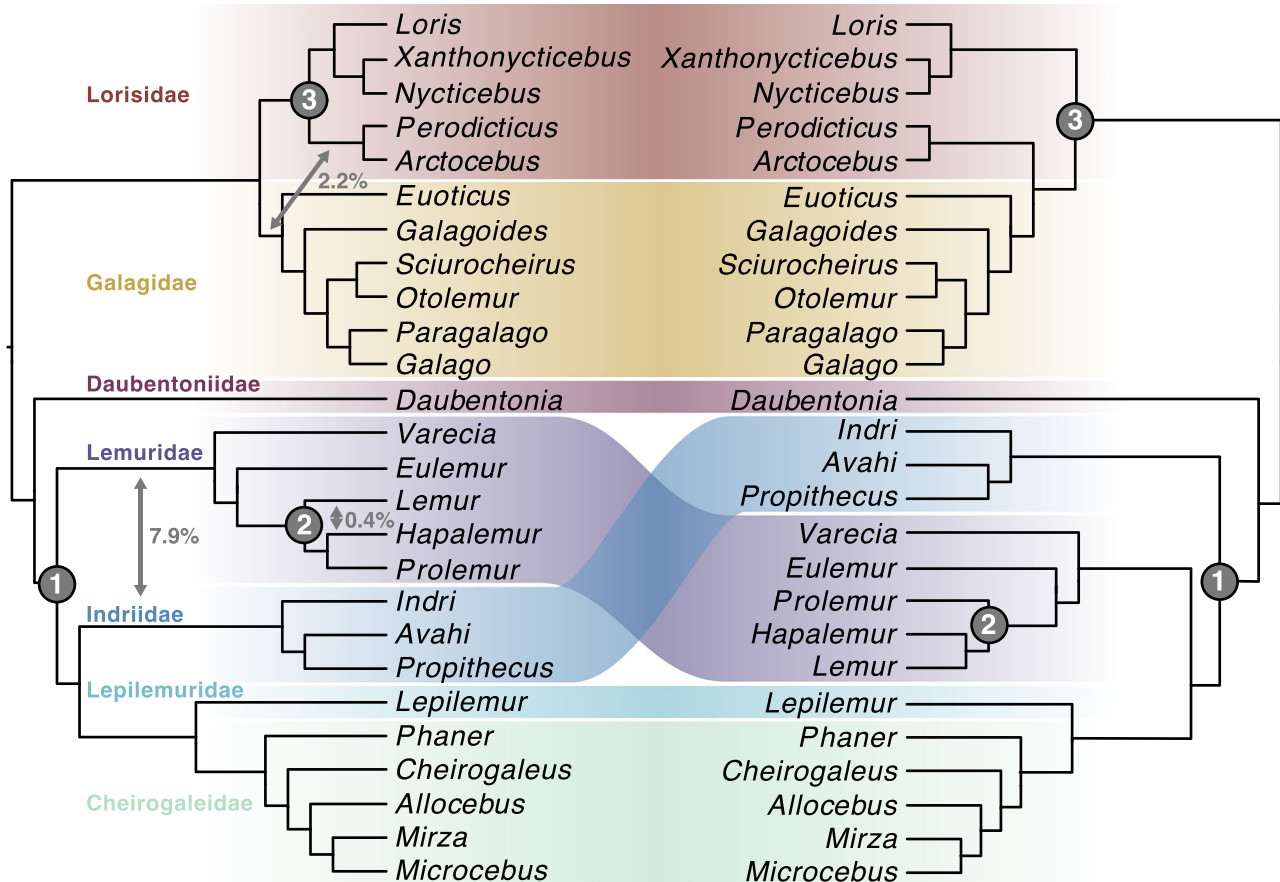
Fig. 3 | Discordance between nuclear (left) and mitochondrial (right) phylogenies of strepsirrhine genera. Both phylogenies were estimated using IQTree with all available individuals, and then species-level branches were manually collapsed to visualize one branch per genus. Fully detailed phylogenies from these analyses are available in Supplementary Figs. 9 and 13. The nuclear and mitochondrial trees are discordant in three locations labeled with gray numbered circles. Gray arrows on the nuclear phylogeny indicate three locations, where gene flow was inferred using QuIBL, with the proportions of introgressed loci labeled. Full details from QuIBL are found in Supplementary Fig. 10. Families are colored to match Fig. 1.

lemuriforms. Indeed, we identified introgression during the early divergence of families ~40 MYA (between Lemuridae and Indriidae), during the divergence of genera ~10 MYA (between *Lemur* and *Hapalemur*), and among species in the same genus within the last ~5 million years (Figs. 3, 4).

Hybridizing species experience higher diversification rates

One interesting finding from studies outside of Strepsirrhini has been that some of the most species-rich clades have experienced the highest amounts of introgression e.g., see ref. 15. To understand whether there is a correlation between diversification rates and introgression in our system, we first scored each species as hybridizing or non-hybridizing, based on this study as well as an extensive literature review (Supplementary Data 7). We then tested the fit of five different models of diversification (Supplementary Data 8) which varied based on character-dependence or -independence, and on the presence or absence of unsampled factors (hidden states); the least complex model (the dull null) assumes a single rate of diversification regardless of whether the taxon hybridizes, whereas the most complex model (the hidden-state speciation and extinction, or HiSSE, model[75]) assumes that diversification rates are influenced both by the presence or absence of hybridization and by hidden states. We found that the top-ranking model of diversification was a binary-state speciation and extinction (BiSSE) model; i.e., a model in which the diversification rate is tightly correlated with the presence or absence of hybridization without additional hidden states (Supplementary Data 8). Under this

state-dependent diversification model, hybridizing species were estimated to have a net diversification rate that was more than four times higher than non-hybridizing species (Table 1). The BiSSE model was supported across multiple variations of this analysis: when lemurs and lorisiforms were analyzed together, when lemurs were analyzed alone, when we treated all unsampled taxa as hybridizing, and when we treated all unsampled taxa as non-hybridizing (Supplementary Data 8).

A caveat of the above results is that taxa were coded using a liberal definition of hybridization, i.e., they were scored as hybridizing if hybridization had been directly observed in the wild or captivity, or if any genetic analysis had detected interspecific admixture or gene flow. When we applied a conservative coding scheme, in which species were only coded as hybridizing if there was direct documentation of present-day hybrid offspring in the wild, the best-supported models were character-independent (Supplementary Data 8). However, given that many of our results above point to pervasive introgression on ancient and modern evolutionary timescales, we place less weight on these results as we feel that the inclusion of only modern-day hybrids is unrealistically restrictive.

One additional caveat is that it may be difficult to disentangle hybridization from taxonomic attention. For example, groups like *Microcebus* that have been featured in multiple species delimitation studies could have higher rates of diversification because more taxa are being split, and these same groups might also have higher rates of hybridization because they are more recently diverged. To explore this idea, we extended the BiSSE models above to fit a multistate speciation
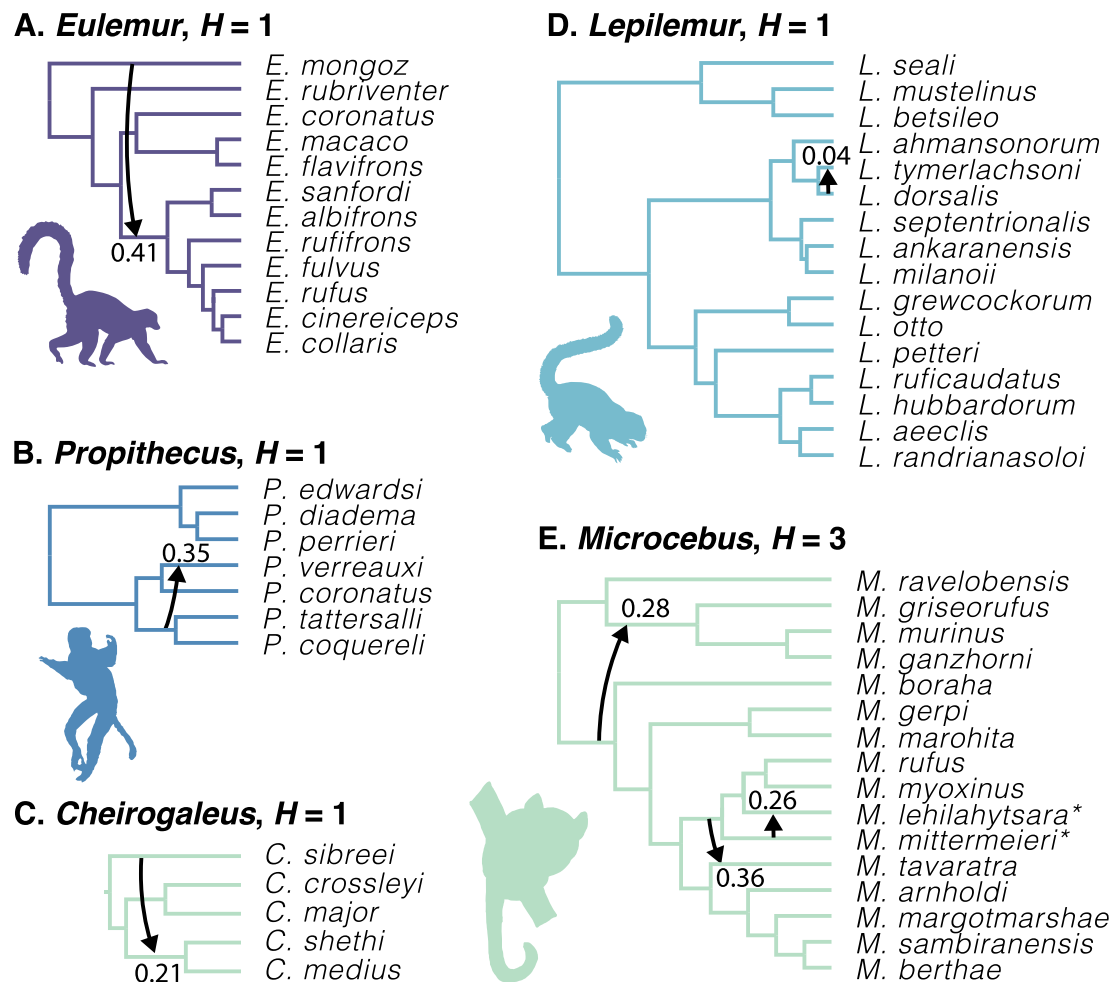
Fig. 4 | Historical introgression events estimated in five lemur clades. Phylogenies with reticulate relationships estimated by PhyloNet for five strepsirrhine genera (**A**–**E**) that had poorly resolved nodes (bootstrap support values < 75%) in our species tree analyses (Fig. 1). Arrows indicate the reticulation events (*H*) and are labeled with the estimated inheritance probabilities. Note that several models received similar support (Supplementary Fig. 11; source data in Supplementary Data 13), and here we show the models with the lowest *H* among the well-supported models. Colors and silhouette images for each genus match the Family-level formatting from Fig. 1. *Note that a recent paper[32] proposed synonymizing *M. mittermeieri* and *M. lehilahytsara* as a single species; however, we treated these as distinct species as our data did not support a sister relationship.

extinction (MuSSE) model with two traits: hybridizing vs. non-hybridizing as well as high taxonomic attention vs. low taxonomic attention (Supplementary Data 7). In this analysis hybridizing taxa still had higher rates of diversification than non-hybridizing taxa, but the magnitude of this difference was impacted by taxonomic attention; specifically, diversification rates were two to four times higher in hybridizing taxa with high taxonomic attention compared to hybridizing taxa with low taxonomic attention (Supplementary Data 9). While this result bolsters support for our finding that hybridization is a significant predictor of diversification, it also highlights an important concern: to what extent do taxonomic practices shape our perception of evolution and biodiversity? This question is particularly relevant in our study, and in other studies of recent lineages that are still experiencing genetic exchange, as these might not be considered distinct species under some conceptual frameworks[76]. It is possible that lineages receiving greater attention are closer to representing true biological diversity, with finer-scale sampling and genomic data allowing for resolution of cryptic species[77]. However, it is also possible that increased scrutiny leads to taxonomic oversplitting, as minor genetic or morphological differences may represent population-level variation rather than evolutionary independence[37]. Although our results suggest a genuine association between hybridization and diversification, they also reinforce the need for caution when interpreting macroevolutionary patterns in groups where the units of analysis—the species—may not be consistently delineated.

Overall, this work contributes to a growing body of evidence that hybridizing species can experience accelerated rates of diversification[13,15], and it demonstrates that this effect can be amplified by taxonomic attention. These results are in contrast to many other examples across the Tree of Life where hybridization erodes species diversity by replacing high-fitness offspring with poor-fitness hybrids, or by homogenizing gene pools before the speciation process can complete[11]. However, it is important to note that our data do not allow us to disentangle cause and effect of this correlation: is introgression merely a byproduct of rapid speciation, resulting from an insufficient amount of time for reproductive barriers to evolve? Or does hybridization itself drive rapid speciation? In the latter case, one mechanism by which hybridization can promote speciation is through the process of reinforcement, or the accumulation of reproductive barriers through selection against hybrids[14]. Alternatively, a combinatorial view of speciation posits that hybridization might fuel rapid diversification by shuffling old genetic variants or introducing novel alleles to new populations[13,78]. This is a fruitful area of research, and we can point to the three genera (*Eulemur*, *Microcebus*, and *Lepilemur*) that we identified with high diversification rates as well as high levels of introgression, which serve as convenient jumping-off points for future studies.

Table 1 | Differences in estimated diversification rates (DR) between hybridizing and non-hybridizing taxa, as estimated by a binary state speciation extinction (BiSSE) model

Model	DR (Spp/100 My): Non-Hybridizing Taxa	DR (Spp/100 My): Hybridizing Taxa
All Strepsirrhines	7.06	30.40
All Strepsirrhines; All unsampled hybridize	7.25	38.38
All Strepsirrhines; No unsampled hybridize	7.98	33.20
Lemurs Only	9.50	35.95
Lemurs only; All unsampled hybridize	9.57	44.32
Lemurs only; No unsampled hybridize	10.49	38.56

The BiSSE model was the top-ranking model in a HiSSE analysis (Supplementary Data 8). The six models listed below varied in whether or not they included lorisiforms, and in how unsampled taxa were treated by the model.

Implications for strepsirrhine conservation and future research

Strepsirrhine primates are in the midst of a biodiversity crisis, with approximately 95% of species being threatened with extinction and 90% experiencing population declines[79,80]. From a conservation perspective our findings provide several important advances. First, they point to species and clades that are most prone to hybridization and gene flow. Another recent genomic study found high levels of gene flow in the same lemur taxa we identified[27], and this result helps explain why lemurs have higher levels of allelic diversity than most other primates despite severe population declines[81,82]. For some taxa gene flow can be a positive force by introducing new genetic variation and adaptive genes, while in others hybridization can lead to genetic swamping and speciation reversal[83]. Conservation practitioners will need to evaluate instances on a case-by-case basis to determine how best to preserve unique genetic variants while also maintaining population sizes, health, and resilience. Second, this study provides a robust phylogenetic framework that future researchers can use to place new species as they continue to be identified. It is worth noting that strepsirrhine taxonomy is a moving target and some groups have received greater taxonomic attention than others[10,84], which is one reason we tested for the effects of undescribed species and taxonomic biases in this study.

Our results also reiterate that certain branches on the strepsirrhine tree are evolutionarily significant, i.e., lineages that diverged a long time ago and that perform important ecosystem functions, but now contain few living species. Examples include the monotypic genera *Lemur* and *Indri*, and—as an extreme example—the lone member of Chiromyiformes, the aye-aye (*Daubentonia*). Our results show that these lineages are even older than previously recognized and have experienced slower rates of evolution relative to other lemurs. Finally, our study provides a nuanced perspective on the often-neglected lorisiforms, which are difficult to sample and are therefore underrepresented in strepsirrhine research (including the present study, which included 50% taxonomic sampling of lorisiforms compared to 79% of lemur species). A major effort will be needed to understand lorisiform distributions, taxonomy, population sizes, and diversity in the future.

Methods
Sampling

We sequenced DNA from 129 individuals obtained as fresh or frozen blood or tissues from a variety of sources including museum collections, the Duke Lemur Center, the German Primate Center, private collections, and field sampling (Supplementary Data 2). For field collected samples, local and international ethical guidelines were followed to minimize disturbance to animals and the environment. Approvals were granted by Madagascar National Parks, the Ministére de l'Environnmement et du Développement Durable de Madagascar and the Committee for Environmental Research (permit numbers 004-MEF/SG/DGEF/DADF/SCB, 072-MINENV.EF/SG/DGEF/DADF/SCB, 100-MINENV.EF/SG/DGEF/DPB/SCBLF, 124/09/MEFT/SG/DGEF/DSAP/

SLRSE, 130/16/MEEF/SG/DGF/DAPT/SCBT.Re, 137/13/MEF/SG/DGF/DCB.SAP/SCB, 186/11/MEF/SG/DGF/DCB.SAP/SCB, 78/17/MEEF/SG/DGF/DSAP/SCB.Re, 79/17/MEF/SG/DGF/DSAP/SCB.Re, and 82/18/MEEF/SG/DGF/DSAP/SCB.Re). These samples were exported under CITES permit 19US36412D/9 and imported to the U.S. under U.S. Fish and Wildlife Service permit numbers 2019NW2505894-905. Capture and handling procedures followed routine protocols approved by the Institute of Zoology, University of Veterinary Medicine Hannover Foundation.

Genomic DNA was extracted from frozen tissues using a Qiagen DNEasy Blood and Tissue kit (Qiagen, Inc.) and double-stranded DNA in each extraction was quantified using a Qubit fluorometer (Invitrogen, Inc.). Where DNA quantities were very low, we used a Repli-G whole-genome amplification kit (Qiagen, Inc.) to increase the amount of DNA prior to library preparation. DNA samples were transported to Florida State University to undergo library preparation and sequencing.

Probe design for AHE library prep

Anchored Hybrid Enrichment (AHE)[85] is a DNA sequencing approach that is widely used in phylogenomics because it targets thousands of conserved protein-coding exons (and their more variable flanking regions) across the taxa of interest. To generate an AHE probe set for strepsirrhines, we adapted the Amniote 2 AHE design[86] using six previously published genomes: *Daubentonia madagascariensis* (Daubentoniidae, NCBI accession GCA_000241425.1), *Microcebus murinus* (Cheirogaleidae, NCBI accession GCA_000165445.3), *Propithecus coquereli* (Indriidae, NCBI accession GCA_000956105.1), *Eulemur flavifrons* (Lemuridae, GCA_001262665.1), *Eulemur macaco* (Lemuridae, ncbi accession GCA_001262655.1), and *Otolemur garnettii* (Galagidae, GCA_000181295.3). We identified sequence regions in the strepsirrhine genomes that were homologous to the Amniote 2 AHE probes and extracted 6000 bp regions containing those homologs using custom scripts from Hamilton et al.[87]. We then aligned the sequences across the six strepsirrhine sequences for each locus using MAFFT (v7.023b)[88] with the "genafpair" algorithm 1000 cycles of iterative refinement. These alignments were trimmed and masked using custom scripts from Hamilton et al.[87] to retain only well-aligned regions. These alignments were further reduced to a set that had no overlapping regions (some loci in the Amniote kit were from neighboring exons that overlapped when extended), The resulting alignment covered ~1.3 Mb. We tiled 120 bp probes across all remaining sequences at 2.8x density to produce 124188 sequences (Supplementary Data 10).

Library preparation and DNA sequencing

We prepared and sequenced libraries using the AHE protocol[85,89], which first involved sonicating the extracted DNA to 250–500 bp using a Covaris Ultrasonicator in 96-well glass plates. We performed blunt-end repair and Illumina adapters ligation (with 8 bp indexes) using a Beckman Coulter FXp liquid-handling robot. The prepared libraries were pooled in groups of 24 samples, then enriched using an Agilent

Sure Design XP kit containing the probes described above. Enriched libraries were pooled, assessed for quality via Bioanalyzer and qPCR (using a Library Quantification Kit from KAPA Biosystems, Inc.), then sequenced and average of 10.9 million read pairs per sample on an Illumina NovaSeq 6000 instrument using paired-end 150 bp chemistry. Sequencing was performed at the Translational Lab in the College of Medicine at Florida State University.

Retrieval of DNA sequence data from previously published genomes

We supplemented our sampling with previously published whole genome data from six primate outgroups (from UCSC genome browser: human-hg38, chimpanzee-panTro6, gorilla-gorGor5, rhesus-rheMac8, squirrel monkey-saiBol1, tarsier-tarSyr2) and 18 previously published strepsirrhines (Supplementary Data 11). We mapped probe region sequences from the strepsirrhine probe design alignments (see above) and extracted the matching sequences from each downloaded genome using the software Geneious v.2022.2[90].

Quality control and AHE Assembly

Newly sequenced reads were demultiplexed and quality filtered using Casava (Illumina, Inc.). Quality-filtered Illumina reads were merged using the software SHE-RA[91]. We assembled the reads using the Assembler.java script [https://doi.org/10.5281/zenodo.28343] from Prum et al.[89], which employs a quasi-de novo approach where the strepsirrhine probe region sequences were used as references for assembly. The resulting consensus sequences were filtered, with those that resulted from at least 83x read depth being kept for downstream analyses. We then performed orthology across the consensus sequences (and genome-derived sequences mentioned above) using a neighbor-joining approach to identify a single othologous sequence per individual at each AHE locus. Specifically, we calculated pairwise distances among all pairs of homologues using the GetPairwiseDistanceMeasures.java script [https://doi.org/10.5281/zenodo.28343] from Prum et al.[89] then used this distance matrix to cluster the sequences using a neighbour-joining algorithm, allowing at most one sequence per species to be in a given cluster. Clusters containing fewer than 50% of the species were removed from downstream processing.

DNA alignment

Sequences determined to be orthologous were aligned using MAFFT (v7.023b)[88] with the "genafpair" algorithm 1000 cycles of iterative refinement. These alignments were then trimmed/masked using the trimandmaskrawalignments3.java script [https://doi.org/10.5281/zenodo.28343] from Prum et al.[89], which used the following procedure: sites with >70% similarity were defined as good, then 20-base-pair windows containing <10 good sites were masked and sites with <10 unmasked bases were trimmed. As a last step, all loci were imported into the software Geneious v.2022.2[90] for a final quality check by eye, with poorly aligned regions being fixed using the Local Realignment tool. Final alignments for each locus were exported from Geneious to nexus, phylip, and fasta files for further analysis.

Evaluation of the effects of missing data

We identified some loci and individuals that had elevated levels of missingness in our dataset (Supplementary Fig. 1; source data in Supplementary Data 12). To evaluate the impact of missing data on phylogenetic analyses, we first created six concatenated fasta files containing:

(1) All loci, all individuals (161 individuals, 1,108,850 bp)

(2) All loci, individuals with > 50% missing data removed (144 individuals, 1,108,850 bp)

(3) All loci, individuals with > 20% missing data removed (106 individuals, 1,108,850 bp; outgroups with > 20% missing data were retained for rooting)

(4) Reduced loci (dropping 37 loci that failed to sequence in lorisiforms and outgroups), all individuals (161 individuals, 969,767 bp)

(5) Reduced loci, individuals with > 50% missing data removed (144 individuals, 969,767 bp)

(6) Reduced loci, individuals with > 20% missing data removed (109 individuals, 969,767 bp; outgroups with > 20% missing data were retained for rooting)

All six datasets were analyzed using IQ-TREE v.2.1.3[92]. Each locus was treated as a separate partition for automatically estimating substitution models, and a maximum-likelihood phylogeny was estimated for each dataset with 1000 ultrafast bootstrap replicates.

We observed that missing data had no effect on the overall topology or node bootstrap support values, except that several important genera and species were removed from the datasets with reduced taxa. However, we observed that many of the taxa with > 50% missing data had long terminal branch lengths (Supplementary Figs. 12–17). Because branch lengths are important in diversification and divergence time analyses, we ran our divergence time analysis (see below) using Dataset 2 (all loci, taxa with > 50% missing data removed).

Phylogenetic analysis

We estimated species trees using two different approaches: (1) SVDquartets[16,17], which is statistically consistent when applied to multilocus sequence data[93]; and (2) ASTRAL[18], which uses gene trees as input. Both are coalescent-based programs that use quartet scores to select the best species-tree topology. We ran SVDquartets in PAUP*[94] using a concatenated sequence file as input. We used multilocus bootstrapping and the evalq = all setting, which specifies that all quartets should be evaluated, and designated the five haplorrhine species as the outgroup. Finally, we ran ASTRAL with default settings using individual gene trees from each locus as input. These gene trees were generated from individual sequence alignments for each locus using RAxML-ng[95] under the GTR model.

Estimation of divergence times

We estimated time-calibrated phylogenies using the MCMCTree algorithm[96], implemented within the program PAML[97]. We used our SVDquartets topology and full concatenated dataset as the inputs for this analysis, but pruned the input files to include only taxa with <50% missing data and only one individual per species (the individual with the lowest proportion of missing data). Divergence time estimation was performed six times using different fossil calibration sets based on recommendations from previous studies (Supplementary Data 3). We used the R package ddBD[98] to estimate the parameters for the birth-death model from our empirical data using the sum of squared errors method for selecting the initial values in grid search (BDparas = 21.011 17.752 0.71). We used the GTR + G model (model = 7) with 5 gamma categories (ncatG = 5), and used the program baseml (distributed with PAML) to estimate the alpha parameter (alpha = 0.40337) and substitution rate (rgene_gamma = 1 14.2282). We ran the MCMCTree analysis using an approximated likelihood approach[99], where the gradient and Hessian of the likelihood function are estimated first (usedata = 3), then divergence times are estimated using Markov Chain Monte Carlo (MCMC; usedata = 2). The first 20,000 iterations of the MCMC were discarded as burn-in, then we ran the MCMC chain for 1 million iterations sampling every 20 for a total of 50,000 samples.

Macroevolutionary rates of speciation

To generate lineages-through-time (LTT) plots, we used our time-calibrated phylogenies as input to the ltt function in the R package phytools[100] To visualize potential variation in these plots that might be caused by incomplete taxonomic sampling, we also generated a suite of 1000 trees for each of our six time-calibrated phylogenies using the program TACT[101], to stochastically add all missing species to the proper genera, and estimated an LTT plot for each of the

6000 stochastically resolved trees. Finally, we used the mccr function in phytools to estimate Pybus and Harvey's γ [a metric that uses internode distances on an ultrametric tree to infer whether accelerations in diversification rate occurred early (negative γ) or late (positive γ) in the phylogeny][36] using the rho parameter to account for sampling fraction.

Some studies have suggested that lemurs are taxonomically oversplit[37,38]. To test whether the results above would be robust to taxonomic synonymization, we wrote a custom R script (PybusGamma_TaxInflation.R)[102] using commands from the phytools package[100] to randomly drop five lemur species from each of our 6000 time-calibrated and stochastically resolved phylogenies, leaving at least one representative from every genus. This process was then repeated with 10, 15, and 20 lemur species dropped from the trees. We estimated Pybus and Harvey's γ for each tree and visualized the distribution of γ values at every level of taxonomic synonymization using ggplot2. It is also possible that lorisiform diversity is *underestimated* due to lack of taxonomic attention; thus, we conducted the same analysis described above, but instead of randomly dropping tips we randomly added five, 10, 15, or 20 new lorisiform species on each tree. The new tips were added to regions of the tree <10 million years old, as we felt that it was unlikely that very ancient lineages have not yet been discovered.

Macroevolutionary rates were estimated using the missing state speciation and extinction model (MiSSE)[40], which belongs to the speciation and extinction family of models e.g., see refs. [75,103–105], and reconstructs diversification rates as a function of one or more hidden states. We performed this analysis on each of our six time-calibrated phylogenies in R using the package hisse[75], setting the estimated proportion of extant species sampled in the phylogeny (f) to 0.71[75]. We tested five models which varied in the number of hidden states from one to five, each with an associated turnover rate and extinction fraction. The top-ranking model was selected using the Akaike Information Criterion (Supplementary Data 6) and this model was then used to reconstruct rates across the trees using the function Margin-ReconMiSSE (Supplementary Figs. 6, 7).

We also estimated tip diversification rates (λ_{DR}; Supplementary Data 5), which reflect the weighted inverse of phylogenetic branch lengths leading to each tip[39]. A median λ_{DR} value was calculated for each tip across all 6000 phylogenies that were estimated previously using TACT. We also simulated λ_{DR} distributions expected under a homogeneous birth-death process in order to identify specific regions of the tree with higher or lower empirical speciation rates than expected, following the procedure outlined in Upham et al.[106]. Tree simulations and calculation of λ_{DR} metrics were performed using a custom R code (TipDR_Calculation.R)[102].

Comparison of mitochondrial and nuclear datasets

Mitochondrial sequences were captured as off-target reads in our sequencing protocol and were harvested from our raw sequence data (forward and reverse fastq.gz files) using the program MitoZ with the Chordata clade setting[107] This pipeline retrieved mitochondrial sequence data in 104 individuals. Sequences were assembled and aligned using Geneious[90] and a mitochondrial phylogeny was estimated using the IQ-TREE web server[108] with default settings, allowing the substitution model to be ascertained automatically (Supplementary Fig. 9). Genera were collapsed into single branches in the main text for visualization purposes (Fig. 3).

Tests of hybridization and gene flow

We used the program QuIBL[71] to distinguish between ILS and ancient introgression (above the species level) in our dataset. We first calculated a set of gene trees (one for each locus), using RaxML-ng[95], with the ultrafast bootstrapping method and the GTR model of substitution. To prepare these gene trees for QuIBL, we used a custom R script

to collapse each genus into a single tip and retained only the gene trees with all genera present. We evaluated all triplets and set the outgroup of our species tree to the Haplorhini. We set the 'numdistributions' parameter to 2, which corresponds to one branch-length distribution for ILS and one for introgression, and we used default recommendations for the remaining parameters (likelihoodthresh, numsteps, and gradascentscalar).

We also used the program PhyloNet[109] to test for introgression in each genus that had topological uncertainty (low node support) in our species-tree analyses (i.e., *Cheirogaleus*, *Eulemur*, *Lepilemur*, *Microcebus*, and *Propithecus*)[95]. The set of gene trees that was previously estimated in RaxML-ng was used as input to PhyloNet, using a custom R script to prune each gene tree to include only the species from the genus of interest. We used the maximum pseudo-likelihood approach to estimate quartet counts under models that varied in the number of hybridization events (H), which we allowed to vary from zero to five. To choose the correct H for each analysis, we visualized the log-likelihood scores for each analysis and used the lowest value of H, beyond which little improvement in likelihood was observed (Supplementary Fig. 11; source data in Supplementary Data 13).

To understand whether there was a correlation between speciation rates and hybridization, we first scored each strepsirrhine species as hybridizing or non-hybridizing based on this study as well as an extensive literature review using the search engine Google Scholar, where the species name was paired with the words "hybrid" and "introgress" and their structural variants (e.g., "hybridize" and "introgression"; Supplementary Data 7). We generated two scoring systems: (1) a conservative system, where species were only classified as hybridizing if there was documentation of that species hybridizing in the wild, and (2) a liberal system, where species were classified as hybridizing if there was any documentation of that species hybridizing in the wild or captivity, or if any previous study had found evidence of gene flow using phylogenetic or population genetic analyses, or if that species was a descendant of a reticulate branch leading to one or two tips in our PhyloNet analyses (Fig. 4). Because we were concerned that hybridization might be artificially inflated in the genera where we explicitly looked for evidence of hybridization (i.e., genera that we included in PhyloNet), we also conducted a second round of PhyloNet analyses where we scanned each Family following the same procedure outlined above. These analyses did not reveal any additional taxa to score as hybridizing in the liberal system (Supplementary Fig. 18). After finalizing our scoring system, we used an approach similar to Patton et al.[15], who applied the hidden-state speciation and extinction (HiSSE) trait-dependent diversification model[75]. We evaluated a total of five competing models using the hisse package in R[75], ranging from a null character-independent model with a single diversification rate, to a full character-dependent HiSSE model accounting for hidden states. Parameter values were estimated from the top-ranking models, which were selected using the Akaike Information Criterion. We applied this model-testing framework to both the liberal and conservative coding schemes. Then, to understand the influence of unsampled taxa where hybridization status is unknown, we re-ran those tests again using two different values for the sampling parameter f: one in which all unsampled taxa on the phylogeny are assumed to hybridize, and one in which all unsampled taxa on the phylogeny are assumed not to hybridize.

Where the top-scoring model was a BiSSE model (see results), we explored how these results were affected by taxonomic attention. To do this we coded taxa as high taxonomic attention or low taxonomic attention by searching Academic Search Complete (EBSCO Industries, Inc.) for peer-reviewed articles with "[genus name]" in the title and any of the words "evolution", "phylogeny", or "population genetics" in the article contents. All members of genera with less than five article hits were coded as low taxonomic attention (n genera = 13) while those with five or more hits were coded as high taxonomic attention (n genera =

13). This trait was then used in conjunction with the hybridizing/non-hybridizing trait to fit a multi-state speciation extinction (MuSSE) model using the R package hisse[75].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Code availability

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