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Letter

Ecological causes of uneven speciation and species richness in mammals

Short title: Ecology of speciation in mammals

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Statement of authorship: NSU and WJ conceived the study; NSU and JAE collected and curated the data; NSU performed all analyses and wrote the first draft of the manuscript, with contributions to revisions from all co-authors.

Data and material availability: All data and code is available in the manuscript and after publication on Dryad (also to be available at github.com/n8upham/).

Keywords: Phylogenetics, macroevolution, trait-associated diversification, dispersal, latitude, diel activity; **Length:** abstract 172 words; main text 4,710 words; 110 references; 5 figures.

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ABSTRACT

Biodiversity is distributed unevenly from the poles to the equator, and among branches of the tree of life, yet how those enigmatic patterns are related is unclear. We investigated global speciation-rate variation across crown Mammalia using a novel time-scaled phylogeny (*N*=5,911 species, ~70% with DNA), finding that trait- and latitude-associated speciation has caused uneven species richness among groups. We identify 24 branch-specific shifts in net diversification rates linked to ecological traits. Using time-slices to define clades, we show that speciation rates are a stronger predictor of clade richness than age. Speciation is slower in tropical than extra-tropical lineages, but only at the level of clades not species tips, consistent with fossil evidence that the latitudinal diversity gradient may be a relatively young phenomenon in mammals. In contrast, species tip rates are fastest in mammals that are low dispersal or diurnal, consistent with models of ephemeral speciation and ecological opportunity, respectively. These findings juxtapose nested levels of diversification, suggesting a central role of species turnover gradients in generating uneven patterns of modern biodiversity.

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INTRODUCTION

Biological diversity is concentrated at the equator more than the poles, and in some evolutionary lineages more than others. Yet whether these organic phenomena are causally connected is an open question. The latitudinal diversity gradient is generally attributed to tropical biomes being stable, productive, and old (1–5), but there is less consensus regarding why species richness is distributed unevenly across the tree of life. Phylogenetic tree shape was first characterized taxonomically (6) and later formalized under the concept of tree imbalance or unevenness (7). To arise, more speciose clades must have been derived from faster rates of net diversification (speciation – extinction), older ages (earlier divergences), or both. However, the relative contribution of clade rates and ages to species richness is widely disputed (e.g., (8–11)). Similarly controversial are the causes of diversification-rate variation in real phylogenies, whether due to stochasticity, determinism via ecological factors or time, or artifacts from how we reconstruct evolutionary history (12–23). Latitude might determine the rates at which new species originate and persist or go extinct (2, 3, 24–26), but so too might species' intrinsic traits (27), some of which are correlated with latitude (e.g., (28)). For mammals and other tetrapods, the Cretaceous-Paleogene (K-Pg) bolide impact is linked to the selective extinction of major lineages (29, 30), adding the wrinkle of historical contingency to how surviving lineages diversified in response (31–33). Thus, understanding the processes underpinning uneven species richness requires connecting levels of indirect (e.g., eco-geographic) and direct (e.g., rates, ages) causes to tease apart their joint influences upon different radiations.

The last ~180-million-years of crown mammalian evolution has resulted in ~6000 living species (34, 35), which collectively inhabit nearly all terrestrial biomes plus the open oceans, and thousands of preserved ancestors described as fossil taxa (36–38). Within this context, similarly

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aged clades in the mammal tree range from mega-diverse rodents (~2500 living species) and bats (~1300 species) to species-poor groups like treeshrews (20 species) and pangolins (8 species; all four share stem ages of ~60-70 million years ago [Ma] (35, 39)). The early availability of a species-level 'supertree' phylogeny of mammals (now cited over 1,800 times; (40)) encouraged initial studies of macroevolutionary-rate covariates (e.g., (18, 22, 41, 42)). However, because that pioneering supertree was assembled from hundreds of overlapping source trees, over 50% of its nodes were initially unresolved and then simulated to obtain a bifurcating time-scaled phylogeny (40, 43). Timings of diversification from this supertree, along with two other mammal supertrees (11, 44), were consequently shown to have inflated precision relative to the large gaps in available fossil age and DNA sequence data (35).

Here, we draw upon a new time-calibrated phylogeny for global Mammalia built from a contiguous DNA supermatrix (31 genes by 4,098 species; completed to 5,911 modern species) and consisting of credible sets of 10,000 trees (35). We used these phylogenies, which jointly model uncertainty in topology and node ages, to better understand the temporal dynamics of mammalian diversification relative to the potentially causal effects of historical, organismal, and environmental factors. Our objectives were three-fold. First, we tested for tree-wide and branch-specific rate variation in relation to the Cretaceous-Paleogene (K-Pg) mass extinction event to explore whether predicted shifts in placental diversification rates (45) are recoverable across extant clades. Second, we used neutrally defined (time-slice based) clades to explore the relative roles of clade ages and speciation rates in explaining current-day species richness. Finally, we linked observed variation in speciation rates to its putative ecological causes, testing whether factors predicted to cause newly formed species to persist or go extinct are, in turn, causing the observed patterns of uneven species richness. Investigating deep-time rate shifts (e.g., relative to

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the K-Pg or other factors) alongside the drivers of modern clade richness is intended to test for time-specific differences in the drivers of mammalian rate variation.

Among clades, we focus on three potential ecological causes of richness differences: species vagility, latitude, and diurnality. First, we tested whether low-vagility species have faster speciation than more dispersive species given their greater likelihood of forming peripheral isolates (46, 47). For this test, we developed an allopatric index of organismal vagility for all mammals (i.e., maximum natal dispersal distance; (48)). Vagility effects have never been assessed across all mammals, although evidence in birds using the hand-wing index supports an inverse vagility-to-speciation rate relationship (e.g., (49, 50)). Second, if unstable environments increase ephemeral speciation via greater species turnover (extinction / speciation (51)), then we expect the recent species-specific (i.e., 'tip') speciation rates of surviving lineages to be higher in temperate latitudes with greater climatic instability (25, 52). To our knowledge, the effects of latitude upon mammal tip rates have yet to be assessed, but clade-level comparisons have either been negative (53) or supported greater temperate than tropical turnover in some clades (24, 42, 54). Lastly, we tested whether diurnality (daytime activity) has increased speciation rates relative to nocturnal clades, following recent evidence that all mammals were nocturnal until daytime niches evolved ~35 Ma (33, 55). A positive influence of diurnality on speciation rates has been found across major tetrapod lineages (56), and in primates specifically (57, 58), but has yet to be investigated at the species-level in all mammals (but see ancestral state reconstructions (55)). We are thus using species-level trait proxies to investigate scenarios of geographic, ephemeral, and adaptive modes of species diversification in mammals, respectively, and across the entire mammal tree of life to avoid ascertainment bias from selecting smaller clades (59).

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Overall, our approach ties together among-clade variation in rates, ages, richness, and traits in a multivariate causal framework (phylogenetic path analysis (60)). By jointly assessing the causal contributions of ecological factors to the inferred tempo of mammalian lineage diversification, we shed new light on their relative importance to generating uneven species richness patterns. We find that vagility and diurnality are greater causes of recent speciation-rate variation than latitude, which effects rates deeper in the tree. Rate variation, in turn, contributes more to uneven species richness than differences in clade age.

RESULTS AND DISCUSSION

Tree-wide lineage diversification relative to the K-Pg event.

The Mammalia tree shows substantial unevenness in species richness across major named clades (Fig 1a). We first evaluated evidence for whether early placentals diverged before, after, or during the K-Pg event, known as the short fuse, long fuse, and explosive models, respectively (45, 61). The first four placental divergences unambiguously preceded the K-Pg (Fig. 2a; filled circles), followed by the next 21 divergences with CIs that overlap it (Fig. 2a–b). Therefore, we detect a Cretaceous "fuse" of ~25-Ma between the radiation of crown Placentalia and nine of 18 crown orders (Fig. 2b), in line with some estimates (39, 62), but longer than others (e.g., (40)).

Modeling branch-specific rates across the tree shows a qualitative pulse in both speciation and extinction near the K-Pg (Fig. 2c) that matches concurrent fossil evidence for increases in origination and extinction (Fig. 2d; synthesized from the Paleobiology Database (37)). However, we find mixed results in formal tests of tree-wide shifts in the 5-Ma following the K-Pg, with TreePar (41) showing a clear signal of increased net diversification rates that is absent in CoMET analyses (63) ((Fig. S5-S6); the latter model allows for time-varying

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diversification rates while the former does not). Based on the patterns reported in fossil eutherians (45, 64), a pulse of lineage turnover following the K-Pg is expected due to selective extinction and recovery of surviving mammal lineages (29, 31). Thus, this fossil-calibrated molecular phylogeny of mammals (35) is capable of recovering dynamics evident from the fossil record alone, albeit as dependent upon assumptions of different tree-wide birth-death models.

Branch-specific rate shifts relative to time and traits.

We recover shifts in net diversification rates associated with 24 consistent nodes in the mammal tree (Fig. 1a, 2c, e; shifts are present in ≥ 50% of maximum shift credibility trees using BAMM (65), see *Supplementary Materials* Fig. S7, Table S1). The earliest rate shift occurs in either crown Placentalia (mean of 1.1x higher over separate BAMM runs, as compared to the median background rate of 0.138 species/lineage/Ma) or Boreoeutheria (1.6x, node C in Fig. 1a). These shifts involve 18 different lineages, 15 of which are consistent increases. The only consistent rate decrease was in the strepsirrhine primates (lemurs, lorises, and galagos; node O). Two other shifts are alternately up or down, depending on the tree sampled (nodes H, P; Fig. 1a). This result compares to 27 rate-shifted clades detected on the original mammal supertree using an earlier method (15 increasing and 12 decreasing (18)—but note caveats about the identifiability of downshifts (66)). Overall, rate increases nearer the present are higher, with a 2.2x mean in the Miocene versus 1.3x in each the Oligocene and Eocene (Fig. 2c; df=2, F=7.772, P=0.003). This result is consistent with the expectation for extinctions deeper in the tree to have reduced our ability to quantify more ancient shifts (65, 67), as well as fossil and molecular evidence that younger clades tend to have faster rates of diversification (20).

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At first glance, species in rate-shifted clades have dissimilar traits of vagility, diurnality, and latitudinal extent (Fig. 1a-b). However, several consistent patterns emerge. On a visual basis, related clades of rodents show a conspicuous latitudinal pattern of alternating south-north-south endemism that may relate to biogeographic incumbency effects previously reported (e.g., (68)). Similarly, the rate shifts present in Cetacea and Carnivora (nodes F and D; Fig. 1a) are associated with high vagility and latitudinal extents, while simian primates (node N) are nearly exclusively tropical and diurnal (Fig. 1b). Strikingly, the two largest rate increases (4.0x and 3.2x) occurred in lineages with disparate life modes but similar propensities for geographic isolation: the fossorial tuco-tucos of South America (*Ctenomys*, node Q), and the Indo-Pacific flying foxes (*Pteropus*, node J; Fig. 1a). Thus, small burrowers and large flyers both show similar signatures of recent and rapid speciation under conditions of insularity, although in subterranean and oceanic realms, respectively. Ecologically selective processes appear to be involved in fostering major mammalian radiations, but are these trait associations idiosyncratic or deterministic?

We next investigated trait-dependent speciation on a tree-wide basis, aiming to look for common ecological causes of rate variation. These tests uncovered that high vagility is marginally associated with novel rate regimes (STRAPP (69) one-tailed test, $P = 0.08$), which is contrary to the inverse vagility-to-speciation relationship we expected (46, 47). However, these tests are complicated by the fact that many high-vagility lineages are also diurnal, and diurnality is clearly associated with shifts to higher speciation-rate regimes ($P = 0.027$; Fig. S8). For example, we find diurnality-associated rate shifts in clades of primates, carnivorans, cows, and whales (shifts N, D-F, and Q; Fig. 1a) that also contain a majority of species with >1 km natal dispersal distance (Fig. 1b). Therefore, these findings highlight the need to jointly consider (i.e.,

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in the same model) the relative contributions of vagility, latitude, and diurnality to understand their effects upon rate heterogeneity in mammalian clades.

Named clade rate variation.

Beyond searching for rate-shifted clades, we also test the five most speciose placental orders for signatures of diversification-rate variation (Fig. 2e-f). Comparing the fit of models of rate-variable processes through time (RV, exponential or linear; (70)) versus rate-constant ones (RC, single rates of birth or death), we find greater fits to RV models in five of the 12 named subclades examined (Fig. 2f; Table S2). The mouse-related clade of rodents (clade 20 in Figs. 1, 2f) has a branching pattern best fit by RV processes in all 100 trees examined, as expected from the seven branch-specific rate shifts already uncovered in that clade (nodes R-X in Figs. 1, 2). Shrews, catarrhine primates, and the cow- and whale-related clades of artiodactyls join mice in showing greater RV fits than expected from RC simulation (clades 6, 15, 10, and 11; Fig. 2f). Overall, these named clade results are consistent with previous evidence (e.g., among mammal families (21)) that lineage diversification rates have been non-constant through time.

In theory, considerably more fossil evidence might be required for the birth-death models evaluated so far to be identifiable (71). This word of caution is particularly relevant for groups like horses and pigs (Perissodactyla (72)), in which we know that periods of diversity decline have been substantial (see (73) for general comparison of BAMM and RPANDA model performance). Nevertheless, clade-specific fossil and molecular evidence supports our assertion that ancestral whales and dolphins entered a novel macroevolutionary regime, including selection toward larger body sizes (65, 69, 70, 74). Bats, on the other hand, display an inconsistent fit to RV models of diversification (clades 12-13, Fig. 2f), and an inconsistent number of rate shifts

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between our study (six, nodes G-L, Fig. 1a) and a previous one (two, nodes H and J; (75)). We suggest that high levels of topological uncertainty, which is arguably greater in bats than other orders (76), is contributing to the equivocal modeling of RC, RV, and branch-specific shift processes across credible tree sets for bats (Table S2).

As an alternative, non-model-based test of within-clade rate variation, we use clade-wide distributions of tip-level speciation rates as assessed using the tip DR metric (77) (Fig. 2f). Tip rates carry the benefit of estimating diversification dynamics at the instantaneous present, and thereby overcome the aforementioned concerns regarding the impact of past extinctions on model identifiability (71, 73, 78, 79). Broadly, we recognize substantial heterogeneity in tip speciation rates across the mammal tree, sometimes with a few high-tip-rate species nested together with lower-rate species (Fig. 1a), resulting in long right-side tails in the tip-rate distributions (positive skew, e.g., bat and rodent clades 12 and 18; Fig. 1a, 2f). We propose that tip rate skew measures aspects of within-clade speciation-rate variation that is otherwise uncaptured by fitting *a priori* models of the diversification process (Table S3), and thus offers a distinct predictor of among-clade variation in species richness.

Time-slice clade richness relative to ages and rates.

The relative importance of clade ages (time) versus rates of speciation and extinction (whether stochastic or ecologically deterministic) as an explanation of extant diversity levels is widely debated (8–12, 16, 21, 80). Original claims that uneven trees are random outcomes of constant-rate diversification (e.g., (81)) have been refuted (10, 13, 17). However, past efforts to separate these hypotheses have focused on named clades (e.g., (10, 21)), which are biased by subjective delineation and often vast age differences (mammal families range 3.8–59.0 Ma in

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mean crown ages; (35)). To avoid problems associated with subjective clade definitions, we sliced phylogenies at five-million-year intervals and took the tipward clades as objective units for analysis (Fig. 3). Time-sliced clades thus account for the 'pull of the present' in modern trees (67) by analyzing successive levels of rootward covariance among clade-level summaries of crown age, species richness, tip rate harmonic mean and skew, and the arithmetic (or geometric) mean of species ecological traits. If time-constant rates predominate (11, 12, 16), crown ages will explain the most among-clade variation in species richness. In contrast, if rate variation is strong, as we already recognized for some nodes and named clades (Fig. 2) and expect from varying ecological regimes (18, 22, 23), diversification rates will have the greater explanatory power.

We find that the clade harmonic mean of tip speciation rates explains most of the variation in species richness across time-sliced clades (Fig. 4, multivariate PGLS). Clade age and richness are positively correlated (Fig. 4a)—yet clade tip rate mean has stronger effects on richness than expected from simulated birth-death trees containing only stochastic rate variation (Fig. 4b). Clade tip rate skew is also significant, especially so at deeper time slices (Fig. 4c), confirming that single speed-ups in diversification within a clade (e.g., due to a rate shift in one lineage) can drive much of its overall species richness today. These analyses are robust to the influence of species that are missing DNA sequences and imputed (see Fig. S10, also for univariate and taxon-based results). Our findings thus support arguments that 'ecology' (broadly defined to include any non-temporal factor that alters macroevolutionary-rate processes, including sexual selection and geographic factors) is a greater cause of species richness variation than time (21–23). However, variation in both rate and age clearly contribute to observed richness (adjusted-R^2: 0.88 full model versus 0.74 with tip rate mean only and 0.26 with crown age only, means of 100-tree PGLS among 35-Ma clades). Jointly analyzing richness

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determinants in time-sliced clades offers an objective way to assess age and rate effects that, in turn, raises questions about which ecological factors are driving that rate variation.

Linking uneven rate variation to ecological factors.

We performed phylogenetic path analysis (60) to assess the hypothesized effects of species vagility (46, 47), latitude (24, 25), and diurnality (33) upon the joint, yet unequal, contributions of rates and ages to extant species richness variation (Fig. 5, *Methods*, Fig. S4). Here, the time-sliced clades allow us to distinguish trait-rate dynamics that are localized near the species level (if traits drive species turnover (51), or if they evolved very recently) from those that occur among clades deeper in the tree (if traits evolved anciently and the lineages persisted). Our assembly of species-level traits across Mammalia (Fig. 1b) enables us to directly pass information to clade-level averages, thereby summarizing the ecological 'essence' of that clade for a given trait. However, we note that other statistical moments (e.g., trait variance or skew) may prove useful for future study.

At the species level, we find that low-vagility mammals have higher tip speciation rates, especially in herbivores and carnivores (Fig. 5a; ecological trait ~ rate PGLS (82)). Effects of vagility on clade tip rate mean in 10-Ma clades are weakened at deeper time slices, where they are instead recorded on tip rate skew (Fig. 5b). We interpret these short-lived effects of vagility on speciation rates as consistent with expectations that incipient species are produced at a high rate, but are ephemeral (51), subject to high species turnover. Under this scenario, speciation rates are roughly constant, but low-vagility lineages have gone extinct at a faster rate than high-vagility forms, presumably due to the stochastic effects of small geographic range size in nascent species (47, 83). In summary, we hypothesize that turnover-driven speciation—i.e., speciation

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rates that are high because extinction rates are high, and a lineage is still observed—is causing the inverse effects of vagility upon tip speciation rates we observe in the mammal tree.

Our interpretation argues for an approximately 10-million-year 'threshold' whereby low-vagility lineages must lower their extinction risk (e.g., find an adaptive zone or evolve greater vagility; (84, 85)) or else vanish. Alternatively, the influence of vagility on mammal diversification might be non-linear as hypothesized in birds (e.g., humped (46) or sigmoidal (50)), in which case our results among shallow clades and tip species may only be capturing one side of the vagility-to-rate relationship. We concede that our allometric vagility index is a rough proxy for dispersal ability, particularly given the potential for island effects in the nearly 20% of living mammals that are endemic to islands (86). Similarly, the vagility index does not explicitly account for the flying abilities of bats, which differ substantially by wing morphology (87). Nevertheless, the described patterns are robust to multiple sensitivity tests (including the exclusion of bats and island endemics; (Fig. S13-S14)), and thus are deemed to convey the macroevolutionary outcome of historical gene flow or isolation among populations of mammals.

To test the causal role of environmental stability in the generation of mammalian tree shape (3, 25, 52), we next evaluated how a climatic proxy—latitudinal centroid distance from the equator—influences speciation rates. Contrary to the expectations of climatic instability driving recent, high rates of speciation at temperate latitudes (24, 25, 52), we find no effect of absolute latitude on tip-level speciation (Fig. 5a). Instead, strong positive associations with latitude only arise among clades at deeper time slices, and without any corresponding effects on clade tip rate skew (Fig. 5b). These results compare to similarly absent latitude-to-tip rate effects in the species-level phylogeny of birds ((77, 88); but see suboscines (89)). For both birds and mammals, New World sister species show higher turnover rates at temperate than tropical

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latitudes (24, 52); however, reliance on the mitochondrial DNA clock renders these results less conclusive for mammals than birds given their more pronounced life-history effects (90). Other mammal studies have yielded inconsistent findings with a variety of methods, including: (i) higher subspecies counts in harsher temperate environments ((54); but note the opposite pattern in birds (91)); (ii) no latitude-to-rate effects at the genus level (53), using genus ages from the Bininda-Emonds et al. (40) supertree of mammals; and (iii) greater rates of temperate extinction and tropical speciation on a Mammalia-wide basis (42), using a modified version of the same supertree. Thus, our finding that temperate clades of mammals have higher tip rates than tropical clades (harmonic mean of species values at 10-, 30-, and 50-Ma time-sliced clades) sheds new light on what, to date, has been a murky understanding of how macroevolutionary rates have influenced the latitudinal diversity gradient.

We hypothesize that high rates of temperate extinction during the Plio-Pleistocene, a period of harsh environmental changes starting ~5 Ma (92), may have erased the modern portion of the latitudinal effect that otherwise would be recorded in species' present-day tip rates. Under this scenario, finding clade-level signatures of faster temperate speciation (as we did) is still expected as long as temperate lineages were not fully extirpated during these climatic oscillations, perhaps as persisting in glacial refugia (93). Key to understanding this result is that the latitude-to-rate signature among, e.g., 30-Ma clades reflects processes occurring *more recently* than 30 Ma, since we are examining clade-level summaries of branching rates leading to each species' instantaneous present. Thus, we are proposing that intensified Pliocene rates of temperate extinction initiated two canonical patterns, at least in mammals if not other taxa: (i) the inverse latitudinal gradient of clade-level speciation rates, as viewed retrospectively on an extant phylogeny; and as a result, (ii) the latitudinal diversity gradient. This hypothesis is supported by

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the North American fossil record (the most complete paleogeographic sampling of mammals), in which richness and latitude are not strongly correlated until ~4 Ma (94), as well as evidence from fossil bivalves that Pliocene extinctions strengthened the latitudinal diversity gradient (95). Overall, we contend that the traditionally invoked tropical 'cradle' (higher speciation) and 'museum' (lower extinction (3)) should instead re-focus upon the *turnover ratio* of those processes. Testing whether species lineages have been 'cycled' faster (i.e., shorter durations) outside than inside the tropics is a prediction in need of greater paleo-to-neontological synthesis.

Lastly, we queried the effect of diurnal diel activity, a core behavioral trait thought of as a temporal niche innovation (33). We find that apparently independent origins of diurnality since the late Eocene (~35 Ma (33, 55)) are associated with faster speciation, both at the present (Fig. 5a) and among time-sliced clades at 10 Ma (Fig. 5b). These findings complement the signature of greater diurnal activity on rate-shifted clades (Fig. S8), as well as place previous findings of rapid diversification in diurnal lineages of primates (57, 58, 96) and whales (70) in a broader context. We suggest that inverse effects of diurnality on tip rate skew at deeper time slices (Fig. 5b) are misleading given the evolution of daytime activity ~35 Ma, well after a 'nocturnal bottleneck' among K-Pg-surviving mammals (33, 55). This bottleneck has been described at broader phylogenetic scales across major extant lineages of tetrapods (family-level sampling for mammals (56)), although fossil evidence suggests that daytime activity also evolved in the extinct sister lineages to mammals (non-mammalian synapsids (97)). The coordinated eco-physiological changes required to evolve diurnality (e.g., eye pigments and corneal size (33)) have presumably carried with them fitness benefits from access to novel resources in the daytime niche. Thus, diurnality may rightly be viewed as an adaptative innovation in mammals, and one that appears to have induced macroevolutionary rate changes.

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To explain faster speciation in diurnal clades and species, we posit that greater daytime activity is an example of a trait that has decreased extinction rates via competitive release (i.e., an 'ecological opportunity'; (84, 98)). In this scenario, evolving diurnality has led to differential lineage persistence (i.e., low rates of species turnover = low extinction / high or moderate speciation) relative to nocturnality because novel niche resources have presumably improved organismal fitness (33, 84). This hypothesis implies that persistence-driven speciation—i.e., speciation rates that appear high because extinction rates are reduced—underlies the diurnal rate signature, in contrast to the turnover-driven speciation we suggest is associated with low-vagility and high-latitude lineages. Alternatively, the more classical narrative of 'key innovation' spurring diversification (84) would suggest that diurnal lineages have increased speciation rates (with no change in extinction) due to specializing on resources within the relatively 'open' diurnal ecospace. While we cannot rule out this speciation-only hypothesis, we find it less probable because the acquisition of diurnal behavior has likely evolved and persisted at least ten times in crown mammals (55). From diurnal primates and squirrels to elephant shrews, there seems to be no characteristic secondary axis of resource specialization that is common to these groups (e.g., diet or locomotor diversity); rather, allopatric speciation—and persistence of those lineages—is more likely the secondary driver of diurnal diversity (e.g., (99)) following the initial adaptation. Overall, we suggest that faster diurnal than nocturnal speciation in mammals is a signature of greater persistence (lower turnover) of lineages due to more ecological opportunity.

CONCLUSION

By taking an uncommonly broad view on the evolutionary history of Mammalia, from tree-wide to branch-specific to tip-level processes, the present study uncovers commonalities in

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the ecological causes of uneven species diversification over geography as well as phylogeny. These general processes might have remained hidden had this study been motivated by publishable units and not global synthesis. Using an innovative time-slice approach to defining clades, we demonstrate that clade rates explain more of the variation in mammal species richness than do clade ages. Connecting those clades rates to both intrinsic (vagility, activity pattern) and extrinsic (latitude) characteristics of the component species, we then detect consistent ecological signatures at nested levels of the mammal phylogeny.

Overall, we hypothesize that two main processes are at work. First, we identify signatures of turnover-driven speciation at shallow levels of the tree due to greater geographic isolation among low-vagility species, and among deeper clades due to the survival of temperate lineages in extratropical climates. We provide phylogenetic evidence supporting the notion that the latitudinal diversity gradient is in fact a relatively young phenomenon in mammals, perhaps originating or steepening during the Pliocene as the fossil record suggests (94). Second, we hypothesize that persistence-driven speciation is occurring in diurnal lineages due to lower extinction rates following access to new daytime niches and subsequent release from nocturnal competitors. In this case, diurnality is an example of an adaptive innovation in mammals that is presumably associated with greater ecological opportunity. Traversing from the first to second macroevolutionary mode may be possible if otherwise ephemeral incipient species can enter novel regimes of lower extinction risk, either via niche evolution or extrinsic opportunity (84, 98), to then differentially persist through time.

In summary, our study shows that coupling two ideas—that new species are formed frequently but rarely persist (51), and extinction risk is related to species-level traits (27)—helps to connect within-species dynamics of dispersal, gene flow, and niche evolution with

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macroevolutionary rates. We logically reason that axes of low-to-high vagility and day-to-night activity are affecting extinction rates in respectively opposite directions (i.e., high extinction and turnover versus low extinction and turnover). However, the lack of direct extinction-rate estimates is a clear shortcoming of this argument that can only be addressed by more fully leveraging the mammal fossil record. Future tests that develop direct skeletal or remotely sensed measurements of mammalian vagility (as opposed to the indirect index used here), along with cranial correlates of diurnal vision (e.g., (97)), will be valuable for assessing whether the relative frequency of turnover- and persistence-driven speciation has changed from fossil to modern ecosystems. Efforts to connect evolutionary levels from individual organisms to speciose clades appear the most promising for comprehending uneven species richness in the tree of life.

METHODS

Mammalian phylogeny and species trait data. We leveraged the recently constructed species-level mammal trees of Upham et al. (35) to conduct all analyses. Briefly, these phylogenies include 5,804 extant and 107 recently extinct species in credible sets of 10,000 trees. They are built using a 'backbone-and-patch' framework that used two stages of Bayesian inference to integrate age and topological uncertainty, and incorporate 1,813 DNA-lacking species using probabilistic constraints (available at vertlife.org/phylosubsets). We compared credible sets of trees built using node-dated backbones (17 fossil calibrations) and tip-dated backbones (matrix of modern and Mesozoic mammals), as well as taxonomically completed trees (5,911 species) versus trees of DNA-only species ($N = 4{,}098$) without topology constraints.

Our workflow for gathering trait data involved (i) unifying multiple trait taxonomies (e.g., EltonTraits v1.0 (100), PanTHERIA (101)) to our phylogeny's master taxonomy; and (ii) interpolating home range area and vagility to the species level using known allometric

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relationships in mammals (Fig. S2). Vagility was calculated as the maximum natal dispersal distance per individual (km) and interpolated for each species following our updated version of Whitmee and Orme's (48) best-fit equation, which applies species means of body mass, home range, and geographic range (Fig. S3). Note that our vagility index does not account for locomotor abilities (e.g., flying or arboreality), but rather captures aspects of space use that scale allometrically across mammals.

Tip-level speciation rates. We calculated per-species estimates of expected pure-birth diversification rates for the instantaneous present moment (tips of the tree) using the inverse of the equal splits measure (77, 102). This metric has been called 'tip-level diversification rate' (tip DR) because it measures recent diversification processes among extant species (103). However, to avoid confusion with 'net diversification', for which tip DR is misleading when extinction is very high (relative extinction >0.8 (78)), we here refer to tip DR as a tip-level speciation rate metric. At the tip level, we show that tip DR is tightly associated with model-based estimators of speciation and net diversification rates in our trees (Fig. S1a). At the clade-level, we measure 'clade tip speciation mean' as the harmonic mean of tip DR among species, which is known to converge to the maximum likelihood estimator of pure-birth diversification rate in clades with >10 species (77, 102). We show that clade tip DR mean indeed best approximates pure-birth clade rates for time-sliced clades in our mammal trees (R^2: ~0.7 versus ~0.5 for birth-death speciation and net diversification rates; Fig. S1b).

Branch-specific and tree-wide rate shifts. We performed searches for macroevolutionary shifts using BAMM v2.5 (65), a reversible-jump algorithm for sampling birth-death rate regimes without a prior hypothesis. We evaluated the number and location of rate shifts on 10 trees from the node-dated sample of complete mammal trees. We summarized

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across the most likely shifts per tree—called maximum shift credibility (MSC) sets (Fig. S7)—using the ratio of the mean net diversification rate of all branches inside the shifted clade (clade rate) and outside that clade (background rate) to calculate the rate shift magnitude and direction for each MSC set (Table S1). For tree-wide rate shifts, we compared results from TreePar (41) and CoMET (63) (see details in Fig. S5-S6).

Comparisons with fossil genus diversification. To assess the congruence of our molecular phylogeny-based rate estimates with rates estimated from the fossil record, we analyzed Mammalia fossil occurrence data from the Paleobiology Database (37). Grouping by genus after excluding ichnotaxa and uncertain genera, we recovered 71,928 occurrences of 5300 genera, which we then binned in 10-Ma intervals (taxa spanning boundaries go in both bins) and used shareholder quorum subsampling (SQS (104); quorum size: 0.5) to maximize the uniformity of coverage. We then calculated corresponding origination and extinction rates per stage using the per-capita rate method (105).

Likelihood testing for models of diversification. We analyzed the branching times of 27 named subclades (11 orders and 16 suborders) that contained ≥ 25 species. For each subclade, we tested 10 models developed by Morlon et al. (70): two rate-constant (RC) models, constant pure-birth and birth-death; and eight rate-variable (RV) models, with exponentially and linearly time-varying rates. We fit models for 100 trees of the empirical subclades and their matching RC-simulated trees (null models, simulated under the empirical extinction fractions of ~ε=0.65 over 100 trees using the "pbtree" function in phytools (106)). Subtracting AICc scores of the best-fitting RC and RV models provided the $\Delta AIC_{RC\text{-}RV}$ test statistic (107) per tree and subclade for comparison to the simulated null distribution (alpha=0.05; see Table S2).

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Time-sliced clades and clade-level tests of species richness variation. To objectively define clades, we arbitrarily drew lines (referred to as "time slices") at 5-Ma intervals and took the resulting *tipward* (all the way to the extant tip) monophyletic clades as non-nested units of analysis. The *rootward* relationships of those clades (the "rootward backbone") was retained for each interval, giving the expected covariance structure among clades when performing phylogenetic generalized least squares (PGLS) analyses (see Fig. 3 for illustration). We used the "treeSlice" function in phytools to construct clade sets across Mammalia trees and the three sets of RC simulations, empirical (ε=0.65), low (ε=0.2), and high (ε=0.8), also comparing our results to analyses on traditional taxon-based clades (genera, families, and orders; Fig. S10-S12). All PGLS was performed excluding extinct species, using Pagel's "lambda" transformation in phylolm (optimized for large trees (108)), and repeating the analysis across 100 or 1000 trees. We also performed multivariate analyses including percent of DNA-sampled species per clade to test whether our results are unaffected by imputing DNA-missing species (Fig. S10).

Tip-level tests of speciation-rate correlates. To examine correlative structures underlying observed tip-rate variation, we performed tip-level PGLS analyses between species' ecological traits and tip DR values across 1000 trees, focusing on a 5675-species data set that excluded all extinct (n=107) and marine (n=129) species. We followed Freckleton et al. (82) in using trait ~ rate models in our tip-level PGLS analyses to avoid identical residuals in the dependent variable (i.e., sister species have identical tip DR values, which otherwise violates the assumed within-variable data independence in bivariate normal distributions). The trait ~ rate approach was previously applied using tip DR in univariate contexts (109) (see Fig. S13-S14 for sensitivity tests).

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Clade-level tests of speciation-rate correlates. At the clade level, univariate PGLS was performed typically (rate ~ trait models), since clade tip DR mean gave independent values to sister clades. These analyses were conducted on 1000 trees by analogy with those previous, except that per-clade trait summaries were standardized predictors (mean centered, standard deviation scaled) using geometric means for vagility and arithmetic means otherwise. We also performed tests for trait-dependent speciation using rate-shifted clades identified in BAMM runs on 10 mammal trees (STRAPP (69) method), which corrects for phylogenetic pseudoreplication similar to PGLS except instead via the covariance structure among rate regimes (see Fig. S8).

Phylogenetic path analyses. We performed path analysis aiming to fully resolve correlational structures and thereby translate from the language of statistical association to causality. For phylogenetic path analyses, we used PGLS to test statements of conditional independence (60) across 27 pre-selected path models (Fig. S4). For each tree and clade set, we used "phylopath" (110) to analyze models and perform conditional model averaging. Time-sliced clades at 10-, 30-, and 50-Ma intervals were analyzed and compared to analogous results using taxon-based clades (Fig. S12; see *Supplementary Information* for further details).

Acknowledgments: We thank I. Quintero, M. Landis, D. Schluter, A. Mooers, A. Pyron, G. Thomas, D. Greenberg, S. Upham and E. Florsheim for conceptual discussions that improved this study; B. Patterson, K. Rowe, J. Brown, T. Colston, T. Peterson, D. Field, T. Stewart, J. Davies, and three anonymous reviewers for comments on earlier drafts; and M. Koo, A. Ranipeta, and J. Hart for database help. Artwork from phylopic.org and open source fonts. **Funding:** The NSF VertLife Terrestrial grant to W.J. and J.E. (DEB 1441737 and 1441634) and NSF grant DBI-1262600 to W.J. supported this work. **Competing interests:** None.

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Figure legends

Fig. 1. Species-level relationships, rates, and traits for 5,911 species of mammals globally. (**a**) The maximum clade credibility topology of 10,000 node-dated trees, with numbered clade labels corresponding to orders and subclades listed in the plot periphery: Eulipoty., Eulipotyphla; Carn., Carnivora; Artio., Artiodactyla. Scale in millions of years, Ma. Branches are colored with tip-level speciation rates (tip DR metric) and marked with 24 inferred shifts in branch-specific net diversification rates (nodes A-X; shifts with multiple circles occurred on either branch, not both, over a sampling of 10 trees from the credible set). Tip-level rates are reconstructed to interior branches using Brownian motion. (**b**) Per-species ecological traits: allometric index of vagility (dispersal ability), diurnality (predominant daytime activity), and north-south latitudinal extent (see *Methods* for details). Silhouettes are from phylopic.org and open source fonts.

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statistically different); and, right: tip-level speciation rate (tip DR metric) distributions of the same simulated and observed subclades (gray versus color, one tree), comparing variation in clade tip rate mean and skew across 100 trees. The last 2 Ma are removed from parts **c-e** to focus on pre-recent rate dynamics.

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crown age, (**b**) clade tip-level speciation rate mean (harmonic mean of species' tip DR in clade), and (**c**) clade tip-level speciation rate skew (asymmetry of species' tip DR in clade; multivariate PGLS [phylogenetic generalized least squares] on standardized data with 95% confidence intervals [CIs] on parameter estimates). Clade tip rate mean explains most of the variation in species richness across time-sliced clades, given its consistently larger unique effects in observed clades (grey symbols and black line) than either clade crown age or tip rate skew. By comparing these observed effects on clade richness to simulated rate-constant effects (colored symbols and dashed lines; different extinction fractions, ε), we find that tip rate mean has significantly stronger effects on richness than expected from simulated birth-death trees containing only stochastic rate variation. Clade tip rate skew also explains significantly more variation in clade richness than expected at deeper time slices, while crown age matches the simulated predictions. Other predictors were also assessed, as were taxon-delimited clades (Fig. S10). Solid black lines connect the observed best-fitting models across time slices and trees.

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slopes; colored if effects are significant, red for negative, blue for positive, else gray). (**b**) Phylogenetic path analysis conducted across time-sliced clades at 10-, 30-, and 50-Ma intervals, delimited as illustrated in Fig. 3 (nested multivariate PGLS on standardized data). This causal framework connects clade-level summaries of species' vagility (geometric mean), diurnality (arithmetic mean), and latitude (arithmetic mean of centroid absolute values) to corresponding clade rates, and those rates to clade species richness. Path thickness, color, and directionality denote median coefficients of model-averaged analyses across 1000 trees (see legend: positive paths in shades of blue, negative in shades of red; time-sliced clades of 10-, 30-, and 50-Ma proceed from left to right as labeled). The bottom panels provide per-estimate uncertainty across time slices (slope ± SE), with non-zero estimates totaled in the right margin. Paths present in >500 trees are bolded and displayed in the upper path model diagram whereas other paths are dashed lines.

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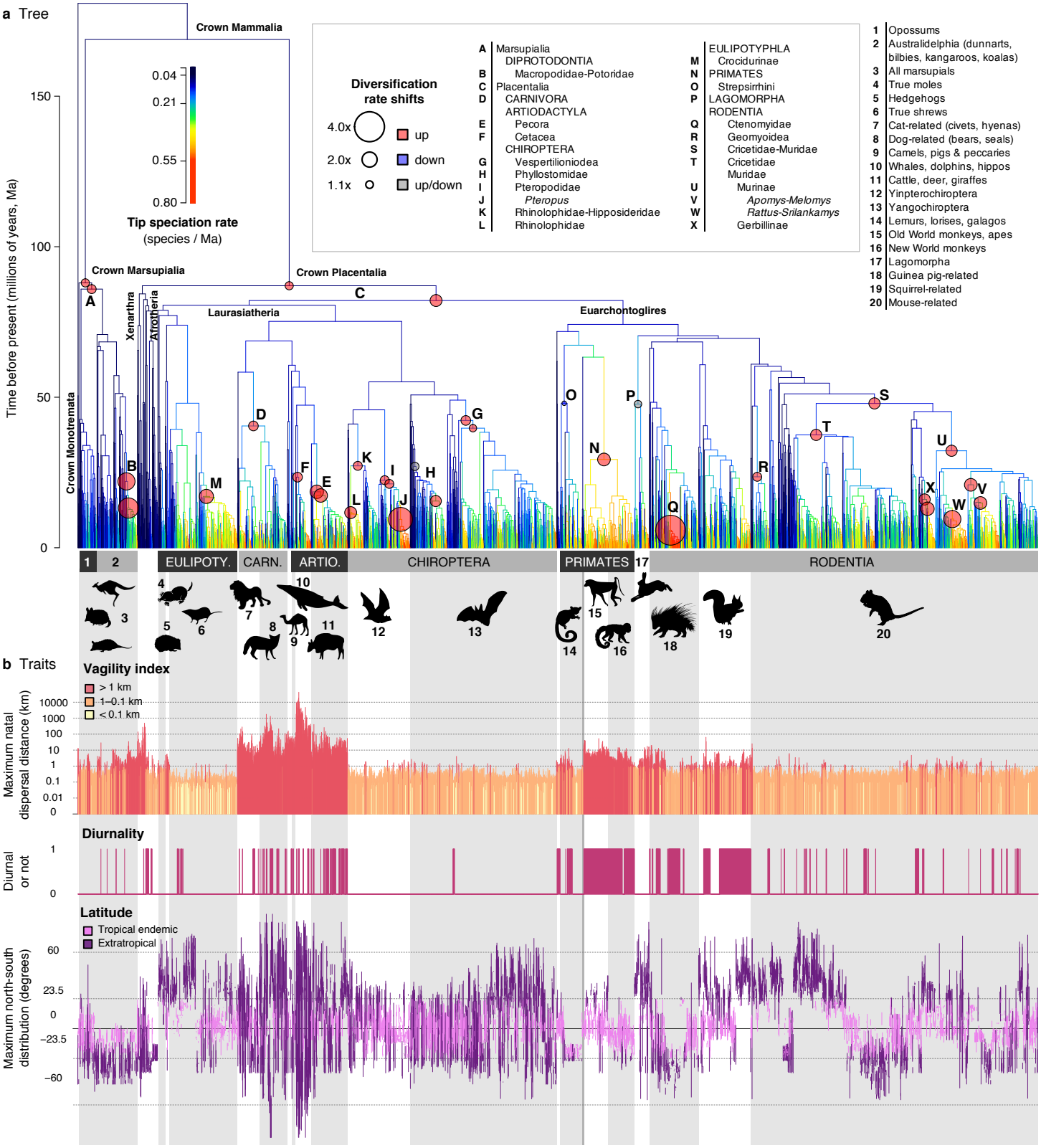

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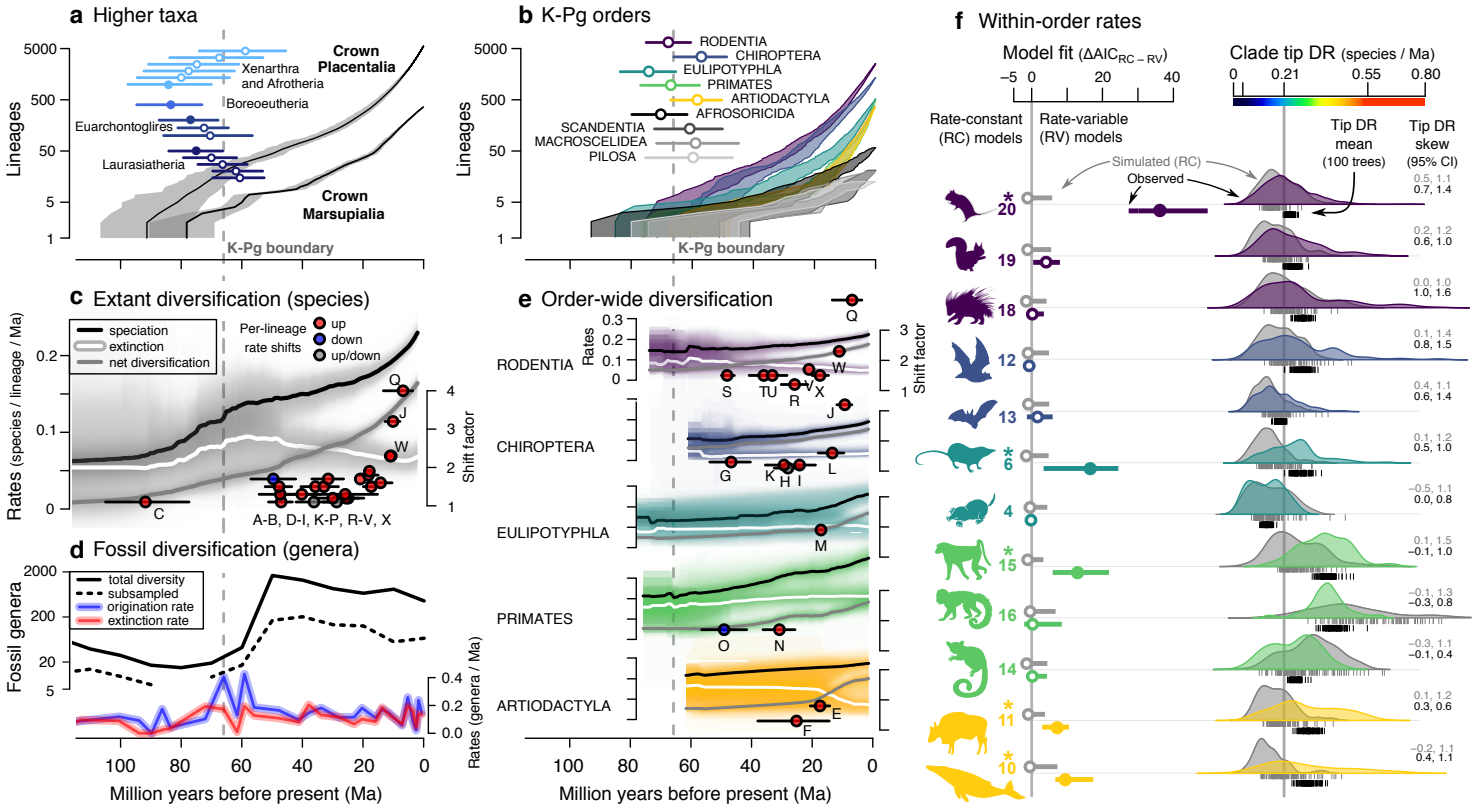

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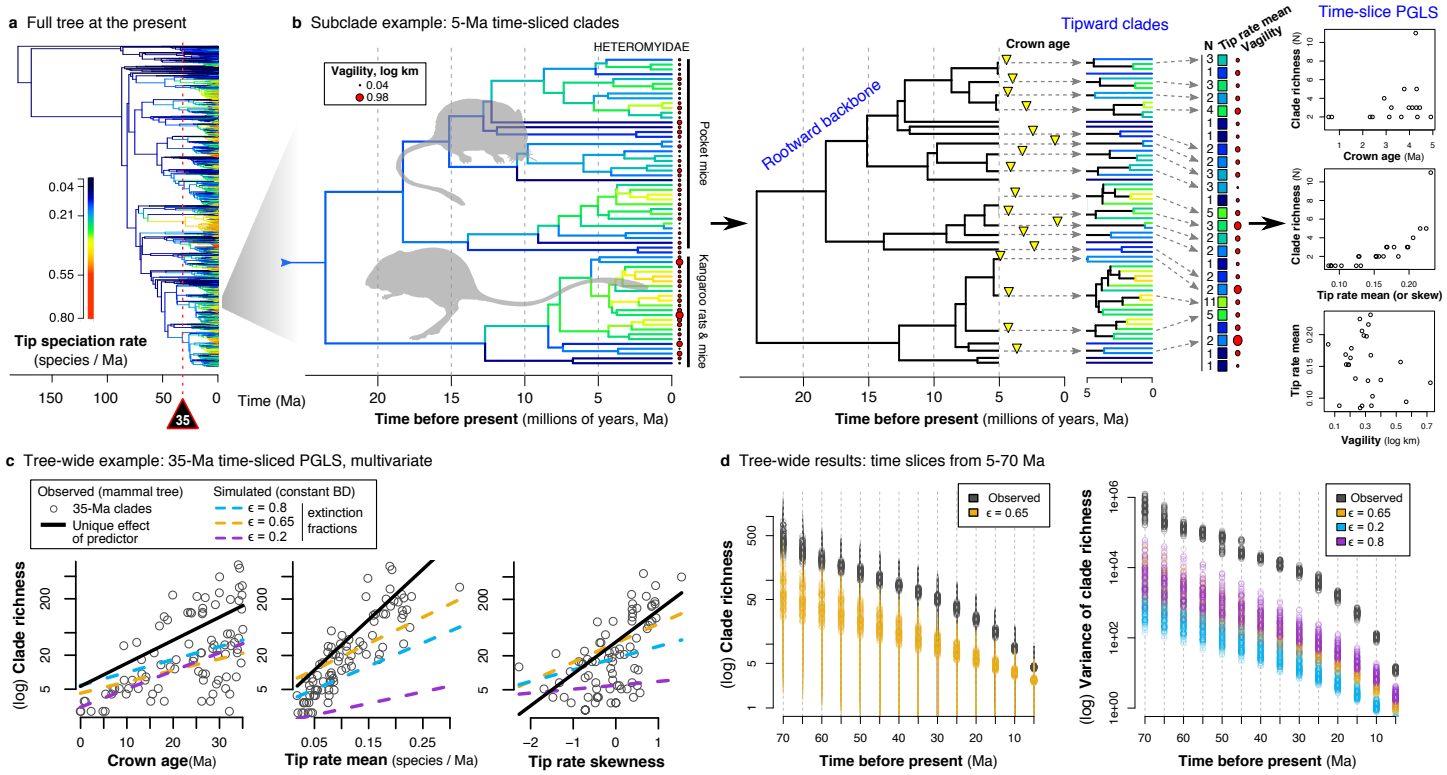

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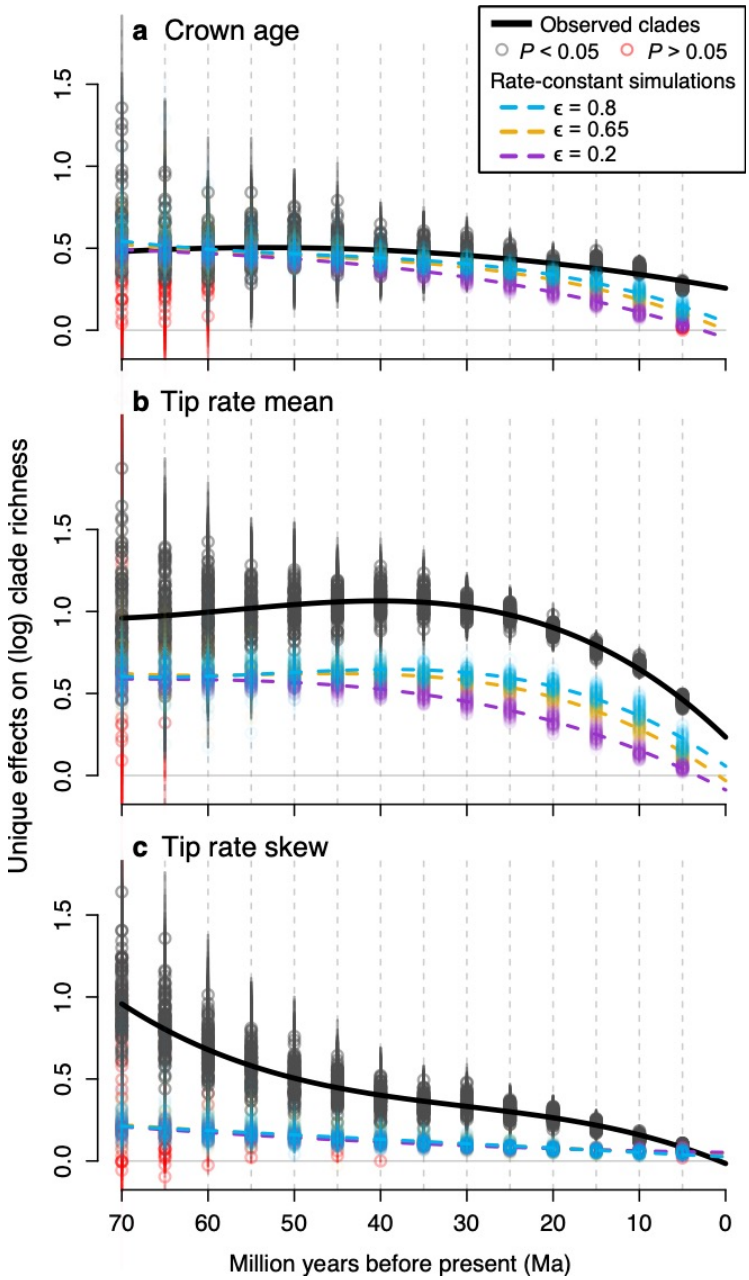

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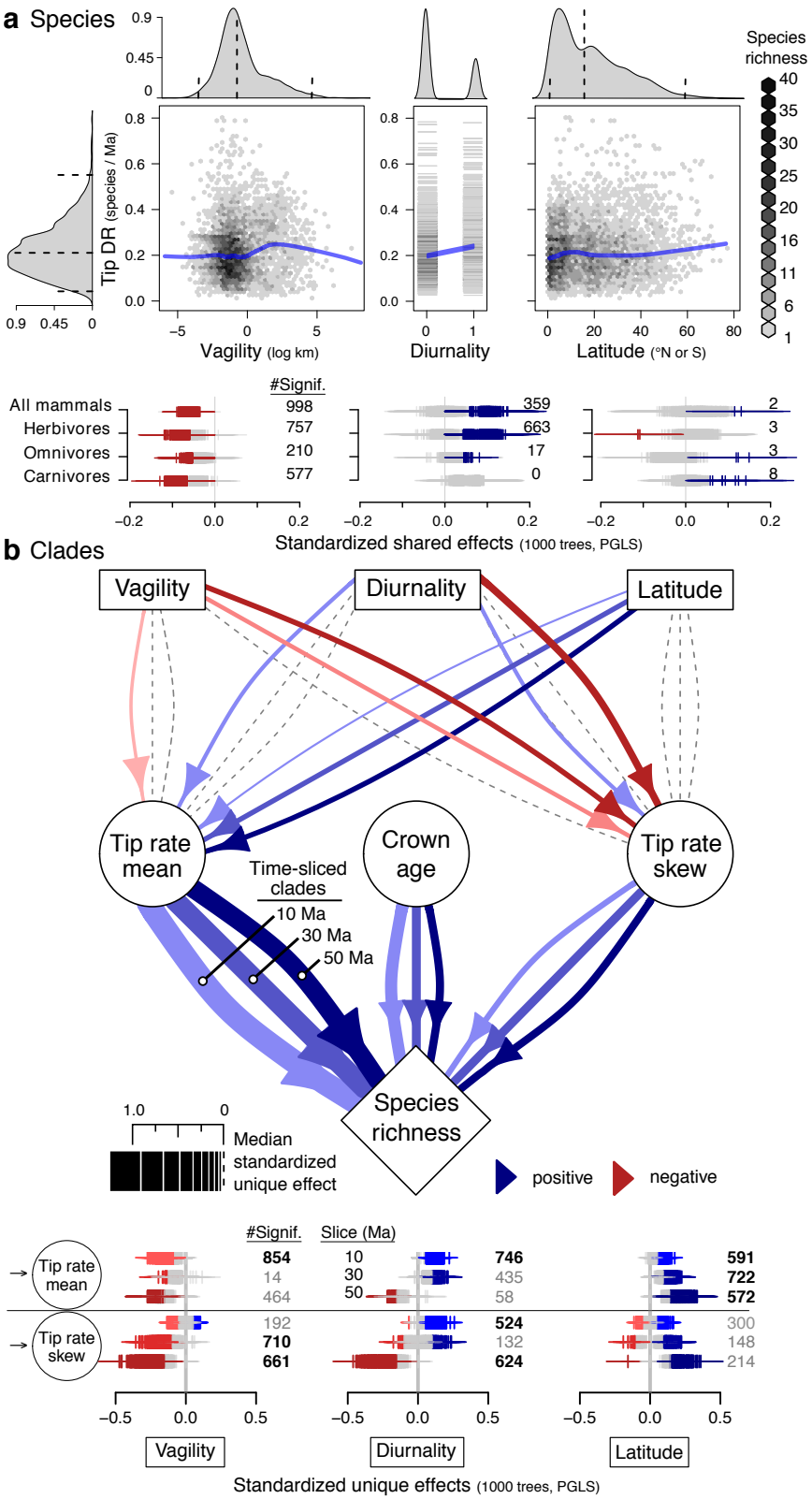

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