

1 Letter

2 **Ecological causes of uneven mammal diversity**

3

4 Short title: Causes of uneven species diversity

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19

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23 **ABSTRACT**

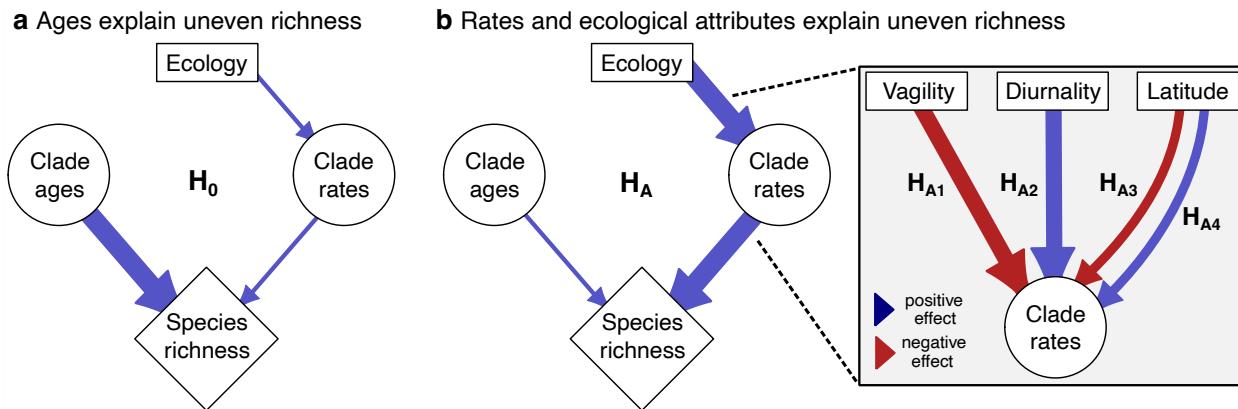
24 The uneven distributions of species over geography (e.g., tropical versus temperate  
25 regions) and phylogeny (e.g., rodents and bats versus the aardvark) are prominent biological  
26 patterns for which causal interconnections remain enigmatic. Here we investigate this central  
27 issue for living mammals using time-sliced clades sampled from a comprehensive recent  
28 phylogeny ( $N=5,911$  species, ~70% with DNA) to assess how different levels of unsampled  
29 extinction impact the inferred causes of species richness variation. Speciation rates are found to  
30 strongly exceed crown age as a predictor of clade species richness at every time slice, rejecting a  
31 clock-like model in which the oldest clades are the most speciose. Instead, mammals that are  
32 low-vagility or daytime-active show the fastest recent speciation and greatest extant richness.  
33 This suggests primary roles for dispersal limitation leading to geographic speciation (peripatric  
34 isolation) and diurnal adaptations leading to ecological speciation (time partitioning). Rates of  
35 speciation are also faster in temperate than tropical lineages, but only among older clades,  
36 consistent with the idea that many temperate lineages are ephemeral. These insights, enabled by  
37 our analytical framework, offer straightforward support for ecological effects on speciation-rate  
38 variation among clades as the primary cause of uneven phylogenetic richness patterns.

39

## 40 INTRODUCTION

41 Biological diversity is concentrated more at the equator than the poles, and more in some  
42 clades than others. Yet whether the latitudinal pattern of variation causes the phylogenetic one is  
43 an open question. The latitudinal diversity gradient is generally attributed to tropical biomes  
44 being stable, productive, and old (Fine & Ree 2006; Jablonski *et al.* 2006; Mittelbach *et al.* 2007;  
45 Jetz & Fine 2012; Jansson *et al.* 2013; Pontarp *et al.* 2019), but there is less consensus regarding  
46 why species richness is distributed unevenly across the tree of life. Phylogenetic tree shape was  
47 first characterized taxonomically (Willis 1922) and later formalized under the concept of tree  
48 imbalance or unevenness (Mooers & Heard 1997). To arise, more speciose clades must derive  
49 from faster net diversification (speciation – extinction), older ages (earlier divergences), or both.  
50 However, the relative contribution of clade rates and ages to species richness is widely disputed  
51 (e.g., (McPeek & Brown 2007; Wiens 2011; Rabosky *et al.* 2012; Hedges *et al.* 2015)).  
52 Empirical phylogenies might record diversification-rate variation due to stochastic factors,  
53 determinism (e.g., via ecological factors), or artifacts of how we reconstruct evolutionary history  
54 (Ricklefs 2003; Blum & François 2006; Phillimore & Price 2008; Rabosky 2009; Venditti *et al.*  
55 2010; Davies *et al.* 2011; Purvis *et al.* 2011; Price *et al.* 2012; Moen & Morlon 2014; Castro-  
56 Insua *et al.* 2018; Machac *et al.* 2018; Diaz *et al.* 2019; Louca & Pennell 2020). Latitude might  
57 alter the rates at which new species originate, persist, or go extinct (Jablonski *et al.* 2006; Weir &  
58 Schlüter 2007; Cutter & Gray 2016; Machac & Graham 2017; Silvestro *et al.* 2020), but so too  
59 might species' intrinsic traits (Jablonski 2008), some of which are correlated with latitude (e.g.,  
60 (Alroy 2019)). Thus, understanding the processes underpinning uneven species richness requires  
61 connecting direct (e.g., rates, ages) and indirect (e.g., ecological) causes to tease apart their joint  
62 influences upon the phylogenetic distribution of species richness.

63 The challenge of disentangling the relative importance of clade ages (time) versus rates  
64 of speciation and extinction (whether stochastic or ecologically deterministic) suggests the need  
65 to establish a hierarchical framework uniting these direct and indirect potential causes of uneven  
66 species richness (Fig. 1). To do so, we propose the following set of hypotheses:  $H_0$ , speciation  
67 and extinction rates among clades do not vary substantially, so clade ages best explain uneven  
68 species richness; or,  $H_A$ , differences in among-clade diversification rates explain species richness  
69 better than clade age. If the alternative hypothesis is supported, then certain ecological attributes  
70 (e.g., patterns of space use, activity period, or environment niche) may explain changes in  
71 diversification rates, and thereby indirectly cause patterns of uneven species richness (Fig. 1b).  
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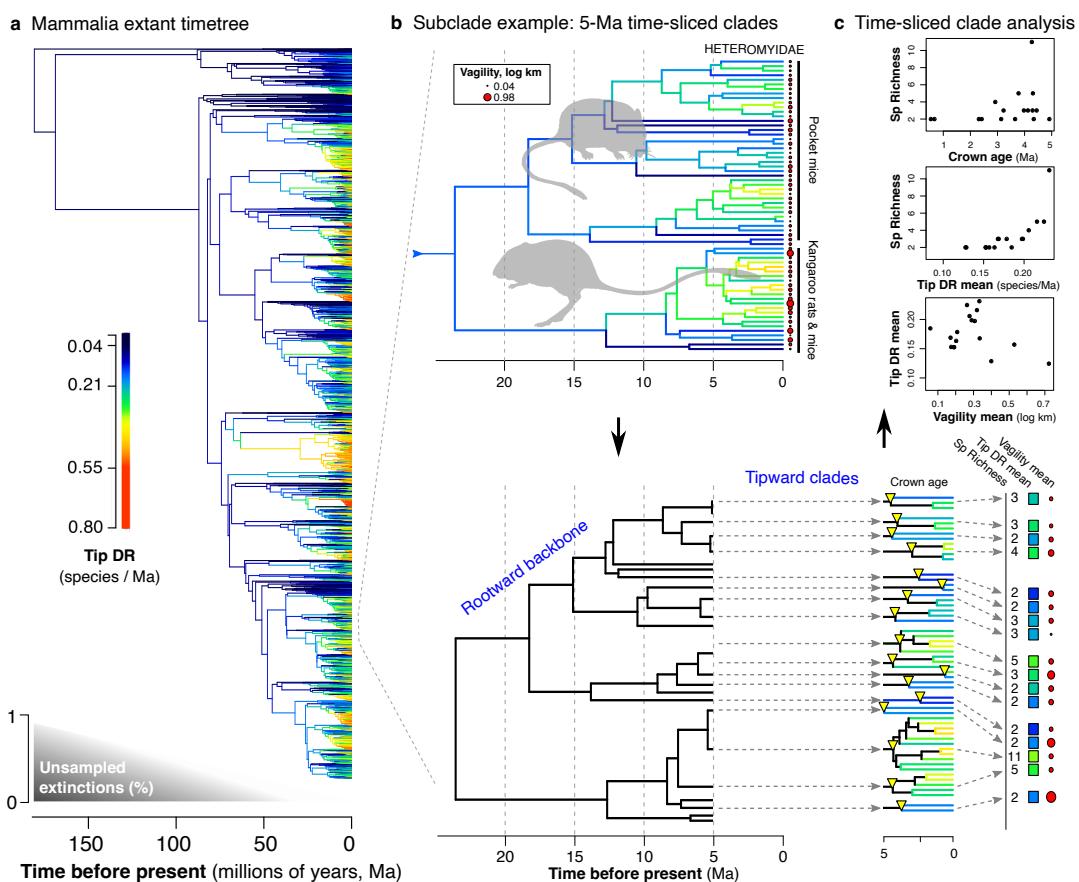


74 **Fig. 1. Hypotheses for uneven species richness among branches in the tree of life.** The  
75 observation that different groups of species (clades) have differing numbers of extant species is  
76 generally explained in one of two ways: (a) by uneven clade ages, in which younger clades have  
77 few species while older clades are the most speciose (null hypothesis,  $H_0$ ); or (b) by uneven  
78 macroevolutionary rates (speciation – extinction = net diversification), in which the most  
79 speciose clades have the fastest rates (alternative,  $H_A$ ).  $H_A$  implies that some varying ecological  
80 attributes of species are, in turn, responsible for the observed variation in clade rates. We  
81 specifically assess three aspects of ecology (inset): vagility, a measure of individual dispersal  
82 ability in a species ( $H_{A1}$ ); diurnality, or the propensity for individuals in a species to be active  
83 during daylight hours ( $H_{A2}$ ); and centroid latitude of a species' geographic range, a surrogate  
84 metric capturing abiotic conditions such as environmental stability ( $H_{A3}$  and  $H_{A4}$ ). See the main  
85 text for explanations of each attribute's expected directions of influence upon clade rates.  
86

87        This framework can be tested using phylogenetic path analysis (von Hardenberg &  
88        Gonzalez-Voyer 2013), which unifies macro-scale approaches from ecology and evolution. In  
89        macroecology, environmental variables or species traits are often related directly to species  
90        richness (e.g., associations between clade richness and mean body size; (Gittleman & Purvis  
91        1998; Isaac *et al.* 2005)). In macroevolution, measurements of clade rates or ages are either  
92        compared to species richness (e.g., (Scholl & Wiens 2016; Sánchez-Reyes *et al.* 2017)) or  
93        ecological traits (e.g., (Beaulieu & O'Meara 2016; Harvey & Rabosky 2018)), but usually not  
94        both. Recently, Harvey *et al.* (2020) used a path analysis of geographic regions to establish  
95        causality between environmental variables, species richness, and speciation rates in suboscine  
96        birds, which revealed the spatial context of uneven species diversification. However, the  
97        phylogenetic context of why species richness varies so dramatically among clades remains  
98        enigmatic, particularly regarding the relative causality of temporal and ecological factors.

99        A major limitation to studying among-clade diversity has been the reliance, as units of  
100        analysis, on higher taxa (e.g., (Rabosky *et al.* 2012; Castro-Insua *et al.* 2018)), which often have  
101        vast differences in age. For example, crown ages of mammal families range from 3.8 to 59.0  
102        million years (Ma; (Upham *et al.* 2019)). To avoid comparing heterogeneously defined clades,  
103        we propose an objective strategy for delimiting analytically equivalent clades, i.e., ‘time-sliced  
104        clades.’ By slicing a phylogeny at a given time, we can then take the tipward groups as objective  
105        units of analysis. As shown for an example family of mammals (Fig. 2), slicing the tree at 5 Ma  
106        results in the delimitation of 17 clades containing two or more species. Those clades are united  
107        by having (i) a stem age  $>5$  Ma and crown age  $< 5$  Ma; and (ii) a rootward backbone of shared  
108        evolutionary history. However, because each clade varies in estimated crown age, species  
109        richness, clade summaries of species attributes, and species-specific ‘tip’ speciation rates, there

110 is a key opportunity for identifying partial associations (Fig. 2c). Critically, defining time-sliced  
111 clades at successively older time-points within a phylogeny of extant species yields the  
112 expectation for progressively greater bias from unsampled extinction events — i.e., Marshall’s  
113 (2017) ‘fifth law of palaeobiology’ (Fig. 2a). As a result, speciation rates will be increasingly  
114 underestimated or ‘pulled’ from the actual rates of the birth-death process in older clades (Kubo  
115 & Iwasa 1995; Louca & Pennell 2020). This general expectation has been confirmed in crown  
116 Mammalia, for which fossil- and molecular-based speciation rates overlap only between 0 and  
117 ~10 Ma (Upham *et al.* 2021). Thus, analyzing clades from shallow to deep time slices of an  
118 extant phylogeny presents a further opportunity for assessing the impact of unsampled  
119 extinctions on among-clade correlations in species attributes, rates, ages, and diversities.



121 **Fig. 2. Approach of using time-sliced clades to test eco-evolutionary hypotheses.** (a) The  
122 mammal timetree is painted with species-specific (tip) speciation rates calculated using the tip  
123 DR metric across the full tree. The fraction of unsampled extinction events is expected to  
124 increase at deeper levels of the extant timetree, with only two surviving lineages (leading to  
125 extant therians and monotremes) sampled at the root of crown Mammalia. (b) Example of how a  
126 subclade of mammals can be divided into time-sliced clades, here the rodent family  
127 Heteromyidae (64 species) with clades delimited tipward of an arbitrary line drawn at 5-million  
128 years (Ma; branch colors correspond to tip DR). (c) The crown age of those clades with two or  
129 more species are by definition < 5 Ma (yellow triangles), and the species richness values range  
130 from 1-11 species in this example. Also summarized are the clade harmonic mean of tip DR (tip  
131 DR mean), and the clade geometric mean of vagility values (or other ecological traits). The  
132 rootward backbone of those time-sliced clades represents their expected covariance structure for  
133 use in comparative analyses (e.g., phylogenetic generalized least squares). Analyses conducted in  
134 Fig. 4 and 5 are based upon summary values for time-sliced clades delimited in this manner.

135

136 Here, we apply this novel clade-level framework to the investigation of temporal and  
137 ecological causes of uneven diversification in Mammalia. Considering the ~6,500 recognized  
138 living species of mammals (Burgin *et al.* 2018; MDD 2023), we see that similarly aged clades  
139 range from mega-diverse rodents (~2,600 living species) and bats (~1,400 species) to species-  
140 poor groups like treeshrews (23 species) and pangolins (8 species, all four clades share stem ages  
141 of ~60-70 Ma; (Meredith *et al.* 2011; Upham *et al.* 2019; Álvarez-Carretero *et al.* 2022; Foley *et*  
142 *al.* 2023)). We here focus on three ecological factors hypothesized to influence rates of mammal  
143 speciation — vagility, diurnality, and latitude (Fig. 1b) — as measured on extant time-calibrated  
144 phylogenies (i.e., timetree). First, we tested whether low-vagility species have faster speciation  
145 than more dispersive species given their greater likelihood of forming peripheral isolates ( $H_{A1}$ )  
146 (Mayr 1963; Kisel & Barraclough 2010). For this test, we developed an allopatric index of  
147 organismal vagility for all mammals (i.e., maximum natal dispersal distance; (Whitmee & Orme  
148 2013)). Vagility effects have never been assessed across all mammals, although evidence in birds  
149 (e.g., (Belluire *et al.* 2000; Claramunt *et al.* 2012)) and reef fishes (Donati *et al.* 2019) supports  
150 an inverse vagility-to-speciation rate relationship. Second, we tested whether clades with greater

151 diurnality have increased speciation rates relative to nocturnal clades, following evidence that  
152 mammalian ancestors were likely nocturnal until daytime niches evolved ~35 Ma ( $H_{A2}$ )  
153 (Gerkema *et al.* 2013; Maor *et al.* 2017). A positive influence of diurnality on speciation rates  
154 has been found across major tetrapod lineages (Anderson & Wiens 2017), and in primates  
155 specifically (Magnuson-Ford & Otto 2012; Santini *et al.* 2015), but has yet to be investigated at  
156 the species-level in all mammals (only ancestral diel states have been examined (Maor *et al.*  
157 2017)). Lastly, we examine the effects of latitude on speciation rates, which could either have a  
158 negative or positive association (fastest rates at low latitudes,  $H_{A3}$ , or high latitudes,  $H_{A4}$ ,  
159 respectively). Previous work in mammals has supported faster tropical than temperate speciation  
160 among orders (Rolland *et al.* 2014), but has been inconclusive among genera (Soria-Carrasco &  
161 Castresana 2012) and found the opposite pattern among sister species (Weir & Schluter 2007).  
162 Faster temperate than tropical speciation contrasts with the observed pattern of peak tropical  
163 mammal richness, meaning that  $H_{A4}$  additionally implies higher temperate rates of extinction and  
164 thus species turnover (extinction / speciation). This type of ‘ephemeral speciation’ (Rosenblum  
165 *et al.* 2012) is supported by observations of faster tip speciation in high-latitude marine fishes  
166 (Rabosky *et al.* 2018) and rosid angiosperms (Sun *et al.* 2020), as well as high-elevation birds  
167 (Quintero & Jetz 2018), but this hypothesis is so far untested in mammals (reviewed in (Cutter &  
168 Gray 2016; Schluter & Pennell 2017)). Drawing upon a comprehensive time-calibrated  
169 phylogeny of mammals and tip rates of speciation calculated across a credible set of 10,000 trees  
170 (Upham *et al.* 2019), we assembled a corresponding set of species-level ecological traits to query  
171 whether factors predicted to cause newly formed species to persist or go extinct are, in turn,  
172 causing the observed patterns of uneven species richness among clades.  
173

174 **METHODS**

175 **Mammalian phylogeny and species trait data.** We used the species-level mammal trees  
176 of Upham et al. (2019) to conduct all analyses. Briefly, these phylogenies include 5,804 extant  
177 and 107 recently extinct species in credible sets of 10,000 trees. They were built using a  
178 ‘backbone-and-patch’ framework that applies two stages of Bayesian inference to integrate age  
179 and topological uncertainty, and incorporates 1,813 DNA-lacking species using probabilistic  
180 constraints (available at [vertlife.org/phylosubsets](http://vertlife.org/phylosubsets)). We compared credible sets of trees built  
181 using node-dated backbones (17 fossil calibrations) and tip-dated backbones (matrix of modern  
182 and Mesozoic mammals), as well as taxonomically completed trees (5,911 species) versus DNA-  
183 only trees (4,098 species) without topology constraints. We calculated phylogenetic signal and  
184 tree imbalance statistics using maximum clade credibility (MCC) consensus trees and the R  
185 packages “phytools” (Revell 2012) and “apTreeshape” (Bortolussi *et al.* 2006), respectively.

186 Our workflow for gathering trait data involved (i) unifying multiple trait taxonomies  
187 (e.g., EltonTraits v1.0 (Wilman *et al.* 2014), PanTHERIA (Jones *et al.* 2009)) to our phylogeny’s  
188 master taxonomy; and (ii) interpolating home range area and vagility to the species level using  
189 known allometric relationships in mammals (Fig. S1). Vagility was interpolated as an index  
190 value for each species following our updated version of Whitmee and Orme’s (2013) best-fit  
191 equation, which applies species means of body mass, home range, and geographic range to  
192 calculate the maximum natal dispersal distance per individual (km; Fig. S2). Note that our  
193 vagility index does not account for locomotor abilities (e.g., flying or arboreality), but rather  
194 captures aspects of space use that scale allometrically across mammals. Collinearity among trait  
195 variables was examined using the “corrplot” package in R (Wei 2017).

196 We identified three species-level traits that are directly related to core hypotheses of  
197 ecological diversification while also having minimal collinearity (Fig. S3). These traits are: (i) an  
198 allometric index of vagility based on a best-fitting equation of  $\log(\text{maximum natal dispersal}$   
199  $\text{distance, km}) = -2.496 + 0.206 \log(\text{body mass, g}) + 0.323 \log(\text{home range size, km}) + 0.216$   
200  $\log(\text{geographic range size, km})$ ; (ii) diurnality as a binary trait of 0 = nocturnal / cathemeral /  
201 crepuscular, and 1 = diurnal; and (iii) latitude calculated as the absolute value of the centroid of a  
202 species' expert geographic range map. As expected (Jetz *et al.* 2004; Whitmee & Orme 2013),  
203 the vagility index captures a multivariate signal of average individual space use per species  
204 (correlation of  $r=0.5-0.8$  with its component variables; Fig. S3). Diurnality and latitude inform  
205 two additional ecological axes, each having low collinearity with vagility or other variables  
206 (maximum  $r=0.34$  and 0.13, respectively).

207 **Tip-level speciation rates.** We calculated per-species estimates of expected pure-birth  
208 diversification rates for the instantaneous present moment (tips of the tree) using the inverse of  
209 the equal splits measure (Steel & Mooers 2010; Jetz *et al.* 2012). This metric has been called  
210 'tip-level diversification rate' (tip DR) because it measures recent diversification processes  
211 among extant species (Quintero & Jetz 2018). However, to avoid confusion with 'net  
212 diversification', for which tip DR is not suited when extinction is very high (relative extinction  
213  $>0.8$  (Title & Rabosky 2019)), we here use tip DR as a tip-level speciation rate metric. At the tip  
214 level, we confirm that tip DR is tightly associated with model-based estimators of tip speciation  
215 and tip net diversification rates in the mammal trees (Fig. S4). At the clade level, Upham *et al.*  
216 (2021) showed that (i) the clade-level harmonic mean of tip speciation rates, as measured by tip  
217 DR (here called 'tip DR mean') approximates the pulled speciation rate for that clade at the  
218 instantaneous present ( $\lambda_0$ ), which is an identifiable value (Louca & Pennell 2020); and (ii) the

219 skewness of tip DR in a clade (here called ‘tip DR skew’) approximates that clade’s extent of  
220 past diversification-rate shifts, as measured using BAMM rate-shift factors (Rabosky 2014).  
221 Thus, we expect tip DR mean and skew to illuminate the speed and heterogeneity of past  
222 speciation in a clade, respectively. A critical caveat here, following the demonstration in fig. 4b  
223 of Upham *et al.* (2021), is that we only expect the most recent ~10 Ma of branching in the extant  
224 mammal timetree to carry a reliable signal of past speciation-rate dynamics as compared to the  
225 fossil record.

226 **Time-sliced clades and clade-level tests of species richness variation.** To objectively  
227 define clades, we arbitrarily drew lines (referred to as “time slices”) at 5-Ma intervals and took  
228 the resulting *tipward* (all the way to the extant tip) clades as non-nested units of analysis. The  
229 *rootward* relationships of those clades (the “rootward backbone”) was retained for each interval,  
230 giving the expected covariance structure among clades when performing phylogenetic  
231 generalized least squares (PGLS) analyses (see Fig. 2 for illustration). We used the “treeSlice”  
232 function in phytools to construct clade sets across mammal timetrees and three sets of rate-  
233 constant birth-death (RCBD) simulated trees. These RCBD simulations were run using the  
234 “pbtree” function in phytools under scenarios of extinction fraction,  $\varepsilon$ , matching the empirical  
235 median ( $\varepsilon=0.65$ ) versus low ( $\varepsilon=0.2$ ) or high ( $\varepsilon=0.8$ ) values, and with simulations set to 5,911  
236 species and re-scaled to crown age of 188 Ma to approximate the branching history of extant  
237 mammals. We also compared the time-sliced clade results to analyses based on traditional named  
238 clades (genera, families, and orders). All PGLS analyses were performed excluding extinct  
239 species, using Pagel’s “lambda” transformation in phylolm (optimized for large trees (Ho & Ané  
240 2014)), and repeating the analysis on 100 or 1,000 trees. We also performed multivariate

241 analyses including percent of DNA-sampled species per clade (for the completed trees) to test  
242 whether any results were affected by the proportion of taxonomically imputed species.

243 **Tip-level tests of speciation-rate correlates.** To examine correlative structures  
244 underlying observed tip-rate variation, we performed tip-level PGLS analyses between species'  
245 ecological traits and tip DR values across 1000 trees, focusing on a 5,675-species data set that  
246 excluded all extinct (n=107) and marine (n=129) species. We followed Freckleton et al. (2008)  
247 in using trait ~ rate models in our tip-level PGLS analyses to avoid identical residuals in the  
248 dependent variable (i.e., sister species have identical tip DR values, which otherwise violates the  
249 assumed within-variable data independence in bivariate normal distributions). The trait ~ rate  
250 approach was previously applied using tip DR in univariate contexts (Harvey *et al.* 2017), and  
251 performs well compared to QuaSSE (Harvey & Rabosky 2018).

252 **Clade-level tests of speciation-rate correlates.** At the clade level, univariate PGLS was  
253 performed typically (rate ~ trait models), since clade tip DR mean gave independent values to  
254 sister clades. These analyses were conducted on 1,000 trees as above, except that per-clade trait  
255 summaries were standardized (mean centered, standard deviation scaled) using geometric means  
256 for vagility and arithmetic means otherwise. For focal species attributes, we took clade-level  
257 average values to be robust ecological summaries of clades in relation to other clade metrics.

258 **Phylogenetic path analyses.** We performed path analysis aiming to fully resolve  
259 correlational structures and thereby translate from the language of statistical association to  
260 causality. For phylogenetic path analyses, we used PGLS to test statements of conditional  
261 independence (von Hardenberg & Gonzalez-Voyer 2013) across 27 pre-selected path models  
262 (Fig. S5). For each tree and clade set, we used the “phylopath” R package (van der Bijl 2018) to  
263 analyze models and perform conditional model averaging. Time-sliced clades at 10-, 30-, and 50-

264 Ma intervals were analyzed and compared to somewhat analogous taxon-based clades of genera,  
265 families, and orders, with the expectation that older clades will contain greater unmeasured  
266 extinction and thus be less reliable indicators of historical speciation rates.

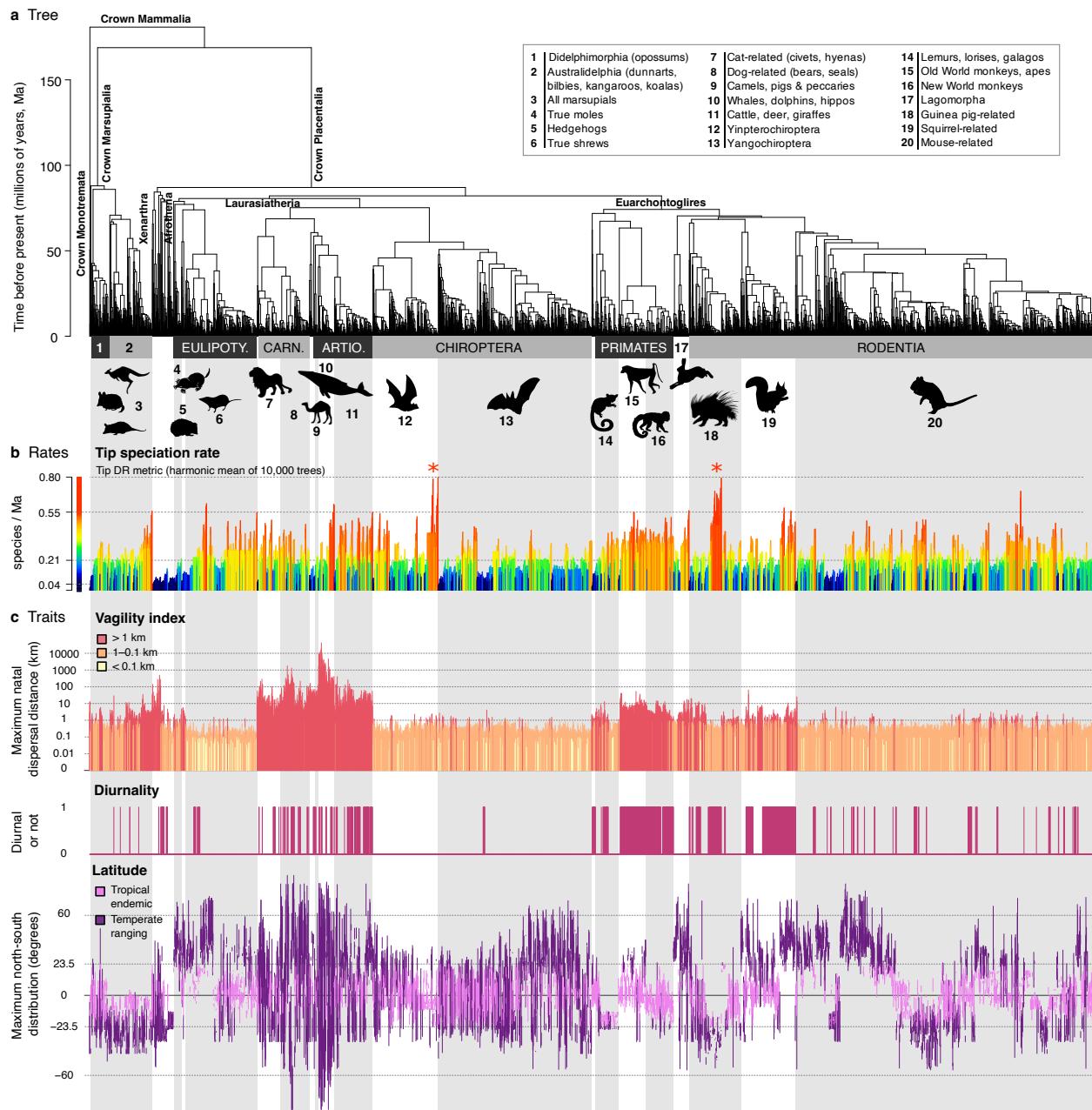
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## 268 RESULTS

269 **Unevenness of traits, rates, and species in the mammal timetree.** We find dramatic  
270 variation in the phylogenetic distribution of mammal biodiversity (Fig. 3). The shape of the  
271 extant phylogeny is highly imbalanced, either as measured on the DNA-only or completed MCC  
272 tree (Colless'  $I$  values of 53591 and 82550, respectively) as compared to Yule expectations (test  
273 statistics of 5.872 and 6.397;  $P < 0.001$ ). For speciation-rate estimates, we similarly find the tip  
274 DR values are non-uniform with respect to taxonomic orders (Kruskal-Wallis  $\chi^2 = 1085.3$ ,  $df =$   
275 26,  $P < 0.001$ ) and families ( $\chi^2 = 2564.4$ ,  $df = 161$ ,  $P < 0.001$ ). Variation among species  
276 attributes is also non-uniform, as illustrated by significant phylogenetic signal with respect to  
277 vagility ( $K = 0.045$ ,  $P = 0.034$  [1,000 randomizations]), diurnality ( $K = 0.137$ ,  $P = 0.001$ ), and  
278 latitude ( $K = 0.062$ ,  $P = 0.001$ ; using the DNA-only MCC tree, as imputed species can bias  
279 studies of trait evolution, see (Rabosky 2015)).

280 Visually, mapping rates and traits on the timetree reveals a macroscopic view of global  
281 mammal diversification history. Two major pulses of recent speciation are apparent in bats and  
282 rodents, corresponding to the largest and most reliable diversification-rate shifts in mammals  
283 ((Upham *et al.* 2021); Fig. 3b, red asterisks in clades 12 and 18). We find greater vagility and  
284 latitudinal extents within Carnivora and Artiodactyla (clades 7–11; Fig. 3c) as compared to other  
285 mammal orders, along with a more heterogenous mix of diurnal or non-diurnal activity. In  
286 contrast, simian primates and squirrel-related rodents show clade-wide sweeps of diurnality

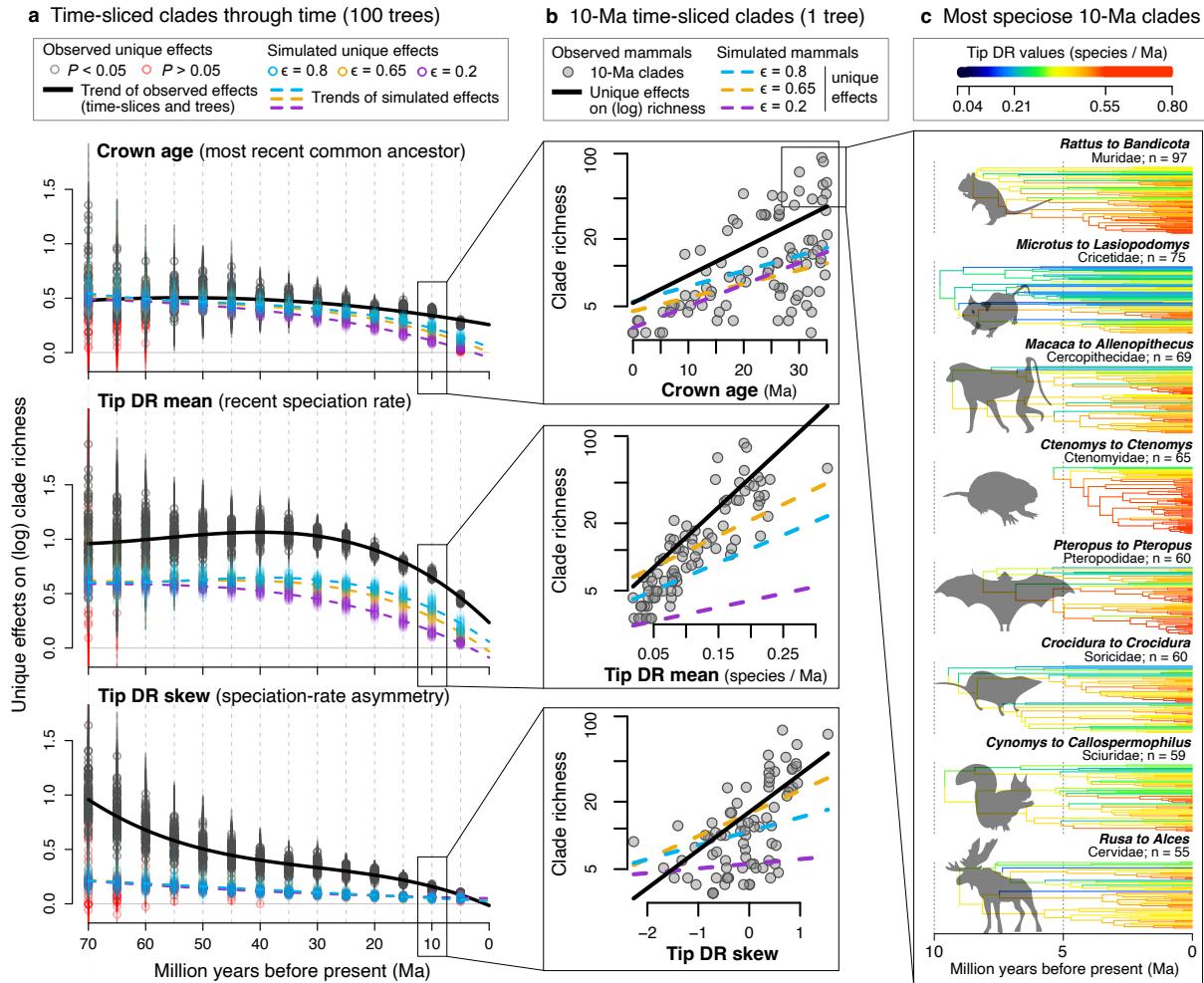
287 (clades 15, 16, 19). We also find a conspicuous latitudinal pattern of alternating north-south-  
288 north-south endemism from Lagomorpha to Rodentia (clades 17–20), which is difficult to  
289 dismiss as randomness given the clade-wise sorting of traits, so it may reflect biogeographic  
290 incumbency effects. We also note the clear signal of Madagascar visible from 12 to 24 degrees  
291 south latitude, representative of endemic radiations of tenrec afrotherians, euplerid carnivorans,  
292 strepsirrhine primates, and nesomyid rodents.



293

294 **Fig. 3. Species-level relationships, rates, and traits for 5,911 living species of mammals**  
295 **globally. (a)** The maximum clade credibility topology of 10,000 node-dated timetrees, with  
296 numbered clade labels corresponding to orders and subclades listed in the plot periphery:  
297 Eulipoty., Eulipotyphla; Carn., Carnivora; Artio., Artiodactyla. Scale in millions of years, Ma.  
298 **(b)** Tip speciation rates, as measured using tip DR values that correspond to the expected rate of  
299 species formation at the instantaneous present for each species (red asterisks refer to the bat  
300 clade *Pteropus*, left, and the rodent clade *Ctenomys*, right, which display significantly elevated  
301 rates of recent speciation). **(c)** Per-species ecological attributes: allometric index of vagility  
302 (dispersal ability), diurnality (predominant daytime activity), and north-to-south latitudinal  
303 extent of geographic range map. Silhouettes are from phylopic.org and open-source fonts.  
304

305        **Effects of ages and rates on clade species richness.** To separate the putative temporal  
306 causes of among-clade richness differences, we performed PGLS analyses on time-sliced clades.  
307 Univariate analyses show that crown age, tip DR mean, and tip DR skew are consistently the best  
308 predictors of log clade richness across time slices and trees (Fig. S7a, b; largest shared effects  
309 using standardized data). The percent of DNA-sampled species per clade is not important for  
310 explaining richness differences in multivariate models (Fig. S7c), indicating that completed  
311 mammal trees are unbiased for this question. In multivariate analyses (top three predictors across  
312 100 mammal trees), we find that crown age has unique effects across all time slices, but not  
313 different to those found in 3 sets of RCBD simulated phylogenies (Fig. 4a, top panel). While  
314 crown age can nominally explain differences in mammal richness, its effect is no larger than  
315 expected if tree-wide speciation rates were constant through time. In contrast, tip DR mean  
316 explains more variation in mammal richness than expected (and double that of crown age),  
317 especially from 5–30 Ma (Fig. 4a, center panel; non-overlapping 95% confidence intervals [CIs]  
318 between mammal trees and simulations). Similarly, tip DR skew has unique effects on mammal  
319 richness that increase for older time slices, especially at >50 Ma (Fig. 4a, bottom panel). Taken  
320 together, these results show that (i) recent speciation-rate variation in mammals is greater than  
321 expected from RCBD rate stochasticity alone; (ii) clade richness differences are better explained  
322 by recent speciation rates (tip DR mean and skew) than origin times (crown ages); and (iii)  
323 variation in both rates and ages is nonetheless important for explaining richness. Named clades  
324 show mostly similar results, but lack a way to generate null RCBD expectations (Fig. S8).



325

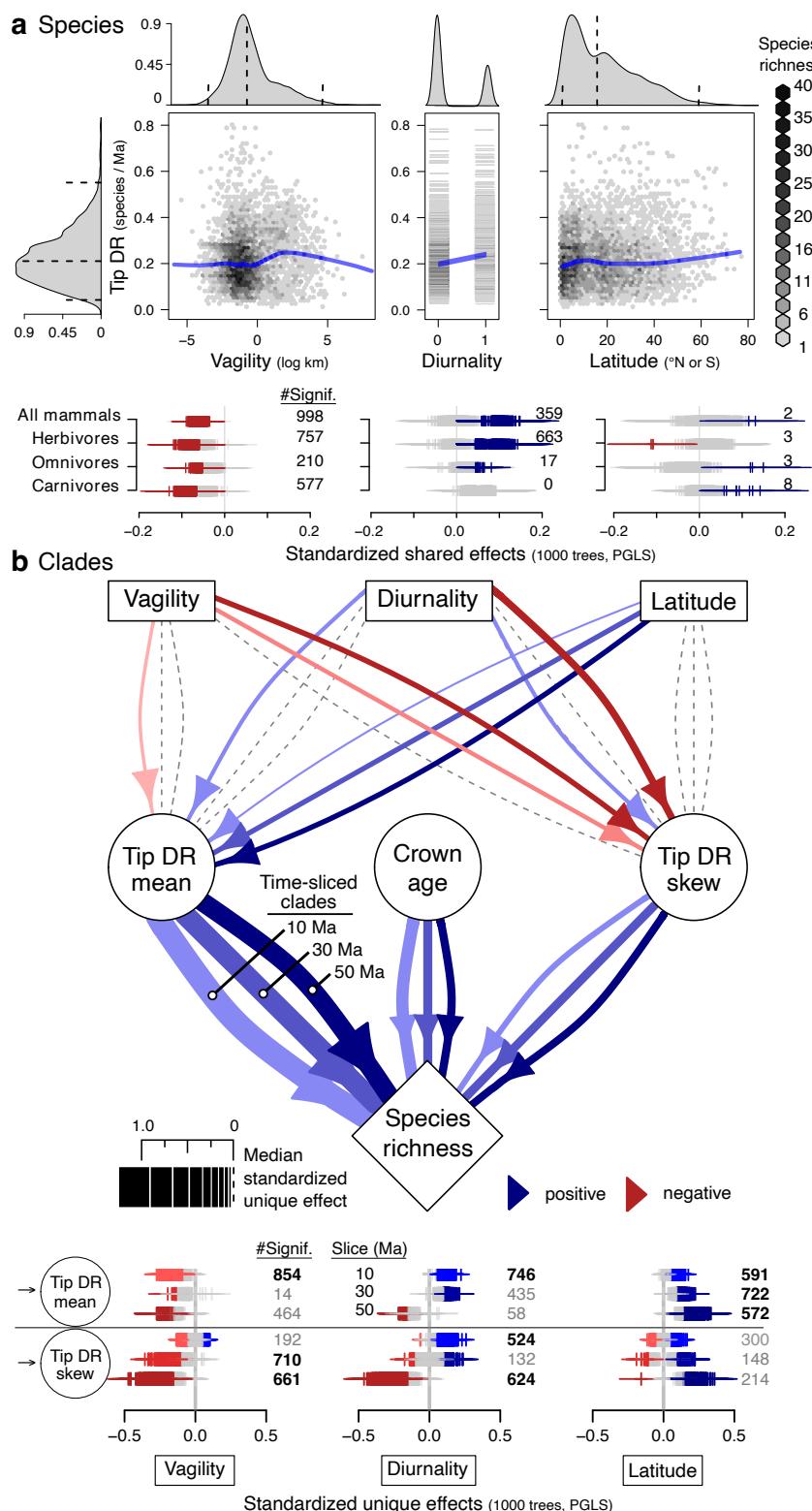
326 **Fig. 4. Temporal causes of species richness variation across time-sliced clades. (a)**  
327 Phylogenetic generalized least squares (PGLS) analyses of tipward time-sliced clades (delimited  
328 as in Fig. 2) at 5-million-year (Ma) intervals from 5–70 Ma. Analyses are repeated across 100  
329 mammal trees and compared to analogous results from trees simulated under a model of rate-  
330 constant birth-death (RCBD). For all clades, partial unique effects are examined on clade  
331 richness (PGLS of log clade species richness  $\sim$  crown age + tip DR mean + tip DR skew;  
332 predictors are standardized). Tip DR mean has consistently stronger unique effects than does  
333 crown age, and stronger than expected from the stochastic rate variation in RCBD simulations  
334 (95% confidence intervals do not overlap from 5–30 Ma). At deeper time slices, tip DR skew  
335 also explains more variation in clade richness than expected from simulations. **(b)** Each gray  
336 point in part **a** represents the unique-effect PGLS slope (solid black line) for a set of mammal  
337 time-sliced clades, here shown for an example of 10-Ma clades in 1 mammal tree compared to  
338 analogous clades from RCBD simulations (dotted colored lines under different extinction  
339 fractions,  $\epsilon$ ). Note the clade-level predictors are shown with original (non-standardized) values  
340 for illustration purposes only. **(c)** Illustration of the most speciose 10-Ma clades delimited from 1  
341 mammal tree (n = species richness of clade). Branches are colored relative to species' tip DR  
342 values (interior nodes painted for visualization purposes using a Brownian motion  
343 reconstruction). Silhouettes are from phylopic.org and open-source fonts.

344       **Ecological effects on speciation rates.** We analyzed the shared effects of standardized  
345    species' ecological traits on tip DR values across 1,000 mammal trees (Fig. 5a, tip-level PGLS  
346    for 5,675 extant non-marine species). We find that vagility is inversely related to tip DR such  
347    that lower vagility mammals have faster recent speciation rates, both overall and especially for  
348    herbivores ( $N = 1,637$ ) and carnivores ( $N = 1,565$ ) versus omnivores ( $N = 1,852$ ). For diurnality,  
349    daytime-active mammal species ( $N = 1,037$ ) also have faster recent speciation, especially for  
350    diurnal herbivores ( $N = 450$ ) as compared to omnivores ( $N = 478$ ) or carnivores ( $N = 109$ ).  
351    Lastly, species' absolute latitudinal centroids are unrelated to their tip DR values, either across  
352    all mammals or within trophic categories ( $P > 0.05$  for nearly all comparisons; Fig. 5a).  
353    Sensitivity analyses show that these tip-level PGLS results are robust to a range of alternatives  
354    (Fig. S9): using tip-dated mammal trees, using node density for recent speciation rates, removing  
355    taxonomically imputed species from completed trees, and removing island endemic species.

356       Phylogenetic path analyses of time-sliced clades and including species attributes confirm  
357    that the unique effects of tip DR mean on clade richness are consistently ~2x greater than crown  
358    age or tip DR skew (Fig. 5b), as found without considering attributes (Fig. 4a). We find that  
359    among 10-Ma clades, low vagility leads to faster rates of recent speciation (Fig. 5b), similar to  
360    the pattern seen at tree tips (Fig. 5a). Vagility effects are weaker among older clades, where  
361    vagility instead shows negative effects on tip DR skew (Fig. 5b), which is similar to the shared  
362    effects pattern seen in univariate PGLS (Fig. S10a). Diurnality shows positive effects on tip DR  
363    mean among 10-Ma clades, which is also analogous to the pattern at tree tips (Fig. 5a, b), and  
364    inconsistent effects on tip DR skew that are similar to the shared effects pattern (Fig. 5b; S10a).  
365    Latitude shows consistent, positive effects on tip DR mean among 10-Ma and older clades (Fig.  
366    5b), which contrasts with the lack of tip-level latitudinal effect (Fig. 5a, S9) and inconsistent

367 clade-level effects seen in univariate analyses (Fig. S10a). Both the time-sliced and taxon-based  
368 path analyses (Fig. S11) differ markedly from the univariate ecological analyses (Fig. S10),  
369 highlighting the importance of connecting both ecological and temporal factors in the  
370 investigation of uneven clade richness patterns. Sensitivity tests show that path analyses of time-  
371 sliced clades are robust to the exclusion of island endemics and imputed species, use of the tip-  
372 instead of node-dated backbone trees, and the use of node density instead of tip DR to  
373 summarize clade-level rate mean and skew (Fig. S12).

374



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**Fig. 5. Connecting ecological and temporal causes of rate and richness variation in the mammal timetree.** (a, top panels) Distribution of tip-level speciation rates (tip DR metric, shown is the harmonic mean of 10,000 trees) relative to per-species estimates of vagility (allometric index of maximum natal dispersal distance), diurnality (0=nocturnal or cathemeral,

380 1=diurnal), and absolute value of latitude (centroid of expert maps). Loess smoothing lines  
381 visualize general trends without considering phylogeny (blue, span=0.33). **(a)**, bottom panels  
382 Species-level effects considering phylogeny between tip DR and ecological attributes, as subset  
383 across trophic levels of herbivores, omnivores, and carnivores (univariate PGLS [phylogenetic  
384 generalized least squares] conducted on standardized predictors across 1,000 trees, showing 95%  
385 confidence intervals of slopes; colored if effects are significant, red for negative, blue for  
386 positive, else gray). **(b)** Phylogenetic path analysis conducted across time-sliced clades at 10-,  
387 30-, and 50-Ma intervals, delimited as illustrated in Fig. 2. Path thickness, color, and  
388 directionality denote median coefficients of model-averaged analyses across 1,000 trees (time-  
389 sliced clades of 10-, 30-, and 50-Ma proceed from left to right as labeled). The bottom panels  
390 provide per-estimate uncertainty across time slices (slope  $\pm$  SE), with non-zero estimates totaled  
391 as '#Signif.' in the right margin. Paths present in >500 trees are bolded and displayed in the  
392 upper path model diagram whereas other paths are dashed lines.  
393

## 394 DISCUSSION

395 Our investigations establish a primary role for ecological over temporal factors in causing  
396 uneven patterns of species richness in living mammals, suggesting that similar processes are  
397 likely also active in other branches of life. To reach this conclusion, we tested a hierarchical set  
398 of causal hypotheses (Fig. 1) for which types and speeds of macroevolutionary processes are  
399 occurring across phylogenetic levels, using an innovative time-slicing approach to define clades  
400 (Fig. 2). This framework enabled us to query evolutionary questions from shallow to deep levels  
401 of the extant timetree, recording macroevolutionary signals in recently diverged clades where  
402 inferences are more accurate and in more ancient clades where unobserved extinctions have  
403 accumulated (Kubo & Iwasa 1995; Marshall 2017; Louca & Pennell 2020; Upham *et al.* 2021).  
404 By connecting clade-level variation in ages and rates to species' ecological attributes—both  
405 intrinsic (vagility, diurnality) and extrinsic (latitude)—this framework also connects two ideas  
406 that are usually investigated separately: phylogenetic unevenness (PU) and the latitudinal  
407 diversity gradient (LDG). Thus, applying this causal time-slice framework quantifies the relative  
408 roles of the PU, LDG, and intrinsic trait-rate processes in producing extant mammal biodiversity.

409 Considering varying clade ages, rates, and attributes of mammals (Fig. 3), we found  
410 evidence that speciation rates explain more of the variation in among-clade species richness than  
411 do crown ages (Fig. 4). This result refutes the idea that ‘clocklike’ rates of speciation  
412 predominate (contra (Ricklefs 2003; Venditti *et al.* 2010; Hedges *et al.* 2015)). We then ask why  
413 some clades have faster rates of speciation than others, finding that vagility and diurnality are  
414 greater causes of recent speciation-rate variation than is latitude (Fig. 5). Low-vagility and  
415 daytime-active species of mammals show the fastest recent speciation rates (supports  $H_{A1}$  and  
416  $H_{A2}$ , respectively), which suggests respective roles for dispersal limitation leading to peripatric  
417 speciation (Jablonski 1986; Kisel & Barraclough 2010) and diurnal adaptations leading to  
418 ecological speciation via time partitioning (Gerkema *et al.* 2013; Maor *et al.* 2017). In contrast,  
419 latitude positively affects speciation rates as measured in older clades, suggesting that faster  
420 speciation in temperate clades—coupled with the extinction of many nascent lineages—has  
421 helped produce the LDG pattern of greater tropical than temperate richness (supports  $H_{A4}$  over  
422  $H_{A3}$ ). Thus, we here present evidence for contrasting modes of nonadaptive and adaptive  
423 speciation occurring in the same large radiation of mammals (*sensu* Czekanski-Moir & Rundell  
424 (2019)). We present arguments to justify these interpretations in the sections below.

425 **Time-sliced clades to test age and rate effects on richness.** Original claims that uneven  
426 trees are random outcomes of constant-rate diversification (Wright 1941) have been refuted by  
427 several authors (Blum & François 2006; Davies *et al.* 2011; Rabosky *et al.* 2012), but with others  
428 continuing to support constant rates of speciation, extinction, or both (Ricklefs 2003; Venditti *et*  
429 *al.* 2010; Hedges *et al.* 2015). Ranked taxa have been the typical units for testing the relative  
430 effects of ages and rates on species richness differences. However, high variance in the crown  
431 ages of same-rank taxa (e.g., Table S1) has yielded proposals for time-standardizing higher taxa

432 to make them comparably aged units (e.g., (Avise & Johns 1999; Dubois *et al.* 2021)). Time-  
433 standardization is both impractical due to regular phylogenetic flux (e.g., see (Franz *et al.* 2016,  
434 2019)) and would disrupt the core principle of prevailing usage in taxonomic classification  
435 (Simpson 1945). Thus, we here embrace an alternative strategy of using tree-wide time slices to  
436 delimit comparable units of phylogenetic analysis (Fig. 2). A key feature of time-sliced clades is  
437 that they are readily delimited across a *sample of trees*—rather than a single consensus tree—so  
438 that clade sets on each tree can be iteratively used in comparative analyses. Doing so propagates  
439 confidence in node ages and relationships into modeled predictor effects, avoiding problems  
440 from assuming that the analyzed tree is the true tree (Huelsenbeck *et al.* 2000).

441 Under this time-slicing approach, we find a greater role for clade-level speciation rates  
442 (tip DR mean and skew) than time since most recent common ancestor (crown age) as the direct  
443 cause of mammal richness unevenness (Fig. 4a; Table 1). However, this explanatory role for  
444 speciation-rate variation is also greater than expected if Mammalia-wide birth and death rates  
445 were constant through time and among clades. Hence, these findings support arguments that  
446 ‘ecology’ (broadly defined as including any non-temporal factor that alters macroevolutionary-  
447 rate processes, including sexual selection and geographic factors) is a greater cause of species  
448 richness variation than is ‘time’ (here as crown age; (Price *et al.* 2012; Castro-Insua *et al.* 2018;  
449 Machac *et al.* 2018)). However, the ‘ecology’ vs. ‘time’ dichotomy is misleading. Variation in  
450 both rate and age clearly contribute to richness.

451 The dual roles of rate and age variation are intuitively illustrated by separating out those  
452 10-Ma clades within 1 tree (Fig. 4b) and comparing subtrees of the most speciose clades (Fig.  
453 4c). A rapid proliferation of species-level branches is needed for a given clade to be among the  
454 most speciose of a particular time slice, but some speciose clades are also near the 10-Ma

455 maximum crown age for that example. Thus, while speciation-rate variation appears to cause the  
456 majority of the mammal PU pattern, it is only warranted to claim a greater *relative role* for  
457 ‘ecology’ over ‘time’ to the extent that rate-covarying ecological factors can also be identified.

458

459 **Table 1. Summary of findings.** Hypotheses refer to those in Fig. 1, and primary claims  
460 regarding how uneven clade richness ( $N$ ) is explained by crown ages ( $A$ ), speciation rates ( $S$ ),  
461 and/or species’ attributes (traits). Levels of support refer to findings in Fig. 4 ( $H_0$  vs.  $H_A$ ) and  
462 Fig. 5 ( $H_{A1-4}$ ), while explanations include the interpretations of *trait-associated lineage turnover*  
463 (TALT) and *key innovation / ecological opportunity* (KIEO) discussed in the main text.

Hypotheses	Primary claims	Levels of support	Explanation
$H_0$	$N \sim A$	rejected	less support than for $H_A$
$H_A$	$N \sim S$ and $S \sim$ traits	5-70 Ma clades	rates vary non-randomly
$H_{A1}$	$S \sim$ vagility (negative)	tips, 10 Ma clades	TALT
$H_{A2}$	$S \sim$ diurnality (positive)	tips, 10 Ma clades	KIEO
$H_{A3}$	$S \sim$ latitude (negative)	rejected	no support
$H_{A4}$	$S \sim$ latitude (positive)	10-, 30-, 50-Ma clades	TALT, but not at the tips

464

465 **How do ecological differences lead to uneven speciation rates and richness?** Given  
466 the known greater influence of unsampled extinction events at deeper levels (older time slices) of  
467 the mammal timetree (Upham *et al.* 2021), we wanted to test how trait-to-speciation rate  
468 relationships differ depending on phylogenetic depth. We find that tip-level rate relationships  
469 with vagility (negative,  $H_{A1}$ ) and diurnality (positive,  $H_{A2}$ ) are only recovered for species’ tip  
470 rates and shallow 10-Ma clade rates, and not among clades at 30- or 50-Ma time slices (Fig. 5).  
471 This finding can be explained in two main ways. Either (i) the trait-to-rate signatures exist in  
472 older clades, but are invisible in the timetree due to unsampled extinct lineages; or (ii) the trait  
473 originated more recently than the 30- or 50-Ma cutoff point, so that the trait-to-rate signatures do  
474 not exist among older clades (younger signatures are swamped out in old clades).

475 In the first explanation, fast trait-associated speciation at the level of tips and 10-Ma  
476 clades is linked to similarly rapid extinction (*trait-associated lineage turnover* model; TALT).

477 This view extends from models of ephemeral speciation, in which incipient species are  
478 frequently forming and going extinct (Mayr 1963; Stanley 1985; Rosenblum *et al.* 2012).  
479 However, here TALT further posits that lineage turnover is non-random with respect to certain  
480 trait or attribute states. In the second explanation, fast speciation among tips and young clades is  
481 a recent phenomenon caused by a trait adaptation that influences macroevolutionary rates (*key*  
482 *innovation / ecological opportunity* model; KIEO). This view stems from adaptive radiation  
483 theory, in which trait innovations can release certain lineages from competition, opening new  
484 ecological space that both promotes speciation and reduces extinction risk (Schluter 2000; Yoder  
485 *et al.* 2010; Gillespie *et al.* 2020). These contrasting TALT and KIEO views both posit that  
486 speciation rates have been higher in lineages with certain trait states, but they differ in their  
487 assumptions about unmeasured extinction rates (higher in TALT, lower in KIEO) and potentially  
488 the timing of historical onset in the trait-to-rate signatures (more recent onset of KIEO would  
489 explain the lack of older clade relationships, but TALT could have begun at any time). This  
490 TALT-or-KIEO framework therefore provides criteria for speculating about how species'  
491 attributes are most likely influencing tree-wide speciation rates (Table 1).

492 **Vagility and turnover.** The negative effects of vagility on tree-wide speciation rates  
493 indicate that low-vagility mammals—here proxied by smaller average body size and  
494 home/geographic ranges—are speciating faster than more vagile, wide-ranging species. The  
495 extremes of vagility within mammals help illustrate this dynamic, from low-vagility subterranean  
496 rodents like *Ctenomys* Tuco-Tucos—for which 68 range-restricted species are currently  
497 recognized ((MDD 2023); see Fig. 3, asterisk in clade 18 is the largest rate shift detected in  
498 Upham *et al.* (2021))—to the single species of highly vagile Mountain Lion, *Puma concolor*,  
499 which ranges from southern Alaska, USA to Tierra del Fuego, Argentina. This observed dynamic

500 is consistent with long-standing theory linking individual-level dispersal ability (i.e., vagility) to  
501 lineage-level dynamics of gene flow versus isolation among geographic populations (Mayr 1963;  
502 Jablonski 1986; Slatkin 1987; Bohonak 1999; Kisel & Barraclough 2010). In this theory, less  
503 frequent dispersal leads to less gene flow and more genetic isolation in peripheral populations,  
504 promoting peripatric speciation (as distinct from allopatric speciation given the latter's emphasis  
505 on physical barriers; (Mayr 1954; Carson & Templeton 1984)). Negative vagility-to-speciation  
506 rate relationships have been shown using the hand-wing index in birds (Claramunt *et al.* 2012;  
507 Sheard *et al.* 2020) and larval ecology in reef fishes (Riginos *et al.* 2014) and bivalves (Jablonski  
508 1986). However, in the TALT-or-KIEO framework, we suggest that low-vagility lineages are apt  
509 to also experience high rates of *extinction* and thus high turnover (i.e., TALT). This is because  
510 the small ranges of low-vagility incipient species should present greater stochastic risk (Jablonski  
511 1986; Kisel & Barraclough 2010), leading to the effects of vagility being erased at deeper levels  
512 of extant timetrees. If correct, the long branch leading to crown *Ctenomys* in the timetree (~13  
513 Ma; (Upham *et al.* 2019)) should be populated by many unsampled extinct taxa, a supposition  
514 that paleontological studies in fact support (6 genera of stem ctenomyids are known; (Verzi *et al.*  
515 2013; De Santi *et al.* 2021)). Thus, we interpret the short-lived effects of vagility on speciation  
516 rates—only recorded at levels of tip species and shallow clades before subsiding—as evidence  
517 for TALT, implying that many low-vagility lineages older than 10 Ma have already gone extinct.

518 How, then, to explain the high rates of speciation detected in *Pteropus* Flying Foxes,  
519 which are among the largest-bodied and most vagile of all bats? We suggest that the influence of  
520 vagility on mammal diversification might be non-linear as hypothesized in birds (e.g., humped  
521 (Mayr 1963) or sigmoidal (Claramunt *et al.* 2012)), in which case our results among shallow  
522 clades and tip species may only be capturing one side of the vagility-to-rate relationship. The 57

523 living species of *Pteropus* (MDD 2023) originate from second highest rate shift in Upham et al.  
524 (2021) (Fig. 3, asterisk in clade 12). Their long-distance dispersal ability (Oleksy *et al.* 2015) has  
525 enabled *Pteropus* to reach most Indo-Pacific islands, a pattern of diversification that best fits a  
526 founder-event model of speciation (Tsang *et al.* 2020) and highlights the additional role of  
527 landscape heterogeneity in determining the shape of vagility-to-speciation rate relationships.  
528 Wing morphology is known to contribute to bat vagility (Norberg & Rayner 1987), similar to the  
529 hand-wing index in birds (Sheard *et al.* 2020), but bat flying abilities are not explicitly modeled  
530 by our vagility index. Instead, we rely on allometric scaling relationships as a rough proxy of  
531 dispersal distances across all mammals (Sutherland *et al.* 2000; Whitmee & Orme 2013). No  
532 morphological trait has yet been identified as a Mammalia-wide vagility metric, but  
533 physiological scaling relationships may offer additional resolution (e.g., the maximal sustainable  
534 metabolic rate divided by the metabolic cost of transport; (Hillman *et al.* 2014)). Nonetheless,  
535 the vagility patterns described here are robust to multiple sensitivity tests (including the  
536 exclusion of island endemics; Fig. S9, S12), and thus convey reliable macroevolutionary  
537 signatures of mammalian space use relative to speciation rates.

538 **Diurnality and persistence.** In contrast, the KIEO perspective of adaptive diversification  
539 following a trait innovation best explains the observed pattern of faster speciation among diurnal  
540 tip species and 10-Ma clades and not thereafter (Fig. 5). The multiple independent origins of  
541 daytime activity started ~35 Ma after a ‘nocturnal bottleneck’ among K-Pg-surviving mammals  
542 (Gerkema *et al.* 2013; Maor *et al.* 2017). This pattern of diurnal-associated speciation has been  
543 described at broader phylogenetic scales across major extant lineages of tetrapods (family-level  
544 sampling for mammals (Anderson & Wiens 2017)), as well as for narrower radiations of diurnal  
545 primates (Magnuson-Ford & Otto 2012; Santini *et al.* 2015; Arbour & Santana 2017) and whales

546 (Morlon *et al.* 2011), but not before at the species level for all mammals. Fossil evidence  
547 suggests that non-mammalian synapsids may also have evolved diurnality (Angielczyk &  
548 Schmitz 2014), but those lineages are extinct and thus unobserved in the molecular timetree.

549 The coordinated eco-physiological changes required to evolve diurnality (e.g., eye  
550 pigments and corneal size (Gerkema *et al.* 2013)) have presumably carried with them fitness  
551 benefits from access to novel resources in the daytime niche. In this context, we posit that  
552 evolving diurnality has led to differential lineage persistence (i.e., low rates of species turnover =  
553 low extinction / high or moderate speciation) relative to nocturnality because novel niche  
554 resources have presumably improved organismal fitness (Yoder *et al.* 2010; Gerkema *et al.*  
555 2013). The KIEO model implies that persistence-driven speciation—i.e., speciation rates that  
556 appear high in extant timetrees mainly because extinction rates are reduced—underlies the  
557 diurnal rate signature, in contrast to the turnover-driven speciation which we suggest is  
558 associated with low-vagility lineages and high latitudes. Interestingly, the acquisition of diurnal  
559 behavior has likely evolved and persisted at least ten times in crown mammals (Maor *et al.*  
560 2017), from diurnal primates and squirrels to elephant shrews. However, there appears to be no  
561 characteristic secondary axis of resource specialization that is common across these groups (e.g.,  
562 diet or locomotor diversity); rather, allopatric/peripatric speciation—and persistence of those  
563 isolated diurnal lineages—is likely the secondary driver of diurnal diversity (e.g., (Zelditch *et al.*  
564 2015)). Overall, we show that faster diurnal than nocturnal speciation is a consistent signature  
565 among recent lineages of mammals, and suggest that it is caused by greater persistence (lower  
566 turnover) of lineages due to ecological opportunity in new daytime niches.

567 **Latitude and uneven clade-level speciation.** Latitude-related hypotheses of climatic  
568 stability accelerating local adaptation and low-latitude speciation ( $H_{A3}$ ; (Mittelbach *et al.* 2007;

569 Etienne *et al.* 2019)) or climatic instability spurring isolation and high-latitude speciation (H<sub>A4</sub>;  
570 (Cutter & Gray 2016; Schluter & Pennell 2017)) align with the aforementioned KIEO or TALT  
571 models of speciation, respectively. However, tropical net diversification must have been greater  
572 than at temperate latitudes to produce the LDG. We find no consistent influence of latitude upon  
573 tip-level speciation rates (Fig. 5a, S9), contrary to evidence from marine fishes (Rabosky *et al.*  
574 2018) and angiosperms (Igea & Tanentzap 2020; Sun *et al.* 2020) that supported negative  
575 latitude-to-tip speciation rate relationships. Instead, we find only a clade-level inverse gradient in  
576 mammals: positive latitudinal effects on speciation rates are increasingly strong among 10-, 30-,  
577 and 50-Ma clades (Fig. 5b, S12) as well as among taxonomic orders (Fig. S11b). However, those  
578 clade-level latitudinal patterns are apparent only in multivariate path analyses (Fig. S10). Thus,  
579 our results bring nuance to the extant timetree-based perspective on the mammal LDG by  
580 showing that (i) the negative latitude-to-rate pattern is mainly present at deeper timetree levels  
581 (older clades); (ii) the pattern may be an artifact of unobserved extinctions biasing speciation-  
582 rate estimates in older clades; and (iii) whether artifact or not, the pattern is hidden unless  
583 covariation in other ecological causes of uneven speciation rates is considered.

584 Our latitudinal results compare to similarly mixed findings from other studies of birds  
585 and mammals. In timetrees of extant birds, latitude-to-tip rate effects are also absent at the global  
586 level (Jetz *et al.* 2012; Rabosky *et al.* 2015), but New World suboscines show faster temperate  
587 than tropical speciation (Kennedy *et al.* 2014; Harvey *et al.* 2020). New World sister species of  
588 birds and mammals similarly show higher turnover rates at temperate than tropical latitudes  
589 using mitochondrial DNA clocks (Weir & Schluter 2007; Schluter & Pennell 2017), but reliance  
590 on molecular clocks is more questionable for mammals than birds given their greater breadth of  
591 generation times (Nabholz *et al.* 2009). Other studies have shown inconsistent results with a

592 variety of methods, including: (i) higher mammal subspecies counts in harsher temperate  
593 environments ((Botero *et al.* 2014); but the opposite pattern in birds (Martin & Tewksbury  
594 2008)); (ii) no latitude-to-rate effects at the genus level (Soria-Carrasco & Castresana 2012)  
595 using consensus ages from the Bininda-Emonds *et al.* (2007) supertree of mammals; and (iii)  
596 greater rates of temperate extinction and tropical speciation (Rolland *et al.* 2014) using a  
597 modified version of that same mammal supertree. Here, using credible sets of mammal timetrees  
598 from the supermatrix-based Bayesian study of Upham *et al.* (2019) we find faster speciation rates  
599 in temperate than tropical clades, but weak relationships among tip species and shallow clades  
600 where speciation rates are most confidently inferred (Louca & Pennell 2020; Upham *et al.* 2021).

601 We speculate that the extinction-filtered lens of extant mammal diversity retains true  
602 signals of faster temperate than tropical lineage turnover, but that greater paleo-to-neontological  
603 synthesis will be needed to corroborate this pattern. Our use of species' geographic range  
604 centroid distance from the equator is likely not capturing dependencies on environmental  
605 stability for widespread species with postglacial range expansions (e.g., red deer (Doan *et al.*  
606 2022)). However, the latitudinal 'essence' of a given clade should be summarized increasingly  
607 well at deeper timetree levels by averaging the values of more modern species. This may be why  
608 we found the strongest latitude-to-rate patterns among 50 Ma clades and taxonomic orders. The  
609 'clades only' pattern of faster high-latitude speciation is also biologically feasible if (i) high-  
610 latitude glaciations during the last ~4 Ma (Mudelsee & Raymo 2005; Clague *et al.* 2020) led to a  
611 pulse of mammal extinctions, and (ii) those extinctions were phylogenetically dispersed enough  
612 to erase only the tip-level portion of the latitude-to-speciation rate effect. Under that scenario,  
613 clade-level signatures of faster temperate speciation are possible as long as temperate lineages  
614 were not fully extirpated during climatic oscillations (e.g., persisting in glacial refugia (Hewitt

615 2000)). This scenario is supported by the North American fossil record, in which mammal  
616 richness and latitude are not strongly correlated until ~4 Ma (Marcot *et al.* 2016), as well as  
617 fossil evidence that high-latitude extinctions steepened the LDG for bivalves and reptiles  
618 (Jablonski *et al.* 2016; Meseguer & Condamine 2020). Overall, we contend that the traditionally  
619 invoked ‘cradle’ (higher tropical speciation) and ‘museum’ (lower tropical extinction (Mittelbach  
620 *et al.* 2007)) should instead re-focus upon the *turnover ratio* of those processes, more similar to  
621 Stebbens’ (1974) original meaning, as was emphasized by Vasconcelos *et al.* (2022). Testing  
622 whether mammal lineages have ‘cycled’ faster (i.e., shorter durations) outside than inside the  
623 tropics is the key question to resolve.

624

## 625 CONCLUSION

626 By taking a broad view on the evolutionary history of Mammalia, from recent species’  
627 tips to ancient clade-level processes, we uncover commonalities in the ecological causes of  
628 uneven species diversification over geography as well as phylogeny. We provide evidence that  
629 ecological factors have had non-random influences on mammalian macroevolutionary rates: far  
630 from stochastic, speciation rates are likely higher in clades that contain more low-vagility,  
631 diurnal, and temperate-distributed species. Ecologically linked speciation rates have, in turn,  
632 driven the majority of the PU pattern of uneven among-clade species richness. The LDG is not  
633 separate from this PU pattern, but rather interconnected with it—both types of unevenness share  
634 underlying causes, both direct (macroevolutionary rates and ages) and indirect (factors affecting  
635 gene flow, isolation, and adaptation). Species’ ecological attributes appear to provide the most  
636 reliable predictor for whether a given lineage will tend to speciate, go extinct, or persist in the  
637 near future (i.e., ‘species selection’ *sensu* Jablonski (2008)). Thus, the extent to which we can

638 reliably unite the ecological, taxonomic, and phylogenetic knowledge of all mammal species—  
639 over 40% of which has only been described since 1993 (Burgin *et al.* 2018; MDD 2023)—is  
640 likely to dictate our ability to determine which aspects of extinction risk are inherent to species  
641 versus external and human-caused (Pyron & Pennell 2022).

642 Overall, we hypothesize that two main macroevolutionary processes are at work in  
643 mammals. First, we identify rate signatures that are consistent with turnover-driven speciation  
644 (TALT model) at shallow levels of the timetree due to greater geographic isolation among low-  
645 vagility species. Second, we hypothesize that persistence-driven speciation (KIEO model) is  
646 occurring in diurnal lineages because of access to new daytime niches and release from nocturnal  
647 competitors. We speculate different explanations for the same speciation signatures due to the  
648 differing circumstantial evidence of vagility acting on space use and diurnality acting on  
649 resource use. However, the value of applying the TALT-or-KIEO framework to our extant  
650 timetree-based analyses lies in it generating plausible hypotheses for more direct future  
651 evaluation using fossil-based extinction rates and species attributes. Developing physiological or  
652 skeletal metrics of mammalian vagility (as opposed to the allometric index used here) along with  
653 cranial correlates of diurnal vision (e.g., (Angielczyk & Schmitz 2014)) will be critical for  
654 assessing whether the relative frequency of turnover- and persistence-driven speciation has  
655 changed from fossil to modern ecosystems. Connecting evolutionary levels from individuals and  
656 species to clades appears promising for explaining uneven diversification across the tree of life.  
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