Macroevolutionary diversification rates show time dependency

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For centuries, biologists have been captivated by the vast disparity in species richness between different groups of organisms. Variation in diversity is widely attributed to differences between groups in how fast they speciate or go extinct. Such macroevolutionary rates have been estimated for thousands of groups and have been correlated with an incredible variety of organismal traits. Here we analyze a large collection of phylogenetic trees and fossil time series and describe a hidden generality among these seemingly idiosyncratic results: speciation and extinction rates follow a scaling law in which both depend on the age of the group in which they are measured, with the fastest rates in the youngest clades. Using a series of simulations and sensitivity analyses, we demonstrate that the time dependency is unlikely to be a result of simple statistical artifacts. As such, this time scaling is likely a genuine feature of the tree of life, hinting that the dynamics of biodiversity over deep time may be driven in part by surprisingly simple and general principles.

phylogenetics | paleobiology | macroevolution | speciation | extinction

Although once controversial, it is now widely accepted that both the traits of organisms and the environments in which they live can influence the pace of evolution of life on Earth (1–3). In particular, there is tremendous variation between groups of organisms in the rate at which species form and go extinct. This variation is reflected both in the wildly uneven diversity of clades in the fossil record and in the imbalanced shape of the tree of life (2–5). Our estimates of speciation and extinction rates vary by orders of magnitude when comparing different clades, locations, or time intervals.

In turn, researchers have suggested a tremendous array of mechanisms that may have accelerated or slowed the accumulation of biodiversity. These mechanisms include aspects of organisms, such as color polymorphism (6), body size (7), and many others, and of the environment, including geographic region (8, 9), temperature (10), and the interactions between the two (11). Taken as a whole, this growing body of work implicates a wide variety of factors that influence speciation and/or extinction rates and suggests that the growth of the tree of life has been largely idiosyncratic.

Despite the rapid expansion of research on variation in speciation and extinction rates, few synthetic studies have been attempted. Consequently, we know little about whether or not there are common factors that predict speciation and extinction rates across diverse taxa (2). One hurdle to such synthesis is that studies, especially those using the tree of life, often focus more on relative than absolute diversification rates. That is, studies are focused more on whether speciation or extinction rates are higher in one part of a phylogenetic tree than in another part, rather than attempting to estimate those rates in absolute terms. This makes comparisons across studies difficult or impossible.

Another compelling reason to gather and compare estimates of speciation and extinction rates across clades is the potential for scale-dependence. In all other instances when macroevolutionary rates have been compared, these rates have shown a pattern of time dependence, with the fastest rates estimated over the shortest time scales. This time scale dependence is apparent in rates of molecular (12) and trait evolution (13, 14) and has even been observed when estimating long-term rates of sedimentation (15). The prevalence of time scaling of rate estimates in other types of data, along with previous hints of a possible similar pattern in speciation rates (16–20), suggest that a broader comparison is needed. Here we explore the time scaling of diversification rates using both phylogenetic data from the tree of life and paleobiological data from the fossil record and find evidence that there are indeed general scaling laws that govern macroevolutionary dynamics of speciation and extinction.

Results and Discussion

Using a Bayesian approach that allows for heterogeneity across the phylogeny (21), we estimated speciation and extinction rates across 104 previously published time-calibrated molecular phylogenies of multicellular organisms that collectively contain 25,864 terminal branches (*SI Appendix*, Table S1). As many other studies have reported, we found substantial variation in both speciation (Fig. 1*A*) and extinction rates (*SI Appendix*, Fig. S5) across groups, ranging from 0.02 to 1.54 speciation events per lineage per million years—a two-orders of magnitude difference (16, 22–25). Remarkably, a substantial amount of this variation in rates can be explained simply by time alone. We found a strong negative relationship between the mean rates of both speciation and extinction and the age of the most recent common ancestor of a group (regression on speciation rates: $\beta = -0.542$; $P < 0.001$; $R^2 = 0.339$; on extinction rates: $\beta = -0.548$; $P < 0.001$;
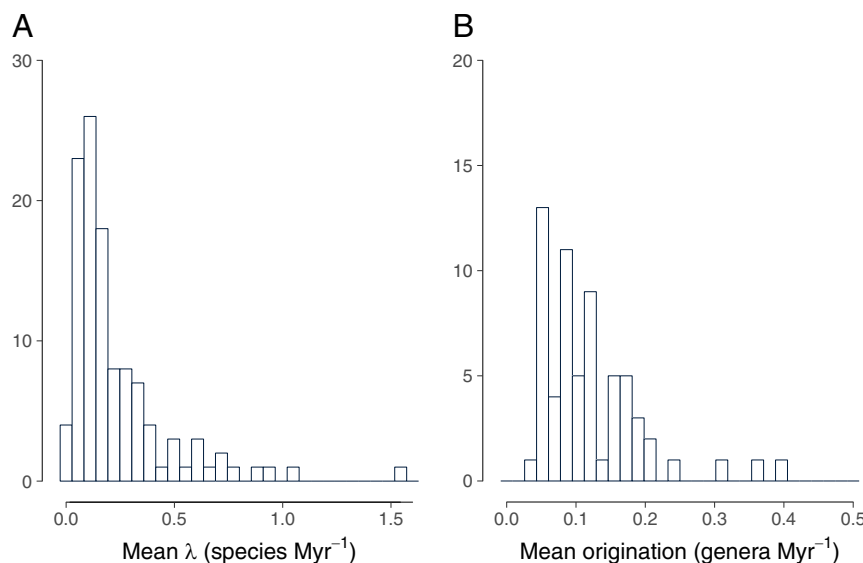
EVOLUTION

Fig. 1. Histogram of mean speciation (λ) and origination rates. (*A*) The lowest speciation rate is for the fern family Matoniaceae (0.02), and the highest is for the subfamily Lobelioidae (1.54). (*B*) The lowest origination rate is for the order Pinales (0.02), and the highest is for the order Cingulata (0.34). Note that the axes have different magnitudes.

$R^2 = 0.155$) (Fig. 2 *A* and *B*). In general, regardless of the taxonomic identity, ecological characteristics, or biogeographic distribution of the group, younger clades appeared to be both speciating and going extinct faster than older groups.

We also recovered this same scaling pattern using an independent dataset of fossil time series, demonstrating that the time dependency of diversification rates is a general evolutionary phenomenon and not simply a consequence of using extant-only data. We estimated origination and extinction rates from a curated set of fossil time series comprising 17 orders of mammals, 22 orders of plants, and 51 orders of marine animals (mostly invertebrates), containing representatives from 6,144 genera (*SI Appendix*, Table S2), using the widely used per capita method (25). For fossil data, we measured time as the duration over which a clade of fossil organisms existed and analyzed the formation and extinction of genera rather than species. We found that both origination (β = −0.227; *P* < 0.001; $R^2 = 0.152$; Fig. 2*C*) and extinction (β = −0.245; *P* < 0.01; $R^2 = 0.126$; Fig. 2*D*) rates of fossil genera were highly dependent on duration.

This result has important consequences for how we measure and interpret rates of diversification. First, this implies that it is not informative to use constant-rate estimators to compare diversification rates of clades of different ages (e.g., refs. 16 and 26); this point has been made previously (27, 28), but our results provide a particularly clear demonstration that the constant-rate approach is inherently problematic. In recent years, there has been a great deal of progress toward more complex models of diversification that allow for heterogeneity in the process through time and across groups (21, 22, 29). In principle, such variable-process models can alleviate these concerns; if young clades are indeed diversifying rapidly, then the methods will recover this pattern, and the analyses will reveal a nested series of upshifts in the rate of diversification (e.g., ref. 30). In this sense, state-of-the-art methods for measuring diversification rate changes are working exactly as designed. However, our results do call into question how we interpret such results. Typically, researchers are not content to merely describe the pattern of rate variation, but rather wish to attribute variation in rates to differences in the organisms or the environments in which they are diversifying. If young groups have faster diversification rates in general, then nearly any feature that has recently evolved or any

environment that organisms have recently colonized will likely be associated with an increase in diversification. It is beyond the scope of the present article to discuss what precisely constitutes evidence of causality in macroevolutionary studies, but we suggest that it is certainly not a coincidence that many of the regions of the world commonly recognized as hotspots of diversification (at least over the past several million years) are also precisely those regions that harbor young groups of organisms, such as the Páramo of the Andes (31), oceanic islands (32), and polar seas (23).

Potential causes of this ubiquitous pattern fall into two main categories. First, our results may be statistically biased; the underlying process of diversification may be consistent with that assumed by diversification models with constant rates, but our statistical methods are biased toward recovering time dependence. Second, our results may reflect biological generality; the true dynamics of diversification over macroevolutionary time scales show patterns that are incompletely described by current models and theories and lead to time dependence in rate estimates. Using a series of simulations and sensitivity analyses, we show that statistical biases are unlikely to account for the entirety of our pattern. We present results investigating a variety of potential artifacts, including bias in the rate estimators, incomplete sampling, errors in divergence time estimation, and acquisition bias (known as the "push of the past" in the macroevolutionary literature; ref. 33), all of which have been invoked when this pattern was previously documented by biologists in studies of individual groups (16–18, 20, 28, 34, 35). While all of these may generate a negative relationship between rate and time, none of the artifactual explanations that we considered can fully account for the patterns we found in both phylogenetic and fossil time series data.

We therefore suggest that the time dependency of rates is indeed a real phenomenon that requires a biological explanation. Perhaps the simplest, and easiest to dismiss, explanation is that there has been a true, secular increase in rates of diversification over time, such that globally, macroevolution is faster now than it has ever been in the past. We fit variable-rate models to each molecular phylogeny individually, but find no evidence of widespread speedups within groups (Fig. 3*A*). While we do find support for shifts in diversification rates within trees (*SI Appendix*, Fig. S1), there is no clear temporal trend. This is inconsistent with
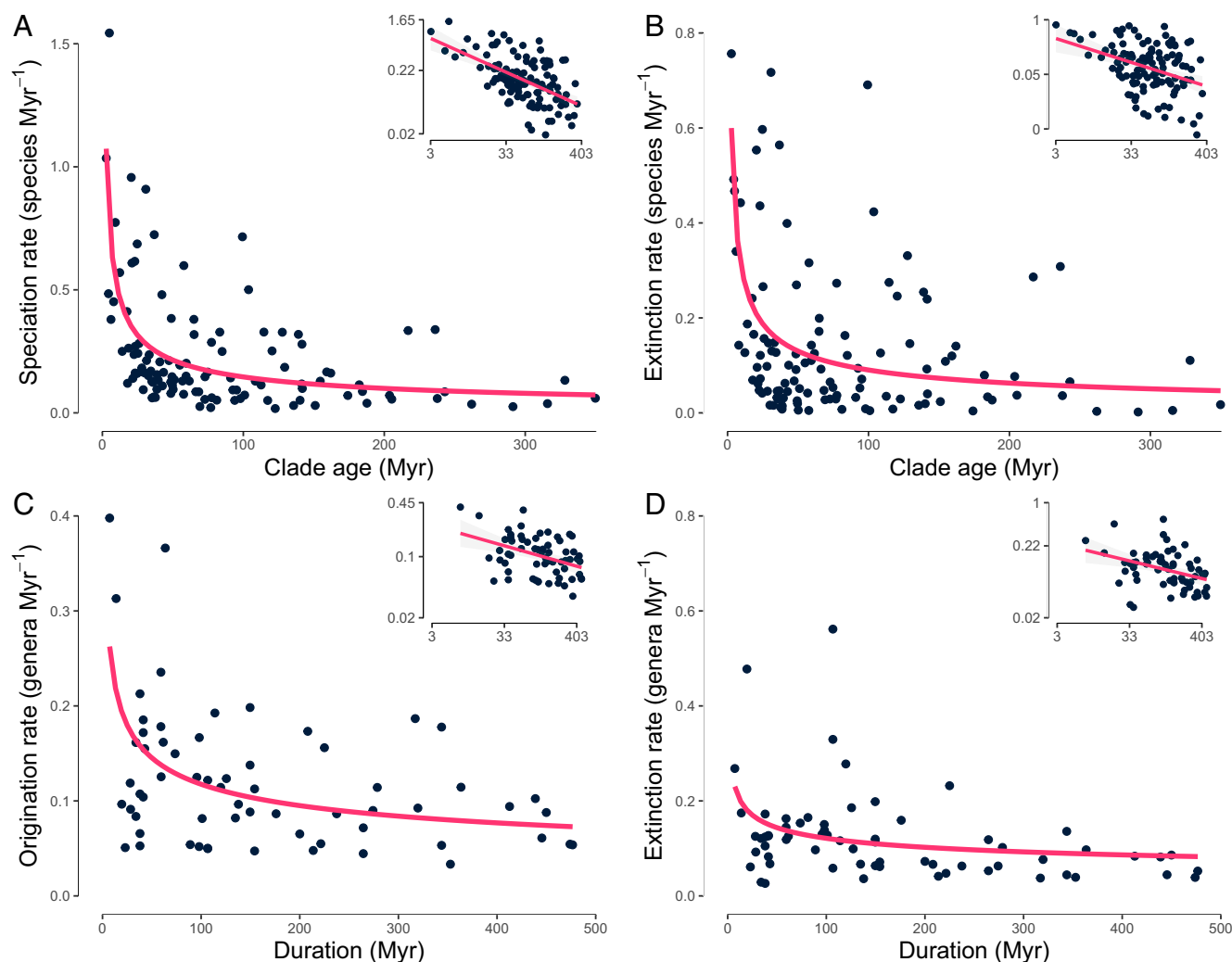
Fig. 2. Time-dependency of macroevolutionary rates. (*A* and *B*) Mean per-lineage speciation (*A*) and extinction (*B*) rates estimated from 104 molecular phylogenies plotted against the age of the most recent common ancestor of each clade. (*C* and *D*) Mean rates of origination and extinction of genera estimated from fossil time series from 16 orders of mammals and 24 orders of plants against the total duration of the group's existence. (*Insets*) The relationships on a log-log scale.

the idea of a global speedup. Consistent with previous studies (34), we do not see an increase in rates over time for fossil data (Fig. 3*B*). Furthermore, previous studies have shown that heterogeneity in rates across groups cannot generate the patterns that we observe under realistic diversification scenarios (28).

The lack of evidence for temporal trends within groups also does not support another commonly invoked explanation for the time dependency of rates—that diversity dynamics are shaped by ecological limits (4, 27). If niche or geographic space were constrained, then diversification should slow as diversity accumulates; this decoupling of clade age and size would then lead directly to time-dependent rates of diversification (28). In this scenario, younger clades are growing nearly exponentially while older clades have reached stationarity, and thus the average rates of evolution would appear to be much faster in younger clades relative to older clades (19). This explanation predicts that slowdowns in rates should be ubiquitously observed within clades, which, as stated above, is incompatible with our findings. Moreover, the signal for a slowdown should be most apparent in older clades, which is also not apparent in either phylogenetic or paleobiological data (Fig. 3 *A* and *B*), although we acknowledge that such a signal is particularly difficult to detect in older clades,

as it may be eroded by subsequent diversification (36). Furthermore, such clade-based explanations depend critically on the premise that higher taxonomic groups (e.g., families, orders) are meaningful units for diversification analyses. This may be because taxonomists have actually identified true evolutionary lineages (37) with dynamics of their own, such as those envisioned by models of taxon cycles (38, 39) or interclade competition (40). It might also be the case that taxonomic practice is biased in some as-yet unknown way (28). We can evaluate the premise that named clades are special by subsampling our data. Using recently published megaphylogenies of birds (32), ferns (41), and flowering plants (42), we tested whether the slope of the time dependency of diversification rates differs between named clades and clades descending from randomly chosen nodes of similar age. We find that it does not (Fig. 4), suggesting that clade-specific ecological limits are unlikely to satisfactorily explain our results.

We favor another explanation, that speciation and extinction events are clustered together in time, with these clusters interspersed among long periods during which species neither form nor go extinct. For inspiration, we turn to a result, strikingly similar to our own, from an entirely different field. Sadler (15) demonstrated that estimated rates of sediment deposition and
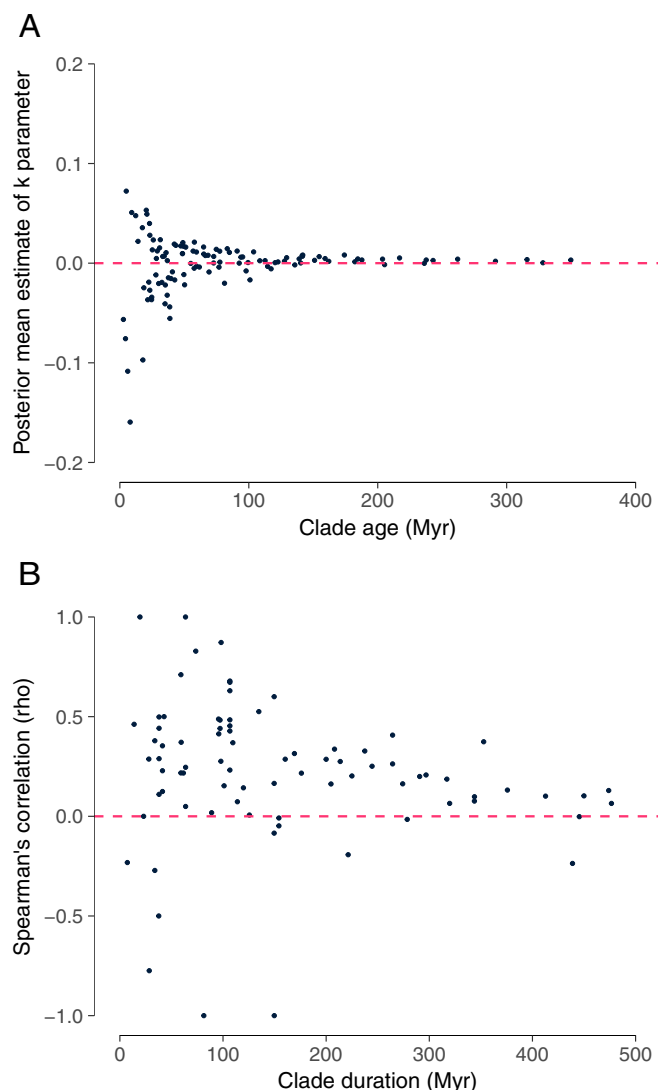
A

B

Fig. 3. Diversification trends through time. (*A*) Temporal change parameters (*k*) estimated for 104 empirical phylogenies as a function of clade age. Each value of *k* is simply the mean of the marginal posterior distribution of temporal "rate shift" parameters estimated using BAMM; positive values indicate a speed up toward the present, and negative values indicate a slowdown toward the present. (*B*) For each fossil dataset, we calculated the Spearman correlation between the diversification rate estimated from each time interval and the interval's ordination in the series. When the correlation is positive, diversification rates later in the series are higher, and when the correlation is negative, diversification rates early in the series are higher. This correlation coefficient is plotted against the total duration of the clade. Neither the *k* parameter nor Spearman correlation coefficients decrease with time. Furthermore, they do not deviate from zero with clade age, suggesting that there is no strong evidence for diversity dependence over time.

erosion are also negatively correlated with the time interval over which they are estimated, a geologic phenomenon known as the "Sadler effect." This time dependency likely results from the unevenness of sedimentation; geological history is dominated by long hiatuses with no or negative sedimentation (i.e., erosion) punctuated by brief periods during which large amounts of sedimentation accumulate (43). Under such a scenario, the mean rate tends to decrease the farther back in time one looks, owing to the fact that an increasing number of hiatuses are observed.

We believe that Sadler's rationale could apply to diversification rates as well. There is evidence that extinction events recorded in

the fossil record are much more clustered in space and time than would be predicted under gradualism (44, 45). Indeed, many of the boundaries of the geological time scale are defined by large-scale faunal and floral turnover. The most widely known example of this is undoubtedly the mass extinction event that separates the Cretaceous from the Paleogene. There is abundant evidence, including our results, that origination and extinction rates tend to be highly correlated over macroevolutionary time and concentrated in clades with high volatility (34, 46). We expect that if extinction events are concentrated in time, then speciation rates will be as well.

We are not the first to propose that pulses of diversification may affect the interpretation of rates estimated based on the assumption that diversity accumulates gradually; paleobiologists have found that short geological intervals tend to show higher rates than longer intervals and have argued that this is caused by the concentration of events at the interval boundaries (44, 45). As we noted above, some phylogenetic analyses have uncovered similar patterns (16–20, 35); however, explanations favored by previous work do not explain the entirety of our observation of the apparent time dependency seen across both phylogenetic trees and fossils.

Some researchers have suggested that clustered speciation and extinction events observed in the fossil record may be due to large-scale, and possibly regular, climatic fluctuations (47) or to an emergent property of complex ecosystems (48). Perhaps a simpler explanation is that species evolve and diversify over a complex geographic landscape, and that successful speciation and persistence seem to require the confluence of multiple factors at the right place and time (49). Most speciation events likely occur in lineages with limited or fragmented ranges, but the resulting species are also highly prone to go extinct before they can leave their mark on macroevolutionary history (50). This verbal model shares much in common with Futuyma's model of ephemeral divergence (51), which itself can be invoked to explain the long-observed negative time dependency of rates of phenotypic evolution (13, 14) and potentially could explain a similar pattern in rates of molecular evolution (12). This scenario, which is consistent with our results, would imply that the scaling of rates of sedimentation, phenotypic divergence, molecular evolution, and diversification with time all might share a common mechanism.

We acknowledge that much more work, both theoretical and empirical, is needed to fully comprehend why diversification rates scale with time, and understand that this research may or may not support our proposed explanation. In either case, we hope that our results call biologists' attention to surprising regularities in the tree of life. Long before well-resolved and robustly dated phylogenies were available for most groups, biologists noted that trees had stereotypical features (5, 52, 53). Macroevolutionary biologists have tended to focus their attention on the particular innovations that may have spurred radiations in particular groups at particular times; a far less well-explored—and completely open—question is why, despite all of the idiosyncrasies and contingencies inherent in the process of diversification, phylogenies from across the tree of life look so remarkably similar.

Methods

Phylogenetic Collection and Data Cleaning. We collected and curated 104 time-calibrated species-level phylogenies of multicellular organisms from published articles and from data repositories. These trees were fully bifurcating and ultrametric and contained more than seven tips and at least 1% of the clade's total richness (*SI Appendix*, Tables S1 and S3). Trees were checked to ensure that branch lengths were in the millions of years (54–57). For each group, the total number of extant species was compiled from the literature.

Phylogenetic Diversification Analysis and Regressions. Diversification rates were estimated for each phylogeny using BAMM with default priors and including sampling fraction (58). From the posterior distribution, we calculated the mean and variance in speciation and extinction rates across all branches, as
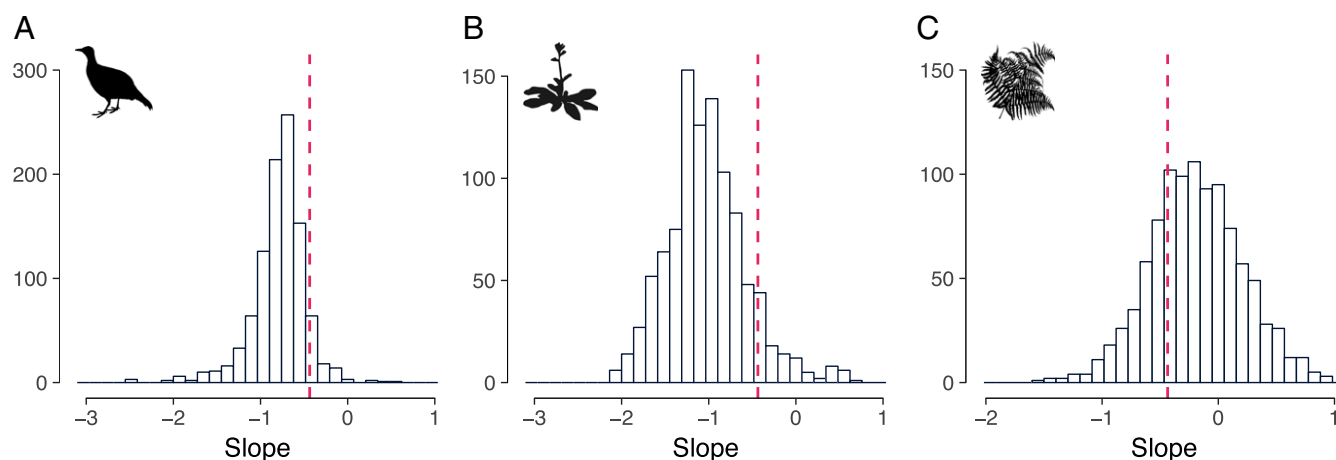
Fig. 4. The random clade selection effect. Empirical slope of diversification rate as a function of time (dashed line) compared with the slope's distribution from randomly sampled clades. In all cases, our empirical estimates lay within the negative slopes distribution from randomly drawn clades, showing that our results are not a sampling artifact due to taxonomic delimitation. (*A*) Bird families. (*B*) Angiosperm orders. (*C*) Fern families.

well as the frequency of shifts. Model mixing and convergence were assessed by examining the effective sample size in CODA (59). To calculate the k parameter, we reran BAMM on each phylogenetic dataset, permitting only a single diversification regime per tree (*SI Appendix, Methods*). We fit linear models between mean and variance rates on a log-log scale compared with crown ages (estimated from the tree heights). We observed qualitatively identical results when fitting the same linear regressions using the maximum likelihood estimates (MLEs) of the rates and the DR statistic (32).

Phylogenetic Simulations. To explore the effect of the "push of the past" (i.e., conditioning on the survival of the clade to the present), we simulated trees with at least six taxa and the same ages as our empirical dataset. We used the diversification parameters from the oldest groups (>150 My), where the curve between rate and age levels off. We repeated this procedure by setting $\mu = 0.5\lambda$ to acknowledge the difficulty in estimating extinction rates and their influence in macroevolutionary dynamics. We repeated both procedures 1,000 times.

To evaluate whether the observed time dependency was a consequence of using named higher taxonomic groups, we developed a novel algorithm for randomly sampling nodes from a tree given the age distribution of a set of named nodes and a tolerance. Using this algorithm, we were able to compare a temporally equivalent set of unnamed random clades with our empirical tree results. We computed the mean MLE for diversification rates of named clades (across several ranks) from megaphylogenies and to the random clades with equivalent ages. We repeated the latter process 1,000 times.

The reconstructed trees usually represented a small proportion of a group's entire diversity, making diversification analysis sensitive to this sampling fraction. This is especially relevant for our purposes, as older groups tend to be more sparsely sampled than younger ones. Even though previous studies have shown that birth-death estimations are consistent when the sampling fraction is provided (60, 61), we wanted to rule out its effect. We simulated a tree corresponding to each tree in the dataset based on empirical ages, mean rates from phylogenies older than 150 My, and sampling fractions using the TreeSim R package (62). We then reestimated the MLE using the R package diversitree (63), repeating this procedure 1,000 times.

Errors in ages of young clades can overestimate diversification rates, leading to a negative relationship between rate and time. Given the heterogeneous nature of the trees that we used, it was infeasible to include uncertainty in

branching times (i.e., from a posterior distribution or set of bootstraps). As an alternative, we explored this possibility using simulations; we repeated the simulations as in the push of the past section but this time added an error to clade ages. To each age, we drew a percentage error from a uniform distribution that modified the branch lengths (by addition or subtraction). Simulations were carried out with maximum error values ranging from 10% to 90%. In all of the simulated cases mentioned, we estimated the slope of the log(speciation rate) ~ log(crown age) regression resulting from each of the trees and then compared these with our empirically estimated slope.

Fossil Collection and Cleaning Data. We collected and curated fossil information on the first and last appearances of each genus for 39 orders of mammals (17) and plants (22) from online databases. Each order included in our analyses consisted of at least 10 genera, each genus had at least two occurrences, and only occurrences assigned to a unique geological stage were considered. We also included 51 orders, each with a minimum of 10 genera, from Sepkoski's marine animal compendium. In total, our dataset consists of 6,144 genera distributed across 90 orders that were analyzed individually (*SI Appendix,* Table S2).

Fossil Diversification Analysis and Regressions. Diversification rates were estimated using Foote's per capita method (25), which uses the first and last occurrences of the genera to estimate the rates of origination (i.e., rate of appearance of new genera) and extinction for each geological stage. We divided the diversification rate (i.e., origination minus extinction) by the duration of each interval, then estimated the average diversification rate for the orders. We also estimated the correlation between the rate estimates and the time bin ordination. We fit linear models on a log-log scale between average diversification rate and clade duration.

1. Jablonski D (2008) Species selection: Theory and data. *Annu Rev Ecol Evol Syst* 39:501–524.
2. Wiens JJ (2017) What explains patterns of biodiversity across the Tree of Life? *BioEssays* 39:1600128.
3. Schluter D, Pennell MW (2017) Speciation gradients and the distribution of biodiversity. *Nature* 546:48–55.
4. Sepkoski JJ (1984) A kinetic model of Phanerozoic taxonomic diversity, III: Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–267.
5. Mooers AO, Heard SB (1997) Inferring evolutionary process from phylogenetic tree shape. *Q Rev Biol* 72:31–54.
6. Hugall AF, Stuart-Fox D (2012) Accelerated speciation in colour-polymorphic birds. *Nature* 485:631–634.
7. Clauset A, Erwin DH (2008) The evolution and distribution of species body size. *Science* 321:399–401.
8. Weir JT, Schluter D (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315:1574–1576.
9. Rolland J, Condamine FL, Jiguet F, Morlon H (2014) Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol* 12:e1001775.
10. Allen AP, Gillooly JF (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol Lett* 9:947–954.
11. Wagner CE, Harmon LJ, Seehausen O (2012) Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487:366–369.
12. Ho SYW, et al. (2011) Time-dependent rates of molecular evolution. *Mol Ecol* 20:3087–3101.
13. Gingerich PD (1983) Rates of evolution: Effects of time and temporal scaling. *Science* 222:159–161.

14. Uyeda JC, Hansen TF, Arnold SJ, Pienaar J (2011) The million-year wait for macro-evolutionary bursts. *Proc Natl Acad Sci USA* 108:15908–15913.
15. Sadler PM (1981) Sediment accumulation rates and the completeness of stratigraphic sections. *J Geol* 89:569–584.
16. Magallón S, Sanderson MJ (2001) Absolute diversification rates in angiosperm clades. *Evolution* 55:1762–1780.
17. McPeek MA, Brown JM (2007) Clade age and not diversification rate explains species richness among animal taxa. *Am Nat* 169:E97–E106.
18. Ricklefs RE (2006) Global variation in the diversification rate of passerine birds. *Ecology* 87:2468–2478.
19. Linder HP (2008) Plant species radiations: Where, when, why? *Philos Trans R Soc Lond B Biol Sci* 363:3097–3105.
20. Marin J, Hedges SB (2018) Undersampling genomes has biased time and rate esti-mates throughout the tree of life. *Mol Biol Evol* 35:2077–2084.
21. Rabosky DL (2014) Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS One* 9:e89543.
22. Alfaro ME, et al. (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc Natl Acad Sci USA* 106:13410–13414.
23. Rabosky DL, et al. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* 559:392–395.
24. Sepkoski JJ, Jr (1998) Rates of speciation in the fossil record. *Philos Trans R Soc Lond B Biol Sci* 353:315–326.
25. Foote M (2000) Origination and extinction components of taxonomic diversity: General problems. *Paleobiology* 26:74–102.
26. Scholl JP, Wiens JJ (2016) Diversification rates and species richness across the Tree of Life. *Proc. R. Soc. B* 283:20161334.
27. Rabosky DL (2009) Ecological limits and diversification rate: Alternative paradigms to explain the variation in species richness among clades and regions. *Ecol Lett* 12:735–743.
28. Rabosky DL, Slater GJ, Alfaro ME (2012) Clade age and species richness are decoupled across the eukaryotic tree of life. *PLoS Biol* 10:e1001381.
29. Stadler T (2011) Mammalian phylogeny reveals recent diversification rate shifts. *Proc Natl Acad Sci USA* 108:6187–6192.
30. Tank DC, et al. (2015) Nested radiations and the pulse of angiosperm diversification: Increased diversification rates often follow whole genome duplications. *New Phytol* 207:454–467.
31. Madriñán S, Cortés AJ, Richardson JE (2013) Páramo is the world's fastest-evolving and coolest biodiversity hotspot. *Front Genet* 4:192.
32. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. *Nature* 491:444–448.
33. Budd GE, Mann RP (2018) History is written by the victors: The effect of the push of the past on the fossil record. *Evolution* 72:2276–2291.
34. Alroy J (2008) Colloquium paper: Dynamics of origination and extinction in the ma-rine fossil record. *Proc Natl Acad Sci USA* 105:11536–11542.
35. Rabosky DL (2016) Challenges in the estimation of extinction from molecular phy-logenies: A response to Beaulieu and O'Meara. *Evolution* 70:218–228.
36. Liow LH, Quental TB, Marshall CR (2010) When can decreasing diversification rates be detected with molecular phylogenies and the fossil record? *Syst Biol* 59:646–659.
37. Barraclough TG (2010) Evolving entities: Towards a unified framework for un-derstanding diversity at the species and higher levels. *Philos Trans R Soc Lond B Biol Sci* 365:1801–1813.
38. Wilson EO (1961) The nature of the taxon cycle in the Melanesian ant fauna. *Am Nat* 95:169–193.
39. Ricklefs RE, Cox GW (1972) Taxon cycles in the West Indian avifauna. *Am Nat* 106:195–219.
40. Quental TB, Marshall CR (2013) How the Red Queen drives terrestrial mammals to extinction. *Science* 341:290–292.
41. Testo W, Sundue M (2016) A 4,000-species dataset provides new insight into the evolution of ferns. *Mol Phylogenet Evol* 105:200–211.
42. Zanne AE, et al. (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature* 506:89–92.
43. Schumer R, Jerolmack DJ (2009) Real and apparent changes in sediment deposition rates through time. *J Geophys Res* 114:481.
44. Foote M (1994) Temporal variation in extinction risk and temporal scaling of ex-tinction metrics. *Paleobiology* 20:424–444.
45. Foote M (2005) Pulsed origination and extinction in the marine realm. *Paleobiology* 31:6–20.
46. Davies TJ, et al. (2011) Extinction risk and diversification are linked in a plant bio-diversity hotspot. *PLoS Biol* 9:e1000620.
47. Crampton JS, et al. (2018) Pacing of Paleozoic macroevolutionary rates by Milankovitch grand cycles. *Proc Natl Acad Sci USA* 115:5686–5691.
48. Solé RV, Manrubia SC, Benton M, Bak P (1997) Self-similarity of extinction statistics in the fossil record. *Nature* 388:764–767.
49. Donoghue MJ, Sanderson MJ (2015) Confluence, synnovation, and depauperons in plant diversification. *New Phytol* 207:260–274.
50. Rosenblum EB, et al. (2012) Goldilocks meets Santa Rosalia: An ephemeral speciation model explains patterns of diversification across time scales. *Evol Biol* 39:255–261.
51. Futuyma DJ (2010) Evolutionary constraint and ecological consequences. *Evolution* 64:1865–1884.
52. Blum MGB, François O (2006) Which random processes describe the tree of life? A large-scale study of phylogenetic tree imbalance. *Syst Biol* 55:685–691.
53. Lewitus E, Morlon H (2016) Natural constraints to species diversification. *PLoS Biol* 14:e1002532.
54. Michonneau F, Bolker B, Holder M, Lewis P, O'Meara B (2016) Package "rncl." Available at https://repo.bppt.go.id/cran/web/packages/rncl/rncl.pdf. Accessed April 18, 2018.
55. Louca S, Doebeli M (2018) Efficient comparative phylogenetics on large trees. *Bioinformatics* 34:1053–1055.
56. Popescu A-A, Huber KT, Paradis E (2012) Ape 3.0: New tools for distance-based phylogenetics and evolutionary analysis in R. *Bioinformatics* 28:1536–1537.
57. Schliep KP (2011) Phangorn: Phylogenetic analysis in R. *Bioinformatics* 27:592–593.
58. Rabosky DL, et al. (2014) BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods Ecol Evol* 5:701–707.
59. Plummer M, Best N, Cowles K, Vines K (2006) CODA: Convergence diagnosis and output analysis for MCMC. *R News* 6:7–11.
60. FitzJohn RG, Maddison WP, Otto SP (2009) Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Syst Biol* 58:595–611.
61. Höhna S (2014) Likelihood inference of non-constant diversification rates with in-complete taxon sampling. *PLoS One* 9:e84184.
62. Louca S, Doebeli M (2017) Efficient comparative phylogenetics on large trees. *Bioinformatics* 34:1053–1055.
63. FitzJohn RG (2012) Diversitree: Comparative phylogenetic analyses of diversification in R. *Methods Ecol Evol* 3:1084–1092.