Title: Macroevolutionary diversification rates show time-dependency

One sentence summary:
Speciation and extinction rates follow a scaling law in which the youngest groups have the fastest apparent rates.

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Abstract:
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 report a hidden generality amongst these seemingly idiosyncratic results: speciation and extinction rates follow a scaling law where both depend strongly on the age of the group in which they are measured. This time-scaling has profound implications for the interpretation of rate estimates and suggests there might be general laws governing macroevolutionary dynamics.

Main Text:

Though 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 life (*1*). Using both fossil time series and phylogenetic trees of extant organisms, thousands of studies have documented variation between groups of organisms in the rate at which species form and go extinct. This variation in rates has been widely invoked to explain the disparity in species richness across different taxa (*2–5*). Individually these studies are fascinating -- researchers have uncovered a tremendous array of mechanisms that may have accelerated or slowed the accumulation of biodiversity -- but together suggest that the inflorescence of the Tree of Life has been largely idiosyncratic and contingent upon series of chance events. However, we have uncovered a general and unexpected pattern that implies that much of the observed variation in macroevolutionary rates may instead be attributable to a deceptively simple factor: time.

We explored the time scaling of diversification rates using both phylogenetic data from the Tree of Life and paleobiological data from the fossil record. Using a Bayesian approach that allows for heterogeneity across the phylogeny (*6*), we estimated speciation and extinction rates across 104 previously published time-calibrated molecular phylogenies of multicellular organisms which collectively contained 25,864 terminal branches (Table S2). 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 a speciation rates: β = -0.536; $P < 0.001$; extinction rates β = -0.498; $P < 0.001$; Fig. 1A,B). In general, no matter what 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.

Remarkably, we also recovered this same scaling pattern using fossil time series. We estimated origination and extinction rates from a curated set of fossil time series consisting of 17 orders

of mammals, 22 orders of plants, and 51 orders of (non-mammalian) marine animals, which in total contain representatives from 6,144 genera, using the widely used per capita method (*7*). 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 (see Supplementary Online Material; SOM). Both origination (β = -0.237; P < 0.001; Fig. 1C) and extinction rates of fossil genera (β = -0.270; P < 0.001; Fig. 1D) were highly dependent on duration.

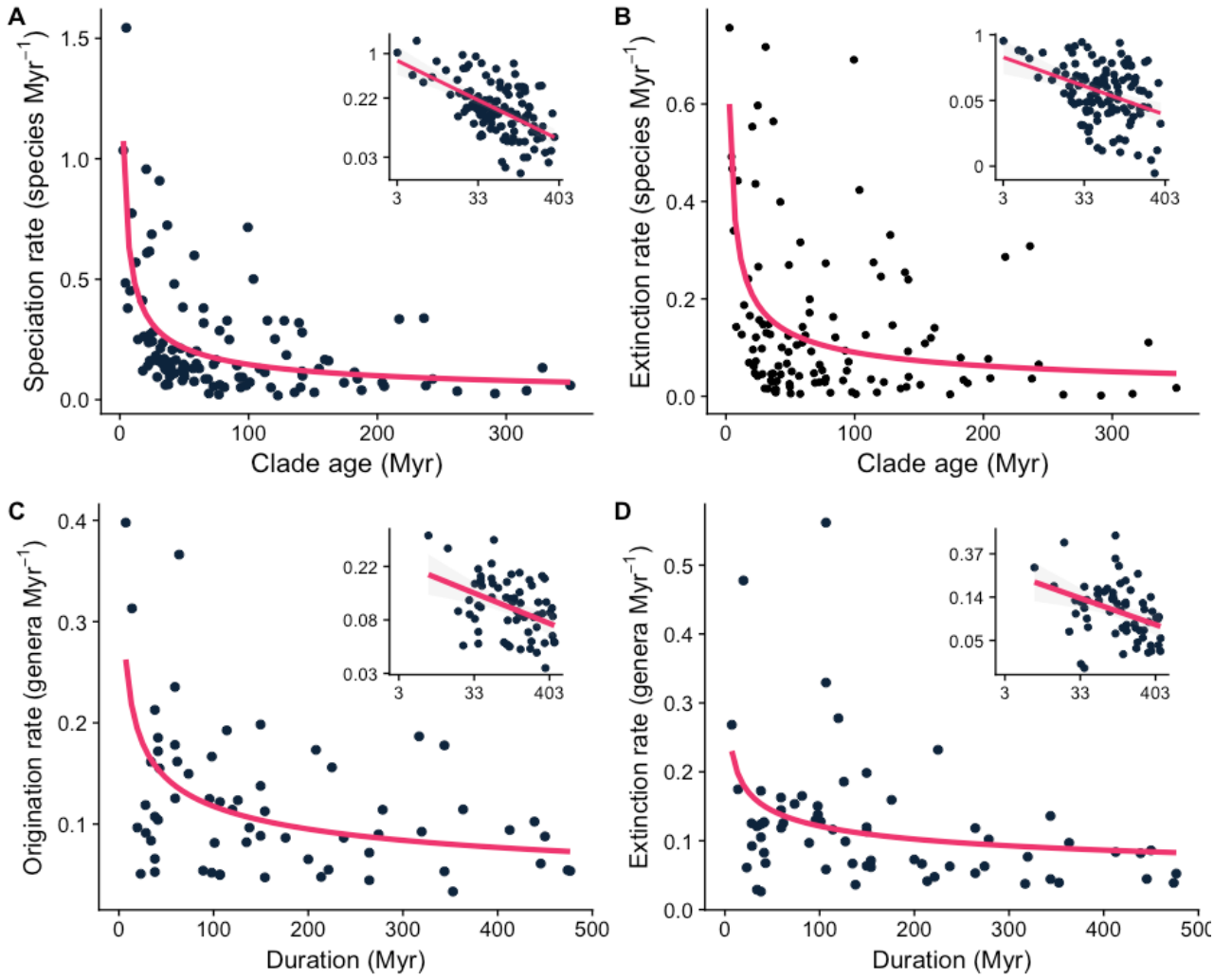

Fig. 1. Time-dependency of macroevolutionary rates. Mean per-lineage speciation (Panel A) and extinction (Panel B) rates estimated from 104 molecular phylogenies plotted against the age of the most recent common ancestor of each clade. Panels C and D show the mean rates of origination and extinction of genera estimated from fossil time series from 90 orders of animals and plants against the total duration each group existed. The insets of each panel show the relationship on a log-log scale.

This result is unexpected and has severe consequences for how we measure and interpret rates of diversification. We suspect that many findings of diversification rate differences among groups will need to be reconsidered in light of our findings. The time-dependency of rates implies that it is incorrect to compare rates of speciation and extinction between groups, areas, traits, etc. without controlling for time -- which our current macroevolutionary approaches fail to do. While we do not re-evaluate any previous studies here, we note that many of the regions of the world that are often recognized as hotspots of diversification (at least over the past several million years) are also precisely those regions that harbour young groups of organisms, such as the Páramo of the Andes (*8*), oceanic islands (*9*), or polar seas (*10*). There is a pressing need for novel methods that can fully account for the time-scaling of rates.

Potential causes of this ubiquitous pattern fall into two main categories: statistical, where this pattern is attributed to biases in the data we use or how we analyze it; and biological, where this pattern is caused by general rules operating over macroevolutionary time scales. Using a series of simulations and sensitivity analyses, we show that statistical biases are unlikely to account for the entirety of our pattern. In the SOM, we present results investigating a variety potential artifacts, such as bias in the rate estimators, incomplete sampling, error in divergence time estimation, taxonomic practice, or acquisition bias (known as the “push of the past” in the macroevolutionary literature), all of which have been invoked when this pattern was previously glimpsed by phylogenetic biologists in studies of individual groups (*11*–*14*). None of these artifactual explanations can fully account for the pattern we find 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, is that there has been a true, secular increase in rates of diversification through time, such that evolution 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. S3, SOM). While we do find support for shifts in diversification rates within trees (Fig. S2), there is no clear temporal trend. This is inconsistent with the idea of a global speedup. And consistent with previous studies (*15*), we do not see an increase in rates through time for fossil data (Fig. S7). We also note that previous studies have shown that heterogeneity in rates across groups cannot generate the patterns we observe under realistic diversification scenarios (*16*).

The lack of support for temporal trends within groups also rules out another commonly invoked explanation for the time-dependency of rates -- that diversity dynamics are shaped by ecological limits (*2*, *17*). If niche or geographic space is constrained, then diversification should slow down as diversity accumulates; this decoupling of clade age and size would then lead directly to time-dependent rates of diversification (*16*) (but see (*18*)). In this scenario, younger clades are growing near exponentially while older clades have reached stationarity; therefore, the average rates of evolution would thus appear much faster in younger clades relative to older ones. This explanation predicts that slowdowns in rates should be ubiquitously observed *within* clades which, as stated above, is incompatible with our findings. Furthermore, the signal for a slowdown should be most apparent in older clades, which is also not apparent in either phylogenetic or paleobiological data (Figs. S5, S7).

We favor another explanation: that speciation and extinction events are clustered together in time, with these clusters interspersed among long periods where species neither form nor go extinct. For inspiration, we turn to a result, strikingly similar to our own, from an entirely different field. Sadler (*19*) demonstrated that estimated rates of sediment deposition and erosion are also negatively correlated with the time interval over which they are estimated (this is now known in geology 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 where large amounts of sedimentation accumulates (*20*, *21*). Under such a scenario, the mean rate tends to decrease the farther back in time one looks owing to the fact that more and more hiatuses are observed.

We think that Sadler's rationale could apply to diversification rates as well. There is evidence that extinction events recorded by the fossil record are much more clustered in space and time that we would predict under gradualism (*22*, *23*). 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. And there is abundant evidence, including from our results, that origination and extinction rates tend to be highly correlated over macroevolutionary time (*15*, *24*). We expect that if extinction events are concentrated in time, speciation rates will be as well.

We are not the first to propose that pulses of diversification may mislead rate estimators built 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 (*22*, *23*). And as we noted above, some phylogenetic analyses have uncovered similar patterns (*11–14*, *25*). However, explanations favored by previous work are idiosyncratic to the particulars of either phylogenetic or paleontological analysis, and do not explain the entirety of our observation of apparent time-dependency found across both phylogenetic trees and fossils.

As additional support for our favored explanation, some researchers have suggested that clustered speciation and extinction events may be due to large-scale, and possibly regular,

climatic fluctuations (*26*) or an emergent property of complex ecosystems (*27*). Perhaps a simpler explanation is that species evolve and diversify over a complex geographic landscape, and successful speciation and persistence seems to require the confluence of multiple factors at the right place and time. 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 (*28*). This verbal model shares much in common with Futuyma's model for ephemeral divergence (*29*), which itself can be invoked to explain the long-observed negative time-dependency of rates of phenotypic evolution (*30*, *31*) and could, potentially, explain a similar pattern in rates of molecular evolution (*32*). This scenario, consistent our results, would imply that the scaling of rates of sedimentation, phenotypic divergence, molecular evolution, and diversification with time all might share a common cause.

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https://github.com/mwpennell/macro-sadler. As we used only previously published (and publicly available) phylogenetic and paleobiological data for this analysis, we will not re-publish the curated datasets; however, the final, curated datasets are available upon request.

List of Supplementary Materials

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Supplementary Materials for

Macroevolutionary diversification rates show time-dependency

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This PDF file includes:

Materials and Methods

Curation of phylogenetic datasets

We collected and curated a set of time-calibrated species level phylogenies from the supplementary materials of published journal articles and from data repositories. Since we needed time-calibrated trees, with branch lengths in standardized units (millions of years), we were unable to rely exclusively on existing compilations (e.g., TreeBase (*33*), OpenTree (*34*)). It was important that we gather data from as many different, independent sources as feasible rather than simply slicing up previously constructed "megaphylogenies" (*35*) for two reasons. First, very large trees are necessarily constructed using only the few genes that are widely available for many taxa; there is thus likely to be substantial uncertainty in both topology and divergence times (*35–37*). Second, we wanted to minimize the correlation of error across datasets.

Our goal in collecting trees was to assemble a dataset that was as taxonomically unbiased as possible -- so as to avoid focusing on groups that have been previously identified as being adaptive radiations, etc. -- and made up primarily of recent studies under the assumption that, in general, more recently estimated trees tend to be more robust than older ones. To do this, we took two approaches; i) first we systematically surveyed issues of eight journals that routinely publish primary phylogenies (the issues we examined are listed in Table S1); and ii) we searched Open Tree of Life (*34*), Figshare (figshare.com), and Dryad (datadryad.org) using the following tags: "time-calibrated", "dated-tree", and "species-time-tree". In order to be included, phylogenies had to be fully bifurcating and ultrametric, include more than 7 tips and contain more than 1% of the total diversity of the group being studied.

Through this process we compiled 104 phylogenies from 69 studies, most of them at family (54), genus (19) and order (11) rank; plant (50) and animal (54) groups were nearly evenly represented (Table S2). The number of taxa included in the trees varied from 7 to 4,161 species, and clade (crown) ages range from 2.74 to 349.8 million years (Myr).

For each group represented by a phylogeny, we searched the literature to estimate the total number of extant taxa in the group. Because speciation rates likely have radically different meanings for unicellular organisms (but see ref. (*38*, *39*)), we limited our search to multicellular organisms. We removed outgroups and duplicated species by hand and ensured that the trees

were ultrametric and had branch lengths in units of millions of years. Tree manipulations and adjustments were done with the R packages ape (*40*), phangorn (*41*), castor (*42*), and rncl (*43*).

Estimating diversification rates from phylogenetic data

We calculated diversification rates (speciation and extinction) for each tree using BAMM v2.5.0 (*44*) . The BAMM model is a variety of a birth-death process where the rates vary both through time and across the tree. BAMM uses reversible-jump MCMC (*45*) to locate breakpoints in the birth-death process on the phylogeny. We used BAMMtools (*46*) to configure the analysis; we used the default priors and incorporated a sampling fraction for each tree (using the true diversity estimated from the literature, as above) to correct the diversification rate estimates (*47*). For each tree, we ran 4 independent chains of 2 million generations each. We assessed mixing using the *effectiveSize* (ESS) function in the coda package (*48*). In cases, where the ESS was less than 100, we continued running the analysis until convergence was reached. For each of the 104 analyses, we computed the following summary statistics from the posterior distribution: i) the mean speciation rate across all branches (**Figure S1**); ii) mean extinction rate across all branches; iii) speciation and extinction rates variance across all branches; and iv) the frequency of well-supported shifts (as identified by the protocol in BAMMtools (*46*)). We estimated the number of detectable shifts (>1) given clade age, and the average waiting times between evolutionary regime changes (**Figure S2**).

The standard BAMM model (*44*) fit to a tree with *n* tips includes *m* evolutionary regimes, where *m* can vary between 1 (single rate) and 2*n*-3 (each branch has its own rate). Each of the evolutionary regimes contains its own speciation and extinction rate, as well as a rate *k* the describes how the diversification process changes through time. The *k* parameter was included in the BAMM model owing to apparent widespread inadequacy of constant rate birth death models (*49*). A negative *k* reflects a slowdown in diversification (perhaps owing to diversity dependent diversification (*17*, *50*), or to other processes and artifacts (*18*, *51*)) whereas a positive value of *k* indicates a speedup. As such, the estimate of the *k* values within a tree can indicate whether the time-dependency of rates across trees reflect true diversification trends. While a *k* parameter is estimated for each evolutionary regime, it is difficult to meaningfully summarize this across the tree (D. Rabosky, pers. comm.). We therefore took an alternative approach: we conducted another BAMM analysis on each tree (following the protocol described above), but this time constrained the model to include only a single evolutionary regime and calculated the mean *k* value across each posterior (**Figure S3**). In addition to *k* we

also computed the γ-statistic (*52*), another metric of changing diversification rates through time, both in its standard form and correcting for tree size (*53*).

BAMM has been criticized as an inappropriate model for diversification analyses (*54*) (though these critiques are themselves potentially problematic; see refs. (*55*, *56*)). However, as we are not primarily interested in detecting the number and location of shifts (the focus of the critiques) we have little reason to believe that our estimates of mean rates are in any way biased. In any case, as an additional check, we computed diversification rates for each phylogeny using two alternative methods: i) the maximum likelihood estimator (MLE) for a constant rate model including incomplete sampling (*47*, *57*), as implemented in diversitree (*58*); and ii) the mean estimate of the DR statistic (*59*) across all species in the tree.

We fit linear models on a log-log scale between mean rates (speciation and extinction estimated from BAMM) and crown ages extracted from the from tree heights (results in main text). Time-dependency explains 34% of variation in diversification rates across the tree of life (R^2 value from fitting a linear model between the mean diversification rate [speciation - extinction] for each group and its crown age). We fit the same linear regression models using the MLE rates (**Figure S4**) and for the DR statistic (**Figure S5**) with qualitatively consistent results. We also tested for correlations between clade age, clade richness, and the γ-statistic (**Figure S6**).

Curation of fossil time series

For the mammalian data, we used the data from Sugawara and Quental (in review). The authors of this study downloaded all occurrences associated with each of the 21 Placentalia orders (i.e., Afrosoricida, Artiodactyla, Carnivora, Cetacea, Chiroptera, Cingulata, Dermoptera, Erinaceomorpha, Hyracoidea, Lagomorpha, Macroscelidea, Perissodactyla, Pholidota, Pilosa, Primates, Proboscidea, Rodentia, Scandentia, Sirenia, Soricomorpha, Tubulidentata) in the Paleobiology Database (PBDB; https://paleobiodb.org/) and in the New and Old Worlds - Database of fossil mammals (NOW; http://pantodon.science.helsinki.fi/now/). After checking for typographical errors and synonyms, Sugawara and Quental removed occurrences that were duplicated in the PDBD and NOW. The mammalian record is very well curated and the taxonomic information is more complete than the plants. The data includes the number of times each genus (the basic unit of paleobiological analyses) was recorded as well as the geological stage of each record. We conducted all analyses at the order level and restricted our

dataset to genera with at least two records and orders that had at least 10 genera. In total, this resulted in a dataset including 16 orders of placental mammals (Artiodactyla, Carnivora, Cetacea, Chiroptera, Cingulata, Erinaceomorpha, Hyracoidea, Lagomorpha, Macroscelidea, Perissodactyla, Pilosa, Primates, Proboscidea, Rodentia, Sirenia, Soricomorpha), which included a total of 107,376 occurences (median number of occurrences per order: 2,260.5) distributed in 3,180 mammalian genera (median number of genera per order: 73.5).

The paleobotanical datasets in the PBDB are not as well curated as the mammalian data so an additional set of data cleaning steps were required. To do this we modified the protocol of ref. (*60*). First, we downloaded (April, 2018) all fossil occurrences for the following groups, individually: Arberiopsida, Bennettitopsida, Cladoxylopsida, Cycadopsida, Dicotyledonae, Equisetopsida, Filicopsida, Ginkgoopsida, Lycopsida, Magnoliopsida, Peltaspermopsida, Pinopsida, Polypodiopsida, Progymnospermopsida, Psilophytopsida, Pteridopsida, Voltziopsida, Zosterophyllopsida, Alismales, Apiales, Arales, Arecales, Asterales, Bennettitales, Buxales, Callistophytales, Caryophyllales, Caytoniales, Celastrales, Ceratophyllales, Coniferales, Cooksoniales, Cordaitales, Cordaitanthales, Cornales, Corystospermales, Cyatheales, Cycadales, Cyperales, Dilleniales, Dioscoreales, Dipsacales, Equisetales, Ericales, Euphorbiales, Fabales, Fagales, Filicales, Gentianales, Geraniales, Gleicheniales, Glossopteridales, Gondwanostachyales, Isoetales, Juglandales, Lamiales, Laurales, Magnoliales, Malpighiales, Malvales, Marsileales, Myrtales, Myrtiflorae, Nelumbonales, Nymphaeales, Osmundales, Peltaspermales, Pinales, Polygonales, Polypodiales, Proteales, Pseudosporochnales, Psilophytales, Ranunculales, Rhamnales, Rosales, Rubiales, Salviniales, Sapindales, Sapotales, Saxifragales, Schizaeales, Scrophulariales, Solanales, Sphenophyllales, Theales, Triuridales, Typhales, Umkomasiales, Urticales, Violales, Voltziales and Zingiberales.

We then removed duplicate entries filtering by the "occurrence_no" and checked the generic names against the Index Nominum Genericorum (ING; (*61*)). We then assigned each genus to a family and order using the following protocol. First, we checked if each genus was listed by the Pteridophyte Phylogeny Group (*62*), which contains all Pteridophyte extant genera and their respective higher-level classification. If it was not included in the list, then we checked if at least two databases (PBDB, ING, TPL) included a family name for a genus and the name was the same across all the databases, we assigned that genus to that family. Then we cross-referenced the family name with The Plant List (TPL) v1.1 http://www.theplantlist.org/. If this was not the case, we searched three databases that aggregated taxonomic information: Encyclopedia of Life (EOL; http://eol.org/), Integrated Taxonomic Information System (ITIS;

https://www.itis.gov/) and Global Biodiversity Information Facility (GBIF; https://www.gbif.org/). In cases of conflict between databases, we chose the most recent evidence-based taxonomy. After we assigned the Family name, we checked both PPG I 2016 and the Angiosperm Phylogeny Group (*63*) to assign the Family to its corresponding Order. For the genera that we could not assign a Family name or the Family name was not found in the Phylogeny Groups (*62*, *63*), we used the most recent evidence-based information about Order in the queried databases (i.e., PBDB, ING, TPL, EOL, ITIS, GBIF). The Family name was used to help us identify the corresponding order. Like the mammals, all analysis were conducted at the order level.

The final dataset contains 17,640 plant fossil occurrences (median number of occurrences per order: 570), distributed in 430 genera (median number of genera per order: 17) and 19 orders (Arecales, Cycadeoideales, Ericales, Fabales, Fagales, Lamiales, Laurales, Malpighiales, Malvales, Myrtales, Pinales, Polypodiales, Proteales, Ranunculales, Rosales, Sapindales, Saxifragales, Schizaeales, Selaginellales).

We also analysed the classical Sepkoski's compendium of marine animals (*64*) (downloaded from http://strata.geology.wisc.edu/jack/). Which includes information about the first and last occurrences for 9 Phyla (i.e., Actinopoda, Annelida, Arthropoda, Brachiopoda, Bryozoa, Chaetognatha, Chordata, Ciliophora, Hemichordata, Hyolitha, Trilobozoa). After removing the orders with less than 10 genera, we are left with 2,851 genera and 51 orders (i.e., Nassellaria, Spumellaria, Agnostida, Asaphida, Bradioriida, Corynexochida, Decapoda, Eurypterida, Lichida, Metacopida, Odontopleurida, Palaeocopida, Phacopida, Podocopida, Proetida, Ptychopariida, Redlichiida, Acrotretida, Atrypida, Lingulida, Orthida, Pentamerida, Rhynchonellida, Spiriferida, Strophomenida, Terebratulida, Thecideida, Cheilostomata, Cryptostomata, Cyclostomata, Cystoporata, Fenestrata, Trepostomata, Alepisauriformes, Antiarcha, Arthrodira, Beryciformes, Chelonia, Coelocanthiformes, Conodontophorida, Crossognathiformes, Elopiformes, Lamniformes, Pachycormiformes, Palaeonisciformes, Petalichthida, Pteraspidomorphes, Rajiformes, Semionotiformes, Hyolithida, Orthothecida).

Estimating diversification rates from fossil time series

To be consistent with the paleobiological literature, we use the term origination rather than speciation as we are working with higher level taxonomic groups. Also, as pointed out by Ezard et al. (*65*), the dynamics of morphological divergence recorded by the fossil record may differ

from those of lineage divergence. Many of the estimators of origination and extinction rates that have been proposed for the analysis of fossil time series are inherently dependent on interval length (*66*). This time dependency was the motivation for the development of the now ubiquitously used Per Capita (PC) rate estimators (*7*) as they, like the rate estimators used with phylogenetic data, explicitly control for time (*66*). The PC rate estimators use only the first and last occurrence of a lineage and bin all observations by geological interval. As with the other analyses in this paper, we summarized the rates by computing mean origination and extinction rates across all intervals over which a group occurred. Unlike the analyses of the molecular phylogenies, crown age was not synonymous with duration as some groups had gone extinct entirely; we therefore measured duration as the time between the very first and very last occurrence of each group.

As with phylogenies we wanted to explore if our results arise from an accelerating secular trend within clades towards the present. We estimated the correlation between the rate estimates and the time-bin ordination (i.e., we wanted to test whether bins later in the series tended to have higher or lower rates than bins earlier in the series). We do not observe a strong or consistent trend of decreasing (or increasing) rates through time (origination: Spearman's ρ = 0.138; extinction: Spearman's ρ = -0.183; **Figure S7**). In concordance with the results from the phylogenetic analyses (above; **Figure S3**), fossils do not show evidence of evolutionary speed-ups towards present nor systematic slowdowns.

For rates estimated we fit a linear regression model between the natural logarithm of the rates and the natural logarithm of the duration of the entire group.

Evaluating purely statistical explanations for our results

We considered a number of artifactual statistical explanations that might explain why macroevolutionary rates scale negatively with time. On their own, it appears that none of these factors are sufficient to explain our results, though we acknowledge that it is difficult to completely rule out that some complex interaction of statistical artifacts could generate the pattern; however, resolving this is beyond the scope of the present paper.

The first, and simplest statistical artifact is that the negative time-dependency simply reflects the fact that in order for a young group to be observed -- and to be large enough to be considered for inclusion in an analysis such as ours -- it must have had high rates of

diversification early in its history. As clades get larger (and older) the rates tend to regress towards the mean, such that young groups would tend to have inflated estimates. This sampling artifact is known as the "push of the past" in the macroevolutionary literature and has been documented in both the paleobiological (*67*) and phylogenetic data (*68*, *69*). (As an aside, we note that this is related to, but distinct from, the "pull of the present/recent", the artifact resulting from the fact that extant taxa have not yet been pruned by extinction; in our data, extinction rates also scale negatively with time, which is inconsistent with the "pull of the present" artifact being an important part of the explanation.) As we show below, even when trees are simulated under a birth-death (speciation and extinction) or pure-birth (speciation only) process conditioned on surviving and containing a sufficient number of lineages, we observe a pattern where rates are inflated for lineages that originated close to the present (as in our empirical data). The key question is whether this effect is strong enough to explain our findings; using simulations designed following some recently developed theory (*67*), we are able to answer that it is not likely to be the case.

We estimated the mean rates of speciation and extinction from the oldest groups (more than 150 million years), where the curve between rates and age levels off (on a natural scale; Figure 1); this gave us parameters of λ = 0.11 and μ = 0.08. We then used TreeSim (*70*) to generate 104 phylogenies with the same ages as our empirical trees. We conditioned the simulations to produce trees with at least 6 taxa (the same as in our empirical trees) such that for younger clades, the only trees that would meet this condition were those that had stochastically high number of speciation events early in their history. We repeated this procedure 1000 times and estimated the slope of the log(speciation rate) ~ log(crown age) regression resulting from each one. We then compared this to our empirically estimated slope. We found that the slopes generated by conditioning alone were indeed negative but not nearly as negative as our empirically estimated slope (**Figure S8**), suggesting that our empirical results do not simply reflect inflated estimates for young groups. As a further check, we repeated this procedure by setting $\mu = 0.5\lambda$ since extinction rates are notoriously difficult to estimate (*71*). This scenario was qualitatively similar to those from the empirically estimated extinction rate.

Second, the groups we have included in this meta-analysis are not random subsets of the Tree of Life; the very fact that they are generally named groups means that taxonomists have identified these as special or distinct in some way (*72*). Rabosky and colleagues (*17*, *49*, *73*) have suggested that some as-yet-unidentified artifact of taxonomic practice may break the correlation between age and species richness -- and consequently, generate a negative

time-dependency of macroevolutionary rates. Even without a clear mechanism, we can test this proposition. To do this, we used recently published megaphylogenies of birds (*59*), ferns (*74*), and Angiosperms (*75*). We first computed the MLE of diversification rates for named clades (families, families, and orders, respectively) consisting of at least 10 taxa using the package diversitree (*58*) and fit a linear regression model log(speciation rate) ~ log(crown age) through all of the subclades. We then randomly selected an equivalent number of nodes from each tree with (approximately) the same age distribution as the named groups. We computed the MLE diversification rates for each of these subtrees and computed the same regression model as with the named nodes. We repeated this process 1000 times. Finally, as with the ascertainment bias simulations, we compared the regression slope from the named nodes to the distribution of slopes from random subtrees and in all cases, found no difference (**Figure S9**). In other words, we see the same pattern of rate-scaling whether we use named clades or random nodes within the Tree of Life. This result strongly suggests that our negative slope results are not a sampling artifact due to taxonomic delimitation. (It is not possible to subset the fossil time series at unnamed clades so we assume that our results from the phylogenetic data can be applied to the fossil data as well.) And while we tried to be as systematic as possible in collecting trees from the literature so as not to bias our results, it is nonetheless possible that scientists themselves are biased in terms of what groups they build trees for; for example, they may tend to study groups that are more diverse than average. If this selection bias is more pronounced for younger groups, then it is possible that our negative time-dependency might reflect this. However, we cannot imagine any way to evaluate this with our data.

Third, many of the trees in our collection were from sparsely sampled groups (and the older groups tended to be more sparsely sampled than younger ones; Spearman's rank correlation between age and sampling fraction: -0.25). While previously simulation studies (e.g., ref. (*47*)) have demonstrated that birth-death estimators are consistent when the correct sampling fraction has been provided, we performed a brief simulation of our own to ensure our results were not susceptible to our particular pattern of sampling. We used the empirically estimated ages and sampling fractions from our phylogenetic analyses and used the TreeSim R package (*70*) to simulate a tree corresponding to each empirical dataset (as above, using the mean rates estimated from empirical phylogenies older than 150 My; λ = 0.11, μ = 0.08). We re-estimated the MLE parameters using diversitree (*58*) and then fit a linear model between the (log) estimates and (log) crown age as we did in the empirical data. We repeated this procedure 1000 times and compare the estimated slopes to our empirically estimated slopes. There is no indication that our pattern of sampling could generate the negative relationship between rates

and age that we observe in our empirical data (**Figures S10**). However, we assume throughout that sampling is randomly distributed across the tree; of course in real life, researchers are likely to preferentially sample some taxa (e.g., to ensure that a phylogeny contains representatives from all major groups) and such sampling schemes can mislead birth-death estimators if not accounted for (*76*–*78*). While we acknowledge that failing to account for nonrandom sampling may bias our results (though in which way, it is not entirely clear), given the breadth of our study, there is no way we could feasibly control for the pattern of sampling in each individual dataset.

Fourth, it is a well known statistical fact that measurement error in the explanatory variable will tend to negatively bias the estimate of the slope. Two previous simulation studies have found that diversification rates are generally fairly robust to errors in divergence time estimation (*79*, *80*) (but see (*81*)). Still, error in ages of young clades could lead to pathological overestimates of diversification rates, potentially driving a negative relationship between rates and time. To investigate this, we repeated the simulations described previously to test the "push of the past" artifact. This time, we added error to clade ages. For each age, we drew a percentage error from a uniform distribution, and then added or subtracted the appropriate amount from the branch length. We ran a set of simulations where maximum error varied from 10% to 90%. Although altering the error did result in negative scaling of diversification rate with clade age, in no case was the slope as extreme as in our empirical data (**Figure S11**). In other words, error in branch length estimation cannot explain our results.

And last, the estimators themselves may be slightly biased in a way that previous simulation studies have missed; a central claim of our paper is that the estimators are not expected to show any time-dependency. We think that this is very unlikely to be driving the pattern. General birth-death estimators have been extremely well studied in the context of macroevolution and have been found to be consistent (e.g., (*82*)). The phylogenetic method used in this study (BAMM (*44*)) can accommodate high levels of heterogeneity in the diversification process (both across time, and across lineages), making them more likely to be adequate than simple, constant rate models. Nonetheless, our results are qualitatively the same whether we use the fits of complex models or much simpler metrics (such as the DR for phylogenies (*59*)).

Table S1 List of journals (and associated issues) that were systematically searched for phylogenetic data.

Journal	Last issue reviewed	First issue reviewed
American Journal of Botany	Vol. 105 (1); 2018	Vol. 103 (12); 2016
BMC Evolutionary Biology	Vol. 18:26; 2018	Vol. 17:248; 2017
Evolution	Vol. 72 (3); 2018	Vol. 70 (12); 2016
Molecular Biology and Evolution	Vol. 35 (3); 2018	Vol. 33 (6); 2016
Molecular Phylogenetics and Evolution	Vol. 120; 2018	Vol. 93; 2015
New Phytologist	Vol. 217(3); 2018	Vol. 217(1); 2018
Systematic Biology	Vol. 67 (1); 2018	Vol. 64 (1); 2015
Systematic Botany	Vol. 42(4); 2017	Vol. 42(1); 2017

Table S2 Summary of phylogenies used in this analysis including the clade name (in some cases, this refers to the nearest named node), age of the most recent common ancestor of lineages present in the tree (in millions of years), total number of tips in the phylogeny, estimate of extant diversity in the group, and the source of the tree.

Clade name	Clade age	Number of tips	Clade size	Reference
Viperidae	49.7	263	329	(*83*)
Costaceae	49.4	75	139	(*84*)
Hordeum	9.2	21	33	(*85*)
Onthophagus	37.6	66	68	(*86*)
Actinopterygii	114.6	1982	27681	(*87*)
Ovalentaria	72.8	103	352	(*88*)
Coronellini	24.6	70	88	(*89*)
Grallariidae	28.0	16	53	(*90*)
Orthorrhapha	20.5	16	8116	(*91*)
Dytiscidae	159.2	164	4196	(*92*)
Cichlidae	64.9	89	1404	
Ceanothus	51.1	51	64	(*93*)
Scolytinae	112.6	651	6000	(*94*)
Pinnipedia	43.4	34	34	(*95*)
Cracidae	23.3	47	50	(*96*)
Ctenitis	26.0	36	53	(*97*)
Quercus	50.2	150	207	(*98*)
Sebastes	8.0	99	107	(*99*)
Anolis	81.2	216	415	(*100*)
Heliconia	38.7	169	194	(*101*)
Cathartidae	6.1	7	7	(*102*)
Amnirana	36.7	11	12	(*103*)
Corvides	30.1	667	780	(*104*)
Coniferophyta; Pinidae	328.2	489	629	(*105*)

Rhododendron section Vireya	55.0	65	200	(*106*)
Agama	23.2	42	45	(*107*)
Odonata	236.1	521	1964	(*108*)
Lobelioidae	5.0	145	550	(*109*)
Phymatinae	77.6	28	29	(*110*)
Balistidaea	18.6	32	42	(*111*)
Monacanthidae	33.2	48	109	(*111*)
Spermacoceae	36.8	365	1346	(*112*)
Cephalotes	42.6	116	118	(*113*)
Testudinata	315.8	294	335	(*114*)
Squamata	174.1	4161	9400	(*115*)
Caniformia	23.0	34	174	(*95*)
Furnariidae	32.6	278	287	(*116*)
Scolopacidae	31.4	6	79	(*117*)
Passeriformes	21.0	191	6263	(*118*)
Euteleostei	216.9	572	17419	(*119*)
Otophysi	349.8	95	6842	(*120*)
Lupinus	12.3	120	159	(*121*)
Columbidae	47.3	55	244	(*122*)
Trochilidae	22.5	293	338	(*123*)
Temnothrorax	35.0	97	390	(*124*)
Psophiidae	2.7	8	11	(*125*)
Mormoopidae & Phyllostomidae	39.6	61	210	(*126*)
Phymaturus	17.5	37	47	(*127*)
Carnivora	48.9	138	288	(*128*)
Poaceae	57.8	3595	11000	(*129*)
Galliformes	56.8	171	291	(*130*)

Columbiformes	24.7	27	315	(*131*)
Elasmobranchii	291.3	585	926	(*132*)
Chimaeriformes	187.7	25	47	(*132*)
Brassicaceae	38.8	222	831	(*133*)
Primates	65.1	233	501	
Ballenidae	35.9	87	91	(*134*)
Salmonidae	42.2	28	176	(*135*)
Chiroptera	57.7	812	1200	(*136*)
Pectinidae	237.6	92	300	(*137*)
Aedes	100.9	247	929	(*138*)
Astacoidea & Parastacoidea	262.0	466	665	(*139*)
Pergidae	140.2	59	450	(*140*)
Phoenicopteridae	4.4	6	6	(*141*)
Myrtaceae	85.0	200	5950	(*142*)
Guibourtia	17.9	17	17	(*143*)
Cetartiodactyla	74.8	182	339	(*144*)
Pradosia	34.4	21	26	(*145*)
Anemiaceae	141.4	23	100	(*74*)
Aspleniaceae	129.4	249	700	(*74*)
Athyriaceae	83.3	197	600	(*74*)
Blechnaceae	59.5	138	200	(*74*)
Cibotiaceae	25.2	9	11	(*74*)
Cyatheaceae	99.4	120	600	(*74*)
Cystopteridaceae	77.4	31	64	(*74*)
Davalliaceae	59.4	13	65	(*74*)
Dennstaedtiaceae	154.6	35	170	(*74*)
Dicksoniaceae	108.5	13	30	(*74*)
Diplaziopsidaceae	76.9	4	4	(*74*)

Dipteridaceae	48.6	5	11	(74)
Dryopteridaceae	139.1	742	1700	(74)
Equisetaceae	151.0	15	15	(74)
Gleicheniaceae	120.4	32	125	(74)
Hymenophyllaceae	242.9	208	600	(74)
Hypodematiaceae	93.9	5	20	(74)
Lindsaeaceae	182.3	166	200	(74)
Lomariopsidaceae	95.2	32	40	(74)
Lygodiaceae	72.7	19	25	(74)
Marattiaceae	162.0	79	150	(74)
Marsileaceae	127.7	46	75	(74)
Matoniaceae	122.6	4	4	(74)
Nephrolepidaceae	61.6	21	21	(74)
Oleandraceae	14.1	4	35	(74)
Onocleaceae	69.2	5	5	(74)
Ophioglossaceae	205.3	63	80	(74)
Osmundaceae	203.7	17	20	(74)
Plagiogyriaceae	48.5	9	15	(74)
Polypodiaceae	91.0	719	1500	(74)
Psilotaceae	66.3	8	12	(74)t
Pteridaceae	184.5	595	950	(74)
Rhachidosoraceae	29.0	4	7	(74)
Saccolomataceae	35.3	4	12	(74)
Salviniaceae	92.6	15	16	(74)
Schizaeaceae	135.7	10	30	(74)
Tectariaceae	141.9	99	230	(74)
Thelypteridaceae	103.7	183	950	(74)
Woodsiaceae	68.4	20	35	(74)

Rhinantheae	30.8	49	528	(*146*)
Rhithrogena	21.6	25	25	(*147*)
Myrteae	40.8	115	2500	(*148*)
Buccinidae	141.6	22	1500	(*149*)
Vitis	28.3	48	60	(*150*)
Anisoptera	117.3	563	1033	(*151*)
Zygoptera	97.9	759	931	(*151*)

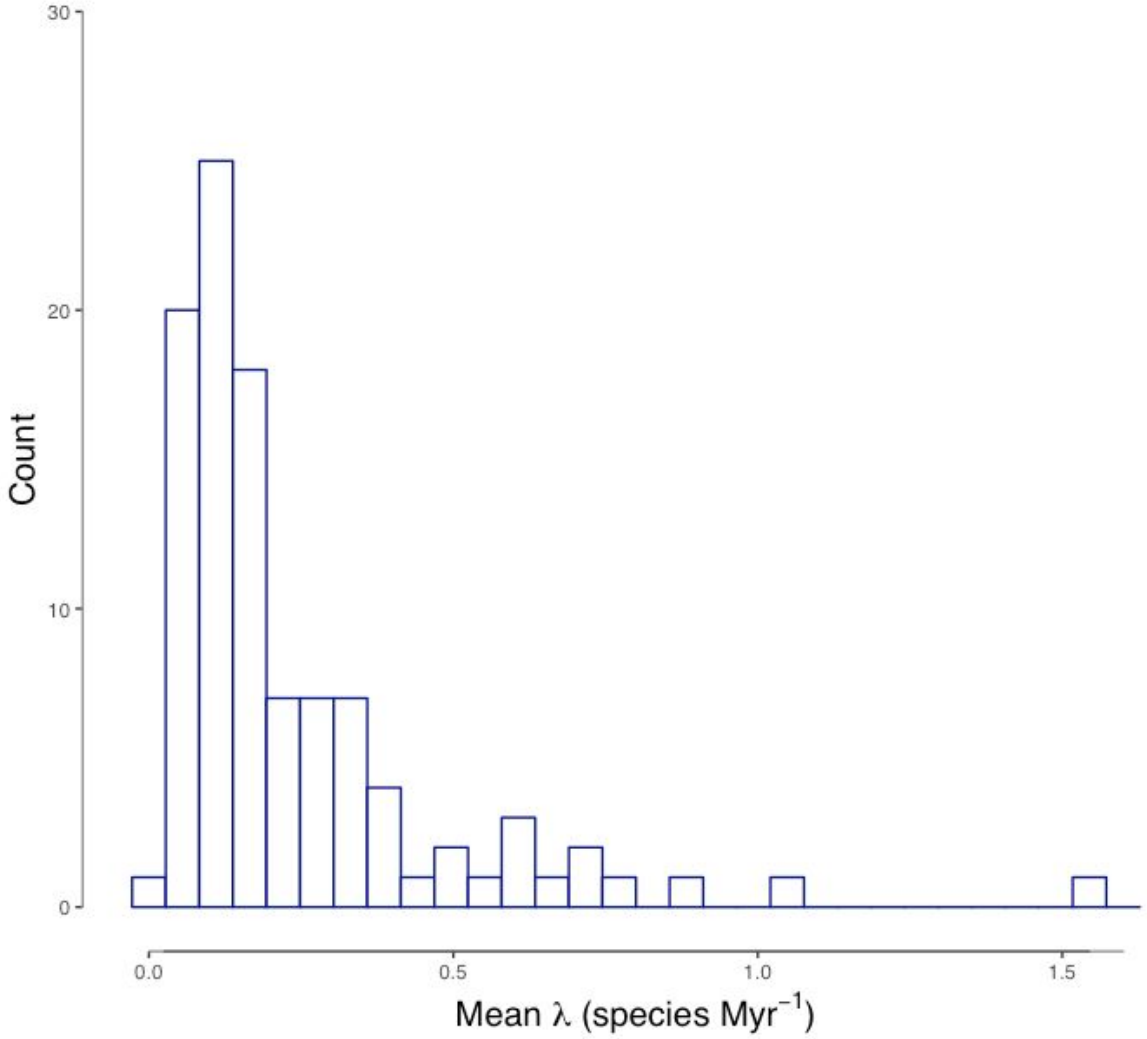

Fig. S1. Histogram of mean speciation rates (λ). The lowest speciation rate corresponds to the fern family Matoniaceae (0.02), the highest is Lobelioidae subfamily (1.54).

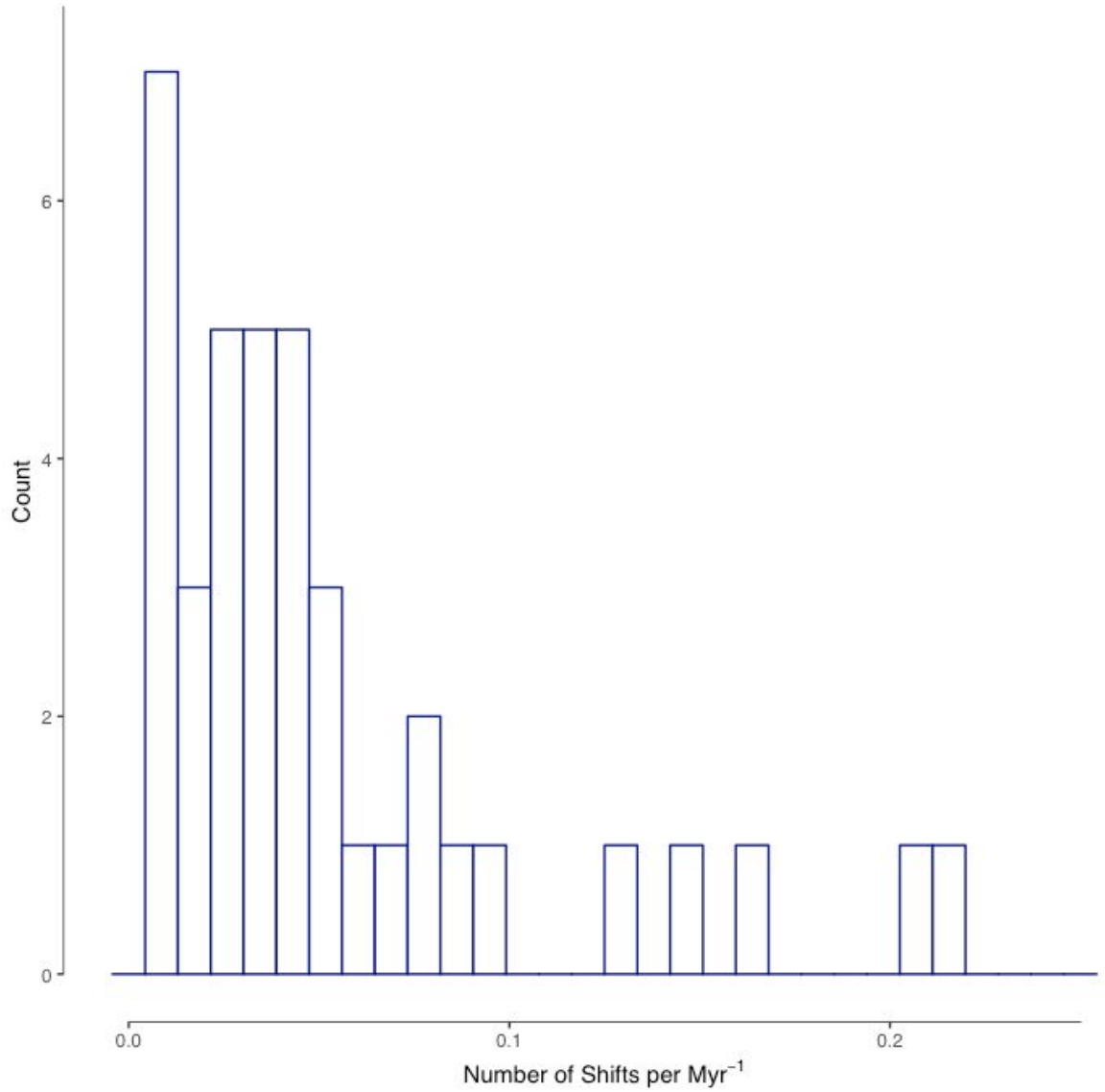

Fig. S2. Frequency of number of highly supported shifts per million years of evolution**.** For each phylogeny we fit a reversible-jump BAMM model and used BAMMtools (*46*) to identify the "Best Number of Shifts" in each analysis. Since the number of highly supported shifts recovered depends highly on the number of taxa in the analysis (Spearman's rank correlation rho: 0.51), we standardized the frequency by dividing my millions of years. On average, highly supported shifts occurred every 24.2 million years (variance: 0.03 My^2). While it is almost certainly just a coincidence, it is noteworthy that this frequency is almost perfectly aligned with that of major shifts in phenotypic evolution (*86*, *87*) and major extinction events observed in the fossil record (*88*–*90*). We will leave it to the reader to speculate about what this might mean.

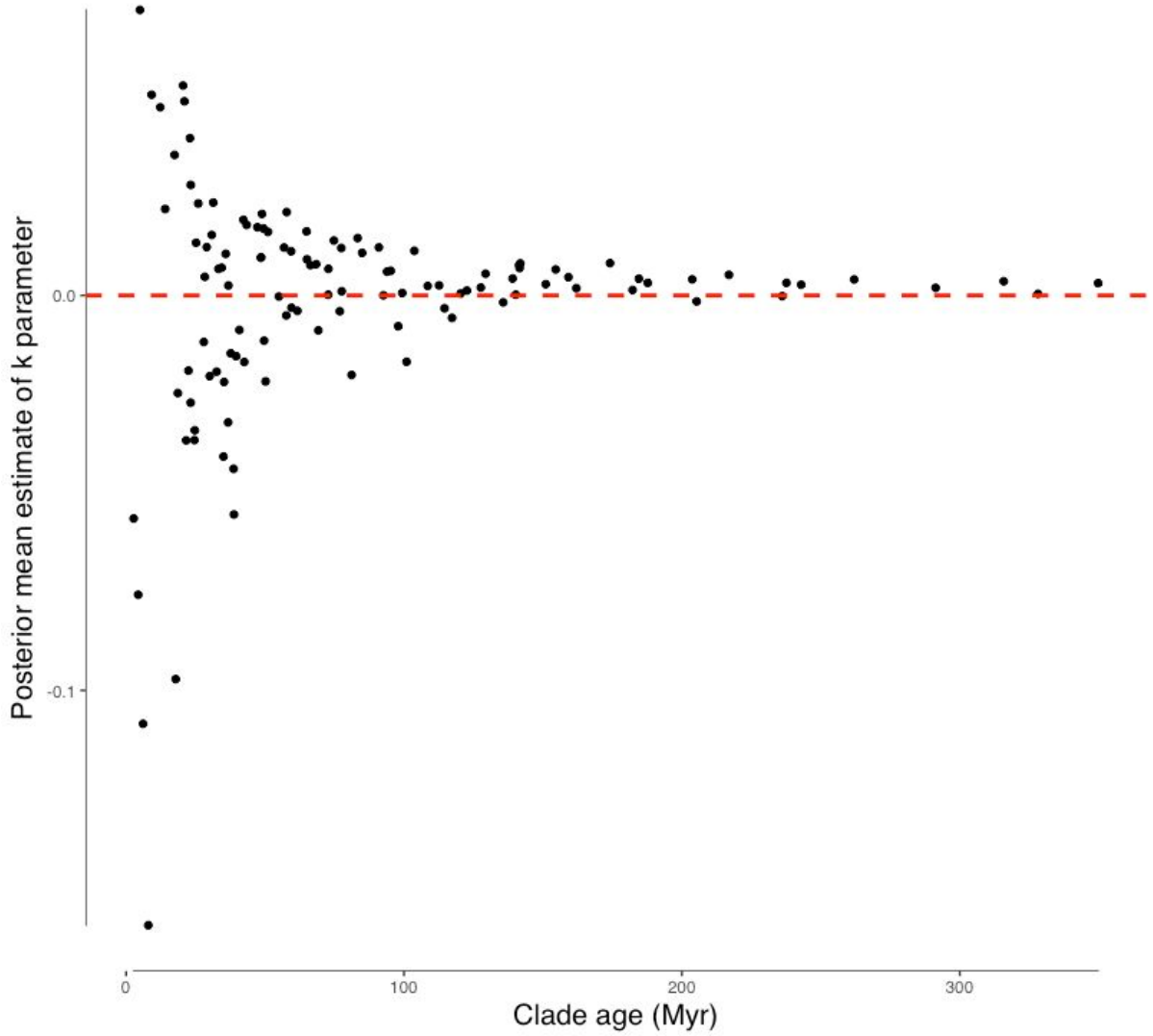

Fig. S3. Mean posterior distribution of shift parameter (*k*) from BAMM against clade age. BAMM analysis on each tree (following the protocol described above) constraining the model to include only a single evolutionary regime (root) and calculated the mean *k* value across each posterior. As seen above the *k* parameter does not decrease with time and furthermore it does not deviate from zero with clade age suggesting that there is no diversity dependence through time.

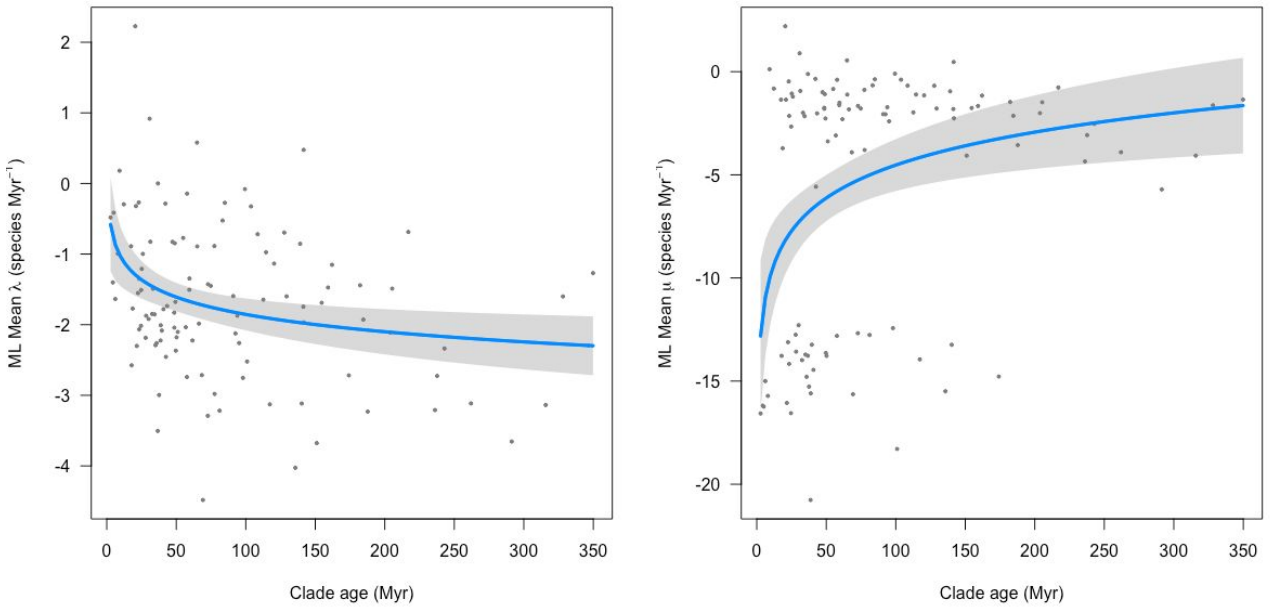

Fig. S4. Maximum likelihood estimates of speciation (λ) and extinction rate (μ) vs clade age. The estimates have been corrected for incomplete sampling. As has been previously noted, MLEs for the extinction parameter are often unreliable, particularly when the sampling fraction is low (*47*, *71*). As such, we do not put much stock in the lack of time-scaling in the extinction rates but include the plot for the sake of completeness.

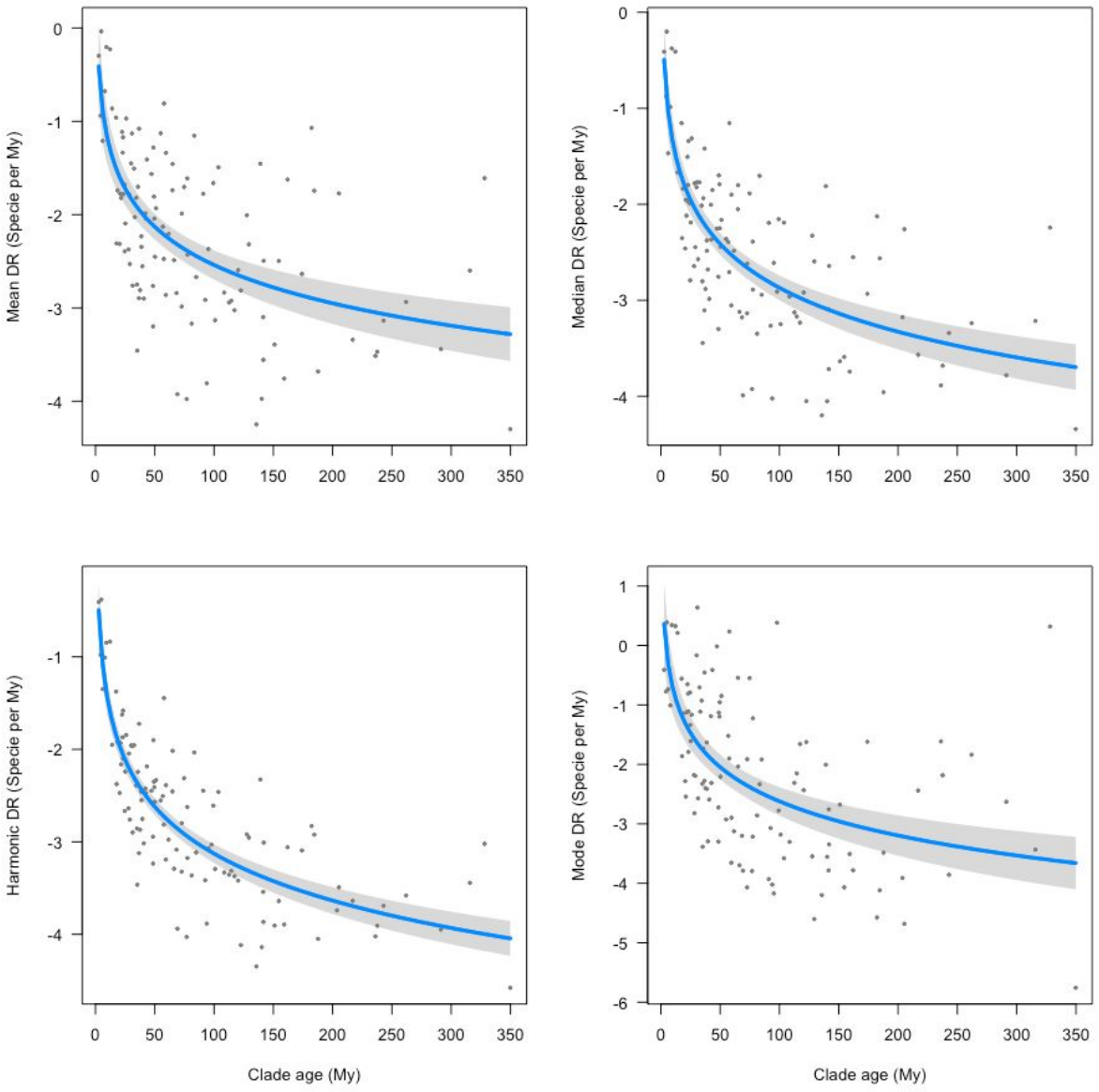

Fig. S5. Tree-wide DR statistic vs clade age. As an alternative to the mean posterior rates estimated in the BAMM analyses, we also computed the DR statistic for every tip, computed the mean, median, harmonic mean, and mode of the values for each tree. The tree-wide DR statistic, which is a non-parametric metric closely related to the speciation rate, shows the same type of time-scaling as the rates estimated from BAMM; this demonstrates that the time-scaling is a general phenomenon and not specific to the BAMM model.

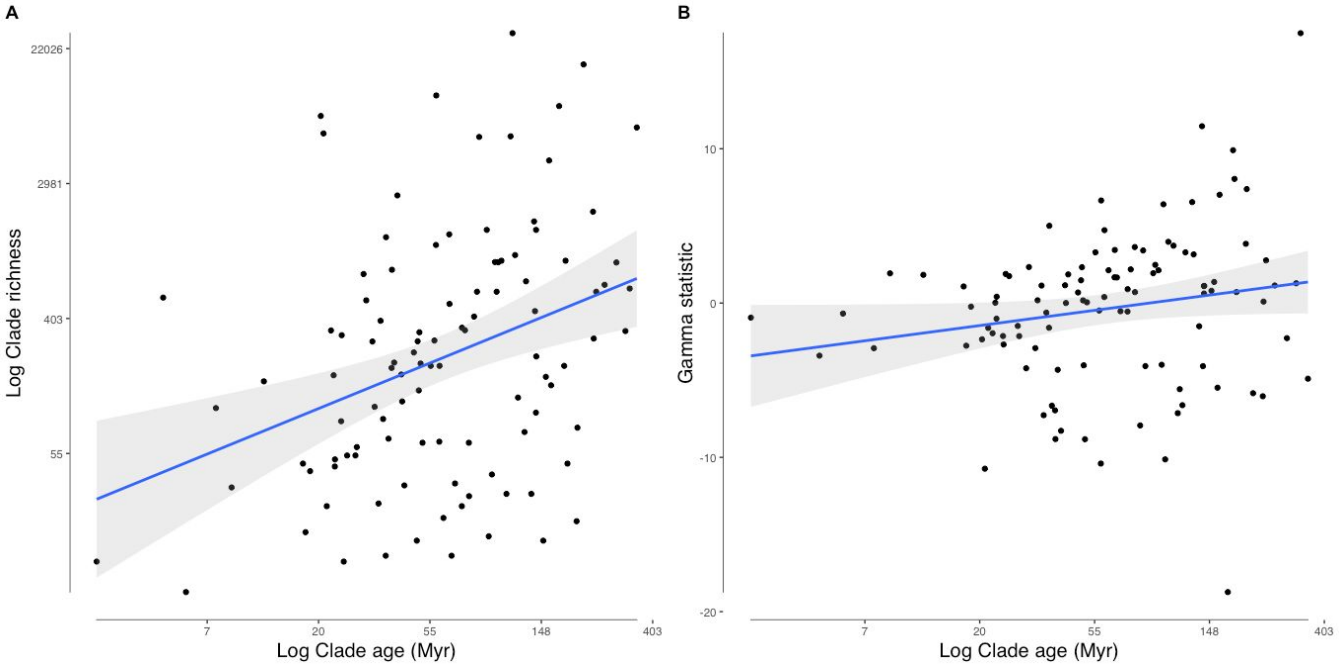

Fig. S6. Relationship between crown clade age and A) clade richness and B) the γ-statistic. Crown age and richness is weakly positively related to clade age (in line with the results of ref. (*81*) but contrary to those of ref. (*16*) who used stem age). We agree with Harmon and Harrison (*18*) that this positive relationship neither refutes or confirms ecological limits as an important factor in the diversification process. However, if the time-dependency of diversification rates did indeed result from widespread slowdowns, we would expect a preponderance of negative values of γ across clades and for slowdowns to be more widespread (i.e., more negative γ values) in older clades. As apparent from the figure, neither of these predictions is supported by the data.

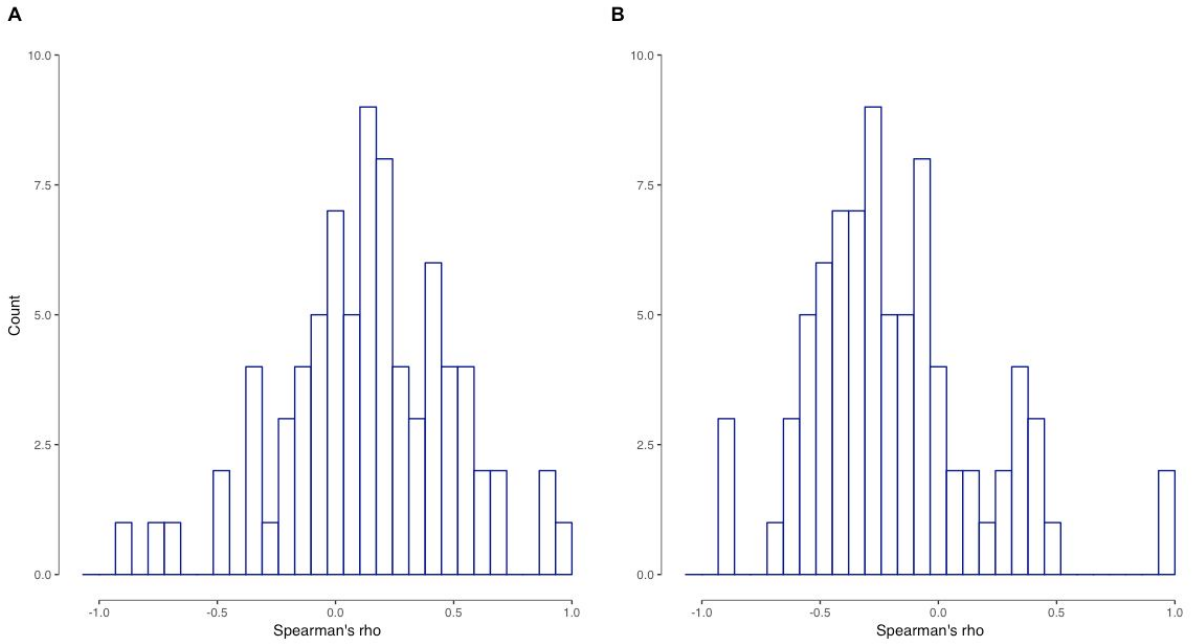

Fig. S7. Trends through time for fossil data. Spearman's correlation between time interval ordination with A) origination and B) extinction rates estimated using the perCapita method for mammals, plants and Sepkoski's marine animals. As with the analyses of the temporal dynamics of diversification rates inferred from molecular phylogenies (**Fig. S3**), secular trends towards faster rates within datasets are not widespread.

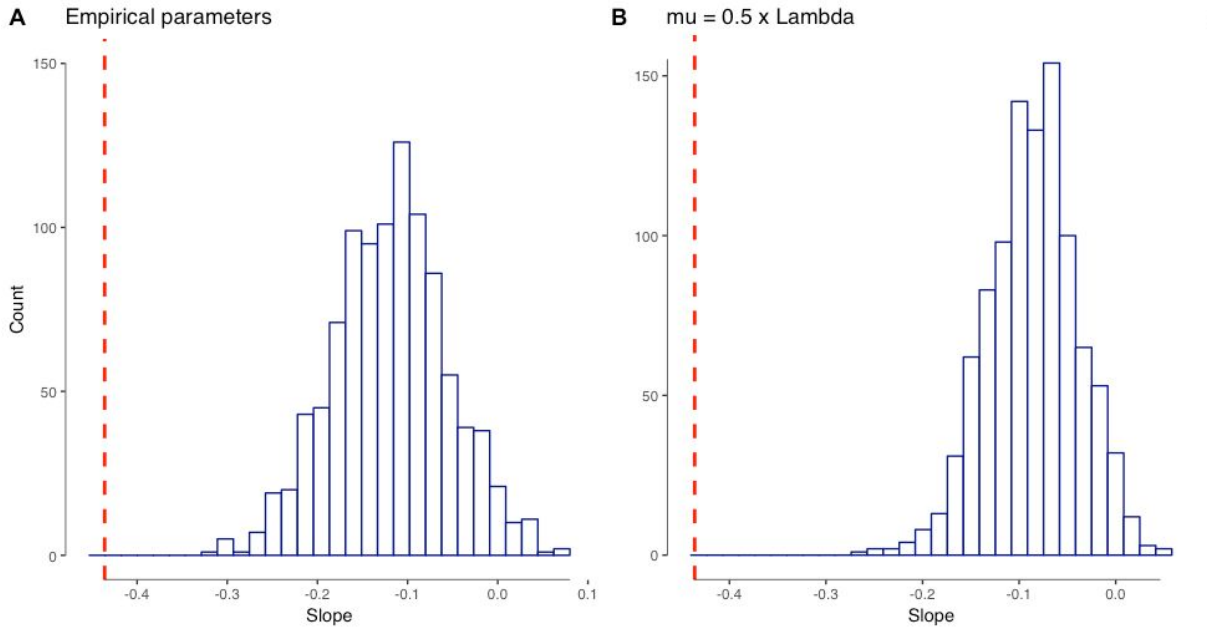

Fig. S8. Empirical slope (dash) compared with slope's distribution from simulated trees (parameters from trees older that 150 Myr.) with λ = 0.11 and differential extinction rates A) μ = 0.08 and B) $\mu = 0.5\,\lambda$. Although the push of the past may generate negative slopes, our empirical slope are far less negative than those in our empirical and alternative scenario discarding it as our results main driver.

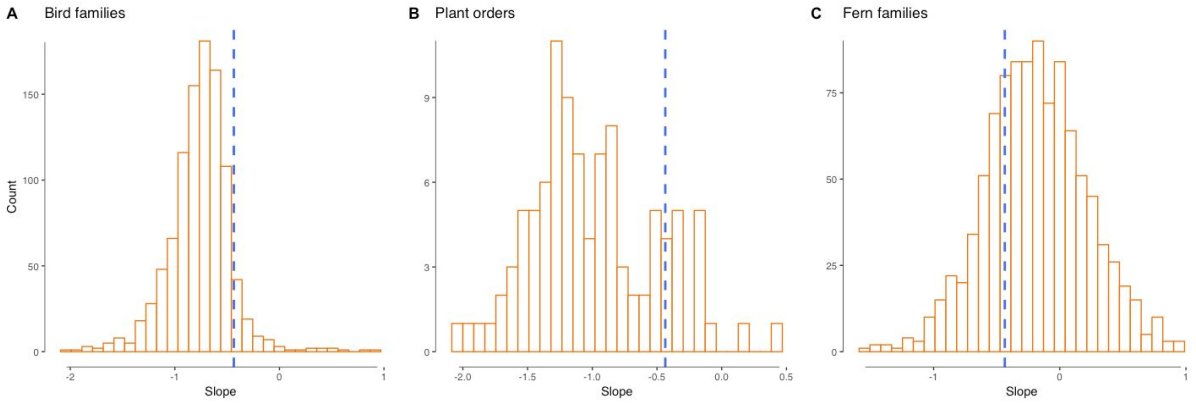

Fig. S9. Empirical slope (dashed) compared with slope's distribution from random sampled clades. In all cases our empirical estimates were within the negative slope's distribution from random drawn clades; showing that our negative slope results are not a sampling artifact due to taxonomic delimitation.

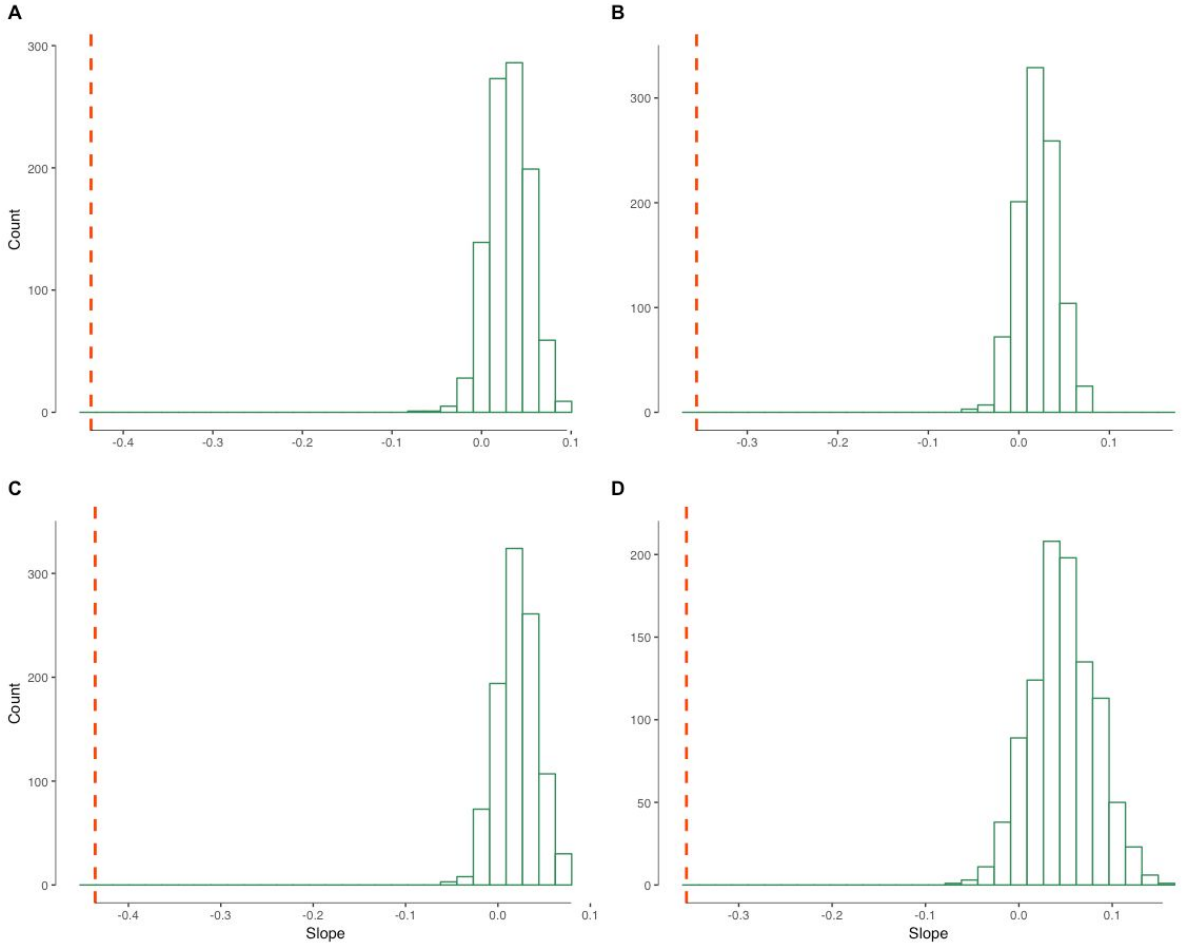

Fig. S10. Empirical slope (dashed) compared with slope's distribution from simulated trees. Speciation (A, C) and extinction rates (B, D). A) and B) Trees simulated with empirical sampling fractions; C and D) Trees simulated with empirical sampling fraction and age. We did not found any significative trend in any of our simulation scenarios nor expeciation or extinction rates; if any it seems to be rather mainly positive. This suggest that in spite of sampling fraction effect in rates estimation it acts in a different direction than our negative dependent results.

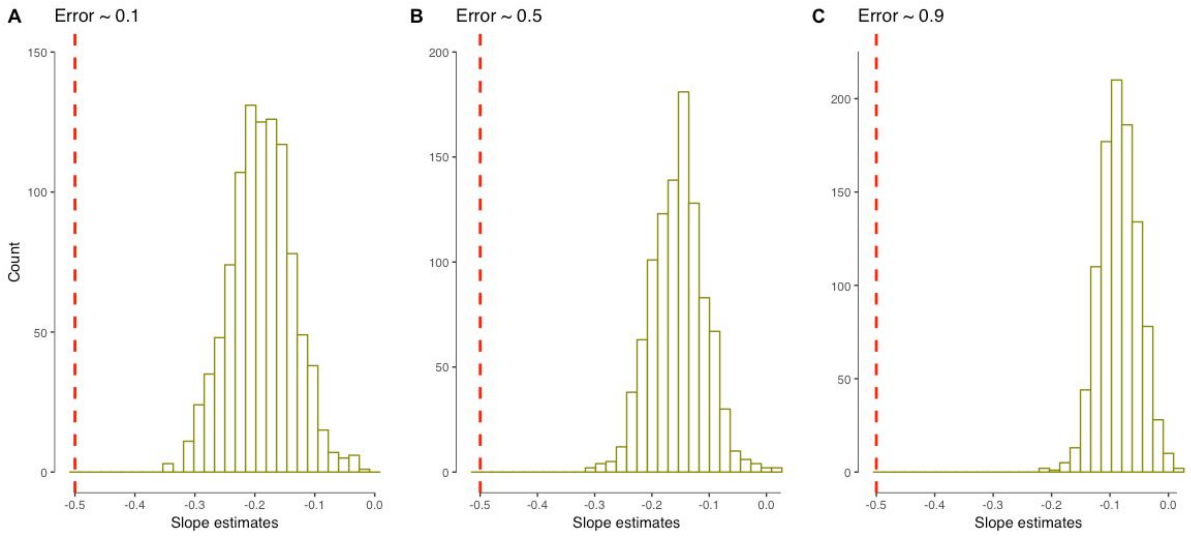

Fig. S11. Empirical slope (dashed) compared with slope's distribution from biased/error in tree's branch lengths. Three different error scenarios A) 0.1 , B) 0.5 and C) 0.9