Title: **Evolutionary change is remarkably time-independent across scales**

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Classification: Biological Sciences, Evolution

Keywords: Evolutionary rate, microevolution, macroevolution, stasis paradox

Abstract Apparent time-scaling of evolutionary rates presents an evolutionary dilemma. Rates of molecular, phenotypic, and lineage diversification typically scale negatively with time interval, raising questions about the processes driving this seemingly general pattern. Here we show that much apparent temporal scaling is an inevitable outcome of plotting a ratio against its denominator. Highly unlikely relationships between timescale and accumulated evolutionary change are required to produce anything other than negative relationships between rate and time. Rate-time scaling relationships reflect unscaled magnitudes of evolution that are largely unrelated to time, consistent with uniformitarianism and reframing the widely-held view of disparate pace of micro- and macroevolution. Time-independence of evolutionary change raises new questions about the factors that generate temporal consistency in evolution.

Significance Statement A longstanding finding across molecular, phenotypic, phylogenetic and fossil data is that evolutionary rates depend strongly on the timescale over which evolution is measured. This seemingly general pattern has stimulated many hypotheses of some shared general features of the underlying processes that shape evolutionary rates. Here, we show that evolutionary rates will inevitably correlate negatively with time interval, even if evolutionary processes are time-independent. While the statistical effects behind this pattern are known, our new analyses demonstrates that evolutionary rate-time relationships are nearly inevitable. Empirical data suggest variable evolutionary rates across time, but no time-dependency or systematic difference between micro- and macroevolutionary scales. Thus, evolutionary change is largely uniform and independent of timescale.

Main Text: Evolutionary rates vary with the time interval over which they are measured. A seemingly general pattern with faster evolutionary rate over short timescales, and slower rates over longer timescales has been recognized for decades (1-5). Such apparent time-dependence has subsequently been documented consistently for nearly every possible measure of evolutionary rate (6), including rates of morphological evolution, rates of molecular evolution (7), and rates of lineage formation on phylogenies and in the fossil record (Figure 1). Negative rate-time scaling relationships were initially proposed as an artifact that needed to be taken in to account, because evolutionary rates over different time intervals were not directly comparable (5). Yet these negative relationships between evolutionary rate and time continue to generate discussions and stimulate new hypotheses about the possible shared features of the underlying evolutionary processes that could explain such general time-scaling (6, 8). Recent technical and statistical explanations to these apparent negative rate-time scaling relationships focus on sampling biases (9), such as a the "push of the past" (6) model mis-specification (2), and measurement error (10). This puzzling and general phenomenon of apparent widespread negative rate-time scaling relationships has been recently highlighted as a major unsolved challenge in evolutionary biology (2, 6, 8). The renewed interest in such apparent time-dependence of evolutionary rates has re-kindled long-standing ideas and hypotheses about fundamental disparities between micro- and macroevolution (11-15).

Here we show that much of this apparent paradox of strong time-dependency of evolutionary rate is readily explained by the inevitable negative correlation generated by plotting a ratio against its own denominator (16). While this is a well-known statistical issue across a range of scientific fields (5, 17-20), recent discussions of rate-time scaling patterns in evolutionary biology have either have either downplayed the importance of the mathematical dependence of rate and time (e.g., Box 1 in 2, 6, 8), or have focused on explanations arising from

specific statistical models used to estimate rates in a single context (9). By revisiting the functional dependence of rates and time, analyzing large existing datasets and using new simulations, we show that a negative relationship between evolutionary rate and time is nearly inevitable, regardless of the underlying evolutionary process. We show that the key feature underlying negative rate-time relationships in empirical data is in fact a weak, null, or variable relationship between magnitude of evolution and time. Uninformed focus on rate-time relationships therefore provide little insight into underlying evolutionary processes even under highly idealized conditions. Instead, the empirical evidence suggest remarkable time-independence and uniformity of evolutionary change across timescales and datasets.

The negative rate-time association is nearly inevitable

Estimates of evolutionary rate can be modelled as a function of evolutionary change scaled by time:

$$y = d/t \tag{1}$$

where y is the rate-measure, d is some measure of evolutionary change (e.g., change in population mean phenotype, base pair substitutions, log change in number of species in a clade) and t is some measure of time interval over which change was observed or inferred (e.g. generations, or years). Some classical estimates of evolutionary rate are calculated directly by dividing phenotypic change with time, the latter typically measured in generations. For example, Darwins (21) and Haldanes (4) have been used to describe morphological rate, and other types of rate estimators measure per-capita origination rate of fossil lineages (22) and phylogenetic net diversification rate (23). Other estimates are obtained from more sophisticated statistical models of evolution (24-26). Regardless, all evolutionary rate measures are, per definition, scaled by

time (e.g., waiting times between observed branching events on a phylogeny are a direct component of the likelihood in in maximum likelihood models of birth-death diversification (24)).

The inevitable mathematical dependence between rate and time is an obvious challenge in interpreting the time-dependence of evolutionary rate (5). Even a random association between evolutionary change and time will result in a strong negative scaling relationship between rate and time (27). The strength of this negative relationship will inevitably increase when a greater range of timescales is sampled (16). The problem of interpreting such inevitable negative relationships between a rate and time interval have been discussed in several fields outside evolutionary biology, including geology (28) and paleontology (29). The problem has also been raised in evolutionary biology, both in the context of rates of morphological evolution (3, 5, 18, 30-32) and lineage diversification (33-35). Here, we revisit and elaborate on the issues with interpreting rates as a function of time.

It is useful to ask, under what scenarios do we expect null or positive relationships between rate and time? Consider rate as a function of time,

$$y = f(t) \tag{2}$$

Where y is evolutionary rate (as in eqn 1). We also consider the amount, or magnitude, of accumulated evolution (rate numerator) as a function of time,

$$d = g(t) \tag{3}$$

where d is the accumulated evolutionary change . This could be the change in trait means between allochronic or synchronic populations, difference in log number of lineages between two sampling points in time (e.g., the stem age of a clade and present), or any other measure of evolutionary change. Rates, $y = d/t$, will be constant over time when d scales linearly with t,

i.e. $g'(t)$ is a positive constant over the timescale in question. Rates will increase with time, i.e. $f'(t) > 0$ when $g''(t) > 0$; that is, rates increase over time when the amount of evolutionary change is an accelerating function of time.

Noteworthy is that under a null relationship between *d* and *t*, such that $g'(t) = 0$, the logarithmic regression of rate versus time ($\log(y) \sim \mu + \beta * \log(t)$) will yield a negative slope estimate of $\beta = -1$ (5). This can be seen most easily by expressing equation 3 as a power function, e.g., $d = t^0$, in which case we can describe the regression of $\log(y) \sim \beta * \log(t)$ as $\log(t^0/t) \sim \beta * \log(t)$; solving for $\beta = \log(t^{-1})/\log(t) = -1$.

This negative slope estimate provides one cutoff of interest in assessing rate-time scaling relationships: log-log regressions of rate vs time that are shallower than or not significantly different from -1 are consistent with either a null relationship evolutionary change and time (time independence) or an increasing relationship between change and time, respectively.

The relationships between equations 1-3 are illustrated in Figure 2, which shows the relationship between rate and time. Figure 2A illustrate differing relationships between rate numerator and time illustrated in Figure 2B for a range of power functions. There are few theoretical models that predict the type of accelerating relationship between magnitude of evolution and time that are needed to produce a positive relationship between evolutionary rate and time. For example, neutral and adaptive models of phenotypic and molecular evolution predict either no relationship with time or linear accumulation (constant change) with time (36). Similarly, birth-death models of lineage accumulation also predict either a linear or a decelerating accumulation of log lineage number through time under most conditions. Even models of time-dependent lineage diversification make no prediction about accelerating log lineage number versus interval time across a sample of clades. Moreover, lineage-through-time

136 (LLT) plots for single clades diversifying under such a process can produce complex lineage
137 through time plots (37) that are consistent with several different underlying diversification
138 processes (38).

139 Some biological and ecological scenarios could potentially lead to accelerating change
140 with time, and thus generate positive relationships between evolutionary rates and time (Figure
141 2). Such scenarios include "diversity begets diversity" models of lineage diversification (24, 39),
142 evolution by positive frequency-dependent selection (40), runaway sexual selection driven by
143 female choice (41-43), "tipping points" in the evolution of reproductive isolation (44) and
144 populations crossing critical thresholds followed by phase transitions between alternative stable
145 states (45). How common such ecological and evolutionary scenarios are in nature is an open
146 empirical question. However, given the transient nature of such rapid and self-reinforcing
147 evolutionary processes driven by positive feedbacks (42, 43), we suspect that positive time-rate
148 scenarios are unlikely to be sustained over longer macroevolutionary time scales and should
149 quickly reach stable equilibria and largely be transient. Thus, such rapid and self-reinforcing
150 evolutionary processes are unlikely to proceed unchecked over millennia (45), as would be
151 required to generate positive rate-time relationships in empirical data such as that shown in
152 Figure 1.

153

154 **Data and simulation reveal persistence of inevitable scaling relationships**

155 Reanalysis of empirical datasets of evolutionary rate-time associations reveals little
156 consistent patterns in the relationship between amount of evolutionary change and time, despite a
157 pervasive negative relationship between rate and time. This holds for body size evolution (Figure
158 1A, E), where past work (18, 30, 31) has shown that body size changes are largely unrelated to

time, and in time-series of extant populations found no detectable change (46). Although a log-log regression of rate vs time yields a slope that is nominally steeper than -1 (β = -1.019, 95%CI -1.031, -1.007) we recover a breakpoint in the relationship between morphological change and time ($F_{2, 5388}$ = 207.2, $P < 2.2 \times 10^{-6}$, breakpoint = -2.63 log MY, SE = 0.147). The result is an estimated weak negative relationship between time and evolutionary change, followed by an increasing slope after the breakpoint (Fig. 1A, E), identical to that found by (30), but no overall slowdown in accumulated evolutionary change across the entire time-series

Similar results are seen in patterns of lineage accumulation in the fossil record (Figure 1B, F). We first found evidence for a strong negative rate-time relationship reflecting weak and variable relationship between evolutionary change and time (breakpoint regression $F_{2, 86}$ = 3.199, P = 0.046, breakpoint = -109 MY, SE = 33.13). However, this regression model was not a significantly better fit than a model with only an intercept; $F_{3, 86}$ = 2.6, P = 0.057. Consistent with this finding, a log-log regression between rate and time yields a slope that is significantly shallower than -1 (β = -0.24, 95%CI -0.36, -0.11)

On phylogenetic trees (Figure 1C, D, G, H), we also find a consistent striking negative relationships between rate and time (8) that in fact corresponds to underlying variable association between diversity and time (33, but see 47). We recover a weak positive linear relationship between diversity and time in one dataset ($F_{1, 112}$ = 14.17, P = 0.000267; Figure 1H) corresponding to a log-log regression that is significantly shallower than -1 (β = -0.53, 95%CI -0.68, -.39), and a piecewise linear relationship in another dataset (breakpoint regression $F_{2, 430}$ = 12.67, $P = 4.474 \times 10^{-6}$, breakpoint = 4.6 log MY, SE = 0.108) corresponding to a log-log regression of rate and time with a slope that is not significantly different from -1 (β = -1.04, 95%CI -1.1, -0.98).

182 Interestingly, we even recover a nonlinear negative relationship between evolutionary
183 rate and time when examining phenotypic change that occurred within a timeframe less than the
184 average generation time of the study organism (in this case, primarily long-lived fish; Figure 1E).
185 This within-generation dataset had a log-log regression of rate and time with a slope that was not
186 significantly different from -1 (β = -0.83, 95%CI -1.08, -0.58). This final example, again
187 demonstrates the appearance of a rate-time scaling relationship for a case that obviously defies
188 evolutionary explanation based on between-generation change. This conclusion is further
189 strengthened by the fact that the slope estimate does not significantly differ from the expectation
190 under a random relationship between rate numerator and time. That is, scaling phenotypic
191 change by time in order to calculate rate generates a non-linear negative relationship with time
192 even for this within-generation change (Figure 1E, J), that is likely to reflect phenotypic
193 plasticity, culling, or other non-evolutionary within-generational environmental effects.

194 In summary: the striking negative rate-time relationship shared by four independent
195 evolutionary datasets and one non-evolutionary (within generation) dataset reflects, primarily, a
196 lack of strong or consistent association between the amount of evolutionary change (rate
197 numerator) and the timescale over which this change took place (Figure 1 F-J). Although some
198 of these case-specific results have been pointed out before (e.g., (30), whose analysis we have in
199 part replicated here), we have shown that a decoupling of amount of evolution and timescale of
200 measurement is likely a general feature across a range of evolutionary datasets, from
201 morphological change to lineage diversification, that together describe the pace of life. In only
202 one case did we find any evidence of a significant negative association between evolutionary
203 change and time that was less than -1 on a log scale. Yet, even in this case, that of vertebrate
204 body size evolution, breakpoint regression indicates that the true relationship between time and
205 evolutionary change involves a complex combination of decreasing and increasing relationships

206 between time and evolutionary change through the history of vertebrates (30). We further note
207 that widespread time-independence of evolutionary change does not imply that magnitudes of
208 evolution are low or "slow". Rather, the vertical axes in Figure 1F-J often correspond to massive
209 changes in the number of lineages or morphology. The crucial point is that these large
210 evolutionary changes are typically decoupled from the time interval over which they occurred
211 and there is no evidence for any systematic time-dependency of accumulated evolutionary
212 change.

213 Simulations of classical constant-rate evolutionary models reveal that negative rate-time
214 associations readily emerge from these existing models. Phenotypic evolution by random
215 genetic drift results in a Brownian motion process wherein phenotypic variance across lineages
216 increases linearly with time (Figure 3A), and evolutionary rate is time-independent when
217 calculated for an entire clade (3E inset panel). Even this simple constant rate model results in a
218 negative scaling relationship between lineage-specific estimates of evolutionary rate and time
219 (Figure 3E). The problem is even further exacerbated an under adaptive model of natural
220 selection towards an optimum (an Ornstein-Uhlenbeck process), where a null relationship
221 between time and divergence (Figure 3B) generates a strong negative relationship between per-
222 lineage rate and time (Figure 3F), reminiscent of empirical data from vertebrate body size
223 evolution (Figure 1).

224

225 Finally, the simplest model of lineage accumulation, a constant-rate pure-birth process, also
226 leads to these types of associations. The log number of lineages accumulates approximately
227 linearly through time in a pure-birth process, as seen when sampling pure-birth phylogenies
228 differing in age (Figure 3C, 3D). Yet, pure-birth estimators of diversification rate from these

229 phylogenies (Kendall-Moran Yule rates, Figure 3G, S1) as well as maximum likelihood
230 estimates of net diversification from a birth-death diversification model (Figure S2) nonetheless
231 show a negative scaling relationship with time. In principle Yule rates do not inherently show
232 time dependence when estimates of zero rates, which rarely result in phylogenies of more than a
233 single taxon, are included. For example this can be shown by the crown-age estimates using
234 clade age – time data (Magellon-Sanderson rate estimates, Figure 3H). However, even in this
235 case non-zero rate estimates show negative time scaling (Figure 3H). Similarly, sampling
236 directly from the theoretical distribution of pure-birth richness and age yields zero-rate estimates
237 that can cancel out non-zero rates for young clades (10), we note that these zero rates are largely
238 unobservable in actual data. Our simulations and others (10) show that non-zero rates show
239 negative time-scaling even under a constant-rate pure-birth diversification process. This negative
240 scaling relationships is driven largely by the inclusion of high evolutionary rates estimated over
241 short timescales (Figure 3G), yet the scaling pattern can sometimes remain even when focusing
242 only on larger and older clades (Figure S1). This illustrates the inherent problems of interpreting
243 evolutionary change scaled by time. Moreover, we recover the same general pattern when
244 simulating phylogenies of varying age under an accelerating time-dependent diversification
245 process (Figure S3). These simulation results are not in any way meant as evaluations of these
246 models, rather a demonstration that constant rate processes readily and almost inevitably will
247 produce negative rate-time scaling relationships at least in some circumstances.

248

249 **Discussion**

250 Here we have demonstrated three main results with direct implications for interpreting
251 evolutionary rate-time relationships and their bearing on the pace of life. First, by simply

formalizing the development of the expected relationship between rate and time, we have demonstrated that there will only exist a limited range of relationships between amount of evolution and time that generate anything other than negative rate-time relationships. Second, our analysis of several independent datasets of evolutionary rates demonstrate that existing, widely-documented negative rate-time scaling relationships clearly suggest weak and inconsistent relationships between the amount of evolution and timescale of measurement, with no evidence for a systematic slowdown in accumulated evolutionary change or time-dependency. Third, using simulation of some of the most common process-based models of constant-rate evolutionary change, we demonstrate that all readily generate negative rate-time scaling relationships. Together, these results unequivocally demonstrate the challenge in interpreting widespread (2, 5, 6, 8) negative rate-time scaling relationships across varying temporal scales.

That evolutionary rates scale negatively with the timeframe over which they are measured is unsurprising given the inevitable statistical dependence between rate and time. Negative scaling relationships are therefore expected under a wide range of relationships between evolutionary change and time, in spite of fundamentally different underlying evolutionary processes behind the patterns (Figure 2). The fact that the scaling pattern is observed consistently across disparate types of data from different sources, for rates estimated in very different ways, and even within generations, strongly suggest that these negative relationships are unlikely to reflect a causal biological process (2). As Gingerich (5) emphasized, the negative scaling relationship that is generated by plotting a rate against time interval must be accounted for before rate variation across time can be meaningfully compared. Although the likely-artifactual nature of evolutionary rate-time scaling relationships has been acknowledged since (2, 3, 5, 11), the pervasive negative relationship between evolutionary rate and time interval continues to inspire evolutionary explanation (2, 6-9, 48).

This renewed interest in rate-time relationships is unfortunate in light of alternative approaches to the analysis of time-dependence of the evolutionary process. For example, relationships between the magnitude of evolutionary change (e.g., phenotypic change or the log number of new lineages arising) and time can be assessed directly, as we have done here and which has also been done by others(30, 49). For example, piece-wise or segmented regression (3, 28, 30, 50) can identify significant breakpoints in evolutionary change across time, an approach that avoids the problem of statistical confounders between rate and time interval that was highlighted by Gingerich (5). These and related statistical approaches (30) can be used to identify temporal shifts in the evolutionary process over time. It is also likely that some estimators of evolutionary rate do not show the types of inevitable time scaling relationships we have reported; for example, clade-level estimates of Brownian motion rate appear to be less affected. A main conclusion from our analysis, however, is that we should generally be surprised when evolutionary rates *do not* show negative time scaling.

Our analyses of rate numerators versus time reveal lack of consistent time-dependency across datasets (Figure 1). We note that these diverse datasets contain information from many thousands of species of extant and extinct plants, animals, and prokaryotes, range in time interval from less than one generation to hundreds of millions of years, and together span the entire history of life. A conclusion from these results, and the finding of log-log rate-time regression slopes that are shallower than null expectations, is that the persistent rate-time relationship do not provide evidence of shared features of evolution across these disparate data, *contra* some recent suggestions (2, 6, 8). In many ways our reanalysis refutes the view that high microevolutionary rates measured over short time intervals and low macroevolutionary rates measured over longer time scales indicate fundamental disparity between micro- and macroevolution. By extension, these results call into question the common view (2, 6, 8) that microevolutionary rates

300 documented in natural populations of extant organisms (51, 52) are exceptionally high in
301 comparison to macroevolutionary change over longer time scales (Fig. 1F-J; (see also 30, 53));
302 our results indicate that such a finding may be a nearly-inevitable outcome of comparing lineage-
303 specific rates of evolution measured over vastly different time intervals.

304 Existing data (Fig. 1F-J) suggest that evolutionary change (rate numerator) is remarkably
305 independent of time, across multiple temporal scales. When significant relationships between
306 time and amount of evolution do exist, they are weak and variable across datasets. Such general
307 and widespread time-independence of evolution becomes a new challenge to explain. Time-
308 independence of phenotypic evolution be explained by relatively-stable or slowly moving
309 adaptive zones, within which lineages may evolve substantially (30, 54). For lineage
310 diversification, disparity in ecological opportunity among diversifying lineages may decouple
311 clade age and species richness across taxa (34). We emphasize that while we find little
312 consistent relationships between amount of evolution and interval time, evolutionary events can
313 still be substantial, as shown in Figure 1. We also note that timing of key events in the history of
314 life has, of course, played a major role shaping the origins of diversity (55). These include shifts
315 in body size evolution (30) or rapid jumps in bill evolution in birds (56). Our results are not
316 inconsistent with such important historical events, but indicate that there is no evidence of a
317 pervasive relationship between amount of evolution and interval time. There is also evidence of
318 substantial variation in evolutionary change in response to different selective agents, including
319 human disturbances and harvesting (46), but such change in response to different environmental
320 agents does not appear to be systematically linked to time interval over which evolution was
321 recorded, as we have shown here.

322 Our results and other recent findings (10, 57) call into question the value of rate-time
323 scaling patterns as empirical evidence underlying the apparent "paradox of stasis", which is an

324 observation of far less evolutionary change observed over long timescales than what is expected
325 based on microevolution (58). For example, consider the widely-appreciated fact that
326 microevolutionary quantitative genetic models of random genetic drift are inconsistent with the
327 amount of evolutionary change in deep time (13, 59); we often find far less evolutionary change
328 in deep time than expected via drift alone, based on patterns of standing extant genetic variance.
329 However, it is noteworthy that even if phenotypic divergence in deep time was generally
330 consistent with drift under observed levels of standing variance, we would still expect to see a
331 negative scaling relationship between lineage specific rates of evolution and time interval (Figure
332 3). Although it is often claimed that stasis is widespread and a predominant mode of evolution
333 (12, 13), the results in the present study and others (57, 60, 61) reframe the view that pure stasis
334 is predominant. Given that the stasis paradox has partly been stimulated by apparent rate
335 disparities through time, which have been interpreted as indicating a fundamental qualitative
336 difference between micro- and macroevolution (6, 62, 63), our results instead indicate that the
337 paradox of stasis could be reformulated as the "paradox of time-independence" of evolutionary
338 change. Such a reformulation is also consistent with more recent interpretations of the paradox
339 (30, 57). Our analysis suggests that the decoupling of amount of evolution and time applies not
340 only to morphological change, but also to lineage accumulation.

341 Time-invariant evolutionary change still poses other challenges for reconciling micro-
342 and macroevolution (30). Constancy of evolutionary rates, and thus linear accumulation of
343 change with time, across temporal scales is expected and often observed at the molecular level
344 (36, 64). It is more difficult to explain relative time-independence in phenotypic evolution, where
345 trait change is expected to accumulate with time given strong and variable natural selection (65,
346 66), or under neutral evolution (67, 68). However, new empirical findings indicate that
347 phenotypic evolution over a range of timescales is proportional to standing phenotypic and

genetic variation (69). Such variation-limited evolution, if general across taxa, could be one possible explanation for time-constancy in evolutionary change, although it raises additional questions on how and why variational properties could be conserved through time. Time-dependence, or rather lack thereof, therefore remains a major open question in evolutionary biology.

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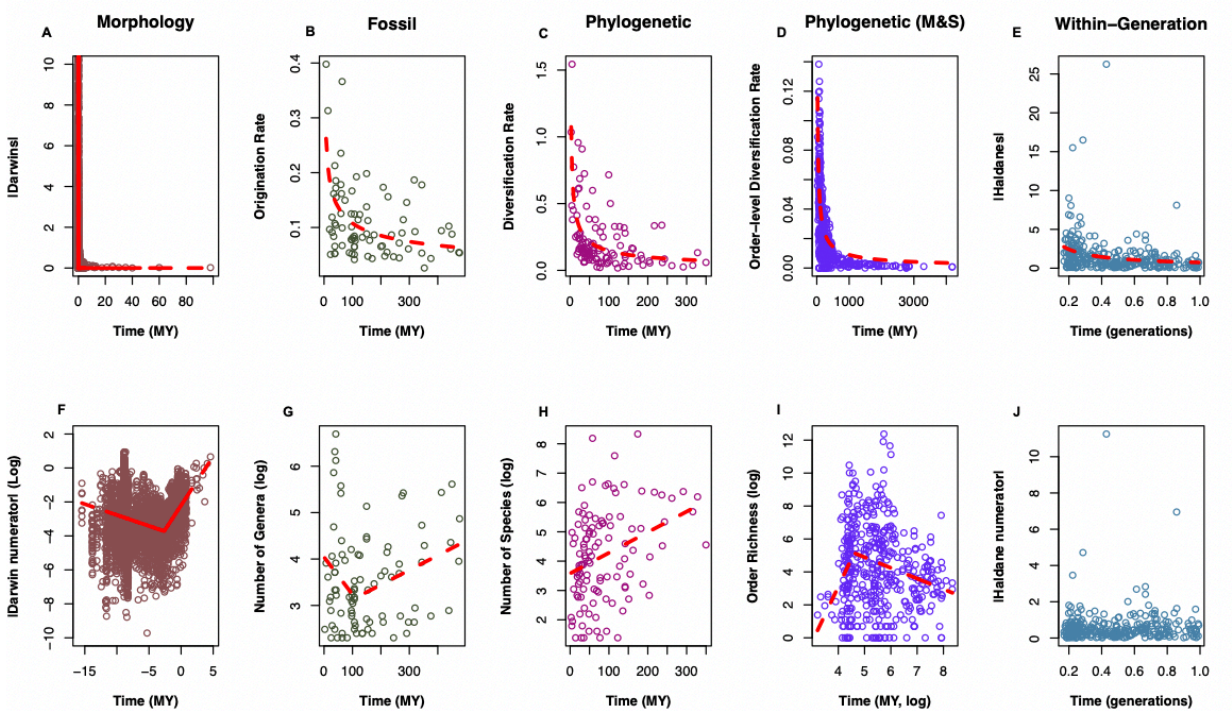


Fig. 1. Evolutionary rate-time relationships reflect null or variable underlying relationships between evolutionary change and time. Panels **A-E** show evolutionary rate plotted against the timescale of measurement (6), with dashed red lines showing the least squares fit of the function $rate = a*time^b$. Panels **F-J** plot the amount of evolutionary change (i.e., a rate numerator) against time frame for the same datasets, with dashed red lines showing the linear piecewise regression, if statistically significant. Panels **A** and **F** show vertebrate body size evolution (30), Panels **B** and **G** show diversification of genera from fossil lineages (plants, mammals, and marine animals)(8), Panels **C** and **H** show diversification data estimated from time-calibrated molecular phylogenies (8), while Panels **D** and **I** show a larger database of phylogenetic diversification rates (47) where rates were inferred directly from age and richness data (23). Panels **E** and **J** show within-generation morphological changes (mainly from fish harvesting). All nonlinear negative relationships plotted in **A-E** were statistically significant, whereas relationships in **F-J** were variable, with statistically significant breakpoints found for morphology, fossil lineage accumulation, and one estimator of phylogenetic diversification, and a positive linear relationship for another estimator of phylogenetic diversification. No significant relationship was found for the within-generation changes in panel **J**. Sample sizes for each column: **A** N = 5392

records of evolutionary change, **B** N = 90 lineages, **C** N = 114 clades, **D** N = 434 Orders, **E** N = 302 records of within-generation change.

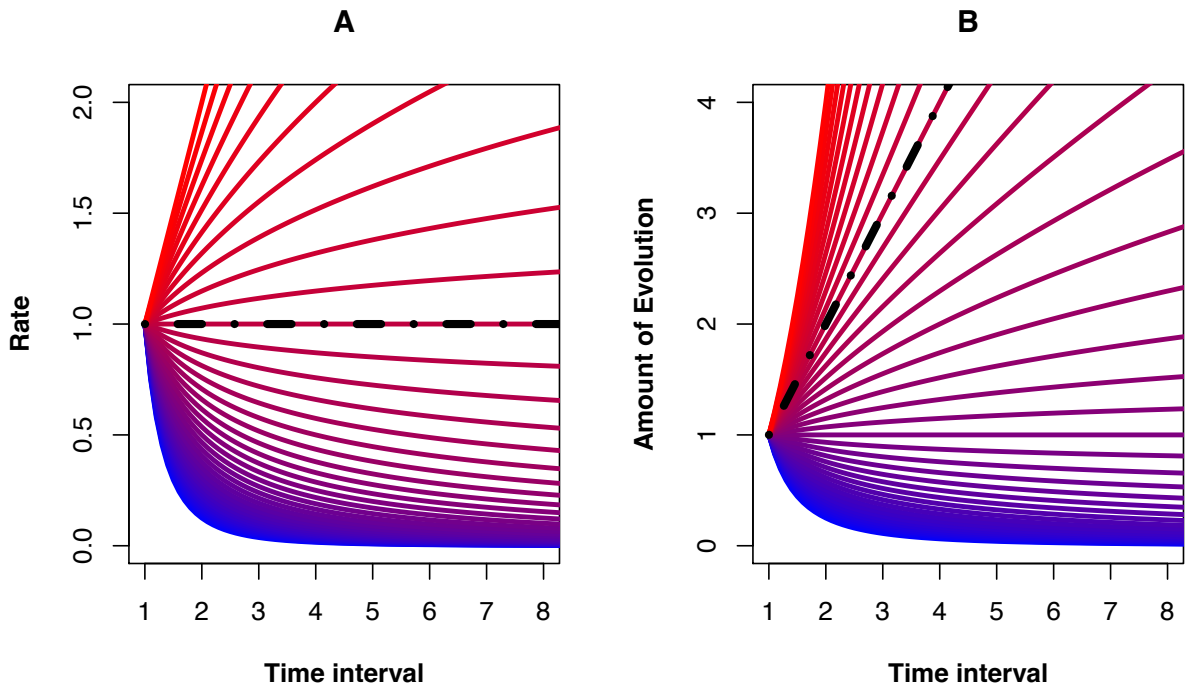


Fig. 2. Extraordinary relationships between the accumulated amount of evolution and time are required to produce positive rate-time relationships. Panel **A** shows the relationship between rate and time for various functions of the rate numerator and time, which are plotted in the same color in Panel **B**. The black line is a reference point, where there is a null relationship between rate and time. Thus, each line in Panel **A** corresponds to a specific relationship between rate numerator and time, plotted in Panel **B**; only cases of an accelerating relationship between amount of evolution and time are expected to produce positive rate-time scaling relationships. We assume for this example a form of the relationship, *amount of evolution* = $time^b$, where the function was plotted for b ranging from -2 (blue) to 2 (red). Similar general patterns are observed for other functions of change and time. Note that because we are considering these relationships in light of large amalgamations of data from disparate groups (e.g., Figure 1), as opposed to within-lineage time series, negative relationships between amount of evolution and interval time are in principle possible, even if unlikely.

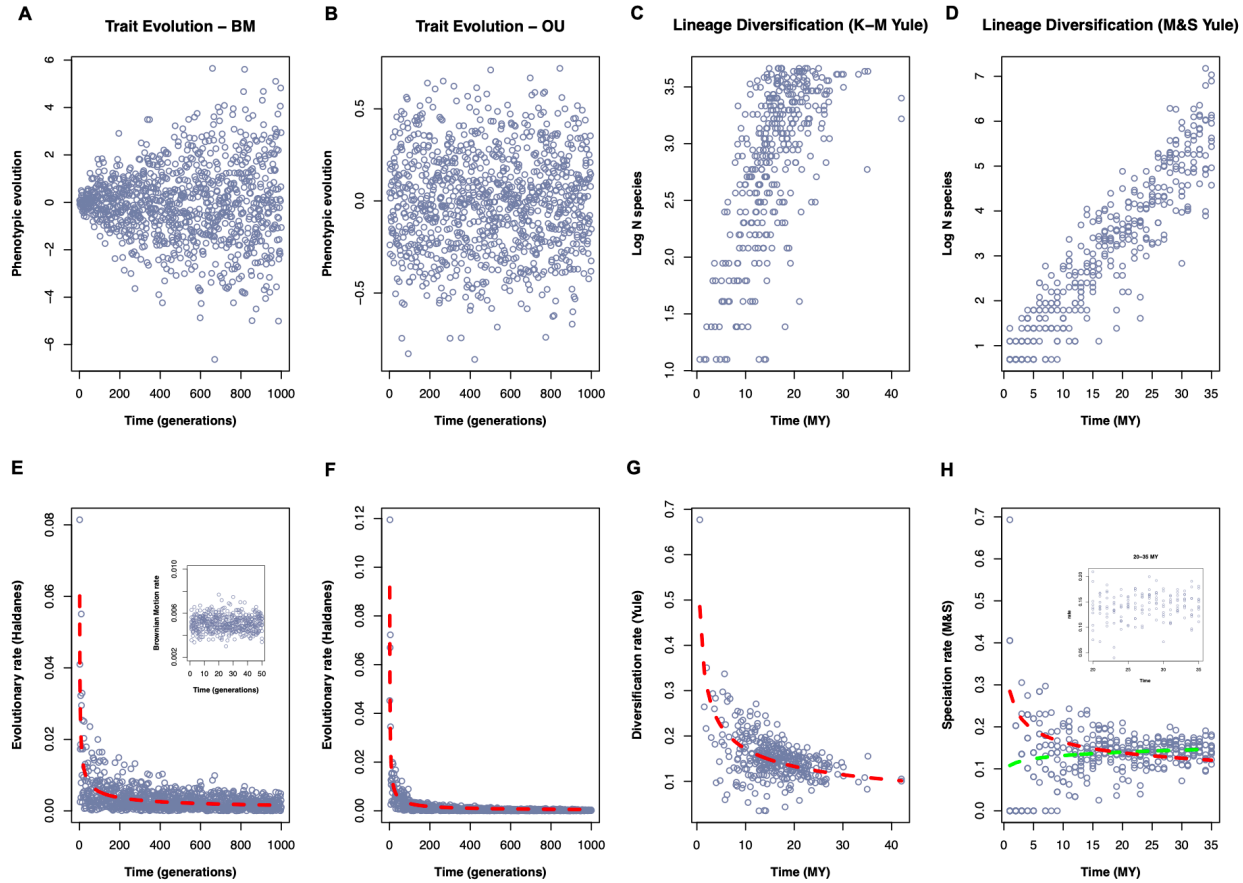


Fig. 3. Simulations of constant-rate evolutionary models reveal persistence of spurious negative rate-time relationships. Panels **A** and **E** show a simulation of phenotypic evolution under random genetic drift in the absence of natural selection, which produces a Brownian motion process (66) where variance among lineages accumulates linearly with time (**A**). Although the rate of drift is constant (**E** inset), we will nevertheless obtain a negative scaling relationship between the lineage-specific per-generation rate of evolution (**E**). Panels **B** and **F** show a simulation of phenotypic evolution under drift and stabilizing natural selection, an Ornstein Uhlenbeck process (70). This process generates no relationship between time and divergence (**B**), but again a strong negative scaling relationship with per-lineage per-generation evolutionary rate and time and hence a similar negative relationship (**F**). Panels **C** and **G** show a constant-rate pure-birth (i.e., no extinction) lineage diversification process (Yule process), where diversity accumulates approximately linearly with time (**C**). This scenario also produces a similar negative scaling relationship between the Kendall-Moran branch-length based rate estimator and time (**G**). Calculating Yule diversification rate for a different set of trees (**D**) based on the crown-age Magellon and Sanderson estimator yields a similar pattern (**H**), but in this case the inclusion of zero rate estimates (which are unlikely to be sampled in actual trees or in the simulated data in panel C) offsets (green line) the negative relationship between non-zero

observable rates and time (red line). The last 15 million years of the simulated data illustrates there is no relationship between rate and time for this time interval (**H** inset).

Methods

Data and code availability: All data is already publicly available, and we provide our complete R script as a supplemental file.

Data. We analyze existing data on rates of vertebrate body size evolution (30), which consists of data on log-fold change in body size as well as time interval over which this change occurred. For phylogenetic lineage diversification, we analyze two datasets, one in which diversification rates were estimated from the branching pattern of species-level phylogenies (8), and another larger dataset (47) where diversification rates were estimated from clade diversity and age information. For fossil data, we analyze an existing dataset (8) of emergence rates of new genera. For each dataset, we plot the standard measure of rate against the timeframe over which that rate was measured, fitting exponential linear models by nonlinear least squares (6). We also plot a measure of the rate numerator against time for each of these datasets, and fit piecewise linear regressions to identify significant linear relationships between amount of evolution and time, as well as any potential shifts in the relationship between evolution and time. For each dataset, we fit nonlinear models of the form $rate = a*time^b$ using nonlinear least squares (nls()) in R, as well as piecewise regression using the segmented package. We compared models fits of an ordinary linear regression to a model with a single breakpoint, and also when appropriate to a null model containing only an intercept, using the anova() function in R. Data presented in Figure 1 were obtained from ref 11 (available at https://github.com/fhenaod/evol_time_scaling/tree/main/data), ref 29 (Dryad doi:10.5061/dryad.7d580), ref 46, and ref 47 (database available at: https://proceeddatabase.weebly.com/).

640 Simulation We simulated three different constant rate evolutionary process. The aim of our
641 simulations was not to evaluate the performance of statistical models used to estimate rates.
642 Rather, our aim was simple to examine scaling patterns observed in the simplest cases of
643 simulated constant rate evolution. For morphological evolution, we simulated random genetic
644 drift for 1-1000 generations assuming a heritability of 0.50 and a population size of 100. We also
645 simulated evolution under genetic drift and stabilizing selection, with the same demographic and
646 genetic assumptions but assuming weak selection ($\omega^2 = 15$) towards an optimum. Each
647 simulation was started with the population at its optimum. For morphological evolution, we
648 plotted rates in units of Haldanes (4), which was natural as we simulated evolution on the scale
649 of phenotypic standard deviations. For lineage diversification, we simulated pure-birth
650 phylogenies with a constant speciation rate of 0.15, corresponding to a expected number of 2.3
651 taxa at timepoint 1 under a continuous time pure birth process. We simulated pure-birth
652 diversification because, while biologically unrealistic, it excludes explanations for rate-time
653 scaling patterns that are based on sampling biases generated by extinction. We also note that
654 although many challenges exist in sampling all possible trees in a simulation, these are identical
655 to challenges observed in actual data; namely, inclusion of trees with zero diversification rate.
656 Given the aims of our simulations noted above, we proceeded by first simulating trees
657 conditioned on number of tips as opposed to clade age, focusing first on trees with at least 3 tip
658 taxa (conclusions remain unchanged by focusing instead on trees with 20 or more tips; Figure
659 S3). We then calculated the Kendall-Moran estimator (71, 72) for the Yule process for these
660 trees using the diversitree package (26). We also estimated maximum likelihood birth-death
661 diversification rates for the same set of trees constraining diversification rates to be positive.
662 Finally, we also generated trees with ages ranging from 1-35 million years, and plot the
663 maximum likelihood estimator of the crown-age Yule diversification rate, $[\log(N)-\log(2)]/t$ (23).

Our simulations of phenotypic evolution were performed using nested for() loops in R and parameterized as described above. Our simulations of constant rate pure birth phylogenetic diversification was performed using the pbtree() function in the phytools package (73). Our simulations of time-dependent pure birth diversification (Figure S3) were performed using the TESS package (74). We provide our complete R script as supplemental material.

Acknowledgments: We thank Masahito Tsuboi and Josef Uyeda for critical feedback that improved the manuscript, as well as Chris Cooney, Charlie Cornwallis, Kjetil Voje, and Miguel Gomez for comments and discussion of these issues. **Funding:** This work was funded by grants from the Swedish Research Council (VR: grants no. 2019-03706 to SPD and no.r 2020-03123 to EIS), The Crafoord Foundation (20220602), Formas (grant 2021-01096), to SPD

Author contributions: SPD and EIS conceived of the problem and designed the study, SPD performed the analysis and drafted the manuscript. Both authors wrote the manuscript.

Competing Interest Declaration: The Authors have no competing interests to declare

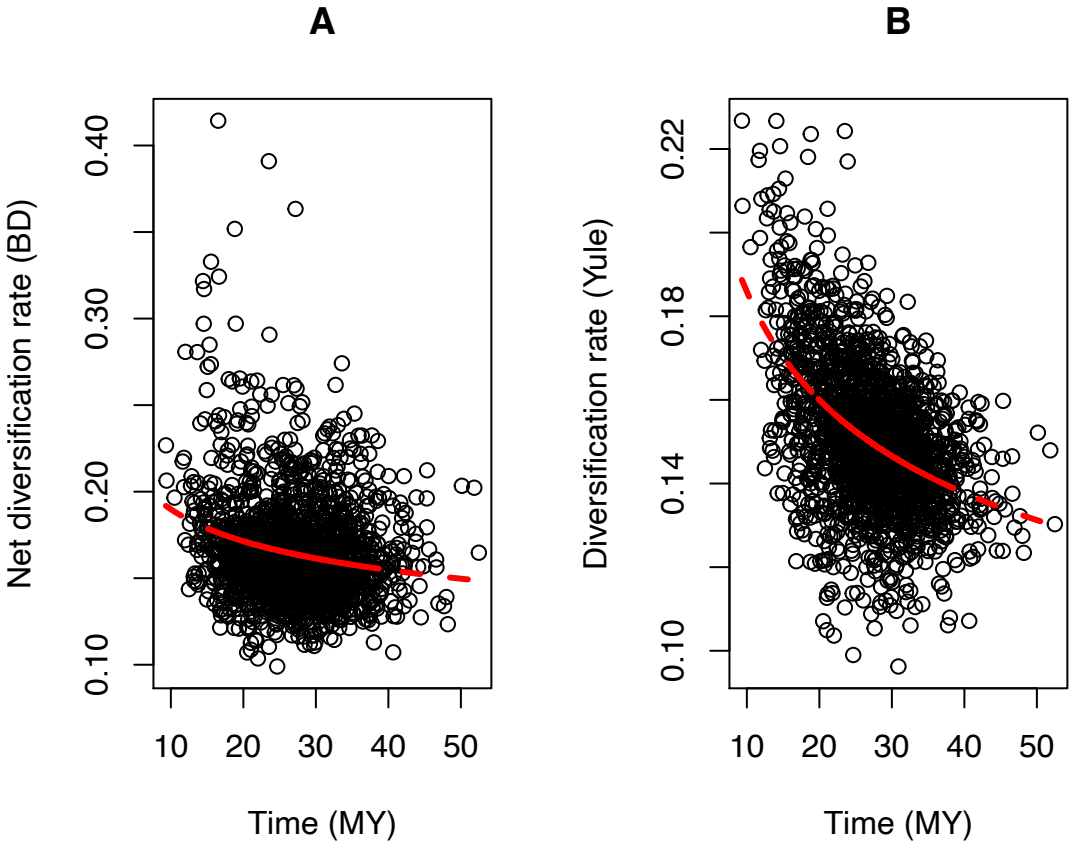
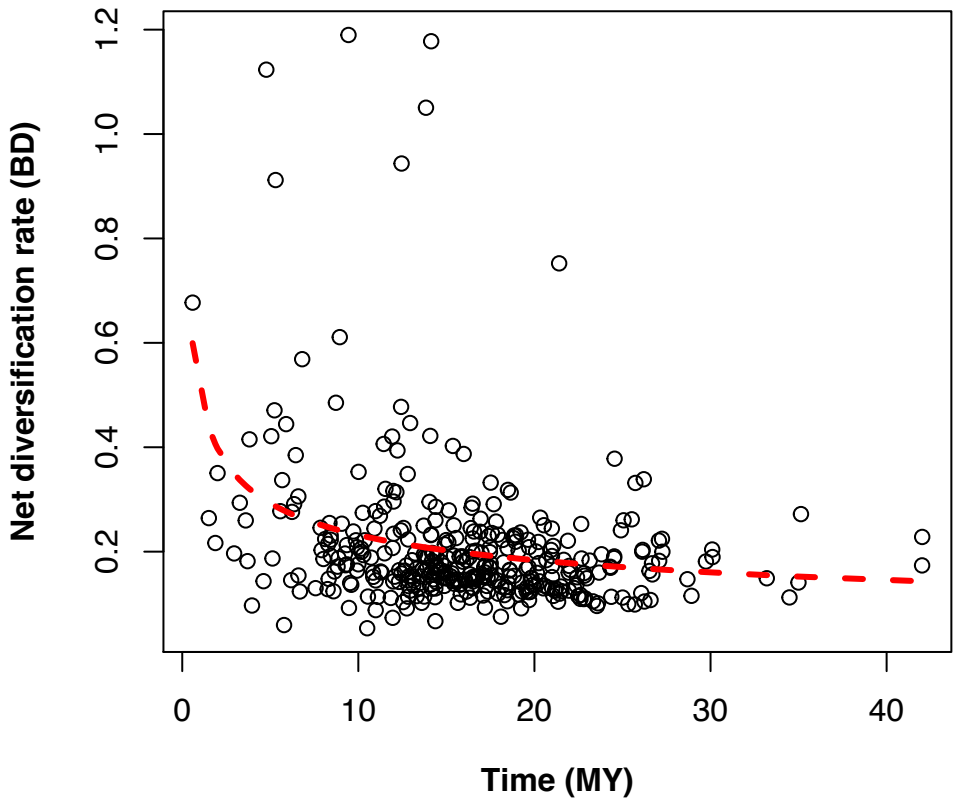


Fig. S1. Negative time-scaling of ML lineage diversification rates for trees greater than or equal to 20 tips. Shown are the scaling relationships for time and diversification estimators for pure-birth phylogenies of size equal to or greater than N = 20. Panel A shows the net diversification rate from a ML birth-death model, panel B shows the Yule estimator for the same set of trees. Other simulation conditions were as in Figure 3C, G.



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715 **Fig S2. Birth-death estimator diversification rate for trees plotted in Figure 3D, H**. Shown

716 is the ML estimate of the birth-death diversification rate λ for the same set of trees shown in

717 Figure 3D, H. Red dashed line shows the least squares fit of the model $rate = a*time^b$.

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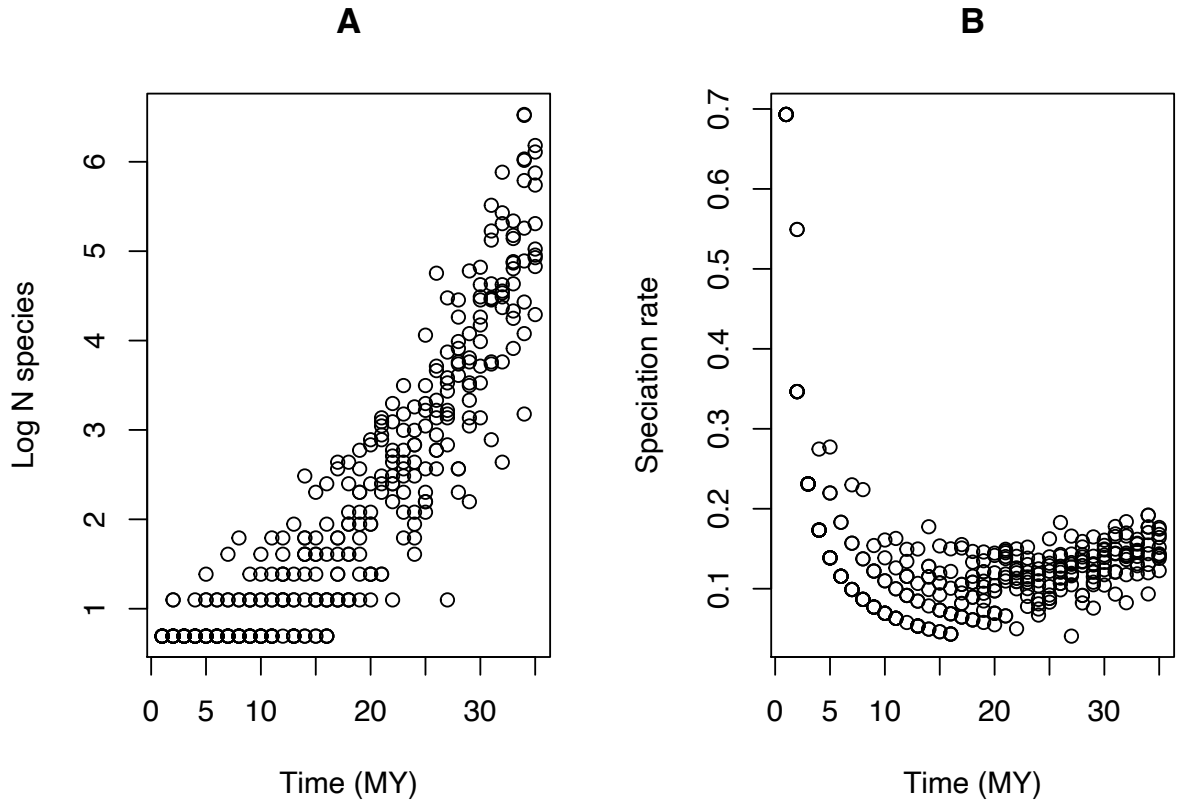

Fig. S3. Accelerating time-dependent diversification produces negative rate scaling patterns. Panels show simulations of time-dependent pure birth diversification, repeated for different timeframes from 1-35 million years under the same time-dependent diversification model. In each simulation birth rates were assumed to be linearly related to time, $\lambda \sim 0.008*time$, extinction rate $\mu = 0$. Panel **A** shows log of total diversity plotted against time for each simulation run. Panel **B** shows the estimate of net speciation rate $\log(N)/t$ as a function of time.

Qualitative conclusions remain unchanged under different parameter values, with the one salient feature being that the expected positive rate-time relationship is only recovered in deep time.