Title: **Evolutionary change is remarkably constant across timescales**

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Apparent time-scaling of evolutionary rates presents an evolutionary dilemma; rates of molecular, phenotypic, and lineage diversification scale strongly negatively with timeframe of measurement, raising questions about the processes driving this general pattern. Here we show that much of this apparent temporal scaling is an inevitable outcome of plotting a ratio against its denominator. Highly unlikely relationships between timescale and amount of evolutionary change are required to produce anything other than artefactual negative relationships between rate and time. Unscaled magnitudes of evolution are largely unrelated to time, are easily explained by existing evolutionary models, and reframe the widely-held view of disparate pace of micro- and macroevolution. Time-independence of evolutionary change raises new questions about the factors that generate such temporal consistency in evolution.

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, in that 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 biological hypotheses for 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] and model mis-specification [2]. 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 [10-14].

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 [15]. While this is a well-known statistical issue across a range of scientific fields [5,16-19], 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 [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, and the empirical evidence instead suggest remarkable time-constancy of evolutionary change across timescales.

The negative rate-time association is nearly inevitable

All measures of evolutionary rate are a function of evolutionary change scaled by time

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

where y is some measure of rate, 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 [20] and Haldanes [4] have been used to describe morphological rate, and other types of rate estimators measure per-capita origination rate of fossil lineages [21] and phylogenetic net diversification rate [22]. Other estimates are obtained from more sophisticated statistical models of evolution [23-25]. Regardless, all of these measures of evolutionary rates are, by definition, scaled by time.

The mathematical dependence between rate and time is an obvious challenge in interpreting the time-dependence of evolutionary rate [5]. Moreover, even a random association

between evolutionary change and time will result in a strong negative scaling relationship between rate and time [26]. The strength of this relationship will only increase with a greater range of timescales sampled [15]. This problem of interpreting relationships between a rate and the timescale over which rates have been measured have been discussed in other scientific fields outside evolutionary biology, including geology [27] and paleontology [28]. This problem has also raised in evolutionary biology, in the context of rates of morphological evolution [3,5,17,29-31] and lineage diversification [32-34]. 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 evolution (rate numerator) as a function of time,

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

where d is evolutionary divergence, the magnitude of evolutionary change. This could be 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 slope estimate of β

91 = -1 [5]. Thus, this slope estimate provides one cutoff of interest in assessing rate-time scaling
92 relationships: log-log regressions of rate vs time that are shallower than or not significantly
93 different from -1 are consistent with either a null relationship evolutionary change and time (time
94 independence) or an increasing relationship between change and time, respectively. Thus, if
95 there would exist a true biological, non-artefactual relationship between evolutionary rates and
96 time driven by accelerating change with time, we would expect log-log regressions with slopes
97 that are steeper than -1.

98 The relationships between equations 1-3 are illustrated in Figure 2, which shows the
99 relationship between rate and time and rate numerator and time illustrated for a range of power
100 functions. There are few existing models of evolution that predict the type of accelerating
101 relationship between magnitude of evolution and time needed to produce a positive relationship
102 between evolutionary rate and time. For example, neutral and adaptive models of phenotypic and
103 molecular evolution predict either no relationship with time or linear accumulation (constant
104 change) with time [35]. Similarly, birth-death models of lineage accumulation also predict either
105 linear or a decelerating accumulation of log lineage number through time under most conditions.
106 Even models of time-dependent lineage diversification, including models of accelerating
107 diversification rate with time before or towards present during the diversification of a single
108 clade [23], make no prediction about accelerating log lineage number versus interval time across a
109 sample of clades. Moreover, lineage-through-time (LLT) plots for single clades diversifying
110 under such a process can produce complex lineage through time plots [36] that are consistent with a
111 range of diversification processes [37].

112 Some specific biological and ecological scenarios could lead to accelerating change with
113 time, and thus potentially generate positive relationships between evolutionary rates and time
114 (Figure 2). Such scenarios include "diversity begets diversity" models of lineage diversification

[23,38], evolution by positive frequency-dependent selection [39], runaway sexual selection driven by female choice [40-42], "tipping points" in the evolution of reproductive isolation [43] and populations crossing critical thresholds followed by phase transitions between alternative stable states [44]. How common such ecological and evolutionary scenarios are in nature is an open empirical question. However, given the transient nature of such rapid and self-reinforcing evolutionary processes driven by positive feedbacks [41,42], we suspect that positive time-rate scenarios are unlikely to be sustained over longer macroevolutionary time scales but should instead rather quickly reach stable equilibria. Thus, such rapid and self-reinforcing evolutionary processes seem unlikely to proceed unchecked over millennia [44], as would be required to generate positive rate-time relationships in empirical data such as that shown in Figure 1.

Data and simulation reveal persistence of inevitable scaling relationships

Reanalysis of well-known examples of evolutionary rate-time associations reveals little consistent patterns in the relationship between amount of evolutionary change and time, despite a pervasive negative relationship between rate and time. This holds for body size evolution (Figure 1A, E), where past work [17,29,30] has shown that body size changes are largely unrelated to time, and in time-series of extant populations found no detectable change [45]. Although a log-log regression of rate vs time yields a slope that is significantly 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).

137 Similar results are seen in patterns of lineage accumulation in the fossil record (Figure
138 1B, F), where we found evidence for a strong negative rate-time relationship reflecting weak and
139 variable relationship between evolutionary change and time (breakpoint regression $F_{2, 86} = 3.199$,
140 $P = 0.046$, breakpoint = -109 MY, SE = 33.13). However, this regression model was not a
141 significantly better fit than a model with only an intercept; $F_{3, 86} = 2.6$, $P = 0.057$. Consistent
142 with this finding, a log-log regression between rate and time yields a slope that is significantly
143 shallower than -1 (β = -0.24, 95%CI -0.36, -0.11)

144 On phylogenetic trees (Figure 1C, D, G, H), we also find a consistent striking negative
145 relationships between rate and time [8] that in fact corresponds to underlying variable association
146 between diversity and time [32,]but see [46]. We recover a weak positive linear relationship between
147 diversity and time in one dataset ($F_{1, 112} = 14.17$, $P = 0.000267$; Figure 1H) corresponding to a
148 log-log regression that is significantly shallower than -1 (β = -0.53, 95%CI -0.68, -.39), and a
149 piecewise linear relationship in another dataset (breakpoint regression $F_{2, 430} = 12.67$, $P = 4.474$
150 $\times 10^{-6}$, breakpoint = 4.6 log MY, SE = 0.108) corresponding to a log-log regression of rate and
151 time with a slope that is not significantly different from -1 (β = -1.04, 95%CI -1.1, -0.98).

152 Interestingly, we even recover a nonlinear negative relationship between evolutionary
153 rate and time when examining phenotypic change that occurred within a timeframe less than the
154 average generation time of the study organism (in this case, primarily fish; Figure 1E). This
155 within-generation dataset had a log-log regression of rate and time with a slope that was not
156 significantly different from -1 (β = -0.83, 95%CI -1.08, -0.58). This demonstrates the appearance
157 of a rate-time scaling relationship for a case that obviously defies evolutionary explanation based
158 on between-generation change. This conclusion is further strengthened by the fact that the slope
159 estimate does not significantly differ from the expectation under a random relationship between

160 rate numerator and time. That is, scaling phenotypic change by time in order to calculate rate
161 generates a non-linear negative relationship with time even for this within-generation change
162 (Figure 1E, J), that is likely to reflect phenotypic plasticity, culling, or other non-evolutionary
163 within-generational environmental effects.

164 In summary: the striking negative rate-time relationship shared by a diverse array of
165 evolutionary datasets reflects, primarily, a lack of strong or consistent association between the
166 amount of evolutionary change and the timescale over which this change took place (Figure 1 F-
167 J). In only one case did we find evidence of a significant negative association between
168 evolutionary change and time that was less than -1 on a log scale. Yet, even in this case, that of
169 vertebrate body size evolution, breakpoint regression indicates that the true relationship between
170 time and evolutionary change involves a complex combination of decreasing and increasing
171 relationships between time and evolutionary change through the history of vertebrates [29]. We
172 further note that widespread time-independence of evolutionary change does not imply that
173 magnitudes of evolution are low or "slow". Rather, the vertical axes in Figure 1F-J often
174 correspond to massive changes in the number of lineages or morphology, yet these evolutionary
175 changes are largely decoupled from the time interval over which they occurred.

176 Simulations of classical constant-rate evolutionary models reveal that negative rate-time
177 associations readily emerge as statistical artifacts. Phenotypic evolution by random genetic drift
178 results in a Brownian motion process wherein phenotypic variance across lineages increases
179 linearly with time (Figure 3A), and evolutionary rate is time-independent when calculated for an
180 entire clade (3D inset panel). Even this simple constant rate model results in a negative scaling
181 relationship between lineage-specific estimates of evolutionary rate and time (Figure 3D). The
182 problem is even further exacerbated an under adaptive model of natural selection towards an
183 optimum (an Ornstein-Uhlenbeck process), where a null relationship between time and

divergence (Figure 3B) generates a strong negative relationship between per-lineage rate and time (Figure 3E), reminiscent of empirical data from vertebrate body size evolution (Figure 1). Finally, the simplest model of lineage accumulation, a constant-rate pure-birth process, also leads to these types of associations. The log number of lineages accumulates approximately linearly through time in a pure-birth process, as seen when sampling pure-birth phylogenies differing in age (Figure 3C). Yet, pure-birth estimates of diversification rate nonetheless show a negative scaling relationship with time (Figure 3F) that cannot be fully explained by the "push of the past" [8], as we recover this effect in the absence of extinction and in model parameterizations that yield high expected values of diversity early in time, minimizing the potential of only sampling clades with stochastically high rates early in their history (see Materials and Methods). This latter negative scaling relationships is driven entirely by the inclusion of high evolutionary rates estimated over short timescales (Figure 3F). This illustrates the inherent problems of interpreting evolutionary change scaled by time even when the evolutionary model is not mis-specified. Moreover, we recover the same general pattern when simulating phylogenies of varying age under an accelerating time-dependent diversification process (Figure S1).

Discussion

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 most likely statistical artifacts [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 [2,3,5,10], the pervasive negative relationship between evolutionary rate and time interval continues to inspire evolutionary explanation [2,6-9,47].

This renewed interest in artefactual 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 [29,48]. For example, piece-wise or segmented regression [3,27,29,49] 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 [29] can be used to identify temporal shifts in the evolutionary process over time.

Our analyses of rate numerators versus time reveal lack of consistent time-dependency across datasets (Figure 1). 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* recent suggestions [2,6,8]. Our reanalysis refutes the view that high microevolutionary rates measured over short time intervals and low macroevolutionary rates measured over longer time scales indicates fundamental disparity between micro- and macroevolution. By extension, the common view [2,6,8] that microevolutionary rates documented in natural populations of extant

organisms [50,51] are exceptionally high in comparison to macroevolutionary change over longer time scales is not empirically supported, neither in this study nor by other empirical evidence (Fig. 1F-J; see also [29,52]).

Existing data (Fig. 1F-J) instead suggest that evolutionary change is remarkably independent of time, across multiple temporal scales. Such time-constancy becomes a new challenge to explain. Time-independence of phenotypic evolution be explained by relatively-stable or slowly moving adaptive zones, within which lineages may evolve substantially [29,53]. For lineage diversification, disparity in ecological opportunity among diversifying lineages may decouple clade age and species richness across taxa [33]. We emphasize that while we find little consistent relationships between amount of evolution and interval time, evolutionary events can still be substantial, as shown in Figure 1. We also note that timing of key events in the history of life has, of course, played a major role shaping the origins of diversity [54]. These include shifts in body size evolution [29] or rapid jumps in bill evolution in birds [55]. Our results are not inconsistent with such important historical events, but indicate that there is no evidence of a pervasive relationship between amount of evolution and interval time. There is also evidence of substantial variation in evolutionary change in response to different selective agents, including human disturbances and harvesting [45], but such change in response to different environmental agents does not appear to be systematically linked to time interval over which evolution was recorded, as we have shown here.

Our results and other recent findings [56] also call into question the empirical evidence underlying the apparent "paradox of stasis", which is an observation of far less evolutionary change observed over long timescales than what is expected based on microevolutionary rates [57]. Although it is often claimed that stasis is widespread and a predominant mode of evolution [11,12], the results in the present study and others [56,58,59] cast doubt on the view that stasis is predominant.

Given that the stasis paradox has partly been stimulated by apparent rate disparities through time, which have been interpreted as indicating a fundamental qualitative difference between micro- and macroevolution [6,57,60,61], our results instead indicate that the paradox of stasis could be reformulated as the "paradox of time-independence" of evolutionary change. Such a reformulation is also consistent with more recent interpretations of the paradox [29,56].

Time-invariant evolutionary change still poses other challenges for reconciling micro- and macroevolution [29]. Constancy of evolutionary rates, and thus linear accumulation of change with time, across temporal scales is expected and often observed at the molecular level [35]. It is more difficult to explain relative time-independence in phenotypic evolution, where trait change is expected to accumulate with time given strong and variable natural selection [62,63], or under neutral evolution [64,65]. However, new empirical findings indicate that phenotypic evolution over a range of timescales is proportional to standing phenotypic and genetic variation [66]. 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, of the evolutionary process therefore remains a major open question in evolutionary biology.

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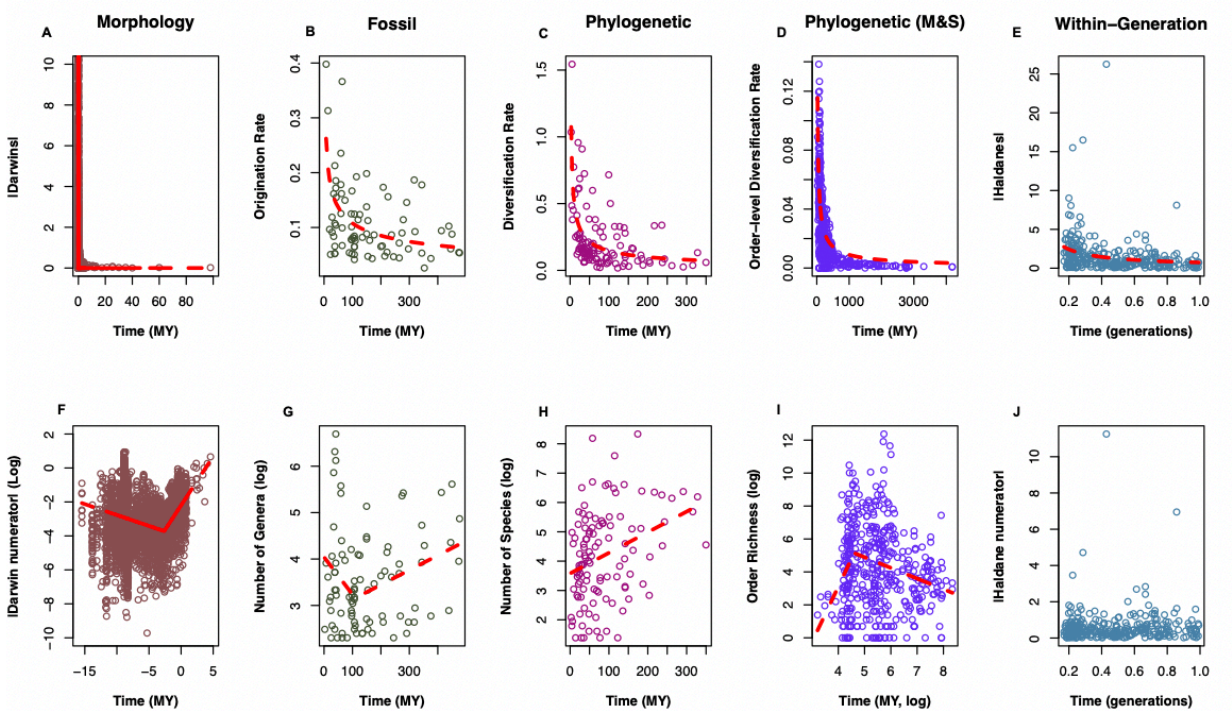

Fig. 1. Evolutionary rate-time relationships reflect null or variable underlying relationships between evolutionary change and time. Panels **A-E** show evolutionary rate plotted against the timescale of measurement [6], with dashed red lines showing the least squares fit of the function $rate = a*time^b$. 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 [29], 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 [46] where rates were inferred directly from age and richness data [22]. 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

439 of phylogenetic diversification. No significant relationship was found for the within-generation
440 changes in panel **J**.

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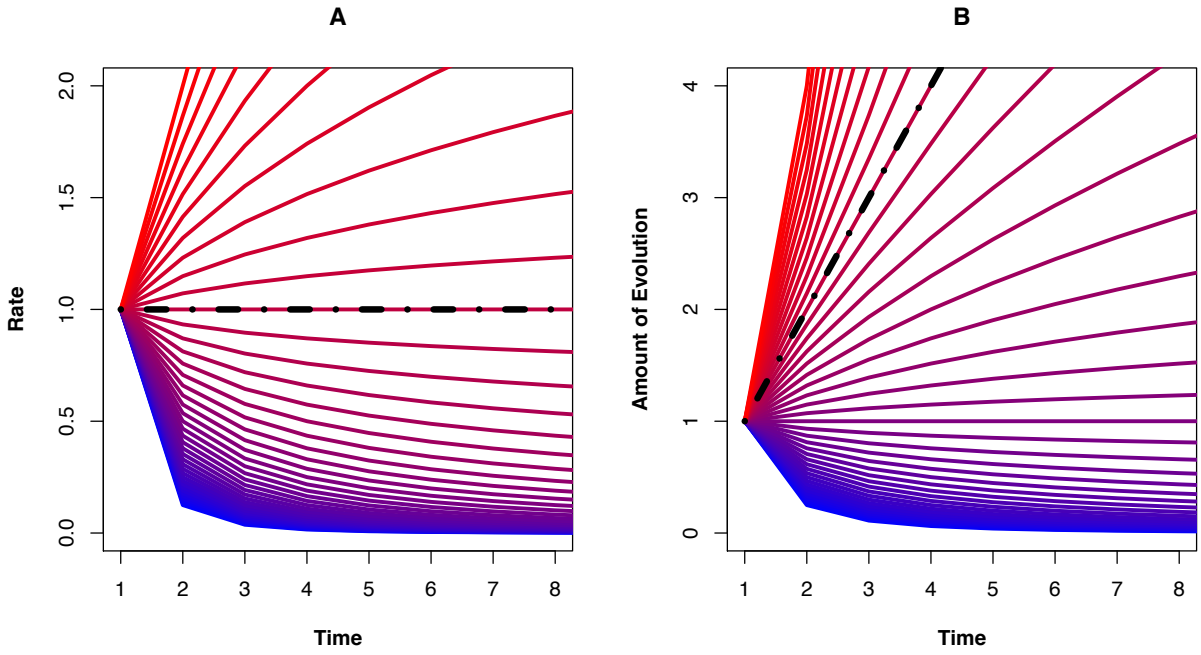

Fig. 2. Extraordinary relationships between the amount of evolution and time are required to produce positive rate-time relationships. Panel **A** shows the relationship between rate and time for various functions of the rate numerator and time, which are plotted in the same color in Panel **B**. The black line is a reference point, where there is a null relationship between rate and time. 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.

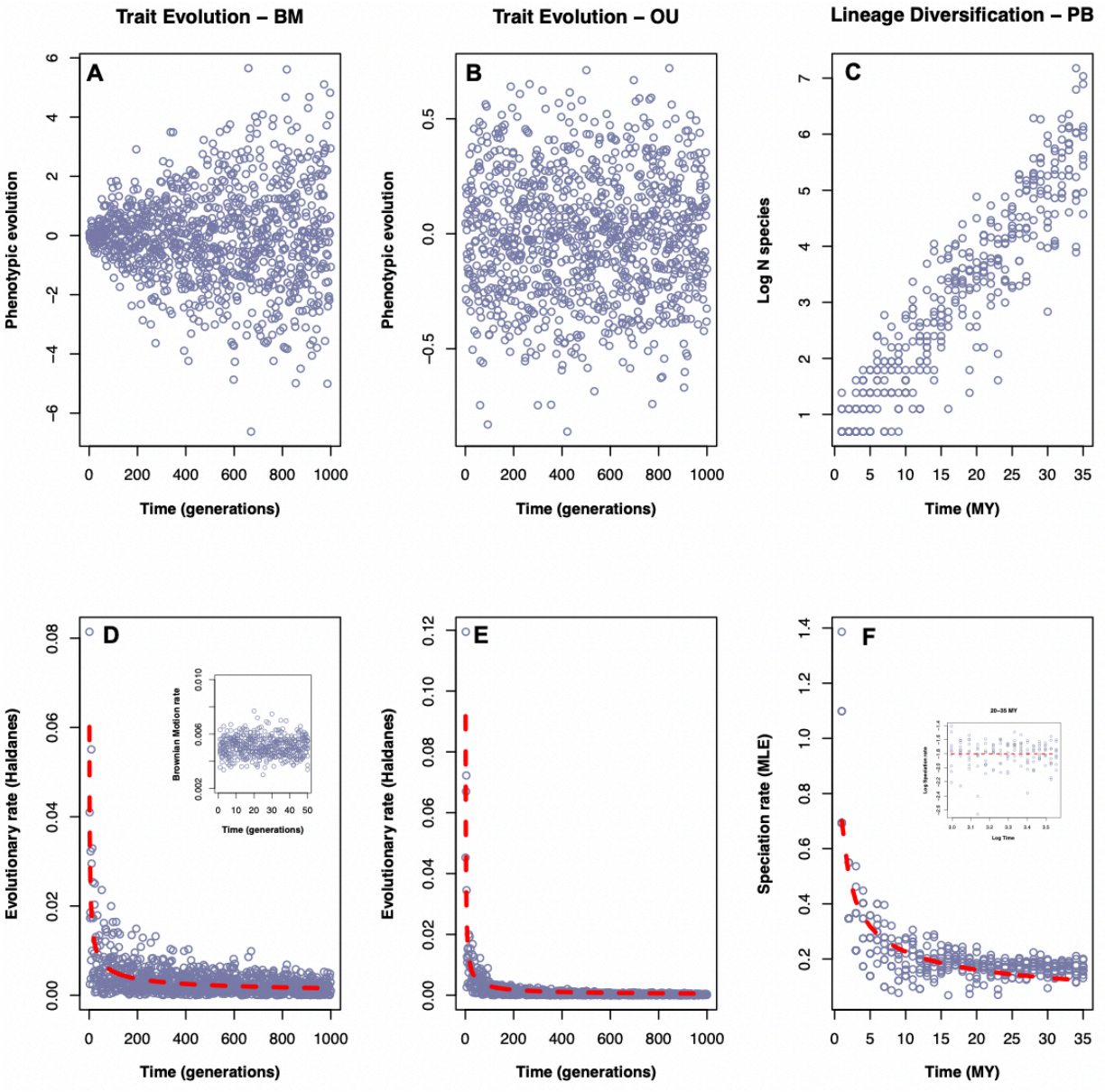

Fig. 3. Simulations of constant-rate evolutionary models reveal persistence of spurious negative rate-time relationships. Panels **A** and **D** show a simulation of phenotypic evolution under random genetic drift in the absence of natural selection, which produces a Brownian motion process [63] where variance among lineages accumulates linearly with time (**A**). Although the rate of drift is constant (**D** inset), we will nevertheless obtain a negative scaling relationship between the lineage-specific per-generation rate of evolution (**D**). Panels **B** and **E** show a simulation of phenotypic evolution under drift and stabilizing natural selection, an Ornstein Uhlenbeck process [67]. 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 spurious negative relationship(**E**). Panels **C** and **F** show a constant-rate pure-birth (i.e., no extinction) lineage diversification process, where diversity accumulates approximately linearly with time (**C**). This scenario also produces a similar spurious a negative scaling relationship between the rate estimator [22] and time (**F**). That this relationship is a

statistical artifact with no need for any evolutionary explanation can be seen by fitting a log-linear model to the last 15 million years of the simulated data, which shows there is no relationship between rate and time for this time interval (**F** 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 [29], 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 [46] 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 6 (available at https://github.com/fhenaod/evol_time_scaling/tree/main/data), ref 24 (Dryad doi:10.5061/dryad.7d580), ref 40, and ref 39 (database available at: https://proceeddatabase.weebly.com/).

Simulation We simulated three different constant rate evolutionary process. For morphological evolution, we simulated random genetic drift for 1-1000 generations assuming a heritability of

532 0.50 and a population size of 100. We also simulated evolution under genetic drift and stabilizing
533 selection, with the same demographic and genetic assumptions but assuming weak selection (ω^2
534 = 15) towards an optimum. Each simulation was started with the population at its optimum. For
535 morphological evolution, we plotted rates in units of Haldanes [4], which was natural as we
536 simulated evolution on the scale of phenotypic standard deviations. For lineage diversification,
537 we simulated pure-birth phylogenies with a constant speciation rate of 0.15, corresponding to a
538 expected number of 2.3 taxa at timepoint 1 under a continuous time pure birth process. We
539 generated trees with ages ranging from 1-35 million years, and plot the maximum likelihood
540 estimator of the pure-birth diversification rate, $\log(N)/t$ [22]. Our simulations of phenotypic
541 evolution were performed using nested for() loops in R and parameterized as described above.
542 Our simulations of constant rate pure birth phylogenetic diversification was performed using the
543 pbtree() function in the phytools package [68]. Our simulations of time-dependent pure birth
544 diversification (Figure S1) were performed using the TESS package [69].

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

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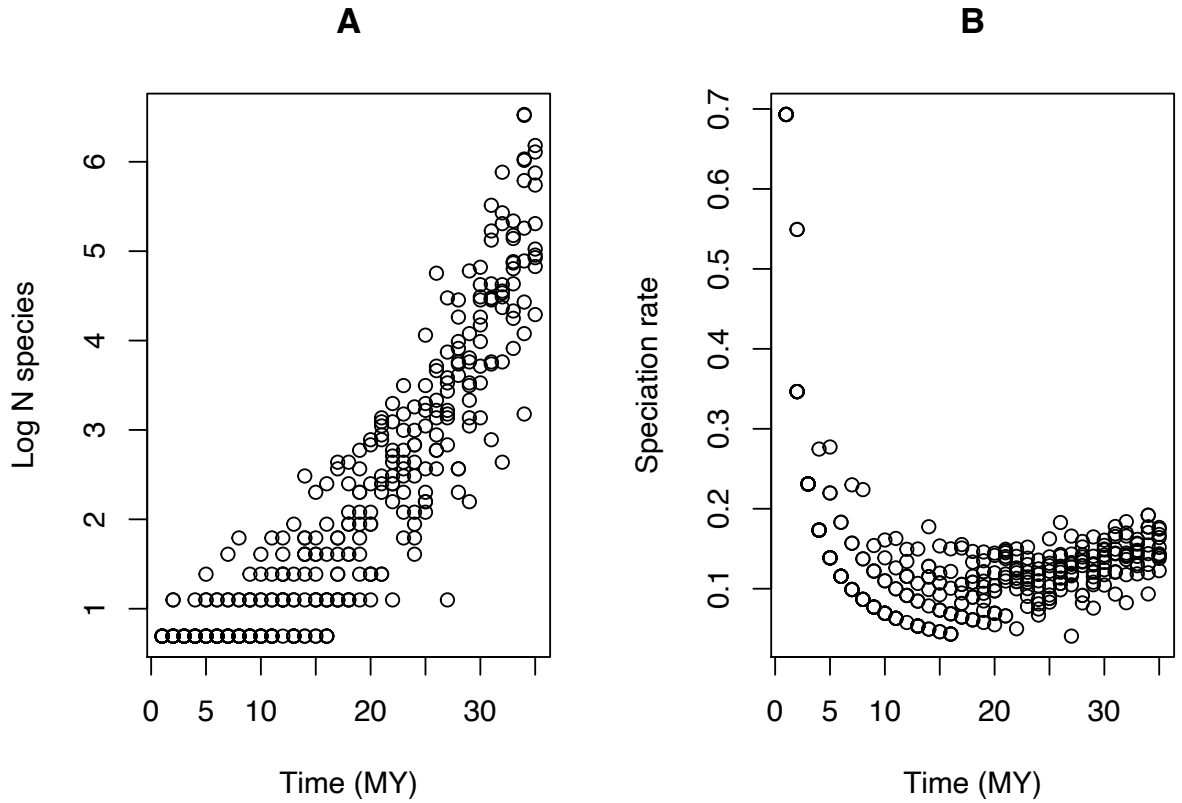

Fig. S1. Accelerating time-dependent diversification produces negative rate scaling patterns. Panels show simulations of time-dependent pure birth diversification, repeated for different timeframes from 1-35 million years under the same time-dependent diversification model. In each simulation birth rates 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.