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

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Abstract

Apparent time-scaling of evolutionary rates presents a potential dilemma. Rates of molecular, phenotypic, and lineage diversification typically scale negatively with time interval, raising questions about the ecological and evolutionary processes driving this pattern. Here we explore the fact that much apparent temporal scaling is an inevitable outcome of plotting a ratio against its denominator. We show that this effect readily explains the qualitative existence of a negative scaling relationship across different types of evolutionary rates. Highly unlikely relationships between timescale and accumulated evolutionary change are required to produce anything other than negative rate-time relationships. Empirical rate-time scaling relationships reflect unscaled magnitudes of evolution that are either unrelated to time and/or vary in their relationship with time. Over 99% of variation in rate-time relationships across five datasets can be explained by time variation alone, and simulations suggest a range of rate-time scaling exponents can be generated by similar evolutionary processes. These results raise challenges in the interpretation of evolutionary rate-time relationships, and highlight segmented regression as one useful approach to understanding temporal variation in evolution. Time-independence of evolutionary change raises new questions about the factors that generate 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 (Gingerich 1983, 1993; Hendry & Kinnison 1999; Gingerich 2001; Harmon *et al.* 2021). Such apparent time-dependence has subsequently been documented consistently for nearly every possible measure of evolutionary rate (Rolland *et al.* 2023), including rates of morphological and molecular evolution (Ho *et al.* 2011), 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 into account, because evolutionary rates over different time intervals were not directly comparable (Gingerich 1983). 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 and ecological environment that could explain such general time-scaling (Henao Diaz *et al.* 2019; Rolland *et al.* 2023). Recent technical and statistical explanations to these apparent negative rate-time scaling relationships focus on sampling biases (Louca *et al.* 2022), such as a the "push of the past" (Rolland *et al.* 2023) model mis-specification (Harmon *et al.* 2021), and measurement error (O'Meara & Beaulieu 2024). 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 (Henao Diaz *et al.* 2019; Harmon *et al.* 2021; Rolland *et al.* 2023). The renewed interest in such apparent time-dependence of evolutionary rates has rekindled long-standing ideas and hypotheses about fundamental disparities between micro- and macroevolution (Eldredge & Gould 1972; Gould & Eldredge 1977; Gould 1984; Gould & Eldredge 1993; Hansen & Houle 2004).

We here focus on elaborating the simplest explanation for such a pattern: the inevitable negative correlation generated by plotting a ratio against its own denominator (Pearson 1897). This is a well-known statistical issue across a range of scientific fields (Atchley *et al.* 1976; Gingerich 1983; Prarie & Bird 1989; Jackson & Somers 1991; Arnold 2014), including research on evolutionary rates (e.g., see Box 1 in Harmon *et al.* 2021). 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 a weak, null, or variable relationship between magnitude of evolution and time. While some of these points have been well-appreciated in the past, our revisit to this phenomenon emphasizes that rate-time plots will nearly always appear to indicate qualitative consistency of the evolutionary process, in the form of negative scaling relationships, across types of evolutionary change. Our analysis also highlights new challenges in interpreting quantitative estimates of rate-time scaling patterns. We highlight the use of segmented regression techniques that can identify significant breakpoints in evolutionary time series

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)

129 and t is some measure of time interval over which change was observed or inferred (e.g.
130 generations, or years) and noting that rates are undefined at $t = 0$. Some classical estimates of
131 evolutionary rate are calculated directly by dividing phenotypic change with time, the latter
132 typically measured in generations or years. For example, Darwins (Haldane 1949)
133 $\left(\frac{\ln(\bar{z}_1-\bar{z}_2)}{\Delta t*10^6}\right)$ and Haldanes (Gingerich 1993)
134 $\left(\frac{(\bar{z}_1-\bar{z}_2)}{\Delta t}, \text{were z is in units of phenotypic standard deviations}\right)$ have been used to describe
135 morphological rate, and other types of rate estimators measure per-capita origination rate of
136 fossil lineages (Foote 2000) and phylogenetic net diversification rate (Magallon & Sanderson
137 2001). Other estimates are obtained from more sophisticated statistical models of evolution (Nee
138 *et al.* 1994; FitzJohn 2012; Rabosky *et al.* 2014). Regardless, all evolutionary rate measures are,
139 per definition, scaled by time (e.g., waiting times between observed branching events on a
140 phylogeny are a direct component of the likelihood in maximum likelihood models of birth-death
141 diversification (Nee *et al.* 1994)).

142 The inevitable mathematical dependence between rate and time is an obvious challenge
143 in interpreting the time-dependence of evolutionary rate (Gingerich 1983). For example, a
144 random association between evolutionary change and time will result in a strong negative scaling
145 relationship between rate and time (Kenney 1982). The strength of this negative relationship will
146 inevitably increase when a greater range of timescales is sampled (Pearson 1897). The problem
147 of interpreting such inevitable negative relationships between a rate and time interval have been
148 discussed in several fields outside evolutionary biology, including geology (Schlager *et al.* 1998)
149 and paleontology (Sheets & Mitchell 2001). The problem has also been raised in evolutionary
150 biology, both in the context of rates of morphological evolution (Gingerich 1983; Hendry &
151 Kinnison 1999; Roopnarine 2003; Estes & Arnold 2007; Uyeda *et al.* 2011; Arnold 2014) and

lineage diversification (Rabosky 2009; Wiens 2011; Rabosky *et al.* 2012). 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, with prime denoting the first derivative. 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 $\beta = -1$ (Gingerich 1983). 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

174 different from -1 are consistent with either a null relationship between evolutionary change and
175 time (time independence) or an increasing relationship between accumulated change and time,
176 respectively. For some cases, such as morphological evolution, it is possible to develop
177 predictions for rate-time scaling parameters under various models of evolutionary change
178 (Hansen 2024; Holstad *et al.* 2024).

179 The relationships between equations 1-3 are illustrated in Figure 2, which shows the
180 relationship between rate and time. Figure 2A illustrate differing relationships between rate
181 numerator and time illustrated in Figure 2B for a range of power functions. There are few
182 theoretical models that predict the type of accelerating relationship between magnitude of
183 evolution and time that are needed to produce a positive relationship between evolutionary rate
184 and time. For example, neutral and adaptive models of phenotypic and molecular evolution
185 predict either no relationship with time or linear accumulation (constant change) with time
186 (Morgan 1998). Similarly, birth-death models of lineage accumulation also predict either a
187 linear or a decelerating accumulation of log lineage number through time under most conditions.
188 Even models of time-dependent lineage diversification make no prediction about accelerating
189 log lineage number versus interval time across a sample of clades. Moreover, lineage-through-
190 time (LLT) plots for single clades diversifying under such a process can produce complex
191 lineage through time plots (Paradis 2015) that are consistent with several different underlying
192 diversification processes (Louca & Pennell 2020).

193 Some biological and ecological scenarios could potentially lead to accelerating change
194 with time, and thus generate positive relationships between evolutionary rates and time (Figure
195 2). Such scenarios include "diversity begets diversity" models of lineage diversification (Nee *et*
196 *al.* 1994; Emerson & Kolm 2005), evolution by positive frequency-dependent selection
197 (Chouteau *et al.* 2016), runaway sexual selection driven by female choice (Fisher 1930; Lande

1981; Kirkpatrick 1982), "tipping points" in the evolution of reproductive isolation (Nosil *et al.* 2017) and populations crossing critical thresholds followed by phase transitions between alternative stable states (Scheffer 2009). Tracking of a constant-rate moving optimum can generate short-term positive rate-time scaling until a population reaches its stable expected lag(Lynch & Lande 1993; Bürger & Lynch 1995) (elaborated below). 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 (Lande 1981; Kirkpatrick 1982), we suspect that positive time-rate scenarios are unlikely to be sustained over longer macroevolutionary time scales and should quickly reach stable equilibria and largely be transient. Thus, such rapid and self-reinforcing evolutionary processes are unlikely to proceed unchecked over millennia (Scheffer 2009), as would be required to generate positive rate-time relationships in empirical data such as that shown in Figure 1.

Finally, we can further decompose the covariance between rate and time, focusing on the log-scaled case, where

$$Cov\left[log\left(\frac{d}{t}\right), \log(t)\right] = Cov[log(d) - \log(t), \log(t)]$$

$$= Cov[log(d), \log(t)] - Var[\log(t)]$$

Which shows that the relationship between rate and time is governed both by the variance in time interval as well as the relationship between accumulated change (*d*) and time.

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

221 Here we revisit five published empirical datasets of evolutionary rate. Reanalysis of
222 these empirical datasets of evolutionary rate-time associations reveals little consistent patterns in
223 the relationship between amount of evolutionary change and time, despite a pervasive negative
224 relationship between rate and time. For our first example, vertebrate body size evolution (Figure
225 1A, E), past work (Estes & Arnold 2007; Uyeda *et al.* 2011; Arnold 2014) has shown that body
226 size changes are largely unrelated to time, and in time-series of extant populations found no
227 detectable change (Sanderson *et al.* 2021). Although a log-log regression of rate vs time yields a
228 slope that is nominally steeper than -1 (β = -1.019, 95% CI -1.031, -1.007), which suggests no
229 accumulation of change with interval time, there is a breakpoint in the relationship between
230 morphological change and time ($F_{2, 5388}$ = 207.2, $P < 2.2 \times 10^{-6}$, breakpoint = -2.63 log MY
231 (0.072 MY), SE = 0.147). The result is an estimated weak negative relationship between time
232 and evolutionary change, followed by an increasing slope after the breakpoint (Fig. 1A, F; or
233 shallower negative slope on the log scale, Figure 1A inset panel), identical to that found by
234 (Uyeda *et al.* 2011). Thus, for body size evolution, amount of change is largely unrelated to time
235 interval except over the deepest periods of evolutionary time (Uyeda *et al.* 2011).

236 Similar results are seen in patterns of lineage accumulation in the fossil record (Figure
237 1B, G), where a strong negative rate-time relationship (found by (Henao Diaz *et al.* 2019) and
238 replotted here) reflects a weak and variable relationship between evolutionary change and time
239 (segmented regression $F_{2, 86}$ = 3.199, P = 0.046, breakpoint = -109 MY, SE = 33.13). However,
240 this segmented regression model was not a significantly better fit than a model with only an
241 intercept; $F_{3, 86}$ = 2.6, P = 0.057. Consistent with this finding, a log-log regression between rate
242 and time yields a slope that is significantly shallower than -1 (β = -0.24, 95%CI -0.36, -0.11) and

243 no significant evidence for a breakpoint ($F_{2, 75}$ = 1.71, P = 0.18), indicating that there is some
244 accumulation of diversity with interval time.

245 On phylogenetic trees (Figure 1C, D, G, H), there is also a consistent striking negative
246 relationships between rate and time (as found by the original studies; Scholl & Wiens 2016;
247 Henao Diaz *et al.* 2019) that corresponds to underlying variable association between diversity
248 and time (Rabosky *et al.* 2012; but see Scholl & Wiens 2016). We recover a weak positive linear
249 relationship between diversity and time in one dataset ($F_{1, 112}$ = 14.17, P = 0.000267; Figure 1H)
250 corresponding to a log-log regression that is significantly shallower than -1 (β = -0.53, 95%CI -
251 0.68, -.39), indicating some accumulation of diversity with time, and a segmented linear
252 relationship in another dataset (segmented regression $F_{2, 430}$ = 12.67, P = 4.474 x10^{-6}, breakpoint
253 = 4.6 log MY, SE = 0.108) corresponding to a log-log regression of rate and time with a slope
254 that is not significantly different from -1 (β = -1.04, 95%CI -1.1, -0.98), indicating the
255 accumulated diversity and interval time are decoupled.

256 Interestingly, we even recover a nonlinear negative relationship between evolutionary
257 rate and time when examining phenotypic change that occurred within a timeframe less than the
258 average generation time of the study organism (in this case, primarily long-lived fish; Figure 1E).
259 This within-generation dataset had a log-log regression of rate and time with a slope that was not
260 significantly different from -1 (β = -0.83, 95%CI -1.08, -0.58), indicating that there is no
261 accumulation of change with interval time for intervals less than one generation, as we may
262 expect since such change is likely an outcome of non-accruing environmental effects. This final
263 example demonstrates the appearance of a rate-time scaling relationship for a case that obviously
264 defies evolutionary explanation based on between-generation change. This conclusion is further
265 strengthened by the fact that the slope estimate does not significantly differ from the expectation

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

270 We can then decompose the covariance between rate and time for each of these datasets
271 into its components associated with variation in time and covariance between accumulated
272 change and time, as in equation 4. A caveat in this exercise is that not all of the rate estimates
273 are calculated directly as in equation 1, for example phylogenetic lineage diversification rates
274 in(Henao Diaz *et al.* 2019), and so we do not expect all of the variance in rate-time relationships
275 to be explained by these two components. Nonetheless, this analysis reveals that 99.7% (54%
276 with morphology data dropped) of the variance in rate-time relationships can be explained by
277 variance in time alone ($F_{1,3} = 916$, $P = 7.9\text{x}10^{-5}$, Figure 3A), while change-time covariance alone
278 explains only 14.6 % (25% with morphology data dropped) of the variance in rate-time
279 relationships ($F_{1,3} = 0.51$, $P = 0.52$, Figure 3B). Placing both predictors in a multiple regression
280 reveals support for variance in time ($t = -25.97$, $P = 0.0015$, df = 2), but not covariance between
281 change and time ($t = 0.764$, $P = 0.52$, df = 2), as a significant predictor of rate-time relationships.
282 While it is true that all covariance relationships will depend strongly on variance in their
283 constituent variables, this analysis reveals the noteworthy contrast in lack of meaningful
284 contribution of covariance between accumulated change and time.

285 In summary: the striking negative rate-time relationship shared by four independent
286 evolutionary datasets and one non-evolutionary (within generation) dataset reflects, primarily, a
287 lack of strong or consistent association between the amount of evolutionary change (rate
288 numerator) and the timescale over which this change took place (Figure 1 F-J). These results
289 largely recapitulate the findings of original studies from which these datasets were obtained,

290 although we have shown that a decoupling of amount of evolution and timescale of measurement
291 is likely a general feature across a range of evolutionary datasets, from morphological change to
292 lineage diversification, that together describe the pace of life.

293 Simulations of classical constant-rate evolutionary models reveal that negative rate-time
294 associations readily emerge from these existing models. Phenotypic evolution by random
295 genetic drift results in a Brownian motion process wherein phenotypic variance across lineages
296 increases linearly with time (Figure 4A), and evolutionary rate is time-independent when
297 calculated for an entire clade (4E inset panel). Even this simple constant rate model results in a
298 negative scaling relationship between lineage-specific estimates of evolutionary rate and time
299 (Figure 4E), resulting in a scaling exponent of – ½ in a log-log regression of rate versus
300 time(Hansen 2024).

301 Lineage specific rates are even more strongly associated with time under adaptive model
302 of natural selection towards a stationary optimum (an Ornstein-Uhlenbeck process), where a null
303 relationship between time and divergence (Figure 4B) generates a strong negative relationship
304 between per-lineage rate and time (Figure 4F) with a log-log slope of -1 over long timescales
305 (Hansen 2024), reminiscent of empirical data from vertebrate body size evolution (Figure 1).
306 However, we note that a stationary OU model readily produces negative rate-time scaling
307 exponents that deviate from -1 when sampling lineages evolving under different values of
308 genetic variance and strength of stabilizing selection (Figure 5). Adding any movement of the
309 optimum in an OU process produces dramatic shifts in the form of rate time scaling, yet also
310 indicates that a range of models incorporating stabilizing selection readily produce scaling
311 relationships similar or identical to that expected under pure genetic drift (Figure 5).

312

313 Finally, the simplest model of lineage accumulation, a constant-rate pure-birth process,
314 also leads to these types of associations. The log number of lineages accumulates approximately
315 linearly through time in a pure-birth process, as seen when sampling pure-birth phylogenies
316 differing in age (Figure 4C, 4D). Yet, pure-birth estimators of diversification rate from these
317 phylogenies (Kendall-Moran Yule rates, Figure 4G, S1) as well as maximum likelihood
318 estimates of net diversification from a birth-death diversification model (Figure S2) nonetheless
319 show a negative scaling relationship with time. In principle Yule rates do not inherently show
320 time dependence when estimates of zero rates, which rarely result in phylogenies of more than a
321 single taxon, are included. For example this can be shown by the crown-age estimates using
322 clade age – time data (Magellon-Sanderson rate estimates, Figure 4H). However, even in this
323 case non-zero rate estimates show negative time scaling (Figure 4H). Similarly, sampling
324 directly from the theoretical distribution of pure-birth richness and age yields zero-rate estimates
325 that can cancel out non-zero rates for young clades (O'Meara & Beaulieu 2024), we note that
326 these zero rates are largely unobservable in actual data. Our simulations and others (O'Meara &
327 Beaulieu 2024) show that non-zero rates show negative time-scaling even under a constant-rate
328 pure-birth diversification process. This negative scaling relationships is driven largely by the
329 inclusion of high evolutionary rates estimated over short timescales (Figure 4G), yet the scaling
330 pattern can sometimes remain even when focusing only on larger and older clades (Figure S1).
331 This illustrates the inherent problems of interpreting evolutionary change scaled by time.
332 Moreover, we recover the same general pattern when simulating phylogenies of varying age
333 under an accelerating time-dependent diversification process (Figure S3). These simulation
334 results are not in any way meant as evaluations of these models, rather a demonstration that
335 constant rate processes readily and almost inevitably will produce negative rate-time scaling
336 relationships at least in some circumstances.

Discussion

Here we have explored the problem of why all evolutionary rates appear to scale negatively with time, and what information may be gleaned from these rate-time relationships. First, it is readily apparent 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, revisiting 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 in evolutionary change. Our analysis of these datasets reveals that variation in rate-time scaling pattern is primarily driven by variation in timespan of the dataset rather than patterns of accumulated evolutionary change. Finally, simulation of some of the most common process-based models of constant-rate evolutionary change reveals that all can readily generate a range of negative rate-time scaling relationships. Although many of these points have been discussed in regards to specific datasets, our results unequivocally demonstrate the challenge in interpreting widespread (Gingerich 1983; Henao Diaz *et al.* 2019; Harmon *et al.* 2021; Rolland *et al.* 2023) negative rate-time scaling relationships. Our results have revealed that a negative rate-time relationship is nearly inevitable under a wide range of biological scenarios and over different temporal scales, and moreover suggest potential limitation in the unique information revealed by quantitative estimates of negative rate-time scaling relationships.

That evolutionary rates scale negatively with the timeframe over which they are measured is unsurprising given the inevitable dependence between rate and time, a point that has

been widely acknowledged (Gingerich 1983; Gould 1984; Hendry & Kinnison 1999; Harmon *et al.* 2021). 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). As Gingerich (Gingerich 1983) emphasized, this suggests that the negative scaling relationship that is generated by plotting a rate against time interval should perhaps be accounted for before rate variation across time can be meaningfully compared or understood.

Yet, there is also widespread interest in understanding the extent to which evolutionary processes may contribute to such a pattern of rate-time scaling (Kinnison & Hendry 2001; Ho *et al.* 2011; Henao Diaz *et al.* 2019; Harmon *et al.* 2021; Louca *et al.* 2022; Rolland *et al.* 2023), and so there is justified interest in understanding the drivers of rate-time scaling relationships beyond the inevitable qualitative expectation of a negative relationship (Harmon *et al.* 2021). For example, analyses of rate-time relationships can provide new insights when coupled with explicit null hypothesis tests against scaling parameters expected under various evolutionary process models (as can be done for the case of morphological evolution; Hansen 2024; Holstad *et al.* 2024). It might also be possible to construct meaningful null expectations for other types of rate-time scaling patterns, such as lineage diversification. For example, in their assessment of negative scaling of diversification rates, Henao Diaz et al. (2019) constructed a null expectation by simulating birth-death trees for the same age ranges as their empirical set of trees, under the mean values of birth and death rate observed for the oldest groups in the study. While such an approach is useful in identifying cases of negative rate-time scaling beyond what may be an inevitable outcome from our imperfect statistical models, for many types of rate estimate we lack the quantitative rate scaling predictions (such as those available for morphological evolution). One point of our paper is that, without some sort of quantitative expectation for a rate scaling

384 relationship, the existence of a negative relationship between empirical rates and time is not very
385 informative.

386 As a counterpoint to the above, however, in some cases it may be difficult to reconcile
387 quantitative rate-time scaling patterns with specific evolutionary process models, especially in
388 large datasets of evolutionary rate spanning disparate lineages. For example, although a
389 stationary OU model can generate a -1 scaling relationship of rate with time (Hansen 2024), this
390 is only strictly true over moderate timescales when selection is strong and genetic variance is
391 moderate to high. Similarly, evolution by Brownian motion produces a scaling relationship of -
392 1/2, but so too can a random walk of the optimum under stabilizing selection (at least under some
393 conditions), a process which itself is not strictly Brownian unless all phenotypic variance has an
394 additive genetic basis. Thus, while dramatic shifts in rate-time scaling relationships certainly
395 imply shifts in the mode of evolution (Hansen 2024), it seems likely that similar rate-time scaling
396 relationships may be generated by many disparate processes.

397 Relationships between the magnitude of evolutionary change (e.g., phenotypic change or
398 the log number of new lineages arising) and time can also be assessed directly, as we have done
399 here and which has also been done by some other researchers (Hendry & Kinnison 1999; Uyeda
400 *et al.* 2011; Svensson 2019). One under-used statistical tool is, for example, piece-wise or
401 segmented regression (Schlager *et al.* 1998; Hendry & Kinnison 1999; Uyeda *et al.* 2011;
402 Clapham & Karr 2012) that can be used to identify significant breakpoints in evolutionary
403 change across time. Such an approach avoids the problem of statistical confounders between rate
404 and time interval that was highlighted by Gingerich (Gingerich), at least when applied to analysis
405 of change-time relationships, and also allow for the possibility of identifying shifts in the form of
406 rate-time scaling relationships (Hansen 2024). These and related statistical approaches (Uyeda *et*
407 *al.* 2011) can be used to identify temporal shifts in the evolutionary process over time. Although

408 analysis of rate-time and change-time plots present the same total information, uninformed
409 comparisons of rate-time relationships will readily generate the appearance of shared features of
410 the evolutionary process. Our analysis revealed that variation in evolutionary rate-time
411 relationships across datasets revealed little information about variation in accumulated
412 evolutionary change.

413 A main conclusion from our analysis is that we should generally be surprised when
414 evolutionary rates *do not* show negative time scaling. However, it is likely that some estimators
415 of evolutionary rate do not show the types of inevitable time scaling relationships we have
416 reported; for example, clade-level estimates of Brownian motion rate appear to be less affected.
417 Indeed, in their review, Harmon et al. (2021) draw a distinction between "summary rates" and
418 "parameter rates"; the former being descriptive summary statistics, such as haldanes, while the
419 latter are inferences of instantaneous rate parameters estimated from a process-based model of
420 evolutionary change, with Brownian motion rate or birth-death lineage diversification rate
421 presenting two examples. In this distinction, and barring inadequate models or data, parameter
422 rates from constant rate models should be free from inevitable time-scaling (Hunt 2012; Harmon
423 *et al.* 2021). Yet a challenge remains in that many maximum likelihood estimators of parameter
424 rates are ultimately simple functions of amount of evolution and time, and noteworthy is that
425 even most summary rates could in fact be considered parameter rates under appropriate
426 evolutionary models (Harmon *et al.* 2021). The haldane, for example is a parameter rate under
427 one very simple model of directional trait change (constant directional selection), but note that it
428 shows positive and negative time scaling in different process-based manifestations of directional
429 evolution models (see Fig. 5C). Given that we can never know the true process model giving
430 rise to an evolutionary dataset, and thus our models will always be wrong to some degree (Box

431 1976), it remains to be seen if there is a general distinction between these categories of rate
432 estimate in regards to prevalence of time scaling.

433 Our analyses of rate numerators versus time reveal lack of consistent time-dependency in
434 accumulated evolutionary change across datasets (Figure 1). This is also reflected in variation in
435 rate-time scaling slopes, where estimates of rate-time slope range from near unity
436 (morphological body size evolution, lineage net diversification rate) to modestly negative (fossil
437 lineage diversification). The former indicates that over some very broad time scales evolutionary
438 change is largely decoupled from time, while the later case indicates that there is some
439 meaningful accumulation of evolutionary change with time over some time intervals. We note
440 that these diverse datasets contain information from many thousands of species of extant and
441 extinct plants, animals, and prokaryotes, range in time interval from less than one generation to
442 hundreds of millions of years, and together span the entire history of life. One conclusion is that
443 the qualitative persistence of negative rate-time relationships do not provide evidence of shared
444 features of evolution across these disparate data. Existing data (Fig. 1F-J) suggest that
445 evolutionary change (rate numerator) is remarkably independent of time, across multiple
446 temporal scales. Such general and widespread time-independence of evolution becomes a new
447 challenge to explain. Time-independence of phenotypic evolution could be explained by
448 relatively-stable or slowly moving adaptive zones, within which lineages may evolve
449 substantially (Simpson 1953; Uyeda *et al.* 2011). For lineage diversification, disparity in
450 ecological opportunity among diversifying lineages may decouple clade age and species richness
451 across taxa (Rabosky 2009). We emphasize that while there is little consistent relationships
452 between amount of evolution and interval time, evolutionary events can still be substantial, as
453 shown in Figure 1. We also note that timing of key events in the history of life has, of course,
454 played a major role shaping the origins of diversity (Gould 1989). These include shifts in body

455 size evolution (Uyeda *et al.* 2011) or rapid jumps in bill evolution in birds (Cooney *et al.* 2017).
456 There is also evidence of substantial variation in evolutionary change in response to different
457 selective agents, including human disturbances and harvesting (Sanderson *et al.* 2021), but such
458 change in response to different environmental agents does not appear to be systematically linked
459 to time interval over which evolution was recorded.

460 Our results and other recent findings (Voje 2016; O'Meara & Beaulieu 2024) call into
461 question the value of the mere existence of rate-time scaling patterns as empirical evidence of a
462 fundamental disparity between micro and macroevolution (Rolland *et al.* 2023), since the
463 qualitative existence of a negative relationship is readily explained by many constant-rate
464 processes. For example, consider the widely-appreciated fact that microevolutionary quantitative
465 genetic models of random genetic drift are inconsistent with the amount of evolutionary change
466 in deep time (Hansen & Houle 2004; Houle *et al.* 2017); we often find far less evolutionary
467 change in deep time than expected via drift alone, based on patterns of standing extant genetic
468 variance. However, it is noteworthy that even if phenotypic divergence in deep time was
469 generally consistent with drift under observed levels of standing variance, we would still expect
470 to see a negative scaling relationship between lineage specific rates of evolution and time
471 interval (Figure 3). Our analysis suggests that the decoupling of amount of evolution and time
472 applies not only to morphological change, but also to lineage accumulation. For morphological
473 evolution, it is indeed possible to construct explicit quantitative hypotheses for the form of
474 negative scaling relationship expected between rate and time (Holstad *et al.* 2024). However, as
475 noted above, currently we lack quantitative predictions for other forms of rate-scaling
476 relationships.

477 Time-invariant evolutionary change still poses other challenges for reconciling micro-
478 and macroevolution (Uyeda *et al.* 2011). Constancy of evolutionary rates, and thus linear

accumulation of change with time, across temporal scales is expected and often observed at the molecular level (Morgan 1998; Bromham & Penny 2003). 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 (Felsenstein 1988; Kingsolver *et al.* 2001), or under neutral evolution (Felsenstein 1985; Lynch 1990). However, new empirical findings indicate that phenotypic evolution over a range of timescales is proportional to standing phenotypic and genetic variation (Hansen & Pélabon 2021). 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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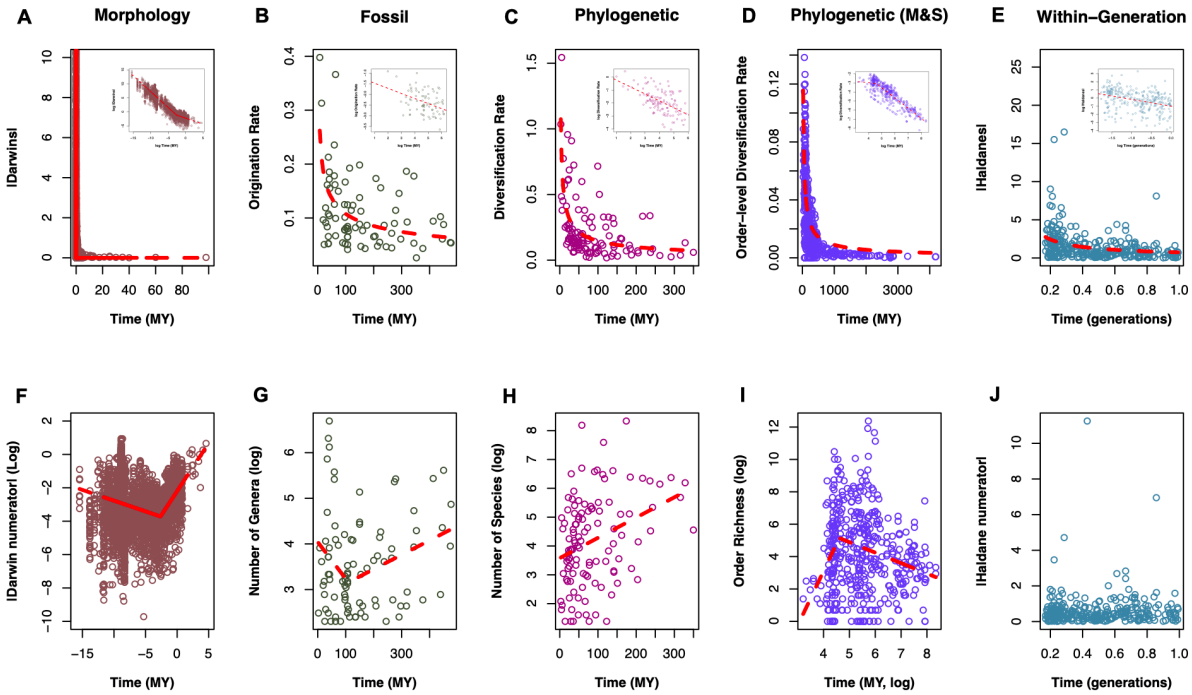

Fig. 1. Evolutionary rate-time relationships reflect null or variable underlying relationships between evolutionary change and time. Panels **A-E** show evolutionary rate plotted against the timescale of measurement (Rolland *et al.* 2023), with dashed red lines showing the least squares fit of the function *rate* = *a**time^b and inset panels showing the linear relationship on a log-log scale. 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 segmented regression, if statistically significant. Panels **A** and **F** show vertebrate body size evolution (Uyeda *et al.* 2011), Panels **B** and **G** show diversification of genera from fossil lineages (plants, mammals, and marine animals)(Henao Diaz *et al.* 2019), Panels **C** and **H** show diversification data estimated from time-calibrated molecular phylogenies (Henao Diaz *et al.* 2019), while Panels **D** and **I** show a larger database of phylogenetic diversification rates (Scholl & Wiens 2016) where rates were inferred directly from age and richness data (Magallon & Sanderson 2001). 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.

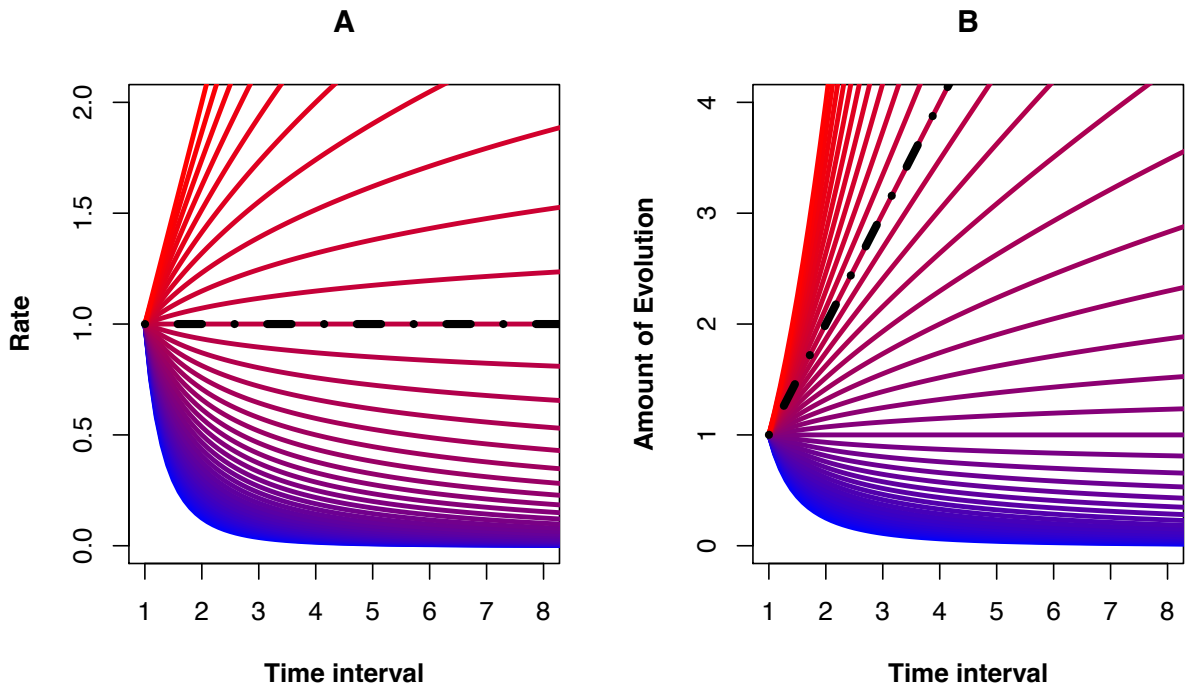

Fig. 2. Extraordinary relationships between the accumulated amount of evolution and time are required to produce positive rate-time relationships. Panel **A** shows the relationship between rate and time for various functions of the rate numerator and time, which are plotted in the same color in Panel **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.

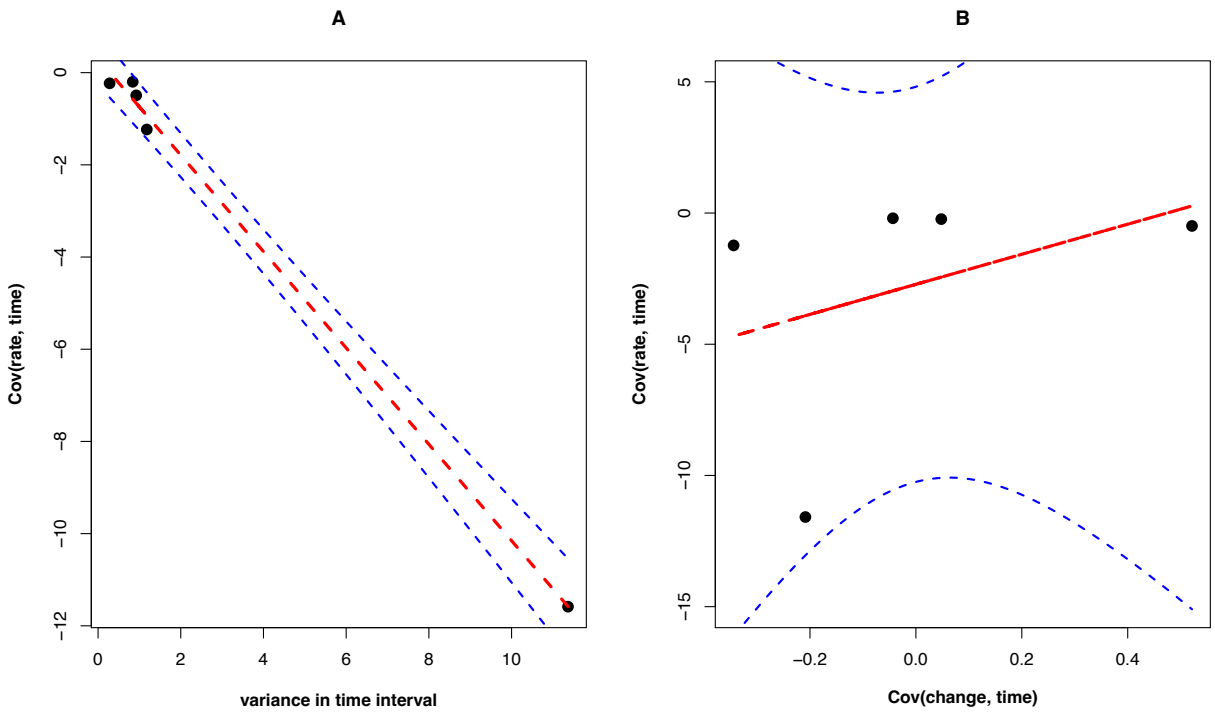

Fig. 3. Time interval determines rate-time relationships across datasets. The covariance between rate and time in the five empirical datasets shown in Figure 1 is almost entirely explained by variance in time (Panel **A**). Covariance between change and time, also expected to be a component of the covariance between rate and time, is not significantly associated (Panel **B**). Lines and 95% confidence intervals are from linear models fit separately to each; a multiple regression with both var(time) and cov(change, time) as predictors yielded equivalent conclusions (see text).

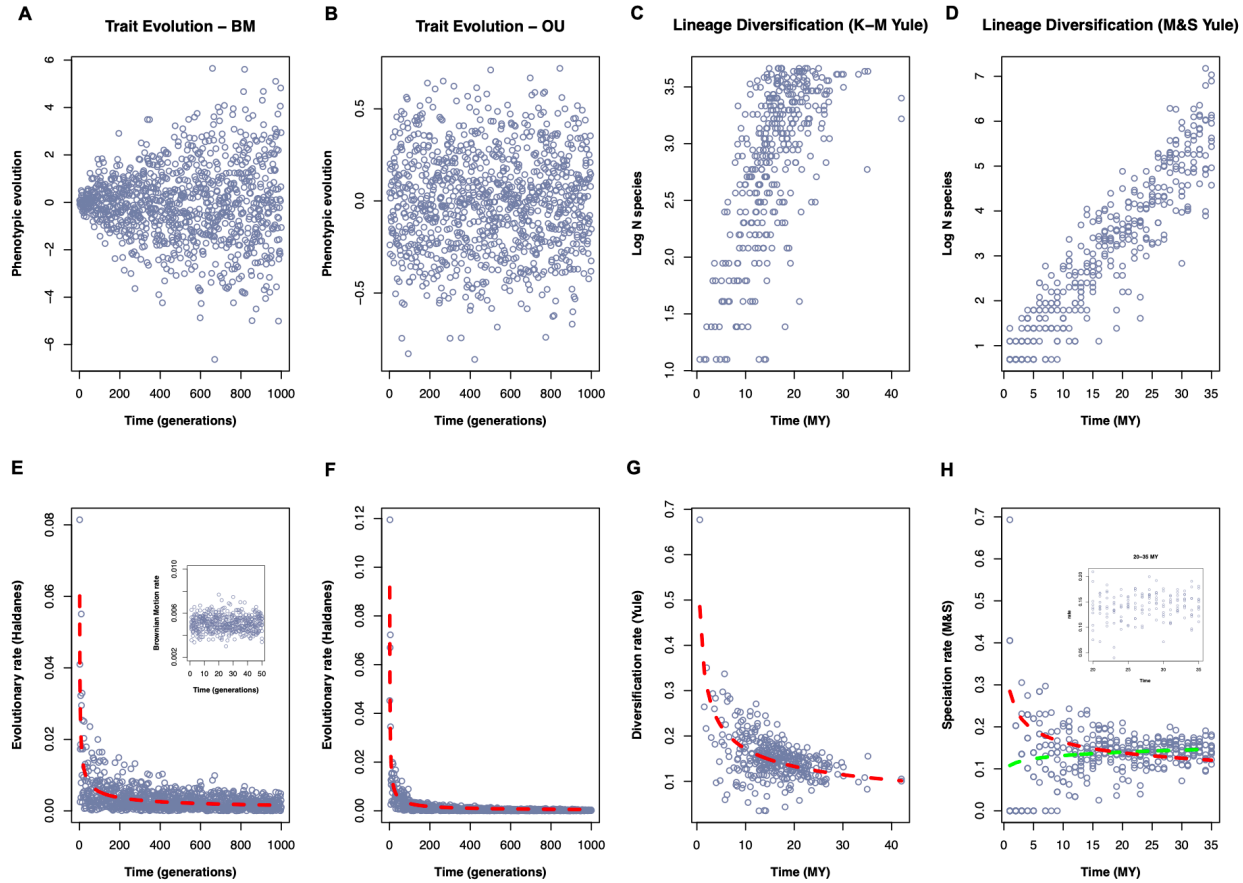

Fig. 4. Simulations of constant-rate evolutionary models reveal persistence of negative rate-time relationships in resulting data. Panels **A** and **E** show a simulation of phenotypic evolution under random genetic drift in the absence of natural selection, which produces a Brownian motion process (Felsenstein 1988) 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 (Lande 1976). 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).

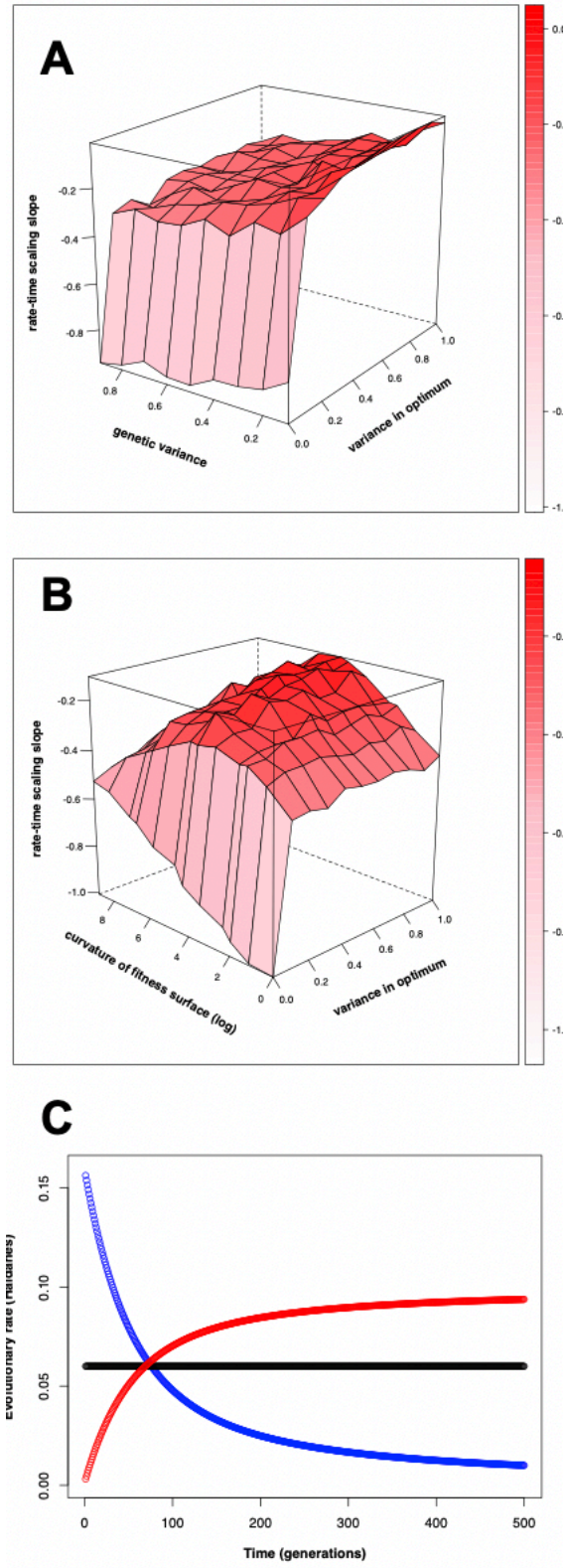

Fig 5. Heterogeneity in rate-time scaling exponents under different forms of morphological evolution. Panels **A** and **B** show simulated evolution under drift and stabilizing selection; an OU process. When there is zero variance in the optimum, this is a stationary OU process generating

a scaling relationship of -1 over this timespan (9000 generations) only when genetic variation is relatively high (Panel **A**), and selection is strong (a low value of ω and thus a strong curvature of the fitness surface, (Panel **B**). Any variance in the optimum leads to a dramatic shift in the scaling relationship. Noteworthy is that a wide range of parameter space, corresponding to models of pure drift as well as models of pure fluctuating selection, can all produce a range of similar scaling relationships particularly in the range of 0 to -1/2. For each parameter value in **A** and **B**, the average scaling slope is shown from 10 simulation runs of 36 lineages each spanning a time range of 1-9000 generations. Panel **C** shows evolutionary rate versus time for three forms of directional evolution. In black is the rate estimate versus time for evolutionary change under the breeders equation, $\Delta\bar{z} = G\beta$. Blue shows the rate estimate for evolution towards an optimum that shifted 5 phenotypic standard deviations at generation 0, assuming the same form of stabilizing selection as in Figure 3B, which is high over short timescales but decelerates as the population adapts. Red shows the relationship for evolution towards an optimum that moves at contant rate of .1 standard deviations per generation, starting at generation 0 with a population on the optimum. In this model the accelerating rate-time relationship is due to the lag between evolutionary rate and rate of peak movement that equilibrates when the population reaches its equilibrium lag behind the optimum(Lynch & Lande 1993; Bürger & Lynch 1995). All of these models produce directional evolutionary change, yet only for one specific model, $\Delta\bar{z} = G\beta$, which is often thought to capture the main features of the two other models of directional change, do we see a lack of time scaling.

Methods Details

Data. We analyze existing data on rates of vertebrate body size evolution (Uyeda *et al.* 2011), 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 (Henao Diaz *et al.* 2019), and another larger dataset (Scholl & Wiens 2016) where diversification rates were estimated from clade diversity and age information. For fossil data, we analyze an existing dataset (Henao Diaz *et al.* 2019) 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 (Rolland *et al.* 2023). We also plot a measure of the rate numerator against time for each of these datasets, and fit segmented linear regressions to identify significant linear relationships between amount of

884 evolution and time, as well as any potential shifts in the relationship between evolution and time.
885 For each dataset, we fit nonlinear models of the form $rate = a*time^b$ using nonlinear least
886 squares (nls()) in R, as well as segmented regression using the segmented package. We compared
887 models fits of an ordinary linear regression to a model with a single breakpoint, and also when
888 appropriate to a null model containing only an intercept, using the anova() function in R. Data
889 presented in Figure 1 were obtained from (Henao Diaz *et al.* 2019) (available at
890 https://github.com/fhenaod/evol_time_scaling/tree/main/data), (Uyeda *et al.* 2011)(Dryad
891 doi:10.5061/dryad.7d580), (Scholl & Wiens 2016), and (Sanderson *et al.* 2021) (database
892 available at: https://proceeddatabase.weebly.com/).

893 Simulation We simulated three different constant rate evolutionary process. The aim of our
894 simulations was not to evaluate the performance of statistical models used to estimate rates.
895 Rather, our aim was simple to examine scaling patterns observed in the simplest cases of
896 simulated constant rate evolution. For morphological evolution, we simulated random genetic
897 drift for 1-1000 generations assuming a heritability of 0.50 and a population size of 100. We also
898 simulated evolution under genetic drift and stabilizing selection, with the same demographic and
899 genetic assumptions but assuming weak selection ($\omega^2 = 15$) towards an optimum. Each
900 simulation was started with the population at its optimum. For morphological evolution, we
901 plotted rates in units of Haldanes (Gingerich 1993), which was natural as we simulated evolution
902 on the scale of phenotypic standard deviations. We then repeated our simulations of OU
903 evolution but exploring a range of parameter values for genetic variance, the strength of selection
904 (curvature of the fitness surface) and the stability of the optimum. For the later, we sampled
905 changes in the optimum from a normal distribution centered at zero and exploring different
906 values of the variance, producing a random walk of the optimum.

907 For lineage diversification, we simulated pure-birth phylogenies with a constant speciation rate
908 of 0.15, corresponding to a expected number of 2.3 taxa at timepoint 1 under a continuous time
909 pure birth process. We simulated pure-birth diversification because, while biologically
910 unrealistic, it excludes explanations for rate-time scaling patterns that are based on sampling
911 biases generated by extinction. We also note that although many challenges exist in sampling all
912 possible trees in a simulation, these are identical to challenges observed in actual data; namely,
913 inclusion of trees with zero diversification rate. Given the aims of our simulations noted above,
914 we proceeded by first simulating trees conditioned on number of tips as opposed to clade age,
915 focusing first on trees with at least 3 tip taxa (conclusions remain unchanged by focusing instead
916 on trees with 20 or more tips; Figure S3). We then calculated the Kendall-Moran estimator
917 (Baldwin & Sanderson 1998; Nee 2001) for the Yule process for these trees using the diversitree
918 package (FitzJohn 2012). We also estimated maximum likelihood birth-death diversification
919 rates for the same set of trees constraining diversification rates to be positive. Finally, we also
920 generated trees with ages ranging from 1-35 million years, and plot the maximum likelihood
921 estimator of the crown-age Yule diversification rate, $[\log(N)-\log(2)]/t$ (Magallon & Sanderson
922 2001). Our simulations of phenotypic evolution were performed using nested for() loops in R
923 and parameterized as described above. Our simulations of constant rate pure birth phylogenetic
924 diversification was performed using the pbtree() function in the phytools package (Revell 2012).
925 Our simulations of time-dependent pure birth diversification (Figure S3) were performed using
926 the TESS package (Hoehna 2013).

927

928

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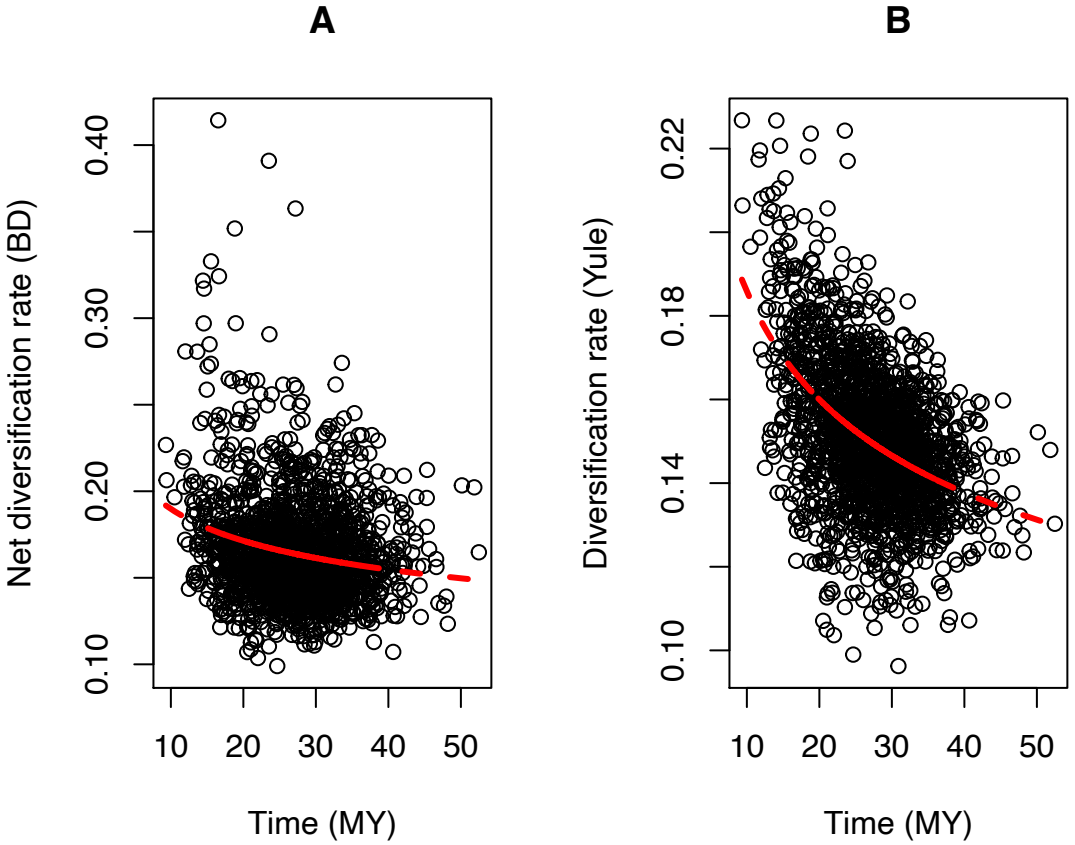
950 **Supplemental Material**



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

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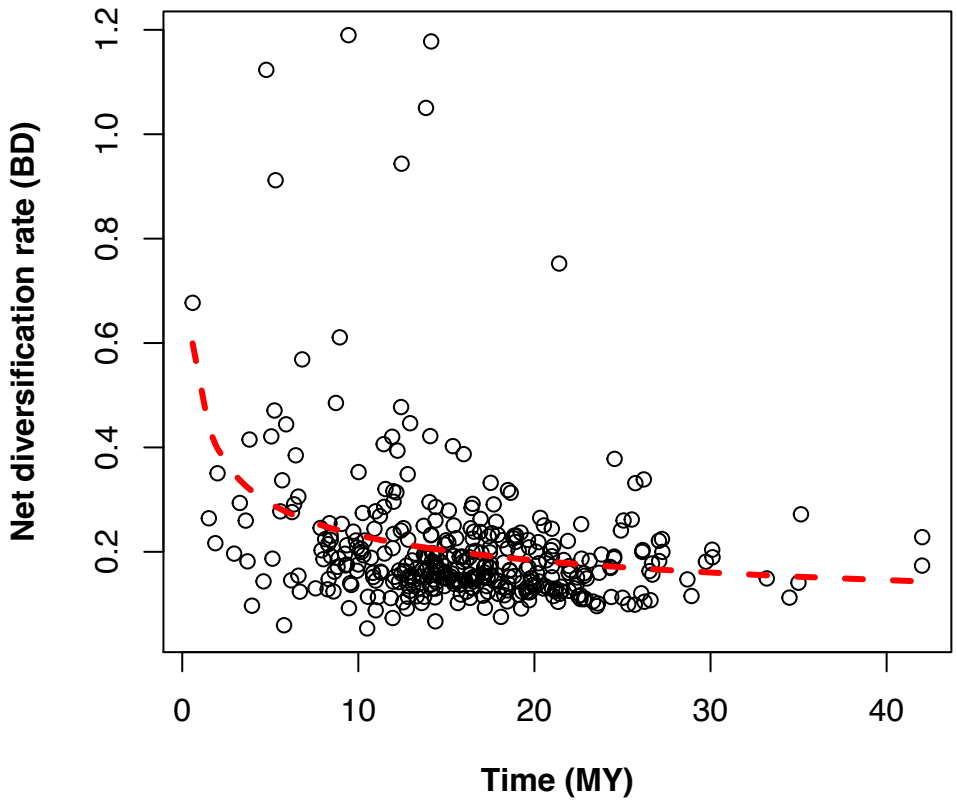

Fig S2. Birth-death estimator diversification rate for trees plotted in Figure 3D, H. Shown is the ML estimate of the birth-death diversification rate λ for the same set of trees shown in Figure 3D, H. Red dashed line shows the least squares fit of the model $rate = a*time^b$.

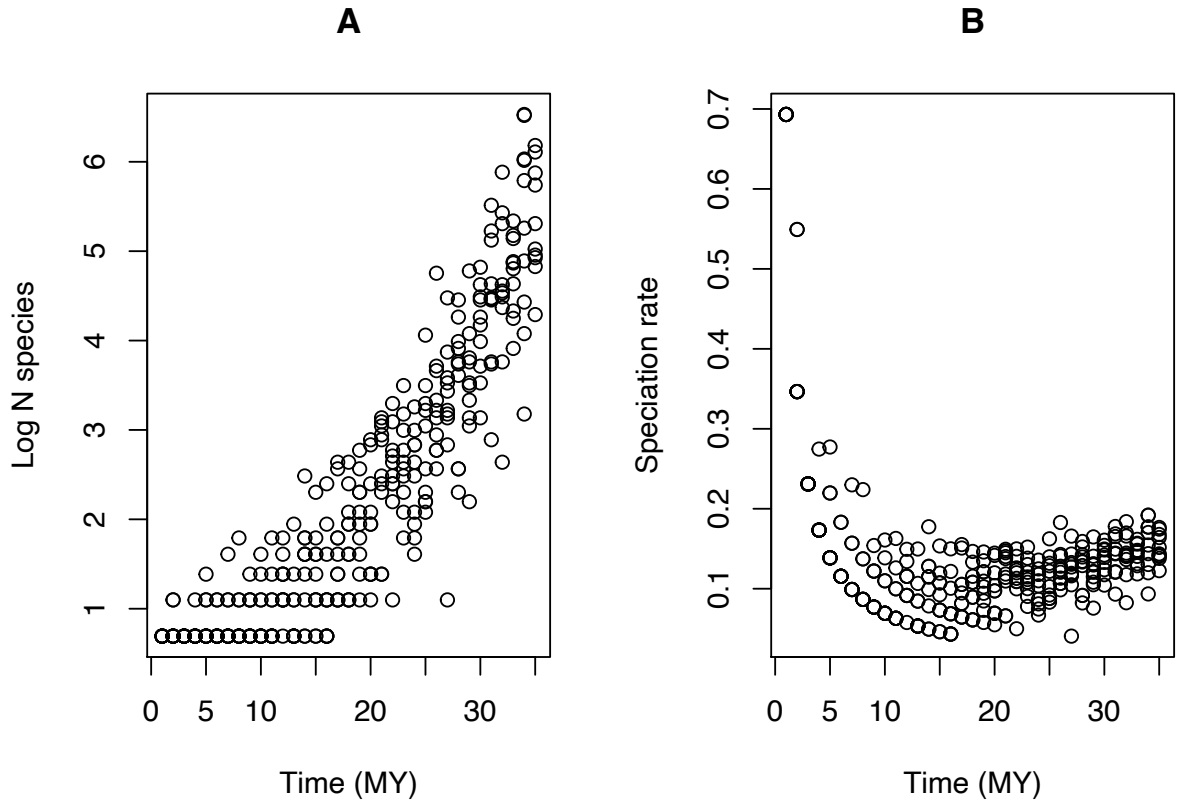

Fig. S3. Accelerating time-dependent diversification produces negative rate scaling patterns. Panels show simulations of time-dependent pure birth diversification, repeated for different timeframes from 1-35 million years under the same time-dependent diversification model. In each simulation birth rates 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.