Non-equilibrium rate heterogeneity explains fat-tailed fluctuations in Phanerozoic biodiversity

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Fluctuations in biodiversity, both large and small, are pervasive through the fossil record, yet we do not understand the processes generating them. Here we use a novel extension of theory from non-equilibrium statistical physics to describe the previously unaccounted for fat-tailed form of fluctuations in marine invertabrate richness through the Phanerozoic. Using this theory, known as super-statistics, we show that orders and the families they subsume, are largely autonomous evolutionary units, each likely experiencing its own unique and conserved region of an adaptive landscape. The separation of timescales between background origination and extinction compared to the origin of major ecological and evolutionary innovations between orders and families allows within-clade dynamics to reach equilibrium, while between-clade diversification is non-equilibrial. This between clade non-equilibrium accounts for the fat-tailed nature of the system as a whole. The distribution of shifts in diversification dynamics across orders and families is consistent with niche conservatism and pulsed exploration of adaptive landscapes by higher taxa. Compared to other approaches that have used simple birth-death processes, equilibrial dynamics, or non-linear theories from complexity science, super-statistics is superior in its ability to account for both small and extreme fluctuations in the richess of fossil taxa. Its success opens up new research directions to better understand the evolutionary processes leading to the stasis of order- and family-level occupancy in an adaptive landscape interrupted by innovations that lead to new orders and families.

Introduction

Biodiversity has not remained constant nor followed a simple trajectory through geologic time (*1–5*). Instead, it has been marked by fluctuations in the richness of taxa, both positive in the case of net origination, or negative in the case of net extinction. Major events, such as adaptive radiations and mass extinctions have received special attention (*6, 7*), but fluctuations of all sizes are ubiquitous (*2, 5, 8*) and follow a fat-tailed distribution, i.e. where large events are more probable compared to models such as the Gaussian distribution. Understanding the fat-tailed nature of these fluctuations continues to elude paleobiologists and biodiversity theoreticians.

The fat-tailed distribution of fluctuations in taxon richness inspired earlier researchers to invoke ideas from complex systems with similar distributions. Such ideas include the hypotheses that biological systems self-organize to the brink of critical phase-transitions (*9, 10*), and that environmental perterbations are highly non-linear (*11*). New data and analyses have not, however, supported these hypotheses at the scale of the entire Phanerozoic marine invertebrate fauna (*5, 12*). Other studies have modeled the mean trend in taxon richness as tracking a potentially evolving equilibrium (*2, 13–15*) and yet ignore the potential role of stochasticity and non-equilibrium dynamics in producing observed patterns (*4, 8, 16–18*). Individual, population, and local ecosystem scale processes that could produce complex dynamics, such as escalatory co-evolutionary interactions (*19*), have not been documented to scale to global patterns (*20*) and indeed should not be expected to scale as such (***?***). Thus, we still lack a new hypothesis to describe the striking fat-tailed nature of fluctuations throught the Panerozoic.

Despite the heterogeneity of explanations of Phanerozoic biodiversity, consensus has emerged on one property of macroevolution: clades experience different rates of morpho-

logical evolution, speciation and extinction (*2,3,21–24*). Here we show that the simple fact of conserved rates within clades and variable rates across clades is sufficient to describe pervasive, fat-tailed fluctuations in taxonomic richness throughout the marine Phanerozoic. This biological mechanism has a precise correspondence to non-equilibrial theory, known as "superstatistics" derived in statistical mechanics (*25*) and applied across the physical and social sciences (*26, 27*). We leverage this correspondence to derive a robust prediction of the distribution of fluctuations in the standing richness of marine invertebrates preserved in the Phanerozoic fossil record. We further show that the specific mathematical derivation of this superstatistical mechanism is consistent with niche conservatism (*28,29*) and pulsed exploration on an adaptive landscape by higher taxa (*29–31*).

Superstatistics (*25*) proposes that non-equilibrial systems can be decomposed into many local sub-systems, each of which attains a unique dynamic equilibrium. The evolution of these dynamic equilibria across sub-systems evolves more slowly. This separation in time scale allows local systems to reach equilibrium while the system as a whole is far from equilibrium (*25*). In the context of macroevolution we propose that a clade with conserved evolutionary rates and life history characteristics corresponds to a sub-system in dynamic equilibrial. We say dynamic equilibrium following MacArthur and Wilson (*32*) in recognition that while the identity and exact number of taxa will fluctuate stochastically from random origination and extinction (taking the place of local immigration and extinction in (*32*)), the overall process determining the number of taxa, and by extension, fluctuations in that number, is in equilibrium. Indeed, the different regions of adaptive space occupied by different clades can be conceptualized as different islands with different dynamic equilibria, albeit with macroevolutionary processes determining the colonization of adaptive peaks, as opposed to short timescale biogeographic processes.

Variation in the magnitudes of origination and extinction rates across these islands of

adaptive space will correspond to the life histories, ecologies, and evolutionary histories that characterize each region. We do not attempt to disagnose which characteristics of different regions of adaptive space account for rate differences, but others have found relationships between larval type (*33*), body plan (*16*), body size (*34*), range size (*34, 35*), and substrate preference (*29*) on rates of origination and extinction. Not all of these traits would be considered dimensions of an ecological niche or characteristics of a guild (*?*), but they all point to different ecological strategies that may be more or less favorable macroevlutionarily and that result from interactions between heritable traits and environments, which may also be viewed as semi-heritable (*?*). Thus different regions of adaptive space, and the clades occupying them, will experience different magnitudes of stochastic fluctuations in taxonomic richness. Indeed, there is evidence that extinction rate as a trait is phylogenetically conserved (*36*). As clades occasionally split to fill new regions of adaptive space their pulsed diversification determines the non-equilibrium nature of the entire biota.

To uncover the superstatistical nature of the marine invertebrate Phanerozoic fauna we analyze the distribution of fluctuations in the number of genera (the lowest reliably recorded taxonomic resolution) using the Paleobiology Database (PBDB; `paleobiodb.org`). We correct these raw data for incomplete sampling and bias using a new approach described in the methods section.

We define potentially equilibrial sub-systems based on taxonomic hierarchies, as a full phylogenetic hypothesis for all marine invertebrates is lacking. Taxa ideally represent groups of organisms that descend from a common ancestor and share similar ecologically and evolutionary relevant morphological traits (*37, 38*). To evaluate the optimal taxonomic level for sub-system designation, we test our superstatistical theory using taxonomic levels from order to phylum. Additionally, we compare our results to randomized

taxonomies and confirm that the observed fit of superstatistical theory is not an artifact of arbitrary classification but instead represent real, biologically relevant diversification processes within and between clades.

Results

In statistical mechanics, local sub-systems can be defined by a simple statistical parameter β often corresponding to inverse temperature. In the context of macroevolution we define the β_k of clade k as the inverse variance of fluctuations x_k in the number of genera within that clade. The β_k thus represent the inverse variances of homogeneous origination-extinction processes of genus richness withing a clade, which will be approximately Gaussian if the clades' diversification dynamics are independent and in local equilibrium (see Appendix S1). Three exemplar dynamics taken from a sampling-corrected (see methods section) aggregation of the Paleobiology Database (PBDB) (*5*) are shown in Figure 1, and indeed all richness fluctuations within orders are well characterized by a Gaussian distribution (Fig. 1).

To predict the super-statistical behavior of the entire marine invertebrate Phanerozoic fauna we must integrate over all possible local equilibria that each clade could experience. The stationary distribution of β_k values describes these possible equilibria, specifying the probability that a given clade, chosen at random, will occupy a region of niche space characterized by β_k.

We estimate the distribution of β_k's simply as the maximum likelihood distribution describing the set of inverse variances for all orders. In both the PBDB and Sepkoski's compendium, Phanerozoic marine invertebrate orders clearly follow a Gamma distribution in their β_k values (Fig. 1).

Using the observation of within order statistical equilibrium and Gamma-distributed

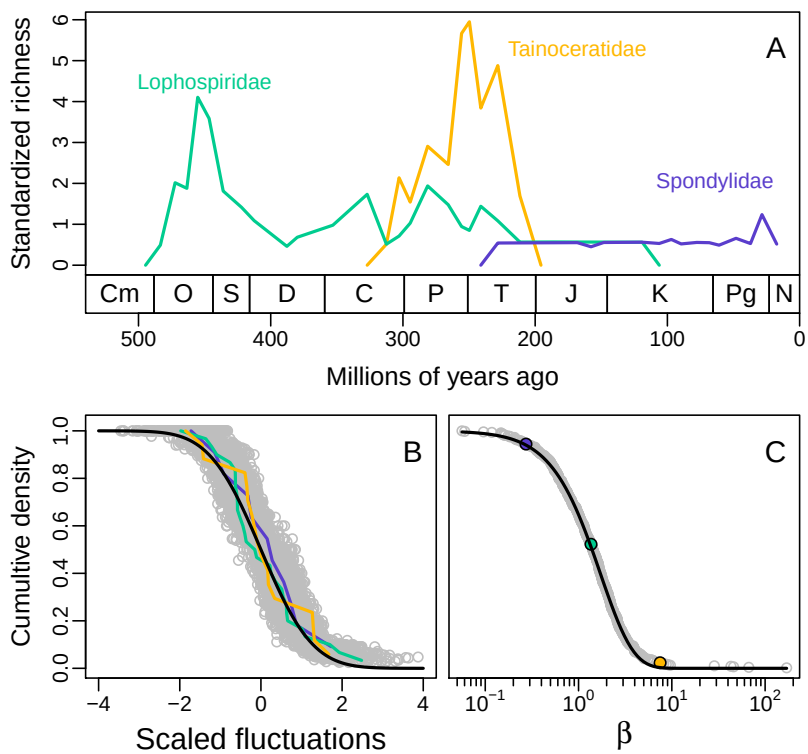

Figure 1: The distributions of within-order fluctuations in genus richness shown for the trajectories of three exemplar orders (A) and shown as an empirical cumulative density aggregated across all orders (B). To display all orders simultaneously we simply collapse their fluctuation distributions by dividing by their standard deviations. If orders conform to the Gaussian hypothesis their scaled fluctuations should fall along the cumulative density line of a normal N(0, 1) distribution, as shown in (B). In (C) the distribution of inverse variances β_k across all orders matches very closely to a Gamma distribution (black line); exemplar orders are again highlighted.

β_k parameters we can calculate, without further adjusting free parameters, the distributions of order-level fluctuations for the entire marine Phanerozoic, $P(x)$, as

$$P(x) = \int_0^\infty p_k(x \mid \beta) f(\beta) d\beta \tag{1}$$

where $p_k(x \mid \beta) = \sqrt{\frac{\beta}{2\pi}} e^{-\frac{\beta x^2}{2}}$ is the distribution of fluctuations within an order and $f(\beta) = \frac{1}{\Gamma(b_1/2)} \left(\frac{b_1}{2b_0}\right)^{b_1/2} \beta^{(b_1/2)-1} \exp\left(-\frac{b_1 \beta}{2b_0}\right)$ is the stationary distribution of inverse variances in

the magnitude of order-level fluctuations in richness. The integral in (1) leads to

$$P(x) = \frac{\Gamma\left(\frac{b_1+1}{2}\right)}{\Gamma\left(\frac{b_1}{2}\right)} \sqrt{\frac{b_0}{\pi b_1}} \left(1 + \frac{b_0 x^2}{b_1}\right)^{-\frac{b_1+1}{2}} \tag{2}$$

This corresponds to a non-Gaussian, fat-tailed prediction for $P(x)$ which matches both the PBDB and Sepkoski data closely (Fig. 2 and Appendix S2.3).

To quantitatively evaluate how well the super-statistical prediction matches the data we constructed a 95% confidence envelope from bootstrapped maximum likelihood estimates for $P(x)$. Observed fluctuations fall within this 95% confidence envelope (Fig. 2), indicating that the data do not reject the super-statistical prediction. For further comparison, we fit a Gaussian distribution to the observed fluctuations, which corresponds to the equilibrium hypothesis that all orders conform to the same dynamic. Using Akaike Information Criterion (AIC) we find that observed fluctuations are considerably better explained by the super-statistical prediction than by the Gaussian hypothesis (ΔAIC = 11285.18). Thus, as expected under the superstatistical hypothesis, the fat tailed distribution of fluctuations arise from the superposition of independent Gaussian statistics of fluctuations within orders.

Computing the distribution of fluctuations using classes instead of orders leads to a substantially poorer fit to the observed data (Fig. **??**). We quantify this shift with the Kolmogorov-Smirnov statistic, which changes from 0.041 for orders to 0.062 for classes (Fig. 3). However, if super-statistical theory explains the data, this worsening fit with increasing taxonomic scale is expected as the different classes should not represent dynamically equilibrial sub-systems in their fluctuation dynamics. Instead, classes aggregate increasingly disparate groups of organisms, and thus effectively mix their associated Gaussian fluctuations, meaning that one statistic should no longer be sufficient to describe class-level dynamics.

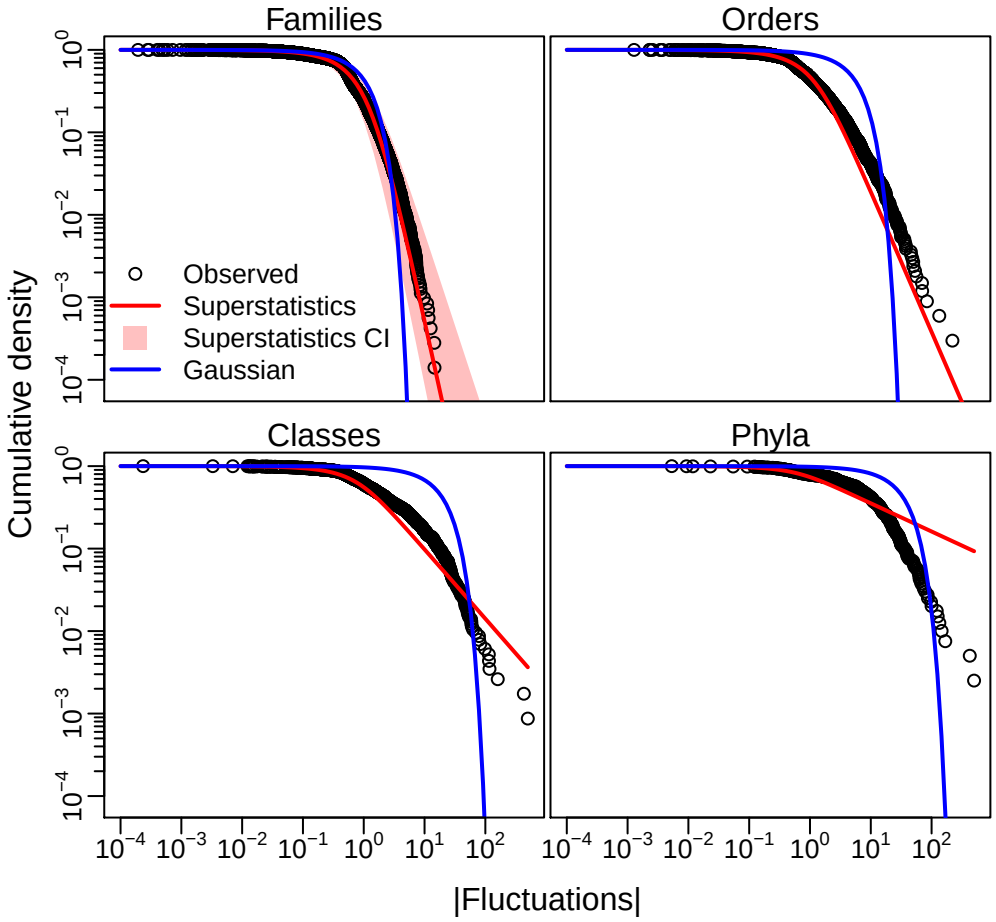

Figure 2: Distribution of fluctuations in genus richness within orders of marine invertebrates in the Paleobiology Database (*5*) after sampling correction. The distribution is fat-tailed as compared to the maximum likelihood estimate of the normal distribution (blue line). At the order level the empirical distribution of fluctuations are well described by our super-statistical approach, both when computed from integrating over the distribution of observed variances (red line) and when fit via maximum likelihood (95% confidence interval; red shading).

Our analysis indicates that orders are evolutionarily equilibrial and independent entities, with all subsumed taxa sharing key ecological and evolutionary attributes allowing them to reach steady state diversification independently from other orders. Both the good fit at the order level and worsening fit at higher taxonomic levels is confirmed in

Sepkoski's compendium.

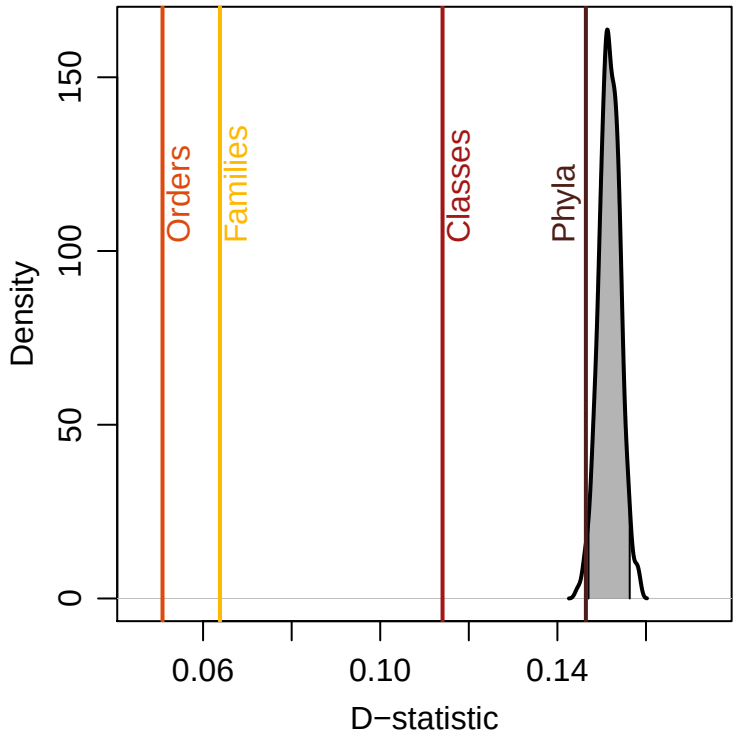

Figure 3: Distribution of Kolmogorov-Smirnov (KS) statistics from randomly permuting genera within orders (gray shading represents 95% confidence interval). Solid black line is observed KS statistic at the order level, while the dashed black line shows the observed KS statistic at the class level.

To further test the evolutionary coherence of orders we conducted a permutation experiment in which genera were randomly reassigned to orders while maintaining the number of genera in each order. For each permutation, we calculated the super-statistical prediction and the Kolmogorov-Smirnov statistic. The permutation simulates a null model in which common evolutionary history is stripped away (genera are placed in random orders) but the total number of observed genera per order is held constant. Repeating this permutation 500 times yields a null distribution of Kolmogorov-Smirnov statistics that is far separated from the observed value (Fig. 3) suggesting the good fit at the order

level is not merely a statistical artifact of classification but carries important biological information.

Discussion

Our analysis makes no assumption that orders should correspond to super-statistical subsystems, but identifies them as the appropriate level for marine invertebrates. As we show, orders differ only in the variances of their richness fluctuations (Fig. 1).

Our study is the first to demonstrate that complex patterns in the fluctuation of taxon richness resulting from the sequence of origination and extinction events in the fossil record are the result of a simple underlying process analogous to the statistical mechanisms by which complexity emerges in large, non-equilibrium physical (*26*) and social systems (*27*). We do so by identifying the biological scale at which clades conform to locally independent dynamic equilibria in fluctuations. This scale is determined by the process of niche conservatism (*28, 29*) within orders. Equilibrium could result from many processes, including neutrality (*32, 39*), diversity-dependence (*14, 40*) and processes that dampen—rather than exacerbate—fluctuations in complex ecological networks (*41*).

Independent and dynamically equilibrial dynamics suggested by these Gaussian fluctuations in genus richness could result from neutral-like processes (*39*), where the dynamics of one taxon are unaffected by those of another, or from dampening mechanisms that stabilize complex networks of interacting taxa (*42*). This is in direct contrast to the instability hypothesis underlying the self-organized criticality theory of paleo-biodiversity (*9, 10*).

We then show that punctuated shifts to different equilibria between order, a consequence of punctuated exploration of niche space by newly evolving clades (*29–31*), leads to a characteristically non-equilibrial distribution of richness fluctuations when the marine Phanerozoic fauna is viewed as a whole macro-system.

The distribution describing this process of evolution in equilibria between orders is clearly Gamma (Fig. 1. A Gamma distribution, while consistent with multiple processes (e.g., (*43*)), could result from evolution of diversification rates across an adaptive landscape that promotes niche conservatism and punctuated exploration of niche space. Specifically, if β_k values are associated with a clade's physiological and life history traits, and those traits evolve via Ornstein-Uhlenbeck-like exploration of an adaptive landscape, the resulting stationary distribution of β_k will be Gamma (*43,44*). For macroevolutionary rates to vary across an adaptive landscape, this landscape cannot be flat, and thus niche conservatism punctuated by adaptive exploration is inevitable (*31*). The specifics of how this adaptive landscape is shaped and is traversed by evolving clades will likely determine the specific distribution (e.g. Gamma versus Chi-squared, etc.) describing punctuated evolution of clades' equilibria. Our work thus motivates study of the trait spaces and evolutionary shifts consistent with Gamma-distributed equilibria in richness fluctuations.

Our work highlights the importance of both niche conservatism and punctuated adaptive radiation in producing the statistical behavior of the Phanerozoic; our theory thus provides new motivation for identifying the eco-evolutionary causes of innovations between lineages and how those innovations are eventually conserved within lineages. Armed with an understanding of the statistical behavior of diversification we can go on to examine mechanisms underlying additional patterns in the mean trend of biodiversity through the Phanerozoic. In particular, clades have been shown to wax and wane systematically through time (*4, 8*), a pattern that we cannot explain with super-statistics alone.

Superstatistics could also be applied to other areas of evolution and macroecology. For example new phylogenetic models already consider heterogeneous rates of diversification (e.g., (*45*)). The superstatistics of clades in adaptive landscapes could provide a means to build efficient models that jointly predict morphological change and diversification. This

framework could also provide a new paradigm in modeling the distributions of richness, abundance and resource use in non-neutral communities. Non-neutral models in ecology are criticized for their over-parameterization (*46*), yet a persistent counter argument to neutral theory (*39*) is the unrealistic assumption of ecological equivalency (*47*) and poor prediction of real dynamics (*48*). If ecosystems are viewed as the super-position of many individualistically evolving clades, each exploiting the environment differently and thus obeying a different set of non-equivalent statistics, then diversity dynamics could be parsimoniously predicted with superstatistics while incorporating real biological information on ecological differences between taxa.

Superstatistics is a powerful tool to derive macro-scale predictions from locally fluctuating sub-systems whose evolution is driven by interesting, but complex and difficult to model, biological mechanisms. As such, applications of superstatistics from islands to populations to clades are ripe for exploration.

Methods and Materials

Paleobiology Database data download and filtering

Data were downloaded from the Paleobiology Database (PBDB; `https://paleobiodb.org`) on 15 November 2018 via the database's API (data retrival and processing script in the supplement). Collections were filtered using the same approach as Alroy (*5*) to insure that only well preserved marine invertebrate occurrences were used in subsequent analyses. This filtering resulted in 221202 genus occurrences. These were further filtered to exclude those occurrences without family-level taxonomy and those collections with age estimate resolutions outside the 10MY time bins proposed by Alroy (*5*) resulting in 189516 occurrences. These timebins were querried from `http://fossilworks.org` with a custum script reproduced in the supplement. The correspondence of these time bins to real

stratographic intervals is reported in Supplamental Table **??**. The first and last of these time bins, corresponding to the earliest Cambrian and the latest Cenozoic, were excluded from analysis because their sampling completeness (see below) could not be assessed..

To focus attention on the variance of fluctuations we center each clade's fluctuation distribution. Because "equilibrium" in the statistical mechanical sense means a system undergoes coherent, concerted responses to perturbation the mean trend line is of less interest than deviations from it. We also note that the distributions of fluctuations for most clades are already close to a mean of 0 (mean across families: 0.038 ± 0.176 SD), and so centering has little influence on clade-specific fluctuation distributions.

Correcting for imperfect and potentially biased sampling

We use a new and flexible method to correct for known sampling incompleteness and biases in publication-based specimen databases (*5, 13*). Incompleteness is inherent in all biodiversity samples, the fossil record being no exception (*?, 13, 49–51*). This incompleteness is only an issue if it varies across the fossil record, as indeed it does (*?, 13, 50, 51*). In addition to variable incompleteness, bias may result from preferential publication of novel taxa (*13*) which exacerbates the difference between poorly-sampled and well-sampled time periods. We therefore develop a simple two-step method: we first correct for incomplete sampling using the "three-timer" correction (*5*) and then further correct this three-timer estimate by accounting for any correlation between the number of genera and the number of publications in a time period.

The three-timer correction estimates the probability of failure to observe a genus in a given time period p_t as the number of times any genus is recorded before and after that period but not during, divided by the number of genera whoes occurrence histories span the period in question. To calculate the sampling-corrected richness $\hat{D}_{kt}$ of a clade k in

the time period in question, the observed genera within that clade and time period are divided by $1 - p_t$ and their occurrences summed:

$$\hat{D}_{kt} = \sum_{j \in k} \frac{I_{jt}}{1 - p_t} \tag{3}$$

where $j \in k$ designates genera in clade k and I_{jt} is an indicator equal to 1 if the genus j occurs in time period t.

The estimator $\hat{D}_{kt}$ is the maximum likelihood estimator of richness in a simple occupancy through time type model assuming binomial sampling (), and in that way mimics other proposed methods for the fossil record (*?,50*). We avoid parametrically modeling the sampling process through time by instead taking a sliding window of time bins from the Cambrian to the Cenozoic. It should be noted that the three-timer correction compares favorably to other similar methods to account for imperfect detection (*52*)

To eliminate further bias due to preferential publication of novel taxa (*13*) we divide the three-timer-corrected number of genera per family per time period by the expected number of genera given publications in that time period. The expected number is calculated by regressing the log-transformed three-timer-corrected number of genera on log-transformed number of publications. There is only a weak trend toward higher richness with more publications (Fig. S1) meaning that the most important correction comes from the three timer correction.

Our new method re-scales each genus occurrence from 0 or 1 (absent or present) to a weighted number continuously ranging between 0 and 1. Because these weighted numbers represent sampling and bias-corrected *occurrences* we can add them arbitrarilly, corresponding to the membership of a genera in any given taxonomic group from the level of family and above. We must, however, choose a taxonomic level at which to evaluate the relationship between richness and publications; we choose the level of family because

this is the most finely resolved option.

This method achieves similar results at the global scale across all clades to more computationally intensive subsampling procedures (*13, 49, 53*). These subsampling would not even be advisable for clades with few genera. We directly compare our predicted time series of global fluctuations in genus richness with results derived from rarifaction and shareholder quarum subsampling (SQS; (*53*)) in Figure S2. Our method shows very minor differences with these subsampling-based predictions and any discrepancies do not impact the statistical distribution of fluctuations (Fig. S2).

Super-statistical methods

We first derive the super-statistical distribution $P(x)$ by fitting Gaussian distributions to clade-level distributions of fluctuations $p_k(x)$, extracting the inverse variances β_k of those $p_k(x)$, testing the best function to describe the distribution of β_k, and then integrating $P(x) = \int_\beta p_k(x|\beta) f(\beta)$. This process allows to free parameters to hone the fit of $P(x)$ to the data. However, each inverse variance must of course be estimated for each clade. To do so we use least squares instead of maximum likelihood because the asymmetric fluctuation distributions of small clades were more reliably fit with curve fitting than with the maximum likelihood estimator.

We then estimated $P(x)$ directly from the raw data using maximum likelihood to compare the fit of our super-statistical prediction and that of a simple Gaussian distribution using AIC. To calculate a likelihood-based confidence interval on our prediction we bootstrapped the data, subsampling fluctuations with replacement from all orders combined, and calculating AIC of the superstatistical and Gaussian models on these bootstrapped datasets.

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Author contributions: AJR, MAF and PAM designed the study; AJR and MAF preformed the analyses; AJR, MAF and PAM interpreted the results and wrote the manuscript.

Competing interests: none.

Data and materials availability: Data are available through the Paleobiology Database (`paleobiodb.org`) and all code needed to interface with the `paleobiodb.org` API, process, clean, and ultimately analyze the data are available online at `github.com/ajrominger/pale` This github repository also hosts the exact download from `paleobiodb.org` used in this analysis. Scripts are also availible and explained in the Supplement.

Supplementary materials

S1 Limit distribution of a time-averaged homogeneous origination-extinction process

Fossil taxa gain and lose taxa according to an origination-extinction process. We assume that most fossil occurrences of a taxon come from the period of its history when it is dominant and in steady state. In a time slice of duration τ during such a period of steady state the latent per capita rates of origination and extinction would be equal (i.e. $\lambda = \mu \equiv \rho$) and the number of origination or extinctions events (call such events Y) each follow an inhomogeneous Poisson process with rate ρN_t where N_t is the number of species or genera in the taxon of interest at time t. Allowing N_t to vary smoothly with time, and recognizing that the sum of Poisson random variables remains Poisson, we arrive at the number Y of extinction *or* origination events in τ being distributed

$$Y \sim \text{Pois}(\rho \int_{t=0}^{\tau} N(t)dt). \tag{4}$$

Under the steady state assumption we can approximate $N(t)$ by $\bar{N}$, the steady state richness, leading to

$$Y \sim \text{Pois}(\rho \bar{N} \tau). \tag{5}$$

Assuming the τ of each time period in the Paleobiology Database or Sepkoski's compendium to be approximately equal (i.e. equal durations of major asymptotic units) then the distribution of fluctuations within taxa will be asymptotically Gaussian.

The Gaussian asymptotics of time-averaged birth-death processes have been proven and explored elsewhere as well (*54, 55*).

S2 Additional super-statistical analyses

To evaluate the sensitivity of our super-statistical analysis on the particular data used and we tested our predictions on different data sets (see below). The fact that it works in all different applications indicates that it is robust to vagaries of different recording strategies and bias corrections in paleobiology. This could mean that much of the raw signal in massive fossil datasets, at least signals regarding fluctuations, are not artifacts of sampling, as has been proposed before (*56*).

S2.1 Raw PBDB data

We calculated the super-statistical prediction at the order level from raw genus richness recorded in the PBDB without correcting for taphonomic or sampling bias (Fig. **??**). The super-statistical calculation also closely fits the raw data as in the case of sampling and publication bias-corrected data.

S2.2 Different taxonomic ranks in PBDB data

As noted in the main text, the super-statistical prediction predictably breaks down at higher taxonomic scales. In Figure **??** we present this worsening fit graphically using class level data with three-timer and publication corrected PBDB data

S2.3 Sepkoski's compendium

Sepkoski's compendium (*57*) provided the first hypothesis of Phanerozoic diversification. As such, it has served as a benchmark for further investigation into large-scale paleobiological patterns (*5*). We conducted the same super-statistical analysis as in the main text and find comparable results. Specifically, the super-statistical prediction far out preforms the null Gaussian model (Fig. **??**) and worsens with increasing taxonomic scale (Fig. **??**),

again implying the uniqueness of orders.

Supplemental Figures

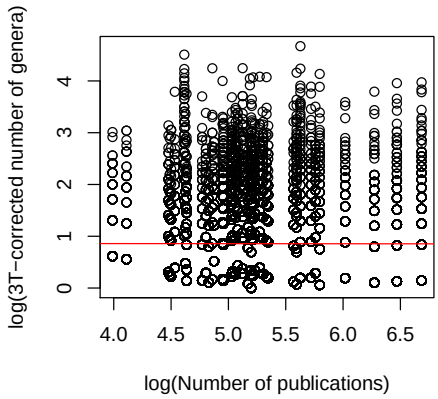

Figure S1: Relationship between number of publications and genus richness as recorded by the PBDB.

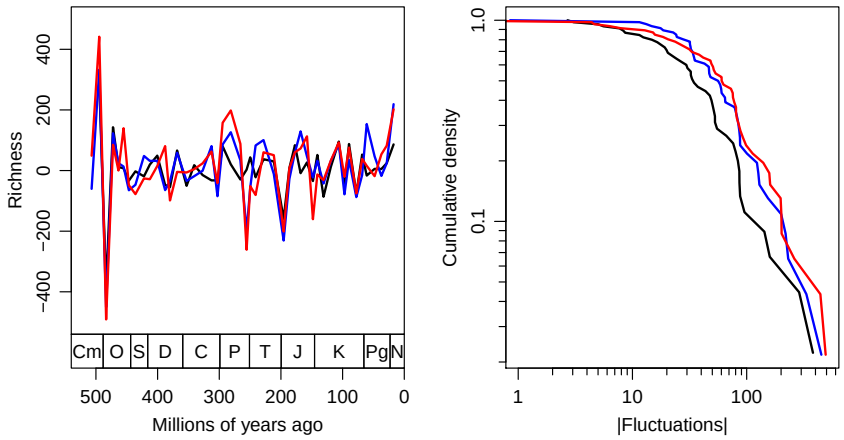

Figure S2: Comparison of SQS method (*13*) (solid black line) with the raw data (dashed black) and our three-timer and publication bias correction method (red). The time-series of all marine invertebrate genera shows general agreement with the only major deviations toward the modern (A). Despite these differences the distribution of fluctuations in genus richness across all marine invertebrates show good agreement (B).