Rate heterogeneity, time scale separation and non-equilibrium evolution explain fat-tailed fluctuations in marine biodiversity of the Phanerozoic

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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 show that three universal properties of macroevolution— *i*) heterogeneity of diversification rates between taxa, likely driven by *ii*) niche conservatism and *iii*) punctuated adaptive radiation— are sufficient to explain the previously unaccounted for fat-tailed form of fluctuations in diversity through the Phanerozoic. Using this theory, known as superstatistics, we identify taxonomic orders as 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 allow within-order dynamics to reach equilibrium, while between-order diversification is non-equilibrial, driven by major evolutionary innovations. Compared to other approaches that have used simple birth-death processes, equilibrial dynamics, or non-linear theories from complexity science, superstatistics is superior in its ability to account for both small and extreme fluctuations in fossil diversity. Its success opens up new research directions to better understand the universal nature of non-equilibrium dynamics across disparate systems of interest—from societal to physical to biological. Specifically in the biological case, research is motivated to understand the evolutionary processes leading to the stasis of order-level occupancy in an adaptive landscape punctuated by innovations between orders.

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Introduction

Biodiversity has not remained constant nor followed a simple trajectory through geologic time (*1–6*). Instead, it has been marked by fluctuations in the number of extant 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 (*7,8*), but fluctuations of all sizes are ubiquitous (*2,5,9*) and follow a distribution with fat tails, i.e. where large events are more probable compared to models such as the Gaussian distribution. Predicting the magnitude of these fluctuations continues to elude paleobiologists and biodiversity theoreticians.

Several approaches have been taken to study the complex trajectory of paleo-biodiversity ranging from the hypothesis that biological systems self-organize to the brink of critical phase-transitions (*10, 11*), to invocations of non-linear environmental perturbations (*12*) and escalatory co-evolutionary interactions (*13*). New data and analyses have not supported these hypotheses at the scale of the entire Phanerozoic marine invertebrate fauna (*5, 14, 15*). Other studies have modeled the mean trend in diversity as tracking a potentially evolving equilibrium (*2, 5, 6, 16*) and yet ignore the potential role of stochasticity and non-equilibrium dynamics in producing observed patterns (*4, 9, 17*). As such, we still lack a synthetic theory of evolving biodiversity through the fossil record.

Despite the heterogeneity of explanations of Phanerozoic biodiversity, consensus has emerged on three properties of macroevolution: *i*) as a consequence of the interaction between their life history characteristics and the environments they inhabit (*18*) different clades experience different rates of morphological evolution, speciation and extinction (*2, 3, 19, 20*). *ii*) those gross ecological and life history attributes of clades are often maintained, a phenomenon known as niche conservatism (*21, 22*); *iii*) long periods of

niche conservatism are interrupted by adaptive diversification and exploration of new ecological niche space (*22–24*); and

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 diversity 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 diversity 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 and punctuated evolution on an adaptive landscape.

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 (*28*) in recognition that while the identity and exact number of taxa will fluctuate stochasticity from random origination and extinction (taking the place of local immigration and extinction in (*28*)), 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 in (*28*).

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Variation in magnitudes of origination and extinction across these islands of adaptive space should correspond to life history and ecological characteristics that define that island or region occupied by a given clade. Larval type (*29*), body plan (*17*), body size (*30*), range size (*30, 31*) and substrate preference (*22*) have all been shown to influence such rates. Thus different regions of niche space, and the clades occupying them, will experience different magnitudes of stochastic fluctuation in diversity. As clades occasionally split to fill new regions of niche space their punctuated 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 two canonical databased of fossil biodiversity, the Paleobiology Database (PBDB; (*5*)) and Sepkoski's compendium (*32*) of fossil marine invertebrates (results from Sepkoski's compendium are presented in Appendix S2.3). We used both data sources because concensus is lacking on the most accurate picture of Phanerozoic biodiversity (*33*).

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 (*34, 35*). 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, which will be approximately Gaussian if 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 diversity fluctuations within orders are well characterized by a Gaussian distribution (Fig. 1).

Independent and dynamically equilibrial dynamics suggested by these Gaussian fluctuations in genus richness could result from neutral-like processes (*36*), where the dynamics of one taxon are unaffected by those of another, or from dampening mechanisms that stabilize complex networks of interacting taxa (*37*). This is in direct contrast to the instability hypothesis underlying the self-organized criticality theory of paleo-biodiversity (*10, 11*).

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 β_k. The form of this stationary distribution could shed interesting light on the biological processes that lead different clades to explore different regions of adaptive landscapes, and thus different equilibria, as discussed below.

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
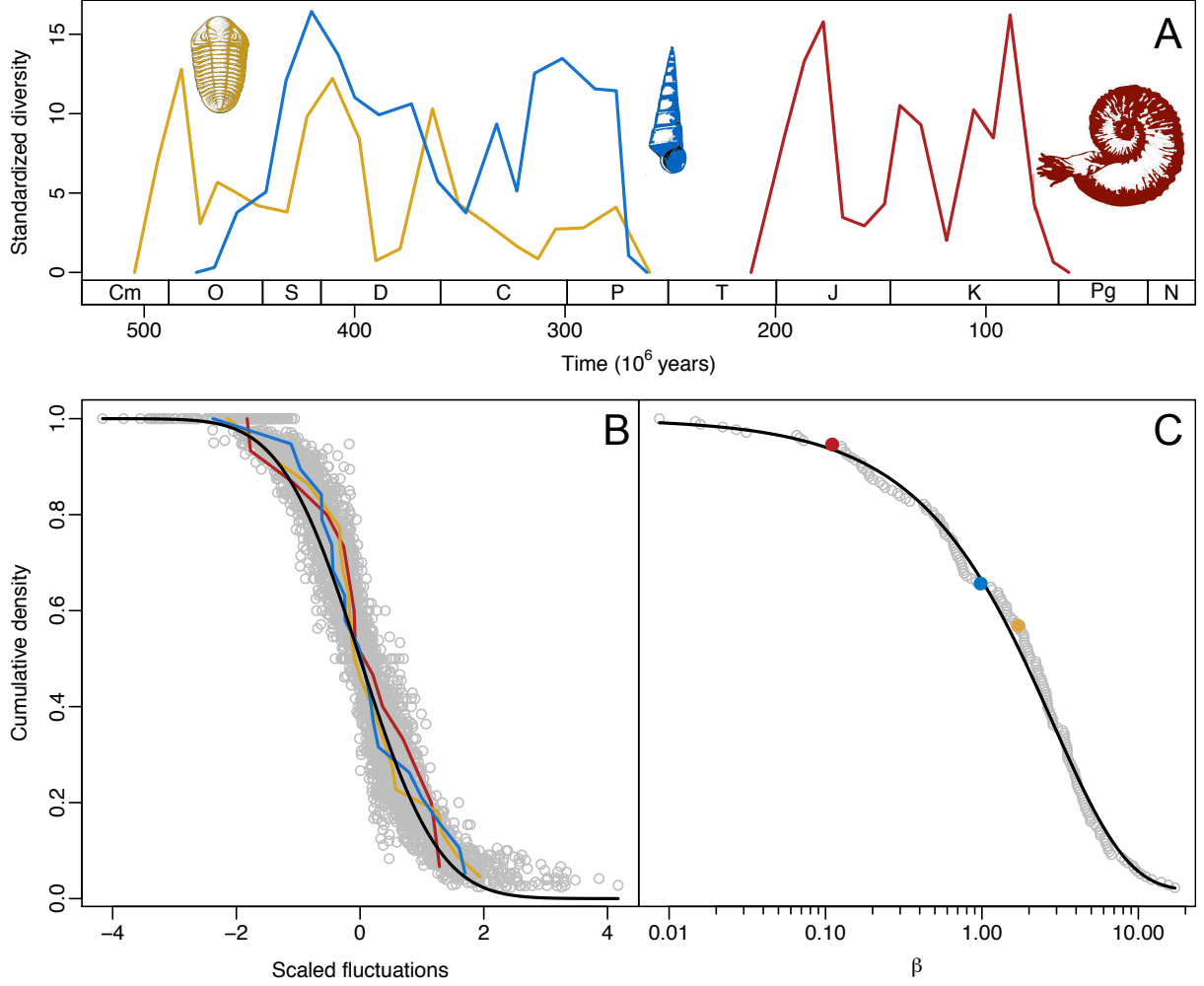
Figure 1: The distributions of within-order fluctuations in genus diversity shown for the trajectories of three exemplar orders (A) and shown as an empirical cumulative density aggregated across all orders (B). To display all orders simultaneously we simply collapse their fluctuation distributions by 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.

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

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124 β_k parameters we can calculate, without further adjusting free parameters, the distribu-

125 tions of order-level fluctuations for the entire marine Phanerozoic, $P(x)$, as

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

126 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 $f(\beta) =$

127 $\frac{1}{\Gamma(b_1/2)} \left(\frac{b_1}{2b_0}\right)^{b_1/2} \beta^{(b_1/2)-1} exp\left(-\frac{b_1\beta}{2b_0}\right)$ is the stationary distribution of inverse variances in the

128 magnitude of order-level fluctuations in diversity. The integral in (1) leads to

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

129 This corresponds to a non-Gaussian, fat-tailed prediction for $P(x)$ which matches both

130 the PBDB and Sepkoski data closely (Fig. 2 and Appendix S2.3).

131   To quantitatively evaluate how well the super-statistical prediction matches the data

132 we constructed a 95% confidence envelope from bootstrapped maximum likelihood esti-

133 mates for $P(x)$. Observed fluctuations fall within this 95% confidence envelope (Fig. 2),

134 indicating that the data do not reject the super-statistical prediction. For further com-

135 parison, we fit a Gaussian distribution to the observed fluctuations, which corresponds to

136 the equilibrium hypothesis that all orders conform to the same dynamic. Using Akaike

137 Information Criterion (AIC) we find that observed fluctuations are considerably better

138 explained by the super-statistical prediction than by the Gaussian hypothesis (ΔAIC =

139 11285.18). Thus, as expected under the superstatitical hypothesis, the fat tailed distri-

140 bution of fluctuations arise from the superposition of independent Gaussian statistics of

141 fluctuations within orders.

142   Computing the distribution of fluctuations using classes instead of orders leads to a

143 substantially poorer fit to the observed data (Fig. S4). We quantify this shift with the

144 Kolmogorov-Smirnov statistic, which changes from 0.041 for orders to 0.062 for classes
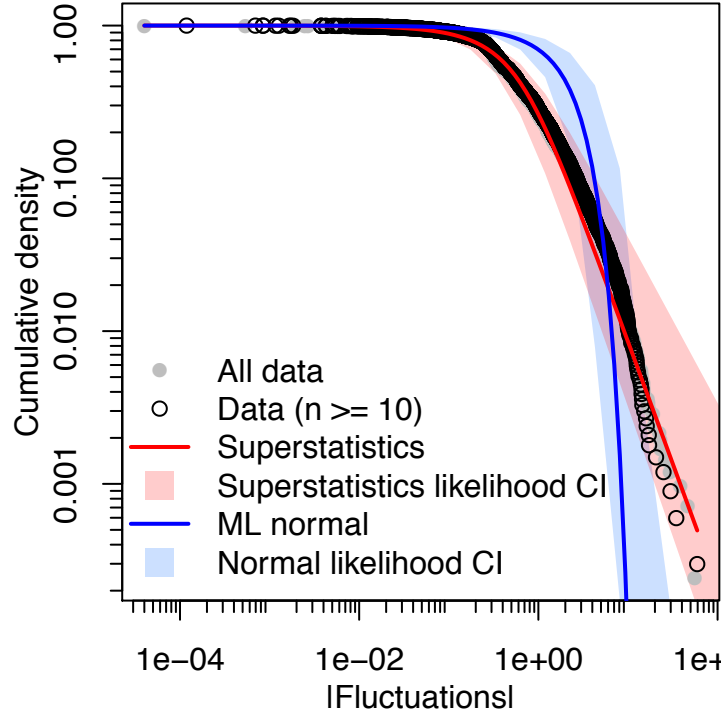
Figure 2: Distribution of fluctuations in genus diversity within orders of marine invertebrates in the Paleobiology Database (*5*) after sampling correction. The distribution is fat-tailed as compared to the maximum likelihood estimate of the normal distribution (blue line). At the order level the empirical 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).

(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.

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.
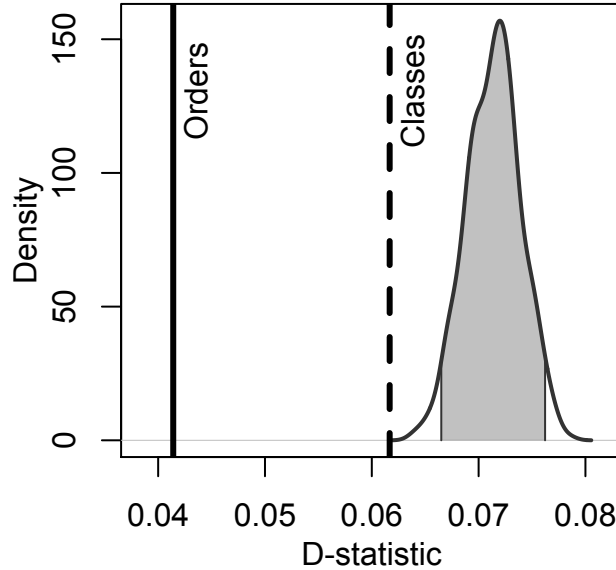

Figure 3: Distribution of Kolmogorov-Smirnov (KS) statistics from randomly permuting genera within orders (gray shading represents 95% confidence interval). Solid black line is observed KS statistic at the order level, while the dashed black line shows the observed KS statistic at the class level.

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 diversity fluctuations (Fig. 1).

Our study is the first to demonstrate that complex patterns in the fluctuation of diversity 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 (*21, 22*) within orders. Equilibrium could result from many processes, including neutrality (*28, 36*), diversity-dependence (*16, 38*) and processes that dampen—rather than exacerbate—fluctuations in complex ecological networks (*39*).

We then show that punctuated shifts to different equilibria between order, a consequence of punctuated exploration of niche space by newly evolving clades (*22–24*), leads to a characteristically non-equilibrial distribution of diversity 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., (*40*)), 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 $(40, 41)$. For macroevolutionary rates to vary across an adaptive landscape, this landscape cannot be flat, and thus niche conservatism punctuated by adaptive exploration is inevitable (24). The specifics of how this adaptive lanscape is shaped and is traversed by evolving clades will likely determine the specific distribution (e.g. Gamma versus Chi-squared, etc.) describing punctuated evoltuion of clades' equilibria. Our work thus motivates study of the trait spaces and evolutionary shifts consistent with Gamma-distributed equilibria in diversity 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 $(4, 9)$, 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., (42)). 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 diversity, abundance and resource use in non-neutral communities. Non-neutral models in ecology are criticized for their over-parameterization (43), yet a persistent counter argument to neutral theory (36) is the unrealistic assumption of ecological equivalency (44) and poor prediction of real dynamics (45). If ecosystems are viewed as the super-position of many

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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 whoes 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

Paleobiology Database data download and filtering

Data were downloaded from the Paleobiology Database (PBDB; www.pbdb.org) on 28 May 2013. Collections were filtered using the same approach as Alroy (5) to insure that only well preserved marine invertebrate occurrences were used in subsequent analysis resulting in 221202 genus occurrences. These were further filtered to exclude those occurrences without order-level taxonomy and those collections with age estimate resolutions outside the 10my default bins of the PBDB resulting in 189516 occurrences left for analysis. To avoid basic sampling concerns we excluded the earliest Cambrian and the latest Cenozoic.

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 most clades are already close to centered and so centering has little influence on clade-specific fluctuation distributions.

Three-timer and publication sampling correction

We use a new and flexible method, described below, to correct for known sampling biases in publication-based specimen databases (5, 6). We were motivated to use this method because rarefaction has been shown to under-perform compared to the more data-intensive shareholder quorum subsampling (SQS) method (6). However, subsampling cannot be applied to small orders (i.e. the majority) because SQS becomes increasingly unreliable as sample size decreases (6). We therefore develop a simple method based on first correcting for detection bias using the "three timer" correction (5) in which the rate of failure to observe a genus is estimated by the number of times a gap occurs in the occurrence history of each genus. To eliminate further bias due to preferential publication of novel taxa we divide observed number of genera per order 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 number of genera on log-transformed number of publications. There is a weak trend toward higher diversity with more publications (Fig. S1) meaning that the most important correction comes from the three timer correction.

Our new method effectively re-scales each genus occurrence from 0/1 (absent/present), to a weighted number continuously ranging between 0 and 1. This method achieves similar results to more computationally intensive sub-sampling procedures (5, 6). We directly compare our predicted time series of global genus diversity with results derived from SQS (6) and the raw data (Fig. S2). Our method shows minor differences with the SQS prediction, However, these discrepancies do not impact the distribution of fluctuations (Fig. S2) and super-statistical analysis on uncorrected PBDB data (see section S2.1) produces a similar result to the analysis on corrected PBDB data presented in the main text.

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Numerical 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 variances 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 asymetric 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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