

LETTER

Biodiversity Trends Show an Excess of Both Near Stasis and of Very Large Change

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ABSTRACT

Temporal trends in biodiversity metrics such as species richness and total community abundance often average close to zero across many assemblages. However, little attention has been given to characterising the variation in trends such as the overall shape of the distribution. For a variety of biodiversity metrics and large data sets, we find that measured rates of change are not well fit by the Normal Distribution but are better characterised by leptokurtic, fat-tailed distributions. The best fit overall is to the Subbotin, with the special case of the Laplace Distribution usually performing well. These findings can improve statistical analysis and simulations, but the most important implication of leptokurtosis is that ecologists should pay more attention to the small number of systems that are experiencing strong temporal trends, rather than focusing on the large majority of cases that exhibit weak trends.

1 | Introduction

The biosphere is being drastically modified by humans in many ways (Vitousek et al. 1997; McGill et al. 2015). It seems unlikely that these extensive and diverse human activities could have no impact on biodiversity. Although investigations of human impacts in specific places and taxa have been longstanding, the recent decade has seen a flurry of meta-analyses analysing the trend of change in biodiversity in the past 50 years (typically under the assumption that these changes are in response to large human impacts). In recognition that biodiversity is a complex concept, a variety of biometric metrics of potential interest (McGill et al. 2015) have received attention. These include classic diversity measures (Vellend et al. 2013; Dornelas et al. 2014), abundance (Dornelas et al. 2019; Van Klink et al. 2020), occupancy (Outhwaite et al. 2020), biomass and body size (Martins et al. 2023), temporal beta diversity (Dornelas et al. 2014) and spatial beta diversity (Blowes et al. 2024) and they are the

subject of a recent review (Dornelas et al. 2023). Most of these meta-analyses have focused on the mean trend, often finding the mean trend to be close to zero or even positive (Dornelas et al. 2023); this finding has proved to be controversial (Primack et al. 2018). Many authors have also noted the considerable variation around the mean trend. For example, the phrase “...biodiversity trends are complex and heterogeneous” is in the title of one recent paper (Wagner et al. 2021). To date, little effort has gone into describing the nature of this variation beyond plotting empirical histograms of the distribution, simply noting that variation in trends seems large and contains some very large trends up or down for a given biodiversity metric.

To be more explicit, we define a biodiversity metric as a number that represents a property of a collection or set of organisms interpreted to be related to biodiversity. It could be species richness, species diversity or evenness, total number of organisms in a population or in a multi-species community, mean phenotype

(e.g., average body size), or one of many other metrics. We can denote this as $D_{i,t}$ for a metric D measured at time t at replicate (e.g., site or taxon) i . A trend in a biodiversity metric is simply the regression slope of a metric versus time, t , and can be denoted T_i . Examining the slope of a linear regression provides a broad brush trend, but ignores details such as curvilinear trends, which have been measured elsewhere (e.g., McGill 2013); we ignore these here for simplicity. T_i will be positive if the metric is increasing through time, zero if it is not changing systematically and negative for declines. We wish to characterise the nature of the set of T_i . Most of the studies cited in the last paragraph focused on the mean slope ($\mu = \text{mean}(T_i)$) or other measures of central tendency of the distribution of T_i , often finding it is closer to zero than expected (Dornelas et al. 2023). Mostly these studies comment only qualitatively and in passing that the variance, $\sigma^2 = \text{var}(T_i)$, seems large.

Rarely even raised as an assumption or question is what the statistical distribution of the T_i is? Probably many (including the authors) might suspect a Normal distribution as a good first guess for the distribution of T_i . Three different lines of argument point to a Normal distribution, explaining its empirical ubiquity (Figure 1). Treating T_i as an observation with error (due in part perhaps to measuring a single location) from a true underlying value of T invokes the theory of measurement errors. Treating T_i as arriving from many random perturbations to the community aligns with the Central Limit Theorem (Lindgren 1976), while adding an additional assumption of a central tendency, with pressure to return to a set point, to the assumption of accumulating random perturbations, invokes Ornstein–Uhlenbeck processes (Uhlenbeck and Ornstein 1930). The simplest and longest standing versions of all of these lines of statistical model point to

a Normal distribution. Less appreciated is that these same three lines can invoke more complex assumptions and point away from the Normal distribution to a wide variety of heavy-tailed distributions (Figure 1). To oversimplify, these complexifications involve more variability, unequal allocation of resources and randomness, and nonlinearity, all ecologically probable (See Table S1 and Figure S3 and associated narrative text for details and citations).

Once this door is opened, the list of possible distributions is large (Figures 1 and S3), but importantly they broadly share the feature of allowing more kurtosis (peakedness) and in most cases heavier tails than the Normal distribution. Figure 1 describes this metaphorically as the “heavy-tailed” world versus the “Normal world”. Although large, complex and less familiar, the heavy-tailed world does contain a few recurring distributions, including the Normal (“normal world” is a special case of, not separate from, “heavy-tailed world”), but also noticeably the Laplace distribution, and its generalisation, the Subbotin distribution (Subbotin 1923) (see Supporting Information for introductions to the Laplace and Subbotin distributions). While none of the aforementioned lines of argument require that the distribution of T_i comes from one of these distributions, they are suggestive, as is the fact that these same distributions have been found to be applicable to economic trends such as growth of GDP across countries (Gibrat 1931). Thus the key question explored in this paper is whether the Normal distribution is an adequate description of the distribution of trends in biodiversity, or whether it is necessary to expand into the “heavy tailed world” to adequately describe the distribution of trends in biodiversity. Although we do additionally explore which distributions of “heavy-tailed world” provide the best fit to our empirical data, we recognise

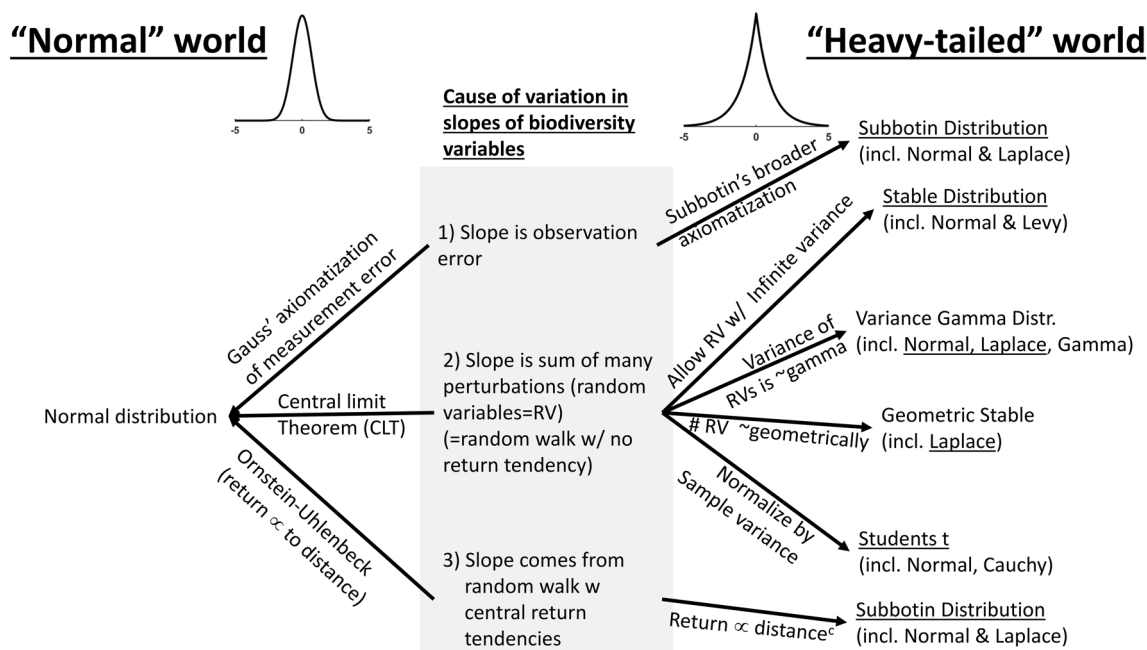


FIGURE 1 | Simplified assumptions derived from: (1) measurement error theory, (2) central limit theorem and (3) random walks with central tendencies lead to the Normal distribution (as widely appreciated). The right hand side shows how less-widely appreciated alternative assumptions lead to a wide variety of distributions which we label “heavy-tailed world”. These distributions are all capable of expressing strong kurtosis (peakedness) where most often events are very close to the centre (e.g., near zero) but the probability of rare very large events is much larger than in a Normal distribution. Note that the Normal distribution is a special case of many of these “heavy-tailed world” distributions so “Normal world” is actually embedded in “heavy-tailed world”, not separate from as suggested in the figure.

that it is essentially impossible to prove that empirical data comes from a specific distribution (especially with finite samples), so that is not our goal. Similarly, fitting distributions is not informative about mechanism (Cohen 1968; McGill et al. 2007) and the highly general statistical arguments we invoke can include literally hundreds of more specific models. Accordingly, this is fundamentally an empirical exploration about the general nature of the distribution of biodiversity trends.

Within the heavy-tailed world, the Variance Gamma and the Geometric Stable distribution have gained significant attention in econophysics (Madan and Seneta 1990; Kozubowski and Rachev 1994) as models of stock market prices, but are analytically complex, difficult to work with and do not have readily available methods and software to fit and estimate parameters (which often can only be done by approximation; see Loregian et al. 2012) or non-maximum-likelihood methods (Kozubowski 1999); we choose not to address those two distributions here. Instead, we will empirically explore the Subbotin, Student's t and Stable distributions as alternatives to the Normal distribution, noting with interest that the Subbotin and its special case of the Laplace show up most often in these high-level statistical models.

Most of these “heavy-tailed world” distributions have not been widely explored in ecology, but many have been used occasionally in ecology. The Subbotin Distribution is sometimes referred to as the Generalised Normal Distribution (Kotz et al. 2012) and has a shape parameter α that gives the Normal Distribution when $\alpha=2$ and gives the Laplace (also known as the double exponential or back-to-back exponential) when $\alpha=1$. See the [Supporting Information](#) section “Subbotin distribution” for more details. The Subbotin has been used to generalise the use of a Normal bell-curve shape to represent niches along a linear axis (Roughgarden 1974). The Laplace distribution has been identified several times in ecology. In particular multiple authors have shown that one time-step population growth rates $r_t = \log(N_{t+1}/N_t)$ follow the Laplace distribution in birds (Keitt and Stanely 1998; Marquet et al. 2007), marine fish (Labra et al. 2005a), freshwater fish (Sun et al. 2015), diverse marine planktonic organisms (Segura et al. 2017) and estuarine fish (Segura et al. 2021). Also, at the population level, one time period changes in phenotype (selection coefficients) have been noted to fit the double exponential (Laplace) (Kingsolver et al. 2001). One time-step population growth rates are clearly conceptually related to the multi-year trends in population size that are the subject of this paper, but no-one has explored the distribution of multi-year trends in population abundance to our knowledge. Additionally, most of these identifications of the Laplace have all been based on visual examination, with only Segura et al. (2017) having performed more quantitative analysis. The Student's t has been most often used in ecological systems as a description of a fat-tailed dispersal kernel for seeds (Clark 1998) (an application which has also used the Subbotin distribution: e.g., Clark 1998). Stable distributions, especially the special case of the Levy distribution, has been widely used as a model of animal movement (Levy flights) (Reynolds and Rhodes 2009). Other heavy-tailed distributions have also been used for dispersal (e.g., Van Houtan et al. 2007). The Levy Distribution, per se, is not an appropriate model for trends as it strictly non-negative, but the more general class of Stable distributions includes those

covering $(-\infty, \infty)$ and are explored here. The Stable Distribution was found to provide a good fit to population growth rates in marine microbes (Segura et al. 2013) and several diverse species (Lan and Chandran 2011), while a poor fit was found in diverse taxa (Halley and Inchausti 2002).

In this paper we pursue two new directions. First, we explore not population but community metrics including various diversity metrics and total community population size (Segura et al. (2013, 2017) also looked at aggregate population sizes but, to our knowledge, nobody has examined diversity in this frame). Second, we address long term (decadal or longer) trends that in most cases include multiple birth and death cycles of the organisms, as opposed to shorter time frames (e.g., a week or a year) that are closer to a single generation time and are explicitly described in the above references as population growth rates, not long term trends. Although we are unable in this paper to attribute results to humans, the timescales are more applicable to recent human-caused global change questions.

In this paper, we assemble a variety of time series of multi-year trends in single population and multi-species biodiversity metrics to examine the distribution of their trends (T_i), explore the fit to the Normal and explore the fit to alternatives including the Student's t , Stable and Subbotin distributions with special attention to the Laplace.

2 | Methods

Here we assemble three datasets, BioTIME, containing measurements of the abundance of every species in a community over time from diverse taxa (Dornelas et al. 2018), the North American Breeding Bird Survey (BBS) containing standardised measurement protocols for one taxa and continent (Sauer et al. 2017), and Kingsolver's database on selection coefficients (change in phenotype for one population) (Kingsolver et al. 2001, Kingsolver et al. 2008) covering 63 studies and 1582 data points spanning weeks to many years. For BioTIME we filter out data from the BBS (to avoid double counting) and limit the data to timeseries with at least ten time periods (to give a good estimate of a trend) spanning at least a decade (to give long term trends), resulting in 7456 communities and 217,678 populations. We then compute trends in $\log(S)$ where S is species richness, trends in Shannon and Simpson Diversity and trends in log total community abundance by summing number of individuals across all species and log transforming, $\log(N_{tot})$. The first three of these can also be described as variants of the Hill Diversity indices (Hill et al. 1995) with $q=0, 1, 2$ respectively. We also examine the Jaccard dissimilarity index (effectively a measure of percent of species that have changed) between the first and last time point as a measure of temporal beta diversity. In the BBS we look at the trend in $\log(S)$. These are all metrics of change in the whole community. We also assess the multi-year population trend in $\log(N)$ of the change in each individual species at each site (i.e., population) in both the BBS and BioTIME. The BBS data includes 12,030 populations and 442 community trends, all over exactly 20 years. These are related to but distinct in temporal span and number of points per trend from the analysis of one year population growth rates previously studied in the BBS (Keitt and Stanely 1998; Marquet et al. 2007) and in other

taxa mentioned in the [Introduction](#). To include evolutionary or phenotypic change we use the strength of selection (the same dataset analysed by Kingsolver, but providing a more quantitative analysis of the shape of the distribution). Note that except for some of the selection coefficients, these are all multiyear trends; and further excepting the selection coefficients these are all OLS regression slopes across at least 10 (BioTIME) or exactly 20 (BBS) time periods.

Using these nine datasets we provide visual comparisons to the Normal distribution, perform a Lilliefors test for normality, and explore statistics of skewness and kurtosis which are combined in the Jarque–Bera test (Jarque and Bera 1980) to see if skewness and kurtosis statistically significantly exceed those found in the normal. We also implement the Hogg T statistic of probability density in the tails to see if the tails are heavier than normal and assign statistical significance (Schmid and Trede 2003).

With the same nine datasets we next explore the fit to alternative distributions using maximum likelihood estimation (MLE) of parameters and information criteria-based model selection. (AIC reported in the main text, BIC reported in the [Supporting Information](#)). Specifically, we fit the following distributions. First, four variants of the Laplace distribution including the simple, traditional Laplace with a single scale parameter, σ (number of parameters $k=1$), asymmetric Laplace ($k=2$), where the scale parameter varies on the left and right sides, σ_{left} and σ_{right} , non-centred Laplace ($k=2$, μ and σ) where the peak occurs elsewhere than zero (μ) and a combined asymmetric, non-centred Laplace ($k=3$, μ , σ_{left} , σ_{right}). Note that the MLE estimate of μ is the same in the two and three parameter cases. Second, we fit a Subbotin distribution ($k=3$) with measure of central tendency, μ , scale of variation σ and shape, α . Note that if $\alpha=1$ this reduces to the non-centred Laplace, and if $\alpha=2$ this is the Normal distribution. Third, we fit a non-centred, scaled Student's t distribution which is commonly used to fit symmetric, heavy-tailed data in ecology (Clark 1998) and which also has centre, scale and shape parameters ($k=3$). If the shape parameter $\nu=1$ then this is the Cauchy distribution (and if $\nu=\infty$ it is the Normal distribution). Finally, we fit the Stable distribution which has four parameters ($k=4$) where μ is a location, σ is scale, γ = skew and α = shape.

To place confidence intervals on the Laplace distribution fit to the data (Figure 3), we perform a parametric bootstrap with 1000 random replicates. For each replicate, we draw points randomly from the Laplace with the MLE estimated parameters, drawing the same number of points as in the original data. Then, for each replicate, we count the number of points falling in each of 41 bins evenly spread across the range of data. After completing the 1000 replicates, we calculate the 2.5th and 97.5th percentiles of each of the 41 bins and draw lines through these percentiles. We also perform a Kolmogorov–Smirnov goodness of fit test to the simple 1-parameter Laplace distribution.

3 | Results

In each of the nine data sets of biodiversity change (see [Methods](#)), the data show some broad similarities to a Normal Distribution (Figure 2), but also exhibit substantial differences which are shared across all of these data sets (Table 1). The Lilliefors test

gives $p < 0.001$ in all nine cases for the data being drawn from a Normal distribution. In each case the skew is small (Table 1), falling within the range of $(-0.5, 0.5)$ that Bulmer (2012) calls “fairly symmetric”. But the kurtosis is in every case greater than 3 (the kurtosis of the Normal distribution), indicating leptokurtosis. The Jarque–Bera test indicates that in all nine cases the combination of skew and kurtosis has $p < 0.001$ for being sampled from a Normal distribution. Since the skew is close to zero as in a Normal Distribution, this is presumably due to high kurtosis, but we are not aware of a statistical significance test that singles out only kurtosis. The Hogg T also trends higher than the Normal distribution (indicating heavier tails) for eight data sets (all but the BBS log(S)), and is statistically significantly higher than it would be in a Normal distribution for six of the nine datasets (Table 1). This confirms more quantitatively the visual impressions of Figure 2.

We give the maximum likelihood estimated parameters of the six variants of distributions tested in Table 2. The Subbotin distribution tended to have a shape parameter close to $\alpha=1$, representing proximity to the Laplace distribution (and in every case closer to $\alpha=1$ than the Normal which has $\alpha=2$). For the Laplace distribution, the parameter estimates from the three and two parameter versions are reported (they have the same MLE estimator for μ so it is only reported once). In every case μ was very close to zero but a simple signed rank test always indicated it was highly statistically significantly different from zero ($p < 1E-6$) except for the BBS log(S) metric which was not significantly different from zero. Other than the fact that these data sets have very large N and thus very high power to detect small deviations, we are unsure what to make of this. It is hard to imagine a biological scenario that would cause trends to average very close to zero but be statistically significantly different to zero. We suspect this is more a case of irregularities or biases in the data rather than having any biological significance. The shape parameter (ν) for the Student's t was typically between about 2.4 and 5, indicative of data that is more leptokurtic and fatter-tailed than the Normal distribution ($\nu=\infty$) but less heavy-tailed than the Cauchy ($\nu=1$). These parameters all confirm that the data are more leptokurtic than the Normal distribution and that within the Subbotin family, the data are closest to Laplace.

To compare the fit of the models we used ΔAIC (Table 3). For all nine datasets the Subbotin distribution was the best model. For eight of the datasets some form of the Laplace was the 2nd best model (the simple 1 parameter model for five and the maximally complex 3 parameter model for three). The BBS population trends dataset was the one exception where the Student's t was the 2nd best fit. This distribution also had the Laplace shape parameter, α , farthest from 1. The Laplace seems an especially poor fit to that data, although it clearly remains more heavy tailed and leptokurtic than a normal, and the Subbotin is the best fit. The BIC (Table S2) tells a largely similar story with the Subbotin usually providing the best fit, some form of the Laplace providing the second best, and only for the BBS population trends does the Student's t fit as the 2nd best. Within the Laplace, adding a parameter for non-centeredness offers more improvement in AIC than a parameter for asymmetry. The Stable and especially the Normal distributions are always much worse, while the Student's t is intermediate but usually (8 of 9 cases) worse than the Subbotin/Laplace family.

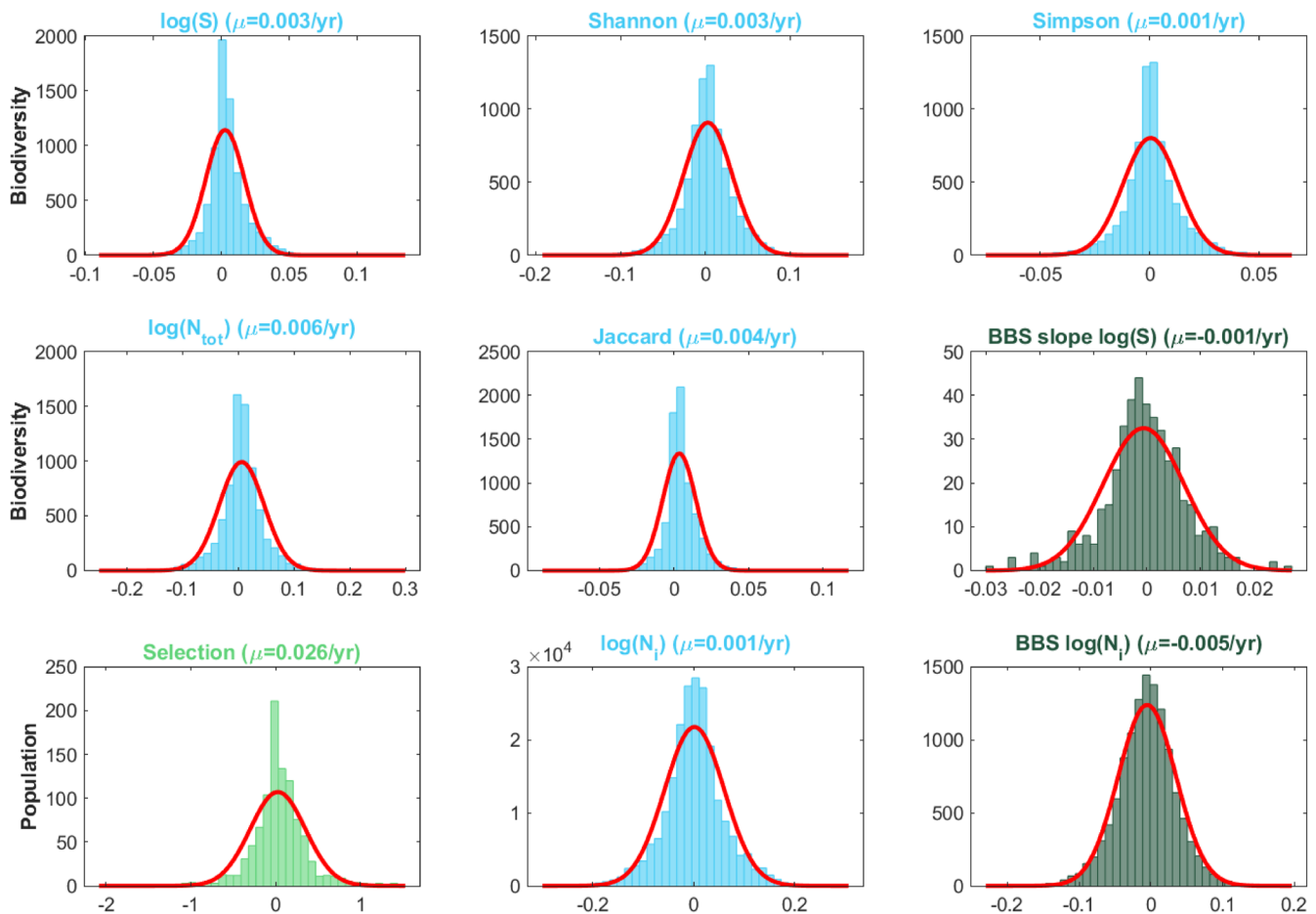


FIGURE 2 | Comparison of empirically observed distribution of trends of 9 biodiversity metrics to a Normal distribution (red line represents MLE best fit Normal distribution) (see main text for descriptions of data and biodiversity metrics). Histograms in light blue are from the BioTIME data. Histograms in dark green are from the North American Breeding Bird Survey. The histogram at the bottom left in blue-green is from Kingsolver's compilation of selection coefficients. The top two rows represent community-level (multi-species) metrics, while the bottom row represents single species population metrics. See the methods for more details on the data.

The two parameter Laplace and its 95% confidence intervals show a good visual fit to the data as well (Figure 3). With 41 bins, about 5% (~2) points should be expected to fall outside of the 95% confidence lines by chance. Three datasets seem to exceed this. The BioTIME $\log(S)$ data shows a clear excess of intermediately large positive trends while fitting the Laplace well elsewhere, for which we have no explanation. The two population abundance trends (N_i) also clearly fall below the 95% confidence intervals in both tails. To some degree, poor fits in the tails are less surprising due to finite samples, but the Subbotin α parameter also suggests these data are intermediate between the Laplace ($\alpha=1$, appears as a triangle in Figure 3) and the Normal ($\alpha=2$, appears as a parabola in Figure 3).

4 | Discussion

Overall, these nine data sets provide strong support for rejecting the Normal Distribution as the default distribution for multi-year trends in biodiversity (or population) data in favour of a heavier tailed, more leptokurtic distribution. Of the three such families of distributions that we explored, the Subbotin was overall the clear winner. If one seeks a simple, easy to work with,

well-known distribution, the Laplace or double-exponential special case of the Subbotin ($\alpha=1$) comes closest, although in no case is the Subbotin α parameter exactly 1 (even to two significant digits), and the KS test rejects the Laplace in 8 of 9 cases. But rejecting an exact fit to a specific distribution is common with the amount of power (high N) in these data sets. Even if most of the data shares a common generating process, there are always a few sampled points that come from another process, or the process is never exactly instantiated. Other heavy tailed distributions, including the earlier mentioned Variance Gamma and Geometric Stable distributions, should be explored as software and methods become more available. Furthermore, the Stable Distribution and the Student's t Distribution clearly beat the Normal, seemingly making almost any symmetric, fat-tailed distribution superior to the Normal. But for now, the most supported course is to proceed with the Subbotin (or, if one prefers simplicity and specificity, the Laplace) rather than with the Normal Distribution as a default assumption for the distribution of trends in biodiversity. And regardless of the exact distribution, the strong peakedness and heavy tails seem to be a fairly general feature in the nine datasets we explored. It is worth noting that these findings are in datasets that are geographically and taxonomically diverse with substantial spatial extent and covering

TABLE 1 | Basic descriptive statistics and significance tests.

	Community					Population			
	BioTIME					BBS	Kingsol	BioTIME	BBS
	log(S)	Shannon	Simpson	log(N _{tot})	Jaccard	log(S)	Selec	log(N _i)	log(N _i)
<i>N</i>	7448	7448	7448	7448	7448	442	993	217,678	12,030
Sign-Rank <i>P</i> ($\mu=0$)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.2697	<0.0001	<0.0001	<0.0001
Skewness	0.249	−0.158	−0.020	0.159	0.344	−0.233	0.113	0.046	−0.142
Kurtosis	6.708	5.610	5.698	7.552	9.000	4.392	7.848	4.266	4.033
Jarque–Barre <i>P</i> (Normal)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
HoggT tails versus 1.7038	1.724	2.239	2.104	1.837	1.972	<i>1.313</i>	1.711	1.724	1.914
KS <i>P</i> (Laplace)	0.00000	0.11218	0.00000	0.00002	0.00000	0.34293	0.04821	0.00000	0.00000

Note: The sign-rank test tests for a mean value of 0. All data had means statistically significantly different than zero. Skewness is the sample skewness statistic. Bulmer (1979) describes skewness <0.5 as “fairly symmetric” which applies to all data. Kurtosis values greater than 3 (the kurtosis of the Normal distribution) indicate leptokurtic distributions (peaked w/heavier tails). Some authors suggest 6 as a cutoff for very strong kurtosis but this is arbitrary. The Jarque–Barre test combines skewness and kurtosis into a single number to test deviation from normality. All data is statistically significantly different from normal in the degree of skewness + kurtosis. Given the weak skewness and strong kurtosis observed this deviation from normality is presumably mostly due to kurtosis. The Hogg percentile test for tails (Schmid and Trede 2003) is a non-parametric method to assess for tails that are heavier than the Normal distribution. Values > 1.7038 indicate heavy tails, which all data shows except for the trend in log(S) for the BBS. A Monte Carlo statistical test for significantly heavy tails is also provided and bold values are statistically significant. The Kolmogorov–Smirnov (KS) test tests whether the data could come from the Laplace 1-parameter distribution. All data reject this null except for the Shannon and BBS log(S) trend.

TABLE 2 | The parameter estimates for the parameters of three families of distributions estimated for nine different data sets of rates of change (trends) in biodiversity metrics.

		Biodiversity					Population			
		BIOTime					BBS	KS	BIOTime	BBS
		log(S)	Shannon	Simpson	log(N _{tot})	Jaccard	log(S)	Selec	log(N _i)	log(N _i)
Laplace	μ	0.003	0.003	0.001	0.006	0.004	−0.001	0.026	0.001	−0.005
	σ	0.010	0.021	0.009	0.027	0.007	0.006	0.218	0.043	0.031
	σ_{left}	0.009	0.020	0.008	0.026	0.006	0.005	0.200	0.043	0.032
	σ_{right}	0.011	0.021	0.009	0.028	0.009	0.006	0.238	0.044	0.030
Subbotin	α	0.943	1.070	0.871	0.882	0.933	1.281	0.882	1.183	1.454
	μ	0.003	0.003	0.001	0.006	0.004	0.000	0.026	0.001	−0.006
	σ	0.009	0.023	0.007	0.022	0.007	0.007	0.179	0.053	0.046
Student's <i>t</i> (Scaled, noncentral)	μ	0.003	0.003	0.001	0.006	0.004	0.000	0.035	0.001	−0.006
	σ	0.008	0.020	0.008	0.023	0.006	0.006	0.187	0.045	0.035
	ν	2.476	3.579	2.614	2.427	2.419	5.067	2.480	4.326	7.680
Stable distribution	α	1.412	1.641	1.475	1.445	1.380	1.791	1.478	1.719	1.887
	γ	0.290	0.070	0.124	0.048	0.315	−0.290	0.095	0.080	−0.306
	μ	0.007	0.016	0.006	0.019	0.005	0.005	0.154	0.036	0.027
	σ	0.003	0.003	0.001	0.006	0.004	0.000	0.032	0.001	−0.005

Note: See [Methods](#) of datasets and metrics. See [Supporting Information](#) “Laplace Distribution” and “Subbotin Distribution” for definitions of parameters and distributions.

TABLE 3 | Δ AIC table for model selection of distributions fit for nine different data sets of rates of change (trends) in biodiversity metrics.

	# param	Biodiversity					Population			
		BIOTime					BBS	KS	BIOTime	BBS
		log(S)	Shannon	Simpson	log(N _{tot})	Jaccard	log(S)	Selec	log(Ni)	log(Ni)
Subbotin	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LapSymCtr	1	<u>24.0</u>	<u>5.7</u>	54.5	<u>40.0</u>	<u>39.4</u>	<u>3.2</u>	4.4	1626.7	410.4
LapSymNonCtr	2	26.0	7.7	56.5	42.0	41.4	5.2	6.4	1628.7	412.4
LapAsymCtr	2	533.0	116.9	81.7	328.1	1573.9	7.9	16.4	1691.9	568.7
LapAsymNonCtr	3	43.4	99.2	<u>12.6</u>	240.4	781.9	7.5	<u>1.7</u>	<u>1602.1</u>	255.4
Student's <i>t</i>	3	219.4	95.8	366.9	100.5	117.9	1.6	13.9	3516.2	<u>10.7</u>
Stable	4	322.2	274.7	576.8	274.0	169.4	10.2	33.8	9381.8	125.6
Normal	2	1495.9	874.9	1488.6	1805.1	1841.9	22.6	253.8	15561.3	318.3

Note: Bolded number is the lowest AIC (best model). Underlined number is 2nd best model. BIC table shown in supplemental material is qualitatively similar.

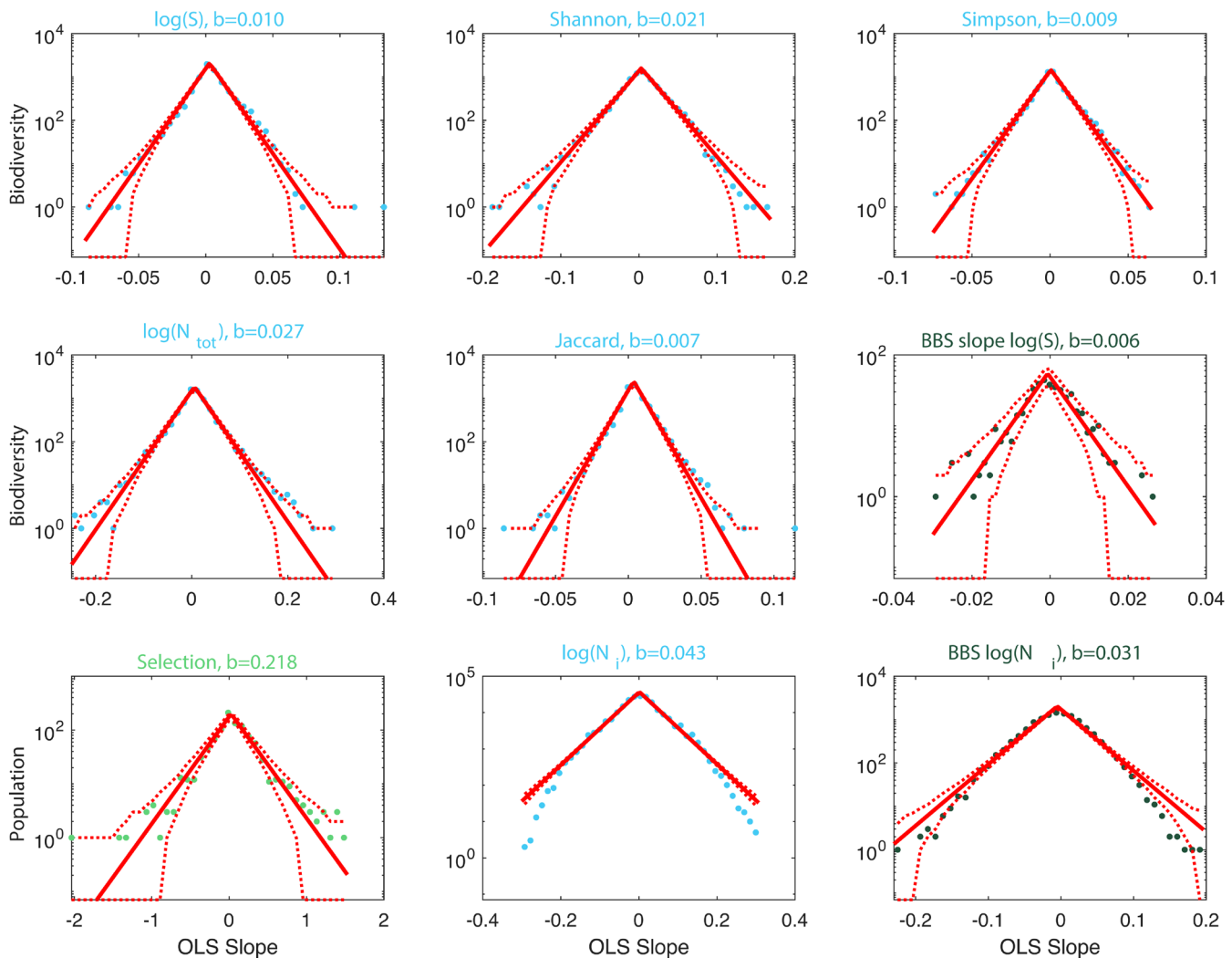


FIGURE 3 | Plot of the distribution of nine assemblages of biodiversity trends on a logged y-axis showing counts. The data sources and metrics in these nine panels are the same as the data sources and metrics in the corresponding nine panels in Figure 2. The Laplace distribution should appear as a pyramid (solid red line). A Normal distribution should appear as a parabola (not shown). Fitted Laplace distributions shown in solid red line. Binned frequency counts of empirical data shown as dots. Monte Carlo 95% confidence intervals resampled from the fitted Laplace are shown in the thin dashed red lines. Note that by chance about 5% of the 41 dots (~2) should appear outside the confidence intervals.

most of the time period over which we have sufficient data (the last two to four decades), and moreover that this pattern occurs in a variety of biodiversity metrics at both the population and community level, suggesting that there is a strong chance these results are general.

As noted in the introduction, five previous papers have found a Laplace distribution in population growth rates (Keitt and Stanely 1998; Labra et al. 2005a; Marquet et al. 2007; Sun et al. 2015; Segura et al. 2017; Segura et al. 2021), one author found the Laplace in population selection coefficients (Kingsolver et al. 2001), and two papers found the Stable distribution in short-term population growth rates (Lan and Chandran 2011; Segura et al. 2013) while one paper found a poor fit for the Stable (Halley and Inchausti 2002). All of these authors have worked on the population (single site and species) level and looked only at short term changes on time scales approximating single birth-death cycles, but did find good fits. It is, therefore, perhaps surprising that the Laplace/Subbotin distribution (and more generally fat-tailed, leptokurtic distributions) has been so little recognised in ecology or tested on other types of trends or change. Many of the recent papers on biodiversity trends (Vellend et al. 2013; Dornelas et al. 2014; Elahi et al. 2015; Blowes et al. 2019) have plotted histograms of rates of change (trends) in biodiversity, and they all clearly look too leptokurtic to be normal. Yet this goes unremarked, including by the authors of this paper (Dornelas et al. 2014; Dornelas et al. 2019). We believe this is due to the over focus to date on the mean trend, because the histograms were centred on zero with a strong mode at zero and rough symmetry around zero, with the result that investigators did not probe further. We hope this paper will encourage ecologists and evolutionary biologists to devote more attention to the nature and distribution of the variance in trends in ecological systems.

The arguments we present (Supporting Information) for the Subbotin and Laplace Distribution of trends in biodiversity metrics are quite generically statistical in nature, and so this pattern joins the status of other statistically generated patterns in macroecology such as the approximately lognormal (or logseries) species abundance distribution (McGill et al. 2007) and the log-normal body size distributions (Blackburn and Gaston 1994). The generic statistical nature suggests that analogous results might be observed in measurements of rates of change in other complex, non-ecological systems (Nekola and Brown 2007; Blonder et al. 2014), and this is indeed the case. There is a long and moderately large history of exploring the rates of growth of the GDP of countries and the size of firms or cities as well as the changes in prices of assets like stocks through time (Gibrat 1931; Sutton 1997). In these systems the observation of a fat-tailed distribution of rates of change is decades old and the Laplace distribution has been frequently invoked (Lee et al. 1998; Bottazzi and Secchi 2006; Alfarano et al. 2012; Arata 2019). Such analyses have also been at the heart of a new field known as econophysics (Mantegna and Stanley 1999). Just as in ecology, where it is possible to derive general statistical distributions like the logseries via highly detailed mechanistic models like neutral theory (Hubbell 2001), a number of econophysics authors have derived rather detailed mechanistic models of a finite number of shocks (innovations) to competing firms (Bottazzi and Secchi 2006) or affiliation switching in networks (Mondani et al. 2014) that

clearly have applicability to ecology as well. However, these arguments are effectively only reproducing a statistical argument with mechanistic clothing. We personally find the general statistical arguments more fundamental and general, but we recognise this preference may vary among ecologists. The Laplace distribution has also been applied to problems like hydrology and engineering (Kotz et al. 2012). Without testing data that predates the Anthropocene, it is an open question whether the fat tails are a signature of human impacts or general to ecological change, although the general statistical nature of the Subbotin distribution suggests the Subbotin or Laplace is probably not any more likely to provide a signature of the Anthropocene than the Normal Distribution does. More likely, change in the Anthropocene is constrained by the same rules and distributions as change predating the Anthropocene.

Although our data and exploratory analysis broadly supports the Subbotin and its special case of the Laplace most strongly, it is not truly possible to prove a single data set follows a specific distribution, let alone that all similar data sets would. It is also not possible to impute a specific mechanism from a given distribution. In the Supporting Information material we identify at least four different mechanisms that can produce the Laplace distribution alone. Moreover, one specific mechanism (the sum of a geometrically distributed random number of normal random variables; 2b in Supporting Information material) can be mapped into very different mechanistic processes such as network linkages preferentially going to nodes that already have linkages (Mondani et al. 2014) or random shocks to company profits that accumulate in a clustered fashion (Bottazzi and Secchi 2006). Thus our exploratory analysis cannot prove any underlying mechanism. Nonetheless, there are at least two shared themes that are suggestive of possible key processes. First, the notion of random drift with a central return tendency (3a) leads to Subbotin distributions which are not hard to imagine in ecological systems and have been observed for community metrics (Brown et al. 2001; Ernest et al. 2008; Gotelli et al. 2017). Second, high heterogeneity (specifically, systems where some subsets show very large variance and more subsets show very low variance) can also produce the Laplace distribution and leptokurtic distributions more generally (arguments 1b, 2b, 2c) and certainly conform to intuitions about the nature of ecological systems. This has been suggested as a mechanism producing the Laplace in one-year growth rates previously (Allen et al. 2001; Segura et al. 2017; Segura et al. 2021). This argument has also been found in econophysics (Bottazzi and Secchi 2006; Mondani et al. 2014). Econophysics has also noted that systems follow a sort of variant of ecology's Taylor's Law where variance of subsets of data grouped by size, S , (e.g., across species grouped by abundance into bins) follows a power law, $\sigma(S) = aS^b$ (Lee et al. 1998), an argument related, but not identical to those made for one-year growth rates in ecology (Allen et al. 2001; Segura et al. 2013; Segura et al. 2017). We can preliminarily confirm this argument works for community-level or biodiversity data (Figure S4), although we have found cases where the exponent b is both positive and negative. This needs more examination than space here provides.

Knowing that rates of change are Laplace distributed has implications for our ability to detect and analyse biodiversity change. The occurrence of a Laplace distribution can bias significance

tests (e.g., testing whether a slope differs from zero). Assuming normality when the data is in fact heavy-tailed would bias the confidence intervals and p -values and make researchers more likely to report significant differences from zero than supported. More generally anything based on likelihood (including AIC) will also be incorrect if the wrong distribution is used. The Laplace is also associated with robust regression (MLE with Laplace errors gives the least absolute deviation regression). Similarly, the MLE estimator of μ (central tendency parameter) of the Laplace Distribution is $\text{median}(x_i)$ while in the Normal Distribution it is mean (x_i). Given the sensitivity of ordinary (Normal error) regression to outliers and the increased frequency of points far from the central tendency in the Laplace Distribution, estimates to identify central tendencies of biodiversity trends may want to move to robust regression methods. Finally, the prevalence of the Laplace distribution opens up the possibility of more accurately simulating changes to ecological systems over long time periods. This knowledge is not predictive of a specific trend for a specific system, but it does allow us to much better simulate and understand the range of changes forthcoming. It also allows the development of improved null models of rates of change. For example, Sun et al. (2015) showed that using Laplace rates of change with additional rules about modified rates of growth at low population sizes very accurately simulates the population dynamics of harvestable fish species and draws conclusions about variation in stocks and covariance between populations.

Although the differences between the Laplace (or the leptokurtic end of the Subbotin distribution or even leptokurtic distributions in general) and Normal might seem too small to have conservation implications, especially on a log scale, we suggest these differences are important. In a simple comparison of a unit Normal distribution versus the best Laplace distribution fitted to that same data (Figure S2), we found that extreme events defined by changes larger than ± 3.5 s.d. make up 1.2% of the cases if Laplace applies (frequent enough to be of management relevance) while these make up only 0.05% if Normally distributed (too rare for most management relevance). Additionally, small changes in the range (-0.5 s.d., $+0.5$ s.d.) are 22% more common in the Laplace distribution and extremely small changes in (-0.2 s.d., 0.2 s.d.) are 40% more common in the Laplace. While the scale of change is arbitrary here, the point that very large changes and very small changes are both meaningfully more frequent in Laplace distributed data is germane. This really argues that conservation efforts, especially at broad policy levels, need to move beyond worrying about mean trends, celebrate that many species or locations will show little to no trend, and devote the limited attention and resources to the handful of cases showing very large trends. In a recent paper, Leung et al. (2020) looked at another large compilation of trends in vertebrate populations (Ledger et al. 2023). Using entirely different and distribution-free methods, they also found that most populations showed little to no trend and a handful (a few percent) of populations showed extreme trends. Leung and colleagues similarly argued for lessened focus on the large majority of species and heightened focus on the extreme trends. Concretely, this suggests that conservation resources should be allocated to broad brush triaging of systems into systems of little change and extreme change. Notably this suggests we need to devote fewer resources to measuring with great precision systems with little

change. This frees more resources to focus on mitigation efforts on the few percent of systems showing very large change. And to understanding if there are properties that predict systems most likely to showing very large change. The finding that extreme declines are roughly balanced by extreme increases is also interesting and may require some rethinking. For example, should conservationists attempt to “squash” extremely increasing populations? This is common thinking for invasives, but not necessarily so for native species at present.

Although more research is needed to cement the generality of fat-tailed, leptokurtic (e.g., Subbotin or Laplace) distributions for the distribution of rates of biodiversity change, this literally has been a pattern staring us in the face for the last decade. However, it has gone largely unnoticed with a few exceptions focused on single year changes (Keitt and Stanely 1998; Kingsolver et al. 2001; Labra et al. 2005b; Marquet et al. 2007; Sun et al. 2015; Segura et al. 2017; Segura et al. 2021), due to our tendency to summarise many species and locations down to single values (mean trend). We argue here that the nature and structure of the variance is at least equally important, if not more important, than the mean trend. We now know there is an excess of near stasis (little to no change) and of extreme change relative to the traditional null model, Normal Distribution assumptions. The Laplace Distribution of biodiversity trends has important implications for our mechanistic understanding of temporal dynamics, of simulating and statistically analysing temporal dynamics and of conservation prioritisation. Although the mechanisms we identify that produce these patterns are more suggestive than determinative, it is deeply intriguing that the prevalence of the Laplace Distribution signals the pivotal roles in ecological systems of heterogeneity in variance and the model that ecological communities may show strong regulation of biodiversity metrics with occasional escapes to new basins of attraction. With ecology's increasing focus on temporal change (Wolkovich et al. 2014), the fat-tailed (e.g., Subbotin and Laplace) distribution of rates of biodiversity change promises to play an increasingly important role.

Author Contributions

All authors conceived the project and interpreted results jointly. Brian J. McGill and Faye Moyes performed statistical analysis. Brian J. McGill wrote a first draft, and all authors significantly improved the writing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data analysed in this paper has been previously published and is available through established repositories. No new or unique data was used in this paper. This data includes the North American Breeding Bird Survey (a US government published data set <https://www.pwrc.usgs.gov/BBS/RawData/Choose-Method.cfm>), the BioTIME data set (<https://zenodo.org/records/5026943>) and the Kingsolver data set on selection (<https://zenodo.org/records/5024624>). About 15% of the data in BioTIME is from government and NGO sources that do not permit us to reshare their data (i.e., not in the Zenodo repository), but make it freely available themselves; these datasets and links to access the data are documented in the R-markdown code in the figshare repository. All code and the trends across all data sets necessary to reproduce all figures and tables are available in the figshare repository <https://doi.org/10.6084/m9.figshare.31297936> with a readme.txt file providing an overview.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70353-sup-0001-FigureS1-S3-TableS1-S2.pdf.