Lognormality in ecological time series

John Halley and Pablo Inchausti


Among ecologists, it is often believed that population abundance is lognormally distributed. To test this hypothesis, we analysed and compared 544 annual time-series of population abundance longer than 30 years ($n \geq 30$). Using Khamis’ modified KS test we found one-half of the long-term datasets were lognormally distributed ($p$-value = 0.05). Among those deviating from lognormality, the most consistent feature was that the skewness was less than that expected under the lognormal hypothesis, implying a shorter upper tail (i.e. fewer extremely high values) than expected. There was little evidence of systematic extreme heavy-tail behaviour characteristic of the Lévy-stable distributions in long ($n \geq 50$ years) time series. Both the standard KS test and the Akaike information criterion (AIC) were used to compare a number of alternative distributions for goodness of fit. Distributions symmetric in logarithmic scale (lognormal and log-sech) were found to fit the data best according to the KS test. However, by the AIC the gamma distribution was most often the best model. Numbers of significant departures from lognormality varied among taxa, with insects having the highest departure from lognormality. There were also trophic differences, with herbivores deviating from lognormality more than carnivores. We found no habitat or geographic dependencies in the incidence of lognormality. The poor fit of the lognormal to real data means that it is not a good substitute for specific population dynamic and distributional information. However, being a superior “universal” descriptor of population abundance than other two-parameter models, it may be useful in applications where such detailed information is unavailable.


The purpose of this paper is to characterise the distribution of population abundance seen in long-term ecological time series. Our specific aim is to test the commonly held belief that ecological abundance follows a lognormal distribution, if indeed it is meaningful to speak of such general behaviour. This question is of great interest as a theoretical issue and of great importance in applied issues such as extinction forecasting.

A number of authors have discussed the issue of lognormality in ecological time series (Williamson 1972, May 1975, Dennis and Patil 1988). However, because it tends to be regarded by ecologists as something of a weakly supported generalisation or “folklore theorem”, actual testing of lognormality has been more limited. We believe that the reliability of the lognormal hypothesis should be quantified more carefully. In this paper, we use systematic statistical procedures to test it against 544 long-term time series of population abundance. We test the absolute goodness of fit of the lognormal model and compare it with some alternatives that could in principle be used to describe the frequency distribution of population data. We will do this by using Kolmogorov-Smirnov and Akaike information statistics, measures of skewness and tail behaviour. Tail behaviour is crucial to Mandelbrot’s fractal motivated family of “L-stable distributions” that he proposed as an alternative to the lognormal model (Mandelbrot 1997), and which is currently enjoying a high level of interest in a number of disciplines (Adler et al. 1997).
The lognormal hypothesis is predicated on the assumption that the abundance distributions of diverse natural populations share some general features, leading to a general or “universal” distribution shape, in spite of differences in detail. We believe this idea to be meaningful and necessary in ecology. For example, a universal distribution could be used to include variability in model parameters to account for food-web interactions. Such a scheme would still be more realistic than ignoring variability of these parameters altogether. Also, in this paper we ignore temporal correlation. This assumes in effect that, although a distribution may change in time, for example its variance may grow due to the more-time-more-variation effect (Pimm and Redfearn 1988, Inchausti and Halley 2001), it does not change in its essential shape or distribution type.

**Biological motivations for lognormal abundance distribution**

Among ecologists, it is widely believed that that population abundance should be lognormally distributed (Whittaker 1970, Williamson 1972, May 1975, Dennis and Patil 1988). The essence of the argument is that population growth is a multiplicative (rather than additive) process, such that if a population grows (or declines) in an exponential fashion with a finite replacement rate \( \lambda \), which is randomly fluctuating over time:

\[
N_{t+1} = \lambda_t N_t = \lambda_0 \lambda_{t-1} N_{t-1} = ... = \lambda_2 \lambda_1 \lambda_0 N_0
\]

then by taking the logarithm of both sides, one arrives at the expression:

\[
\log(N_{t+1}) = \log(N_0) + \sum_{k=0}^{t} \log(\lambda_k)
\]

If \( \log(\lambda) \) are independent, normally-distributed variates (or indeed any independent identically-distributed variate with finite moments), then their summation in the above equation, and hence \( \log N_{t+1} \), will tend to be normally-distributed, and thus \( N_{t+1} \) to be lognormally distributed. This argument is essentially the central limit theorem working multiplicatively for \( N_{t+1} \). The lognormal model gains further credibility from the fact that its support, zero to infinity, is the same as the domain of values wherein any population count or density is naturally constrained.

An important weakness of the above argument is that the result is only true for populations in exponential growth or decline. For the equilibrium regime it has been argued (Whittaker 1970, May 1975) that the dynamics of populations embedded in communities with a large number of species in a variable environment are liable to be governed by the compounded effect of many ‘more-or-less’ factors acting multiplicatively, again leading to lognormal statistics. More formal approaches have also investigated how a lognormal population abundance distribution might emerge at equilibrium. For example, Dennis and Patil (1984, 1988) argue that although the equilibrium distribution for the stochastic version of the logistic model is gamma distributed, a lognormal distribution emerges naturally from the stochastic Gompertz model. Diserud and Engen (2000), in a different context, have analysed a model which yields either lognormal or gamma distributions as alternate ends of a spectrum of distributions.

Mandelbrot offered a spirited attack on the widespread use of the lognormal distribution (“a wolf in sheep’s skin”) as a universal distribution in economics (Mandelbrot 1997). Mandelbrot identified at least three problems with the lognormal distribution, (a) extreme sensitivity of the all moments of the distribution to small departures from precise lognormality. Thus he argues that while a normal distribution may fit \( N_t \) acceptably well, the moments of the \( N_t \) itself may be very differ drastically from the corresponding lognormal distribution. (b) Slow convergence of the estimates of moments (e.g. mean, variance, skewness) to their asymptotic values (c) Intractability when dealing with additive, rather than multiplicative, effects. Instead, he suggested the family of scaling or Lévy-stable, or L-stable, distributions based on fractal ideas (Mandelbrot 1963, 1997). A notable feature of L-stable distributions is a slow (power law) decay in the tails, so that extreme values are generated naturally. All L-stable variates have the nice property of additive invariance: adding two or more independent realisations yields another variate of the same type. The normal distribution is a limiting case of this generalised central limit theorem (Zolotarev 1986). Although Mandelbrot’s arguments were directed at economists, L-stable distributions have also been applied in biology (Mandelbrot 1973, West 1995, Provata and Almirantis 1997). Dynamical similarities between economic and ecological systems, and the fundamental importance of fractal ideas for ecology, suggest this possibility might be relevant to ecological population abundance.

**Types of probability models and their importance**

As well as being of interest in itself, the probability distribution of abundance is important for population dynamic models. Such models contain three essential elements: (a) the number of interacting species (or ‘dimension’) of the model (b) the type of ecological interactions or processes that determine the population dynamics, (c) the form of environmental variation, if included. In this paper we will be concentrating on the third of these. In addition to abiotic factors such as...
weather, the parameters of populations suffer serious perturbation due to the fluctuations of other species in its food-web. That is why analysis of population fluctuations gives important insights into the fluctuations of model parameters.

Figure 1 shows six different probability models (see Appendix A for details) that might describe the frequency distribution of population abundance. These probability distributions are the normal, Cauchy and hyperbolic secant (sech) which are all symmetric, and the lognormal, gamma, and log-hyperbolic secant (log-sech) which are asymmetric. The normal and gamma distributions have been widely applied in ecology (Fisher et al. 1943, Dennis and Patil 1984, Diserud and Engen 2000). The Cauchy distribution turns up frequently in economics (Mikosch 1997). In contrast, the sech and log-sech distributions have not been used in ecology and are included here because they are the simplest bell-shaped distributions with two exponential and two power-law tails respectively. The symmetrical distributions (normal, Cauchy and sech) are defined for all values in the interval \((-\infty, +\infty)\) and thus may generate negative values. Therefore it might be argued that they should be rejected a priori as candidates for describing the distribution of population abundance, which cannot be negative. However, many natural non-negative quantities are well-defined over most of their range by such distributions (e.g. people’s heights are well-described by the normal).

The importance of the probability model can be illustrated with an application to extinction forecasting, on which much continues to be written (Wissel and Stocker 1991, Boyce 1992, Lande 1993, Lawton and May 1995, Halley and Iwasa 1998). Figure 2 shows the average extinction time (defined here as the inverse of the extinction probability per year) as a function of median size for populations assumed to fluctuate according to gamma, lognormal and log-sech distributions. Notice that when population abundance has a lognormal distribution the expected survival time increases (on logarithmic scales) faster than linear with median population size, while the curves corresponding to the other two distributions increase only linearly, with a slope of approximately two. This is due to the fact that at low values of population (for these parameters), the relevant gamma and log-sech distributions both have the form \(f(x) \sim x^{-2}\), while the lognormal has a sharper cut-off, so that moving the distribution upwards has a more pronounced effect on extinction time.

**Methods and sources of data**

For the analysis of population time series we used the global population dynamics database (GPDD). Analy-
sis using this database (Inchausti and Halley 2001) allows us to draw more general conclusions than have been possible so far, since the GPDD is one of the largest databases of its kind in the world. From the GPDD we extracted all annual time series longer than 30 years (meaning at least 30 non-blank data points), resulting in a total of 544 time series of 123 species (Fig. 3). Besides population counts, we considered auxiliary data such as the taxonomic group and trophic level.

**Data processing**

*Goodness-of-fit test for lognormality*

The Kolmogorov-Smirnov or KS test (Press et al. 1992, Sokal and Rohlf 1995) measures the maximum departure of the data from a theoretical cumulative distribution function, and can be used as a goodness-of-fit test for the lognormal distribution. This is most easily done by first taking natural logarithms and then testing for normality in the log-domain (Fig. 4). We used Khamis’ (1992) “δ-modified” version of the KS test that has greater statistical power for small sample sizes than the original KS test, and Khamis’ tables of significance for the case where mean and variance are calculated from the observed data. Some of the series contain zero counts, which raises problems when taking logarithms. These are often met by using transformation log (1 + \( N_t \)) instead of log \( N_t \) to avoid infinities at zero. In addition to problems discussed by MacArdle et al. (1990), this approach was unsuitable for us because of the variety of units in which the populations were expressed. Therefore we treated the zeroes as blanks and excluded them from analyses involving logarithms. Although this solution is unsatisfactory in some ways, the distortion is not so great because the actual number of zeroes is not a large fraction of the observations of these time series.

**Ecological correlates of the analyses of goodness of fit**

The goal of this part of the analysis is to compare the incidence of lognormality among various explanatory factors of ecological interest. The 544 datasets were divided into the following taxonomic groups: Mammalia, Insecta, Aves, Osteichyes, Crustacea and Mollusca. The datasets were further classified by trophic level (herbivores, carnivores and secondary carnivores), and type of habitat (aquatic, terrestrial). In addition, we used all available data on latitude and body size for those species and populations for which it was available. Data for all explanatory variables were not available for all taxa or populations, so the sample size varies between analyses and thus the total number of datasets analysed was not the same in all tests. The (square root transformed) length of each time series was used as a covariate in all logistic regressions to control for the fact that spurious results could be generated because of the unequal number or lengths of the datasets for particular combinations of explanatory factors.

We fitted four separate logistic regression models, using the fit to the lognormal (preceding section) of each data set as the dependent binary variable. The first model evaluated latitudinal and taxonomic effects; the
second model included latitudinal, taxonomic, habitat and trophic effects; the third, contrasted vertebrates and invertebrates, while the fourth model included taxonomic and functional effects (trophic level, log-transformed adult biomass). The fitting of all regressions started with the saturated model including all single-level effects and interactions up to the highest possible level between the explanatory factors and the covariate. Each saturated model was then simplified by systematic backward deletion of either interaction terms or single-factor effects. The statistical significance of each term in the regression model was determined by a G test with the significance level set to 0.01 because of the numerous G tests made for each regression model. The G test indicates whether the deletion of a term or interaction led to a significant decrease in the goodness of fit compared to another regression equation that included the deleted term (Hosmer and Lemeshow 1989). This stepwise procedure was repeated until we found the most parsimonious logistic regression equation that could not be further simplified without causing significant decrease of fit between the statistical model and the observed data. The coefficients of multiple logistic regression when there is a combination of categorical and continuous explanatory variables cannot be interpreted in the same way as in multiple linear regression (Hosmer and Lemeshow 1989). For the sake of clarity and interpretability, the results of all logistic regressions are reported as the incidence of lognormality predicted by the single-factor effects and their interactions retained in each logistic regression equation. The estimated parameters of all logistic regressions can be found in Appendix B.

Skewness of population abundance data.
Skewness is of special importance because the degree of asymmetry can help distinguish between various probability distributions that might fit the population time series data. If population abundance has a symmetric distribution, the skewness coefficients should be close to zero in the arithmetic scale, \( N_a \), and negative in the logarithmic scale \( \log N_b \). Conversely, if the distribution of population abundance were close to Lognormal in arithmetic scale, one should expect skewness to be positive in the arithmetic scale, and approximately zero in logarithmic scale. For each of the 544 time series, we calculated the basic descriptive statistics and invertebrates, while the fourth model included taxonomic and functional effects (trophic level, log-transformed adult biomass). The fitting of all regressions started with the saturated model including all single-level effects and interactions up to the highest possible level between the explanatory factors and the covariate. Each saturated model was then simplified by systematic backward deletion of either interaction terms or single-factor effects. The statistical significance of each term in the regression model was determined by a G test with the significance level set to 0.01 because of the numerous G tests made for each regression model. The G test indicates whether the deletion of a term or interaction led to a significant decrease in the goodness of fit compared to another regression equation that included the deleted term (Hosmer and Lemeshow 1989). This stepwise procedure was repeated until we found the most parsimonious logistic regression equation that could not be further simplified without causing significant decrease of fit between the statistical model and the observed data. The coefficients of multiple logistic regression when there is a combination of categorical and continuous explanatory variables cannot be interpreted in the same way as in multiple linear regression (Hosmer and Lemeshow 1989). For the sake of clarity and interpretability, the results of all logistic regressions are reported as the incidence of lognormality predicted by the single-factor effects and their interactions retained in each logistic regression equation. The estimated parameters of all logistic regressions can be found in Appendix B.

Skewness was measured using the 3rd moment formula:

\[
\kappa = \frac{n}{(n-1)(n-2)} \sum_{k=1}^{n} \left( \frac{N_k - \bar{N}}{S} \right)^3
\]

where \( n \) is the number of non-blank observations, \( \bar{N} \) is the mean, \( S \) is the standard deviation. Although the skewness coefficient \( \kappa \) has the advantage of having an estimate of the standard error (Jolicoeur 1983) that allows testing of its statistical significance for each data set, it tends to behave badly with ‘noisy’ data (Press et al. 1992) and may reflect extreme values rather than true skewness. We used a second measure of skewness to check for this:

\[
T = \frac{(Q_3 - M) - (M - Q_1)}{Q_3 - Q_1}
\]

\( M \) is the median of the series, and \( Q_1 \) and \( Q_3 \) are the 25% and 75% percentiles of the time series. This second measure of skewness, \( T \), measures the distance from the median to the upper and to the lower quartiles as a proportion of the total inter-quartile distance. Because \( T \) is based on order statistics, this estimate is robust in the face of extreme values, but it lacks an estimate of standard error thus precluding any statistical testing. The values of both skewness coefficients are positive for right-skewed distributions, and negative for left-skewed ones. In what follows, we will focus on \( \kappa \) and will only refer to \( T \) as a check for consistency.

Comparing the goodness of fit to different probability distributions
The goodness of fit of time series to the different probability models of Fig. 1 were computed using the standard KS test (Press et al. 1992). Each of these distributions has only two parameters, which can be calculated from median and the inter-quartile distance (Appendix A). For each model, the two parameters were estimated from the data and then used to generate the expected cumulative distribution function for use in the KS test.

For a given series, the “best” model was that whose the \( p \)-value indicated the smallest difference between the data and the model. The best overall model was that which had the largest number of such wins.

An alternative way of choosing the best overall model is to compare them using the Akaike information criterion (AIC). This is a likelihood-based comparison and is widely used as an alternative to hypothesis-testing (Anderson et al. 2000). The AIC is calculated as follows:

\[
\text{AIC} = 2k - 2 \log(L)
\]

Here \( L \) is the maximum-likelihood function, for the given data, \( k \) is the number of parameters in the model: for the distributions considered in this paper \( k = 2 \), broadly corresponding to the centre, \( a \), and width, \( b \). For the \( L \)-stable family \( k = 4 \). For most of the distributions of interest in this paper the maximum likelihood estimator is hard to derive, so we used a Monte-Carlo search to find the best parameters. Starting with the pair of parameters \( (a, b) \) found by the procedures in Appendix A, we searched uniformly the region between \([b/2, b \times 2]\) for the width and \([a-b/2, a+b/2]\) for the
centre (except for the gamma distribution, for which we searched instead for the shape parameter over \([c/2, c \times 2]\)). We chose the pair of parameters \((\hat{\alpha}, \hat{\beta})\) giving the maximum value of likelihood, \(L\), out of 10,000 runs.

Estimators of the power-law decay in the tails of the distribution

The tests for lognormality and model comparisons above have greatest power in the region of the central bell of a distributions, but they say little about the behaviour in the tails. The rate of decay of the tail of a distribution is a measure of the weight of the tail and the degree to which extreme values will be produced. The degree of prevalence of ‘extreme events’ of environmental fluctuations is an important issue in its own right (Lande 1993, Mangel and Tier 1993). As mentioned earlier, when discussing Fig. 2, the behaviour of the tail may be crucial in determining important features of the population. Also, it is the tail, not the central portion, which will determine whether the central limit theorem applies to sums of \(N_i\) and thus it is desirable to determine how heavy are the tails of the distribution.

We use the conditioned maximum likelihood estimator introduced by Hill (1975), to investigate tail behaviour. If one assumes that the tail of the cumulative frequency distribution of \(N_i\) satisfies relations of the form:

\[
F(x) \sim 1 - |M - x|^{-\alpha}, \quad \alpha > 0, \quad x \gg M
\]  

(5a)

then the corresponding Hill estimator for the tail index \(\hat{\alpha}\) is:

\[
\hat{\alpha} = \frac{1}{n} \sum_{i=1}^{n} \ln \frac{|N_i - M|}{|N_i - M|}
\]  

(5b)

where the sum in the denominator is carried out over the upper 10% (in our case) of observations, \(N_i\) being the smallest of these. The parameter \(\alpha\) is called the tail index (which need not be the same for the upper and lower tails) and describes the rate of decay from the median \(M\) towards the tail of the distribution. The distribution is said to be “heavy-tailed” whenever \(\alpha < 2\) (Hill 1975). Such heavy-tailed distributions generate more extreme value than the lognormal model does.

Since by definition most of the values of a probability distribution lie within the central lobe, fitting the shape of the tail is generally difficult, and only accurately possible for large datasets. We attempted to estimate the exponent \(\alpha\) only for data series longer than 50 observations. The precision of the majority of estimates of \(\alpha_{\text{obs}}\) is low since most datasets are shorter than 100 observations. Thus, we calculated 95% confidence intervals of \(\alpha\) to assess the reliability of individual estimates of \(\alpha_{\text{obs}}\). The width of these confidence intervals depend on the value of \(\alpha_{\text{obs}}\) on the number of observations \(n\), on the fraction of them used in tail estimation (here 10%), and on the proposed functional form (log-sech) of the distribution (Pictet et al. 1997). We constructed two look-up tables, for the upper and lower ends of the confidence interval respectively, covering a range of values of \(n\) and \(\alpha_{\text{obs}}\). For each entry, 10,000 simulated series were produced for a range of hypothetical values of \(\alpha\). The confidence interval contains all values of \(\alpha\) consistent with the null hypothesis of \(\alpha = \alpha_{\text{obs}}\). Because of problems of interpretation for the lower tail (due to integer counts and the finite lower limit, \(N_t = 0\), we only considered the upper tail of the distribution.

Results

Goodness-of-fit test to the lognormal distribution and its ecological correlates

We found that, contrary to theoretical expectations, the lognormally hypothesis can be rejected (at significance level \(p \leq 0.05\) for just over half of long-term time series data (Table 1). A total of 133 series (24.4%) were highly lognormal \((p \geq 0.25)\), while 185 series (34.0%) were far from lognormal \((p < 0.01)\). The occurrence of lognormality was highly variable among major taxa, being low for insects (26.1%) and high for Crustacea (76.9% of datasets). Mammals and birds were intermediate with 49.3% and 39.7% respectively of datasets being lognormally distributed. The incidence of lognormality varied among aquatic than in terrestrial habitats (higher incidence of lognormality in aquatic than in terrestrial populations) and showed that the difference between vertebrates and invertebrates was not statistically significant. The incidence of lognormality varied among trophic levels, but this variation was modulated by body size; it decreased with body size for herbivores and secondary carnivores, and increased with body size for carnivore species (Appendix B). When accounting for the number and length of the datasets, the incidence of lognormality increased for higher trophic levels for both terrestrial and aquatic populations (Appendix B).
Table 1. Goodness of fit to the lognormal distribution and analysis of skewness in the ln \( N_t \) scale. Lognormality was decided using the Khamis-modified Kolmogorov-Smirnov test, and the statistical significance of skewness in the ln \( N_t \) scale using the test of Jolicoeur (1983); see text for further details. The number of series for each category is given in parentheses. The table is to be read as follows: 37/63 equivalent to 58.7% of the avian series showed significant departures from lognormality, 20/37 equivalent to 54.0% of the non-lognormal, vertebrate series were significantly skewed, and 20/20 equivalent to 100.0% of the non-lognormal and significantly skewed avian series, were left-skewed.

<table>
<thead>
<tr>
<th>Category</th>
<th>% Non-lognormal datasets</th>
<th>% Signif. skewed among non-lognormal datasets</th>
<th>% Left-skewed of non-lognormal, signif skewed datasets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aves</td>
<td>58.7 (63)</td>
<td>54.0 (37)</td>
<td>100 (20)</td>
</tr>
<tr>
<td>Crustacea</td>
<td>23.1 (13)</td>
<td>66.6 (3)</td>
<td>100 (2)</td>
</tr>
<tr>
<td>Insecta</td>
<td>69.6 (223)</td>
<td>43.7 (16)</td>
<td>42.9 (7)</td>
</tr>
<tr>
<td>Mammalia</td>
<td>50.4 (345)</td>
<td>66.6 (174)</td>
<td>75.9 (116)</td>
</tr>
<tr>
<td>Osteichthyes</td>
<td>42.6 (94)</td>
<td>40.0 (40)</td>
<td>100 (16)</td>
</tr>
<tr>
<td>Mollusca</td>
<td>66.7 (6)</td>
<td>50.0 (4)</td>
<td>100 (2)</td>
</tr>
<tr>
<td>Aquatic</td>
<td>40.9 (115)</td>
<td>46.8 (47)</td>
<td>100 (22)</td>
</tr>
<tr>
<td>Terrestrial</td>
<td>52.5 (429)</td>
<td>62.6 (225)</td>
<td>77.3 (141)</td>
</tr>
<tr>
<td>Vertebrates</td>
<td>49.3 (499)</td>
<td>61.0 (246)</td>
<td>81.3 (150)</td>
</tr>
<tr>
<td>Invertebrates</td>
<td>57.8 (45)</td>
<td>50.0 (26)</td>
<td>69.2 (13)</td>
</tr>
<tr>
<td>Herbivores</td>
<td>61.1 (108)</td>
<td>68.2 (66)</td>
<td>77.7 (45)</td>
</tr>
<tr>
<td>Carnivores</td>
<td>47.1 (394)</td>
<td>57.0 (186)</td>
<td>81.1 (106)</td>
</tr>
<tr>
<td>Secondary Carnivores</td>
<td>47.6 (42)</td>
<td>60.0 (20)</td>
<td>83.3 (12)</td>
</tr>
<tr>
<td>Overall</td>
<td>50.0 (544)</td>
<td>59.2 (272)</td>
<td>80.3 (163)</td>
</tr>
</tbody>
</table>

**Skewness**

Overall the histograms of \( N_t \) are characterised by a strong positive skew, implying a long upper tail (Fig. 5a). This pattern prevailed for each major taxa with the median of the skewness coefficient (for \( N_t \)) of major taxa ranging from 0.68 to 1.28. However this skewness is slightly less than would be expected on the basis of the lognormal model, so log \( N_t \) is not symmetric but slightly negatively skewed (Fig. 5b). This negative skew ranged from −0.56 to −0.21 (medians) for different taxa, except for insects for which the median skewness was +0.09. Results for the rank-based estimator, \( T \), corroborate these findings (data not shown).

Skewness is an important reason for deviation from lognormality, 59.2% of the non-lognormal data sets being significantly skewed (Table 1). Interestingly, there is a clear dominance (80.3%) of negative or left-skewness (i.e. longer lower tail) in logarithmic scale in most datasets that showed a statistically significant departure from lognormality (Table 1). This feature is observed across all trophic levels, habitats and type of population dynamics (Table 1).

**Comparative goodness-of-fit for various distributions**

Despite of the fact that the lognormal hypothesis can be rejected in about half of the time series (Table 1), compared with other probability distributions it performs well (Table 2a). However, its edge is not in itself decisive and the order of the first 3 distributions is changed when we look at the results of the AIC, for which the gamma gives the best results (Table 2b).

The gamma distribution is a particularly good model for birds. The typical bird’s population is also less positively skewed and closer to normal behaviour than other taxonomic groups. Note that all of the asymmet-

![Fig. 5. Results for the skewness of ecological time series. (a) The skewness coefficient \( \kappa \) for the raw values of population \( N_t \) for time series of various taxonomic groups. (b) The skewness coefficient \( \kappa \) for the corresponding values of the logarithms ln \( N_t \). Note that the width of the box-plots is a measure of the number of series in each group (width \( \propto \sqrt{n} \).](image-url)
Small values of the Hill exponent (\(x_{\text{obs}} < 2\)) are associated with heavy-tailed behaviour. We found plenty of variability in the estimates of the tail index for the 171 time series with more than 50 observations (Fig. 6a). However, despite this variability, it is clear that for most series, the tail index \(x_{\text{obs}} > 2\). The associated confidence intervals (Fig. 6b) sustain this finding: only for 16% of the 171 time series analysed was the entire 95% confidence interval for \(x\) below the critical value of \(x = 2\), while in 52% of cases all of this confidence interval was above 2 (Fig. 7). There does not seem to be any taxonomic or ecological bias in this pattern.

**Discussion**

Our analysis shows that about one-half of the 544 long-term population time series are lognormally distributed (\(p = 0.05\)). We find no common geographic or habitat-related variation in the incidence of lognormality. Departures from lognormality changed significantly among taxa and across trophic levels and in relation to body size.

The clearest reason for departures from the lognormal expectation is a persistent “skewness deficit”. In the histogram of the log-transformed abundance, this deficit appears as a persistent negative skew (longer lower tail or shorter upper tail or both) something that is not expected for truly lognormally distributed populations. In ecological terms, these patterns of skewness imply that a typical population would tend to spend less time at values very high compared to the mean abundance, and more at low values, than would be expected for a lognormal distribution. Therefore, assuming the lognormal as the default probability distribution will tend to over-estimate the length of the upper tail (i.e. the number of values much higher than the mean) and underestimate the extinction probability. This feature has also been reported in other sciences, for example in geostatistics by Clark (1987), who suggests the use of the three-parameter lognormal as an corrected model.

The lognormal performs at least as well as any of the other models but its margin was not very large and it was sensitive to the type of statistic chosen to measure

### Table 2. Number of best fits using different probability models for the 544 time series from the GPDD

<table>
<thead>
<tr>
<th>Taxonomic Group</th>
<th>Normal</th>
<th>Cauchy</th>
<th>Sech</th>
<th>Gamma</th>
<th>Lognormal</th>
<th>Log-sech</th>
<th>None</th>
<th>Median p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aves</td>
<td>13</td>
<td>2</td>
<td>3</td>
<td>13</td>
<td>22</td>
<td>6</td>
<td>1</td>
<td>7%</td>
</tr>
<tr>
<td>Crustacea</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>10</td>
<td>3</td>
<td>1</td>
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<td>4%</td>
</tr>
<tr>
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<td>37</td>
<td>10</td>
<td>1</td>
<td>6</td>
<td>11</td>
<td>9</td>
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<td>7%</td>
</tr>
<tr>
<td>Mammalia</td>
<td>18</td>
<td>7</td>
<td>1</td>
<td>6</td>
<td>11</td>
<td>1</td>
<td>1</td>
<td>4%</td>
</tr>
<tr>
<td>Osteichthyes</td>
<td>1</td>
<td>1</td>
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<td>1</td>
<td>1</td>
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<tr>
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<td>13</td>
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<tr>
<td>All taxa</td>
<td>6%</td>
<td>1%</td>
<td>3%</td>
<td>3%</td>
<td>38%</td>
<td>45%</td>
<td>1%</td>
<td>7%</td>
</tr>
</tbody>
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Discussion

Our analysis shows that about one-half of the 544 long-term population time series are lognormally distributed (\(p = 0.05\)). We find no common geographic or habitat-related variation in the incidence of lognormality. Departures from lognormality changed significantly among taxa and across trophic levels and in relation to body size.

The clearest reason for departures from the lognormal expectation is a persistent “skewness deficit”. In the histogram of the log-transformed abundance, this deficit appears as a persistent negative skew (longer lower tail or shorter upper tail or both) something that is not expected for truly lognormally distributed populations. In ecological terms, these patterns of skewness imply that a typical population would tend to spend less time at values very high compared to the mean abundance, and more at low values, than would be expected for a lognormal distribution. Therefore, assuming the lognormal as the default probability distribution will tend to over-estimate the length of the upper tail (i.e. the number of values much higher than the mean) and underestimate the extinction probability. This feature has also been reported in other sciences, for example in geostatistics by Clark (1987), who suggests the use of the three-parameter lognormal as an corrected model.

The lognormal performs at least as well as any of the other models but its margin was not very large and it was sensitive to the type of statistic chosen to measure

<table>
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<tr>
<th>Taxonomic Group</th>
<th>Normal</th>
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<th>Sech</th>
<th>Gamma</th>
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<th>Log-sech</th>
<th>None</th>
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<td>1</td>
<td>1</td>
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<td>1</td>
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<td>1</td>
<td>1</td>
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<td>7</td>
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<td>18</td>
<td>94</td>
<td>6</td>
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<td>All taxa</td>
<td>345</td>
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<td>55</td>
<td>35</td>
<td>94</td>
<td>6</td>
<td>6</td>
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</tr>
</tbody>
</table>

### Estimating the power-law exponent of the distributions’ tails

Small values of the Hill exponent (\(x_{\text{obs}} < 2\)) are associated with heavy-tailed behaviour. We found plenty of variability in the estimates of the tail index for the 171 time series with more than 50 observations (Fig. 6a). However, despite this variability, it is clear that for most series, the tail index \(x_{\text{obs}} > 2\). The associated confidence intervals (Fig. 6b) sustain this finding: only for 16% of the 171 time series analysed was the entire 95% confidence interval for \(x\) below the critical value of \(x = 2\), while in 52% of cases all of this confidence interval was above 2 (Fig. 7). There does not seem to be any taxonomic or ecological bias in this pattern.
the overall goodness of fit. We found that right-skewed distributions such as lognormal, log-sech and gamma (defined over positive numbers only) were better models than the symmetric distributions (which are defined over the entire range of real numbers) such as the normal, Cauchy, and sech. Despite their skewness deficit, two of the distributions which perform best overall were those that are symmetric on a logarithmic scale: the lognormal and the log-sech. This fact underlines the fundamental importance of working in log-space rather than with raw data. Given that the logarithmic transformation “overcompensates” for the right-skew in \( N_t \), that is \( \log N_t \) is not normal but left-skewed, it is worth asking if normality might be achieved by some other simple transformation. We tested square, cubic and higher root transforms as alternative methods of getting a non-skewed population distribution. However, these were in general insufficient to eliminate the right-skew: only on the (biologically unlikely) sixth root did the skewness (on average) change sign (right- to left-skewed). Therefore we did not pursue this approach.

Whenever several models fit the data equally well, often the case in ecology, models must be selected on the basis of other criteria, such as simplicity, explanatory power and conceptual clarity. In particular, it is desirable that any “universal” probability distribution (should it exist) have at least a plausible mechanistic connection with population growth models, rather than being just a convenient statistical description of the abundance data. Given that the lognormal does not overwhelmingly outperform other asymmetric distributions in purely statistical terms, these considerations are especially important. Obvious advantages of the lognormal distribution are its simplicity and relatively clear biological basis, via the multiplicative nature of population growth. Although the gamma distribution also has a biological basis, since it is the expected equilibrium (stationary) distribution for the stochastic logistic model (Dennis and Patil 1984, 1988), its goodness of fit to ecological time series is less satisfactory than that of the lognormal.

Ecological time series usually contain extreme values, there are some “enormously high data points typically arising in every study” (Dennis and Patil 1988). Thus Mandelbrot’s L-stable family, based on fractal concepts and characterised by power-law tails, deserves serious consideration by ecologists. This is especially important in the light of the growing importance of fractal ideas in ecology (Cole 1995, Halley 1996, Keitt and Stanley 1998, Kunin 1998, Ritchie and Olff 1999, Solé et al. 1999). The L-stable family suffers a number of drawbacks, such as requiring four parameters and that most members of the family have no closed form. However, in order to seriously consider the L-stable family as an alternative universal model for ecology, the most important thing is to demonstrate that ecological distributions are typified by large numbers of extreme values consistent with heavy power-law upper tails, as seems indeed to be the case for many types of economic time-series (Adler et al. 1997). Ecological time series usually contain extreme values, but is this pattern enough to suggest heavy-tailed behaviour in the technical sense (\( \alpha < 2 \)) consistent with L-stable distributions? The answer is no. Our analysis found no pattern to suggest that heavy-tailed behaviour occurs often in ecological time series since only 16% of cases did the confidence interval for the tail-index \( \alpha \) lie below the critical value of \( \alpha < 2 \). Thus, the evidence supporting the L-stable family of distributions is weak.

In analysing hundreds of long-term ecological time series in a very general way, we have been seeking broad patterns rather than detail. Thus, our statements about the departures from lognormality, patterns of...
Fig. 7. It makes sense to use a universal model (however bad our best model may be) because whenever we ignore the variability of ecological parameters we already assume a universal model of zero fluctuations. (a) The temporal fluctuation in each parameter of the discrete logistic equation may be viewed as the composition of the effects of biotic interactions through the food-web. (b) The cascade of ecological dependence in each parameter is replaced by a random effect having a universal distribution, reflecting the biotic dependencies.

skewness and their ecological implications should be interpreted as generic features of an ensemble of populations and species rather than to individual datasets. Only such large-scale analysis can address the issue of what is the best distribution to use for the distribution of population abundance in the absence of detailed knowledge and measurement. In using the GPDD, which, to our knowledge the largest compilation of population-dynamic data available to ecologists, we are accepting long-term data that reflect a various political, economic and historical factors, both in how they were censused and in which ones were censused at all. From this it is obvious that there is scope for statistical refinement of this analysis in later studies. However, the main features of our results are universal and unlikely to change substantively.

An example illustrates how such knowledge might be useful. Suppose, we wish to estimate the probability of extinction, over 30 years, for a species whose intraspecific dynamics is reasonably well described by the discrete logistic (or Ricker) equation and that the dynamics of this population is results from the effect exerted by other species in the food web. A “full” population-dynamic model, based on the branching network in Fig. 7, in addition to the exogenous abiotic effects, would have to take into account a potentially enormous number of interactions among species. Even if we could construct and solve numerically such a large model we would seldom have the required simultaneous census data of interacting species, or measurements of relevant environmental factors, needed to parameterise the model. Without the resources to measure all of the links many users simply resort to assigning constant values to the model parameters. Obviously, such “constants” never remain constant. The general statistical portrait that we have been seeking to test this paper can be thus used to account for variability arising from interactions with other species, on whom detailed information is unavailable.

As a “universal” distribution to describe population abundance, the lognormal model may be considered good or bad, depending on one’s perspective. Given the complexity and importance of the phenomena that are implicitly ignored in such a scheme (which replaces the population-dynamic variable \( N_t \) with a universal random variable), its performance is not too bad. The lognormal model fits about half of all the series tolerably well, has a clear connection with population-dynamic principles, and is at least as good as any simple alternative. However, our findings reinforce the common-sense approach that any universal distribution should be used with appropriate caution.

Acknowledgements – We wish to thank Jörgen Ripa and another referee for helpful comments on this manuscript. The work was partially funded by a TMR Marie Curie Postdoctoral Fellowship to PI. The support of the Programme de Sciences de la Vie du Centre National de la Recherche Scientifique (CNRS) is also gratefully acknowledged by PI. JH was supported by grant 97EL-6 from the General Secretariat for Research and Technology, Greece.

References


\[ \hat{\mu} = M \]
\[ \hat{\sigma} = \frac{Q_3 - Q_1}{2} \]  

(A4)

(c) sech random variable
The sech (hyperbolic secant) random variable, with centre \( a \) and width \( b \) has the probability density function:

\[ f(x) = \frac{1}{\pi b} \operatorname{sech}\left(\frac{x - a}{b}\right) \]  

(A5)

For a dataset with median \( M \) and hinges \( Q_1 \) and \( Q_3 \), the parameters \( a \) and \( b \) are estimated by:

\[ \hat{a} = M \]
\[ \hat{b} = \frac{Q_3 - Q_1}{2[\ln[\tan(\pi/8)]]} \]  

(A6)

(d) gamma random variable
The gamma random variable, with shape parameter, \( c \), and a scale parameter, \( b \), has the probability density function:

\[ f(x) = \frac{1}{b^c \Gamma(c)} \left(\frac{x}{b}\right)^{c-1} e^{-x/b} \]  

(A7)

The gamma distribution has a power-law in the lower tail \( f(x) \sim x^{c-1} \) and a negative exponential upper tail. There is no simple closed formula to calculate the parameters \( c \) and \( b \) from the median and hinges of a dataset \( \{x_1, x_2, \ldots, x_N\} \). However, a change of the scale parameter changes the median and hinges by the same factor, so the ratio \( T = (Q_3 - Q_1)/M \) is independent of \( b \), depending only on the shape parameter. Therefore, we estimated the shape parameter numerically from \( T \) for the standard gamma distribution \( (b = 1) \) and then calculated \( b \) according to the formula \( b = M/m \), where \( m \) is the median for the standard gamma distribution with shape parameter \( \hat{c} \).

(e) lognormal distribution
If a random variable \( X \) has a lognormal distribution, with parameters \( \mu \) and \( \sigma \), then its pdf is:

\[ f(x) = \frac{1}{x \sigma \sqrt{2\pi}} \exp\left[\frac{-(\ln x - \mu)^2}{2\sigma^2}\right] \]  

(A8)

The parameters \( \mu \) and \( \sigma \) are the mean and standard deviation of the corresponding normal distribution, which is obeyed by the random variable \( Y = \ln X \). Thus, they can be found simply by taking the natural logarithm of all the observations \( \{\ln x_1, \ln x_2, \ldots, \ln x_N\} \), and finding the mean and standard deviation, using Eq. (A2) above, of the corresponding normal distribution.

(f) log-sech distribution
If a random variable \( X \) obeys a log-sech model, it has the following pdf:

\[ f(x) = \frac{2/(\pi bx)}{(xe^{-a})^{1/b} + (xe^{-a})^{-1/b}} \]  

(A9)

The parameters \( a \) and \( b \) are the centre and width of the corresponding Sech distribution, which is obeyed by the random variable \( Y = \ln X \). Thus, as for the lognormal model, they can be found simply by taking the natural logarithm of all the observations \( \{\ln x_1, \ln x_2, \ldots, \ln x_N\} \) and estimating the centre and width of the corresponding sech distribution.

Note that the log-sech has a lower power-law tail where \( f(x) \sim x^{1/b-1} \) and an upper tail where \( f(x) \sim x^{-1/b-1} \).

Appendix B
In this appendix we summarise the parameter estimates of the multiple logistic regressions carried out to evaluate the incidence (yes, no) of lognormality for the main taxa, trophic levels, latitude, body mass, and habitat. The evaluation of the incidence of lognormality was based on 544 time series. The choice of the four combinations of explanatory factors for each model, as well as the procedure followed in arriving at the final regression equations shown below are explained in the main text. When a variable listed in the headings does not appear in a table, it is because its single effect and interactions with other variables were not retained during the simplification of the fully saturated model.

1. Effects of major taxa, latitude and length of the time series

<table>
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<th></th>
<th>Slope</th>
<th>Std Error</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
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<td>1.204</td>
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<td>0.331</td>
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<td>Molluscs</td>
<td>−0.693</td>
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2. Effect of trophic level, latitude, habitat and length of the time series

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3. Vertebrates/Invertebrates, and length of each time series.

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4. Mass, trophic level, class, length

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