



Species-abundance distributions and Taylor's power law of fluctuation scaling

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Abstract

Two widely investigated areas of theory in ecology over the past half century are species-abundance distributions (SADs) and Taylor's power law of fluctuation scaling (TL). This paper connects TL with a classic SAD, MacArthur's broken-stick model. Each of these models is more than 60 years old, but apparently the connection has not been observed previously. For large numbers of species, the broken-stick model asymptotically obeys TL with exponent 2: the variance of species abundance equals the square of the mean species abundance. Equivalently, in the broken-stick model, the coefficient of variation of abundance is asymptotically 1. Because both the broken-stick model and TL have interpretations and applications beyond ecology, the connection established here has broader than purely ecological interest. This simple but previously unnoticed relationship between the broken-stick model and the power-law variance function raises the question of how other species-abundance distributions are related to power law or other variance functions.

Keywords Coefficient of variation · Fluctuation scaling · Order statistics · Spacings · Taylor's law

Introduction

“Demonstrating the connection between apparently unrelated theories” is one of six types of useful theory in Caswell's (1988, p. 38) “beginning of a list of types of theoretical problems” in science. For example, Zaoli et al. (2017) analyzed connections and constraints among the species-area relationship, the fraction of individuals in a community that have a given body mass regardless of species (community-size spectrum), the probability distribution of typical or adult body masses, the average abundance of a species with given typical body mass (Damuth's law), and the scaling of an individual's consumption or metabolic rate with the individual's body mass. Notable earlier examples of efforts to integrate diverse

quantitative ecological relationships include those of Brown et al. (2004) and Marquet et al. (2005).

Two widely investigated areas of ecological theory over the past half century are species-abundance distributions (SADs) (Alroy 2015; Baldrige et al. 2016) and Taylor's power law of fluctuation scaling (TL) (Taylor 2019). It has been suggested that TL describes the SAD of bacterial strains in the human microbiome (Ma 2015), but no mathematically exact demonstration of a connection between any SAD model and any form of TL appears to have been published so far. The purpose of this paper is to connect TL with a classic SAD, the broken-stick model (MacArthur 1957), by means of a precise calculation. Though both TL and the broken-stick model are more than 60 years old, the connection between them has not been observed until now. This example opens a field of investigation of the relation of other SADs to TL and other variance functions. Because the broken-stick model and TL have interpretations and applications beyond ecology, the connection established here has broader than purely ecological interest.

MacArthur (1957, p. 293) proposed a “broken-stick” model for the relative abundance of species in a community: “The environment is compared with a stick of unit length on which $n - 1$ points are thrown at random. The stick is broken at these points, and the lengths of the n resulting segments are

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proportional to the abundances of the n species.” MacArthur (1960) and others (reviewed by King 1964) found empirical support for this model.

Independently, Bliss (1941), Fracker and Brischle (1944), Hayman and Lowe (1961), and Taylor (1961) proposed and showed empirically that the variance of population size or population density changed in proportion to a power function of the mean population size or population density in multiple samples. Such a power-law relationship of variance to mean is called a power-law variance function.

Here we show that, in an ensemble of multispecies ecological communities (or, more generally, in a set of samples of some nonnegative random variable), if the relative abundances of the species within each community (or the relative magnitudes within each sample) obey the broken-stick model, then the variance of relative abundance (across species in a given community) is related to the mean of relative abundance (across species in a given community), asymptotically for large numbers of species, by the power-law variance function, variance = $a(\text{mean})^b$ with $a = 1$, $b = 2$. In words, asymptotically for large numbers of species (or large sample sizes), the variance equals the square of the mean of relative abundance. Equivalently, the coefficient of variation of species relative abundance is asymptotically 1. Communities with small, finite numbers of species (or small sample sizes) approach this asymptotic behavior rapidly.

Both the broken-stick model and the power-law variance function are widely studied under different names in sciences other than ecology. The relative abundances generated by the broken-stick model are known in statistics as “spacings” and have a long history (Pitman 1937; Feller 1966, 1971). Barton and David (1956), the source of information about this model for MacArthur (1957), trace spacings back to 1887. Holst (1980, p. 624) reports and cites some of a “huge literature” on spacings. Statistical research on spacings continues (e.g., Devroye 1986, chapter 5; Kochar 2012). None of the publications I have seen on the broken-stick model or spacings refers to Taylor’s law or to a power-law variance function.

In parallel, and apparently independently, Eisler et al. (2008) and Taylor (2019) review physical, meteorological, hydrological, financial, and other empirical applications and theories of the power-law variance function, usually known in the physical sciences as “fluctuation scaling.” Neither review mentions the broken-stick model, spacings (in the statistical sense), or MacArthur (1957). Because interest in spacings and the power-law variance function is widespread, our demonstration that they are closely connected has relevance beyond ecology.

The connection demonstrated here between the broken-stick model and the power-law variance function with exponent 2 suggests a much broader study of the connection between species-abundance distributions (Baldrige et al. 2016) and variance functions generally (power law or otherwise).

Methods

Notation and definitions

We consider $K > 1$ communities, indexed by $k = 1, 2, \dots, K$. We suppose that community k has $n(k) > 1$ species, indexed by $j = 1, 2, \dots, n(k)$. We assume $\lim_{K \rightarrow \infty} n(K) = \infty$, i.e., asymptotically as the number K of communities becomes large, the number $n(K)$ of species per community becomes large.

We write the absolute (not relative) abundance, i.e., number of individuals, of species j in community k as $X_{jk} > 0$ and we include only species with positive abundance. Then the total abundance in community k is $X_{1k} + X_{2k} + \dots + X_{n(k), k}$, and the relative abundance of species j in community k is $R_{jk} = X_{jk} / (X_{1k} + X_{2k} + \dots + X_{n(k), k}) > 0$. The sum of the relative abundances of all species in a community equals 1.

Power-law variance function

The power-law variance function has exact, approximate, and asymptotic forms. If one considers a family of random variables with positive population mean and positive population variance, then the exact form of TL states variance = $a(\text{mean})^b$, or equivalently (1) below. If one considers multiple samples of a nonnegative random variable such as species abundance with sample mean and sample variance, then an approximate form of TL states sample variance $\approx a(\text{sample mean})^b$, with some error term. If one considers the limiting behavior of a family of random variables or samples, then an asymptotic form of TL states variance/(mean) $^b \rightarrow a$ in some limit. In this last case, the moments may be population moments (exact) or sample moments (subject to sampling variation).

More precisely, let p be the label of each community, random variable, or sample, and let $P \neq \emptyset$ be the nonempty set of all labels or distributions being considered. A family of random variables $\{X(p) | p \in P\}$ has a power-law variance function if and only if, for all $p \in P$, $0 < E(X(p))$ and $0 < \text{Var}(X(p))$ and there exist finite real constants $a > 0$ and b such that

$$\log \text{Var}(X(p)) - b \log E(X(p)) = \log a. \quad (1)$$

In this log-log form of the power-law variance function, $\log \text{Var}(X(p))$ is plotted on the ordinate as a function of the abscissa $\log E(X(p))$. Then, $\log(a)$ is called the intercept, and b is called the slope. We refer to b interchangeably as the slope (of the log-log form) or the exponent (of the power-law form).

In empirical applications of (1), the exact equality is replaced by approximation, since the sample mean and the sample variance are subject to sampling variation. In theoretical extensions of (1), exact equality may be replaced by asymptotic convergence as the parameter p approaches some limit.

In this note, the parameter p is the number $n(k)$ of species in the k th community and we prove convergence as $n(k) \rightarrow \infty$.

The coefficient of variation CV of a random variable with finite variance is defined to be its standard deviation divided by its mean, so $CV^2 = \text{variance}/\text{mean}^2$. Then, $CV^2 = CV = 1$ if and only if the power-law variance function (1) holds with $a = 1, b = 2$.

Broken-stick model

To define the broken-stick model for each community $k = 1, \dots, K$, let $\{U_{jk}|j = 1, \dots, n(k) - 1\}$ be $n(k) - 1$ uniformly and independently distributed random variables on the interval $(0, 1)$. Within the k th community, if the $\{U_{jk}|j = 1, \dots, n(k) - 1\}$ are sorted in increasing size, their values from left to right on the real line are the corresponding so-called order statistics, $0 < U_{(1)}, k < U_{(2)}, k < \dots < U_{(n(k)-1)}, k < 1$, where the strict inequalities hold with probability 1. (Events of probability 0 are ignored.) Define $U_{(0)}, k = 0$ and $U_{(n(k))}, k = 1$. Thus $0 = U_{(0)}, k < U_{(1)}, k < U_{(2)}, k < \dots < U_{(n(k)-1)}, k < U_{(n(k))}, k = 1$. In the broken-stick model, the relative abundance R_{jk} of species j in community k is modeled by the distance between successive pairs of adjacent points, namely, $R_{jk} = U_{(j), k} - U_{(j-1), k}$ for $j = 1, \dots, n(k); k = 1, \dots, K$.

Exponential distribution

A random variable $X \geq 0$ is defined to be exponentially distributed with scale parameter $\lambda > 0$ if, for all $x \geq 0, \Pr \{X > x\} = e^{-\lambda x}$. In this case, we write $X =_d \text{Exp}(\lambda)$, where $=_d$ means “has the same distribution as.” The mean of $\text{Exp}(\lambda)$ is λ^{-1} , and its variance is λ^{-2} . The family of exponential distributions $\{\text{Exp}(\lambda) | \lambda \in P \neq \emptyset\}$ obeys Taylor’s law exactly with $a = 1, b = 2$ because, for every $\lambda, \text{Var}(\text{Exp}(\lambda)) = [E(\text{Exp}(\lambda))]^2$.

Results

First, we give a heuristic argument to suggest that, for every $j = 1, \dots, n(k), \lim_{n(k) \rightarrow \infty} \text{Var}(R_{jk}) / (E(R_{jk}))^2 = 1$, which is an asymptotic version of Taylor’s law with $a = 1, b = 2$. Then, we give a simple, exact proof.

Heuristic argument

Let $X_1, X_2, \dots, X_{n(k)}$ be independently and identically distributed as $\text{Exp}(\lambda(k))$ and let

$$S_{n(k)} = X_1 + X_2 + \dots + X_{n(k)}. \tag{2}$$

The scale parameter $\lambda(k)$ may vary from one community (or sample) to another but is the same for all observations (or

random variables, or species abundances in the ecological interpretation) X_j in community k . Then

$$(R_{1k}, R_{2k}, \dots, R_{n(k),k}) =_d \left(\frac{X_1}{S_{n(k)}}, \frac{X_2}{S_{n(k)}}, \dots, \frac{X_{n(k)}}{S_{n(k)}} \right). \tag{3}$$

In words, the joint distribution of the relative abundances in the broken-stick model (on the left side in (3)) is identical to the joint distribution generated by a set $\{X_1, X_2, \dots, X_{n(k)}\}$ of independent and identically distributed exponential random variables, taking the ratio of each exponential random variable to the sum of them all (on the right side in (3)). This beautiful fact appears in Feller (1966, 1971, Sections I.6 and III.3), Holst (1980, p. 625), and elsewhere. Cohen (1968) observed that the expected values of the order statistics of $\{R_{jk}|j = 1, \dots, n(k)\}$ are the same as the expected values of the order statistics of $\{X_j/S_{n(k)}|j = 1, \dots, n(k)\}$, but not that their joint distributions are identical, as stated above.

Since the denominator $S_{n(k)}$ of each ratio $X_j/S_{n(k)}$ is the same for all $j = 1, \dots, n(k)$, it is tempting (though wrong) to imagine that the mean and variance of each ratio are determined by the numerators $\{X_j|j = 1, \dots, n(k)\}$ alone. Under this false supposition, the numerators $X_1, X_2, \dots, X_{n(k)}$ are a random sample of size $n(k)$ from $\text{Exp}(\lambda(k))$. As noted, $\text{Exp}(\lambda(k))$ has finite mean and variance that obey Taylor’s law with $a = 1, b = 2$, so large samples will too. The temptation is to suppose that large samples of $X_j/S_{n(k)}$ will behave likewise.

This heuristic argument, though it leads to the right answer, suffers from three problems. First, each X_j appears alone in the numerator and also as one term in the sum $S_{n(k)}$ in the denominator. Therefore, the numerator and denominator of each ratio $X_j/S_{n(k)}$ are not independent. Second, the fractions $\{X_j/S_{n(k)}|j = 1, \dots, n(k)\}$ are not independent because they sum to 1. Third, $S_{n(k)}$ is not constant.

We present two proofs that solve these problems. The proof in the following subsection determines exactly the distribution and moments of each R_{jk} on the left side of (3). The proof in the Appendix determines exactly the distribution and moments of each $X_j/S_{n(k)}$ on the right side of (3). Each proof is revealing in a different way. Happily, both proofs reach the same conclusion (6).

Proof

Feller (1971, p. 22, I.7(b)) proved the following fact, which even he called “surprising”: in the broken-stick model that partitions the unit line into $n(k)$ segments of length $\{R_{jk}|j = 1, \dots, n(k)\}$, every one of the segments has the same distribution of length with upper tail probability or survival function

$$\Pr\{R_{jk} > t\} = (1-t)^{n(k)-1}, \quad 0 < t < 1, \quad j = 1, \dots, n(k). \tag{4}$$

For any continuous nonnegative random variable X , the r th moment $\mu_r := E(X^r)$ about the origin is given in terms of the survival function $\Pr\{X > x\}$, $x \geq 0$ by (Feller 1971; Hong 2012; Chakraborti et al. 2019)

$$\mu_r = r \int_0^\infty x^{r-1} \Pr\{X > x\} dx, \quad r \geq 1. \tag{5}$$

When $X = R_{jk}$, the survival function $\Pr\{X > x\}$ becomes $\Pr\{R_{jk} > t\}$ from (4) and the upper limit of integration in (5) becomes 1. Then (5) gives, by elementary calculus,

$$\mu_1 = \frac{1}{n(k)}, \quad \mu_2 = \frac{2}{n(k)(n(k)+1)}, \quad \mu_3 = \frac{6}{n(k)(n(k)^2 + 3n(k) + 2)},$$

$$\mu_4 = \frac{24}{n(k)(n(k)^3 + 6n(k)^2 + 11n(k) + 6)}.$$

Therefore $\text{Var}(R_{jk}) = \mu_2 - (\mu_1)^2 = (n(k) - 1)/(n(k)^2(n(k) + 1))$. Thus

$$CV^2(R_{jk}) := \frac{\text{Var}(R_{jk})}{\mu_1^2} = \frac{n(k)-1}{n(k)+1}, \tag{6}$$

$$\lim_{n(k) \rightarrow \infty} CV^2(R_{jk}) = \lim_{n(k) \rightarrow \infty} \frac{\text{Var}(R_{jk})}{[E(R_{jk})]^2} = 1.$$

The last equality in (6) is the asymptotic power-law variance function $\text{variance}/(\text{mean})^b \rightarrow a$ with $a = 1$, $b = 2$. The difference between the limiting value of $a = 1$ and the value of $CV^2(R_{jk})$ for finite $n(k)$ is

$$a - CV^2(R_{jk}) = 1 - \frac{n(k)-1}{n(k)+1} = \frac{2}{n(k)+1} \leq 0.1 \text{ for } n(k) \geq 19. \tag{7}$$

Numerical illustration

To illustrate this result, we simulated one realization of the broken-stick model for each of $K = 20$ communities (or samples) with $n(k) = 2^k$ species, $k = 1, 2, \dots, K$. For the k th community, we simulated $n(k) - 1 = 2^k - 1$ independent, uniformly distributed pseudorandom points $\{U_{jk}, j = 1, \dots, n(k) - 1\}$ on the unit interval $(0, 1)$, sorted those points in increasing order $0 = U_{(0),k} < U_{(1),k} < U_{(2),k} < \dots < U_{(n(k)-1),k} < U_{(n(k)),k}$, $k = 1$, and took the first differences of these order statistics $R_{jk} = U_{(j),k} - U_{(j-1),k}$ as the predicted relative abundance of species (or as the sampled spacings). The spacings, intervals, or line segments R_{jk} are not necessarily in increasing order; they are simply labeled from left ($j = 1$) to right ($j = n(k)$). For this unique realization, we calculated the sample mean and the sample variance of this single realization of the spacings:

$$m(k) := \frac{1}{n(k)} \sum_{j=1}^{n(k)} R_{jk} = \frac{1}{n(k)}, \tag{8}$$

$$v(k) := \frac{1}{n(k)} \sum_{j=1}^{n(k)} (R_{jk} - m(k))^2 = \frac{1}{n(k)} \sum_{j=1}^{n(k)} R_{jk}^2 - \left(\frac{1}{n(k)}\right)^2. \tag{9}$$

In the expressions in (9) for the variance $v(k)$, the denominator to the left of the summations is $n(k)$ and not $n(k) - 1$ because the simulation enumerates completely all $n(k)$ relative abundances (or spacings), not a random sample of them. The simulation was independent for each k , that is, the uniformly distributed pseudorandom points were generated afresh for each different k .

For small k (in the upper right corner of Fig. 1), the asymptotic variance (red circle) deviates slightly below or above the variance of the simulation (blue x). For $n(k) \geq 19$, from (7), the difference is small since $2/(19 + 1) = 0.1$.

The order statistics of relative abundance are defined as the values of relative abundance arranged in order of increasing size, with the least abundant species first and the most abundant species last. The order statistics are written with parentheses around the relevant subscript. Thus, the order statistics of relative abundance in community k (or of spacings or of segment or interval lengths) are $0 < R_{(1),k} \leq R_{(2),k} \leq \dots \leq R_{(n(k)),k}$. Like the sum of the relative abundances, the sum of the order statistics of relative abundance of all species in a community equals 1.

Empirical tests of the broken-stick model usually compare the order statistics of the observed relative abundances of the species in community k with the expected value of the order statistics of relative abundance. According to the broken-stick model (MacArthur 1957 and many others), the expected value of the j th order statistic of relative abundance is

$$E(R_{(j),k}) = \frac{1}{n} \left(\frac{1}{n} + \frac{1}{n-1} + \dots + \frac{1}{n+1-j} \right), \quad j = 1, \dots, n(k). \tag{10}$$

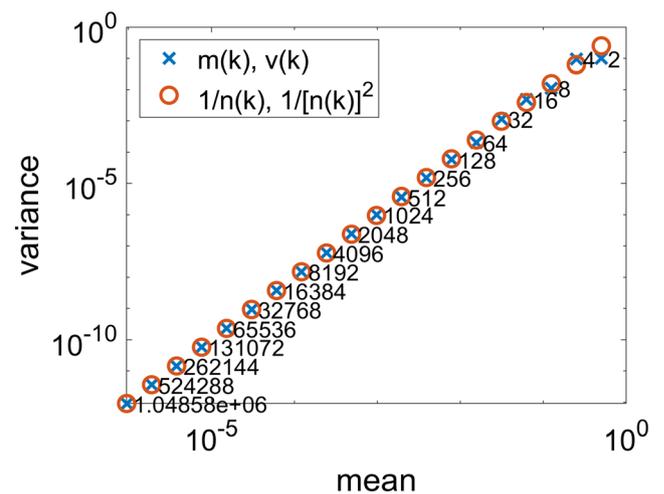


Fig. 1 On log-log coordinates, for each $k = 1, \dots, 20$, $(m(k), v(k))$ (blue x) based on one independent realization and $(1/n(k), 1/[n(k)]^2)$ (red circle) considering that necessarily $m(k) = 1/n(k)$ and assuming $v(k) = [m(k)]^2$ exactly. The number to the right of each blue x is $n(k) = 2^k$

For example, in a hypothetical community with $n = 2$ species, the expected relative abundance of the less abundant species is $1/4$ and the expected relative abundance of the more abundant species is $3/4$. With three species, the expected relative abundances are, in increasing order, $1/9 = 2/18$, $5/18$, and $11/18$. With four species, the expected relative abundances are $1/16 = 3/48$, $7/48$, $13/48$, and $25/48$.

To calculate the means and variances in Fig. 2, we replaced each in R_{jk} in (8) and (9) with the expected order statistic $E(R_{(j), k})$ from (10). For small k (in the upper right corner of Fig. 2), the asymptotic variance (red circle) is above the variance of the expected values of the order statistics (blue x), but for large $n(k)$, the difference is small.

The empirical cumulative distribution function of the simulation and the empirical cumulative distribution function of the expected order statistics both converge to the cumulative distribution function of the broken-stick model for large numbers of species. Hence it is expected that Figs. 1 and 2 show good agreement with the asymptotic theory for large numbers of species or large samples.

Discussion and conclusions

The goal of this paper is to give an example of a mathematical analysis of the connection between SADs and TL. Here, exact calculations connect the broken-stick model of the relative abundance of species (or “spacings” in statistics) and Taylor’s power law (a power-law variance function in statistics and fluctuation scaling in physics). We showed analytically that, for large numbers of species (or large samples of spacings), asymptotically the relative abundances of the broken-stick model have variance equal to the square of their mean; equivalently, the coefficient

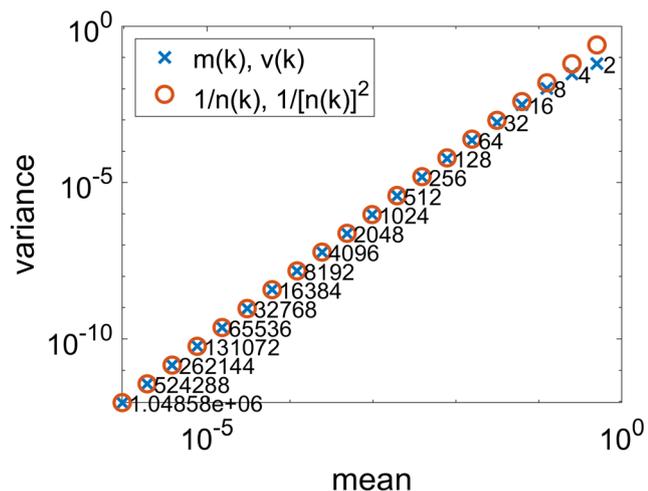


Fig. 2 On log-log coordinates, for each $k = 1, \dots, 20$, $(m(k), v(k))$ (blue x) based on the expected values of the order statistics (10) and $(1/n(k), 1/[n(k)]^2)$ (red circle) considering that necessarily $m(k) = 1/n(k)$ and assuming $v(k) = [m(k)]^2$ exactly. The number to the right of each blue x is $n(k) = 2^k$

of variation of relative abundance converges to 1. We confirmed this result by simulations and exact numerical calculations. Communities with as few as 19 species conformed closely to the predicted asymptotic behavior.

The SAD of the broken-stick model asymptotically obeys $\text{variance} = a(\text{mean})^b$ with $a = 1$, $b = 2$, but observing that TL holds with $a = 1$, $b = 2$ does not imply a broken-stick SAD. Infinitely, many families of probability distributions give rise to Taylor’s law with $a = 1$, $b = 2$ or with any other parameters (Cohen 2020). For example, Cohen (2014b) showed that Taylor’s law with $b = 2$ can (but need not necessarily) arise in three different density-independent stochastic population models: a scalar discrete-time Markovian multiplicative growth model, the discrete-generation Galton–Watson branching process, and the continuous-time linear birth and death process. Giometto et al. (2015) showed that for multiplicative growth models in Markovian environments, if the duration of observation exceeds a logarithmic function of the number of replicates, then the exponent of TL estimated from the replicates will be close to 2, regardless of the exact exponent that mathematical analysis of the underlying model would yield. For this class of models, a reported sample exponent of 2 could be a statistical artifact of too few observations. Other theoretical examples also lead to Taylor’s law with exponent 2.

Another widely confirmed model of SADs is the lognormal distribution or its discretized form, the Poisson lognormal distribution (e.g., Baldridge et al. 2016). In an analysis of tornado outbreaks, Tippet and Cohen (2016) showed that a family of lognormal distributions can obey TL exactly with exponent 2, approximately with exponent 4, or approximately with exponent $2 + 2/3$, depending on how the parameters of the lognormal are assumed to vary or covary. Other values of the TL exponent are also possible for other relationships of the lognormal parameters. This example shows that the broken-stick model is not the only SAD to have a variance function given by TL.

On the other hand, not every SAD has a variance function given by TL. One of the four SADs tested empirically by Baldridge et al. (2016) is the negative binomial distribution (NBD). The negative binomial distribution has two parameters. If one of these parameters varies while the second parameter remains constant, the family of NBDs obeys TL with exponent 1 (Cohen et al. 2016). But if the second parameter varies while the first remains constant, then the variance is a quadratic function of the mean and log variance is a strictly convex function of log mean, so TL does not hold exactly, though TL may sometimes be a plausible approximation (Cohen et al. 2016).

These lognormal and NBD SADs show that the broken-stick model is not the only SAD that can be consistent with TL, and that not every SAD is consistent with TL. It is therefore desirable to find out whether and how other species-abundance distributions are related to power-law or other variance functions.

This paper's demonstration of a theoretical link between TL and the broken-stick SAD is part of a larger project of exploring the connections of TL to the rest of ecological theory, e.g., to Damuth's law of allometry of population density and body mass (Marquet et al. 2005; Cohen et al. 2012), to stochastic multiplicative population growth models (Cohen et al. 2013; Cohen 2013; 2014b), to abrupt change in a smoothly changing environment (Cohen 2014a), to the parasitic mode of life and the negative binomial distribution (Laguerre et al. 2015; Cohen et al. 2016), to models of age-specific human mortality by Gompertz, Makeham, and Siler (Bohk et al. 2016; Cohen et al. 2018), to the Gompertz model of density dependence for rodent populations (Cohen and Saitoh 2016; Saitoh and Cohen 2018), to estimation of fisheries stocks to specified precision (Xu et al. 2019), to synchrony (Reuman et al. 2017), to Chagas disease vector control (Cohen et al. 2017), and beyond ecology even to the prime number theorem in number theory (Cohen 2016). This exploration is far from complete.

Acknowledgments I thank Roseanne Benjamin for assistance during this work.

Appendix. Alternate proof that variance/(mean)² → 1 in the broken-stick model

Gamma distribution

A random variable $X \geq 0$ is defined to have the gamma distribution with shape parameter $k > 0$ and scale parameter $\lambda > 0$, and we write $X \stackrel{d}{=} \Gamma(\lambda, k)$, if its probability density function at $x \in (0, \infty)$ is $\lambda^k e^{-\lambda x} x^{k-1} / \Gamma(k)$, where $\Gamma(k)$ is the gamma function. The mean of $\Gamma(\lambda, k)$ is $E(\Gamma(\lambda, k)) = k/\lambda$ and its variance is $\text{Var}(\Gamma(\lambda, k)) = k/\lambda^2$. For fixed k and varying λ , the family of gamma distributions $\{\Gamma(\lambda, k) \mid \lambda \in P \neq \emptyset, k \text{ fixed}\}$ obeys Taylor's law exactly with $a = 1/k$, $b = 2$ because, for every λ , $\text{Var}(\Gamma(\lambda, k)) = k^{-1}[E(\Gamma(\lambda, k))]^2$. By contrast, for varying k and fixed λ , the family of gamma distributions $\{\Gamma(\lambda, k) \mid k \in P' \neq \emptyset, \lambda \text{ fixed}\}$ obeys Taylor's law exactly with $a = 1/\lambda$, $b = 1$ because, for every λ , $\text{Var}(\Gamma(\lambda, k)) = \lambda^{-1}[E(\Gamma(\lambda, k))]^2$. As this example shows, in parametric families of distributions with more than one parameter, the behavior of each parameter must be specified explicitly when Taylor's law is asserted to hold.

Beta distribution

A random variable $0 < X < 1$ is defined to have the beta distribution with shape parameters $k_1 > 0$, $k_2 > 0$, and we write $X \stackrel{d}{=} B(k_1, k_2)$, if its probability density function at $x \in (0, 1)$ is $\{\Gamma(k_1 + k_2) / [\Gamma(k_1)\Gamma(k_2)]\} x^{k_1-1} (1-x)^{k_2-1}$. Marshall and

Olkin (2007) graph the diverse forms of the exponential, gamma, and beta probability density functions.

The mean and variance of the beta distribution are (Feller 1971, p. 50, II.4(c), Marshall and Olkin 2007, p. 485)

$$E(B(k_1, k_2)) = \frac{k_1}{k_1 + k_2},$$

$$\text{Var}(B(k_1, k_2)) = \frac{k_1 k_2}{[(k_1 + k_2)^2 (k_1 + k_2 + 1)]}$$

$$= \frac{[EB(k_1, k_2)(1-EB(k_1, k_2))]}{(k_1 + k_2 + 1)}.$$

It follows that

$$\text{CV}^2 = \frac{\text{Var}(B(k_1, k_2))}{[EB(k_1, k_2)]^2} = \frac{k_2}{k_1(k_1 + k_2 + 1)}.$$

If $k_1 = 1$, $k_2 = n - 1$, then $\text{CV}^2 = (n - 1)/(n + 1)$. If k_1 is any positive constant and $k_2 \rightarrow \infty$, then $\text{CV}^2 \rightarrow 1/k_1$, and in the special case when $k_1 = 1$, $\text{CV}^2 \rightarrow 1$.

Connections among exponential, gamma, and beta distributions

The exponential, gamma, and beta probability distributions are closely connected.

For $\lambda > 0$ and positive integer n , $\Gamma(\lambda, k)$ is distributed as the sum of k independently and identically distributed copies of $\text{Exp}(\lambda)$, i.e., if X_1, X_2, \dots, X_k are independently and identically distributed as $\text{Exp}(\lambda)$, then $S_k = X_1 + X_2 + \dots + X_k \stackrel{d}{=} \Gamma(\lambda, k)$. As immediate consequences, $\Gamma(\lambda, 1) \stackrel{d}{=} \text{Exp}(\lambda)$, and if $\Gamma(\lambda, k_1)$ and $\Gamma(\lambda, k_2)$ are independent, then $\Gamma(\lambda, k_1) + \Gamma(\lambda, k_2) \stackrel{d}{=} \Gamma(\lambda, k_1 + k_2)$.

Any function f of $n > 0$ real arguments x_1, \dots, x_n is defined to be scale-free (or homogeneous of degree 0) if and only if, for all $c > 0$ and all $x_1, \dots, x_n, f(cx_1, \dots, cx_n) \equiv f(x_1, \dots, x_n)$. For example, $f(x, y) = x/y$ and $f(x, y) = x/(x + y)$ for $xy \neq 0$ are both scale-free. If $X_i \stackrel{d}{=} \Gamma(\lambda, k_i)$, $i = 1, \dots, n$, are independently distributed (but not necessarily identically, as k_i may vary with i), and if $S_n = X_1 + X_2 + \dots + X_n$, then $S_n \stackrel{d}{=} \Gamma(\lambda, \sum_{i=1}^n k_i)$ and any scale-free function $f(X_1, \dots, X_n)$ of the X_i are independent (Pitman 1937, pp. 216–217).

If $\Gamma(\lambda, k_1)$, $\Gamma(\lambda, k_2)$ are independent, then $\Gamma(\lambda, k_1) / [\Gamma(\lambda, k_1) + \Gamma(\lambda, k_2)] \stackrel{d}{=} B(k_1, k_2)$ (Çınlar 2011, p. 62).

Proof that $\text{variance}/(\text{mean})^2 \rightarrow 1$.

By (3), for every $j = 1, \dots, n(k)$, $k = 1, \dots, K$, we have

$$R_{jk} \stackrel{d}{=} \frac{\Gamma(\lambda(k), 1)}{\Gamma(\lambda(k), 1) + \Gamma(\lambda(k), n(k) - 1)} \stackrel{d}{=} B(1, n(k) - 1)$$

where $\Gamma(\lambda(k), 1)$ refers to the same exponential random variable $\text{Exp}(\lambda(k))$ in the numerator and denominator, and where $\Gamma(\lambda(k), 1)$ and $\Gamma(\lambda(k), n(k) - 1)$ are independent. Consequently,

$$\frac{\text{Var}(R_{jk})}{[E(R_{jk})]^2} = CV^2 \text{ of } B(1, n(k)-1) = \frac{n(k)-1}{n(k)+1} \rightarrow 1 \text{ as } n(k) \rightarrow \infty.$$

This completes the proof.

Incidentally, our argument also yields a proof of Feller's formula given above as Eq. (4). Specifically, if $k_1 = 1$, $k_2 = n - 1$, then the probability density function at $x \in (0, 1)$ of $B(1, n(k) - 1)$ simplifies to $\{\Gamma(n(k))/[\Gamma(1)\Gamma(n(k) - 1)]\}(1-x)^{n(k)-2} = (n(k) - 1)(1-x)^{n(k)-2}$. The survival function at $t \in (0, 1)$ is the integral of this probability density function from t to 1, which is (4).

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