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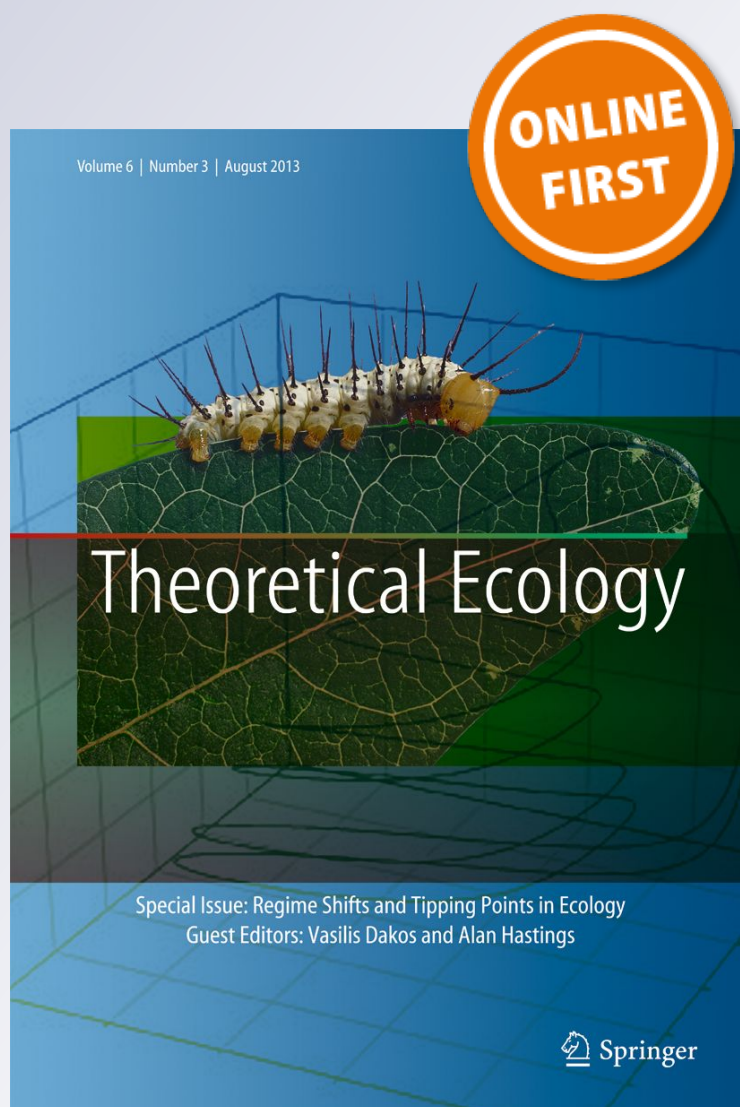
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# Every variance function, including Taylor's power law of fluctuation scaling, can be produced by any location-scale family of distributions with positive mean and variance

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## Abstract

One of the most widely verified empirical regularities of ecology is Taylor's power law of fluctuation scaling, or simply Taylor's law (TL). TL says that the logarithm of the variances of a set of random variables or a set of random samples is (exactly or approximately) a linear function of logarithm of the means of the corresponding random variables or random samples:  $\log \text{variance} = \log a + b \log \text{mean}$ ,  $a > 0$ . Ecologists have argued about the interpretation of the intercept  $\log a$  and slope  $b$  of TL and about what the values of these parameters reveal about the underlying probability distributions of the random samples. We show here that the form and the values of the parameters of TL and of any other variance function (relationship of variance to mean in a set of samples or a family of random variables) say nothing whatsoever about the underlying probability distributions of the random samples (or random variables) other than that they have finite mean and variance. Specifically, given any real-valued random variable with a finite mean and a finite variance, and given any variance function (e.g., TL with specified intercept  $\log a$  and slope  $b$ ), we construct a family of random variables with probability distributions of the same shape as the probability distribution of the given random variable (i.e., that are the same up to location and scale, or in the same "location-scale family") and that obeys the given variance function exactly (e.g., TL exactly with the given intercept  $\log a$  and slope  $b$ ). Every variance function can be produced by the location-scale family of any random variable with finite positive mean and finite positive variance. We illustrate some consequences of these findings by examples (e.g., for presence-absence sampling in agricultural pest control).

**Keywords** Taylor's power law · Variance function · Presence-absence · Exponential dispersion model · Tweedie distribution · Power law · Bartlett's variance function · Negative binomial distribution

## Introduction

The mean and the variance of the abundance of organisms are central concerns of basic and applied ecology, including agriculture, fisheries, forestry, and conservation. The development of statistical methods for analyzing agricultural experiments in the early twentieth century led to models of the relation of the

variance to the mean of abundance. Such a relationship of variance to mean is now known as a variance function.

It has long been known that the Poisson distribution, a common model of "purely random" counts, has a mean equal to its variance. In multiple samples from Poisson distributions with different means and variances, if  $X(\lambda)$  is a Poisson-distributed random variable with a mean and variance equal to  $\lambda$ , then a plot of the variance  $\text{Var}(X(\lambda)) = \lambda$  as a function of the mean  $E(X(\lambda)) = \lambda$  on log-log coordinates for varying values of  $\lambda$  will have a slope equal to 1, and therefore, a log-log plot of the sample variance against the sample mean, for samples from Poisson distributions with varying values of  $\lambda$ , will have a slope that approximates 1 with increasing precision as the sample sizes increase.

In a study of insecticide tests in the laboratory and in the field, Bartlett (1936, p. 193) wrote: "In practice, however, it has been observed that a better fit for the variance is often obtained if we write"  $\text{variance} = b_1 \cdot \text{mean} + b_2 \cdot \text{mean}^2$ ,  $b_1 >$

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$0, i = 1, 2$ . We call this relationship Bartlett's law (BL). BL includes the variance function variance = mean of the Poisson distribution as the special case  $b_1 = 1, b_2 = 0$ . BL also includes as a special case the variance function variance = mean +  $k \cdot \text{mean}^2, k > 0$  (e.g., Taylor 1961, p. 732, his eq. (1)) of the negative binomial distribution, in one way of parameterizing that distribution. Taylor (1961, p. 732) and others noticed that "Unfortunately  $k$  is not always independent of [the mean]  $m$ ."

In an early example of what later came to be known as Taylor's law (TL, sometimes called Taylor's power law of fluctuation scaling; the best review is Taylor 2019), namely,  $\log \text{variance} = \log a + b \log \text{mean}, a > 0$ , Bliss (1941) observed that his data on the distribution of Japanese beetle larvae had slopes  $b > 1$ . These slopes rejected the family of Poisson distributions as a possible model of the distributions of abundance.

Widely diverse views have been expressed concerning the interpretation of the slope of  $b$  in empirical applications of TL (Taylor 1961; Eisler et al. 2008; Taylor 2019). While it is true that a family of Poisson distributions implies  $b = 1$ , some ecologists have been tempted to assume, conversely, that if a log-log plot of the sample variance as a function of the sample mean, for a set of samples with differing sample means, has a slope approximating 1, then the underlying distribution of observations is Poisson. That this assumption is false appears not to be widely known.

Here we show, much more generally, that the form and the values of the parameters of TL and of any other variance function say nothing whatsoever about the shape of the underlying probability distributions of the random samples (or random variables) other than that they have a finite mean and variance. Specifically, given any real-valued random variable with a finite mean and a finite variance, and given any variance function (e.g., TL with specified intercept  $\log a$  and slope  $b$ ), we construct a family of random variables with probability distributions of the same shape as the probability distribution of the given random variable (i.e., that are the same up to location and scale, or in the same "location-scale family") and that obey the given variance function exactly (e.g., TL exactly with the given intercept  $\log a$  and slope  $b$ ). Every variance function can be produced by the location-scale family of any random variable with finite positive mean and finite positive variance. We illustrate some theoretical and practical consequences of these findings by examples.

## Results

We consider real-valued random variables  $X, Y, Z$ , real constants  $a > 0, b_i, i = 1, 2, \dots, c, d \neq 0$ , and a real parameter  $p$  in any non-empty subset of the positive real line  $(0, \infty)$ .

We say that  $X, Y$  have the same distribution up to location and scale, and we write  $X \sim Y$ , if and only if, for some  $c, d \neq 0, X$

has the same distribution as  $c + dY$ . This relation is reflexive, symmetric, and transitive. Therefore  $\sim$  partitions all probability distributions into equivalence classes with respect to  $\sim$ . For example, all normal distributions have the same distribution up to location and scale. Likewise, all uniform distributions on finite intervals of the real line have the same distribution up to location and scale. Discrete distributions require attention. A Poisson distribution assigns positive probability to every non-negative integer and nowhere else. If  $Y$  is a discrete distribution that assigns positive probability to every non-negative integer and nowhere else, then  $c + dY$  assigns positive probability to  $S = \{c + nd \mid n = 0, 1, 2, \dots\}$ .  $S$  may not be the set of non-negative integers and may contain no integers at all. Thus, a Poisson distribution has the same distribution up to location and scale as infinitely many distributions that are not Poisson distributions, but all these distributions have the same shape as a Poisson distribution.

## Taylor's law and its polynomial generalizations

**Definition 1** (Taylor's law and quadratic Taylor's law). A family of random variables  $\{X(p) \mid p \in P \neq \emptyset\}$  with parameter  $p$  in any non-empty set of possible parameter values  $P$  is said to obey Taylor's law (TL) if and only if  $0 < E(X(p)) < \infty, 0 < \text{Var}(X(p)) < \infty$ , and there exist real constants  $a > 0$  and  $b$  such that, for all  $p \in P$ ,

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

A related but different form of TL holds for non-negative random variables with infinite mean and variance (Brown et al. 2017).

A family of random variables  $\{X(p) \mid p \in P \neq \emptyset\}$  with parameter  $p$  in any non-empty set of possible parameter values  $P$  is said to obey a quadratic Taylor's law (QTL, from Taylor et al. (1978, p. 388, their eq. (14)) if and only if  $0 < E(X(p)) < \infty, 0 < \text{Var}(X(p)) < \infty$ , and there exist real constants  $a > 0$  and  $b_1, b_2$  such that, for all  $p \in P$ ,

$$\log \text{Var}(X(p)) = \log a + b_1 \log E(X(p)) + b_2 (\log E(X(p)))^2. \tag{2}$$

**Theorem 1** Let  $Z$  be any real-valued random variable with  $EZ = \mu \in (0, \infty), \text{Var}Z = \sigma^2 \in (0, \infty)$ . Let  $a, b_1, b_2$  be any real numbers such that  $a > 0$ . Then there exists a family of random variables  $\{X(p) \mid p \in P \subset (0, \infty)\}$  such that QTL (2) holds for the chosen  $a, b_1, b_2$  and  $X(p) \sim Z$  for every  $p \in P$ . When  $b_2 = 0$ , TL (1) holds for the chosen  $a, b = b_1$ .

Proof. Define  $q = -\frac{1}{b_1 + 2b_2}$  and for each  $p \in P$ , define

$$X(p) := pa^q + p^{\frac{b_1}{2} + b_2} (Z - \mu) / \sigma. \tag{3}$$

Then  $X(p) \sim Z$  for all  $p \in P$  because  $X(p) = \left[ pa^q - p^{\frac{b_1}{2} + b_2} \mu / \sigma \right] + \left[ p^{\frac{b_1}{2} + b_2} / \sigma \right] Z = c + dZ$  with  $c = pa^q - p^{\frac{b_1}{2} + b_2} \mu / \sigma, d = p^{\frac{b_1}{2} + b_2} / \sigma$ . Since  $E((Z - \mu) / \sigma) = 0$ , we have  $EX(p) = pa^q$ . Taking logarithms of both sides gives  $\log EX(p) = \log p + q \log a$  or

$$\log p = \log EX(p) - q \log a. \tag{4}$$

Also since  $\text{Var}((Z - \mu) / \sigma) = 1$ , we have

$$\begin{aligned} \text{Var}X(p) &= 0 + \text{Var}\left(p^{\frac{b_1}{2} + b_2} (Z - \mu) / \sigma\right) \\ &= p^{b_1 + 2b_2} \text{Var}[(Z - \mu) / \sigma] = p^{b_1 + 2b_2}. \end{aligned}$$

Taking logarithms of the left and right members and using (4) and the definition of  $q$  gives

$$\begin{aligned} \log \text{Var}X(p) &= (b_1 + 2b_2) \log p = (b_1 + 2b_2) [\log EX(p) - q \log a] \\ &= (b_1 + 2b_2) \log EX(p) - q(b_1 + 2b_2) \log a \\ &= \log a + b_1 \log EX(p) + b_2 (\log EX(p))^2. \end{aligned} \tag{5}$$

The first and last members of these equalities (5) are QTL (1) for the chosen  $a, b_1, b_2$ .

**Generalization of Theorem 1** Let  $Z$  be any real-valued random variable with  $EZ := \mu \in (0, \infty), \text{Var}Z := \sigma^2 \in (0, \infty)$ . Let  $a, b_i, i = 1, 2, \dots$  be any real numbers such that  $a > 0$ . Then there exists a family of random variables  $\{X(p) | p \in P \subset (0, \infty)\}$  such that  $\log \text{Var}(X(p)) = \log a + \sum_{i=1}^{\infty} b_i [\log E(X(p))]^i$  ("polynomial Taylor's law" or PTL) holds for the chosen  $a, b_i, i = 1, 2, \dots$  and  $X(p) \sim Z$  for every  $p \in P$ .

*Proof.* Define

$$q = -\left\{ \sum_{i=1}^{\infty} i b_i \right\}^{-1}, \quad r = \frac{1}{2} \left\{ \sum_{i=1}^{\infty} i b_i \right\}. \tag{6}$$

Thus  $-2qr = 1$ . For each  $p \in P$ , define

$$X(p) := pa^q + p^r (Z - \mu) / \sigma. \tag{7}$$

Then as in the prior proof,  $\log p = \log EX(p) - q \log a$  and  $\text{Var}X(p) = p^{2r}$  so

$$\begin{aligned} \log \text{Var}X(p) &= 2r(\log EX(p) - q \log a) \\ &= \left\{ \sum_{i=1}^{\infty} i b_i \right\} \log EX(p) + \log a \\ &= \log a + \sum_{i=1}^{\infty} b_i (i \log EX(p)) \\ &= \log a + \sum_{i=1}^{\infty} b_i (\log EX(p))^i. \end{aligned} \tag{8}$$

**Bartlett's law and its polynomial generalizations**

**Definition 2** (Bartlett's law; Bartlett 1936). A family of random variables  $\{X(p) | p \in P \neq \emptyset\}$  with parameter  $p$  in any non-empty set of possible parameter values  $P$  is said to obey

Bartlett's law (BL) if and only if  $0 < E(X(p)) < \infty, 0 < \text{Var}(X(p)) < \infty$ , and there exist real constants  $b_i > 0, i = 1, 2$ , such that, for all  $p \in P$ ,

$$\text{Var}(X(p)) = b_1 E(X(p)) + b_2 [E(X(p))]^2. \tag{9}$$

**Theorem 2** Let  $Z$  be any real-valued random variable with  $EZ := \mu \in (0, \infty), \text{Var}Z := \sigma^2 \in (0, \infty)$ . Let  $b_i > 0, i = 1, 2$ . Then there exists a family of random variables  $\{X(p) | p \in P \neq \emptyset\}$  such that BL (9) holds for the chosen  $b_i > 0, i = 1, 2$  and  $X(p) \sim Z$  for every  $p \in P$ .

*Proof.* For each  $p \in P$ , define

$$X(p) := p + \left[ pb_1 + p^2 b_2 \right]^{\frac{1}{2}} (Z - \mu) / \sigma. \tag{10}$$

Then  $X(p) \sim Z$  for all  $p \in P$  by the same elementary calculation as in Theorem 1. Since  $E((Z - \mu) / \sigma) = 0$ , we have  $E(X(p)) = p$ . Since  $\text{Var}((Z - \mu) / \sigma) = 1$ , we have  $\text{Var}X(p) = 0 + \text{Var}\left(\left[ pb_1 + p^2 b_2 \right]^{\frac{1}{2}} (Z - \mu) / \sigma\right) = pb_1 + p^2 b_2 = b_1 E(X(p)) + b_2 [E(X(p))]^2$ , which is BL (9) for the chosen  $b_i, i = 1, 2$ .

**Generalization of Theorem 2** Let  $Z$  be any real-valued random variable with  $EZ := \mu \in (0, \infty), \text{Var}Z := \sigma^2 \in (0, \infty)$ . Let  $b_i \geq 0, i = 1, 2, \dots$  be any real non-negative numbers, at least one of which is positive. Then there exists a family of random variables  $\{X(p) | p \in P \neq \emptyset\}$  such that, for every  $p \in P, X(p) \sim Z$  and  $\text{Var}X(p) = \sum_{i=1}^{\infty} b_i [EX(p)]^i$  ("polynomial Bartlett's law" or PBL) holds for the chosen  $b_i, i = 1, 2, \dots$ .

*Proof.* For each  $p \in P$ , define

$$X(p) := p + \left[ \sum_{i=1}^{\infty} b_i p^i \right]^{\frac{1}{2}} (Z - \mu) / \sigma. \tag{11}$$

Then, as before, for all  $p \in P$ , we have  $X(p) \sim Z$  and  $E(X(p)) = p$  since  $E((Z - \mu) / \sigma) = 0$ . Since  $\text{Var}((Z - \mu) / \sigma) = 1$ , we have  $\text{Var}X(p) = 0 + \text{Var}\left(\left[ \sum_{i=1}^{\infty} b_i p^i \right]^{\frac{1}{2}} (Z - \mu) / \sigma\right) = \sum_{i=1}^{\infty} b_i p^i = \sum_{i=1}^{\infty} b_i [EX(p)]^i$ , which is PBL for the chosen  $b_i, i = 1, 2, \dots$

**Arbitrary variance function**

**Definition 3** (variance function; Bartlett 1947, p. 39, his Eq. (1)). A positive-valued function  $f: (-\infty, \infty) \rightarrow (0, \infty)$  is said to be the variance function of a family of random variables  $\{X(p) | p \in P \neq \emptyset\}$  with parameter  $p$  in any non-empty set  $P$  of possible parameter values if and only if, for all  $p \in P, \text{Var}(X(p)) = f(EX(p))$ . (The domain of  $f$  is the entire real line to allow for cases where  $EX(p) < 0$ .)

**Theorem 3** Let  $Z$  be any real-valued random variable with finite expectation  $EZ := \mu \in (-\infty, \infty)$  and finite positive

variance  $\text{Var}Z := \sigma^2 \in (0, \infty)$ . Let  $f: (-\infty, \infty) \rightarrow (0, \infty)$  be any function. Then there exists a family of random variables  $\{X(p) | p \in P \neq \emptyset\}$ , namely,  $X(p) := p + \sqrt{f(p)}(Z - \mu)/\sigma$ , such that, for every  $p \in P$ ,  $X(p) \sim Z$  (i.e., every member  $X(p)$  has the same distribution as  $Z$  up to location and scale) and  $\text{Var}(X(p)) = f(EX(p))$ , i.e.,  $f$  is the variance function of the family  $\{X(p) | p \in P \neq \emptyset\}$ .

*Proof.* Given  $f, Z$ , define, for every  $p \in P$ ,  $X(p) := p + \sqrt{f(p)}(Z - \mu)/\sigma$ . Then  $X(p) \sim Z$  and  $EX(p) = p$  and  $\text{Var}X(p) = f(p)\text{Var}(Z - \mu)/\sigma = f(p) = f(EX(p))$ .

Theorems 1 and 2 are obviously special cases of Theorem 3. They are nevertheless useful and worth stating because they demonstrate the relevance of Theorem 3 to cases most familiar to pure and applied ecologists.

To illustrate an application of Theorem 3, we give an alternate proof of Theorem 1 in the special case of Theorem 1 where  $b_1 = b, b_2 = 0$ , which is TL. The power-law form of TL, equivalent to TL (1), is:

$$\text{Var}(X(p)) = a[EX(p)]^b. \tag{12}$$

So TL is the variance function  $f(p) = ap^b, a > 0, p > 0$ . Let  $Z$  be any real-valued random variable with finite expectation  $EZ := \mu \in (-\infty, \infty)$  and finite positive variance  $\text{Var}Z := \sigma^2 \in (0, \infty)$ . Then  $X(p) := p + \sqrt{f(p)}(Z - \mu)/\sigma = p + \sqrt{ap^b}(Z - \mu)/\sigma$  satisfies  $EX(p) = p$  and  $\text{Var}X(p) = ap^b \cdot 1$ . Since  $EX(p) = p$ , we have  $\text{Var}X(p) = a[EX(p)]^b$ , which is the power-law form of TL (12).

Because this result holds for any such  $Z$ , TL can give no information about the shape of the underlying probability distribution.

## Discussion

### Example 1: Poisson distributions

The family of Poisson distributions  $\{X(p) | 0 < p < \infty\}$  satisfies  $\text{Var}(X(p)) = E(X(p)) = p$ , which is TL (1) or (12) with  $a = b = 1$ . The converse is false: TL (1) with  $a = b = 1$  in no way implies

that the data are Poisson or “randomly” distributed. To see why, choose  $a = b = 1$  in TL (1). Let  $Z$  be any real-valued random variable with mean  $EZ := \mu \in (0, \infty)$  and variance  $\text{Var}Z := \sigma^2 \in (0, \infty)$ . Then  $X(p) = p + \sqrt{p}(Z - \mu)/\sigma$  obeys TL (1) with exactly the same intercept and slope as the family of Poisson distributions but every  $X(p)$  has the same distribution, up to location and scale, as the arbitrarily chosen  $Z$ .

### Example 2: Two-point distributions

We consider four families of random variables  $\{X(p) | p > 0\}$  that take only two values, 0 and an upper value  $p > 0$  (Table 1). Here the upper value  $p$  serves as the parameter of each family of distributions.

For any fixed  $\pi \in (0, 1)$ , families 1 and 2 both have identical parameters of TL, namely,  $a = \pi(1 - \pi), b = 2$ . But the fraction of observations that are positive is  $\pi$  in family 1 and is  $1 - \pi$  in family 2. This dramatic contrast (when  $\pi \neq 1/2$ ) between families 1 and 2 (same TL parameters, different probabilities of being equal to 0) shows that the parameters of TL cannot be used to infer the proportion of infested plants, as some have desired to do in agricultural pest control (e.g., Wilson and Room 1983). For example, if  $\pi = 0.01$ , then in large samples, approximately 99% of observations in family 1 are 0 (uninfested) while in family 2 only 1% of observations are 0 (uninfested). Because it is not possible to infer the prevalence of infestation of plants by insect pests, for example, from the intercept and slope of TL, more detailed analysis of each sample is required.

Wilson and Room (1983, p. 51, their eq. (7)) derived a formula for the proportion of infested cotton plants based on the sample mean and the sample variance of an assumed negative binomial distribution of the number of insects per plant. They then (in their eq. (8)) used TL to replace the sample variance with a power function of the sample mean, overlooking the problem that, in their parameterization of the negative binomial distribution, the variance function of a family of negative binomially distributed random variables is strictly convex on log-log coordinates, not linear on log-log coordinates, and is therefore not compatible with TL (Cohen et al. 2016, pp. 3–4; see proof in supplementary materials).

**Table 1** Four families of two-point distributions that take only two values, 0 and  $p > 0$  with positive probability, with positive means and positive variances, and the parameters of Taylor’s law (TL) where TL is applicable. Here  $\pi$  is a probability,  $0 < \pi < 1$

Family	1	2	3	4
Upper value $p > 0$	Parameter $p$	Parameter $p$	$p = \mu^2/(\mu - 1)$	$p = \mu^2$
$\Pr\{X(p) = 0\}$	$0 < 1 - \pi < 1$	$0 < \pi < 1$	$1/\mu$	$1 - 1/\mu$
$\Pr\{X(p) = p\}$	$0 < \pi < 1$	$0 < 1 - \pi < 1$	$1 - 1/\mu$	$1/\mu$
$EX(p)$	$p\pi$	$(1 - \pi)p$	$\mu > 1$	$\mu > 1$
$E(X^2(p))$	$\pi p^2$	$(1 - \pi)p^2$	$\mu^3/(\mu - 1)$	$\mu^3$
$\text{Var}X(p)$	$\pi(1 - \pi)p^2$	$\pi(1 - \pi)p^2$	$\mu^2/(\mu - 1)$	$\mu^2(\mu - 1)$
TL $a$	$\pi(1 - \pi)$	$\pi(1 - \pi)$	Not exactly TL	Not exactly TL
TL $b$	2	2	$\rightarrow 1$ as $\mu \rightarrow \infty$	$\rightarrow 3$ as $\mu \rightarrow \infty$

Unfortunately, Taylor (2019, p. 467, his eq. (14.6)) repeated (without giving its source) this unreliable formula of Wilson and Room (1983).

Families 3 and 4 show that not all two-point distributions obey TL exactly for all values of  $\mu > 1$ , and when TL describes the variance-mean relation asymptotically, the parameter  $b$  may be greater or less than 2.

### Example 3: $0 < b < 1$

Theorem 1 applies to TL for any  $a > 0$  and all finite real  $b$ , in particular, when  $0 < b < 1$ . Consequently, as Cohen (2014, p. 33) noted, Tweedie distributions and exponential dispersion models do not include all distributions that obey TL, because  $0 < b < 1$  is impossible for Tweedie distributions and exponential dispersion models (Jørgensen 1987, p. 133, Theorem 2; Jørgensen 1997, p. 130, his Table 4.1). This result greatly extends a single, very specific example of stochastic multiplicative population dynamics in a Markovian environment with  $0 < b < 1$  given by Cohen (2014, p. 33). Theorem 1 shows that TL with  $0 < b < 1$  is compatible with the location-scale equivalent class of any random variable with finite positive mean and finite positive variance.

### Example 4: $b < 0$

Theorem 1 applies to TL when  $b < 0$ . Fujiwara and Cohen (2015) simulated stochastic stage-structured density-dependent models of exploited fish populations. When density-dependence was overcompensatory, for certain parameter values, TL with a negative slope was an excellent approximation to the variance-mean relationship (Fujiwara and Cohen 2015, p. 8, their Fig. 4(b,c)). Theorem 1 shows that TL with a negative slope is compatible with an arbitrary family of probability distributions with a positive mean and positive variance.

## Conclusion

Taylor's law, Bartlett's law, and other variance functions are widely applicable but not magically universal summaries of relations of variance to mean. They are extremely useful for statistically transforming data for ANOVA, evaluating projections, designing more efficient sampling, and other purposes. But Taylor's law, Bartlett's law, and every other variance function provide no shortcut to understanding the underlying

distributions of abundance, and the distributions of abundance provides no shortcut to understanding the mechanisms (stochastic or deterministic) that generate the distributions of abundance (e.g., Cohen 1968). Each requires analysis.

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## References

- Bartlett MS (1936) Some notes on insecticide tests in the laboratory and in the field. *Suppl J R Stat Soc* 3(2):185–194 Stable URL: <http://www.jstor.org/stable/2983670>
- Bartlett MS (1947) The use of transformations. *Biometrics* 3(1):39–52 Stable URL: <http://www.jstor.org/stable/3001536>
- Bliss CI (1941) Statistical problems in estimating populations of Japanese beetle larvae. *J Econ Entomol* 34:221–232. <https://doi.org/10.1093/jee/34.2.221>
- Brown M, Cohen JE, de la Peña V (2017) Taylor's law, via ratios, for some distributions with infinite mean. *J Appl Probab* 54(3):1–13. <https://doi.org/10.1017/jpr.2017.25>
- Cohen JE (1968) Alternate derivations of a species-abundance relation. *Am Nat* 102:165–172
- Cohen JE (2014) Stochastic population dynamics in a Markovian environment implies Taylor's power law of fluctuation scaling. *Theor Popul Biol* 93:30–37. <https://doi.org/10.1016/j.tpb.2014.01.001>
- Cohen JE, Poulin R, Lagrue C (2016) Linking parasite populations in hosts to parasite populations in space through Taylor's law and the negative binomial distribution. *Proc Natl Acad Sci U S A* 114(1):E47–E56 [www.PNAS.org/cgi/doi/10.1073/PNAS.1618803114](http://www.PNAS.org/cgi/doi/10.1073/PNAS.1618803114)
- Eisler Z, Bartos I, Kertész J (2008) Fluctuation scaling in complex systems: Taylor's law and beyond. *Adv Phys* 57(1):89–142. <https://doi.org/10.1080/00018730801893043> Cite as: arXiv:0708.2053v2 [physics.soc-ph]
- Fujiwara M, Cohen JE (2015) Mean and variance of population density and temporal Taylor's law in stochastic stage-structured density-dependent models of exploited fish populations. *Theor Ecol* 8(2):175–186. <https://doi.org/10.1007/s12080-014-0242-8>
- Jørgensen B (1987) Exponential dispersion models. *J R Stat Soc Ser B Methodol* 49(2):127–162 Stable URL: <http://www.jstor.org/stable/2345415>
- Jørgensen B (1997) The theory of dispersion models. Chapman & Hall, London
- Taylor LR (1961) Aggregation, variance and the mean. *Nature* 189(4766):732–735. <https://doi.org/10.1038/189732a0>
- Taylor RAJ (2019) Taylor's power law: order and pattern in nature. Elsevier Academic Press, Cambridge, MA
- Taylor LR, Woiwod IP, Perry JN (1978) The Density-Dependence of Spatial Behaviour and the Rarity of Randomness. *The Journal of Animal Ecology* 47 (2):383
- Wilson LT, Room PM (1983) Clumping Patterns of Fruit and Arthropods in Cotton, with Implications for Binomial Sampling. *Environmental Entomology* 12 (1):50–54