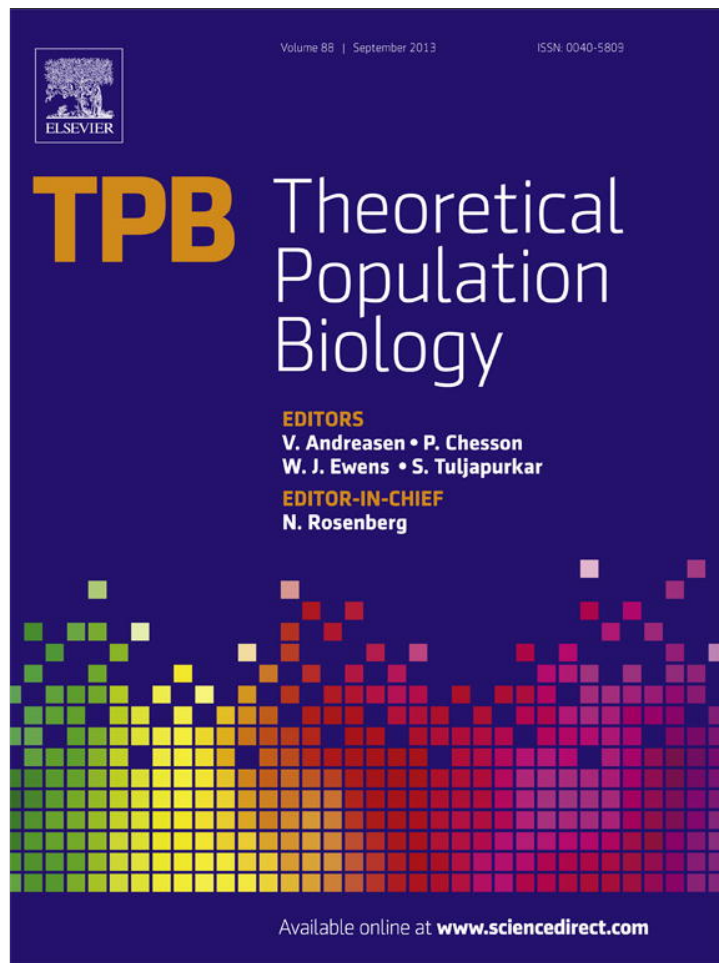


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# Taylor's power law of fluctuation scaling and the growth-rate theorem



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## ABSTRACT

Taylor's law (TL), a widely verified empirical relationship in ecology, states that the variance of population density is approximately a power-law function of mean density. The growth-rate theorem (GR) states that, in a subdivided population, the rate of change of the overall growth rate is proportional to the variance of the subpopulations' growth rates. We show that continuous-time exponential change implies GR at every time and, asymptotically for large time, TL with power-law exponent 2. We also show why diverse population-dynamic models predict TL in the limit of large time by identifying simple features these models share: If the mean population density and the variance of population density are (exactly or asymptotically) non-constant exponential functions of a parameter (e.g., time), then the variance of density is (exactly or asymptotically) a power-law function of mean density.

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## 1. Introduction

Taylor's (1961) law (TL) of fluctuation scaling states that the variance of population density is proportional to some power, denoted  $b$ , of the mean population density. The growth-rate theorem (GR) states that, in a subdivided population, the rate of change of the overall growth rate is proportional to the variance of the subpopulations' growth rates. Until now, it appears that GR and TL have not been linked. Here we derive both GR and TL from a simple model of exponential population dynamics and display a link between them.

In addition, we show why very different population-dynamic models lead to Taylor's law. If the mean of population density behaves as a non-constant exponential function of any parameter (such as time) and the variance of population density behaves as any exponential function of the same parameter, then TL holds. This argument is not limited to the class of exponential functions.

## 2. Exponential model

Consider  $n$  clones,  $1 < n < \infty$ , labeled  $i = 1, \dots, n$ . We think of clone  $i$  as an exponentially changing population of idealized bacteria reproducing asexually at a constant rate in continuous time. The population density  $N_i(t)$  of clone  $i$  at time  $t$  satisfies:

$$\frac{dN_i(t)}{dt} = r_i N_i(t), \quad -\infty < t < +\infty, \\ -\infty < r_i < +\infty, \quad i = 1, \dots, n. \quad (1)$$

Abbreviations: TL, Taylor's law; GR, growth-rate theorem.

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The coefficient  $r_i = (dN_i(t)/dt)/N_i(t)$  is the rate of change of the population density per capita, or the population growth rate, or "Malthusian parameter" of clone  $i$ . Time does not appear as a variable in (1), only as a parameter, and translating time on both sides of (1) by any amount would not change the equation. Hence it is natural to include negative time in the analysis because the choice of an origin of time is arbitrary. Suppose that, at some arbitrary time called  $t = 0$ , clone  $i$  has population density  $N_i(0) > 0$ . Then at any time  $t$ , clone  $i$  has positive population density

$$N_i(t) = N_i(0)e^{r_i t}, \quad -\infty < t < +\infty, \quad i = 1, \dots, n. \quad (2)$$

Assume that  $r_i \neq r_j$  if  $i \neq j$ . Some  $r_i$  might be positive, some negative. At most one  $r_i$  might be zero. Label the clones in decreasing order of population growth rate so that  $r_1 > r_2 > \dots > r_n$ .

Suppose that each clone is present in multiple copies, and that the proportion of all copies that are clone  $i$  is  $p_i$ ,  $0 < p_i < 1$ , where  $p_1 + \dots + p_n = 1$ . The proportion  $p_i$  does not change in time. For example, if in a laboratory experiment each Petri dish is seeded with exactly one clone,  $p_i$  might represent the proportion of all Petri dishes seeded with clone  $i$ . In island biogeography,  $p_i$  might represent the proportion of all islands occupied by clone  $i$ . The proportion of the total population represented by individuals of clone  $i$  changes constantly as at least one clone grows or declines exponentially. Variability enters this deterministic model only through the different population growth rates  $r_i$ , proportions  $p_i$  and population densities  $N_i(0)$  at time  $t = 0$ .

### 2.1. Taylor's law (TL) of fluctuation scaling

Taylor (1961) and colleagues (Taylor et al., 1978, 1980; Taylor and Woiwod, 1980, 1982; Taylor, 1984; Perry and Taylor, 1985; Taylor, 1986) observed that, in many species, the logarithm of the variance of the density (individuals per area or volume) of

comparable populations was an approximately linear function of the logarithm of the mean density. This relationship came to be known as Taylor's law (TL). TL was verified in hundreds of species (Eisler et al., 2008) ranging in size from, recently, bacteria (Ramsayer et al., 2011; Kaltz et al., 2012) to trees (Cohen et al., 2012, 2013). TL is one of the most widely verified empirical relationships in ecology. TL has also been widely discussed from many theoretical points of view (e.g., Eisler et al., 2008, Engen et al., 2008, Fronczak and Fronczak, 2010, and their extensive references).

We show (see the Appendix) that the exponential model predicts a spatial TL in the limit of large time. Here we explain what this means. We say that a spatial TL applies to  $N(t)$  exactly for all times  $t$  if and only if there exist real constants  $a > 0$  and  $b$  such that, for all  $t$ ,  $\text{Var}(N(t)) = a(E(N(t)))^b$ , where the mean  $E(N(t))$  and the variance  $\text{Var}(N(t))$  refer to the mean and variance of population density over space at time  $t$ , and do not refer to a mean and variance over a set of time points. (In a temporal TL, which we do not consider here, the mean and variance are taken over a set of time points separately for each population.)

In an important special case of TL, the coefficient of variation (standard deviation divided by the mean, or CV) of population density is constant if and only if  $b = 2$ . (If  $b = 2$ , then  $\text{Var}(N(t)) = a(E(N(t)))^2$ , hence  $\text{Var}(N(t))/(E(N(t)))^2 = a$ , and taking the square root of both sides yields  $\text{CV} = a^{1/2}$ . Conversely, if  $\text{CV} = k$ , then  $(\text{CV})^2 = k^2$ . Because by definition  $(\text{CV})^2 = \text{Var}(N(t))/(E(N(t)))^2$ , we have  $\text{Var}(N(t)) = k^2(E(N(t)))^2$ , which is TL with  $a = k^2$  and  $b = 2$ .)

Taking logs of both sides of  $\text{Var}(N(t)) = a(E(N(t)))^b$  and moving both functions of time  $t$  to the left side gives an equivalent log-linear form of TL:

$$\log \text{Var}(N(t)) - b \log E(N(t)) = \log a. \quad (3)$$

We say that TL applies to  $N(t)$  in the limit as  $t$  approaches some limit, e.g.,  $t \rightarrow \pm\infty$ , if and only if there exist real constants  $a > 0$  and  $b$  such that

$$\lim_{t \rightarrow \pm\infty} [\log \text{Var}(N(t)) - b \log E(N(t))] = \log a. \quad (4)$$

These definitions intentionally leave unspecified the base of the logarithms (e.g.,  $e$ , 10, or 2) because TL is equally valid for logarithms to any base. In the following mathematical analysis,  $\log = \log_e$ .

In TL,  $b$  does not depend on the units chosen to measure  $N(t)$ . For example, if TL holds when population density is measured in organisms per cubic meter, it will also hold with the same value of  $b$  when population density is measured in organisms per cubic kilometer or any other units. By contrast, the coefficient  $a$  depends on the units of measurement. Hence we focus on  $b$ .

In the exponential model at time  $t$ , the average population density is

$$E(N(t)) = \sum_{i=1}^n p_i N_i(t) = \sum_{i=1}^n p_i N_i(0) e^{r_i t}. \quad (5)$$

The variance of population density is

$$\begin{aligned} \text{Var}(N(t)) &= E(N^2(t)) - [E(N(t))]^2 \\ &= \sum_{i=1}^n p_i (N_i(0))^2 e^{2r_i t} - [E(N(t))]^2. \end{aligned} \quad (6)$$

A main result of this paper is that, in the exponential model, in the limit as  $t \rightarrow \pm\infty$ , TL (4) holds with  $b = 2$  (see the Appendix Theorem 4 for the proof).

The exponential model obeys TL only in the limit of large times (positive or negative). How is the variance related to the mean in the exponential model at finite time  $t$ ? We assume the log mean

and the log variance are differentiable functions of  $t$  and introduce  $b(t)$  as a finite-time approximation to  $b$ :

$$b(t) = \frac{d \log \text{Var}(N(t))}{d \log E(N(t))} = \frac{\left\{ \frac{d \text{Var}(N(t))}{dt} \right\}}{\left\{ \frac{d E(N(t))}{dt} \right\}}. \quad (7)$$

This  $b(t)$ , when it is defined, is the slope at a finite time  $t$  of  $\log \text{Var}(N(t))$  as a function of  $\log E(N(t))$ . (It is defined when  $\text{Var}(N(t)) \neq 0$  and  $E(N(t)) \neq 0$  and  $dE(N(t))/dt \neq 0$ .) When TL holds exactly, as in (3), the right side of (7) is just  $b$ . If  $\lim_{t \rightarrow \pm\infty} b(t)$  exists and is a finite constant, TL holds in the limit as  $t \rightarrow \pm\infty$  and  $\lim_{t \rightarrow \pm\infty} b(t) = b$ . If  $\lim_{t \rightarrow \pm\infty} b(t)$  does not exist or is not a finite constant, TL does not hold in the limit as  $t \rightarrow \pm\infty$ .

A numerical example (Fig. 1) shows that, for finite  $t$ , the behavior of the mean  $E(N(t))$ , the variance  $\text{Var}(N(t))$ , and  $b(t)$  may be surprisingly complex, even in a model as simple as the exponential model. Specifically,  $b(t)$  may be positive, negative, increasing, or decreasing, and may pass through singularities.

### 3. Growth-rate theorem

The growth-rate theorem (GR) states that, in a subdivided population, the rate of change of the overall growth rate of population density is proportional to the variance of the subpopulations' growth rates. The origins of GR will be reviewed in the Discussion. In the exponential model, the overall growth rate of the population at time  $t$  is the mean of  $r_i$ ,  $i = 1, \dots, n$ ,

$$E(r(t)) = \frac{\sum_{i=1}^n p_i N_i(t) r_i}{\sum_{i=1}^n p_i N_i(t)} = \frac{\sum_{i=1}^n p_i r_i N_i(0) e^{r_i t}}{\sum_{i=1}^n p_i N_i(0) e^{r_i t}}. \quad (8)$$

The denominator on the right side of (8) is  $E(N(t))$  in (5). From (5), the first derivative of  $E(N(t))$  with respect to time is

$$E'(N(t)) = \sum_{i=1}^n p_i N_i'(t) = \sum_{i=1}^n p_i N_i(0) r_i e^{r_i t}. \quad (9)$$

But this is just the numerator of the fraction on the right side of (8). Putting together the numerator and the denominator gives

$$E(r(t)) = E'(N(t))/E(N(t)) = d \log E(N(t))/dt. \quad (10)$$

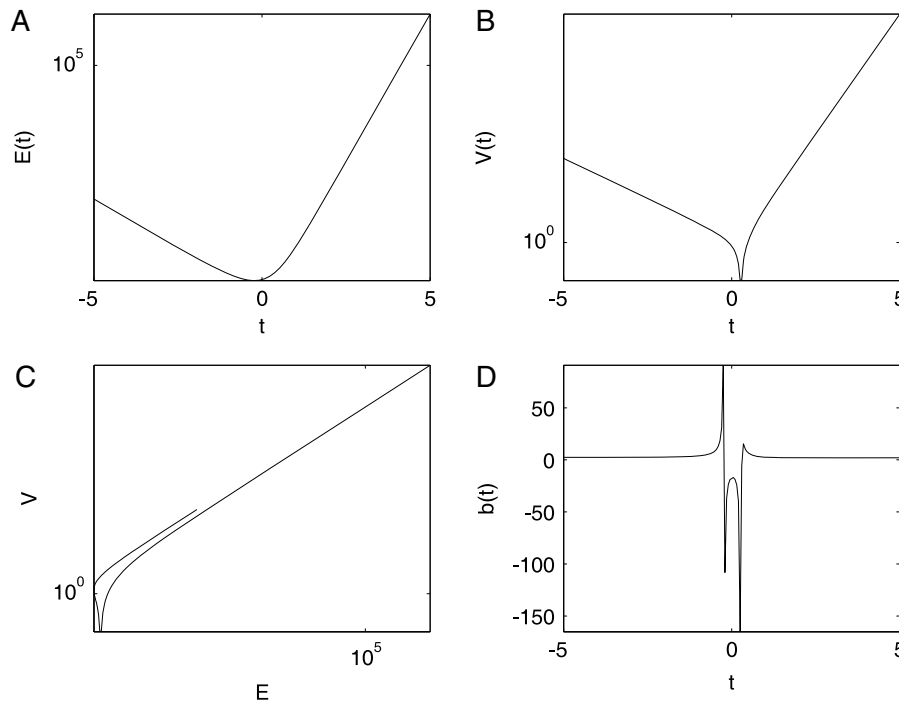
In the exponential model, the mean population growth rate equals the per capita rate of change of the mean population size. The mean population growth rate  $E(r(t))$  in (10) is also the denominator of the local slope of Taylor's law  $b(t)$  in (7). Taking the second derivative of (5) with respect to time gives

$$E''(N(t)) = \sum_{i=1}^n p_i N_i''(t) = \sum_{i=1}^n p_i N_i(0) r_i^2 e^{r_i t} > 0. \quad (11)$$

The variance of the population growth rate is the variance of  $r_i$ ,

$$\begin{aligned} \text{Var}(r(t)) &= E(r^2(t)) - (E(r(t)))^2 \\ &= \frac{E''(N(t))}{E(N(t))} - \left( \frac{E'(N(t))}{E(N(t))} \right)^2 = \frac{d^2 \log E(N(t))}{dt^2}. \end{aligned} \quad (12)$$

In words, the variance of the population growth rate in the exponential model equals the acceleration (second derivative) of the log mean population density. Obviously the derivative with respect to  $t$  of the first derivative  $d \log E(N(t))/dt$ , the right member of (10), equals the second derivative, which is the right member of (12), so the derivative of the mean population growth rate  $E(r(t))$ , the left member of (10), exactly equals the left



**Fig. 1.** Finite-time behavior of the mean and variance of population density and the local slope of an example of the exponential model. For  $t \in [-5, +5]$ , the panels show (A) the mean  $E(t) = E(N(t))$ , (B)  $V(t) = \text{Var}(N(t))$ , (C)  $V(t)$  as a function of  $E(t)$  on log–log coordinates, and (D)  $b(t)$ . Here  $n = 3$ ,  $p = [5/12, 1/3, 1/4]$ ,  $N(0) = [1, 2, 3]$ ,  $r = [1.6, 0.7, -1.2]$ .  $E(t)$  reaches a minimum value  $\approx 1.7479$  around  $t \approx -0.20$  while  $V(t)$  reaches a minimum value  $\approx 0.0085$  at  $t \approx 0.25$ . For  $t < -0.20$ , both  $E(t)$  and  $V(t)$  decrease with increasing  $t$ , so  $b(t) > 0$ . For  $t > 0.25$ , both  $E(t)$  and  $V(t)$  increase with increasing  $t$ , so again  $b(t) > 0$ . When either  $E(t)$  or  $V(t)$  passes through its minimum,  $b(t)$  becomes singular or undefined. When  $-0.20 < t < +0.25$ , the time derivatives  $E'(t)$  and  $V'(t)$  have opposite signs so  $b(t) < 0$ . In (C), a log–log plot of  $V(t)$  as a function of  $E(t)$ , a straight line would correspond to TL. In the curve shown, the short upper limb corresponds to  $t$  in  $(-5, -0.20)$  and the long lower limb to  $t$  in  $(+0.25, +5)$ . For  $t$  near  $\pm 5$ , these limbs display the asymptotic slope near  $+2$ , the limiting value calculated theoretically. The small segment with negative slope in the lower left corner of (C) connects these two limbs for  $t$  in approximately  $(-0.20, +0.25)$  where  $V(t)$  decreases and  $E(t)$  increases. This small segment shows that the same dynamic processes that generate asymptotically perfect agreement with TL at large time (positive or negative) can also generate a nonlinear relationship and a decreasing variance of density with increasing mean density at finite times.

member of (12), the variance of population growth rate  $\text{Var}(r(t))$ . This proves GR with a constant of proportionality equal to 1.

Both the variance of population growth rate and the rate of change of the variance of population growth rate approach zero for large (positive or negative) time (Appendix Theorem 8).

Because  $r_1 > r_2 > \dots > r_n$  by assumption,  $\exp(r_1 t)$  grows faster than any other  $\exp(r_j t)$ ,  $j = 2, \dots, n$ . Hence for any  $j > 1$ ,  $\exp(r_j t)/\exp(r_1 t) \rightarrow 0$  as  $t \rightarrow \infty$ . Hence the upper limit of  $d \log E(N(t))/dt$  as  $t \rightarrow \infty$  is  $r_1$  and the upper limit of mean population growth rate is also  $r_1$ . The intuitive reason for this conclusion is that clone 1 has the highest population growth rate, hence as time increases clone 1 increasingly dominates the population, hence the per capita growth rate of the overall population density gets increasingly close to the per capita growth rate of clone 1, which is  $r_1$ . Symbolically, as  $t \rightarrow \infty$ ,  $E(r(t)) = d \log E(N(t))/dt \rightarrow r_1$ . A parallel result is that  $d \log \text{Var}(N(t))/dt \rightarrow 2r_1$  (see the proof of Appendix Theorem 4). In the limit  $t \rightarrow -\infty$ , clone  $n$  dominates the population, and parallel reasoning yields  $E(r(t)) = d \log E(N(t))/dt \rightarrow r_n$ ,  $d \log \text{Var}(N(t))/dt \rightarrow 2r_n$ , and again  $b(t) \rightarrow 2$ .

#### 4. Why very different models lead to Taylor's law

Cohen et al. (2013) showed that the model of stochastic population dynamics by Lewontin and Cohen (1969) (no relation to this author) leads to an asymptotic spatial TL. The Lewontin–Cohen (hereafter LC) model is a multiplicative random walk. It assumes that the density of a population changes from one point in discrete time to the next point in discrete time as a result of multiplication by some positive-valued random variable which may be called a

“growth factor”, and that successive values of this “growth factor” are independently and identically distributed. The deterministic exponential model and the stochastic LC model make very different assumptions about population dynamics, but both lead to an asymptotic spatial TL. Why? We will answer this question at two different levels, first phenomenological, and second mechanistic.

Suppose the mean of population density changes (exactly or asymptotically) as a non-constant exponential function of time,

$$E(t) = Ae^{Bt}, \quad A > 0, B \neq 0. \quad (13)$$

Suppose also that the variance of population density behaves (exactly or asymptotically) as an exponential function of time,

$$V(t) = Ce^{Dt}, \quad C > 0, \text{ for any real } D. \quad (14)$$

Then  $t = (1/B) \log(E(t)/A)$  from (13), and substituting this expression for  $t$  into (14) gives, by elementary algebra,

$$\begin{aligned} V(t) &= Ce^{Dt} = C \exp\left(\left[\frac{D}{B}\right] \log\left(\frac{E(t)}{A}\right)\right) \\ &= C \left(\frac{E(t)}{A}\right)^{\frac{D}{B}} = CA^{-\frac{D}{B}} (E(t))^{\frac{D}{B}} = a (E(t))^b. \end{aligned} \quad (15)$$

This is a power-law relationship between the mean  $E(t)$  and the variance  $V(t)$ , equivalent to TL (3) with  $a = CA^{-\frac{D}{B}}$ ,  $b = D/B$ . This calculation assumes exact exponential behavior of the mean and the variance. The conclusion remains valid when the mean and variance change asymptotically exponentially.

Cohen et al. (2013) showed that the mean and the variance of population density in the LC model asymptotically change

exponentially. The mean and the variance of population density in the exponential model also asymptotically change exponentially (Appendix Theorem 4) with  $D = 2r_1, B = r_1, b = 2$  as  $t \rightarrow \infty$ . This shared feature explains why the exponential model, the LC model, and many other population models (Cohen, submitted for publication) lead to TL.

The exponential function (13) is not the unique route to a power-law relationship. An identical argument would work equally well for many other invertible functions. For example, if  $E(t) = At^B, A > 0, B \neq 0, V(t) = Ct^D, C > 0$ , then  $E(t)$  is invertible,  $t = \left(\frac{E(t)}{A}\right)^{\frac{1}{B}}$  and  $V(t) = C\left(\frac{E(t)}{A}\right)^{\frac{D}{B}} = CA^{-\frac{D}{B}}(E(t))^{\frac{D}{B}}$ , which is TL exactly as in (15).

This phenomenological answer leads to a question about mechanisms: why do both the exponential model and the LC model have asymptotically exponentially changing means and variances? The answer is that both are multiplicative with multipliers whose distribution does not change with time. In the LC model, the multipliers are independent and identically distributed random variables. In the exponential model, the multipliers are the time-invariant constants  $r_i$  in (1). It does not matter whether the multipliers have exactly the same distribution for all time. As long as the multipliers asymptotically converge sufficiently rapidly to a fixed distribution, the repeated multiplications give exponential change in the mean and the variance.

## 5. Discussion

The exponential model implies Taylor's law (TL) in the limit of large time. The limiting exponent  $b = 2$  of TL is independent of the population growth rate of the clones (provided the population growth rates are distinct), independent of the proportions of clones (provided the proportions are positive), and independent of whether the limit of time is taken toward  $+\infty$  or  $-\infty$ .

Viewing the exponential model from the perspective of TL gave a simple proof of the growth-rate theorem (GR) and new insight into the population-dynamic interpretation of the quantities in GR. Specifically, the mean population growth rate (10) is the first derivative with respect to time of the logarithm of the mean population density, and the variance of population growth rate (12) is the second time derivative of the mean population density. Unlike the approximate derivation of GR by Sato et al. (2003), our proof of GR is exact.

Our proof of GR could be interpreted to apply to any quantity  $N_i(t)$  that satisfies (2), and would imply that the rate of change of the mean of the "population growth rates"  $\{r_i\}$  equals the variance of the "population growth rates" of that quantity (see Edwards, 1987). Likewise, our derivation of an asymptotic spatial TL could be interpreted to apply to any quantity  $N_i(t)$  that satisfies (2), and not only to population density. For example, if  $N_i(t)$  were interpreted as the valuation (number of shares times market price) of the outstanding stock of company  $i$  at time  $t$ , then to the extent that (2) applied one should expect TL to apply to the valuations of companies' stocks and GR to apply to the rate of change of their mean "population growth rates" or percentage growth rates of valuation per unit of time. In fact, TL does describe some aspects of stock market transactions (Eisler et al., 2008), but the specific form of TL suggested here may not yet have been tested.

History dependence in multiplicative population growth models may range from complete (as in the deterministic exponential model) to absent (as in the LC model). Yet both models yield TL in the limit of large time. Considering the differences in underlying assumptions between the exponential model and the LC model, the value of the exponent  $b$  of TL and agreement with the log-linear form (3) of TL cannot shed light on the detailed dynamics of population growth.

In statistical physics, probabilistic models are often viewed as falling along a continuum of models from "quenched" to "annealed". A model is quenched if its defining parameters are random variables that are constant in time (they are "quenched", like the configuration of molecules in a piece of metal that was heated, then dropped in cold water). The population growth rates  $r_i$  of the exponential model are quenched, unchanging in time, though they may have been generated by some random variable. By contrast, in an annealed model, the defining parameters are random variables that evolve in or toward some equilibrium distribution (they are "annealed", like the configuration of molecules in a piece of metal that was heated, then allowed to cool slowly). The statistically independent "growth factors" of the LC model are annealed parameters. Both the quenched exponential model and the annealed LC model (Cohen et al., 2013) lead to TL in the limit of large time. So agreement with TL cannot shed light on whether the underlying process is quenched or annealed.

Taylor (1986, p. 25) described "the interpretation of the power-law relationship between mean and variance" as "one of the most contentious and potentially far-reaching" of the lines of research originating from the Rothamsted Insect Survey. In Taylor's view, the "question [is] whether the power law has stochastic roots as claimed by Anderson et al. (1982) or behavioural as claimed by Taylor" and colleagues in multiple publications. According to Anderson et al. (1982, p. 248), "The patterns of dispersion generated by simple models of population growth lead us to believe that observed relationships between variability in population abundance and average density, highlighted by the work of Taylor, are in general a simple and inevitable consequence of demographic and environmental stochasticity. It is not necessary to invoke explanations based on the behavioural tendencies of species to aggregate and migrate in order to...account for the approximately linear relationship between the logarithms of variance and mean abundance and for the slopes of such relationships lying on average between 1 and 2...". This stochastic perspective continues (e.g., Jørgensen et al., 2009, Cohen et al., 2013). By contrast, Arruda-Neto et al. (2012) wrote, in accord with Taylor's perspective: "The ubiquity of Taylor's power-law slopes in the interval  $1 < b < 2$  is intimately associated with long-range interactions among all the elements of a given system, plus negative interactions among species in a community...".

The exponential model indicates that complex behavioral interactions are not necessary to generate TL, though they may be sufficient. Perhaps the conflict between stochastic and behavioral models results from emphasis on different levels of description. The behavioral models have the potential to explain how the interactions of individuals could generate the population-level phenomenology summarized by the stochastic models.

The results obtained here raise questions for further research. First, the exponential model (2) may be written in vector-matrix form  $\vec{N}(t) = \vec{N}(0) \exp(Rt)$  where  $\vec{N}(t)$  is an  $n$ -element row vector,  $R$  is an  $n \times n$  diagonal matrix with diagonal elements  $r_1 > r_2 > \dots > r_n$ , and  $t$  is a real scalar. It assumes no migration between clones or subpopulations. Now suppose migration occurs. Mathematically, let  $Q$  be an  $n \times n$  matrix with non-negative elements (rates of migration from clone  $i$  to clone  $j$ ) off the main diagonal and zero row sums (so that  $Q$  has the form of the intensity matrix of a continuous-time Markov chain). Does the dynamical system  $\vec{N}(t) = \vec{N}(0) \exp([R + Q]t)$  satisfy an asymptotic TL in the limit of large positive or negative time, and if so, does  $b(t) \rightarrow 2$ ? Second, does a growth-rate theorem apply to this more general model, i.e., is the rate of increase of the growth rate of total population proportional to the variance of the growth rates of the clones or subpopulations, either exactly for all time or asymptotically for large times? Third, in the version of Fisher's Fundamental Theorem of Natural Selection (1958) stated and proved by Ewens

(1989), fitnesses are rescaled so that only the relative frequencies of genes and genotypes are considered. In effect, every generation has the same size. If, instead, fitnesses are interpreted as factors of absolute change from one generation to the next, can an exact or asymptotic TL be proved for the mean and variance of the absolute frequency (abundance) of different genes or genotypes?

I conclude with some remarks on the provenance of GR. Crow and Kimura (1970, p. 10) proved a continuous-time version of GR with interpopulation selection only and called it a rather special example of Fisher's Fundamental Theorem of Natural Selection. Fisher's Fundamental Theorem is based on the genetic make-up of a single population and relies heavily on the concept of the additive genetic variance in fitness in that population (Edwards, 2000). Only in simplified models of the Fundamental Theorem with no selection and epistasis is there a formal mathematical similarity with GR, which has no genetic content. Since the definitive explication of Fisher's Fundamental Theorem by Ewens (1989), it seems no longer acceptable to refer to GR as a simplified form of Fisher's Fundamental Theorem (Edwards, 1994; Plutynski, 2006), notwithstanding earlier (Crow, 1955, p. 58; Li, 1955, pp. 272–273; Crow and Kimura, 1970, p. 10) and some continuing (Sato et al., 2003) confusion on this point.

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**Appendix. Proofs of mathematical claims**

All the following results are in the context and the notation of the exponential model.

**Theorem 1.**  $d \log E(N(t))/dt$  is positive for all  $t$  if all  $r_i \geq 0$ , negative for all  $t$  if all  $r_i \leq 0$ , and zero for exactly one value of  $t$  if there exist  $i \neq j$  such that  $r_i r_j < 0$ .

**Proof.** In the identity  $(d \log E(N(t)))/dt = E'(N(t))/E(N(t))$ , the denominator,  $E(N(t)) = \sum_{i=1}^n p_i N_i(0) e^{r_i t}$ , must be positive for all finite  $t$ . If  $r_i \geq 0$  for all  $i$ , the numerator  $\sum_{i=1}^n p_i r_i N_i(0) e^{r_i t}$  cannot vanish for any  $t$  since every term in it must be non-negative for all  $t$  and (since  $n > 1$ ) at least one term must be positive for all  $t$ . Similarly, if  $r_i \leq 0$  for all  $i$ , the numerator  $\sum_{i=1}^n p_i r_i N_i(0) e^{r_i t}$  cannot vanish for any  $t$  since every term in it must be non-positive for all  $t$  and (since  $n > 1$ ) at least one term must be negative for all  $t$ . If  $r_i = 0$ , then  $p_i r_i N_i(0) e^{r_i t}$  vanishes and at most one term can vanish. So  $\sum_{i=1}^n p_i r_i N_i(0) e^{r_i t} = 0$  at time  $t$  if and only if  $r_i > 0$  for at least one  $i$  and  $r_i < 0$  for at least one  $i$  and

$$-\sum_{i:r_i < 0} p_i r_i N_i(0) e^{r_i t} = +\sum_{i:r_i > 0} p_i r_i N_i(0) e^{r_i t}. \tag{16}$$

The left side of (16) is a strictly decreasing function of  $t$ , while the right side of (16) is a strictly increasing function of  $t$ , so equality can hold in (16) for at most one  $t$ . Moreover, equality must hold in (16) for one  $t$  if  $r_i < 0$  for one or several clones  $i$  and  $r_i > 0$  for one or several clones  $i$ . For as  $t \rightarrow -\infty$ , the left side of (16) becomes arbitrarily large and the right side of (16) becomes arbitrarily close to 0 from above, while as  $t \rightarrow +\infty$ , the left side of (16) becomes arbitrarily close to 0 from above and the right side of (16) becomes arbitrarily large, so the two sides must coincide exactly once.  $\square$

We shall use Lagrange's identity (Steele, 2004, p. 39). For real numbers  $a_1, \dots, a_n, b_1, \dots, b_n$ ,

$$\sum_{i=1}^n a_i^2 \sum_{i=1}^n b_i^2 - \left( \sum_{i=1}^n a_i b_i \right)^2 = \sum_{1 \leq i < j \leq n} (a_i b_j - a_j b_i)^2.$$

If not all  $b_j = 0$ , then the right side is zero if and only if there exists a constant  $c$  such that  $a_i = c b_i, i = 1, \dots, n$ .

**Theorem 2.** The variance of population density is the mean squared difference in population density of all pairs of clonal types weighted by the proportions of clonal types in the population:  $\text{Var}(N(t)) = \sum_{1 \leq i < j \leq n} p_i p_j (N_i(t) - N_j(t))^2$ .

**Proof.** Use Lagrange's identity with  $a_i = \sqrt{p_i}, b_i = \sqrt{p_i} N_i(0) e^{r_i t}$ . Then  $\sum_{i=1}^n a_i^2 = \sum_{i=1}^n p_i = 1, \sum_{i=1}^n b_i^2 = \sum_{i=1}^n p_i (N_i(0))^2 e^{2r_i t} = E((N_i(t))^2)$ , and  $\sum_{i=1}^n a_i b_i = \sum_{i=1}^n p_i N_i(0) e^{r_i t} = E(N(t))$ . Hence from (6),  $\text{Var}(N(t)) = E((N_i(t))^2) - [E(N(t))]^2 = \sum_{1 \leq i < j \leq n} (a_i b_j - a_j b_i)^2 = \sum_{1 \leq i < j \leq n} p_i p_j (N_i(t) - N_j(t))^2$ .  $\square$

**Theorem 3.**  $\text{Var}(N(t)) > 0$  except possibly for at most one value of  $t$ .

**Proof.** By assumption,  $p_i \neq 0, i = 1, \dots, n$ . Suppose there exists a constant  $c$  such that  $a_i = c b_i, i = 1, \dots, n$ . Equivalently,  $1 = c N_i(0) e^{r_i t}$  hence  $c \neq 0$  hence  $1/c = N_i(0) e^{r_i t}, i = 1, \dots, n$ , hence for all  $i \neq j, N_i(0) e^{r_i t} = N_j(0) e^{r_j t}$  or  $N_i(0)/N_j(0) = \exp((r_j - r_i)t)$ . Because  $r_i \neq r_j$  for all  $i \neq j, \exp((r_j - r_i)t)$  is strictly monotone (increasing or decreasing) and can equal  $N_i(0)/N_j(0)$  for at most one value of  $t$ . Hence  $a_i = c b_i, i = 1, \dots, n$  can hold for at most one value of  $t$ . Hence  $\text{Var}(N(t)) > 0$  except possibly for at most one value of  $t$ .  $\square$

An example when  $\text{Var}(N(t)) = 0$  is  $t = 0$  and  $N_1(0) = \dots = N_n(0) > 0$ .

**Theorem 4.** In the limit as  $t \rightarrow \pm\infty$ , the spatial log-linear TL (4) holds with  $b = 2$ . This limit  $b = 2$  is independent of  $N_i(0), r_i$  and  $p_i, i = 1, \dots, n$ , when the  $r_i$  are all distinct and the  $p_i$  and  $N_i(0)$  are all positive.

**Proof.** We calculate  $\lim_{t \rightarrow \pm\infty} b(t)$ . The assumption that  $r_1 > \dots > r_n$  implies that  $\exp(tr_1) > \dots > \exp(tr_n)$  if  $t > 0$  and that  $\exp(tr_1) < \dots < \exp(tr_n)$  if  $t < 0$ . Combining (10), (9) and (5) gives

$$\frac{d \log E(N(t))}{dt} = \frac{E'(N(t))}{E(N(t))} = \frac{\sum_{i=1}^n p_i r_i N_i(0) e^{r_i t}}{\sum_{i=1}^n p_i N_i(0) e^{r_i t}}. \tag{17}$$

We proved above that  $d \log E(N(t))/dt$  is positive for all  $t$  if all  $r_i \geq 0$ , negative for all  $t$  if all  $r_i \leq 0$ , and is zero for exactly one value of  $t$  if there exist  $i \neq j$  such that  $r_i r_j < 0$ . Now divide the numerator and denominator of (17) by the largest exponential factor  $\exp(tr_1)$  (if  $t > 0$ ) or  $\exp(tr_n)$  (if  $t < 0$ ), and pass, respectively, to the limits  $+\infty$  or  $-\infty$  to find

$$d \log E(N(t))/dt \rightarrow r_1 \text{ as } t \rightarrow +\infty, \tag{18}$$

$$d \log E(N(t))/dt \rightarrow r_n \text{ as } t \rightarrow -\infty.$$

From (6),

$$\frac{d \log \text{Var}(N(t))}{dt} = \frac{\frac{d \text{Var}(N(t))}{dt}}{\text{Var}(N(t))} = 2 \left[ \frac{\left( \sum_{i=1}^n p_i r_i (N_i(0))^2 e^{2r_i t} \right) - \left( \sum_{i=1}^n p_i r_i N_i(0) e^{r_i t} \right) \left( \sum_{i=1}^n p_i N_i(0) e^{r_i t} \right)}{\left( \sum_{i=1}^n p_i (N_i(0))^2 e^{2r_i t} \right) - \left( \sum_{i=1}^n p_i N_i(0) e^{r_i t} \right)^2} \right]. \tag{19}$$

Divide the numerator and denominator of (19) by the largest exponential factor  $\exp(2tr_1)$  or  $\exp(2tr_n)$ , and

$$\begin{aligned} d \log \text{Var}(N(t))/dt &\rightarrow 2(p_1 - p_1^2)r_1/(p_1 - p_1^2) = 2r_1 \\ &\text{as } t \rightarrow +\infty, \\ d \log \text{Var}(N(t))/dt &\rightarrow 2(p_n - p_n^2)r_n/(p_n - p_n^2) = 2r_n \\ &\text{as } t \rightarrow -\infty. \end{aligned} \tag{20}$$

Substituting (17) and (19) into the definition (7) and taking the limit gives

$$\lim_{t \rightarrow \pm\infty} b(t) = 2 = b. \quad \square \tag{21}$$

**Theorem 5.** If  $r_i$  are all distinct,  $p_i$  are all positive,  $\sum p_i = 1$ , and  $t \in (-\infty, +\infty)$ , then  $\text{Var}(r(t)) > 0$ .

**Proof.** Multiply (12) by  $(E(N(t)))^2$  to get

$$\text{Var}(r(t)) (E(N(t)))^2 = E''(N(t))E(N(t)) - (E'(N(t)))^2. \tag{22}$$

So  $\text{Var}(r(t)) > 0$  if and only if the right side of (22) is positive. But from (5), (9), and (11),

$$\begin{aligned} &E''(N(t))E(N(t)) - (E'(N(t)))^2 \\ &= \left( \sum_{i=1}^n p_i N_i(0) r_i^2 e^{r_i t} \right) \left( \sum_{i=1}^n p_i N_i(0) e^{r_i t} \right) \\ &\quad - \left( \sum_{i=1}^n p_i N_i(0) r_i e^{r_i t} \right)^2. \end{aligned} \tag{23}$$

By Lagrange's identity (Steele, 2004, p. 39) with  $a_i = \sqrt{p_i N_i(0) r_i^2 e^{r_i t}}$ ,  $b_i = \sqrt{p_i N_i(0) e^{r_i t}}$ , we have  $a_i b_i = p_i r_i N_i(0) e^{r_i t}$  and

$$\begin{aligned} &\text{Var}(r(t)) (E(N(t)))^2 \\ &= \sum_{1 \leq i < j \leq n} \left( \sqrt{p_i N_i(0) r_i^2 e^{r_i t}} \sqrt{p_j N_j(0) e^{r_j t}} \right. \\ &\quad \left. - \sqrt{p_j N_j(0) r_j^2 e^{r_j t}} \sqrt{p_i N_i(0) e^{r_i t}} \right)^2 \\ &= \sum_{1 \leq i < j \leq n} p_i N_i(0) p_j N_j(0) e^{(r_i+r_j)t} (r_i - r_j)^2 \\ &= \sum_{1 \leq i < j \leq n} p_i N_i(t) p_j N_j(t) (r_i - r_j)^2. \end{aligned} \tag{24}$$

This is the population-weighted mean squared difference of population growth rate over all pairs of types of clones. Because all  $p_i N_i(t) > 0$  and  $r_i \neq r_j$  if  $i \neq j$  by assumption, the right member of (24) is positive, hence  $\text{Var}(r(t)) > 0$ .  $\square$

**Theorem 6.** The rate of increase per capita  $(E'(N(t)))/E(N(t)) = d \log E(N(t))/dt$  is strictly increasing with  $t$ . The mean population growth rate is strictly increasing with  $t$ .  $\log E(N(t))$  is strictly convex.

**Proof.** We prove the three statements in the theorem in sequence. First,  $d(d \log E(N(t))/dt)/dt = d^2 \log E(N(t))/dt^2 = \text{Var}(r(t)) > 0$ , where the inequality is proved in the previous theorem. Second, by GR,  $dE(r(t))/dt = \text{Var}(r(t)) > 0$  so the mean population growth rate is strictly increasing with  $t$ . Third,  $\log E(N(t))$  is strictly convex if and only if its second derivative with respect to  $t$  is positive, and that follows from (12) and  $\text{Var}(r(t)) > 0$ .  $\square$

**Theorem 7.** The variance of population growth rate is

$$\text{Var}(r(t)) = \frac{\sum_{1 \leq i < j \leq n} p_i N_i(t) p_j N_j(t) (r_i - r_j)^2}{\left( \sum_{i=1}^n p_i N_i(t) \right)^2}. \tag{25}$$

**Proof.** Combine (5) and (24).  $\square$

**Theorem 8.** The variance of population growth rate and the rate of change of the variance of population growth rate approach zero for large (positive or negative) time.

**Proof.** We use the abbreviations  $E, E', E'', E'''$  for, respectively, the mean population density (5), its first derivative (9), its second derivative (11), and its third derivative

$$E'''(N(t)) = \sum_{i=1}^n p_i N_i'''(t) = \sum_{i=1}^n p_i N_i(0) r_i^3 e^{r_i t}. \tag{26}$$

From (12), we write the variance of population growth rate as

$$\text{Var}(r(t)) = \frac{E \cdot E'' - (E')^2}{E^2}. \tag{27}$$

Divide the numerator and the denominator of the fraction on the right by  $\exp(2r_1 t)$ . As  $t \rightarrow \infty$ , only the leading terms will not vanish. In the denominator, the leading term will be  $(p_1 N_1(0))^2 > 0$ . In the numerator, the leading term will be  $(p_1 r_1 N_1(0))^2 - (p_1 r_1 N_1(0))^2 = 0$ . As  $t \rightarrow -\infty$ , the same argument applies to clone  $n$  instead of clone 1. From the time derivative of (12) or (27), the rate of change of the variance of population growth rate is the third derivative of the log mean population growth rate:

$$\frac{d \text{Var}(r(t))}{dt} = \frac{d^3 \log E(N(t))}{dt^3} = \frac{E^2 E''' - 3E E'' + 2(E')^3}{E^3}. \tag{28}$$

By the same argument, as  $t \rightarrow \infty$ , in the denominator, the leading term will be  $(p_1 N_1(0))^3 > 0$ . In the numerator, the leading term will be  $3(p_1 r_1 N_1(0))^3 - 3(p_1 r_1 N_1(0))^3 = 0$ . A similar argument applies to clone  $n$  as  $t \rightarrow -\infty$ .  $\square$

Numerical examples show that  $d \text{Var}(r(t))/dt$  may be positive or negative for finite  $t$ .

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