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Taylor's law and abrupt biotic change in a smoothly changing environment

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Abstract Taylor's law (TL), widely verified in empirical ecology, states that the variance of population density approximates a power function of the mean population density, with exponent denoted b. A model of multiplicative increments in population density, where the increments are determined by a Markovian environment, predicts TL with an explicit formula for b. We give a simple theoretical example where, unexpectedly, smooth changes in environmental autocorrelation lead to an abrupt, infinite discontinuity in b. As the daily probability of change in environmental state increases from 0 to 1, b rises from 2 slowly at first, then explodes to $+\infty$ when the population becomes critical, drops to $-\infty$, and rises again to 2. In this model, an exponent b of large magnitude (positive or negative) signals the proximity of a population's criticality and of a singularity in b. A comparable real-world singularity in b could adversely affect fisheries, forestry, agriculture, conservation, and public health.

Keywords Markovian environment · Regime change · Power spectra · Population density · Fluctuation scaling

Introduction

Earth's climate (Broecker 2003) and biota (Barnosky et al. 2012) have experienced what Broecker (2003, p. 1522) described as "large and abrupt changes so richly recorded in ice and sediment." Sometimes, an abrupt biotic change resulted from an abrupt environmental change, such as an asteroid impact or volcanic eruption. Sometimes, an abrupt biotic change was a non-linear response to a smooth environmental change (Scheffer et al. 2001). For example (deMenocal et al. 2000), the vegetation cover of much of the Sahara disappeared abruptly ~5,700–5,200 years before the present, at the end of the so-called African Human Period (AHP), though the transition was more gradual in some places. The AHP ended when summer monsoons dropped off as a result of a smooth decline in summer insolation, a decline driven by the precession (wobble) of the Earth's axis. The abruptness, timing, magnitude, and spatial localization of the biotic changes in different parts of northern Africa remain under investigation (deMenocal and Tierney 2012).

Some dynamical systems exhibit recognizable precursors of dramatic shifts in state or behavior (Scheffer et al. 2009; D'Odorico et al. 2013) and some do not (Hastings and Wysham 2010). In a simplified model of the thermohaline circulation system in the North Atlantic, Kleinen (2005) showed that a change in the flux of fresh water into the ocean could push the thermohaline circulation to a saddle-node bifurcation. In this model, as the freshwater flux approaches its critical value at the bifurcation point, the power spectrum of the circulation strength shifts upward. Consequently, the total variance of circulation strength (the area under the spectral density function) increases, mainly at low frequencies (Kleinen 2005, p. 18, his Fig. 2.2). In this theoretical example, as the freshwater flux approaches its critical value, the system gives premonitory signals of increasing variance in the circulation strength. The variance increases because of increased amplitudes of oscillations of very low frequencies. Such increases in the amplitudes of low-frequency oscillations would be very difficult to detect from short-term observations. In the real world, it could be difficult to identify with assurance the precursors of dramatic shifts in the thermohaline circulation.

The causes, necessary and sufficient conditions, leading indicators, and consequences of abrupt biotic responses to

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smooth environmental changes remain insufficiently understood (Scheffer and Carpenter 2003; Russell et al. 2012) and new ideas continue to be proposed (Lorenzo and Ohman 2013; Doney and Sailley 2013; D'Odorico et al. 2013). In this context, we investigated theoretically the effect on Taylor's law (TL), one of the most widely verified empirical patterns in ecology, of a gradual, continuous increase in the daily probability of a change in the environment. This change, we show, is equivalent to an increase in the slope of the environmental power spectral density from the negative slope of a reddened power spectrum (dominated by low frequencies of environmental change) to the zero slope of a white (flat) power spectrum and then the positive slope of a blue power spectrum (dominated by high frequencies of environmental change).

We show here, apparently for the first time, that a dramatic and abrupt shift (a singularity) can occur in the slope b of the log-linear form of TL (which is also the exponent b of the power-law form of TL) as a consequence of a sufficiently large, gradual, and continuous increase or decrease in the temporal autocorrelation of environmental states. The singularity occurs when the population becomes critical (the average population density neither declines towards extinction nor explodes in the long run). Quantifiable precursors of population criticality and of a singularity in b are values of b of large magnitude, positive or negative.

For the sake of transparency, and to avoid an extensive mathematical apparatus that underlies the result presented here, we focus on a highly idealized, simplified abstraction of real ecological dynamics, and on a simple example of the abstraction. This strategy of exploration and exposition identifies phenomena not previously suspected, and is therefore useful. But this example is not intended to replace subsequent, more realistic, more complex modeling, data analysis, and quantitative testing. By analogy, understanding a deterministic model of exponential population growth is useful, even though no biological population can grow exponentially forever.

This work forms part of a large and long-flowing stream of research on population dynamics in randomly varying environments, which includes the early Pimm and Redfearn (1988) and Lawton (1988) and the recent Schreiber et al. (2011) and Evans et al. (2013).

Material and methods

(a) Taylor's power law of fluctuation scaling

Taylor's law presumes the following framework of observations. Suppose we have a large number O of observations of the density (number of individuals per unit of area or volume) of a set of populations. Suppose these observations are partitioned into B blocks. (A block is simply a subset of the observations, but the term "block" is conventional in the statistical theory of experimental design.) Suppose the blocks are labeled $j=1, \ldots, B$ and the number of observations in block j is n_j, so that $n_1 + \ldots + n_B = O$. For every block j, we calculate the sample mean m_j and the sample variance v_j of the observations in block j. Since there are B blocks, we have B pairs (m_j, v_j). Suppose none of the means and none of the variances is zero, and all are finite. Then we may plot these B points on log–log coordinates.

Taylor (1961, 1984) and colleagues (e.g. Taylor et al. 1980) observed that, in many species, the logarithm of the sample variance was an approximately linear function of the logarithm of the sample mean: for some $a > 0$, $\log(v_j) \approx \log(a) + b \times \log(m_j)$. This relationship, equivalent to the power law, $v_j \approx a(m_j)^b$, was previously observed in the spatial distribution of *Ribes* by Fracker and Brischle (1944), but because Taylor et al. emphasized its generality and importance, it became known as Taylor's law (henceforth TL). Most empirical tests of TL have ignored the sampling error in $\log(m_j)$ when fitting a linear regression by the usual least-squares formulas. For large enough numbers n_j of observations per block and a sufficiently wide range of values of $\log(m_j)$, the error introduced by this procedure may not be serious.

TL has multiple forms depending on how the blocks and samples within each block are defined. For example, suppose the observations are organized in a rectangular table with R rows and C columns, and suppose each row is a sampling site or quadrat and each column is a census date. In a spatial TL, each block is one census date, i.e., the observations in that block are the elements in one column of the data matrix, and the mean and variance of density are calculated over different sites (rows) at a given time; here, $B = C$. Alternatively, with the same array of data, in a temporal TL, each row is a block, and the mean and variance of density are calculated over different censuses (columns) at a given site; here, $B = R$. In a hierarchical spatial TL, each quadrat is subdivided into smaller subplots, and the mean and variance of density are calculated over the subplots within each quadrat. In a hierarchical temporal TL, each block is a longer time interval (e.g., decade) and each observation within that block refers to density observed in a shorter time interval (e.g., a year) within each decade. There are other forms of TL as well.

In its various forms, TL has been verified in hundreds of species (Eisler et al. 2008) including, recently, bacteria in laboratory experiments (Ramsayer et al. 2012; Kaltz et al. 2012) and trees in a temperate forest (Cohen et al. 2012a, 2013). TL also describes the relation of variance to mean in populations of stem cells (Klein and Simons 2011), stock market trading, precipitation, packet switching on the Internet, measles cases, and the occurrence of single nucleotide polymorphisms (see the review by Eisler et al. 2008).

Here, we focus on a spatial TL. In theoretical models of TL, the sample mean and sample variance are replaced by the population mean and population variance, respectively. A spatial TL applies exactly to the population moments, by definition, if and only if there exist real constants $a>0$ and b such that the population mean $E(N(t))$ and the population variance $Var(N(t))$ of the density $N(t)$ satisfy, at every time t,

$$\log\ Var(N(t)) – b\ \log\ E(N(t)) = \log\ a. \tag{1}$$

Here, the approximate equality (≈) in the empirical form of TL is replaced by exact equality (=). We emphasize that $E(N(t))$ in Eq. (1) pertains to an average over space (ensemble average) at a given time t, and $Var(N(t))$ pertains to a variance over space at a given time t, *not* to an average or variance over time. TL applies in the limit as t gets large, by definition, if and only if there exist real constants $a>0$ and b such that

$$\lim_{t\to\infty}[\log\ Var(N(t)) – b\ \log\ E(N(t))] = \log\ a. \tag{2}$$

If TL holds for any base of logarithms, it holds for all choices. For the following mathematical analysis, $\log = \log_e$. The value of b remains the same for any choice of the base of logarithms and regardless of the units in which $N(t)$ is measured (e.g., cells per cubic millimeter or cells per cubic kilometer), though the value of $\log\ a$ changes. Hence attention here, and in much work on TL, focuses on the slope b rather than on the intercept.

(b) Example

In this example, we first create a model of an environment and then create a model of a population whose dynamics depend on this environment. This population has no stage-, age-, sex-, or other structure; it is "single-type." For expository convenience, we select the unit of time in this model as 1 day.

In defining the model of the environment, we distinguish between "climate" (a pattern of weather) and "weather" (the conditions on a particular day). We model a climate as a sequence of transitions among different states of weather, and we model these transitions by using a finite-state, homogeneous Markov chain (the Appendix gives details). Suppose a climate has two states of weather. State 1 represents "good weather" and state 2 represents "bad weather." Assume that the probability that tomorrow's weather will differ from today's weather is λ, so the probability that tomorrow's weather will be the same as today's is $1-\lambda$, where $0\leq\lambda\leq1$. Assume that initially (at time 0), good weather occurs with probability $\pi_1=1/2$ and bad weather occurs with probability $\pi_2=1/2$. We summarize the transition probabilities $P(\lambda)$ and the initial probability distribution π of the climate in matrix form:

$$P(\lambda) = \begin{pmatrix} 1-\lambda & \lambda \\ \lambda & 1-\lambda \end{pmatrix}, \pi = \begin{pmatrix} 1/2 \\ 1/2 \end{pmatrix}. \tag{3}$$

Then it is easy to check that $P(\lambda)\pi = \pi$, regardless of λ. This means that in every climate, no matter what the value of λ, $\pi_1=1/2$ and $\pi_2=1/2$ is the stationary probability distribution of the weather, i.e., these probabilities of good and bad weather, respectively, are the same for all times $t=0, 1, 2, \ldots$. Intuitively, that is because the transition from good to bad weather is just as likely as the reverse transition, so by symmetry, the two states of weather are equally likely at every time.

Now we add to this model of a Markovian environment a highly simplified model of multiplicative population dynamics. Assume that a population starts with some positive initial population density $N(0)>0$. Since we will be interested only in long-run growth rates, the initial population density has no effect, provided it is positive, so no generality is lost if we assume $N(0)=1$. Assume that in good weather, the population density increases by a factor of $A(t)=d_1>1$. Assume that in bad weather, the population density falls by a factor of $A(t)=d_2<1$. We chose $d_1=2$, so that the population density doubles in good weather, and $d_2=1/4$, so that the population is reduced to 1/4 its previous density in bad weather.

The choices $d_1=2$ and $d_2=1/4$ guarantee that the average multiplicative growth factor is $E(A(t))=(2+1/4)/2=9/8>1$ but that $E(\log A(t))=(\ln 2+\ln(1/4))/2=(\ln 2–2 \ln 2)/2=(-\ln 2)/2<0$.

An elementary (but long) calculation shows that, regardless of the values of d_1 and d_2, the first-order autocorrelation of the time series $\{A(t)\}$ is exactly $p_{11}(\lambda)–p_{12}(\lambda)=1–2\lambda$, which is also the second eigenvalue of $P(\lambda)$ (the first eigenvalue being 1). When $\lambda\approx 0$, the autocorrelation is near 1 and the power spectrum of $\{A(t)\}$ is red. The climate has long runs (sojourn times) of good weather (the population grows by a factor of $A(t)=d_1>1$ on each such day), and the climate also has long sojourn times of bad weather (the population falls by a factor of d_2 on each such day), and the weather changes rarely from good to bad or vice versa. When $\lambda\approx 1$, the autocorrelation is near -1 and the power spectrum is blue. Two days in a row rarely have the same weather.

When $\lambda=1/2$, the autocorrelation is 0, successive values of $A(t)$ are independent, and the power spectrum is white. This special case of serial independence of successive values of

$A(t)$ is assumed in the model of Lewontin and Cohen (1969) [no relation to the present author]. The Lewontin–Cohen model cannot be used to investigate how differences in environmental autocorrelation affect TL because its environmental autocorrelation is always 0. From Eq. (3),

$$\begin{aligned}\lim_{t\to\infty}(1/t)\ \log\ E(N(t)) &= \lim_{t\to\infty}(1/t)\ [\log\ E(N(0)) \\ &\quad + \log\ E(A(0)) + \cdots + \log\ E(A(t-1))] \\ &= \log\ E(A(0)) > 0. \end{aligned} \tag{4}$$

The mean population density (averaged over an infinite ensemble of infinitely precise simulations or bacterial dishes of infinite capacity) at time t diverges to +∞ with increasing time t, because some of those realizations will have long runs of good weather. But

$$\begin{aligned}\lim_{t\to\infty}(1/t)E(\log\ N(t)) &= \lim_{t\to\infty}(1/t)\ [E(\log\ N(0)) \\ &\quad + E(\log\ A(0)) + \cdots + E(\log\ A(t-1))] \\ &= E(\log\ A(0)) < 0, \end{aligned} \tag{5}$$

so almost every realization of the process (trajectory of population density) approaches (but never reaches) 0 with increasing time t. This apparently paradoxical situation was discussed extensively by Lewontin and Cohen (1969).

For each fixed value of λ from 0 to 1, we calculated an exact, explicit formula for the log-linear TL slope $b = b(\lambda)$. This method is known as "comparative statics" in mechanics and economics. It assumes λ is permanently fixed at different values in different climates and compares the TL parameter $b = b(\lambda)$ in different climates. When we speak of the effects of changes in λ, we are comparing the outcomes in the limit of large time t in different climates in which λ is constant at different values. This method approximates usefully what should be expected if λ, rather than being assumed constant, changed much more slowly than $(1/t)$ log $Var(N(t))$ converges to a linear function of $(1/t)$ log $E(N(t))$. We summarize the results in the following section and give detail in the Appendix.

Results: a singularity in the slope of Taylor's law

In terms of sample paths (or infinitely precise simulations with no underflow and no overflow) of the population density $N(t)$ in this model generally (under broad conditions) and in this example, the spatial mean density $E(N(t))$ grows or declines exponentially or is constant with increasing time t. Thus log $E(N(t))$ is a linear function of t and log $r_1(\lambda)$ is the slope of that linear function. Likewise, the spatial variance of density $Var(N(t))$ grows or declines exponentially or is constant with increasing time t. Thus log $Var(N(t))$ is a linear function of t and log $r_2(\lambda)$ is the slope of that linear function.

For each possible climate with a fixed probability λ of a change in the weather from 1 day to the next, Fig. 1a shows the limiting exponential growth rate per unit time of the mean density, $r_1(\lambda)$, and the limiting exponential growth rate per unit time of the variance of population density, $r_2(\lambda)$. These quantities are defined mathematically in (9) (Appendix) and are calculated explicitly there for this example. Both $r_1(\lambda)$ and $r_2(\lambda)$ are positive for all $0 \le \lambda \le 1$, but are greater than 1 for λ near 0 and less than 1 for λ near 1. Consequently, the slopes of both log $E(N(t))$ and log $Var(N(t))$ as functions of t are positive for λ near 0 and negative for λ near 1. Since the slopes are continuous functions of λ, they must pass through 0 for some value of λ between 0 and 1. The surprising singularity happens precisely where the slope of log $E(N(t))$ passes through 0, as now described in further detail.

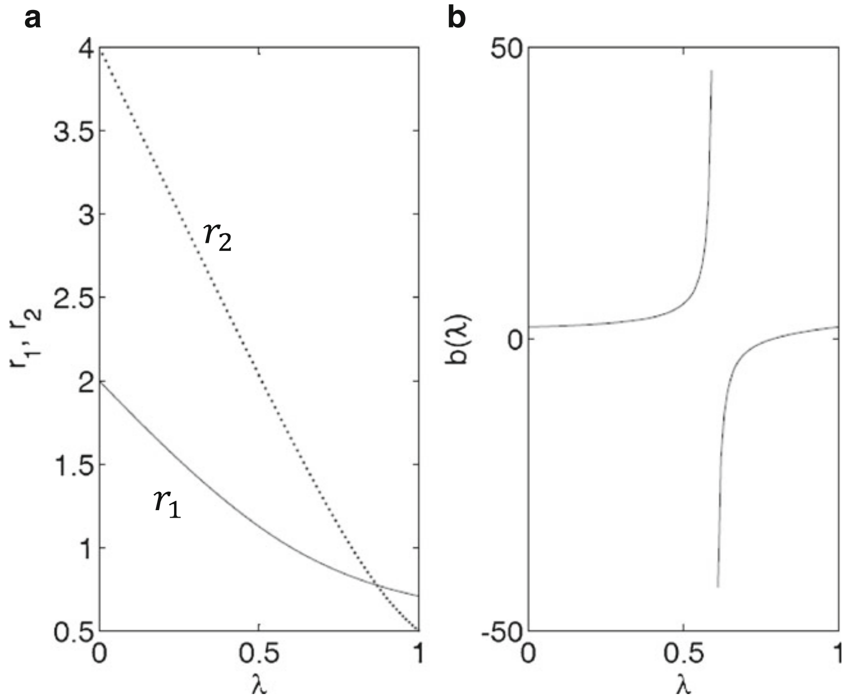
Figure 1b shows $b(\lambda)$, the limiting value at large time of the log-linear TL slope b in Eq. (2). It is derived from the two curves in Fig. 1a as the ratio of their logarithms (see Eq. (5)), $b(\lambda) = \log r_2(\lambda)/\log r_1(\lambda)$. This formula shows that $b(\lambda)$ is a ratio of the two slopes described in the previous paragraph. We now describe the behavior of $r_1(\lambda)$ and $r_2(\lambda)$ and $b(\lambda)$ from left to right as λ increases from 0 to 1.

When $\lambda=0$, the weather never changes so the only randomness is in the initial conditions: does day 0 have good weather or bad? In this case, the long-run rate of growth of the mean density is $r_1(0)=2$, meaning that, in the long run, the mean density doubles every day. Half of all realizations, or sample paths, are stuck initially and permanently with bad weather. For them, the density is multiplied by $d_2=1/4$ every day. These realizations approach 0 but never vanish. The other half of all realizations have good weather initially and permanently, and the density in those realizations doubles at every time step because $d_1=2$. So the mean density (over all realizations, including the half of all realizations that approach zero) also asymptotically doubles at every time step, and that mean is just half of the density in the realizations with permanent good weather. Hence the absolute difference between the mean and the minimum density (as well as the absolute difference between the mean and the maximum density) asymptotically doubles at every time step. So the variance, which is the average of the *squared* deviations from the mean, asymptotically quadruples with each time step.

When $0<\lambda<1$, both $r_1(\lambda)$ and $r_2(\lambda)$ decrease with increasing λ (Fig. 1a). A plot of log $E(N(t))$ as a function of t has slope 2 when $\lambda=0$, and this slope, log $r_1(\lambda)$, decreases as λ increases. When $\lambda=3/5$, the slope of log $E(N(t))$ as a function of t is exactly 0. Hence, for large t, changes in log $E(N(t))$ are negligible compared to t, and a plot of log $E(N(t))$ as a function of t is asymptotically flat when $\lambda=3/5$.

Meanwhile, a plot of log $Var(N(t))$ as a function of t has slope 4 when $\lambda=0$, and this slope, log $r_2(\lambda)$, also decreases as

Fig. 1 **a** The long-run rate of growth r_1 of mean population density (*solid curve*) and the long-run rate of growth r_2 of the variance of population density (*dotted curve*) and **b** the slope $b(\lambda)$ of Taylor's law (*solid curves*) depend strongly on the daily probability λ of change in the weather from good to bad or from bad to good. **a** The larger the probability λ, the smaller r_1 and r_2. **b** As λ increases, the slope $b = b(\lambda)$ of TL increases slowly at first, then more rapidly, and then explodes when the mean population density becomes critical at $\lambda=3/5$, i.e., $r_1(3/5)=1$ or $\log r_1(3/5)=0$, so the denominator of Eq. (8) is 0 when $\lambda=3/5$. When $\lambda>3/5$, $b(\lambda)$ increases rapidly through negative values and more slowly through positive values toward 2



λ increases. But when $\lambda=3/5$, the slope $\log r_2(\lambda)$ of $\log Var(N(t))$ as a function of t is still positive, meaning that the variance of $N(t)$ is still growing exponentially (or $\log Var(N(t))$ is still growing linearly) while $\log E(N(t))$ is changing negligibly compared to t. In this situation, when $\lambda=3/5$, if you try to regress a linearly changing quantity $\log Var(N(t))$ as a function of an essentially unchanging quantity $\log E(N(t))$, you get an infinite slope. This explains why the slope $b(\lambda)$ of TL becomes singular at $\lambda=3/5$. As $\lambda\rightarrow 3/5$ from below, $b(\lambda)$ diverges to $+\infty$ because $\log r_1(\lambda)$, the denominator of $b(\lambda)$, approaches 0, and *not* because the variance explodes.

In the vicinity of $\lambda=3/5$, a very small difference in λ (which implies a very small difference in the autocorrelation) may alter $b(\lambda)$ dramatically and discontinuously. A very slight deviation of λ below 3/5 makes the regression slope $b(\lambda)$ extremely positive. A very slight deviation of λ above 3/5 makes the regression slope $b(\lambda)$ extremely negative.

In the interval $0\leq\lambda<3/5$, the increase of $b(\lambda)$ with increasing λ means that any given fractional increase in mean density is associated (in the long term) with an ever greater fractional increase in the variance of density as λ increases.

The singularity in $b(\lambda)$ and the large absolute values of $b(\lambda)$ show (Fig. 1b) that the relation of variance to mean population density described by TL can be exquisitely sensitive to smooth changes in the pattern of environmental variability, even when the mean and variance of density separately are well behaved and changing smoothly (Fig. 1a). The sharp singularity at $\lambda=3/5$ looks just as sharp on a plot of $\log b(\lambda)$ as on the linear scale in Fig. 1b.

In climates with $3/5<\lambda<15/19$, $b(\lambda)$ increases rapidly from $-\infty$ through negative values. A negative value $b(\lambda)<0$ means that the log variance of density *decreases* with increasing log mean density. Then as λ increases from 15/19 toward 1, $b(\lambda)$ increases slowly toward 2.

When $\lambda=1$, the weather alternates deterministically between good and bad. Again, the only randomness is in the initial conditions: half the realizations start out with good weather, half with bad, but all realizations alternate weather daily. Therefore, over any two successive days, the mean density grows deterministically for all realizations by a factor of $d_1 d_2=2\times(1/4)=1/2$, so $r_1(\lambda)=\lim_{t\rightarrow\infty} [E(N(t))]^{1/t}=(1/2)^{1/2}<1$, so $\log r_1(\lambda)<0$, i.e., $\log E(N(t))$ has a negative slope as a function of t, and the population is subcritical. In both extreme cases, $\lambda=0$ and $\lambda=1$, the TL slope is $b(0)=b(1)=2$, i.e., the variance is proportional to $(\text{mean})^2$, or the coefficient of variation (standard deviation divided by mean) of population density is constant. This behavior is expected for deterministic dynamics (Ballantyne 2005; Cohen 2013a).

Discussion

(a) Principal findings

Under certain broad conditions specified in the Appendix, but not under all conditions, a simple model of multiplicative population growth in a Markovian environment implies TL in the limit of large time, and the limiting slope b of TL (Eq. 8) can be any real number, positive or negative (Cohen 2013c). The variation in population growth may be driven by environmental variation and/or demographic stochasticity. In the model, b depends on the values of the multiplicative factors in different environments (summarized in this particular example by d_1 and d_2) and on the sequential dependence in the occurrence of different environmental states (summarized by the transition probabilities in the matrix $P(\lambda)$ in this example), even when the long-run relative frequency of different environmental states (summarized by the stationary probability vector π) is held constant.

TL has been studied theoretically from many different perspectives (e.g., Anderson et al. 1982; Tweedie 1984; Perry and Taylor 1985; Gillis et al. 1986; Jørgensen 1987; Kemp 1987; Perry 1988; Jørgensen 1997; Keeling 2000; Azevedo and Leroi 2001; Kilpatrick and Ives 2003; Kendal 2004; Ballantyne and Kerkhoff 2007; Eisler et al. 2008; Engen et al. 2008; Fronczak and Fronczak 2010; Cohen et al. 2012b, 2013; Cohen 2013a, c). Probability distributions in which the variance is a power-law function of the mean were studied (Tweedie 1946, 1947) even before the "law" was named for Taylor. Nevertheless, there is little consensus about why TL is so widely observed and how its estimated parameters should be interpreted.

Here, in a simple example, we compared hypothetical climates with differing rates of change from good weather to bad and vice versa, holding constant the probability of good or bad weather on an average day. As the daily probability λ of a change in weather increased from 0 to a threshold value of 3/5 in this example, the slope of TL rose from $b=2$ with increasing rapidity and then diverged to $+\infty$ when the mean population density became critical (Fig. 1b), i.e., when $\log(r_1(\lambda))=0$ or $r_1(\lambda)=1$. This critical case includes, but is not limited to, constant mean population density. Variations in mean population density that are sufficiently small compared to large time are not excluded. With further increase in λ beyond the threshold 3/5, the slope of TL dropped instantaneously to $-\infty$ and then rose, first rapidly then more slowly, approaching $b=2$ from below as λ approached 1. In this example, a slope b of very large magnitude, positive or negative, was a premonitory signal of a population's approach to criticality (the dividing line between ultimate extinction and exponential growth in mean population density).

This discovery of a singularity in b resulting from smooth change in λ in a simple example was unexpected. It may stimulate and contribute to a theory of abrupt biotic change.

(b) Generality and significance

From Fig. 1, it is clear that a singularity in b would occur in any dynamical model with three characteristics. First, the long-run exponential rate of growth r_1 of mean population density and the long-run exponential rate of growth r_2 of the variance of population density are both functions of some parameter θ. (In our example, $\theta=\lambda$.) Second, there exist two distinct values of θ, say, θ_1 and θ_2, such that r_1 is positive at one of these values and negative at the other, i.e., $r_1(\theta_1)r_1(\theta_2)<0$, and r_1 is continuous in the closed interval from θ_1 to θ_2. Then there exists at least one intermediate value, say θ^*, such that $r_1(\theta^*)=0$, by the intermediate value theorem of the calculus. Third, $r_2(\theta^*)\neq 1$. Under these three conditions, $b(\theta^*)=\log r_2(\theta^*)/\log r_1(\theta^*)$ is singular at $\theta=\theta^*$.

These conditions seem likely to be satisfied by a very wide variety of models. The condition that $r_1(\theta)$ be positive at one value of θ and negative at another requires that the parameter θ be good for population growth at some value and bad for population growth at some other value. Temperature, salinity, precipitation, pH, and a host of other environmental factors all satisfy such a condition.

The example given here could be generalized immediately to models of population dynamics in Markovian environments with $s>2$ environmental states, general multiplicative growth factors $d_1, \ldots, d_s$, general transition probabilities, and an age- or stage-structured population instead of a single-type population, provided only that the three conditions above be satisfied.

The model of multiplicative population dynamics in a Markovian environment (Appendix (a)), and not only the example above, allows, as a special case, independent multiplicative increments, as assumed in the Lewontin and Cohen (1969) model. The Lewontin–Cohen model satisfies TL (Cohen et al. 2013, p. 3). In the Lewontin–Cohen model, for a given fixed positive variance in the multiplicative factors $A(t)$, the TL slope b is less than 2 if and only if $E(A(t))<1$ (the mean population density approaches zero), and b is greater than 2 if and only if $E(A(t))>1$ (the mean population density explodes). In the present model where the successive multiplicative factors $A(t)$ are selected by a Markov chain, under broad conditions, and not merely for the specific example given here, similar relationships hold. Specifically (Cohen 2013c), $b(\lambda)>2$ if and only if $r_1(\lambda)>1$ and $b(\lambda)<2$ if and only if $r_1(\lambda)<1$.

The probability λ of a change in weather from 1 day to the next in the model is reflected in the shape of the power spectrum of environmental variation. Caswell and Cohen (1995, p. 308) showed that the nth order autocovariance function of an environmental function of a Markov chain specified by Eq. (3) decays exponentially with increasing n. The spectral density function is dominated by low frequencies (is said to be "red," as the spectral density function decreases with increasing frequency) when $0<\lambda<1/2$, is dominated by high frequencies (is "blue," as the spectral density function increases with increasing frequency) when 1/2

$<\lambda<1$, and is white (the spectral density function is flat, or the same for every frequency) when $\lambda=1/2$. Caswell and Cohen (1995, p. 303, their Fig. 1) graphed illustrative sample paths of a function of the environment with two states and $\lambda=1/10$, 1/2, and 9/10.

The comparison of hypothetical climates with different values of λ and therefore with different spectral colors has some relevance to the real world, though there is a large gap between reality and the idealized model analyzed here. García-Carreras and Reuman (2011, p. 1046) demonstrated a statistically significant global shift towards bluer power spectral densities of mean summer temperature time series from 1911–1950 to 1951–1990. Not all regions experienced the same shift. The spectra of North and South America and Europe became bluer, those of Asia and Australasia redder, and that of Africa was not significantly changed. Had values of b in TL been estimated during 1911–1950 and 1951–1990, and had all of those values been positive (as is commonly the case today), the example analyzed here would predict that the values of b should be larger in the second period than in the first where spectra became bluer (North and South America and Europe), and should be smaller in the second period than in the first where spectra became redder (Asia and Australasia), and should not be changed much where spectra did not shift significantly (Africa). It is not clear whether the observed shifts in the power spectra would have been enough to cause a singularity in b. See also García-Carreras and Reuman (2013).

In fisheries, forestry, and agriculture, efforts to increase yields or harvests may sometimes be associated with efforts to increase mean population densities of harvested species. TL applies in all these fields (for fisheries, Cohen et al. 2012b; for forestry, Fracker and Brischle 1944; Cohen et al. 2012a, 2013; for agriculture, Smith 1938; Wilson et al. 1989). TL implies that increased mean population densities should be associated with increases (if $b>0$) or decreases (if $b<0$) in the variance of population density. For positive b, the greater b is, the greater the increase in variance for a given increase in mean population density. Increases in the variance of the population density of the species that produce food and fiber could increase the fluctuations in the supplies available for human consumption, increase the variability of prices of these products, and increase the probability of demographic collapse (with genetic bottlenecks) or extinction of species. Increases in the variance of the population density of the species that carry, transmit, or cause human, animal, and zoonotic infections could increase the risk of outbreaks of diseases for humans and their domestic and game animals. At extremes of population density, density-dependence (e.g., positive Allee effects when density is low, negative effects of competition when density is high) may weaken the applicability of TL.

(c) Experimental testing and further theoretical analysis

This example's predictions could be tested experimentally using, for example, bacterial microcosms (Ramsayer et al. 2012; Kaltz et al. 2012) in incubators with differing probabilities λ of daily (or even hourly) change in temperature or other environmental factors that promote or reduce population growth.

This model has no density dependence. In future empirical work, it would be desirable to examine whether populations of the flour beetle *Tribolium castaneum*, which are known to be density-dependent, satisfy TL. A parallel theoretical question is whether empirically validated density-dependent models of *Tribolium* population dynamics such as the Larvae–Pupae–Adult family of models (Dennis et al. 1997, 2001; Reuman et al. 2006, 2008) satisfy TL. If these data and models do satisfy TL, they can be used to investigate how the TL slope b depends on the parameters of the laboratory experiments and models. If these data and models do not satisfy TL, they can be used to shed light on the conditions under which TL succeeds or fails.

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Appendix

(a) Multiplicative population dynamics in a Markovian environment

In a model of multiplicative population dynamics in a Markovian environment (Cohen 2013c), the density $N(t)$ of a single-type population changes in discrete time $t=0, 1, 2, \ldots$ as a result of multiplication by a stochastic factor $A(t)$:

$$N(t) = A(t-1)N(t-1), t = 1, 2, \ldots \tag{6}$$

The factor $A(t\text{-}1)$ by which population density changes from $t\text{-}1$ to t is selected by a finite-state Markov chain from a finite set of possible values $\{d_1, \ldots, d_s\}$, where $d_i>0$, $i=1, 2, \ldots, s$. Specifically, suppose the environment has a finite number $s>1$ of possible states (e.g., of temperature, wind velocity, sunshine, precipitation, or some combination of measurable factors) that translate into net population changes with no time delays. Let the probability that environmental state j on day t-1 is followed by state i on day t be given by p_{ij} and let $P = (p_{ij})$ be the $s \times s$ transition matrix of these transition probabilities. The prior state corresponds to column j of P, the next state to row i of P, and the sum of each column equals 1. If P is a positive matrix (all elements satisfy $p_{ij}>0$), then a stationary distribution π (a column vector of s positive probabilities π_j, $j=1,\ldots, s$) exists such that $P\pi=\pi$ (such a stationary distribution exists under much weaker assumptions on the transition matrix P, but those assumptions are not needed in the example investigated here). This means that if the probability distribution of the states of the environment at the initial time $t=0$ has the stationary distribution π, then for all future times, the probability distribution of states of the Markov chain will remain π. If $A(t\text{-}1)=d_j$, then $N(t)=d_jN(t\text{-}1)$, for $j=1, \ldots, s$ and $t=1,2, \ldots$. The multiplicative factor changes from one time step to the next according to the transition probabilities of the Markov chain starting from its stationary distribution:

$$Pr\{A(t) = d_i | A(t-1) = d_j\} = p_{ij}, Pr\{A(0) = d_i\} = \pi_i, i, j = 1, \ldots, s \ \ and \ \ t = 1, 2, \ldots \tag{7}$$

Define the $s \times s$ diagonal matrix $D = \text{diag}(d_i)$ to be zero everywhere except on the diagonal. The ith diagonal element d_i is the value of $A(.)$ when the environment is in state i. The spectral radius of a square matrix, denoted $r(\cdot)$, is the maximum of the absolute value (or modulus) of the eigenvalues of the matrix. If P is a positive matrix and at least two values of d_i are different, and if log $Var(N(t))$ is graphed as a function of log $E(N(t))$ for a succession of values of t, then the plotted points will approximate a straight line, as in Eq. (2), and, provided $\log[r(DP)]\neq 0$, the slope b of that line will be

$$b = \log\left[r\left(D^2P\right)\right] / \log[r(DP)]. \tag{8}$$

The formula for a is more complicated (Cohen 2013c) and is not needed here. Formula (8) is less mysterious than it might seem at first sight. Under the assumed conditions that $P>0$ and at least two elements of $\{d_i, \ i=1,\ldots, s\}$ are different (Altenberg 2013, Cohen 2013b, c), the numerator is $\log[r(D^2P)]=\lim_{t\to+\infty}$ [log $Var(N(t))]/t$, which is the limiting linear growth rate of the log variance, and the denominator is $\log[r(DP)]=\lim_{t\to+\infty}$ [log $E(N(t))]/t$, which is the limiting linear growth rate of the log mean. The condition before Eq. (8) that $\log[r(DP)]\neq 0$ means that the population is not critical, i.e., that mean population density is either increasing or decreasing for large t. Dividing TL in Eq. (1) by t and letting t get large gives $\lim_{t\to+\infty}$ [log $Var(N(t))$ - b log $E(N(t))]/t=0$, and solving this equation for b gives Eq. (8). The assumption that all elements of P are positive is stronger than necessary to guarantee that

$$\log\left[r\left(D^2P\right)\right] = \lim_{t\to+\infty}[\log \ Var(N(t))]/t$$

is the limiting linear growth rate of the log variance. The weaker necessary and sufficient conditions (Altenberg 2013, Cohen 2013b, c) are more complex and are not needed here.

This model is a special case of a widely studied model of age-structured populations in Markovian environments (Cohen 1976; Tuljapurkar 1990; see review by Caswell 2001).

(b) Example

For $D = \begin{pmatrix} 2 & 0 \\ 0 & 1/4 \end{pmatrix}$, we calculated $r(DP(\lambda)) \equiv r_1(\lambda)$ and $r(D^2P(\lambda)) \equiv r_2(\lambda)$ explicitly by using the quadratic formula to calculate the eigenvalues of the 2×2 matrices $DP(\lambda)$ and $D^2P(\lambda)$. We then computed $b = b(\lambda)=\log(r_2(\lambda))/\log(r_1(\lambda))$ from Eq. (8). The results are:

$$\begin{aligned}
&r_1(\lambda) = \lim_{t\to\infty}(E(N(t)))^{(1/t)} = r(DP(\lambda)) = \frac{\left(81\lambda^2-98\lambda+49\right)^{\frac{1}{2}}}{8} + \frac{9}{8}(1-\lambda),\\
&r_1(0) = 2, r_1\left(\frac{1}{2}\right) = \frac{9}{8}, r_1\left(\frac{3}{5}\right) = 1, r_1(1) = \frac{1}{\sqrt{2}},\\
&r_2(\lambda) = \lim_{t\to\infty}(Var(N(t)))^{(1/t)} = r\left(D^2P(\lambda)\right) = \frac{\left(4225\lambda^2-7938\lambda+3969\right)^{\frac{1}{2}}}{32} + \frac{65}{32}(1-\lambda)\\
&r_2(0) = 4, r_2\left(\frac{1}{2}\right) = \frac{65}{32}, r_2\left(\frac{3}{5}\right)\approx 1.66, r_2\left(\frac{15}{19}\right) = 1, r_2(1) = \frac{1}{2},\\
&b(\lambda) = \frac{\log r_2(\lambda)}{\log r_1(\lambda)}, \ \ b(0) = 2, b\left(\frac{1}{2}\right)\approx 6.02, b\left(\left(\frac{3}{5}\right)^-\right) = +\infty, b\left(\left(\frac{3}{5}\right)^+\right) = -\infty, b(1) = 2.
\end{aligned} \tag{9}$$

From Eq. (9), it may be proved that $dr_1(\lambda)/d\lambda < 0$ and $dr_2(\lambda)/d\lambda < 0$, as observed numerically.

At the extremes $\lambda = 0$ and $\lambda = 1$, $P(\lambda)$ is no longer a positive matrix. Because $r_1(\lambda)$ and $r_2(\lambda)$ are continuous functions of λ, we may evaluate these functions at the extremes $\lambda = 0$ and $\lambda = 1$ by using the same formulas as when $0 < \lambda < 1$.

In this example, it was observed numerically that, with increasing λ in $0 \le \lambda \le 1$, $b(\lambda)$ increases (except for the singularity in $b(\lambda)$ at $\lambda = 3/5$) and that $b(\lambda)$ is convex for λ in $0 \le \lambda < 3/5$ and concave for λ in $3/5 < \lambda \le 1$. There have been no mathematical proofs of these conjectures.

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