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Population age and initial density in a patchy environment affect the occurrence of abrupt transitions in a birth-and-death model of Taylor's law

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ABSTRACT

Taylor's power law describes an empirical relationship between the mean and variance of population densities in field data, in which the variance varies as a power, b, of the mean. Most studies report values of b varying between 1 and 2. However, Cohen (2014a) showed recently that smooth changes in environmental conditions in a model can lead to an abrupt, infinite change in b. To understand what factors can influence the occurrence of an abrupt change in b, we used both mathematical analysis and Monte Carlo samples from a model in which populations of the same species settled on patches, and each population followed independently a stochastic linear birth-and-death process. We investigated how the power relationship responds to a smooth change of population growth rate, under different sampling strategies, initial population density, and population age. We showed analytically that, if the initial populations differ only in density, and samples are taken from all patches after the same time period following a major invasion event, Taylor's law holds with exponent $b=1$, regardless of the population growth rate. If samples are taken at different times from patches that have the same initial population densities, we calculate an abrupt shift of b, as predicted by Cohen (2014a). The loss of linearity between log variance and log mean is a leading indicator of the abrupt shift. If both initial population densities and population ages vary among patches, estimates of b lie between 1 and 2, as in most empirical studies. But the value of b declines to ~1 as the system approaches a critical point. Our results can inform empirical studies that might be designed to demonstrate an abrupt shift in Taylor's law.

1. Introduction

Taylor's power law (Taylor, 1961; Taylor et al., 1978, 1980) is a relationship between the mean and variance of population density that has been found in empirical studies. According to this law, the variance is a power, b, of the mean; that is, $\mathrm{Var}(N(t))=a[E(N(t))]^b$, where $E(N(t))$ is the mean and $\mathrm{Var}(N(t))$ is the variance of population density $N(t)$. Empirical values of b are usually between 1 and 2. A number of explanations have been offered for this empirical law (e.g., Gillis et al., 1986; Kilpatrick and Ives, 2003; Kendal, 2004), some of which have been reviewed by Engen et al. (2008). The law has been found to extend far beyond the ecology, where it was first discovered; it describes data from many areas of biology, physics, and the stock market (Eisler et al., 2008).

Taylor's law has multiple forms, depending on the sampling schemes in a space-time diagram (Fig. 1). Assume there are K patches of distinct populations, where each population is censused at L points in time (referred to as population ages in this paper). The form of Taylor's law depends on how one calculates means and variances of population density. For a temporal Taylor's law, one calculates, separately for each of K patches, ln(mean) and ln(variance) as a point for each row (across time), resulting in K points. Then the K points are plotted to produce a relationship of ln(variance) vs. ln(mean), as in Kilpatrick and Ives (2003). For a spatial Taylor's law, one calculates, separately for each of L times, ln(mean) and ln(variance) for each column (across space). The resulting L points are then plotted, as in Taylor et al. (1978, 1980). A hierarchical spatial Taylor's law calculates ln(mean) and ln(variance) over subplots within a patch at particular time (within

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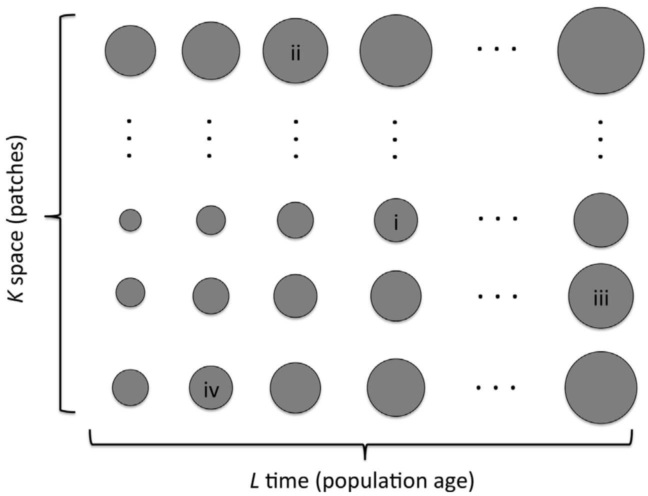

Fig. 1. A space–time diagram shows K patches (rows) of distinct populations censused at L points in time (columns) arranged in a K by L matrix. Population densities are represented as proportional to the size of gray circles, and population ages are represented as the distance from the initial time, which is show in the left column.

one single circle in Fig. 1). Then K points from all the patches are plotted to examine the variance–mean relationship. In some lab experiments, i.e., Petri dishes of bacteria, the "subplots" are replicates and "patches" are treatments or plate environments (Kaltz et al., 2012; Ramsayer et al., 2012). In these experiments the populations are usually controlled to have the same population age at the end of experiments (the last column in the K by L matrix). However, in field surveys, i.e., plots of trees, one may lack information on population age, even though the plots are surveyed in the same year (Cohen et al., 2012). In these cases, the sampling scheme is analogous to picking one time of observation for each row (patch) in the space-time diagram, i.e., as indicated by the illustrative Roman numerals in Fig. 1. The combined effects of different initial population densities and population ages on Taylor's law have apparently not been investigated previously.

Cohen (2014a) recently found an abrupt transition in the exponent b of Taylor's power law in a model that follows the growth of a single population in a stochastic environment. Specifically, he modeled varying environmental conditions (climate) with a two-state, discrete-time Markov chain in which the states represent weather conditions and in which different levels of temporal autocorrelation of weather conditions from one day to the next represent different climates. One state of weather causes population growth and the other state of weather causes reductions in population density. By assuming discrete multiplicative population growth with any finite number of states, Cohen (2014b) derived analytically a long-term rate of change in mean density and variance in the Markovian stochastic environment. The slope b of Taylor's law in log–log form is thus a function of the transition probabilities in the Markovian transition matrix, by which temporal autocorrelation could be tuned. The change in b in response to changes of the autocorrelation was computed numerically from the analytical formulas.

What is remarkable about the model is that, under certain conditions for the average multiplicative growth factor, when the climate is changed smoothly by gradually increasing the level of autocorrelation, at a certain point b undergoes an abrupt singularity in response. Although b stays close to 2 over most of the range of autocorrelation values, near the singularity it increases towards infinity, followed by a jump to an infinitely negative value, and then returns towards 2 as the autocorrelation parameter increases further beyond where the singularity occurs. Cohen (2014a) provides mathematical details and discussion of the general circumstances under which this sort of shift might occur.

This appears to be the first finding of a possible dramatic shift in Taylor's law. Cohen's (2014a) paper raises questions about the nature of the singularity that emerged in his model. Does this singularity appear for a smoothly changing environment in other types of models? Is the singularity something that may be noticed in empirical data? Does the appearance of the singularity depend on how sampling is done? Under what circumstances in nature might the singularity occur? Does it have ecological consequences?

One of many alternatives to Cohen's Markovian multiplicative model, the linear birth-and-death model, was used by Anderson et al. (1982) to show that Taylor's law holds as a result of the natural demographic stochastic processes of individual births and deaths. Their simulations did not reveal the singularity found by Cohen (2014a). In the setting of the linear birth-and-death model, we examine here whether and under what conditions Taylor's law experiences abrupt change (singularity) in response to a smoothly changing environment as predicted by Cohen's model. We are interested in how differences in population age and initial density, which affect the final range of mean population density, can affect the occurrence of abrupt transition. Our approach is through mathematical analysis and simulations aimed at exploring possible implications for field studies.

2. Model analysis

The linear birth-and-death process assumes that each individual in a population has a probability $\lambda\Delta t$ of giving birth to one offspring and a probability $\mu\Delta t$ of dying in each small interval of time, Δt. The difference, $\lambda-\mu$, is the intrinsic rate of growth per individual of the population. Each individual is assumed to be independent of all others. Let $N(t)$ be the integer-valued random variable that gives the density of a population in the birth-and-death model at t. The population density is measured in whole numbers of individuals, not in arbitrary positive real numbers, unlike the Markovian multiplicative model in Cohen (2014a,b). The expected population density at time t of a population with constant initial density N_0 at time 0 is

$$E(N(t)) = N_0 e^{(\lambda-\mu)t} \tag{1}$$

and the variance is

$$\mathrm{Var}(N(t)) = N_0 \frac{\lambda+\mu}{\lambda-\mu} e^{(\lambda-\mu)t}(e^{(\lambda-\mu)t}-1) \quad \text{if} \quad \lambda \neq \mu \tag{2a}$$

$$\mathrm{Var}(N(t)) = 2N_0\mu t \quad \text{if} \quad \lambda = \mu \tag{2b}$$

(Pielou, 1977). In the birth-and-death model, the probabilities of births and deaths are density independent, so that if $\lambda \neq \mu$, as time goes to infinity, the average population goes either to infinity or to zero.

Cohen (2014b) demonstrated for this linear birth-and-death process that, if $\lambda > \mu$, then as $t \to \infty$, a spatial Taylor's law holds with $b = 2$, whereas, if $\lambda < \mu$, as $t \to \infty$, a spatial Taylor's law holds with $b = 1$. If $\lambda = \mu$, then b is not defined. (He also demonstrated a similar abrupt transition in b for the Galton–Watson branching process.) Cohen (2014b) did not estimate the exponent, b, for finite time periods t and he assumed all populations start with same initial population density N_0.

Our objective is to investigate the behavior of the birth-and-death model for finite time periods and with varying initial population densities, to relate model results more closely to what will be encountered in field studies. First, following Cohen (2013, p. 95, his Eq. (7)), we approximated a "transient" value of $b = b(t)$ at a finite time t as the slope of the line tangent to the curve of $\ln \mathrm{Var}(N(t))$ as a function of $\ln E(N(t))$, or explicitly