

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



Jiang Jiang^{a,*}, Donald L. DeAngelis^{b,c}, Bo Zhang^c, Joel E. Cohen^d

^a National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, TN 37996, United States

^b U.S. Geological Survey, Southeast Ecological Science Center, Gainesville, FL 32653, United States

^c Department of Biology, University of Miami, Coral Gables, FL 33124, United States

^d Laboratory of Populations, The Rockefeller University and Columbia University, 1230 York Avenue, Box 20, New York, NY 10065, United States

ARTICLE INFO

Article history:

Received 2 May 2014

Accepted 29 June 2014

Keywords:

Taylor's law

Power law

Regime shift

Demography stochastic

Fluctuation scaling

Leading indicators

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.

© 2014 Elsevier B.V. All rights reserved.

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, $\text{Var}(N(t)) = a[E(N(t))]^b$, where $E(N(t))$ is the mean and $\text{Var}(N(t))$ 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, $\ln(\text{mean})$ and $\ln(\text{variance})$ as a point for each row (across time), resulting in K points. Then the K points are plotted to produce a relationship of $\ln(\text{variance})$ vs. $\ln(\text{mean})$, as in Kilpatrick and Ives (2003). For a spatial Taylor's law, one calculates, separately for each of L times, $\ln(\text{mean})$ and $\ln(\text{variance})$ 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 $\ln(\text{mean})$ and $\ln(\text{variance})$ over subplots within a patch at particular time (within

* Corresponding author. Tel.: +1 3055867856.

E-mail address: jjiang@nimbios.org (J. Jiang).

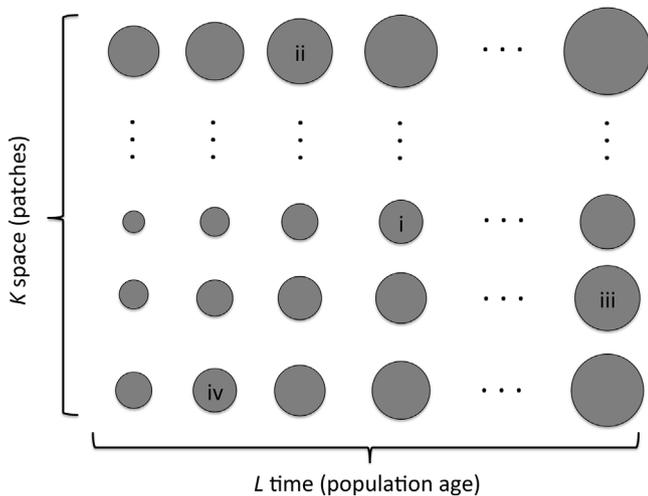


Fig. 1. A space–time diagram shows K patches (rows) of distinct populations censused at L points in time (columns) arranged in a K by L matrix. Population densities are represented as proportional to the size of gray circles, and population ages are represented as the distance from the initial time,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

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

and the variance is

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

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

(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 $t \rightarrow \infty$, a spatial Taylor’s law holds with $b = 2$, whereas, if $\lambda < \mu$, as $t \rightarrow \infty$, 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 $\ln \text{Var}(N(t))$ as a function of $\ln E(N(t))$, or explicitly

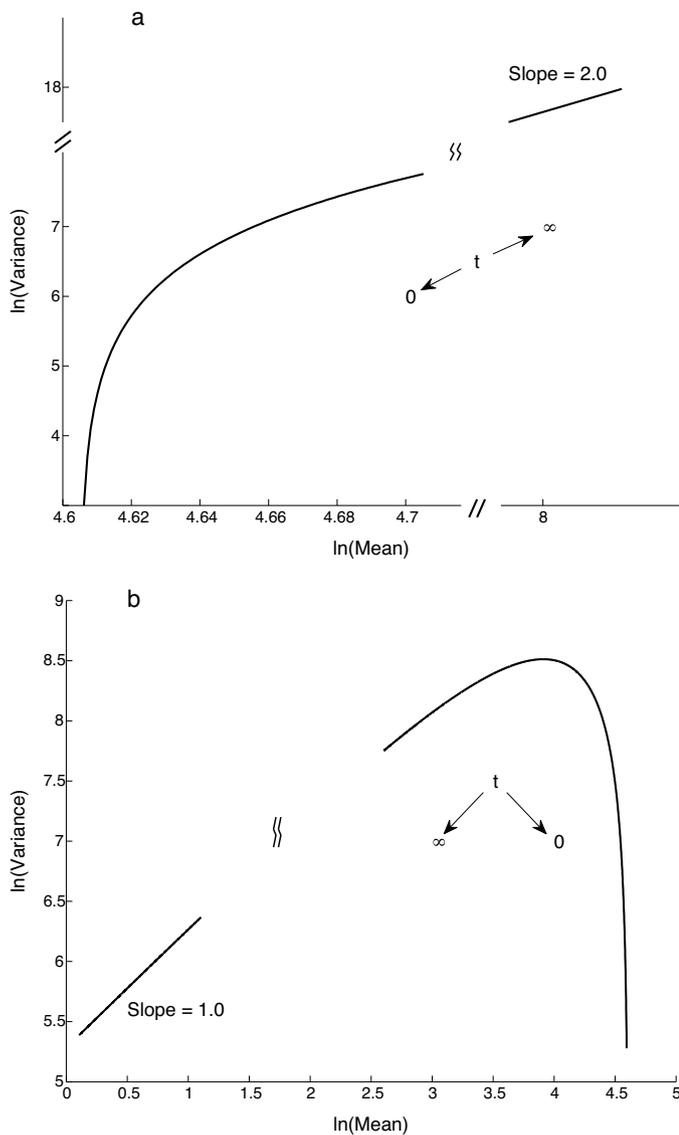


Fig. 2. Relationships of variance and mean on a log-scale, for (a) population increasing with time, $\lambda = 0.0101$ and (b) population decreasing with time, $\lambda = 0.0099$. Initial population density starts at $N_0 = 100$, with mortality rate $\mu = 0.01$. Arrows indicate direction of time t on the relationship curve. When $\lambda > \mu$, the ranges of t are [10 1000] and [40,000 41,000] before and after the break, respectively; when $\lambda < \mu$, the ranges of t are [100 20,000] and [35,000 45,000] before and after the break, respectively. Slopes after breaks are calculated from Eq. (3) as $t \rightarrow \infty$, and labeled here for illustration.

$b(t) = d \ln \text{Var}(N(t)) / d \ln E(N(t))$. We approximated the slope $b(t)$ by evaluating (1) and (2) at times t and $t + \Delta t$. This parameter $b(t)$ pertains neither to a spatial nor to a temporal Taylor’s law in the meanings described above, but to a “transient” Taylor’s law with a temporally changing $b(t)$. The “transient” $b(t)$ can be obtained exactly via limits of $\Delta t \rightarrow 0$, as

$$b(t) = \frac{2 - e^{-(\lambda - \mu)t}}{1 - e^{-(\lambda - \mu)t}} \quad (3)$$

Mathematical details of the derivation are provided in Appendix S1. If $t \rightarrow \infty$, then Eq. (3) yields the same results as in Cohen (2014b). However, Eq. (3) also indicates that for finite times $b(t)$ depends on time t , and that it can never lie between 1 and 2. The result of this model for finite times differs dramatically from empirical estimates of b usually found for both the spatial and temporal versions of Taylor’s law, in which b generally lies between 1 and 2. Fig. 2 illustrates the relationship between $\ln E(N(t))$ and $\ln \text{Var}(N(t))$ over a range of

time intervals. The slope $b(t)$ of tangent lines at time t in Fig. 2 is given by Eq. (3). When λ is slightly greater than μ (Fig. 2a), for small initial t (in the lower left corner of Fig. 2a), $b(t) \gg 0$ and $b(t)$ approaches $b = 2$ as $t \rightarrow \infty$. When λ is slightly less than μ (Fig. 2b), the population is declining and for small initial t (in the lower right corner of Fig. 2b), $b(t) \ll 0$, but $b(t)$ becomes positive at a very early time (after the peak in Fig. 2b), then approaches $b = 1$ as $t \rightarrow \infty$ (in the lower left corner of Fig. 2b).

Fig. 2 rests on the assumption that all populations start with the same initial population density N_0 . We next evaluated Eqs. (1) and (2) at different initial population density, N_0 and $N_0 + M$, where M is a small integer $M \ll N_0$. We then linearized to obtain an expression for the b at N_0 as $M \rightarrow 1$, which yields $b = 1$ (see Appendix S1). This is different from a stochastic population with randomly varying initial population density, observed at time t (Appendix S2). In more general cases, where both assumptions, equal time periods t and equal initial population density N_0 , are relaxed, we had to estimate b using simulations, as described in the following section.

3. Simulations

We consider populations of one species that are distributed across patches, and are independent of each other (Fig. 1). The populations can differ in their initial densities, their lengths of occupation of the different patches (population age), or both. Sometimes each patch will be divided into subplots, each with its own population. Each patch’s population or population of a subplot goes through its birth-and-death process independently.

We ignore migration among patches, or subplots if applicable, for simplicity. Migration contributes to stochastic birth or death implicitly, if immigration occurs at a rate per unit of time that is proportional to the resident population of the patch of destination or if emigration occurs at a rate per unit of time that is proportional to the resident population of the patch of origin.

We simulated each population as a birth-and-death process and mimicked taking samples from the patches. We followed the sampling scheme in the space–time diagram (Fig. 1). When we examined the temporal form of Taylor’s law, we calculated the means and variances over a particular time period (see Scenario 4 later for detail on how to choose the time period). When we examined the hierarchical spatial form of Taylor’s law, each patch was equally divided into one thousand subplots ($M_s = 1000$). We calculated the mean and variance of population densities of the subplots for that patch as indicated by the Roman numerals in Fig. 1. We assumed that the population within each patch, or subplot, if sampled from subplots, went through a birth-and-death process independently, coded as Monte Carlo time steps for each 1 birth or 1 death (see Appendix S3 for the Matlab codes). We sampled 100 patches, which resulted in 100 means and variances, and then performed linear regression of $\ln(\text{Var}(N))$ as a function of $\ln(E(N))$ to obtain the slope b . In all the simulations, we fixed the death rate, $\mu = 0.01$, and decreased the birth rate λ in small decrements, representing smoothly changing environmental conditions. The birth rate λ was constant in any given simulation, but different simulations differed by small decrements of λ . We were interested in whether the exponent b could experience an abrupt change when the population growth rate changed smoothly from positive to negative; i.e., changed from $\lambda > \mu$ to $\lambda < \mu$. We investigated the stochastic demography close to the equilibrium of the deterministic model; that is, around the net zero growth rate, $\lambda = \mu$. The population under these conditions approached neither infinity nor extinction in our simulations.

Four different scenarios were simulated, representing different sampling strategies, differences in initial population density, and differences in population age (Table 1). In this paragraph, we summarize the scenarios. In the following paragraphs, we describe the

Table 1
Summary of scenarios' assumptions and main results. To calculate one mean and variance, we sampled 1000 subplots in Scenarios 1, 2 and 3; and sampled 1000 time points in Scenario 4. In all scenarios, there were 100 patches.

Scenario	Initial population density was assumed to be	Time of observation was assumed to be	Result
1	Same for all patches and subplots	Different for different patches	b has singularity, Fig. 3
2	Same for subplots in each patch, different for different patches	Same for all patches and subplots	$b \approx 1$, Fig. 4
3	Same for subplots in each patch, different for different patches	Different for different patches, one time per patch	b is U-shaped function, Fig. 5
4	No subplots, different for different patches	Different ages, multiple times per patch	b is U-shaped function, Fig. 6

scenarios in detail. The first three scenarios approximated spatial Taylor's laws, in which sampling across space (subplots) was performed to calculate means and variances. Scenario 1 assumed all patches were occupied with same initial population density. All the subplots within any patch were of a uniform age associated with that patch, but the patches were of different ages. In Scenario 2, we picked one column (time of observation) from the K by L matrix, and we chose different initial population densities. Scenario 3 combined differences in both population age and initial density. Scenario 4 approximated the usual temporal Taylor's law, but we added differences in population age and initial density.

In Scenario 1, all patches were occupied with the same initial population density, and within each patch the same initial population density was assigned to each of the M_s subplots. Different patches were assumed occupied for different periods of time. The age of the population on each patch, T_{age} , was selected randomly from a uniform distribution between 1000 and 2000. We took samples across space, where each patch consisted of M_s subplots with initial population density of each subplot $n_0 = 50$, and calculated the mean and variance of population density over the subplots for that patch. In this scenario, the values of the "transient" $b(T_{\text{age}})$ should be the same as the values calculated from Eq. (3). However, in our Monte Carlo sampling, we picked 100 patches with different values of T_{age} chosen randomly across a time interval and then calculated the slope b through regression. We have already seen from Fig. 2 and Eq. (3) that the "transient" slope $b(t)$ is not constant over the whole time period, especially when t (called T_{age} in the simulations that follow) is small. We expected the same would occur in our simulations. Therefore, to make sure in our simulations that any changes in b were caused by changes in λ , as predicted by Cohen (2014a), and not by T_{age} , we picked the ranges of T_{age} where $b(t)$ varies only slightly, i.e., from the relatively linear parts in Fig. 2.

In Scenario 2, all the patches were assumed occupied by their populations for the same period of time, $T_{\text{age}} = 2000$, for example, as if they were settled simultaneously through a major invasion event. But all the patches were assumed to differ in initial population density. Again, we took samples across space, where each patch consisted of M_s subplots. Initial population densities of subplots were the same within a patch but were assumed to be integer values distributed uniform randomly between 10 and 100 initial individuals per subplot for different patches, to produce different initial population densities for the patches. On the basis of analysis of the birth-and-death model for the situation in which only the initial population densities differed among patches (see Appendix S1), we expected the slope b to remain approximately 1.0 in this case, regardless of the birth rate; therefore, no singularity was expected.

In Scenario 3 we again sampled across space (subplots of each patch), and both initial population density and age of the patches were randomly selected using the same distributions as in the previous scenarios. All M_s subplots within a given patch had the same initial population density within a patch but differed among patches as in Scenario 2. Age differed among patches, as in Scenario 1. Scenario 3 was therefore a combination of Scenarios 1 and 2. Our analytic results for b in Scenario 2 were close to $b = 1$ (see Appendix S1), and thus we assumed that in the simulations the effect of different initial densities would overwhelm the tendency

for large values (positive or negative) of the slopes that occur in Scenario 1 and Cohen (2014a) when $\lambda \approx \mu$. Therefore, we did not expect a singularity. Empirical observations tend to find values of the slope, b , that lie between 1 and 2.

In Scenario 4 we sampled across time to evaluate a form of temporal Taylor's law. Again, we sampled 100 patches that differed in both initial population densities and the ages. The initial population density of each patch was chosen from a uniform random distribution between 10 and 100. The age T_{age} of a patch was chosen independently from a uniform distribution between 1000 and 2000. We chose 1000 temporal samples for each patch, with sampling at multiple time points that were uniformly distributed between $[T_{\text{age}}/2, T_{\text{age}}]$. These simulations used an alternative approach such that there were multiple runs, and in each run there was a different sampling time. This alternative method was used because our simulation of Monte Carlo time steps for birth-and-death process could not produce a fixed number of samples for a given time period in a single run. To make sure the final population density of this scenario was comparable to population density in the previous three scenarios, we scaled the initial population densities of patches in this scenario to that of subplots in previous scenarios.

We performed 20 replicates for each value of λ in Scenario 3 and Scenario 4. No replications for Scenario 1 and Scenario 2 were performed, because they were analyzed mathematically above. All the simulations were done in Matlab 2012b.

4. Results

4.1. Cases in which a singularity could occur

Output from Scenario 1, in which all the populations were assumed to have the same initial density but different final ages, matched results predicted by Eq. (3) (Fig. 3, details are shown in Fig. S1). Therefore, as predicted from Eq. (3), the "transient" exponent $b(t)$ can have a singularity when $\lambda = \mu$ (Fig. 3). The simulation shows that $b(t)$ jumps from a very large positive value to a highly negative value, when λ passes from $\lambda > \mu$ to $\lambda < \mu$, for every $t > 0$. The relationship between $\ln(\text{Var}(N))$ and $\ln(E(N))$ loses linearity close to $\lambda = \mu$ (Fig. S1), which corresponds to Cohen's conclusion (2014b) that b is not defined when $\lambda = \mu$.

4.2. Cases of shifts without singularity

The remaining scenarios, when numerically evaluated, showed no singularities. When all the patches were assumed to differ in initial population densities but to have the same population age (Scenario 2), Taylor's law holds around $b \approx 1.0$ for all values of λ (see Fig. 4, and compare with the results for this case in Appendix S1).

When both the initial population density and the age of the population were different (Scenario 3 and Scenario 4), the exponent b displayed U-shaped patterns, lying between 1 and 2, as a function of λ (Figs. 4 and 5). b moved toward 1 when λ approached μ , reaching a minimum value close to 1. In both sampling strategies, b declined rapidly when λ decreased from $\lambda > \mu$ to $\lambda \approx \mu$. But b subsequently

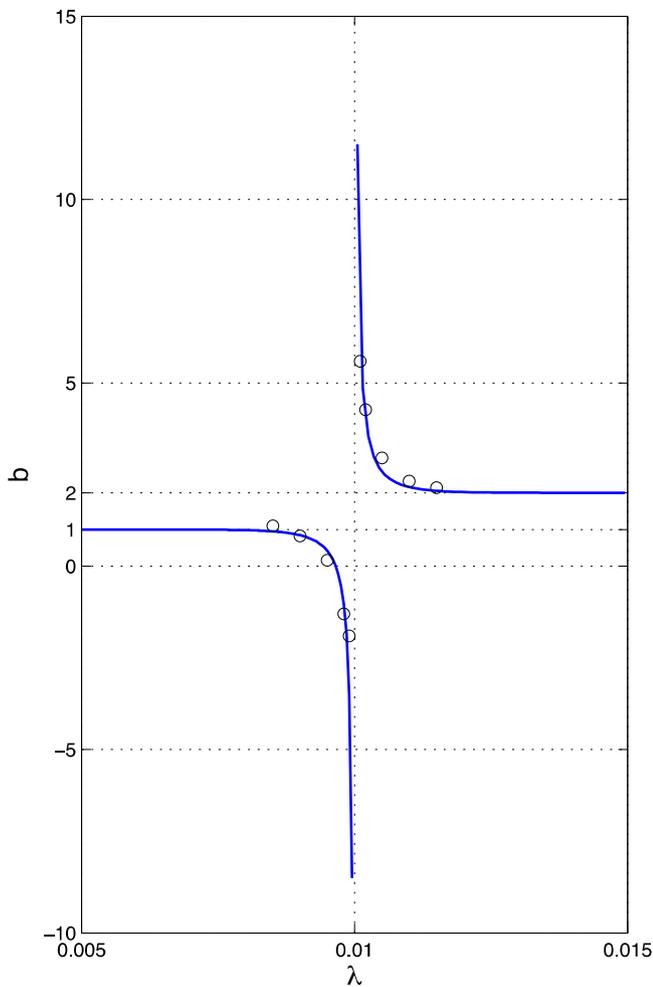


Fig. 3. Predicted “transient” Taylor’s law’s exponent $b(t)$ at time $t=2000$ against birth rate λ in the birth-and-death process (solid line plots Eq. (3)). Dots are values derived from sampling from Scenario 1, assuming that population age varies between 1000 and 2000. Other parameters are $\mu = 0.01$, $n_0 = 50$, number of subplots, $M_s = 1000$. Details of the dots are shown in Fig. S1.

bounced back to larger values when λ continued decreasing away from $\lambda \approx \mu$ in the case of sampling across space (Fig. 5). When sampling was performed across time (Scenario 4), b displayed a similar pattern, but with lower values than in Scenario 3 (Fig. 6).

5. Discussion

Motivated by Cohen’s analytical finding that Taylor’s power law can experience an abrupt shift in the values of b along a smoothly changing environment (Cohen, 2014a), we investigated this phenomenon by simulating linear birth-and-death processes in different environments with smoothly changing values of λ , the birth rate per individual. Cohen (2014a) argued that the abrupt shift can be general as long as the long-term rate of increase in mean population density and variance are functions of some environmental conditions, and if there exists at least a critical point where the mean density is long-run stationary but the long-run variance of population density is positive. However, most empirical studies have reported that b lies between 1 and 2, although exponents greater than 2 or less than 1 have occasionally been observed (Anderson et al., 1982; Kendal, 2004).

We found that the abrupt shift can occur in certain situations. We further found that, under other conditions and other sampling designs, the shift in b may not be abrupt but that b may move more

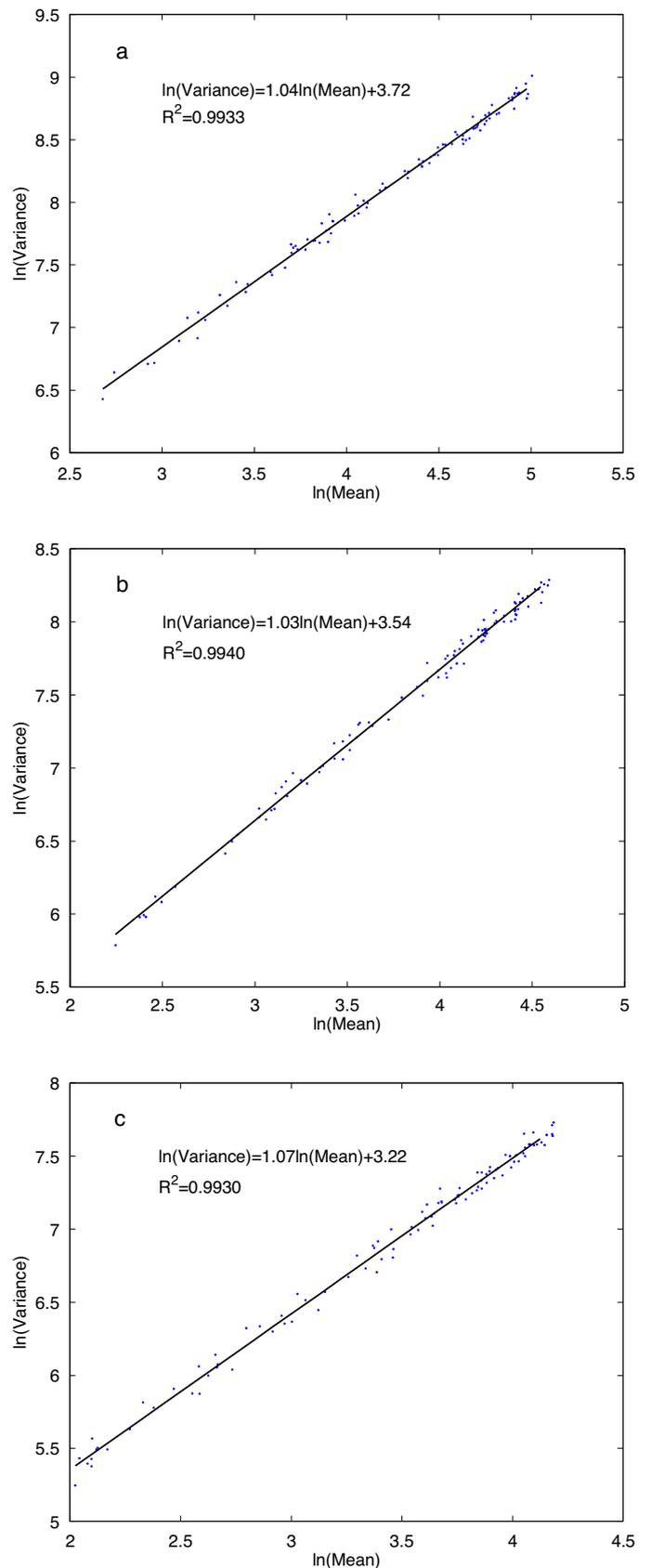


Fig. 4. Selected outputs from Scenario 2, in which the sampling is across space, and in which all the populations of the patches were assumed to differ in initial density but to have the same age. Three cases were plotted here when (a) $\lambda = 0.0102$, (b) $\lambda = 0.01$, and (c) $\lambda = 0.0098$. In all cases, $\mu = 0.01$.

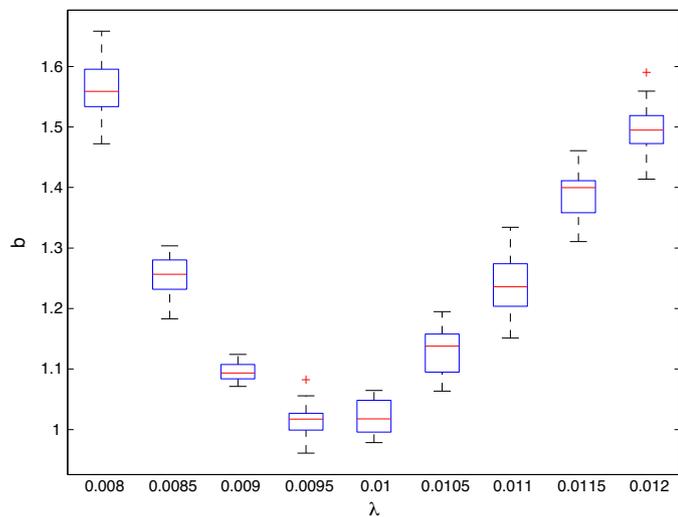


Fig. 5. Outputs from Scenario 3, in which sampling was across space, and all the populations had different initial densities and different ages. Box plots are from 20 replications for each λ . On each box, the central mark is the median, the top and bottom edges of the box are the 25th and 75th percentiles. By definition, outliers, plotted individually (+), are values that are more than 1.5 times the interquartile range away from the top or bottom of the box. The whiskers extend to the most extreme data points that are not outliers.

gradually towards a lower bound as the system approaches a critical point. When both initial population densities and occupancy histories were allowed to vary (in Scenarios 3 and 4), the following situation occurred around $\lambda \approx \mu$. When the population declined, on average, to the left of the critical point (i.e., for $\lambda < \mu$), the slope could be considered to have been a combination of two vectors, one with a large negative slope (as in Scenario 1) and the other with $b = 1$ (as in Scenario 2). But the data points that could result in large negative slope were very close to the initial population densities. Therefore, the tendency towards $b = 1$, caused by the different initial population densities, overwhelmed the tendency toward a large negative slope, caused by different population ages, and prevented a singularity in the overall slope. At some point of $\lambda < \mu$, the large negative slopes might have increased in strength and dragged down the overall slope below 1 slightly (Fig. 5).

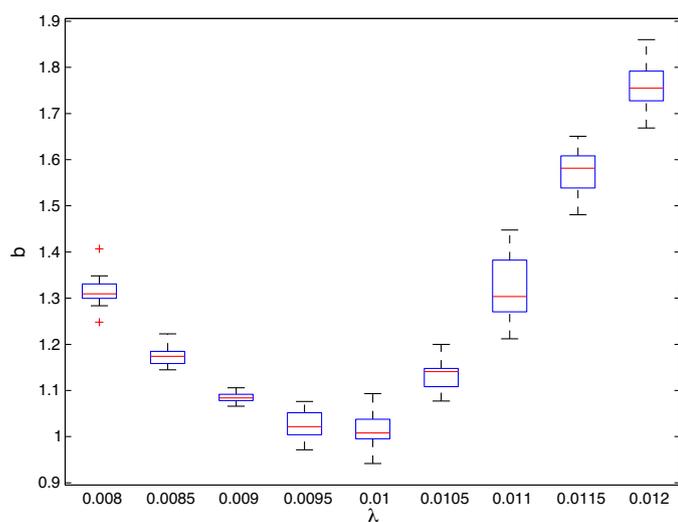


Fig. 6. Output from Scenario 4, in which sampling was across time, and in which all populations had different initial densities and different ages. Box plots are from 20 replications for each λ , same as Fig. 5.

To calculate the slope of the relationship between $\ln(\text{Var}(N))$ and $\ln(E(N))$, we need at least two data points. Different factors can lead to the differences between the two data points, and therefore different factors can contribute the value of b in Taylor's law. Our simulations suggest that in density-independent models, differences in both the initial population density and the population age influenced the value of the slope. Data points of populations that differ in initial population density will maintain the same slope at a value of 1. However, if the amount of time following the establishment of populations of the same density differs, then a singularity can occur when the birth rate λ approaches the death rate μ . For the latter case, in field studies a loss of linearity in the relationship between $\ln(\text{Var}(N))$ and $\ln(E(N))$ could in principle be observed. A large slope, which has very wide range of values of $\ln(\text{Var}(N))$ over a narrow range of values $\ln(E(N))$, may be difficult to observe. Any errors in sampling or estimating the mean or the variance of population density can change the slope significantly. We suggest that the loss of a linear relationship between $\ln(\text{Var}(N))$ and $\ln(E(N))$ could be an indicator of approaching singularity in field studies (Fig. S1). By doing multiple repeated simulations with $\lambda = \mu$, we found that the coefficients of determination (R^2) were very close to 0 (Fig. S1 showing $R^2 = 0.0038$ when $\lambda = \mu$; results of multiple simulations are not shown). When both factors (differences in initial population density, differences in population age) were present (Scenario 3), then, near the critical point, $\lambda = \mu$, we found that the first factor dominates, and hence the slope does not approach a singularity, but approaches 1.

The results of this work are based on a linear birth-and-death process, which is a highly simplified model. The model assumes no density dependence and purely demographic rather than environmental stochasticity. No population is entirely free of density-dependence at the extremes of high and low population density. Density dependence regulates population density over the long term by increasing death rates or decreasing birth rates at high densities. However, density independence may be a good approximate description of a population's dynamics in many cases. Strong (1986) reviewed evidence of 'density vagueness', or the condition in which stochasticity is dominant over a wide range of population densities, with density dependence becoming strong only at 'density floors' or 'density ceilings'. Evidence from populations of many taxa supports the view that density has little influence on dynamics over wide ranges of density. Similar conclusions go back to Ehrlich et al. (1972) and Southwood and Comins (1976). Anderson et al. (1982), who studied the emergence of Taylor's law from a linear birth-and-death model, argued that patterns of population dispersion observed in nature tended to reflect dominance of density-independent processes. Based on this information, the populations most likely to display the effects studied here would be small to intermediate in density relative to their available resources, so that competition or other density-dependent effects are not likely to be important.

Some studies on Taylor's law have investigated the fluctuation of population density under the assumption that populations are at steady state in the long run (Kilpatrick and Ives, 2003). In the setting of the linear birth-and-death model, that is equivalent to the birth rate equaling the death rate. If this is the case, we should have seen many large values of b in Taylor's law, with a narrow range of $\ln(\text{mean})$ and a wide range of $\ln(\text{variance})$. It is probable, however, that other factors overwhelm the singularity. For example, carrying capacities were different for each simulation to obtain a data point ($\ln(\text{mean})$, $\ln(\text{variance})$) in Kilpatrick and Ives (2003). Nutrient levels of the Petri dishes of the bacterial study of Ramsayer et al. (2012) differed from one treatment to another (though nutrient levels were constant for replicated Petri dishes within each treatment), and singularities were not observed in the experiments of Ramsayer et al. (2012). Some large values of b have been reported

in literature. For example, Kaltz et al. (2012) found that bacterial populations treated with antibiotic rifampicin had a narrow range of mean population densities. In Taylor et al. (1980), half of the slopes in moths and aphids in the dataset were greater than 2. Hanski (1987) explained this as low cross-correlation in local populations, which resulted in high variance. However, because we did not include density dependence in our model, we cannot say whether discontinuities might be observed in such situations.

Thus there are strong limitations on our model results. Our questions and methods are probably applicable to many other stochastic population models, but so far our findings have not been shown to be valid in general. However, the implication of the model that the variance of population densities can continue to increase even in the vicinity of zero net growth ($\lambda \approx \mu$) is probably common among models of growth of populations distributed across patches. Our simulations showed a singularity in b at $\lambda \approx \mu$ when sampling was done for populations that differed in age. This finding reflects very slow changes in average population density across time, while variance continued to increase due to random births and deaths. However, past researches tried to avoid sampling small range of mean population density. We suggest that future experiments should identify causes of variation in mean population density. Although a singularity in b occurs in certain special situations, robust statistical analysis to distinguish the two factors of initial population density and population age might be able to reveal the abrupt shift in additional circumstances and to interpret extreme (large or small) values of the exponent b .

Acknowledgments

J.J. was supported as Postdoctoral Fellow at the National Institute for Mathematical and Biological Synthesis (NSF Award #EF-0832858). D.L.D. was partially supported by the FISCHS Project (Future Impacts of Sea Level Rise on Coastal Habitats and Species) at the USGS Southeast Ecological Science Center, funded by USGS Ecosystems Mapping and the USGS Greater Everglades Priority Ecosystems Science. J.E.C. was partially supported by U.S. National Science Foundation grants EF-1038337 and DMS-1225529 and thanks Priscilla K. Rogerson for assistance. Any use of trade, product, or firm names in this article is for descriptive purposes only and does not imply endorsement by the U.S. Government

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2014.06.022>.

References

- Anderson, R.M., Gordon, D.M., Crawley, M.J., Hassell, M.P., 1982. Variability in the abundance of animal and plant species. *Nature* 296, 245–248.
- Cohen, J.E., Xu, M., Schuster, W.S.F., 2012. Allometric scaling of population variance with mean body size is predicted from Taylor's law and density-mass allometry. *PNAS* 109, 15829–15834.
- Cohen, J.E., 2014a. Taylor's law and abrupt biotic change in a smoothly changing environment. *Theor. Ecol.* 7, 77–86.
- Cohen, J.E., 2013. Taylor's power law of fluctuation scaling and the growth-rate theorem. *Theor. Popul. Biol.* 88, 94–100.
- Cohen, J.E., 2014b. Stochastic population dynamics in a Markovian environment implies Taylor's power law of fluctuation scaling. *Theor. Popul. Biol.* 93, 30–37.
- Ehrlich, P.R., Breedlove, D.E., Brussard, P.F., Sharp, M.A., 1972. Weather and the 'regulation' of subalpine populations. *Ecology* 53, 243–247.
- Eisler, Z., Bartos, I., Kertész, J., 2008. Fluctuation scaling in complex systems: Taylor's law and beyond. *Adv. Physiol.* 57, 89–142.
- Engen, S., Lande, R., Saether, B.E., 2008. A general model for analyzing Taylor's spatial scaling laws. *Ecology* 89, 2612–2622.
- Gillis, D.M., Kramer, D.L., Bell, G., 1986. Taylor's power law as a consequence of Fretwell's ideal free distribution. *J. Theor. Biol.* 123, 281–287.
- Hanski, I., 1987. Cross-correlation in population dynamics and the slope of spatial variance – mean regressions. *Oikos* 50, 148–151.
- Kaltz, O., Escobar-Paramo, P., Hochberg, M.E., Cohen, J.E., 2012. Bacterial microcosms obey Taylor's law: effects of abiotic and biotic stress and genetics on mean and variance of population density. *Ecol. Proc.* 1, 5.
- Kendal, W.S., 2004. Taylor's ecological power law as a consequence of scale invariant exponential dispersal models. *Ecol. Complex.* 1, 193–209.
- Kilpatrick, A.M., Ives, A.R., 2003. Species interactions can explain Taylor's power law for ecological time series. *Nature* 422, 65–68.
- Pielou, E.C., 1977. *Mathematical Ecology*. John Wiley & Sons, New York, pp. 15–18.
- Ramsayer, J., Fellous, S., Cohen, J.E., Hochberg, M.E., 2012. Taylor's law holds in experimental bacterial populations but competition does not influence the slope. *Biol. Lett.* 8, 316–319.
- Southwood, T.R.E., Comins, H.M., 1976. A synoptic population model. *J. Anim. Ecol.* 45, 949–965.
- Strong, D.R., 1986. Density vagueness: abiding the variance in the demography of real populations. In: Diamond, J., Case, T.J. (Eds.), *Community Ecology*. Harper & Row Publishers, New York, pp. 257–268.
- Taylor, L.R., 1961. Aggregation, variance and the mean. *Nature* 189, 732–735.
- Taylor, L.R., Woiwod, I.P., Perry, J.N., 1978. The density dependence of spatial behavior and the rarity of randomness. *J. Anim. Ecol.* 47, 383–406.
- Taylor, L.R., Woiwod, I.P., Perry, J.N., 1980. Variance and the large scale spatial stability of aphids, moths and birds. *J. Anim. Ecol.* 49, 831–854.

Supplementary Materials

Figure S1. Selected outputs from Scenario 1, in which sampling was across space and all the populations were assumed to have the same initial size but different ages. $\mu=0.01$ for all the graphs. All these slopes are shown in Figure 2 except when $\lambda = \mu$.

Appendix S1. Mathematical analysis of birth and death model in Scenarios 1 and 2.

Appendix S2. Mathematical analysis of birth and death model in which patches have randomly varying initial population size.

Appendix S3. Matlab scripts to do simulations and to produce figures.

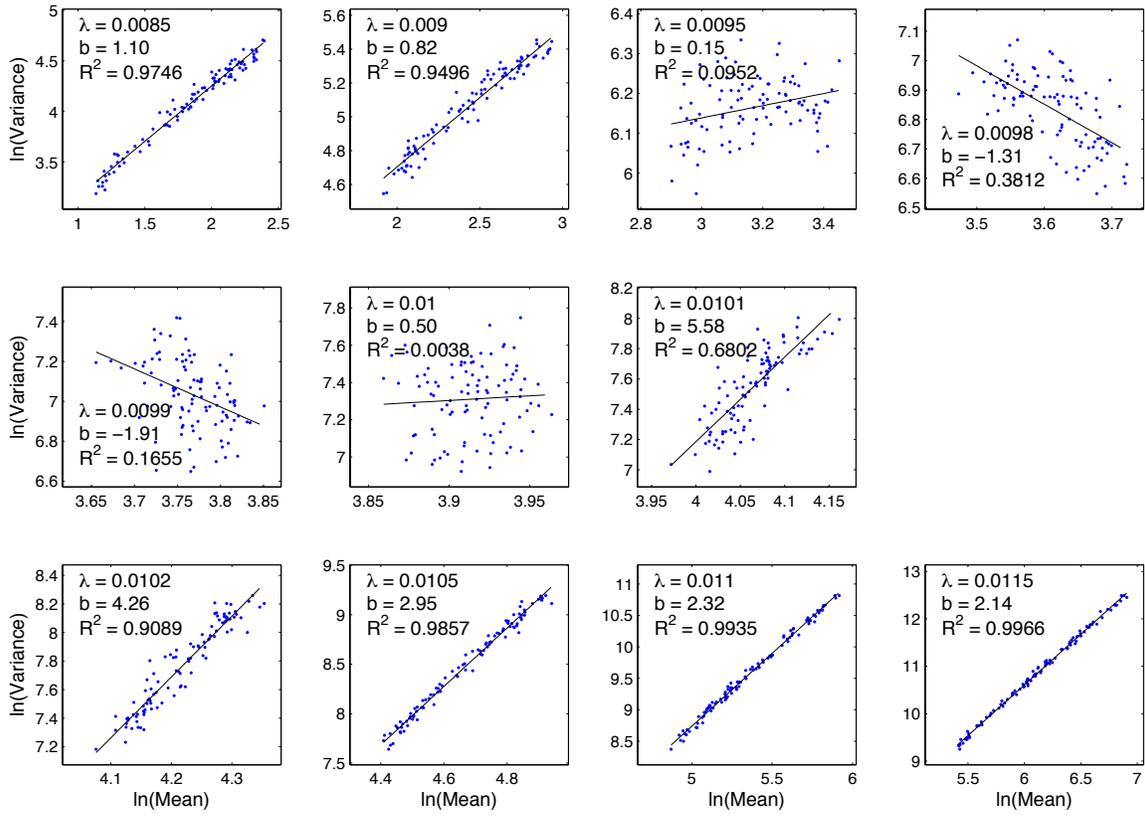


Figure S1.

Appendix S1: Mathematical analysis of birth and death model in Scenarios 1 and 2

The simple birth-and-death process assumes that an individual in a population has a probability $\lambda\Delta t$ of giving birth to another individual and $\mu\Delta t$ of dying in each sufficiently small increment of time, Δt , independently for all individuals. The difference, $\lambda - \mu$, is the intrinsic rate of growth of the population. The expected population size at time t of a population with initial size N_0 at time $t = 0$, is

$$E(N(t)) = N_0 e^{(\lambda-\mu)t} \quad (\text{A1})$$

and the variance is

$$\text{Var}(N(t)) = N_0 \frac{\lambda+\mu}{\lambda-\mu} e^{(\lambda-\mu)t} (e^{(\lambda-\mu)t} - 1) \quad \text{if } \lambda \neq \mu \quad (\text{A2})$$

$$\text{Var}(N(t)) = 2N_0\mu t \quad \text{if } \lambda = \mu \quad (\text{A3})$$

(Pielou 1977).

The logarithmic forms are

$$\ln E(N(t)) = \ln(N_0) + (\lambda - \mu)t$$

$$\ln \text{Var}(N(t)) = \ln\left(\frac{N_0(\lambda+\mu)}{\lambda-\mu}\right) + (\lambda - \mu)t + \ln(e^{(\lambda-\mu)t} - 1)$$

To calculate slope of the relationship between $\ln \text{Var}(N(t))$ and $\ln E(N(t))$, at least two data points are needed. The slope between the two points $[\ln E(N_1), \ln \text{Var}(N_1)]$ and $[\ln E(N_2), \ln \text{Var}(N_2)]$ is

$$b_{12} = \frac{\ln \text{Var}(N_2) - \ln \text{Var}(N_1)}{\ln E(N_2) - \ln E(N_1)} \quad (\text{A4})$$

We investigated the change of slope as function of the intrinsic rate of growth $\lambda - \mu$ of the population, assuming the intrinsic growth rate to be same for the two data points. We derived slopes for data points that differ in N_0 and t separately.

For different initial population sizes

Assume two populations have size N_{n_0} and N_{n_0+m} at time t if the initial population size is n_0 and n_0+m , respectively, where $m \ll n_0$. Then

$$\begin{aligned}
 b &= \frac{\ln \text{Var}(N_{n_0+m_0}) - \ln \text{Var}(N_{n_0})}{\ln E(N_{n_0+m_0}) - \ln E(N_{n_0})} \\
 &= \frac{\ln \frac{(n_0 + m)(\lambda + \mu)}{\lambda - \mu} - \ln \frac{(n_0)(\lambda + \mu)}{\lambda - \mu}}{\ln(n_0 + m) - \ln(n_0)} \\
 &= 1.
 \end{aligned}$$

For fixed initial population size, different times t :

Assume a fixed initial population size; let N_t and $N_{t+\Delta t}$ represent the population size at time t and $t+\Delta t$, respectively. A “transient” value of $b=b(t)$ at time t can be obtained via limits of $\Delta t \rightarrow 0$.

$$\begin{aligned}
 b(t) &= \lim_{\Delta t \rightarrow 0} \frac{\ln \text{Var}(N_{t+\Delta t}) - \ln \text{Var}(N_t)}{\Delta t} \bigg/ \frac{\ln E(N_{t+\Delta t}) - \ln E(N_t)}{\Delta t} \\
 &= 1 + \lim_{\Delta t \rightarrow 0} \frac{\ln[e^{(\lambda-\mu)(t+\Delta t)} - 1] - \ln[e^{(\lambda-\mu)t} - 1]}{(\lambda - \mu)\Delta t} \\
 &= 1 + \lim_{\Delta t \rightarrow 0} \frac{(\lambda - \mu)e^{(\lambda-\mu)(t+\Delta t)} \big/ [e^{(\lambda-\mu)(t+\Delta t)} - 1]}{(\lambda - \mu)} \\
 &= 1 + \frac{1}{1 - e^{-(\lambda-\mu)t}} = \frac{2 - e^{-(\lambda-\mu)t}}{1 - e^{-(\lambda-\mu)t}}.
 \end{aligned}$$

Appendix S2: Mathematical analysis of birth and death model in which patches have randomly varying initial population size

$N(t)$ is found from a birth and death model at time t following Equations (A1), (A2) and (A3). Now we assume that the initial value $N(0)$ varies randomly with a mean value $E(N(0))$ and variance $Var(N(0))$. To find the logarithms of the variance, we use the general formula for the variance of a product (Goodman 1960):

$$Var(XY) = [E(X)]^2 Var(Y) + [E(Y)]^2 Var(X) + Var(X)Var(Y) \quad (A5)$$

where $E(X)$ and $E(Y)$ are the mean values of X and Y .

Assuming that the initial population size $N(0)$ is a random variable and we look at the difference between two times, we use the relation for $Var(XY)$ to get

$$Var(N(t)) = [E(N(0))]^2 \frac{\lambda + \mu}{\lambda - \mu} e^{(\lambda - \mu)t} (e^{(\lambda - \mu)t} - 1) + [e^{(\lambda - \mu)t}]^2 Var(N(0)) \\ + Var(N(0)) \frac{\lambda + \mu}{\lambda - \mu} e^{(\lambda - \mu)t} (e^{(\lambda - \mu)t} - 1)$$

and

$$Var(N(t + \Delta t)) = [E(N(0))]^2 \frac{\lambda + \mu}{\lambda - \mu} e^{(\lambda - \mu)(t + \Delta t)} (e^{(\lambda - \mu)(t + \Delta t)} - 1) \\ + [e^{(\lambda - \mu)(t + \Delta t)}]^2 Var(N(0)) \\ + Var(N(0)) \frac{\lambda + \mu}{\lambda - \mu} e^{(\lambda - \mu)(t + \Delta t)} (e^{(\lambda - \mu)(t + \Delta t)} - 1) \\ \approx [E(N(0))]^2 \left[\frac{\lambda + \mu}{\lambda - \mu} e^{(\lambda - \mu)t} (e^{(\lambda - \mu)t} - 1) + (\lambda + \mu) e^{(\lambda - \mu)t} (2e^{(\lambda - \mu)t} - 1) \Delta t \right] \\ + Var(N(0)) e^{2(\lambda - \mu)t} [1 + 2(\lambda - \mu) \Delta t] \\ + Var(N(0)) \left[\frac{\lambda + \mu}{\lambda - \mu} e^{(\lambda - \mu)t} (e^{(\lambda - \mu)t} - 1) + (\lambda + \mu) e^{(\lambda - \mu)t} (2e^{(\lambda - \mu)t} - 1) \Delta t \right]$$

Then, expanding $\ln Var(N(t))$ and $\ln E(N(t))$, we use the expansions

$$\ln Var(N(t + \Delta t)) \approx \ln Var(N(t)) + \frac{[dVar(N(t))/dt] \Delta t}{Var(N(t))} \quad (A6)$$

$$\begin{aligned}\ln E(N(t + \Delta t)) - \ln E(N(t)) &= \ln E(N(0))e^{(\lambda-\mu)(t+\Delta t)} - \ln E(N(0))e^{(\lambda-\mu)t} \\ &= (\lambda - \mu)\Delta t\end{aligned}\quad (A7)$$

Therefore, substituting (A6) and (A7) into the expression for b (A4), we find

$$b(t) = \frac{\ln \text{Var}(N(t + \Delta t)) - \ln \text{Var}(N(t))}{\ln E(N(t + \Delta t)) - \ln E(N(t))} \approx \frac{d\text{Var}(N(t))/dt}{(\lambda - \mu)\text{Var}(N(t))}$$

where

$$\begin{aligned}\frac{d\text{Var}(N(t))}{dt} &= [E(N(t))]^2 (\lambda + \mu)e^{(\lambda-\mu)t} (2e^{(\lambda-\mu)t} - 1) \\ &\quad + 2\text{Var}(N(0))(\lambda - \mu)e^{2(\lambda-\mu)t} \\ &\quad + \text{Var}(N(0))(\lambda + \mu)e^{(\lambda-\mu)t} (2e^{(\lambda-\mu)t} - 1)\end{aligned}$$

Then, $b(t)$ can be further expressed as

$$b(t) \approx \frac{2 + 2A - AB}{1 + A - AB}$$

where

$$A = \frac{\text{Var}(N(0)) + [E(N(0))]^2}{\text{Var}(N(0))} \frac{\lambda + \mu}{\lambda - \mu}$$

$$B = e^{-(\lambda-\mu)t}$$

It can be show that

$$\lim_{t \rightarrow \infty} b = 2, \text{ when } \lambda > \mu;$$

$$\lim_{t \rightarrow \infty} b = 1, \text{ when } \lambda < \mu.$$

Citation:

Goodman, L.A., 1960. On the exact variance of products. J. Am. Stat. Assoc., 55, 708–713.

Appendix S3. Matlab scripts to do simulations and to produce figures.

Texts from 7 Matlab M-files are attached here.

File “birthdeathExample.m” gives an example run of birth-and-death process

File “birthdeathSimulator.m” is a function of Monte Carlo time steps simulation of birth-and-death process, which is called by other files when needed.

Files “Codes_for_Scenario1.m”, “Codes_for_Scenario2.m”, “Codes_for_Scenario3.m”, and “Codes_for_Scenario4.m” are simulation experiments. See paper for detail descriptions.

File “Codes_for_Figures.m” generates all the figures except Figure 1. Need data outputs from the above simulation experiments to run this file.

File “birthdeathExample.m”

```
% Example for Birth-death stochastic simulation
%       (Monte Carlo steps, 1 birth or 1 death each time step)
%
% Equation:  $dN/dt = (\lambda - \mu) * N$ 
%
% Contact: Jiang Jiang (jjiang@nimbios.org)
% Date:      14 January, 2014

mu = 0.01;           % Death rate
lambda = 0.012;     % Birth rate

n = 10;             % Initial population size
tMax = 1000;       % Maximum time span (e.g. 1000 years)

M = n.*exp((lambda-mu).*[0:tMax]); % Mean population size
figure(1)
hold on
plot([0:tMax],M,'r','LineWidth',1.4)
xlim([0 tMax])
xlabel('Time')
ylabel('Population size')

for rep = 1:20      % Repeat 20 times
    clear tjump state n
    n = 10;
    tjump(1) = 0;   % Start at time 0
    state(1) = n;   % at time 0, number of population = n
    k = 1;          % Index used for store tjump(k) and state(k)
    tcum = 0;       % Cumulate time
    while tcum < tMax % Run the loop until time reach tMax
        k = k + 1;
        lambda_n = lambda*n; % This can be changed by the Equation
        mu_n = mu*n; % This can be changed by the Equation
        time_lambda = -log(rand)/lambda_n; % Waiting time for one birth
        time_mu = -log(rand)/mu_n; % Waiting time for one death
        time = min(time_lambda,time_mu); % Inter-step times
        if time_lambda < time_mu
            n = n + 1; % Birth
        else
            n = n - 1; % Death
        end
        state(k) = n; % Record the population size
        tjump(k) = time; % Record the time interval
        tcum = tcum + time; % Update the cumulate time
    end
    tjump = cumsum(tjump);
    stairs(tjump,state); % Plot a staircase graph

end
M = mean(state(end,:))
```

File “birthdeathSimulator.m”

```
% Birth-death stochastic simulation
% (Monte Carlo steps, 1 birth or 1 death each time step)
%
% Equation:  $dN/dt = (\lambda - \mu) * N$ 
% This code is a function called by other scenario simulations
% to see how this function works, run birthdeathExample.m
%
% Contact: Jiang Jiang (jjjiang@nimbios.org)
% Date: 14 January, 2014

function storeN=birthdeathSimulator(lambda,mu,subplots,sampletime,n0)

tMax = sampletime; % Maximum time span (e.g. 1000 years)
storeN = zeros(1,subplots);
for rep = 1:subplots

n = n0;
%tjump(1) = 0; % Start at time 0
%state(1) = n; % at time 0, number of population = n
k = 1; % Index used for store tjump(k) and state(k)
tcum = 0; % Cumulate time
while tcum<tMax % Run the loop until time reach tMax
    k = k + 1;
    lambda_n = lambda*n; % This can be changed by the Equation
    mu_n = mu*n; % This can be changed by the Equation
    time_lambda = -log(rand)/lambda_n; % Waiting time for one birth
    time_mu = -log(rand)/mu_n; % Waiting time for one death
    time = min(time_lambda,time_mu); % Inter-step times
    if time_lambda<=time_mu
        n = n + 1; % Birth
    else
        n = n - 1; % Death
    end
    %state(k) = n; % Record the population size
    %tjump(k) = time; % Record the time interval
    tcum = tcum + time; % Update the cumulate time
end
%tjump = cumsum(tjump);
storeN(rep) = n;

end

end
```

Files “Codes_for_Scenariol.m”

```
% Codes for Scenario 1 in
% Jiang et al. http://dx.doi.org/10.1016/j.ecolmodel.2014.06.022
%
% Contact: Jiang Jiang (jjiang@nimbios.org)
% Date:      14 January, 2014

clear all
time_begin = cputime;
mu = 0.01;           % Death rate
n0 = 50;            % Initial subplots population size
subplots = 1000;    % Number of subplots
% Selected points for lambda
pointx = [0.0085 0.009 0.0095 0.0098 0.0099 0.01 0.0101 ...
          0.0102 0.0105 0.011 0.0115];

% For each lambda we selected, sample 100 patches,
% each plot has different age varies between 1000–2000 years.
len = length(pointx);
r2 = zeros(1,len); % Store R2
b = zeros(1,len);  % Store slope b
x_save = zeros(100,len); % Store data for log(Mean)
y_save = zeros(100,len); % Store data for log(Variance)

% Seeds the random number generator. If you use older version of
matlab, rng(2014) may doesn't work. use rand('seed',0) instead.
rng(2014)
% rand('seed',0)

for k = 1:len % Select lambda
    lambda = pointx(k)
    meansav = zeros(1,100);
    varsav = zeros(1,100);
    for i = 1:100 % 100 patches
        sampletime = 1000+(rand*1000);
        % Call the simulator function, and return population size
        StoreN = birthdeathSimulator(lambda,mu,subplots,sampletime,n0);
        meansav(i) = mean(StoreN);
        varsav(i) = var(StoreN);
    end
    x = log(meansav);
    y = log(varsav);
    [p s] = polyfit(x,y,1);
    r1 = corrcoef(x,y);
    r2(1,k) = r1(1,2)^2;
    b(1,k) = p(1);
    x_save(:,k) = x';
    y_save(:,k) = y';
end

% Save data on a file named Scenariol
save Scenariol x_save y_save b r2 pointx
time_end = cputime;
time_elapse = (time_end-time_begin)/60;
disp(['Scenariol COMPLETED! Elapsed time = ' num2str(time_elapse) '
Minutes']);
```

Files “Codes_for_Scenario2.m”

```
% Codes for Scenario 2 in
% Jiang et al. http://dx.doi.org/10/1016/j.ecolmodel.2014.06.022
%
% Contact: Jiang Jiang (jjiang@nimbios.org)
% Date:      14 January, 2014

clear all
time_begin = cputime;
mu = 0.01;           % Death rate
sampletime = 2000;  % Age of patches
subplots = 1000;    % Number of subplots

% Selected points for lambda
pointx = [0.0098 0.01 0.0102];
% For each lambda we selected, sample 100 patches,
% each plot has different age varies between 1000-2000 years.
len = length(pointx);
r2 = zeros(1,len);   % Store R2
b = zeros(1,len);    % Store slope b
x_save = zeros(100,len); % Store data for log(Mean)
y_save = zeros(100,len); % Store data for log(Variance)

% Seeds the random number generator. If you use older version of
matlab, rng(2014) may doesn't work. use rand('seed',0) instead.
rng(2014)
% rand('seed',0)

for k = 1:len
    lambda = pointx(k)
    % Record mean and variance of subplots for each of the 100 patches
    meansav = zeros(1,100);
    varsav = zeros(1,100);
    for i = 1:100      % 100 plots
        n0 = 10+fix(rand*90);
        % Call the simulator function, and return population size
        StoreN = birthdeathSimulator(lambda,mu,subplots,sampletime,n0);
        meansav(i) = mean(StoreN);
        varsav(i) = var(StoreN);
    end
    x = log(meansav);
    y = log(varsav);
    [p s] = polyfit(x,y,1);
    r1 = corrcoef(x,y);
    r2(1,k) = r1(1,2)^2;
    b(1,k) = p(1);
    x_save(:,k) = x';
    y_save(:,k) = y';
end

% Save data on a file named Scenario2
save Scenario2 x_save y_save b r2 pointx
time_end = cputime;
time_elapse = (time_end-time_begin)/60;
disp(['Scenario2 COMPLETED! Elapsed time = ' num2str(time_elapse) '
Minutes']);
```

Files “Codes_for_Scenario3.m”

```
% Codes for Scenario 3 in
% Jiang et al. http://dx.doi.org/10.1016/j.ecolmodel.2014.06.022
%
% Contact: Jiang Jiang (jjjiang@nimbios.org)
% Date:      14 January, 2014

clear all
time_begin = clock;
mu = 0.01;          % Death rate
subplots = 1000;   % Number of subplots

% Selected points for lambda
pointx = [0.008:0.0005:0.012];
% For each lambda we selected, sample 100 patches, repeat 20 times
% each plot has different age varies between 1000-2000 years.
% each subplot has different initial population size between 10-100.
len = length(pointx);
r2 = zeros(20,len); % Store R2
b = zeros(20,len);  % Store slope b

% Seeds the random number generator. If you use older version of
matlab, rng(2014) may doesn't work. use rand('seed',0) instead.
rng(2014)
% rand('seed',0)

for k = 1:len % Select lambda
    lambda = pointx(k)
    for m = 1:20 % Repeat 20 times
        Repeat = m
        % Record mean and variance of subplots for each of the 100 patches
        meansav = zeros(1,100);
        varsav = zeros(1,100);
        for i = 1:100 % 100 patches
            sampletime = 1000+(rand*1000); % Age of patches
            n0 = 10+fix(rand*90); % Initial subplot population size
            % Call the simulator function, and return population size
            StoreN = birthdeathSimulator(lambda,mu,subplots,sampletime,n0);
            meansav(i) = mean(StoreN);
            varsav(i) = var(StoreN);
        end
        x = log(meansav);
        y = log(varsav);
        [p s] = polyfit(x,y,1);
        r1 = corrcoef(x,y);
        r2(m,k) = r1(1,2)^2;
        b(m,k) = p(1);
    end
end

% Save data on a file named Scenario3
save Scenario3 b r2 pointx
time_end = clock;
time_elapse = (time_end-time_begin);
hours = time_elapse(3)*24+time_elapse(4)+time_elapse(5)/60;
disp(['Scenario3 COMPLETED! Elapsed time = ' num2str(hours) ' Hours']);
```

Files “Codes_for_Scenario4.m”

```
% Codes for Scenario 4 in
% Jiang et al. http://dx.doi.org/10/1016/j.ecolmodel.2014.06.022
%
% Contact: Jiang Jiang (jjiang@nimbios.org)
% Date:      14 January, 2014

clear all
time_begin = clock;
mu = 0.01;          % Death rate
% Selected points for lambda
pointx = [0.008:0.0005:0.012];
% For each lambda we selected, sample 100 patches, repeat 20 times
% Sample across time, between [Tage/2 Tage]
% each plot has different age varies between 1000-2000 years.
% each subplot has different initial population size between 10-100.
len = length(pointx);
r2 = zeros(20,len); % Store R2
b = zeros(20,len);  % Store slope b
% Seeds the random number generator. If you use older version of
matlab, rng(2014) may doesn't work. use rand('seed',0) instead.
rng(2014)
% rand('seed',0)
for k = 1:len          % Select lambda
    lambda = pointx(k)
for m = 1:20          % Repeat 20 times
    Repeat = m
    % Record mean and variance for each of the 100 patches
    meansav = zeros(1,100);
    varsav = zeros(1,100);
for j = 1:100        % 100 patches
    n0 = 10+fix(rand*90); % Initial population size
    Tage = 1000+(rand*1000); % Age of patches
    StoreNs = zeros(1,1000); % Record population size at sampling time
for i = 1:1000      % Pick 1000 sample times
    samplertime = Tage/2+rand*Tage/2;
    StoreNs(i) = birthdeathSimulator(lambda,mu,1,samplertime,n0);
end
meansav(j) = mean(StoreNs);
varsav(j) = var(StoreNs);
end
x = log(meansav);
y = log(varsav);
[p s] = polyfit(x,y,1);
r1 = corrcoef(x,y);
r2(m,k) = r1(1,2)^2;
b(m,k) = p(1);
end
end

% Save data on a file named Scenario4
save Scenario4 b r2 pointx
time_end = clock;
time_elapse = (time_end-time_begin);
hours = time_elapse(3)*24+time_elapse(4)+time_elapse(5)/60;
disp(['Scenario4 COMPLETED! Elapsed time = ' num2str(hours) ' Hours']);
```

File "Codes_for_Figures.m"

```
% Codes for Figures in
% Jiang et al. http://dx.doi.org/10/1016/j.ecolmodel.2014.06.022
%
% Figure 2. Two break plots illustrate relationship between Var and Mean
% Figure 3. Illustration of Equation (3) overlaps points from Scenario 1
%           (needs data produced by "Codes_for_Scenario1.m")
% Figure 4. Three sample plots for Scenario 2 (need data produced by
%           "Codes_for_Scenario2.m")
% Figure 5. Boxplot for Scenario 3 (Data from "Codes_for_Scenario3.m")
% Figure 6. Boxplot for Scenario 4 (Data from "Codes_for_Scenario4.m")
% Figure S1. Four sample plots for Scenario 1, each plot produce a
% point in Figure 3. (Data from "Codes_for_Scenario1.m")
%
% Contact: Jiang Jiang (jjjiang@nimbios.org)
% Date:      14 January, 2014

clear all
close all
%% Figure 2.
% Relationships of variance and mean in log scale
%
% Figure 2a. when lambda greater than mu, both mean and variance of
% population increase with time from the birth-and-death process.
% I set up a break for axis and the relationship curve. Right and above
% of the break (larger time) are scaled for illustration purpose.
%
% Figure 2b. when lambda smaller than mu, mean of population decrease,
% variance increases when t is small, then decreases as t increase.
% No break for axis, but a break for the relationship curve.

lambda = 0.0101;
mu = 0.01;
n0 = 100;
% Two sample times, before and after break
sampletimel = [10:10:1000];
sampletimel2 = [40000:10:41000];
% Mean and variance are calculated from birth-death process (Pielou
1977)
M_est1 = n0.*exp((lambda-mu).*sampletimel);
V_est1 = n0.*(lambda+mu)./(lambda-mu).*exp((lambda-mu).*sampletimel).*
...
    (exp((lambda-mu).*sampletimel)-1);
x1 = log(M_est1);
y1 = log(V_est1);
M_est2 = n0.*exp((lambda-mu).*sampletimel2);
V_est2 = n0.*(lambda+mu)./(lambda-mu).*exp((lambda-mu).*sampletimel2).*
...
    (exp((lambda-mu).*sampletimel2)-1);
x2 = log(M_est2);
y2 = log(V_est2);

figure
set(gcf, 'Color', 'White')
hold on
% Plot first half before break
```

```

plot(x1,y1,'k','LineWidth',1.5)
xtick=get(gca,'XTick');
xbreak = xtick(xtick>x1(end));
xbreak = xbreak(1);
ytick=get(gca,'YTick');
ybreak = ytick(ytick>y1(end));
ybreak = ybreak(1);

% Rescale second half after break, and then plot
x2_rescale_coef = (x1(end)-x1(1))/(x2(end)-x2(1))/3;
y2_rescale_coef = (y1(end)-y1(1))/(y2(end)-y2(1))/10;
x2_rescale = (x2 - x2(1))*x2_rescale_coef + xbreak+0.01;
y2_rescale = (y2 - y2(1))*y2_rescale_coef + ybreak+0.5;
plot(x2_rescale,y2_rescale,'k','LineWidth',1.5)
axis([4.6 4.78 3 10])
xlabel('ln(Mean)','FontSize',14)
ylabel('ln(Variance)','FontSize',14)

% Set up axis tick labels
set(gca,'XTick',[4.6:0.02:4.7 4.74])
set(gca,'XTickLabel',{'4.6';'4.62';'4.64';'4.66';'4.68';'4.7';...
    num2str(fix(x2(end)))})
set(gca,'YTick',[3:7 9])
set(gca,'YTickLabel',{'';'4';'5';'6';'7';num2str(fix(y2(end)))})

% Plot the break sign "//" on axis
annotation('rectangle',[0.63 0.08 0.05
0.05],'EdgeColor','None','FaceColor','White')
annotation('line',[0.64 0.65],[0.09 0.12],'LineWidth',1.5,'Color','k')
annotation('line',[0.65 0.66],[0.09 0.12],'LineWidth',1.5,'Color','k')
annotation('rectangle',[0.11 0.7 0.05
0.05],'EdgeColor','None','FaceColor','White')
annotation('line',[0.12 0.14],[0.70 0.72],'LineWidth',1.5,'Color','k')
annotation('line',[0.12 0.14],[0.715
0.735],'LineWidth',1.5,'Color','k')

% Plot the break sign on the curve
line([4.713 4.714],[8.1 8.2],'LineWidth',1.1,'Color','k')
line([4.713 4.714],[8.1 8.05],'LineWidth',1.1,'Color','k')
line([4.714 4.713],[8.05 7.95],'LineWidth',1.1,'Color','k')
line([4.715 4.716],[8.1 8.2],'LineWidth',1.1,'Color','k')
line([4.715 4.716],[8.1 8.05],'LineWidth',1.1,'Color','k')
line([4.716 4.715],[8.05 7.95],'LineWidth',1.1,'Color','k')

% Write notes on graphs, showing which direction t is larger or smaller
text(4.7, 6,'0','FontSize',14)
text(4.72,6.5,'t','FontSize',14)
text(4.74,7,'\infty','FontSize',14)
text(4.73,9.2,'Slope = 2.0','FontSize',14)
text(4.62,10,'a','FontSize',14)
annotation('arrow',[0.63 0.58],[0.505 0.47],'Color','k')
annotation('arrow',[0.67 0.72],[0.53 0.56],'Color','k')

% Save graph as .eps file, resolution 600.
print('-depsc','-r600','Fig2a')

```

```

%% Figure 2b
n0 = 100;
lambda = 0.0099;
mu = 0.01;
% Two sample times, before and after break
samplertime1 = [100:10:20000];
samplertime2 = [35000:10:45000];
% Mean and variance are calculated from birth-death process (Pielou
1977)
M_est1 = n0.*exp((lambda-mu).*samplertime1);
V_est1 = n0.*(lambda+mu)./(lambda-mu).*exp((lambda-mu).*samplertime1).*
...
    (exp((lambda-mu).*samplertime1)-1);
x1 = log(M_est1);
y1 = log(V_est1);
M_est2 = n0.*exp((lambda-mu).*samplertime2);
V_est2 = n0.*(lambda+mu)./(lambda-mu).*exp((lambda-mu).*samplertime2).*
...
    (exp((lambda-mu).*samplertime2)-1);
x2 = log(M_est2);
y2 = log(V_est2);

% Combine the break as Not a Number
x = [x1 NaN x2];
y = [y1 NaN y2];

figure
set(gcf, 'Color', 'White')
hold on
plot(x,y, 'k', 'LineWidth', 1.5)
xlabel('ln(Mean)', 'FontSize', 14)
ylabel('ln(Variance)', 'FontSize', 14)

% Write notes on graphs, showing which direction t is larger or smaller
text(4, 7, '0', 'FontSize', 14)
text(3.5, 7.5, 't', 'FontSize', 14)
text(3, 7, '\infty', 'FontSize', 14)
text(0.5, 5.6, 'Slope = 1.0', 'FontSize', 14)
text(0.5, 9, 'b', 'FontSize', 14)
annotation('arrow', [0.66 0.61], [0.6 0.53], 'Color', 'k')
annotation('arrow', [0.69 0.74], [0.6 0.53], 'Color', 'k')

% Plot the break sign on the curve
line([1.7 1.72], [7.1 7.2], 'LineWidth', 1.1, 'Color', 'k')
line([1.7 1.72], [7.1 7.05], 'LineWidth', 1.1, 'Color', 'k')
line([1.72 1.7], [7.05 6.95], 'LineWidth', 1.1, 'Color', 'k')
line([1.74 1.76], [7.1 7.2], 'LineWidth', 1.1, 'Color', 'k')
line([1.74 1.76], [7.1 7.05], 'LineWidth', 1.1, 'Color', 'k')
line([1.76 1.74], [7.05 6.95], 'LineWidth', 1.1, 'Color', 'k')

% Save graph as .eps file, resolution 600.
print('-depsc', '-r600', 'Fig2b')

%% Figure 3
% Illustration of Equation (3), overlap data points from Scenario 1
mu = 0.01;
t = 2000;

```

```

k=0;
xs = [];      % Record lambda

% When lambda=mu,singularity.
% So we plot two parts separately lambda<mu and lambda>mu
clear b1 b2
for lambda = 0.005:0.00005:0.00999999 % When lambda<mu
    k=k+1;
    xs = [xs lambda];
    b1(k) = 1 + 1/(1-exp(-(lambda-mu)*t));
    b2(k) = NaN;
end
k2 = k;
xs2 = xs;
for lambda = 0.01005:0.0001:0.015 % When lambda>mu
    xs2 = [xs2 lambda];
    k2=k2+1;
    b2(k2) = 1 + 1/(1-exp(-(lambda-mu)*t));
end

% Set up figure properties
fig1=figure;
set(fig1,'Units','inches');
set(fig1,'Position',[5 4 5 8])
set(gcf,'PaperPositionMode','auto')
plot(xs,b1,'linewidth',1.4)
hold on
plot(xs2,b2,'linewidth',1.4)
xlabel('\lambda','fontsize',14)
ylabel('b','fontsize',14)
set(gca,'YTick',[-10 -5 0 1 2 5 10 15])
grid on

% Load data from Scenario 1
% first need to run "Codes_for_Scenario1.m", which generate
% a data file named "Scenario1.mat"
load Scenario1.mat
b(pointx==0.01)=[];
pointx(pointx==0.01)=[];
plot(pointx,b,'k0')
hold off

print('-depsc','-r600','Fig3')

%% Figure 4
% Three selected outputs from Scenario 2.
% first need to run "Codes_for_Scenario2.m", which generate
% a data file named "Scenario2.mat"
load Scenario2.mat

for index = 3:-1:1 % Index for lambda values stored in Scenario 2
    lambda = pointx(index);
    x = x_save(:,index); % Extract stored log(Mean)
    y = y_save(:,index); % Extract stored log(Variance)

    % Linear regression. p1 is slope; p2 is intercept
    [p s] = polyfit(x,y,1);

```

```

p1 = sprintf('%0.2f', p(1));
p2 = sprintf('%0.2f', p(2));
% Calculate R2
r1 = corrcoef(x,y);
r2 = r1(1,2)^2;
r2 = sprintf('%0.4f', r2);

% Plot dots and linear regression
figure
plot(x,y, '.')
xx = min(x):0.1:max(x);
yy = p(1).*xx+p(2);
hold on
plot(xx,yy, 'k', 'LineWidth', 1.4)
xlabel('ln(Mean)', 'FontSize', 14)
ylabel('ln(Variance)', 'FontSize', 14)

% Write equation on each graph
switch index
    case 3
        text(3,8.9,['ln(Variance)=', num2str(p1), 'ln(Mean)+', ...
            num2str(p2)], 'FontSize', 14)
        text(3,8.7,['R^2=', num2str(r2)], 'FontSize', 14)
        text(2.75,9.2, 'a')
        print('-depsc', '-r600', 'Fig4a')
    case 2
        text(2.5,8,['ln(Variance)=', num2str(p1), 'ln(Mean)+', ...
            num2str(p2)], 'FontSize', 14)
        text(2.5,7.8,['R^2=', num2str(r2)], 'FontSize', 14)
        text(2.25,8.25, 'b')
        print('-depsc', '-r600', 'Fig4b')
    case 1
        text(2.4,7.5,['ln(Variance)=', num2str(p1), 'ln(Mean)+', ...
            num2str(p2)], 'FontSize', 14)
        text(2.4,7.3,['R^2=', num2str(r2)], 'FontSize', 14)
        text(2.2,7.75, 'c')
        print('-depsc', '-r600', 'Fig4c')
end

end

%% Figure 5
% Outputs for Scenario 3.
% first need to run "Codes_for_Scenario3.m", which generate
%     a data file named "Scenario3.mat"

load Scenario3.mat
lambda = pointx;
figure
boxplot(b,lambda)
xlabel('\lambda', 'FontSize', 14)
ylabel('b', 'FontSize', 14)
print('-depsc', '-r600', 'Fig5')

%% Figure 6
% Outputs for Scenario 4.
% first need to run "Codes_for_Scenario4.m", which generate

```

```

%       a data file named "Scenario4.mat"
load Scenario4.mat
lambda = pointx;
figure
boxplot(b,lambda)
xlabel('\lambda', 'FontSize',14)
ylabel('b', 'FontSize',14)
print('-depsc', '-r600', 'Fig6')

%% Figure S1
% Four selected outputs from Scenario 1.
% first need to run "Codes_for_Scenario1.m", which generate
%       a data file named "Scenario1.mat"

load Scenario1.mat

% Set up figure properties
fig1=figure;
set(fig1, 'Units', 'inches');
set(fig1, 'Position', [4 4 12 8])
set(gcf, 'PaperPositionMode', 'auto')

len = length(pointx); % How many lambdas
for index = 1:len % Index for lambda values stored in Scenario 1
    lambda = pointx(index);
    x = x_save(:,index); % Extract stored log(Mean)
    y = y_save(:,index); % Extract stored log(Variance)

    % Linear regression. p1 is slope; p2 is intercept
    [p s] = polyfit(x,y,1);
    r1 = corrcoef(x,y);
    r2 = r1(1,2)^2;
    r2 = sprintf('%0.4f', r2);
    b = sprintf('%0.2f', p(1));

    % Plot dots and linear regression
    position = index;
    if index>=8; position=index+1;end
    subplot(3,4,position)
    plot(x,y, '.')
    xx = min(x):0.01:max(x);
    yy = p(1).*xx+p(2);
    hold on
    plot(xx,yy, 'k')
    if position>=9
        xlabel('ln(Mean)', 'FontSize',12)
    end
    if mod(position-1,4)==0
        ylabel('ln(Variance)', 'FontSize',12)
    end
    axis([min(x)-0.2*(max(x)-min(x)) max(x)+0.1*(max(x)-min(x)) ...
        min(y)-0.1*(max(y)-min(y)) max(y)+0.2*(max(y)-min(y))])

    % Write lambda, b, and R2 on each graph
    if index==4 | index==5
        text(min(x)-0.1*(max(x)-min(x)),max(y)-0.6*(max(y)-min(y)), ...)

```

```

    ['\lambda = ', num2str(lambda)], 'FontSize', 12)
text(min(x)-0.1*(max(x)-min(x)), max(y)-0.75*(max(y)-min(y)), ...
    ['b = ', num2str(b)], 'FontSize', 12)
text(min(x)-0.1*(max(x)-min(x)), max(y)-0.9*(max(y)-min(y)), ...
    ['R^2 = ', num2str(r2)], 'FontSize', 12)
else
text(min(x)-0.1*(max(x)-min(x)), max(y)+0.1*(max(y)-min(y)), ...
    ['\lambda = ', num2str(lambda)], 'FontSize', 12)
text(min(x)-0.1*(max(x)-min(x)), max(y)-0.05*(max(y)-min(y)), ...
    ['b = ', num2str(b)], 'FontSize', 12)
text(min(x)-0.1*(max(x)-min(x)), max(y)-0.2*(max(y)-min(y)), ...
    ['R^2 = ', num2str(r2)], 'FontSize', 12)
end

end

print('-depsc', '-r600', 'Fig_s1')

```