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# Temporal fluctuation scaling in populations and communities

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*Abstract.* Taylor's law, one of the most widely accepted generalizations in ecology, states that the variance of a population abundance time series scales as a power law of its mean. Here we reexamine this law and the empirical evidence presented in support of it. Specifically, we show that the exponent generally depends on the length of the time series, and its value reflects the combined effect of many underlying mechanisms. Moreover, sampling errors alone, when presented on a double logarithmic scale, are sufficient to produce an apparent power law. This raises questions regarding the usefulness of Taylor's law for understanding ecological processes. As an alternative approach, we focus on short-term fluctuations and derive a generic null model for the variance-to-mean ratio in population time series from a demographic model that incorporates the combined effects of demographic and environmental stochasticity. After comparing the predictions of the proposed null model with the fluctuations observed in empirical data sets, we suggest an alternative expression for fluctuation scaling in population time series. Analyzing population fluctuations as we have proposed here may provide new applied (e.g., estimation of species persistence times) and theoretical (e.g., the neutral theory of biodiversity) insights that can be derived from more generally available short-term monitoring data.

*Key words: birds; demographic noise; environmental stochasticity; population abundance variance; sampling error; Taylor's law; temporal variance; trees; variance–mean relations.*

## INTRODUCTION

One of the major challenges in the study of ecological systems, and complex systems in general, is to characterize and explain patterns of temporal variability and stability. Understanding such patterns is important for both basic ecology, where the degrees of population and community stability are debated, and applied conservation, where temporal fluctuations affect the likelihood of species persistence across human-managed landscapes. A typical scenario where this problem arises is the analysis of time series showing the abundance of a given species at a particular location. Such a time series is usually quite noisy, and one would like to utilize this noisiness in order to characterize the stability properties of the population.

In this context, many studies have reported that the variance ($S$) of population size grows as a simple power of the mean ($N$)

$$S = c \times N^z, \quad 1 \leq z \leq 2 \quad (1)$$

where $c$ and $z$ are constants. This pattern, known as

Taylor's law (Taylor 1961, Taylor and Woiwod 1980, 1982), is considered one of a few general quantitative laws in ecology (Keitt et al. 2002, Kilpatrick and Ives 2003) and other complex systems (de Menezes and Barabasi 2004, Eisler et al. 2008). In fact, this law is used in two distinct contexts (Kendal 2004): to assess spatial clustering and patchiness, and to characterize time series (Taylor and Woiwod 1980, 1982, Kilpatrick and Ives 2003). We consider only Taylor's law for time series, which is recognized as a general scaling relation between a population's mean abundance and its variance over time (Anderson et al. 1982).

Observed variations in population abundance are expected to be caused by a few underlying mechanisms. The simplest of these is sampling errors. Even if the actual size of the population is fixed, the survey may sample different individuals leading to variation in counts across repeated surveys. The stochastic nature of the birth–death process provides us with another source of variation, demographic noise, where individuals vary in their reproductive success in an uncorrelated manner. If, for example, every individual produces, on average, one offspring and then dies, the abundance will fluctuate without an overall trend, and the variation per generation is proportional to the square root of the population size (Van Kampen 1981). Environmental stochasticity, on the other hand, simultaneously affects

all the individuals in the population, causing periods when the growth rate, when averaged over the population, grows or is positive or negative. Accordingly, variation scales linearly with population size (Engen et al. 1998, Lande et al. 2003). It has been shown that if dynamics are governed solely by demographic noise, then the exponent $z$ in Eq. 1 approaches one. Conversely, if environmental stochasticity is the main driver of the change, then $z = 2$ (Ballantyne and Kerkhoff 2007). Finally, stabilizing forces, like a finite carrying capacity, may balance the effects of stochasticity and limit the range of possible population sizes.

Our aim is to reevaluate the validity and usefulness of Taylor's law (as expressed in Eq. 1) and to suggest an alternative framework for the analysis of short-term fluctuations in empirical data sets. Applying our method to relatively clean (error-free) data sets, we can suggest a new empirical law. One of the applied benefits of this approach is that it can be implemented with short-term data which is more widely available, across many more species, than long-term data.

In particular, regarding Taylor's law, we will point out the following obstacles: (1) the variance-to-mean ratio depends strongly on the length of the time series, (2) the apparent agreement of empirical data sets with Eq. 1 may be an artifact of sampling errors and the (mis)use of the double logarithmic scale, and (3) even in the best-case scenario, when the variance-to-mean ratio has converged to its long-term value, it reflects a nontrivial interplay between the noise and the stabilizing mechanisms, rendering it difficult to interpret.

Given the difficulties associated with evaluating and interpreting Taylor's power law, we suggest separating the question of population variability and stability into two components: long-term behavior, governed by stabilizing mechanisms (or lack thereof; Pimm and Redfearn 1988, Hanski 1990) and short-term fluctuations and their scaling with population size. The latter is the focus of our analysis.

The question of short-term fluctuation scaling, i.e., how are survey-to-survey changes in population size dependent on population size itself, addresses a fundamental aspect of the behavior of the system. Without a good assessment of these fluctuations, it is very difficult to interpret the long-term properties of the system and to extract information about regulating forces (Freckleton et al. 2006). Moreover, population viability analyses usually depend on the balance between stabilizing mechanisms and stochasticity, and the latter should be well characterized if we are to have confidence in estimated persistence probabilities. Finally, the neutral theory of community dynamics (Hubbell 2001), a central (although hotly debated) paradigm in contemporary ecology, assumes dynamics are driven by pure demographic stochasticity, an assumption that may be examined within our framework.

As an alternative to Taylor's law, we present and solve a null model for populations under both demographic and environmental stochasticity and explain how to present the results in a way that enables an informative comparison between the model and the data. Comparing the results obtained using high quality data sets and this null model, we can rule out a simple combination of demographic and environmental noise and suggest an alternative nontrivial expression for fluctuation scaling. Finally, we will discuss the implications of our results, including its relevance to the debate surrounding the neutral theory of biodiversity.

## SHORT- VS. LONG-TERM DYNAMICS

To consider the relation between time series length and the variance-to-mean ratio, let us begin with a qualitative analysis. In general, when a system is affected by noise and stabilizing mechanisms, the noise is dominant over short time scales, and the relative importance of stabilizing forces grows in time, eventually dominating the dynamics over long time horizons.

As an example, let us consider a local population fluctuating around an average size $n$. For simplicity, we represent the stabilizing forces as reflecting boundaries at $n + p$ and $n - p$ as in Stong's density-vague dynamics (Strong 1986); see the illustration in Fig. 1. That is to say, the stochasticity-driven fluctuations are not restricted as long as the population size remains between the boundaries. We discuss several alternative versions of this model in Appendix A. In particular, we consider the case of a population driven by pure demographic noise, as well as one driven by both demographic and environmental noise. Another parameter one can modify is the band width ($p$) of the stabilizing force. The width may be taken to be proportional to $n$, and Appendix A presents cases where $p \sim \sqrt{n}$ and $p \sim n$ are simulated.

Both demographic and environmental noise cause the population to perform a random walk between the two boundaries. Over short time scales, before the typical trajectory hits one of the boundaries, the exponent $z$ reflects pure stochastic motion, with $z = 1$ for demographic and $z = 2$ for environmental noise (Van Kampen 1981, Engen et al. 1998, Lande et al. 2003). Over longer time series, the typical trajectory uniformly covers the allowed band of abundances, and the variance scales with $p^2$. Accordingly, the variance-to-mean ratio is determined by the relationship between $n$ and $p$. If $p$ is proportional to $n$, then $z = 2$, and if $p \sim \sqrt{n}$, then $z = 1$, both results being independent of the underlying stochastic process. Hence, if the noise is purely demographic and $p \sim n$, the exponent $z$ approaches 1 over short time intervals and will increase to 2 over long time intervals. Conversely, for environmental stochasticity and $p \sim \sqrt{n}$, estimates of $z$ will start at 2 in the short term and relax to $z = 1$ in the long term. See Appendix A for a summary and a few numerical demonstrations.

All of the above is true for the case of sharp, perfectly reflecting boundaries. If we relax this constraint and let
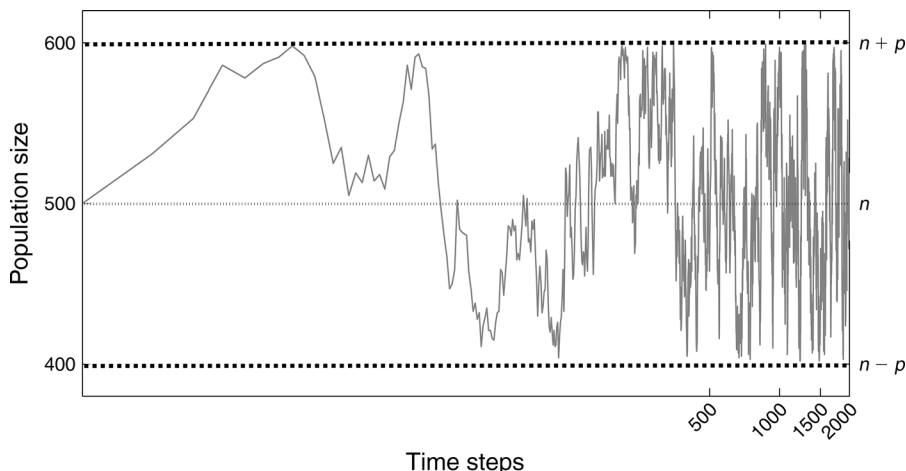
Fig. 1. An illustration showing typical density-vague dynamics with population size $n = 500$ (gray line, middle) and bandwidth $p = 100$ (black dotted lines). A logarithmic scale is used for the $x$-axis (time), to emphasize the distinction between the free random walk in the short-term and the effects of stabilizing mechanism at the long-term.

the strength of the stabilizing force behave more generally (e.g., proportional to the distance from $n$, as in logistic or Gompertz population growth models), then interpretations of $z$ become more complicated. In this case, the nature and strength of the noise affects the width of the allowed band. Accordingly, when the empirical Taylor's exponent $z$ is estimated for time series of arbitrary length (as is usually the case), its magnitude reflects a balance between stochastic fluctuations and the restoring forces in a nontrivial way.

This poses a serious problem for the interpretation of empirical variance–mean relations. Based on the above considerations, we generally expect the scaling to depend on the length of the time series in a manner that depends on the (unknown) properties of the stabilizing force, rendering unequivocal understanding of underlying mechanisms difficult. Furthermore, these difficulties arise even when the empirical measurements of population size are exact and free of errors. We now point out another problem: sampling errors alone may produce almost any exponent.

## TAYLOR'S POWER LAW AS AN ARTIFACT

Sampling noise associated with surveys of population abundance over time poses an often unrecognized obstacle to the assessment of Taylor's law. McArdle et al. (1990) have already noted that sampling causes a bias in the estimate of population variability. We stress another difficulty, arising from the fact that population surveys are subject to two types of sampling errors. When superimposed on each other, these errors may yield any value of $z$ in the appropriate range.

The first type of sampling noise is binomial. If there is a fixed chance to sample each individual animal or plant, two surveys of a population of size $n$ will yield results that typically differ proportionally to $\sqrt{n}$, hence mimicking the $z = 1$ behavior associated with real

demographic fluctuations. A second type of sampling noise is proportional. The observer may miss a whole cluster (flock, patch) leading to an error that scales with population size $n$ (thus $z = 2$) that could be mistakenly interpreted as evidence for environmental noise. The lognormal sampling errors reported in the literature (Dennis et al. 2006, Knape et al. 2011, Knape and de Valpine 2012) also belong to this second class of proportional inaccuracies.

Accordingly, even if the actual population is fixed, sampling errors of both types can yield any ratio between $z = 1$ (only errors of the first kind) and $z = 2$ (mainly errors of the second kind). In Appendix B, we give examples of these artifacts. An analogous problem with the estimation of the exponent in the spatial version of Taylor's law was already pointed out by Titmus (1983).

Given the ubiquity of sampling errors, we argue that the evidence provided thus far in the literature supporting the power law (Eq. 1) is inconclusive. A reliable analysis of fluctuation scaling must start with highly accurate data, for which the sampling errors are negligible, or with data that were corrected for the potential effects of sampling errors.

A related issue (see Appendix B), is the problematic use of the double logarithmic scale. The use of these plots seems to be a natural choice when dealing with power laws like Eq. 1, since a power law appears as a straight line and the log scale allows one to present data that spans many orders of magnitude in the same plot. However, the compression involved in the logarithmic transformation leads to a typical misrepresentation of the results (Avnir et al. 1998): a data set that shows widely scattered points on an arithmetic scale may appear almost as a straight line on a double logarithmic scale.
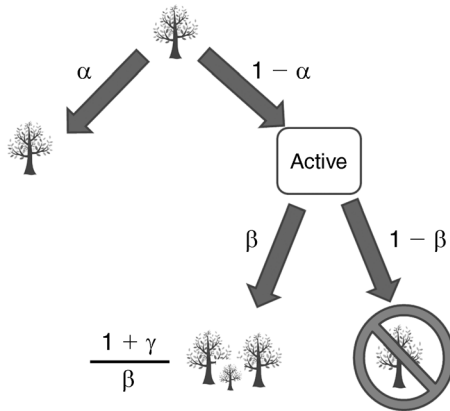
FIG. 2. The alpha-beta-gamma model, $\alpha$ dictates the generation time, $\beta$ sets the scale of demographic stochasticity, and $\gamma$ reflects environmental noise. The growth rate is fluctuating in time, at any given time the population is either decreasing or increasing deterministically. The parameter $\gamma(t)$ defines the instantaneous growth rate of a population (or its relative fitness) at time $t$ and so characterizes the environmental stochasticity. The parameter $\gamma(t)$ is picked independently for every period of time and every species, from a distribution of zero mean and variance $\Delta$. Between censuses a tree may remain inactive with probability $\alpha$. If it is active, it dies with probability $\beta$ or produces $(1 + \gamma)/\beta$ offspring.

All in all, we claim that the empirical support for Taylor's power law is questionable, and even if the law is valid, the $z$ exponent carries little information about the underlying forces that govern population dynamics. We wish to propose an alternative methodology for the analysis of population monitoring data. Long-term monitoring data are expensive and therefore not generally available for many species. To address this data limitation, we focus on presenting an approach that can identify underlying forces contributing to observed population dynamics with short-term data. In those cases where data on long-term dynamics are available, one may implement the variance–time lag technique as presented in Pimm and Redfearn (1988), Hanski (1990), and Keitt and Stanley (1998).

### Short-term Fluctuation Scaling: a Null Model

Let us present a generic and simple null model for population fluctuations that are caused by any combination of demographic and environmental stochasticity. The model is solvable and designed to produce predictions that can be easily tested using empirical data. The outcome of the model is a prediction about the ratio between fluctuation strength and abundance. This provides many technical benefits.

A basic feature of the model is the focus on within-generation fluctuations in abundance, i.e., on time series where the interval between consecutive observations is smaller than the generation time. Such time series are typical for many types of organisms (e.g., time series of tropical trees (Condit 1995) and annual breeding bird surveys (Sauer et al. 2011). Under these conditions, one

can safely assume that an offspring born during the survey interval did not itself give birth within this period, i.e., that the contribution of grandchildren to the variations between survey periods is negligible. Moreover, on such short time scales, one may hope that the effect of stochasticity is more pronounced than the effect of stabilizing forces.

We will present the model using trees as the example taxon, but the concepts are also relevant to surveys of other kinds of organisms, with appropriate modifications of the generation time and survey-to-survey intervals. The model has three parameters: $\alpha$ is related to the ratio between the survey interval and the generation time, $\beta$ is the strength of demographic stochasticity, and a random variable $\gamma$ is taken from a distribution of variance $\Delta$ that is proportional to the environmental noise. Fig. 2 illustrates the model dynamics.

Let us assume that within a single interval (say, five years), the chance of a tree to be inactive is $\alpha$. An inactive tree just stays there, does not reproduce and does not die. When the time interval between two consecutive surveys approaches zero, $\alpha$ approaches 1 and decreases as the time interval increases, reaching zero around the generation time. This parameter links the generation time to the time interval between surveys. If the tree is active (with probability $1 - \alpha$), it either dies with probability $(1 - \beta)$ or produces a random number of offspring, taken from a Poisson distribution with mean $(1 + \gamma)/\beta$.

For $\Delta = 0$ (hence $\gamma = 0$), the average size of the population is fixed over time. Only a fraction $\beta(1 - \alpha)$ of the individuals are reproducing, but each of them produces $1/\beta$ offspring. Therefore, in this model $\beta$ controls the strength of demographic stochasticity. For example, if $\alpha = 0.5$, $\beta = 0.2$, and the initial population size is 100, half of the individuals stay inactive, 40 die, and the remaining 10 produce five offspring and die (or produce four offspring and stay alive), so the overall population is kept fixed.

If $\beta = 1$ then one observes standard (Poissonian) demographic noise. If $\beta << 1$, only a few active trees reproduce, each one of them producing many offspring. For such a Genghis Khan scenario, the demographic noise is huge but still $z = 1$ in Eq. 1 (only the coefficient $c$ in Eq. 1 is larger). Finally, the value of $\gamma$ reflects the strength of environmental noise. In the simplest case, one may pick $\gamma$ at random for every species between any two surveys from some distribution with zero mean.

This model is solvable (see Appendix C and Supplement 2 for the software used to verify the results). In particular, it is useful to look at the quantity

$$Y = \frac{n_t - n_0}{\sqrt{n_0}} \qquad (2)$$

where $n_0$ is the size of the population at $t = 0$ and $n_t$ is the abundance at time $t$. $Y$ is the size of the population variation normalized by the square root of the

population size, i.e., by the scale of the variation if the stochasticity is purely demographic. Therefore, for populations that are subject to purely demographic noise, $\text{Var}(Y)$ is independent of the population size. Accordingly, when calculating the variance of $Y$ using many pairs of data points with the same $n_0$, it is independent of $n_0$. Since, for large populations, one can rarely find multiple measurement with the same $n_0$, we calculate $\text{Var}(Y)$ over bins of population size, denoting the average in every bin as $m$. If environmental noise is dominant, $n_t - n_0$ scales with $n_0$ and $\text{Var}(Y)$ grows linearly with $m$. For populations satisfying the α–β–γ dynamics, we show in Appendix C that $\text{Var}(Y)$ is the sum of two terms, an $m$-independent constant and a linear term

$$\text{Var}(Y \mid m) = \left( \left(\frac{1-\alpha}{\beta}\right)(1 + \Delta) - \Delta(1 - \alpha)^2 \right) + \Delta(1 - \alpha)^2 m. \qquad (3)$$

Here $\Delta = \text{Var}(\gamma)$ reflects the strength of the environmental noise. When $\Delta = 0$ (no environmental stochasticity) $\text{Var}(Y)$ is independent of the mean $m$ as expected. Even if $\Delta > 0$, the effect of demographic noise appears in Eq. 3 only in the intercept, and the dependence of $\text{Var}(Y)$ on $m$ reflects only the environmental noise. Therefore, plotting $\text{Var}(Y)$ vs. $m$ should give us a horizontal straight line if the stochasticity is purely demographic (even if it is very strong, $\beta \ll 1$). Any form of $m$ dependence indicates that the noise is not purely demographic, and in particular, a linear relation between $\text{Var}(Y)$ and $m$ suggests environmental stochasticity.

For a comparison with empirical data, the representation of $\text{Var}(Y)$ against $m$ possesses other advantages. It avoids the use of a double logarithmic scale that obscures the details of the plot, clearly separates the demographic component from other types of noise, and may be used to estimate the strength of environmental stochasticity by the slope of the curve. Moreover, it allows for identification of other types of stochasticity that are neither demographic nor environmental, a feature that turns out to be quite important.

Accordingly, we consider the $\text{Var}(Y)$–$m$ plot the most appropriate tool to identify the nature of short time fluctuations.

### Empirical Analysis

We applied our approach to two data sets. One is the result of consecutive large-scale censuses of trees in different tropical forests provided by the Center of Tropical Forest Science (CTFS; Condit 1995) the other consists of time series obtained from the North American Breeding Bird Survey (NABBS; Sauer et al. 2011). The tree censuses are carried out every five years and are nearly free of sampling noise. The BBS data are very noisy, but we can filter out measurement noise using the variance through time plots as explained in

Appendix D and the software used is presented in Supplement 3.

The $\text{Var}(Y)$–$m$ diagrams are presented in Fig. 3 (for three tropical forests, Barro Colorado Island [BCI], Pasoh, and Lambir) and in Fig. 4 (for fluctuations in bird communities, extracted from the NABBS data). In both figures, the value of $\text{Var}(Y)$ is clearly growing with the mean, so the noise must have a nondemographic component.

Does Eq. 3 fit the empirical findings? It seems that the growth of $\text{Var}(Y)$ with $m$ in Figs. 3 and 4 is sublinear, but it is hard to determine its precise functional form. This sublinearity may reflect an internal structure within the population (Ballantyne and Kerkhoff 2007, Violle et al. 2012) as would be the case if individuals of a population are not all exposed to the same environmental stressor ($\gamma$), but are divided into groups that are exposed to independent random $\gamma$. Alternatively, sublinearity may result from modifications of the scale of fluctuations resulting from interspecific competition (Kilpatrick and Ives 2003, Mellin et al. 2010).

While it is hard to extract an exact functional form from Figs. 3 and 4, and one may wonder if there is a simple and general law that relates the $\text{Var}(Y)$ to the mean, we can still propose a possible relation. First, as demographic noise appears in any population dynamics system, any suggested law must include a term (e.g., the constant term for $\text{Var}(Y)$ plots) that reflects it. Such a term corresponds to the pronounced intercept in Fig. 3 (see inset). The superposition of environmental stochasticity, competition, and other possible forces yields the $m$ dependence in $\text{Var}(Y)$ plots. In the empirical systems, this term grows more slowly than expected for pure environmental noise. Accordingly, we believe that if there is a simple law connecting fluctuations to the mean, it perhaps takes the form

$$\text{Var}(Y) = a + bm^{z-1}, \qquad 1 \le z \le 2. \qquad (4)$$

In Appendix E (see supplementary Fig. E2), we present the fit of the BCI data set to Eq. 4, and it shows good agreement with intercept $a = 1$ and $z \approx 3/2$. The other data sets, although cleaned from sampling errors, are still too noisy to allow for a reliable fit. Indeed, even the BCI fit should be taken with a grain of salt, as different binning methods may yield different exponents. Therefore, we do not argue that the empirical results presented here provide unequivocal support for Eq. 4, but that this expression cannot be ruled out, unlike Eqs. 1 or 3.

### Discussion

The growth in fluctuation amplitude with the mean of a time series is a well-established fact (Eisler et al. 2008). Quantifying this ratio and providing a mathematical expression that describes the variance-to-mean relationship is much harder. Based on his empirical data, Taylor (Taylor and Woiwod 1980) suggested that the ratio is a simple power law (Eq. 1). Given the analysis we
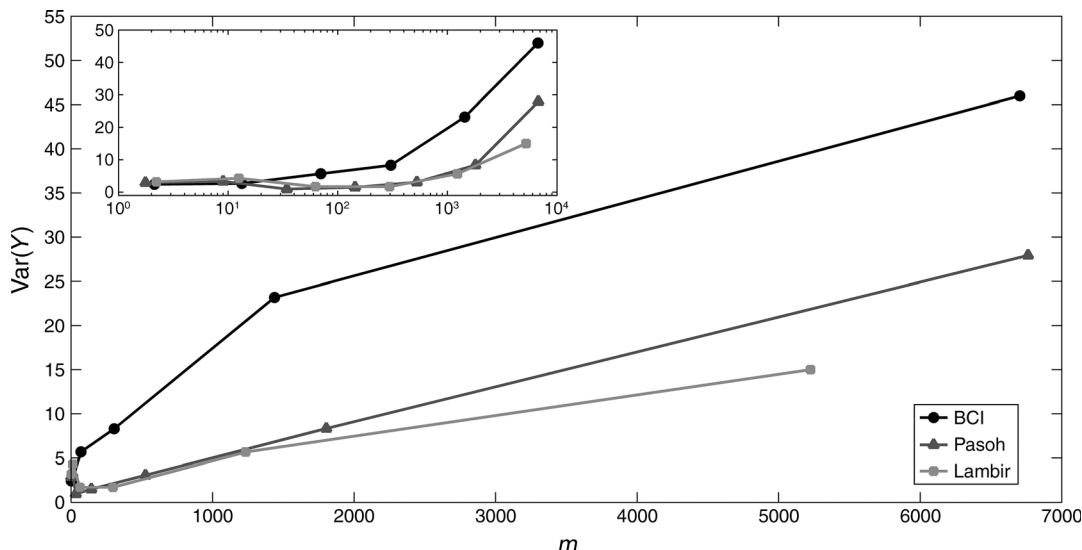
Fig. 3. Var($Y$)–$m$ plot for tropical tree communities, where $Y$ is the size of the population variation normalized by the square root of the population size. The value of Var($Y$) was extracted for >1 cm trees in three 50-ha Center of Tropical Forest Science (CTFS) plots: the Barro Colorado Island (BCI, five censuses, 320 species), Pasoh (three censuses, 823 species), and Lambir (two censuses, 1202 species). Only censuses that are five years apart were considered. Every two consecutive records of population size provide one value of $Y$ for a specific $n_0$ (size of the population at $t = 0$). These values were collected into logarithmic bins, where all values of $Y$ attained from $n_0$ between $5^n$ and $5^{n+1}$ are collected into the $(n + 1)$th bin. Finally, we have calculated Var($Y$) for every bin and plotted it against $m$, the average value of $n_0$ in that bin. The main panel depicts the results on an arithmetic scale, in which the small $m$ behavior is blurred because of the logarithmic binning; the inset shows the same results using a logarithmic scale for the $x$-axis, emphasizing the intercept associated with the constant $a$ in Eq. 4. The growth of Var($Y$) with $m$ is clear, indicating the effect of nondemographic stochastic events. Sublinearity is also self-evident. We have omitted the last point for the BCI forest ($n_0 > 1 \times 10^4$) to keep the scale the same for all three cases. The figure with this extra point is shown in Appendix E.

presented, we feel that this proposal is problematic from a few perspectives. First, Taylor's exponent $z$ depends on many underlying parameters, from the length of the time series to the interplay between stabilizing and destabilizing forces, it is difficult to connect it directly to the mechanisms driving the system. Second, demographic noise affects all ecological population, for every system with $z > 1$, the fluctuation must have at least two sources: demographic and something else, where the extra noise is perhaps related to a superposition of environmental stochasticity and some kind of restoring force. If the net result of these multiple mechanisms is a single power law like Eq. 1, then they must balance each other in a nontrivial and precise way. Fine tuning of this type is extremely rare in nature and to find it in complex systems like those considered here is very unlikely. Adding the demographic term to the additional mechanisms is a more plausible formulation as in Eq. 4. A third line of criticism has to do with the empirical variance–mean graphs. We have shown that the effect of sampling noise, when superimposed on the data compression associated with log-log plots, can lead to a misinterpretation of the simple power law even when the system has no dynamics at all (see Appendix B: Fig. B1).

Accordingly, we put forward two methodological suggestions. The first is either use high quality data coming from full sampling of populations (like in the

CTFS censuses) or to filter out the measurement errors like what was done here for the NABBS. The second is to focus on short-term analysis and to replace the plots of variance vs. mean on a double logarithmic scale by Var($Y$)–mean diagrams using an arithmetic scale. These diagrams allow for a direct comparison with the result of a simple null model (Eq. 3) and make a sharp distinction
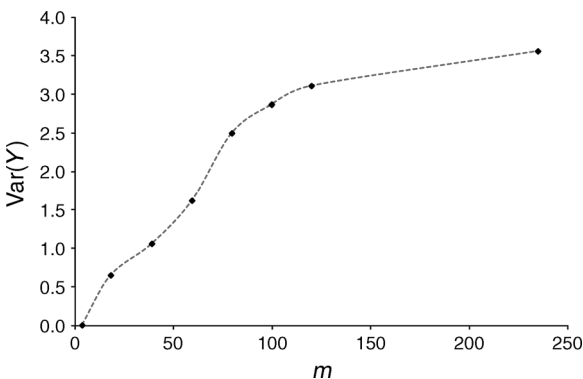


Fig. 4. Normalized variance, Var($Y$), against population size $m$, plotted for bird communities. The value of $Y$ is extracted from the differences between consecutive years in the North American Breeding Bird Survey (NABBS), after filtering the sampling noise as explained in Appendix D. The analysis technique is the same as in Fig. 3, but the binning is linear since in the NABBS data set there are many more species with a smaller range of population sizes.

between the effect of demographic noise, which appears only in the intercept, and other effects that lead to the growth of Var($Y$) with $m$.

The two sets of empirical time series that we have used show a sublinear growth of Var($Y$) with the average abundance, thus they may fit Eq. 4. However, in both cases we do not have enough data points for any specific species; to implement our technique we had to adopt a macroecological approach (Keitt and Stanley 1998, Keitt et al. 2002), assuming that different species and different populations all share the same characteristic dynamics.

Our theoretical and empirical analyses have direct implications for the debate over Hubbell's neutral theory of biodiversity (NTB; Hubbell 2001, Volkov et al. 2003). The NTB assumes that all species in a community have the same fitness, and the dynamics are governed solely by demographic noise and (relatively rare) migration events. Accordingly, the NTB (for a metacommunity, without spatial structure) has a very strong prediction about the fluctuation scaling: the variance of a time series must grow linearly with the mean, independent of species identity, and the variance of $Y$ is independent of $m$. This property is depicted in Fig. 5, where a simulation of Hubbell's zero-sum dynamics provides the time series for the analysis (see Supplement 1 for the software we have used). Fig. 5 provides also the expected magnitude of the variance in this $Y$ vs. mean population plot due to the use of a finite number of relatively short time series. Substantial deviations from this pattern imply nondemographic processes and rule out a purely demographic theory. Although the results shown in Fig. 5 were generated for some set of specific values assigned to the total population and migration/mutation rates, the pattern observed is general; in particular, the value of Var($Y$) is independent of $m$ and the fluctuations (confidence intervals) are smaller than one unit. Clearly, this feature of a purely demographic process is inconsistent with the empirical results presented in Figs. 3 and 4.

The fact that the size of fluctuations is larger than the prediction of the NTB was already noted by several authors (Leigh 2007, Seri et al. 2012). In particular, Feeley et al. (2011) considered these large changes (which they call directional changes) in the BCI forest as resulting from specific nonstationary dynamics (e.g., el Nino events, carbon fertilization), in either the short- or long-term.

Another possible explanation to this puzzle was suggested recently in Keil et al. (2010). The authors showed that a nontrivial variances–mean pattern may appear when a neutral dynamic is simulated on a set of local communities (archipelago model) connected by migration.

We would like to suggest a third possibility within the neutral theory framework: the directional changes are not the exception but rather the rule. That is, the stochasticity affecting ecological communities is mainly
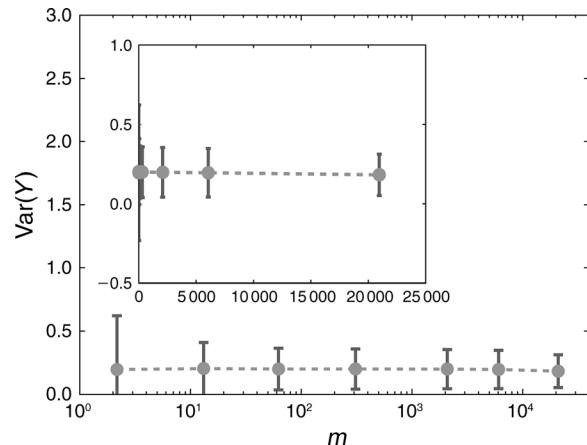


FIG. 5. The variance-to-mean ratio in Hubbell's neutral theory of biodiversity metacommunity dynamics. Time series were gathered from a simulation of a zero sum dynamics for a community (forest) of $N = 25\,000$ trees. At every time step a tree is chosen at random to die, and the vacancy is filled with the descendent of another, randomly chosen tree. The vacancy is replaced by a new species, reflecting the effect of migration (or mutations in a metacommunity) with probability $\mu = 1 \times 10^{-5}$. A generation is defined as the number of time steps for which a tree has a chance $1/e$ to survive. Species' populations were monitored every 1/10th generation (in the tropical forest, the generation time is about 50 years) and the fluctuations monitored along the run to give the variance-to-mean ratio. The figure shows Var($Y$) vs. $m$ with logarithmic binning based on powers of five (this is the binning used for the real data in Fig. 3). The main panel uses logarithmic scaling of the $x$-axis to show clearly the small $m$ data, the inset is the same in arithmetic scale. Error bars stand for 95% ($2\sigma$) confidence intervals.

environmental, or at least nondemographic (one can argue here about terminology, claiming that once the model allows for differential response to exogenous factors it is not neutral anymore, but see Alonso et al. [2006]). This implies that at any given moment different species have different fitnesses, but the relative fitness fluctuates in time and all species are equal on average, like in the $\alpha$–$\beta$–$\gamma$ model considered above.

If this is the case, the deviations from the prediction of the null model (Eq. 3) should be related to the effects of stabilizing mechanisms like restoring forces or to the effect of competition considered in Kilpatrick and Ives (2003). We hope to present a detailed analysis of this possibility in a subsequent publication.

Finally, we would like to stress that any community model that admits a stable equilibrium state (including those based on generalized Lotka-Volterra equations and interaction matrices) and includes only demographic noise should be dismissed (given empirical data sets akin to those presented in Figs. 3 and 4). Fluctuations in such models will be smaller than in the (marginally stable) NTB, and there is a restoring force that limits the amplitude of populations' variations, while the neutral dynamics are free of such stabilizing mechanisms. Community models that are able to fit the data presented here must include either substantial environ-

mental noise or an intrinsic mechanism that generates strong population variations, such as chaotic dynamics (Huisman and Weissing 1999).

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#### Supplemental Material

#### Appendix A

The dependence of the exponent $z$ on the width of the time window (*Ecological Archives* E095-148-A1).

**Appendix B**

Artifacts of sampling errors and the double logarithmic scale (*Ecological Archives* E095-148-A2).

**Appendix C**

The alpha-beta-gamma model (see Fig. 2) (*Ecological Archives* E095-148-A3).

**Appendix D**

Cleaning the Breeding Bird Survey (BBS) data from sampling errors (*Ecological Archives* E095-148-A4).

**Appendix E**

Fluctuation scaling in the tropical forest—a supplement to Fig. 3 (*Ecological Archives* E095-148-A5).

**Supplement 1**

Fortran code simulating a neutral community with demographic noise, used to generate Fig. 5 (*Ecological Archives* E095-148-S1).

**Supplement 2**

Matlab code simulating the alpha-beta-gamma model to check Eq. 3 (*Ecological Archives* E095-148-S2).

**Supplement 3**

Matlab code calculating the variance of $Y$ for different time lags, used to analyze the BBS data (*Ecological Archives* E095-148-S3).