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1 Temporal fluctuation scaling in 2 populations and communities.

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10 Abstract

11
12 Taylor's law, one of the most widely accepted generalizations in ecology, states that the variance
13 of a population abundance time series scales as a power-law of its mean. Here we re-examine
14 this law and the empirical evidence presented in support of it. Specifically we show that the
15 exponent generally depends on the length of the time series and its value reflects the combined
16 effect of many underlying mechanisms. Moreover, sampling errors alone, when presented on a
17 double logarithmic scale, are sufficient to produce an apparent power-law. This raises questions
18 regarding the usefulness of Taylor's law for understanding ecological processes. As an
19 alternative approach, we focus on short-term fluctuations and derive a generic null model for the
20 variance-mean ratio in population time-series from a demographic model that incorporates the

21 combined effects of demographic and environmental stochasticity. After comparing the
22 predictions of the proposed null model with the fluctuations observed in empirical datasets, we
23 suggest an alternative expression for fluctuation scaling in population time series. Analyzing
24 population fluctuations as we have proposed here may provide new applied (e.g., estimation of
25 species persistence times) and theoretical (e.g., the neutral theory of biodiversity) insights that
26 can be derived from more generally available short-term monitoring data.

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

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Introduction

One of the major challenges in the study of ecological systems, and complex systems in general, is to characterize and to 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 timeseries 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):

$$S = c \cdot N^z \quad 1 \leq z \leq 2, \tag{1}$$

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 and Stanley 1998, 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). Here 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).

53 Observed variations in population abundance are expected to be caused by a few
 54 underlying mechanisms. The simplest of these is *sampling errors*: even if the actual size of the
 55 population is fixed, the survey may sample different individuals leading to variation in counts
 56 across repeated surveys. The stochastic nature of the birth-death process provides us with
 57 another source of variation, *demographic noise*, where individuals vary in their reproductive
 58 success in an uncorrelated manner. If, for example, every individual produces, on average, one
 59 offspring and then dies, the abundance will fluctuate without an overall trend, and the variation
 60 per generation is proportional to the square root of the population size (Van Kampen 1981).
 61 *Environmental stochasticity*, on the other hand, affect all the individuals in the population,
 62 causing periods where the birth/death rate, when averaged over the population, grows or
 63 declines, hence the variation scales linearly with population size (Lande et al. 2003) It has been
 64 shown that if dynamics are governed solely by demographic noise, then the exponent z in Eq.
 65 (1) approaches one. Conversely, if environmental stochasticity is the main driver of the change,
 66 then $z=2$ (Ballantyne and Kerkhoff 2007). Finally, *stabilizing forces* like a finite carrying
 67 capacity may balance the effects of stochasticity and limit the range of possible population sizes.
 68
 69 The aim of this paper is to re-evaluate the validity and usefulness of Taylor's law (as expressed in
 70 Eq. [1]), and to suggest an alternative framework for the analysis of short-term fluctuations in
 71 empirical datasets. Applying our method to relatively "clean" (error free) datasets, we can
 72 suggest a new empirical law. One of the applied benefits of this approach is that it can be
 73 implemented with short-term data which is more widely available, across many more species,
 74 than long-term data.
 75

76 In particular, regarding Taylor's law (Eq. [1]) we will point out the following obstacles

77

- 78 1. The variance-mean ratio depends strongly on the length of the time series.
- 79 2. The apparent agreement of empirical datasets with Eq. (1) may be an artifact of sampling
80 errors and the (mis)use of the double logarithmic scale.
- 81 3. Even in the best-case scenario, when the variance-mean ratio has converged to its long-
82 term value, it reflects a nontrivial interplay between the noise and the stabilizing
83 mechanisms, rendering it difficult to interpret.

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

90

91 The question of short-term fluctuation scaling, i.e., how are survey to survey changes in
92 population size dependent on population size itself, addresses a fundamental aspect of the
93 behavior of the system. Without a good assessment of these fluctuations it is very difficult to
94 interpret the long-term properties of the system and to extract information about regulating
95 forces (Freckleton et al. 2006). Moreover, population viability analyses usually depend on the
96 balance between stabilizing mechanisms and stochasticity, and the latter should be well
97 characterized if we are to have confidence in estimated persistence probabilities. Finally, the
98 neutral theory of community dynamics (Hubbell 2001), a central (although hotly debated)

99 paradigm in contemporary ecology, assumes dynamics are driven by pure demographic
 100 stochasticity, an assumption that may be examined within our framework.

101 In what follows, we expand on the limitations associated with Taylor's law, as
 102 enumerated above. As an alternative, we present and solve a null model for populations under
 103 both demographic and environmental stochasticity, and explain how to present the results in a
 104 way that enables an informative comparison between the model and the data. Comparing the
 105 results obtained using high-quality datasets and this null model, we can rule out a simple
 106 combination of demographic and environmental noise, and suggest an alternative non-trivial
 107 expression for fluctuation scaling. Finally, we will discuss the implications of our results,
 108 including its relevance to the debate surrounding the neutral theory of biodiversity.

109 **Short versus long-term dynamics**

110
 111 To consider the relation between timeseries length and the variance-mean ratio, let us
 112 begin with a qualitative analysis. In general, when a system is affected by noise and stabilizing
 113 mechanisms, the noise is dominant over short time scales, and the relative importance of
 114 stabilizing forces grows in time, eventually dominating the dynamics over long time horizons.
 115 As an example, let us consider a local population fluctuating around an average size N . For
 116 simplicity, we represent the stabilizing forces as reflecting boundaries at $N+p$ and $N-p$ as in
 117 Stong's "density vague" dynamics (Strong 1986); see the illustration in Fig. 1. That is to say, the
 118 stochasticity driven fluctuations are not restricted as long as the population size remains between
 119 the boundaries. We discuss several alternative versions of this model in supplement A. In
 120 particular, we consider the case of a population driven by pure demographic noise, as well as one
 121 driven by both demographic and environmental noise. Another parameter one can modify is the

122 band width (p) of the stabilizing force. The width may be taken to be proportional to N , and
 123 supplement A presents cases where $p \sim \sqrt{N}$ and $p \sim N$ are simulated.

124 Both demographic and environmental noise cause the population to perform a random
 125 walk between the two boundaries. Over short time scales, before the typical trajectory hits one
 126 of the boundaries, the exponent z reflects pure stochastic motion, with $z=1$ for demographic and
 127 $z=2$ for environmental noise (Van Kampen 1981, Lande et al. 2003) . Over longer time series,
 128 the typical trajectory uniformly covers the allowed band of abundances, and the variance scales
 129 with p^2 . Accordingly, the variance-mean ratio is determined by the relationship between N and
 130 p . If p is proportional to N , then $z=2$; and if $p \sim \sqrt{N}$, then $z=1$ – both results being independent
 131 of the underlying stochastic process. Hence, if the noise is purely demographic and $p \sim N$ the
 132 exponent z approaches 1 over short time intervals and will increase to 2 over long time intervals.
 133 Conversely, for environmental stochasticity and $p \sim \sqrt{N}$, estimates of z will start at 2 in the
 134 short term and relax to $z=1$ in the long term. See supplement A for a summary and a few
 135 numerical demonstrations.

136 All of the above is true for the case of sharp, perfectly reflecting boundaries. If we relax
 137 this constraint and let the strength of the stabilizing force behave more generally (e.g.,
 138 proportional to the distance from N as in logistic or Gompertz population growth models), then
 139 interpretations of z become more complicated. In this case the nature and strength of the noise
 140 affects the width of the allowed band. Accordingly, when the empirical Taylor's exponent z is
 141 estimated for timeseries of arbitrary length (as is usually the case), its magnitude reflects a
 142 balance between stochastic fluctuations and the restoring forces in a nontrivial way.

143 This poses a serious problem for the interpretation of empirical variance-mean relations.
 144 Based on the above considerations, we generally expect the scaling to depend on the length of

145 the timeseries in a manner that depends on the (unknown) properties of the stabilizing force,
 146 rendering unequivocal understanding of underlying mechanisms difficult. Furthermore, these
 147 difficulties arise even when the empirical measurements of population size are exact and free of
 148 errors. In the next section we point out another problem: sampling errors alone may produce
 149 almost any exponent.

150 **Taylor's power law as an artifact**

151
 152 Sampling noise associated with surveys of population abundance over time poses an
 153 often unrecognized obstacle to the assessment of Taylor's law. McArdle (McArdle et al. 1990)
 154 has already noted that sampling causes a bias in the estimate of population variability. Here we
 155 stress another difficulty, arising from the fact that population surveys are subject to two types of
 156 sampling errors. When superimposed on each other, these errors may yield any value of z in the
 157 appropriate range.

158 The first type of sampling noise is binomial: if there is a fixed chance to sample each
 159 individual animal or plant, two surveys of a population of size n will yield results that typically
 160 differ by \sqrt{n} , hence mimicking the $z=1$ behavior associated with real demographic fluctuations.
 161 A second type of sampling noise is proportional: the observer may miss a whole cluster (flock,
 162 patch) leading to an error that scales with population size n (thus $z=2$) that could be mistakenly
 163 interpreted as evidence for environmental noise. The lognormal sampling errors reported in the
 164 literature (Dennis et al. 2006, Knappe et al. 2011, Knappe and de Valpine 2012) also belong to this
 165 second class of proportional inaccuracies.

166 Accordingly, even if the actual population is fixed, sampling errors of both types can
 167 yield any ratio between $z=1$ (only errors of the first kind) and $z=2$ (mainly errors of the second

168 kind). In supplement B we give examples of these artifacts. An analogous problem with the
 169 estimation of the exponent in the spatial version of Taylor's law was already pointed out by
 170 (Titmus 1983).

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

175 A related issue (see supplement B), is the problematic use of the double-logarithmic
 176 scale. The use of these plots seems to be a natural choice when dealing with power-laws like
 177 (Eq. 1), since a power law appears as a straight line, and since the log scale allows one to present
 178 data that spans many orders of magnitude in the same plot. However, the compression involved
 179 in the logarithmic transformation leads to a typical misrepresentation of the results (Avnir et al.
 180 1998): a dataset that shows widely scattered points on an arithmetic scale, appears almost as a
 181 straight line on a double logarithmic scale.

182 All in all, we claim that the empirical support for Taylor's power law is questionable, and
 183 even if the law is valid, the z exponent carries little information about the underlying forces that
 184 govern population dynamics. We wish to propose an alternative methodology for the analysis of
 185 population monitoring data. Long-term monitoring data are expensive and therefore not
 186 generally available for many species. To address this data limitation we focus on presenting an
 187 approach that can identify underlying forces contributing to observed population dynamics with
 188 short-term data. In those cases where data on long- term dynamics are available, one may
 189 implement the variance-time lag technique as presented in (Pimm and Redfearn 1988, Hanski
 190 1990, Keitt and Stanley 1998)

191 **Short-term fluctuation scaling – a null model**

192

193 Let us present a generic and simple null model for population fluctuations that are caused
194 by any combination of demographic and environmental stochasticity. The model is solvable, and
195 designed to produce predictions that can be easily tested using empirical data. The outcome of
196 the model is a prediction about the ratio between fluctuation strength and abundance; this
197 provides many technical benefits, as will be discussed towards the end of this section.

198 A basic feature of the model is the focus on within-generation fluctuations in abundance,
199 i.e., on timeseries where the interval between consecutive observations is smaller than the
200 generation time. Such time series are typical for many types of organisms (e.g., time series of
201 tropical trees (Condit 1995), and annual breeding bird surveys (Sauer et al. 2011). Under these
202 conditions one can safely assume that an offspring born during the survey interval did not itself
203 give birth within this period, i.e., that the contribution of "grandchildren" to the variations
204 between survey periods is negligible. Moreover, on such short timescales one may hope that the
205 effect of stochasticity is more pronounced than the effect of stabilizing forces.

206 We will present the model using trees as the example taxon, but the concepts are relevant
207 also to surveys of other kinds of organisms, with appropriate modifications of the generation
208 time and survey to survey intervals. The model has three parameters: α is related to the ratio
209 between the survey interval and the generation time, β is the strength of demographic
210 stochasticity, and a random variable γ is taken from a distribution of variance Δ that is
211 proportional to the environmental noise. Figure 2 illustrates the model dynamics.

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

220 For $\Delta=0$ (hence $\gamma=0$), the average size of the population is fixed over time. Only a
 221 fraction $\beta(1-\alpha)$ of the individuals are reproducing, but each of them produces $1/\beta$ offspring.
 222 Therefore, in this model β controls the strength of demographic stochasticity. For example, if
 223 $\alpha=0.5$, $\beta=0.2$ and the initial population size is 100, half of the individuals stay inactive, 40 die
 224 and the remaining 10 produce 5 offspring and die (or produce 4 offspring and stay alive), so the
 225 overall population is kept fixed.

226
 227 If $\beta=1$, then one observes "standard" (Poissonian) demographic noise. If $\beta \ll 1$, only a
 228 few active trees reproduce, each one of them producing many offspring. For such a "Genghis
 229 Khan" scenario the demographic noise is huge but still $z=1$ in Eq. (1) (only the coefficient c in
 230 Eq. 1 is larger). Finally, the value of γ reflects the strength of environmental noise. In the
 231 simplest case one may pick γ at random for every species between any two surveys, from some
 232 distribution with zero mean.

233 This model is solvable (see supplement C, and supplement F2 for the software used to
 234 verify the results). In particular, it is useful to look at the quantity

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

235 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
 236 population variation, normalized by the square root of the population size, i.e., by the scale of the
 237 variation if the stochasticity is purely demographic. Therefore, for populations that are subject to
 238 purely demographic noise, $\text{Var}(Y)$ is independent of the population size. Accordingly, when
 239 calculating the variance of Y using many pairs of datapoints with the same n_0 , it is independent
 240 of n_0 . Since, for large populations, one can rarely find multiple measurement with the same n_0 ,
 241 we calculate $\text{Var}(Y)$ over bins of population size, denoting the average in every bin as m . If
 242 environmental noise is dominant, $n_t - n_0$ scales with n_0 and $\text{Var}(Y)$ grows linearly with m . For
 243 populations satisfying the α - β - γ dynamics, we show in supplement C that $\text{Var}(Y)$ is the sum of
 244 two terms: an m -independent constant and a linear term:

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

245 Here $\Delta = \text{Var}(\gamma)$ reflects the strength of the environmental noise. When $\Delta = 0$ (no
 246 environmental stochasticity) $\text{Var}(Y)$ is independent of the mean m as expected. Even if $\Delta > 0$,
 247 the effect of demographic noise appears in (3) only in the intercept, and the dependence of
 248 $\text{Var}(Y)$ on m reflects only the environmental noise. Therefore, plotting $\text{Var}(Y)$ versus m should
 249 give us a horizontal straight line if the stochasticity is purely demographic (even if it is very
 250 strong, $\beta \ll 1$). Any form of m -dependence indicates that the noise is **not** purely demographic,
 251 and in particular a linear relation between $\text{Var}(Y)$ and m suggests environmental stochasticity.

252 For a comparison with empirical data, the representation of $\text{Var}(Y)$ against m possesses
 253 other advantages. It avoids the use of a double-logarithmic scale that obscures the details of the

254 plot, clearly separates the demographic component from other types of noise and may be used to
 255 estimate the strength of environmental stochasticity by the slope of the curve. Moreover, it
 256 allows for identification of other types of stochasticity that are neither demographic nor
 257 environmental, a feature that turns out to be quite important.

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

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Empirical analysis

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264 We applied our approach to two datasets. One is the result of consecutive large-scale
 265 censuses of trees in different tropical forests, provided by the Center of Tropical Forest Science
 266 (CTFS) (Condit 1995) the other is the timeseries obtained from the North American Breeding
 267 Bird Survey (NABBS) (Sauer et al. 2011). The tree censuses are carried out every five years and
 268 are nearly free of sampling noise. The BBS data are very noisy, but we can filter out
 269 measurement noise using the variance through time plots as explained in supplement D, and the
 270 software used is presented in supplement F3.

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

275 Does Eq. (3) fit the empirical findings? It seems that the growth of $\text{Var}(Y)$ with m in
 276 **Error! Reference source not found.**3 and Figure 4 is sublinear, but it is hard to determine its precise
 277 functional form. This sublinearity may reflect an internal structure within the population

278 (Ballantyne and Kerkhoff 2007, Violle et al. 2012) as would be the case if individuals of a
 279 population are not all exposed to the same environmental stressor (γ), but are divided into groups
 280 that are exposed to independent random γ . Alternatively, sublinearity may result from
 281 modifications of the scale of fluctuations resulting from interspecific competition (Kilpatrick
 282 and Ives 2003, Mellin et al. 2010).

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

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

292 In supplement E (see supplementary Fig. E2), we present the fit of the BCI dataset to (Eq.
 293 4), and it shows good agreement with intercept $a=1$ and $z \approx 3/2$. The other datasets, although
 294 cleaned from sampling errors, are still too noisy to allow for a reliable fit. Indeed, even the BCI
 295 fit should be taken with a grain of salt, as different binning methods may yield different
 296 exponents. Therefore, we do not argue that the empirical results presented here provide
 297 unequivocal support for Eq. (4), but that this expression cannot be ruled out, unlike Eq. (1) or Eq.
 298 (3).

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Discussion

The growth in fluctuation amplitude with the mean of a timeseries is a well-established fact (Eisler et al. 2008). Quantifying this ratio and providing a mathematical expression that describes the variance-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 presented above, we feel that this proposal is problematic from a few perspectives:

1. Because 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.
2. Because 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.

321 3. Another line of criticism has to do with the empirical Var-mean graphs.

322 We have shown that the effect of sampling noise, when superimposed on the data
 323 compression associated with log-log plots, can lead to a misinterpretation of the simple
 324 power law even when the system has no dynamics at all (see supplement B, Fig. B1).

325 Accordingly, we put forward two methodological suggestions. The first is either use
 326 high-quality data coming from full sampling of populations (like in the CTFS censuses) or to
 327 filter out the measurement errors like what was done here for the NABBS. The second to focus
 328 on short-term analysis and to replace the plots of Var vs. mean on a double logarithmic scale by
 329 Var(Y)-mean diagrams using an arithmetic scale. These diagrams allow for a direct comparison
 330 with the result of a simple null model (Eq. 3), and make a sharp distinction between the effect of
 331 demographic noise, which appears only in the intercept, and other effects that lead to the growth
 332 of Var(Y) with m .

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

338 Our theoretical and empirical analyses have direct implications for the debate over
 339 Hubbell's neutral theory of biodiversity (NTB) (Hubbell 2001, Volkov et al. 2003). The NTB
 340 assumes that all species in a community have the same fitness, and the dynamics is governed
 341 solely by demographic noise and (relatively rare) migration events. Accordingly, the NTB (for a
 342 metacommunity, without spatial structure) has a very strong prediction about the fluctuation
 343 scaling: the variance of a timeseries must grow linearly with the mean, independent of species

344 identity, and the variance of Y is independent of m . This property is depicted in Figure 5, where
 345 a simulation of Hubbell's zero-sum dynamics provides the timeseries for the analysis (see
 346 supplement F1 for the software we have used). Figure 5 provides also the expected magnitude of
 347 the variance in this Y versus mean population plot due to the use of a finite number of relatively
 348 short time series. Substantial deviations from this pattern imply *non-demographic* processes, and
 349 rule out a purely demographic theory. Although the results shown in Figure 5 were generated for
 350 some set of specific values assigned to the total population and migration/mutation rates, the
 351 pattern observed is general; in particular, the value of $\text{Var}(Y)$ is independent of m and the
 352 fluctuations (confidence intervals) are smaller than one unit. Clearly, this feature of a purely
 353 demographic process is inconsistent with the empirical results presented in Figure 3 and Figure
 354 4.

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

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

363 We would like to suggest a third possibility within the neutral theory framework: that the
 364 directional changes are not the exception but rather the rule. That is, the stochasticity affecting
 365 ecological communities is mainly environmental, or at least non-demographic (one can argue
 366 here about terminology, claiming that once the model allows for differential response to

367 exogenous factors it is not neutral anymore, but see (Alonso et al. 2006). This implies that at any
 368 given moment different species have different fitnesses, but the relative fitness fluctuates in time
 369 and all species are equal on average, like in the α - β - γ model considered above.

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

374 Finally, we would like to stress that any community model that admits a *stable*
 375 equilibrium state (including those based on generalized Lotka-Volterra equations and interaction
 376 matrices) and includes only demographic noise should be dismissed (given empirical datasets
 377 akin to those presented in Figures 3 and 4). Fluctuations in such models will be smaller than in
 378 the (marginally stable) NTB and there is a restoring force that limits the amplitude of
 379 populations' variations, while the neutral dynamics is free of such stabilizing mechanisms.
 380 Community models that are able to fit the data presented here must include either substantial
 381 environmental noise or an intrinsic mechanism that generates strong population variations, such
 382 as chaotic dynamics (Huisman and Weissing 1999).

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- 471 **Ecological Archive materials:**
- 472 **Appendices**
- 473 [Appendix A](#): The dependence of the exponent z on the width of the time window.
474 *Ecological Archives* ##.
- 475
- 476 [Appendix B](#): Artifacts of sampling errors and the double logarithmic scale.
477 *Ecological Archives* ##.
- 478 [Appendix C](#): The alpha-beta-gamma model (see figure 2 in main text).
479 *Ecological Archives* ##.
- 480 [Appendix D](#): Cleanings the BBS data from sampling errors.
481 *Ecological Archives* ##.
- 482 [Appendix E](#): Fluctuation scaling in the tropical forest—a supplement to figure 3.
483 *Ecological Archives* ##.
- 484 **Supplements**
- 485 [Supplement 1](#): Fortran code simulating a neutral community with demographic noise, used
486 to generate Fig 5.
487 *Ecological Archives* #####.
- 488
- 489 [Supplement 2](#): Matlab code simulating the alpha-beta-gamma model to check eq.3.
490 *Ecological Archives* #####.
- 491
- 492 [Supplement 3](#): Matlab code calculating the variance of Y for different time lags, used to
493 analyze the BBS data.
494 *Ecological Archives* #####.
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Figure Captions

Figure 1. An illustration showing a typical “density vague’ dynamics with $N=500$ (bright line, middle) and $p=100$ (dark lines) reflecting boundaries. 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.

Figure 2. The α - β - γ model: α dictates the generation time, β sets the scale of demographic stochasticity, and γ reflects environmental noise. The growth rate is fluctuating in time: at any given time the population is either decreasing or increasing deterministically. The parameter $\gamma(t)$ define the instantaneous growth rate of a population (or its relative fitness) and so characterizes the environmental stochasticity. $\gamma(t)$ is picked independently for every period of time and every species, from a distribution of zero mean and variance Δ . Between censuses a tree may remain inactive with probability α . If it is active, it dies with probability β or produces $(1+\gamma)/\beta$ offspring.

Figure 3. $\text{Var}(Y)$ - m plot for tropical tree communities. The value of $\text{Var}(Y)$ was extracted for $>1\text{cm}$ trees in three 50-ha CTFS plots: the Barro Colorado Island (BCI, 5 censuses, 320 species) Pasoh (3 censuses, 823 species) and Lambir (2 censuses, 1202 species). Only censuses that are 5 years apart were considered. Every two consecutive records of population size provide one value of Y for a specific n_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 $(n+1)^{\text{th}}$ bin. Finally, we have

519 calculated $\text{Var}(Y)$ for every bin, and plotted it against m , the average value of n_0 in that bin. The
 520 main panel depicts the results on an arithmetic scale, in which the small- m behavior is blurred
 521 because of the logarithmic binning; the inset shows the same results using a logarithmic scale for
 522 the x-axis, emphasizing the intercept associated with the constant a in Eq. (4). The growth of
 523 $\text{Var}(Y)$ with m is clear, indicating the effect of non-demographic stochastic events. Sublinearity
 524 is also self-evident. We have omitted the last point for the BCI forest ($n_0 > 10^4$) to keep the scale
 525 the same for all three cases. The figure with this extra point is shown in the supplement E.

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528 **Figure 4.** Normalized variance, $\text{Var}(Y)$, against population size m , plotted for bird communities.
 529 The value of Y is extracted from the differences between consecutive years in the NABBS, after
 530 filtering the sampling noise as explained in supplement D. The analysis technique is the same as
 531 in Fig. 2, but the binning is linear since in the birds dataset there are many more species with a
 532 smaller range of population sizes.

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535 **Figure 5.** The variance-mean ratio in NTB metacommunity dynamics. Timeseries were gathered
 536 from a simulation of a zero sum dynamics for a community ("forest") of $N=25,000$ trees. At
 537 every timestep a tree is chosen at random to die, and the vacancy is filled with the descendent of
 538 another, randomly chosen tree. The vacancy is replaced by a new species, reflecting the effect of
 539 migration (or mutations in a metacommunity), with probability $\mu = 10^{-5}$. A "generation" is

540 defined as the number of time-steps for which a tree has a chance $1/e$ to survive. Species'
541 populations were monitored every 1/10th generation (in the tropical forest the generation time is
542 about 50 years), and the fluctuations monitored along the run to give the variance-mean ratio.
543 The figure shows $\text{Var}(Y)$ vs. m with logarithmic binning based on powers of 5 (this is the binning
544 used for the real data in Figure 3). The main panel uses logarithmic scaling of the x-axis to show
545 clearly the small- m data, the inset is the same in real scale. Error bars stand for 95% (2σ)
546 confidence intervals.

preprint









