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Heterogeneous 'proportionality constants' – A challenge to Taylor's Power Law for temporal fluctuations in abundance ☆

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HIGHLIGHTS

- We consider fluctuations in populations that follow stochastic logistic growth.
- We suggest why such populations should vary in their per-capita-variability (PCV).
- Variation in PCV implies abundance changes do not scale according to a power law.
- Correlation between PCV and mean abundance can explain empirical scaling exponents.

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ABSTRACT

Taylor's Power Law for the temporal fluctuation in population size (TL) posits that the variance in abundance scales according to aM^b; where M is the mean abundance and a and b are the 'proportionality' and 'scaling' coefficients. As one of the few empirical rules in population ecology, TL has attracted substantial theoretical and empirical attention. Much of this attention focused on the scaling coefficient; particularly its ubiquitous deviation from the null value of 2. Here we present a line of reasoning that challenges the power-law interpretation of the empirical log-linear relationship between the mean and variance of population size. At the core of our reasoning is the proposition that populations vary not only with respect to M but also with respect to a; which leaves the log-linear relationship intact but forfeits its power-law interpretation. Using the stochastic logistic-growth model as an example, we show that ignoring among-population variation in a is akin to ignoring the variation in the intrinsic rate of growth (r). Accordingly, we show that the slope of the log-linear relationship (b) is a function of the among-population (co)variation in r and the carrying-capacity. We further demonstrate that local environmental stochasticity is sufficient to generate the full range of observed values of b, and that b can in fact be insensitive to substantial differences in the balance between variance-generating and stabilizing processes.

1. Introduction

Taylor's Power Law (TL) (Taylor, 1961; Taylor and Woiwod, 1980, 1982) invokes a power-law scaling relationships between the variance in population size (V) and the mean size (M): $V = aM^b$. Support for the law has accumulated over studies spanning hundreds of species, with the slope of the linearized relationship showing considerable variation; predominantly between 1 and the 2 (Fig. 1; Maurer and Taper, 2002, Keil et al., 2010). The temporal TL, where the means and variances are calculated over time for a set of geographically separated populations, is generally thought to reflect processes that affect population dynamics and is one of the fundamental empirical rules in population ecology.

When two quantities exhibit a power-law relationship, relative change in one quantity will result in a proportional relative change in the other; independent of the initial size of the quantities. Viewing the mean-variance relationship as a power-law has two attractive ecological implications. First, large and small populations within the set are all scaled versions of a shared basic quantity: the 'proportionality constant' or 'per-capita variability';

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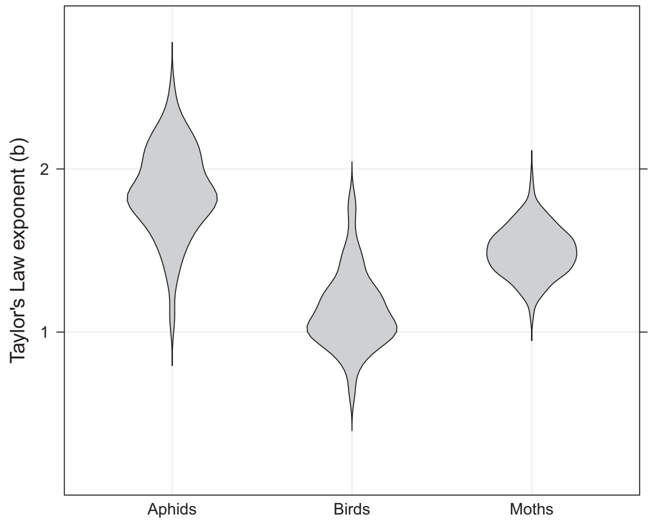

Fig. 1. Violin plots of Taylor's Law exponents for Aphids (n=97), moths (263) and birds (n=88) in Great Britain (data from Taylor and Woiwod, 1980, 1982).

a; with M as the scaling factor. Secondly, systems that share the same scaling coefficient, b, potentially share the same underlying dynamics (i.e. scale invariance). These implications, along with the departure of most observed values of b from the null expectation of 2 (Hanski, 1982; Kilpatrick and Ives, 2003), attracted numerous attempts to explain TL. As TL has been documented also in non-ecological systems (reviewed in Eisler et al., 2008), some of these attempts focused on universal, context-independent explanations (Kendal 2004; Cohen and Xu, 2015; Xiao et al., 2015); including the potential for statistical artifacts due to sampling (Kalyuzhny et al., 2014; Giometto et al., 2015). Others remained focused on the ecological processes that may underly the empirical phenomenon, such as demographic stochasticity (Anderson et al., 1982), negative interspecies interactions (i.e. direct and indirect competition; Kilpatrick and Ives, 2003) and uncorrelated reproductive effort among individuals (Ballantyne and Kerkhoff, 2007).

A common feature of the ecological explanations is that the effect of the putative mechanism on the variance is itself dependent on population-size. This dependency is needed as fluctuations driven solely by environmental stochasticity are expected to result in b=2 (Hanski, 1982; Kilpatrick and Ives, 2003). A second feature is that the second TL parameter – the per-capita variability a, has attracted far less attention. A power-law is defined when observations are homogenous with respect to a. Hence, the inference of TL from a log-linear mean-variance relationship necessarily assumes that all the populations within the set under consideration share the same the per-capita variability. Below we question this assumption; proposing that it lacks ecological justification and has thus led to a potentially flawed perspective of the mean-variance relationship. We begin with a general view of what it means for a to vary across populations, and of the statistical consequences of this variation, before moving to consider how such variation may arise in natural populations.

2. Statistical perspective

Conceptually, the per-capita variability equals the expected variance of population-size when its mean abundance is 1. Since a random variable which is multiplied by a constant has its variance multiplied by that constant squared, a randomly fluctuating population of mean size M should exhibit a variance of aM^2. For a set of such populations, each with a different value of a, the ordinary-least-squares slope (b) of the mean-variance relationship can be shown (Appendix A, Eqs. (A.1a)–(A.1d)) to be a function of the correlation between $\ln(a)$ and $\ln(M)$, $r_{a,M}$, and the ratio of their standard deviations, $q_{a,M}$

$$b=2+\frac{r_{a,M}}{q_{a,M}} \tag{1}$$

As expected, with zero variance in a, the slope equals 2. However, once a is allowed to vary among populations, negative values of $r_{a,M}$ will necessarily drive b below 2; more so for smaller values of $q_{a,M}$ (Fig. 2A. See Table 1 for a summary of the symbols). We are thus left with the task of identifying how such a negative correlation ($r_{a,M} < 0$) could arise in natural populations?

3. Ecological perspective

Consider, for analytical simplicity, the logistic growth model with environmentally-induced stochastic fluctuations: $\frac{1}{N}\frac{dN}{dt}=r\left(1-\frac{N}{u}\right)+\sigma z$. Here σ represents the extent of environmentally-induced stochastic fluctuations in the maximum per-capita rate of change, r; z is a Gaussian noise variable with a zero mean and unit variance; and u is the carrying-capacity. The (approximated) stationary distribution arising from this model is gamma (Dennis and Patil, 1984), with mean $M_i = E(N_i) = \alpha_i\theta_i$ and variance $V(N_i) = \alpha_i\theta_i^2$; where α_i and θ_i are the shape and scale parameters of the i^{th} population, respectively. We can thus rewrite the variance as

$$V(N_i) = 1/\alpha_i(\alpha_i\theta_i)^2 = 1/\alpha_i E(N_i)^2. \tag{2}$$

This formulation suggests that the proportionality constant in TL, $V_i=aM_i$, should be replaced by $a_i = 1/\alpha_i$. Hence, by keeping a_i constant across populations one necessarily assumes that α, or the factors that affect it, are of little ecological consequence (i.e. they do not contribute to among-population variation in M or V).

With the stochastic version of the logistic growth model, α and θ themselves are a function of the demographic parameters r and u (Maurer and Taper, 2002, Linnerud et al., 2013. Appendix A, Eq. (A.2)). Accordingly, we can write,

$$V(N_i)=\frac{1}{\nu_i-1}\left[u_i\left(1-\frac{1}{\nu_i}\right)\right]^2=\frac{1}{\nu_i-1}M_i^2, \tag{3}$$

$$V(N_i)=\frac{1}{\nu_i-1}\left[\frac{\nu_i-1}{\delta_i}\right]^2=\frac{1}{\nu_i-1}M_i^2 \tag{4}$$

where $\nu = 2r/\sigma^2$ is the relative intrinsic growth rate and $\delta=2c/\sigma^2$ is the relative density dependence, with c as the intensity of density-dependence (see Appendix A, Eqs. (A.3) and (A.4) for derivation).

Eqs. (3) and (4) show the dependence on ν of both the mean-abundance (M) and its 'proportionality constant'; the per-capita variability: $a_i = 1/(\nu_i-1)$. Hence, studies that keep a constant across populations must either: 1) fail to recognize the dependence of a on ν - e.g. Maurer and Taper (2002), who allowed for variation in ν, kept a constant and continued to investigate how a and b dictate the relationship between ν and δ; or 2) implicitly assume that variation in M is driven solely by variation in δ and that ν is constant across populations - e.g. Linnerud et al. (2013), who used a form of Eq. (2) to demonstrate b=2 under environmental stochasticity.

Variation in r is common among natural populations (e.g. Sibly et al., 2005). As such, it can be shown (Appendix A, Eqs. (A.5a–f)) that, for populations that follow Eq. (2), the mean-variance relationship should have a slope of