

1 Synchrony affects Taylor's law in theory and data

2 Daniel C. Reuman^{a,b,c,*}, Lei Zhao^{a,b}, Lawrence W. Sheppard^{a,b}, Philip C. Reid^{d,e,f}, Joel E. Cohen^{c,g,h,*}
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^a Department of Ecology and Evolutionary Biology, University of Kansas, 1200 Sunnyside Ave., Lawrence, KS, 66045, USA

^b Kansas Biological Survey, University of Kansas, 2101 Constant Ave., Lawrence, KS, 66047, USA

^c Laboratory of Populations, Rockefeller University, 1230 York Ave, New York, NY, 10065, USA

^d The Laboratory, Sir Alister Hardy Foundation for Ocean Science, Citadel Hill, Plymouth PL1 2PB, UK

^e Plymouth University, Drake Circus, Plymouth PL4 8AA, UK

^f The Laboratory, Marine Biological Association of the UK, Citadel Hill, Plymouth PL1 2PB, UK

4 ^g The Earth Institute and Department of Statistics, Columbia University, New York, NY 10027, USA

5 ^h Department of Statistics, University of Chicago, Chicago, IL 66037, USA

6 * Authors for correspondence: reuman@ku.edu, cohen@rockefeller.edu

7 Abstract

8 Taylor's law (TL) is a widely observed empirical pattern that relates the variances to the means of groups
9 of non-negative measurements via an approximate power law: $\text{variance}_g \approx a \times \text{mean}_g^b$, where g indexes
10 the group of measurements. When each group of measurements is distributed in space, the exponent b of
11 this power law is conjectured to reflect aggregation in the spatial distribution. TL has practical application
12 in many areas since its initial demonstrations for the population density of spatially distributed species in
13 population ecology. Another widely observed aspect of populations is spatial synchrony, which is the
14 tendency for time series of population densities measured in different locations to be correlated through
15 time. Recent studies showed that patterns of population synchrony are changing, possibly as a
16 consequence of climate change. We use mathematical, numerical, and empirical approaches to show that
17 synchrony affects the validity and parameters of TL. Greater synchrony typically decreases the exponent
18 b of TL. Synchrony influenced TL in essentially all of our analytic, numerical, randomization-based, and
19 empirical examples. Given the near ubiquity of synchrony in nature, it seems likely that synchrony
20 influences the exponent of TL widely in ecologically and economically important systems.

21 Significance statement

22 Two widely confirmed patterns in ecology are Taylor's law (TL), which states that the variance of
23 population density is approximately a power of mean population density; and population synchrony, the
24 tendency of species' population sizes in different areas to be correlated through time. TL has been applied
25 in many areas, including fisheries management, conservation, agriculture, finance, physics, and
26 meteorology. Synchrony of populations increases the likelihood of large-scale pest or disease outbreaks
27 and shortages of resources. We show that changed synchrony modifies and can invalidate TL.
28 Widespread recent changes in synchrony, possibly resulting from climate change, may broadly affect TL
29 and its applications.

30 \body

31 Introduction

32 Taylor's law (TL) is a widely observed empirical pattern that relates the variances to the means of groups
33 of measurements of population densities or other non-negative quantities via a power law: $\text{variance}_g = a$
34 $\times \text{mean}_g^b$, where g indexes the groups of measurements, $a > 0$, b is usually positive, and a and b are both
35 independent of g . Equivalently, $\log(\text{variance}_g) = b \times \log(\text{mean}_g) + \log(a)$. The parameter b has the same
36 numerical value whether it appears as the exponent of the power law or as the slope of the linear relation
37 between $\log(\text{variance}_g)$ and $\log(\text{mean}_g)$. Thus b may be referred to as the exponent or the slope of TL.

38 TL has been verified in data on the population sizes and population densities of hundreds of taxa,
39 including aphids (1), crops (2), fish (3, 4), birds (5), and humans (6). TL has also been discovered in

40 many other non-negative measurements (7), including recently tornados per outbreak (8) and stocks (9).
 41 In physics, TL is sometimes called “fluctuation scaling”. TL has been generalized (10), and applied to or
 42 proposed for application to fisheries management (3, 4), estimation of species persistence times (11), and
 43 agriculture (2, 12, 13). Potential mechanisms of TL have been explored extensively (e.g., 9, 14, 15).
 44 Because of its ubiquity, it has been suggested that TL could be another “universal law,” like the central
 45 limit theorem (16).

46 There are multiple versions of TL. “Temporal TL” and “spatial TL,” on which we focus, use time
 47 series, $Y_i(t)$, of population densities measured in locations $i = 1, \dots, n$ at times $t = 1, \dots, T$. For temporal
 48 TL, the groups, g , consist of all measurements made in a location, i (means and variances are computed
 49 over time). For spatial TL, groups are measurements at a single time, t (means and variances are over
 50 space).

51 Synchrony (metapopulation synchrony, spatial synchrony) is another ubiquitous and fundamental
 52 ecological phenomenon. It is the tendency for time series of population densities of the same species
 53 measured in geographically separated locations to be correlated through time. It has been observed in
 54 organisms as diverse as protists (17), insects (18), mammals (19, 20) and birds ((21); see also (22) for
 55 many other examples). It relates to large-scale pest or disease outbreaks and shortages of resources (23,
 56 24), and has implications for conservation because populations are at greater risk of simultaneous
 57 extinction if they are simultaneously rare (24).

58 Although some empirical and theoretical connections have been made between synchrony and TL
 59 (7, 14, 20, 25), the connections are far from completely understood, and do not encompass all versions of
 60 TL. Synchrony, like TL, may reflect aggregation because the spatial extent of correlations among
 61 population time series indicates the geographic size of outbreaks (26). Engen, Lande and Saether (25)
 62 connected TL with synchrony theoretically, but did not use spatial or temporal TL. Temporal TL has been
 63 related to a kind of synchrony that occurs on spatial scales smaller than that of sampling (7, 14).

64 The “Moran effect” refers to synchrony caused by synchronous environmental drivers. Changes
 65 in Moran effects as a consequence of climate change may alter synchrony. Long-term increases in the
 66 synchrony of caribou populations in Greenland were associated with increases in the synchrony of
 67 environmental drivers in the area, apparently through modified Moran effects (19). The latter were in turn
 68 linked to global warming. Similar associations held for North American bird species (21). Large-scale
 69 climatic changes in the North Atlantic Oscillation caused changes in winter temperature synchrony, which
 70 in turn caused changes in the synchrony of pest aphid species in the UK (27). Changes in the synchrony
 71 of plankton (26) and tree rings (28) have been associated with climate change. If synchrony influences
 72 TL, then changes in synchrony may change TL in ecologically and economically important systems.

73 We analyze connections between synchrony and spatial TL to answer the following questions. Do
 74 the presence and strength of synchrony in population time series influence whether TL holds, and if so,
 75 how? Do the presence and strength of synchrony influence the slope b of TL, and if so, how? Because of
 76 the fundamental importance of both TL and synchrony to population ecology, illuminating connections
 77 between these phenomena is of intrinsic interest, but we are also motivated by the applied importance of
 78 TL and by concern that climate change may modify synchrony.

79 **Results**

80 *Analytic results*

81 Suppose the population size or density in location i at time t is modeled by the non-negative random
 82 variable $Y_i(t)$, for $i=1, \dots, n$. Assume that the multi-variate stochastic process $Y(t) = (Y_1(t), \dots, Y_n(t))$ is
 83 stationary and ergodic (29); these are standard assumptions (SI Appendix S1). We use the standard spatial
 84 sample mean and sample variance: $m(t) = \frac{1}{n} \sum_{i=1}^n Y_i(t)$ and $v(t) = \frac{1}{n-1} \sum_{i=1}^n Y_i(t)^2 - \frac{n}{n-1} m(t)^2$. The
 85 traditional plot to test spatial TL is the $\log(v(t))$ -versus- $\log(m(t))$ scatter plot for a finite realization of
 86 these processes. TL hypothesizes that this plot will be approximately linear. The linear regression slope is
 87 $b_t = \frac{\text{cov}_t(\ln(m(t)), \ln(v(t)))}{\text{var}_t(\ln(m(t)))}$ (30). The subscripts t indicate that the variance var_t and the covariance cov_t are

88 computed across time for the finite realization, while each value of $m(t)$ and $v(t)$ is computed across space
 89 at time t . A standard (22) measure of average synchrony, $\Omega_t = \frac{1}{n^2} \sum_{i,j=1}^n \text{cor}_t(Y_i(t), Y_j(t))$, averages the
 90 temporal correlations of every pair of population-dynamic time series. This summation includes the terms
 91 with $i = j$, which equal 1, and hence Ω_t is $1/n$ when the correlations with $i \neq j$ are 0. Ω_t is 0 when the
 92 spatial-average time series is constant, and Ω_t cannot be negative (SI Appendix S1). We are interested in
 93 how Ω_t may affect whether the relationship between the log-mean and the log-variance is linear, and the
 94 value of the slope b_t when linearity holds. For long time series, it suffices (SI Appendix S1) to consider
 95 the population quantities $b = \frac{\text{cov}(\ln(m), \ln(v))}{\text{var}(\ln(m))}$ and $\Omega = \frac{1}{n^2} \sum_{i,j=1}^n \text{cor}(Y_i, Y_j)$, assuming all the expectations,
 96 variances and covariances in these and other expressions exist (details in SI Appendix). Thus we work
 97 with the time-independent distribution $Y=(Y_1, \dots, Y_n)$. Autocorrelation in time series will not influence the
 98 relationships we study if time series are long enough for empirical and true marginal distributions to be
 99 similar (SI Appendix S1).

100 Applying the delta method (31), $\ln(m) \approx \ln(E(m)) + \frac{m-E(m)}{E(m)}$, $\ln(v) \approx \ln(E(v)) + \frac{v-E(v)}{E(v)}$, and
 101 $\text{var}(\ln(m)) \approx \frac{\text{var}(m)}{E(m)^2}$, so (SI Appendix S1)

$$102 \quad b \approx \frac{(n-1)E(m)}{n} \frac{\text{cov}(m,v)}{(A-\text{var}(m))\text{var}(m)}, \quad (\text{Eq. 1})$$

103 where the first factor in this expression and the quantity $A = \frac{1}{n} \sum_{i=1}^n E(Y_i^2) - E(m)^2$ depend solely on the
 104 marginal distributions, Y_i , and not on the correlations, $\text{cor}(Y_i, Y_j)$. On the other hand, $\text{var}(m)$ equals
 105 $\frac{1}{n^2} \sum_{i,j=1}^n \text{cov}(Y_i, Y_j)$, which relates to synchrony, Ω , and is similar in form. Eq. 1 therefore provides the
 106 intuition behind our subsequent analyses: if synchrony (Ω or $\text{var}(m)$) changes and the marginals, Y_i ,
 107 remain fixed, then one expects the slope b to change. The following theorem supports this intuition.

108 **Theorem.** Suppose Y_i are identically distributed (but not necessarily independent) with $E(Y_i) = M > 0$
 109 and finite $\text{var}(Y_i) = V > 0$. Assume $\mu_{ij} = E((Y_i - M)(Y_j - M))$, $\mu_{ijk} = E((Y_i - M)(Y_j - M)(Y_k -$
 110 $M))$, and $\mu_{ijkl} = E((Y_i - M)(Y_j - M)(Y_k - M)(Y_l - M))$ are finite for all i, j, k, l , and define $\rho_{ij} =$
 111 $\text{cor}(Y_i, Y_j) = \frac{\mu_{ij}}{V}$ and $\rho_{ijk} = \frac{\mu_{ijk}}{\mu_{iii}}$. Then

$$112 \quad b \approx \left(\frac{M\mu_{iii}}{V^2} \right) \left(\frac{\sum_{i,j=1}^n \rho_{ijj} - \frac{1}{n} \sum_{i,j,k=1}^n \rho_{ijk}}{n^2(1-\Omega)\Omega} \right). \quad (\text{Eq. 2})$$

113 The approximation is better whenever the coefficients of variation of the sample mean $\frac{\sqrt{\text{var}(m)}}{E(m)} = \frac{\sqrt{V\Omega}}{M}$ and
 114 sample variance $\frac{\sqrt{\text{var}(v)}}{E(v)}$ are smaller, and is asymptotically perfect as these quantities approach 0.

115 Additional details, alternative mathematically equivalent expressions for b , and a proof of the theorem are
 116 in SI Appendix S2.

117 This theorem extends a theorem of Cohen and Xu (15) which assumes that the Y_i are independent
 118 and identically distributed (iid). In that case, the second factor on the right of Eq. 2 is 1 and $b \approx \left(\frac{M\mu_{iii}}{V^2} \right)$,
 119 which equals the skewness $\frac{\mu_{iii}}{V^{3/2}}$ of Y_i divided by its coefficient of variation $V^{1/2}/M$. Independence of the
 120 Y_i is not necessary here: the same formula holds if $\rho_{ij} = 0$ for $i \neq j$ and $\rho_{ijk} = 0$ whenever i, j , and k are
 121 not all equal. Cohen and Xu (15) concluded that, in the iid case, skewness of Y_i is necessary and sufficient
 122 for TL to have slope $b \neq 0$. Our theorem extends this result to the case of identically distributed Y_i that
 123 may be non-independent.

124 The denominator $n^2(1 - \Omega)\Omega$ in Eq. 2 is a \cap -shaped function of Ω (i.e., it increases, has a
 125 maximum and then decreases again as Ω increases). So Eq. 2 may seem to suggest that b is a U-shaped
 126 function of synchrony (it decreases, has a minimum, and then increases again). But the numerator of the
 127 second factor of Eq. 2 may, *a priori*, also be a \cap -shaped function of synchrony, so a U-shaped

128 dependence of b on synchrony is not mathematically certain, nor are any of the components of such a
 129 dependence (the initial decrease, and the internal minimum and subsequent increase of b as Ω increases).
 130 Dependence of the numerator of Eq. 2 on Ω also means $\lim_{\Omega \rightarrow 0} b$ and $\lim_{\Omega \rightarrow 1} b$ can be finite even though
 131 $\lim_{\Omega \rightarrow 0} (1 - \Omega)\Omega$ and $\lim_{\Omega \rightarrow 1} (1 - \Omega)\Omega$ are 0.

132 *Numeric results*

133 To illustrate the identically distributed case, we performed numerical simulations based on multivariate
 134 normal random variables $X = (X_1, \dots, X_n)$ with mean $(0, \dots, 0)$ and covariance matrix with diagonal
 135 entries 1 and off-diagonal entries equal to a parameter, $\rho \geq 0$. We let $Y_i = \varphi(X_i)$, where the
 136 transformations $\varphi(\cdot)$ were chosen, in different simulations, to make the Y_i a variety of Poisson, negative
 137 binomial, gamma, exponential, chi-squared, normal and log-normal distributions. Increases in ρ produced
 138 increases in Ω . Exponential and chi-squared distributions are special cases of gamma distributions. We
 139 produced separate results for these distributions because they are widely used. Results are in SI Appendix
 140 S3; fig. 1 shows typical results for Poisson and gamma examples.

141 Results generally agreed with the above intuitions and analyses. The linearity hypothesis of TL
 142 was usually, but not always, an adequate approximation in that linearity and homoscedasticity could not
 143 be rejected statistically (SI Appendix S6 for details on how this was tested). In agreement with our
 144 theorem and Cohen and Xu (15), when a shifted normal distribution (which has skewness 0) was used for
 145 Y_i , b was approximately 0 for all values of Ω . For skewed distributions, the slope b was generally smaller
 146 for larger values of Ω , confirming the prediction that b depends on synchrony. Although b decreased
 147 steeply as Ω increased from 0 for all skewed distributions, b most commonly continued to decrease
 148 monotonically as Ω increased further, even for large values of Ω , except for a few cases using gamma
 149 distributions, for which modest increases were observed (SI Appendix figs S14-S20): the b -versus-
 150 synchrony relationship was only occasionally U-shaped, and then only mildly so. The right side of Eq. 2
 151 was computed analytically (i.e., with formulas) for gamma, exponential, chi-squared, normal, and log-
 152 normal examples, and the formulas were compared with numerical results. For some distributions and
 153 parameters, the approximation was very accurate, and it was always at least qualitatively accurate (in the
 154 sense that it showed similar declines of b with increasing synchrony), except for the log-normal
 155 distribution, for which it was very inaccurate for some parameters, due to insufficient sampling, as
 156 previously observed (15). As expected from the theorem, Eq. 2 was a better approximation for smaller Ω .

157 We also constructed non-identically distributed examples by applying transformations to
 158 multivariate normal random variables. Our theorem, which assumed identically distributed Y_i , did not
 159 apply here. The random variable X was the same as above and $Y_i = \varphi_i(X_i)$ where the $\varphi_i(\cdot)$ differed for
 160 different i . The $\varphi_i(\cdot)$ were chosen so that all the Y_i were from the same family (Poisson, negative binomial,
 161 gamma, exponential, chi-squared, normal or log-normal), though with different parameters. For gamma,
 162 normal, exponential, and log-normal examples, the $\varphi_i(\cdot)$ were chosen so that Y_i was distributed in the same
 163 way as (but was not equal to) $f_i Y_1$, where $0 < f_1 < \dots < f_n$. This procedure was not possible for negative
 164 binomial, Poisson, or chi-squared distributions because these families are not closed under multiplication
 165 by positive real numbers. Distributions used for these families and the results are described in SI
 166 Appendix S4.

167 Results reinforced most of the generalities that emerged from the above analytical results and
 168 simulations, although a U-shaped dependence of b on Ω was more common and stronger in these
 169 examples (SI Appendix S4). Exceptions to general tendencies did occur. For gamma, exponential, normal,
 170 and log-normal examples, TL was usually a good approximation. Although linearity was often
 171 statistically rejected, departures from linearity were modest: $\log(v)$ -versus- $\log(m)$ plots stayed very close
 172 to the regression line. The slope b always showed an initial steep decrease as Ω increased from 0 for all
 173 gamma, exponential, normal, and log-normal examples. As $\Omega \rightarrow 1$, these examples approached the case
 174 for which Y_i equals $f_i Y_1$ almost surely in addition to having the same distribution as $f_i Y_1$. In that limit, $m =$
 175 $\text{mean}_i(Y_i) = \text{mean}_i(f_i Y_1) = Y_1 \text{mean}_i(f_i)$, whereas $v = \text{var}_i(Y_i) = \text{var}_i(f_i Y_1) = Y_1^2 \text{var}_i(f_i)$. Therefore
 176 TL should hold exactly with slope 2. This argument holds even for symmetric distributions like the

177 normal. Our numeric simulations confirmed that as Ω increased toward 1, root mean squared errors from
178 $\log(v)$ -versus- $\log(m)$ regressions went to 0 and b went to 2, sometimes from above and sometimes from
179 below. An approach from below was paired with U-shaped dependence of b on Ω , which was common
180 and often pronounced in these examples. The earlier result (15) that skewness is required for TL to have
181 slope $b \neq 0$ if Y_i are identically distributed does not hold when Y_i are not identically distributed:
182 simulations with Y_i normally distributed had $b \neq 0$ (SI Appendix figs S45-S50). For Poisson and chi-
183 squared examples, TL was usually a reasonable approximation, and b declined steeply as Ω increased
184 from 0 and continued to decrease for larger Ω . Negative binomial examples often strongly violated TL,
185 especially for large values of Ω (e.g., SI Appendix figs S63, S64). Nonetheless, the slope b tended to
186 decrease with increasing Ω whenever linearity held approximately.

187 Another way to create families of random variables Y with fixed marginal distributions but
188 varying synchrony is based on sums of independent random variables representing local and regional
189 influences on populations (32). It is well known that for independent Poisson random variables X and X_i ,
190 the sum $X+X_i$ is Poisson distributed. Similar facts are also true for the negative binomial, gamma, and
191 normal families. Therefore Y was generated by setting $Y_i = X + X_i$ for independent X and X_i for $i = 1, \dots, n$.
192 The variable X can be interpreted as the influence of a large-spatial-scale environmental or other factor
193 that affects all populations; the X_i are local effects. Different relative variances of X and the X_i led to
194 different amounts of correlation (synchrony) among the Y_i . By this approach, we constructed Y such that
195 the Y_i were identically distributed according to a desired Poisson, negative binomial, gamma, exponential,
196 chi-squared, or normal distribution, with a desired level of synchrony among the Y_i . Details of this
197 construction and the results are in SI Appendix S5.

198 Results were the same in some respects as the results above, and differed in others. Larger values
199 of synchrony always decreased the slope b (except for normal Y_i , for which b was always 0, as expected
200 from the theorem since Y_i are again identically distributed). The slope b went to 0 as Ω approached 1. The
201 approximation Eq. 2 applied reasonably accurately. In all cases, the right side of Eq. 2 reduced to simple,
202 monotonically decreasing functions of Ω . However, contrary to prior simulations, $\log(v)$ -versus- $\log(m)$
203 plots often strongly violated the linear hypothesis of TL. Values of synchrony Ω larger than 0 smeared
204 points rightward in $\log(v)$ -versus- $\log(m)$ space, destroying the linear relation expected from TL. This
205 smearing decreased b , but also changed its meaning from representing the slope of a linear pattern to
206 representing the slope of a linear approximation to a nonlinear pattern. The decrease in b did not reflect
207 maintenance of a linear pattern with a changed slope, as in prior examples (fig. 1, SI Appendices S3-S4).
208 SI Appendix S5 gives an explanation for this effect.

209 *Empirical results*

210 We examined the influence of synchrony on empirical data using 82 spatiotemporal population data sets.
211 The datasets included annual time series of population density for 20 species of aphid sampled for 35
212 years in 11 locations across the UK, annual density time series for 22 plankton groups sampled in 26
213 regions in the seas around the UK for 56 years, and chlorophyll-*a* density time series measured at several
214 locations at each of 10 depths in four distance categories from the coast of Southern California over 28
215 years. We henceforth refer to distance categories from shore in the chlorophyll-*a* data as groups 1-4,
216 where 1 refers to the closest category to shore, and larger group numbers correspond to farther categories
217 from shore. See Methods for further descriptions of the data and their processing.

218 The spatial TL was reasonably well supported by all 82 datasets. SI Appendix figs. S91-S96 plot
219 $\log(v)$ versus $\log(m)$ and give statistical tests of TL. Conformity to TL was not perfect, but was quite good
220 overall, except for the chlorophyll-*a* data in group 3 (SI Appendix fig. S95). Linearity or
221 homoskedasticity of the $\log(v)$ versus $\log(m)$ relationship was rejected at the 1% level for 7 of 82 data sets
222 (1 aphid species; 1 depth from group 1; 5 depths from group 3).

223 We examined correlations across species, taxonomic groups, or depths (for the aphid, plankton,
224 and chlorophyll-*a* data sets, respectively) between measurements of b and Ω . Factors other than
225 synchrony may have influenced these results and are accounted for below after examining the raw
226 correlations here. Fig. 2 (left panels) shows that b and Ω were significantly negatively correlated across

227 aphid species, and across depths in the chlorophyll-*a* data, groups 1 and 2, and were non-significantly
228 negatively correlated across plankton groups in the plankton data. Higher synchrony Ω was associated
229 with lower slope b in these data, despite possible confounding influences.

230 However, significant positive correlations occurred in the chlorophyll-*a* data, groups 3 and 4 (fig.
231 2m, p). These positive associations appear to conflict with simulation results, which generally support a
232 negative association between b and Ω , unless confounding factors overwhelmed a negative influence of
233 synchrony on b in these data. For instance, changes across depths in b may be influenced for the
234 chlorophyll-*a* data, groups 3 and 4, by changes across depths in Ω and by possible changes in time series
235 marginal distributions. Simulations carried out above held time series marginal distributions constant
236 when synchrony was varied.

237 To control for changes in time series marginal distributions that may have occurred in concert
238 with changes in synchrony, we decomposed slopes $b = b_{\text{marg}} + b_{\text{sync}}$ into contributions due to synchrony,
239 b_{sync} , and due to time series marginals, b_{marg} , to separate influences of synchrony and time series marginal
240 distributions on the slope b . We computed the marginal contribution, b_{marg} , by independently randomizing
241 time series and then re-computing the $\log(v)$ -versus- $\log(m)$ slope (Methods) to eliminate synchrony and
242 ensure that it cannot contribute to b_{marg} . Then we defined b_{sync} as $b - b_{\text{marg}}$. Fig. 2 (right panels) shows that
243 b_{sync} was negatively associated with Ω in all cases (albeit not always significantly), even for chlorophyll-*a*
244 data, groups 3 and 4 (fig. 2o, r). For these groups, b_{marg} was strongly positively associated with Ω (fig. 2n,
245 q). This positive association overwhelmed the negative association of b_{sync} with Ω to produce the overall
246 positive association of b with Ω observed in fig. 2m, p. Thus group 3 and 4 results did not conflict with
247 simulation results, but rather showed that other factors dominated. The change in time series marginal
248 distributions for the chlorophyll-*a* data was not surprising because these data were gathered across
249 different depths, and chlorophyll-*a* density varies with depth in the ocean. SI Appendix fig. S99 is like
250 fig. 2, but identifies the species/groups/depths of plotted points; panels for the chlorophyll-*a* data show
251 that depth probably played a role. Differing thermocline depths across groups 1-4 (SI Appendix fig. S101)
252 may also have been important.

253 To examine in more detail the influence of synchrony on spatial TL in empirical data, we
254 performed further randomizations (Methods). Randomizations reduced or increased the synchrony in each
255 of our 82 spatiotemporal population data sets while not modifying the marginal distributions in each
256 sampling location. In virtually every case, increasing synchrony decreased b , while decreasing synchrony
257 increased b (fig. 3). The strength of the effect varied across data sets and was typically steeper for smaller
258 values of synchrony. Values of b_{marg} correspond to the y-axis intercepts of the curves in fig. 3. In a few
259 cases, b appeared to depend in a U-shaped way on synchrony, as in some simulations, but the U shape
260 was modest when it occurred, also in agreement with simulations (i.e., only modest increases in b with
261 increasing Ω were observed on the right portions of plots in fig. 3). The linearity of TL was approximately
262 supported across the range of synchrony values except possibly for the highest synchrony values and the
263 chlorophyll-*a* data in group 3 (SI Appendix figs S97, S98).

264 All results are summarized, with hyperlinks to supporting figures and derivations, in SI Appendix
265 tables S3-S4.

266 Discussion

267 Understanding the relationship of synchrony with TL is important because both patterns are widespread in
268 population ecology, and because TL and recent observed climate-change-induced modifications in
269 synchrony have applied importance (19, 21, 26-28).

270 We showed that the strength of synchrony substantially influences the $\log(\text{variance})$ -versus-
271 $\log(\text{mean})$ scatter plot, of which TL is one special form. It can destroy linearity of TL, but more
272 commonly it preserves linearity and changes the slope b of the plot. Synchrony influenced the slope of TL
273 in essentially all of our analytic, numeric, empirical, and randomization-based examples. The one
274 systematic exception occurred when the marginal distributions of time series in different locations were
275 normally and identically distributed so that a nonzero-slope of TL was not expected with or without
276 synchrony (15). As synchrony increased from 0, slope b almost always decreased quite sharply. For some

277 theoretical and randomization examples, increasing synchrony starting from higher levels of synchrony
278 increased the slope b modestly, but analogous increases were not seen in empirical examples when
279 confounding changes in time-series marginal distributions were controlled. Our analytic results generalize
280 a theorem of Cohen and Xu (15). We provided a simple method of decomposing b into its contributions
281 due to synchrony, b_{sync} , and due to time-series marginal distributions, b_{marg} .

282 Ballantyne and Kerkhoff (14) and Eisler, Bartos and Kertesz (7) (their section 3) described
283 interesting links between small-spatial-scale synchrony and temporal TL. To explain the basic idea, we
284 construct an idealized example using aphids monitored by suction traps. Suppose trap i for $i = 1, \dots, n$ has
285 A_i agricultural fields that can produce aphids within its sampling range. Suppose traps are placed so that
286 no fields contribute to more than one trap. Suppose field ij ($i = 1, \dots, n, j = 1, \dots, A_i$) contributes a random
287 variable $V_{ij}(t)$ to trap i in year t , and suppose all the $V_{ij}(t)$ are identically distributed with mean μ and
288 variance σ^2 . Then if, for fixed i , $V_{ij}(t)$ are perfectly correlated so that all fields near i produce the same
289 number of sampled aphids per year (this is very strong small-spatial-scale synchrony, the spatial scale
290 being smaller than the spatial resolution of sampling), the mean of the number of aphids $\sum_j V_{ij}(t)$
291 sampled by trap i in year t is $\mu_i = A_i \times \mu$, and the variance is $\sigma_i^2 = A_i^2 \times \sigma^2$. Assuming random variables for
292 different times t are independent, the mean and variance across time of numbers of aphids sampled by
293 trap i will converge almost surely, in the limit of long time series, to these same values (strong law of
294 large numbers). Log transforming and doing basic algebra gives $\ln(\sigma_i^2) = 2 \times \ln(\mu_i) + C_1$ for a constant C_1 ;
295 this is a temporal TL with slope 2. If, for fixed i , $V_{ij}(t)$ are independent, then the mean of $\sum_j V_{ij}(t)$ is
296 again $\mu_i = A_i \times \mu$, but the variance is now $\sigma_i^2 = A_i \times \sigma^2$. Log transforming and doing basic algebra gives
297 temporal TL with slope 1. (This example shows, incidentally, that observing TL with slope 1 need not be
298 evidence that the aphids or other organisms are Poisson-distributed, even though Poisson-distributed
299 aphids or other organisms lead to TL with slope 1.)

300 The above example differs in at least two important ways from our results. First, it concerns
301 temporal TL, whereas we studied spatial TL. Second, the above example concerns synchrony at a
302 different spatial scale from our study. Although dependence between numbers of aphids sampled at
303 different traps seems likely to imply dependence between numbers contributed by fields within the range
304 of individual traps, the reverse need not be true.

305 It seems worthwhile, in future research, to examine the possibly complex relationships between
306 the above example (7, 14) and our study. While Eisler, Bartos and Kertesz (7) focus on temporal TL, they
307 state without proof or details that many of their results also apply to TL more generally. Relationships
308 between spatial and temporal TL have recently been examined (20) and may help connect the TL in the
309 above example to the spatial TL of our study. Perhaps all these versions of TL could be formally related
310 to each other and to synchrony.

311 Engen, Lande and Saether (25) produced a general model for analyzing a version of TL in which
312 each group of measurements of population density comes from plots of the same size, but different groups
313 use different plot sizes (distinct from spatial and temporal TL). On p. 2620 they remind the reader that
314 increasing population migration leads to increasing synchrony, which causes “the slope [of this version of
315 TL] ... to increase from 1 to 2 ... as the migration increases.” Engen, Lande and Saether (25) seem to
316 indicate in the final sentences of their paper that their model could be extended to address spatial TL,
317 possibly helping to illuminate connections among spatial, temporal, and their versions of TL and
318 synchrony.

319 Cohen and Saitoh (20) examined relationships among synchrony and spatial and temporal TL in
320 voles. Their example is consistent with our work and illustrates the value of our general results for
321 understanding TL in specific systems. Using 31 years of population density data for the grey-sided vole,
322 *Myodes rufocanus*, at 85 locations in Hokkaido, Japan, Cohen and Saitoh (20) verified that spatial and
323 temporal TL held for the data, as well as for simulations of a previously validated Gompertz model of the
324 dynamics of these populations. However, simulated time series had spatial and temporal TL slopes
325 substantially steeper than those from data. Cohen and Saitoh (20) observed that most pairs of vole
326 populations were significantly temporally correlated, and modified the Gompertz model accordingly.

327 When density-independent perturbations in model dynamics were synchronized, inducing synchrony in
328 simulated population time series, and when simulated populations with higher mean density had a
329 reduced variance of density-independent perturbations, the modeled slopes of spatial and temporal TL
330 were reduced to values similar to those of the data. Our results here account qualitatively for the effect on
331 TL slopes of the first of these two modifications of the Gompertz model, i.e., the introduction of
332 synchrony.

333 Our theoretical models and our randomizations kept the marginal distributions of time series
334 fixed as synchrony changed, to exclude confounding factors. In our empirical analyses, we separated the
335 contribution of synchrony, b_{sync} , to the empirical TL slope b . In reality, synchrony may change jointly
336 with marginal distributions across species, or depths, or some other axis of variation, as in some of our
337 empirical data (fig. 2). Covariation between changes in b_{sync} and b_{marg} should be context dependent, may
338 be biologically revealing, and is worth examining when multiple values of b are computed.

339 Increasing evidence shows that Moran effects, possibly due to climate change, modify synchrony
340 (19, 21, 26-28). The present work indicates that changed synchrony will modify the slope and possibly
341 the validity of TL, with ramifications for applications of TL in many areas including resource
342 management (3), conservation (11), human demography (6), tornado outbreaks (8), and agriculture (2, 12,
343 13). Given the ubiquity of synchrony in nature (22), it seems highly likely that synchrony often affects
344 values of TL slopes in real populations, as Hokkaido voles showed. It is important to understand better
345 how TL is affected by synchrony and other factors.

346 **Methods**

347 *Analytic and numeric methods*

348 Full details of analytic results are in SI Appendix S1-S2, and full details of numeric simulations are in SI
349 Appendix S3-S6.

350 *Data.*

351 Rothamsted Insect Survey (RIS) runs a network of suction traps that sample flying aphids. Daily aphid
352 counts are collected throughout the flight season for many species at multiple locations. Data were
353 processed to produce annual total counts for 20 species (SI Appendix table S1) at 11 locations (SI
354 Appendix table S2) for the years 1976 through 2010, forming 20 spatiotemporal population datasets.

355 The Continuous Plankton Recorder (CPR) survey, now operated by the Sir Alister Hardy
356 Foundation for Ocean Science (SAHFOS), has sampled the seas around the UK for plankton abundances
357 since before World War II, using a sampling device towed behind commercial ships. Data were processed
358 to produce annual abundance time series for 22 phytoplankton and zooplankton taxa (SI Appendix table
359 S1) for $26^{\circ} \times 2^{\circ}$ areas around the UK for the years 1958 through 2013, forming 22 spatiotemporal
360 population datasets.

361 The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has surveyed the
362 California Current System since 1949 measuring chlorophyll-*a* regularly since 1984. Time series of
363 spring chlorophyll-*a* were based on measurements at 55 sites which were divided into four groups based
364 on distance from shore, with group 1 near to shore (average 87.7 km) and group 4 far from shore (average
365 539.3 km). For each site and sampling occasion, annual chlorophyll abundances were calculated for 0, 10,
366 20, 30, 50, 75, 100, 125, 150, and 200 m depths, forming 10 spatiotemporal datasets for each group.

367 Further data details are in SI Appendix S7.

368 *Randomizations and the decomposition of b*

369 Given an $T \times n$ matrix with each column containing a time series of population size or density from one
370 location (so T is the length of time series and n is the number of sampling locations), synchrony was
371 reduced without affecting time series marginal distributions for the sampling locations by selecting k rows
372 randomly, and then randomly replacing the entries in those rows with randomly chosen (with
373 replacement) values from the same column; this replacement was done independently within each
374 column. Larger values of k destroy a larger fraction of any synchrony that was originally present in the
375 time series. Setting $k = T$ completely eliminates synchrony by randomizing each complete time series

376 independently. To increase the synchrony, starting from the original time series, k rows were again
377 selected randomly. Within each column of this $k \times n$ submatrix separately, entries were sorted into
378 increasing order. For each value of k , k rows were selected randomly in 100 ways, with values of b and Ω
379 averaged for fig. 3. The value b_{marg} was computed by randomizing time series with $k = T$ as described
380 above, to destroy synchrony, and then computing $b = b_{\text{marg}}$ for the randomized dataset.

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- 453

454 **Figure Legends**

455 **Figure 1.** Effects of spatial synchrony on spatial Taylor’s law (TL) for a model with populations
456 identically distributed in different sampling locations and identically distributed and independent (iid)
457 through time at each location. Examples use Poisson (a; $\lambda=5$) and gamma (b; shape $\alpha=8$, rate $\beta=2$)
458 distributions (see SI Appendix S3 for parameterization of the gamma distribution). Top panels: m is
459 spatial sample mean and v is spatial sample variance. Confirming TL visually, approximately linear
460 $\log_{10}(v)$ -versus- $\log_{10}(m)$ relationships held with selected values of ρ . Slopes were shallower for greater
461 synchrony. Middle panels: TL had a shallower slope for greater synchrony. Black lines show the average
462 (across the 50 simulations) TL slope plotted against average synchrony (error bars are standard
463 deviations), and average root mean squared deviations of $\log_{10}(v)$ values from $\log_{10}(v)$ -versus- $\log_{10}(m)$
464 linear regressions; red lines (b) are analytic approximations (Eq. 2, theorem 5 of SI Appendix S2.3),
465 computable with readily available software for continuous distributions (SI Appendix S3), with + and \times
466 symbols respectively indicating points for which approximations were deemed adequate via two different
467 methods, both symbols plotted when both methods indicate an adequate approximation. Each simulation
468 consisted of 25 populations sampled 100 times each. Bottom panels: fractions of m and v values which
469 were 0 and therefore ignored; and fractions of 50 simulations for which statistical tests rejected linearity
470 or homoskedasticity of the $\log_{10}(v)$ -versus- $\log_{10}(m)$ relationship with 95% confidence. See SI Appendix
471 figs. S1-S32 for other parameters and distributions, which often showed similar patterns. See SI Appendix
472 S3 and S6 for additional details.

473
474 **Figure 2.** Plots of TL slope b against synchrony Ω for 20 species of aphid in the UK (a), 22 plankton
475 groups in the seas around the UK (d), and chlorophyll- a density time series measured at 10 depths in
476 groups 1-4 (g, j, m, p; Methods), which are distance categories from shore. Panels are paired with
477 contributions to the slope, b , of marginal-distribution structure (b_{marg} ; b,e,h,k,n,q) and synchrony (b_{sync} ;
478 c,f,i,l,o,r; Methods). Associations between synchrony and TL slope b (left panels) can be due to
479 associations between synchrony and b_{marg} or b_{sync} or both, since $b = b_{\text{marg}} + b_{\text{sync}}$. SI Appendix fig. S99
480 shows another version of the figure that labels individual species/groups/depths.

481
482 **Figure 3.** The dependence of the spatial TL slope b on synchrony Ω , where synchrony was manipulated
483 through randomizations or sorting of time series (Methods), for aphid species (a), plankton groups (b),
484 and a chlorophyll- a density index measured at 10 depths (c-f). Panel c is for the 19 group-1 locations,
485 panel f is for the 12 group-4 locations, and panels d and e are for 12 locations in each of two intermediate
486 distance categories (groups 2, 3; Methods). Red points on plotted lines correspond to individual,
487 unrandomized aphid species (a), plankton groups (b), and sampling depths (c-f), detailed in SI Appendix
488 table S1. Grey points are averages over randomizations or sortings (Methods). Values for individual
489 randomizations are shown in SI Appendix fig. S100.