

# 1 Synchrony affects Taylor's law in theory and data

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## 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  $\text{var}_t$  and the covariance  $\text{cov}_t$  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  $\Omega_t$  is  $1/n$  when the correlations with  $i \neq j$  are 0.  $\Omega_t$  is 0 when the  
 92 spatial-average time series is constant, and  $\Omega_t$  cannot be negative (SI Appendix S1). We are interested in  
 93 how  $\Omega_t$  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,  $\Omega$ , and is similar in form. Eq. 1 therefore provides the  
 106 intuition behind our subsequent analyses: if synchrony ( $\Omega$  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  $\Omega$  (i.e., it increases, has a  
 125 maximum and then decreases again as  $\Omega$  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  $\Omega$  increases).  
 130 Dependence of the numerator of Eq. 2 on  $\Omega$  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  $\rho$  produced  
 138 increases in  $\Omega$ . 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  $\Omega$ . For skewed distributions, the slope  $b$  was generally smaller  
 146 for larger values of  $\Omega$ , confirming the prediction that  $b$  depends on synchrony. Although  $b$  decreased  
 147 steeply as  $\Omega$  increased from 0 for all skewed distributions,  $b$  most commonly continued to decrease  
 148 monotonically as  $\Omega$  increased further, even for large values of  $\Omega$ , 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  $\Omega$ .

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  $\Omega$  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  $\Omega$  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  $\Omega$  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  $\Omega$ , 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  $\Omega$  increased  
184 from 0 and continued to decrease for larger  $\Omega$ . Negative binomial examples often strongly violated TL,  
185 especially for large values of  $\Omega$  (e.g., SI Appendix figs S63, S64). Nonetheless, the slope  $b$  tended to  
186 decrease with increasing  $\Omega$  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  $\Omega$  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  $\Omega$ . However, contrary to prior simulations,  $\log(v)$ -versus- $\log(m)$   
203 plots often strongly violated the linear hypothesis of TL. Values of synchrony  $\Omega$  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  $\Omega$ . 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  $\Omega$  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  $\Omega$  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  $\Omega$ , 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  $\Omega$  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  $b_{\text{sync}}$ , and due to time series marginals,  $b_{\text{marg}}$ , to separate influences of synchrony and time series marginal  
240 distributions on the slope  $b$ . We computed the marginal contribution,  $b_{\text{marg}}$ , 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  $b_{\text{marg}}$ . Then we defined  $b_{\text{sync}}$  as  $b - b_{\text{marg}}$ . Fig. 2 (right panels) shows that  
243  $b_{\text{sync}}$  was negatively associated with  $\Omega$  in all cases (albeit not always significantly), even for chlorophyll-*a*  
244 data, groups 3 and 4 (fig. 2o, r). For these groups,  $b_{\text{marg}}$  was strongly positively associated with  $\Omega$  (fig. 2n,  
245 q). This positive association overwhelmed the negative association of  $b_{\text{sync}}$  with  $\Omega$  to produce the overall  
246 positive association of  $b$  with  $\Omega$  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  $b_{\text{marg}}$  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  $\Omega$  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,  $b_{\text{sync}}$ , and due to time-series marginal distributions,  $b_{\text{marg}}$ .

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  $\mu$  and  
288 variance  $\sigma^2$ . 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,  $b_{\text{sync}}$ , 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  $b_{\text{sync}}$  and  $b_{\text{marg}}$  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  $\Omega$   
379 averaged for fig. 3. The value  $b_{\text{marg}}$  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  $\rho$ . 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  $\Omega$  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 ( $b_{\text{marg}}$ ; b,e,h,k,n,q) and synchrony ( $b_{\text{sync}}$ ;  
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  $b_{\text{marg}}$  or  $b_{\text{sync}}$  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  $\Omega$ , 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.