biology letters

Population ecology

Taylor's Law holds in experimental bacterial populations but competition does not influence the slope

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Populations vary in time and in space, and temporal variation may differ from spatial variation. Yet, in the past half century, field data have confirmed both the temporal and spatial forms of Taylor's power Law, a linear relationship between log(variance) and log(mean) of population size. Recent theory predicted that competitive species interactions should reduce the slope of the temporal version of Taylor's Law. We tested whether this prediction applied to the spatial version of Taylor's Law using simple, well-controlled laboratory populations of two species of bacteria that were cultured either separately or together for 24 h in media of widely varying nutrient richness. Experimentally, the spatial form of Taylor's Law with a slope of 2 held for these simple bacterial communities, but competitive interactions between the two species did not reduce the spatial Taylor's Law slope. These results contribute to the widespread usefulness of Taylor's Law in population ecology, epidemiology and pest control.

Keywords: Taylor's Law; populations; competition; bacteria; *Pseudomonas fluorescens*; *Serratia marcescens*

1. INTRODUCTION

Starting half a century ago, Taylor *et al.* [1−4] and nearly a thousand other papers [5] demonstrated a linear relationship (commonly called 'Taylor's Law') between the log(variance) of the population size or density of a species and the log(mean) of population size or density. This relationship applies to both spatial and temporal population samples [4]. Numerous mechanisms affecting the slope of this linear relationship have been examined theoretically [6,7−10], but few have been investigated experimentally [11].

Kilpatrick & Ives [10] suggested that interspecific competition might reduce the slope of the temporal form of Taylor's Law, i.e. lower the rate at which log(variance) increases with log(mean) when mean and variance are calculated over time. In a simple dynamic community model, they demonstrated that direct and

'apparent' competition could reduce slopes from 2 to a lower value between 1 and 2.

The effect of competition on the spatial form of Taylor's Law has not been investigated either theoretically or empirically. The spatial form of Taylor's Law calculates the mean and the variance of populations sampled (possibly simultaneously) at different points in space, when replicate populations are grouped by some external condition such as available nutrients. We examined experimentally the validity of the spatial form of Taylor's Law and the effect of competition on the slope of Taylor's Law in simple, well-controlled laboratory experiments. We cultured two species of bacteria, both separately and together, in media of widely varying nutrient richness. The bacterial species interacted competitively when they were together, and the spatial form of Taylor's Law usefully described the approximately linear increase of log(variance) with increasing log (mean). The slopes were not significantly different from 2. The presence of a competitor had no statistically significant effect on the slope. On the contrary, the slope was slightly (not statistically significantly) higher in the presence of competition.

2. MATERIAL AND METHODS

We used the Gram-negative bacterium *Serratia marcescens* [12] and a smooth-type stabilized strain of *Pseudomonas fluorescens* SBW25 [13]. Each of these two species was cultured alone or in competition with the other (i.e. three types of culture). These cultures were grown in 24 well plates each containing 1.5 ml of King's B (KB) medium (glycerol $10 \, ml \, l^{-1}$; proteose peptone H3 $20 \, g \, l^{-1}$; dipotassium phosphate K_2HPO_4 $1.5 \, g \, l^{-1}$; magnesium sulphate $MgSO_4$ $1.5 \, g \, l^{-1}$; distilled water qs 1 l). To create a gradient of environmental richness, we used pure KB medium and KB medium diluted 3, 9, 27, 81, 243, 729 and 2187 times (eight levels). Each of the $3 \times 8 = 24$ treatments was replicated eight times. We inoculated all the cultures containing *P. fluorescens* or *S. marcescens* with bacteria harvested from two diversified mass cultures (one per species). The initial density of bacterial cells was proportional to the richness of the medium used. In pure KB medium, we introduced approximately 3×10^7 *P. fluorescens* cells, or 3×10^7 *S. marcescens* cells or 3×10^7 cells of each species into 1.5 ml. Initial densities were thus approximately 2×10^7 colony forming units (CFUs) per millilitre for each species whether alone or in combination. Cultures that contained KB medium diluted three times received one-third of these cell numbers, cultures that contained KB medium diluted nine times received one-ninth of these numbers, etc. All populations were grown at $28°C$ under constant agitation for 24 h, that is, until they reached carrying capacity. Although we cannot rule out that some evolution occurred in the microcosms, we expect that ecological forces dominated dynamics over the 24-h period (over which a maximum of 10 and seven generations would have occurred in *S. marcescens* and in *P. fluorescens*, respectively).

Population densities were then estimated by counting the number of CFUs that appeared after plating 15 μl of (serially diluted) cultures on 1 per cent KB agar. After 24- to 36-h growth, colonies of the two bacterial species were readily recognized and counted under a stereomicroscope based on their colour and morphology. Bacterial density in each culture was estimated by averaging counts from two different 15 μl samples. We calculated the mean and the variance of the population density of each bacterial species over the eight replicates in each of the 24 treatments. After log_{10} transformation, we obtained 32 points (log(mean), log(variance)): 16 from bacteria grown in monoculture and 16 from bacteria grown with a competitor. Electronic supplementary material, appendix table S1 gives the raw data.

We tested for evidence of competition using ANOVAs, and investigated the effect of competition on the slope of the regression of log(variance) to log(mean) with linear models and ANCOVAs. All statistical computing was performed using R v. 2.9.0 [14].

3. RESULTS

(a) *Evidence for competition*

If *P. fluorescens* and *S. marcescens* competed for resources, then the presence of each species in a microcosm should reduce the mean population density of the other species.
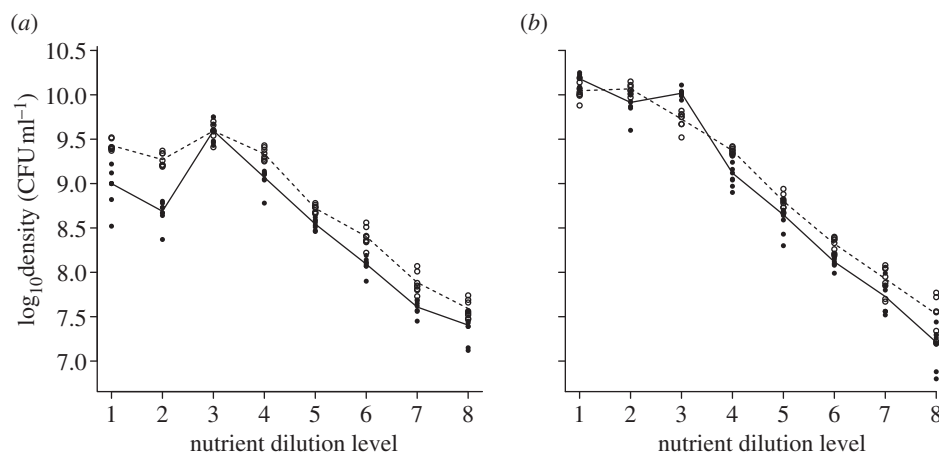
Figure 1. Competition lowers abundance. The effect of competitor presence on bacterial densities (expressed in $\log_{10}$ of CFU ml^{-1}) for (a) *P. fluorescens* and (b) *S. marcescens*, by level of KB dilution, between treatments alone and in competition. (a,b) Filled circles with solid line, in competition; open circles with dashed line, alone. Dilution levels 1 through 8 correspond to actual dilutions of 1, 3, 9, 27, 81, 243, 729, and 2187 times, respectively.

Table 1. Bacterial species compete. Competition, KB dilution and their interaction (competition × KB) affected *P. fluorescens* and *S. marcescens* population densities with very high statistical significance, by ANOVA.

	d.f.	sum-squared	mean-squared	*F*-value	Pr($>F$)
ANOVA table for *P. fluorescens*. Response: log(density)					
competition	1	5.91	5.91	75.42	3.961e−14***
KB dilution	7	339.45	48.49	618.75	<2.2e−16***
competition × KB	7	4.65	0.66	8.4765	2.860e−08***
residuals	110	8.62	0.08		
ANOVA table for *S. marcescens*. Response: log(density)					
competition	1	0.97	0.97	11.807	0.000836***
KB dilution	7	625.19	89.31	1090.763	<2.2e−16***
competition × KB	7	7.76	1.11	13.534	1.739e−12***
residuals	109	8.93	0.08		

***$p < 0.001$.

Experimentally, the density of each species was usually lower in the presence of the other species (figure 1). We defined $\log(\text{mean})_{\text{competition}} - \log(\text{mean})_{\text{monoculture}}$ as 'competitive intensity' and interpreted more negative values of competitive intensity as indicating greater competition. Most values of competitive intensity were negative (figure 1a,b). ANOVAs of competitive intensity rejected the null hypothesis of no competitive effects of *S. marcescens* and *P. fluorescens* on each other with high statistical significance ($p < 0.001$; table 1). In most cases, competitor presence lowered the $\log_{10}$(bacterial concentration) by more than 0.5 units (figure 1), which represents an almost threefold reduction in the absolute number of bacteria. Competition had thus a very strong effect on population density.

We further tested with ANCOVAs whether competitive intensity was strongest when culture medium richness was lowest. We found no statistically significant support for this hypothesis with *S. marcescens* ($F_{1,6} = 4.86$, $p = 0.07$) or *P. fluorescens* ($p > 0.1$; figure 1). Competition was generally less intense at an intermediate KB dilution (electronic supplementary material, figures S1 and S2), and at some intermediate KB dilutions mean abundance of one bacterial species in the presence of the other exceeded mean abundance in the absence of the other. This U-shaped pattern was more pronounced for *P. fluorescens* than for *S. marcescens*. The U-shaped

pattern probably occurs because *P. fluorescens* grows better in slightly diluted KB medium.

(b) *Effect of competition on the relation between log(variance) and log(mean)*

Mean bacterial densities varied by approximately 2.2 orders of magnitude for *P. fluorescens* ($2.5 \times 10^7 - 3.9 \times 10^9$ CFU ml^{-1}) and 3.0 orders of magnitude for *S. marcescens* ($1.6 \times 10^7 - 1.5 \times 10^{10}$ CFU ml^{-1}) across all treatments when pooling all data. The variance of bacterial population densities varied among treatments by approximately 4.5 orders of magnitude for *P. fluorescens* ($5.4 \times 10^{13} - 1.6 \times 10^{18}$) and 5.1 orders of magnitude for *S. marcescens* ($4.6 \times 10^{13} - 5.8 \times 10^{18}$). Hence, if the relation between log(variance) and log(mean) were approximately linear, then the slope of log(variance) as a linear function of log(mean) would be expected to be approximately $4.5/2.2 = 2.0$ for *P. fluorescens* and $5.1/3.0 = 1.7$ for *S. marcescens*.

To investigate the effect of competition on the relation between log(variance) and log(mean), we performed linear regressions, for each species separately, of the dependent variable log(variance) on the independent variable log(mean), for the treatments with and without competition. Then, we used ANCOVAs to test for a slope difference. ANCOVAs did not indicate any statistically significant differences in slopes (interactions
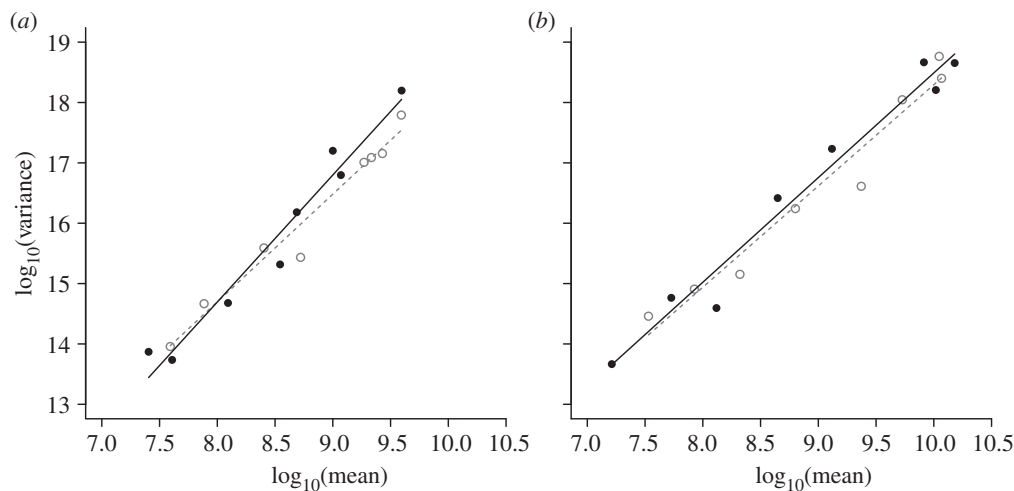
Figure 2. Taylor's Law holds. Linear regression of log(variance) to log(mean) of the bacterial densities of (*a*) *P. fluorescens* and (*b*) *S. marcescens* either grown alone in monoculture or in competition with one another. (*a*,*b*) Filled circles with solid line, in competition; open circles with dashed line, alone.

Table 2. Competition does not change slopes. Neither competition nor species identity had a statistically significant effect ($p > 0.1$) on the slope of log(variance) as a function of log(mean), nor were there statistically significant effects on the slope of interactions of log(mean) with competition or interactions of log(mean) with species identity, by ANCOVA.

	d.f.	sum-squared	mean-squared	*F*-value	Pr($>F$)
ANCOVA table to test for the effect of competition on regressions slopes. Response: log(variance)					
log(mean)	1	78.626	78.626	706.1704	$<2e-16$***
competition	1	0.186	0.186	1.6662	0.2081
species	1	0.131	0.131	1.1747	0.2884
log(mean) × competition	1	0.096	0.096	0.8630	0.3614
log(mean) × species	1	0.296	0.296	2.6541	0.1153
residuals	26	2.895	0.111		

***$p < 0.001$.

between log(mean) and the competition term; $p > 0.1$). For *P. fluorescens*, the slopes without and with the competitor were 1.784 ± 0.33 (95% confidence interval) and 2.104 ± 0.426, respectively (figure 2a). For *S. marcescens*, the slopes without and with the competitor were 1.677 ± 0.346 and 1.734 ± 0.304, respectively (figure 2b). Though the slopes are not significantly different from one another, for both species the slope in the presence of the competitor was higher than the slope without the competitor. This finding for the spatial relationship between log(variance) and log(mean) is contrary to the prediction of Kilpatrick & Ives [10] for the temporal version of Taylor's Law.

When we fitted *P. fluorescens* and *S. marcescens* data together in a single model that contained factors describing whether observations originated from competitive microcosms and the identity of the bacterial species, the interaction between competition and log(mean) was not significant. As in the previous analysis, this analysis provided no evidence that slopes for the spatial form of Taylor's Law were lower in the presence of a competitor (table 2). The terms describing the bacterial species and its interaction with log(mean) were not significant either ($p > 0.1$).

4. DISCUSSION

Theory has identified numerous processes that could influence relationships between log(variance) and log(mean) [4,6,9,10] in population data, but experimental demonstrations of their role have been elusive. We found that the spatial version of Taylor's Law described well the linear increase in log(variance) with increasing log(mean) for each of two bacterial species grown with or without the other. A reduction in mean population size in the presence of the other species demonstrated competition between the bacterial species when they were grown together. The slope of Taylor's Law was not reduced by interspecific competition in our experiments.

These findings suggest that the spatial version of Taylor's Law does not always satisfy the prediction by Kilpatrick & Ives [10] that interspecific competition lowers slopes in the temporal form of Taylor's Law. The confirmation of the spatial form of Taylor's Law and the failure to detect a reduction in slope from values near 2 as a result of competition in these experiments means that an ecological understanding of at least the spatial version of Taylor's Law remains an open challenge. In light of the widespread usefulness of Taylor's Law in areas such as population ecology [15,16], epidemiology [17], and the spatial and temporal dynamics of agricultural pests [18–20], it is a challenge of significance.

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