Parasitism alters three power laws of scaling in a metazoan community: Taylor's law, density-mass allometry, and variance-mass allometry

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How do the lifestyles (free-living unparasitized, free-living parasitized, and parasitic) of animal species affect major ecological power-law relationships? We investigated this question in metazoan communities in lakes of Otago, New Zealand. In 13,752 samples comprising 1,037,058 organisms, we found that species of different lifestyles differed in taxonomic distribution and body mass and were well described by three power laws: a spatial Taylor's law (the spatial variance in population density was a power-law function of the spatial mean population density); density-mass allometry (the spatial mean population density was a power-law function of mean body mass); and variance-mass allometry (the spatial variance in population density was a power-law function of mean body mass). To our knowledge, this constitutes the first empirical confirmation of variance-mass allometry for any animal community. We found that the parameter values of all three relationships differed for species with different lifestyles in the same communities. Taylor's law and density-mass allometry accurately predicted the form and parameter values of variance-mass allometry. We conclude that species of different lifestyles in these metazoan communities obeyed the same major ecological power-law relationships but did so with parameters specific to each lifestyle, probably reflecting differences among lifestyles in population dynamics and spatial distribution.

parasite | metazoan | power law | Taylor's law | allometry

Variation in population density has long been a central topic in ecology (e.g., ref. 1). Taylor's law (TL) (2, 3) is a pattern of variation that has been widely verified for population density in basic and applied ecology and for other quantities in other fields. In its ecological interpretations, TL asserts that, in multiple sets of populations, the sample variance in population density within each set is proportional to a power (usually positive) of the sample mean population density within that set. We specify TL in greater detail below.

Morand and Guégan (4) showed that TL described well the variations of abundance per host in 828 populations of parasitic nematodes from 66 terrestrial mammalian species. Morand and Krasnov (5) reviewed examples of TL in parasitology and epidemiology and interpreted the exponent of the TL power law in terms of the aggregation of parasites and epidemiological dynamics. These studies used the number of individual parasites per individual host as the measure of population density. Following a suggestion of Taylor (2), these studies interpreted the exponent of the power-law relationship of variance of population density to mean of population density as an index of parasite aggregation among hosts. A purely random distribution of parasites per host leads to a Poisson distribution, which gives a TL exponent equal to 1 as the mean population density varies. A TL exponent greater than 1 reflects greater heterogeneity in numbers of individuals per host than expected from a purely random distribution. More importantly, the TL exponent may also be used to assess the strength of parasite population regulation via processes such as interspecific competition or vaccination, and may distinguish between epidemic and endemic infections (5–7).

Here we ask how three lifestyles (free-living unparasitized, free-living parasitized, and parasitic) of animal species affect major ecological power-law relationships, including TL, using new data on all metazoans from the littoral zone of four lakes in coastal and central Otago, South Island, New Zealand. Unlike previous studies of TL in parasitology, we measured the population density of parasites as the number of individuals per square meter of habitat, not per individual host. Additionally, unlike previous studies, in addition to quantifying the population density of parasitic species (separately for each life stage), we quantified the population density of the free-living parasitized species and of the free-living unparasitized species in the same habitat. Contrasting TL and other power-law relationships among organisms with different lifestyles can reveal differences in the degree to which spatial heterogeneity in their abundance is regulated.

Using these data, we tested the validity of TL for metazoans of each lifestyle in the same habitat. Intuitively, it seemed plausible, and we investigated the hypothesis, that the interactions of free-living parasitized species and parasites added variability to the population dynamics of species of both lifestyles compared with free-living unparasitized species. This qualitative argument led us to expect larger values of the exponent of TL for free-living parasitized species and parasites compared with the exponent of TL for free-living unparasitized species.

Significance

Power laws of scaling are major achievements of ecology. Such empirical laws say that one quantity varies as some power of another quantity. For example, Taylor's law says that the variance of population density changes as a power of the mean population density. Density-mass allometry says that the mean population density is a power-law function of the mean body mass. We show, to our knowledge for the first time in any animal community, that the variance of population density is a power-law function of mean body mass, and that the parameters of all three power laws just mentioned are influenced by whether the animals are parasites, free-living parasitized species, or free-living unparasitized species. Lifestyle matters in ecology.

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In addition to testing TL and the effects of lifestyle on the parameters of TL, we examined the allometric relationship between mean population density and mean body mass (density-mass allometry, or DMA). Marquet et al. (8) and Cohen et al. (9) independently showed theoretically that TL and DMA combine to predict the form and parameters of an allometric relationship between the variance of population density and mean body mass (variance-mass allometry, or VMA). (The details of these predictions are in *SI Appendix*.) We tested and verified all three relations empirically for each lifestyle in the same habitat. The parameter values of all three relationships depended on lifestyle.

Although DMA has been very widely confirmed for a great variety of organisms (e.g., refs. 10–18), including parasitic nematodes (19) and other parasites (20), VMA has previously been confirmed empirically only for congeneric trees (*Quercus* spp.) in a temperate forest (9). These new data permitted us to verify the predicted VMA empirically, to our knowledge for the first time for any animals and for the first time for all metazoans in a local community. Empirical confirmation of VMA for all metazoans in a local community makes it possible to use average body mass to predict the variability of population densities of different species, in addition to predicting the mean population density from DMA. This variability bears on risks of extinction, population outbreaks, and epidemics. The ability to predict this variability from a factor as easily measured as average body mass could be valuable for economically important species.

Materials and Methods

We classified each species as belonging to one of three lifestyles: parasitic, free-living parasitized, and free-living unparasitized. Parasitic species were defined as species that derive all their energy from another organism without directly killing the latter. Parasites included mostly endoparasitic helminths at all stages of their life cycles, as well as some ectoparasitic mites. Free-living parasitized species were defined as those in which at least one individual sampled harbored a parasite, whereas free-living unparasitized species were defined as those in which no individual sampled harbored parasites. The free-living species included invertebrates (such as mollusks, crustaceans, aquatic insects, oligochaetes, leeches) and fish. Although free-living unparasitized species might harbor parasites at prevalences undetectable given our sample sizes, parasitized and unparasitized free-living species differ in the likelihood that parasitism affects variability in their population dynamics.

The vast majority of parasitic species considered here were helminths with complex life cycles, in which different life stages have distinct morphologies and different body sizes, and inhabit different host taxa. For these reasons, here we treated each life stage of parasitic species (only) as a separate "species."

We collected all metazoan species in the littoral zones of four modestly sized lakes in Otago, South Island, New Zealand. For all species, whether free-living or parasitic, we measured population density as individuals per square meter. This choice of a standard metric for all species made it possible, to our knowledge for the first time in a study of TL, to compare relationships for parasites with those for free-living organisms. Details of the study sites, sampling techniques, and measures of abundance and body mass, along with the details of statistical procedures and software, are described in *SI Appendix*.

Results

Descriptive Statistics of Three Lifestyles. The distribution of parasitic species across major taxonomic groups differed greatly from the distributions of free-living unparasitized and free-living parasitized taxa: 94% of the parasitic samples were nematodes or trematodes, whereas none of the free-living species was a nematode or a trematode (Table 1). A χ^2 test of the homogeneity across lifestyles rejected the null hypothesis that the distributions of the taxa were the same for all three lifestyles in Table 1 ($\chi^2 = 937.4577$, df = 20, $P < 10^{-185}$). Setting aside the parasitic species, the two free-living lifestyles also differed significantly from one another in their distribution across major taxonomic groups ($\chi^2 = 143.9563$, df = 6, $P < 10^{-27}$). The numbers of samples of taxa in each lifestyle (Table 1) were large enough to make these comparisons meaningful.

The median body mass of parasitic species was an order of magnitude smaller than that of free-living unparasitized species, which was in turn almost an order of magnitude smaller than that of free-living parasitized species (Table 2), despite some overlaps in the range of body masses. Because the smallest fish was much larger than the largest invertebrate, and there were no other organisms of intermediate size, a gap in body sizes represented a natural discontinuity in the size spectrum of species in our study communities.

These differences in taxonomic distribution and in body mass distribution between free-living unparasitized and free-living parasitized species indicated that free-living unparasitized and free-living parasitized species could not be regarded as samples from the same universe of taxa, as if they differed only by the absence or presence of parasites, respectively.

Table 1. Numbers (counts) and percentages of samples from broad taxonomic groups for each lifestyle separately

	Free-living unparasitized		Free-living parasitized		Parasitic	
Taxonomic group	Count	%	Count	%	Count	%
Acanthocephalans	0	0	0	0	8	3
Annelids	26	8	18	12	0	0
Cestodes	0	0	0	0	2	1
Crustaceans	107	33	18	12	0	0
Fish	5	2	58	38	0	0
Insects	122	37	45	30	0	0
Mites	12	4	0	0	4	2
Molluscs	35	11	12	8	0	0
Nematodes	0	0	0	0	26	10
Trematodes	0	0	0	0	213	84
Other	22	7	0	0	0	0
Total	329	100	151	100	253	100
Median of total sample sizes	28		36		20	
2.5th percentile of total sample sizes	1		1		1	
97.5th percentile of total sample sizes	10,743		16,419		8,055	

"Other" comprises planarians, hydrozoans, and nemerteans. "Total sample size" is the total number of organisms in each estimate of the mean and variance of population density.

Table 2. Parameter estimates using ordinary least squares linear regression to fit TL, DMA, and VMA to log-transformed data on the spatial variation of population density (individuals per square meter) of free-living unparasitized species, free-living parasitized species, and parasitic species; and the distribution of average body masses of species in each lifestyle

Parameter	Lifestyle		
	Free-living unparasitized	Free-living parasitized	Parasitic
No. of samples	329	151	253
TL: variance = $a \times$ (mean density)^b			
$\text{Log}_{10}\ a$	0.8060	0.2903	0.4333
Lo	0.7528	0.2043	0.3549
Hi	0.8592	0.3762	0.5118
b	1.6802	2.0193	2.1020
Lo	1.6441	1.9739	2.0568
Hi	1.7163	2.0646	2.1473
Adjusted R^2	0.9623	0.9810	0.9708
DMA: Mean density = $u \times$ (mean body mass)^v			
$\text{Log}_{10}\ u$	0.8577	1.9905	−0.2538
Lo	0.7315	1.7359	−0.4752
Hi	0.9839	2.2452	−0.0323
v	−0.2167	−0.7983	−0.9088
Lo	−0.2963	−0.8815	−1.0650
Hi	−0.1372	−0.7152	−0.7527
Adjusted R^2	0.0779	0.7055	0.3436
VMA: variance = $c \times$ (mean body mass)^d			
$\text{Log}_{10}\ c$	2.2423	4.4773	−0.0572
Lo	2.0228	4.0047	−0.5386
Hi	2.4618	4.9498	0.4242
$\text{Log}_{10}(a) + b \times \log_{10}(u)$	2.2470	4.3097	−0.1001
d	−0.2967	−1.6841	−1.8657
Lo	−0.4351	−1.8383	−2.2052
Hi	−0.1582	−1.5298	−1.5262
$b \times v$	−0.3642	−1.6120	−1.9104
Adjusted R^2	0.0487	0.7559	0.3155
Log_{10} body mass (mg)			
Median of samples	0.3037	1.1752	−0.7214
2.5th percentile	−3.0134	−0.1791	−3.1570
97.5th percentile	4.1204	6.2048	0.6201

Lo, lower limit of 95% confidence interval; Hi, upper limit of 95% confidence interval.

Taylor's Law. TL provided an excellent description of the interspecific relation of log variance of population density to log mean of population density for species of each lifestyle separately (Fig. 1). Visually, the relationships were close to linear. For (a) free-living unparasitized species and (b) free-living parasitized species, regression of log variance as a quadratic function of log mean revealed no statistically significant evidence of nonlinearity (details in *SI Appendix*). For (c) parasites, the coefficient of the quadratic term was slightly but statistically significantly negative ($P \sim 0.0014$), indicating a concavity of small magnitude in the relationship of log variance to log mean. For parasites, the quadratic model had adjusted $R^2 = 0.9718$, whereas the linear model (shown in Table 2) had adjusted $R^2 = 0.9708$. Thus, the quadratic term improved the explanatory

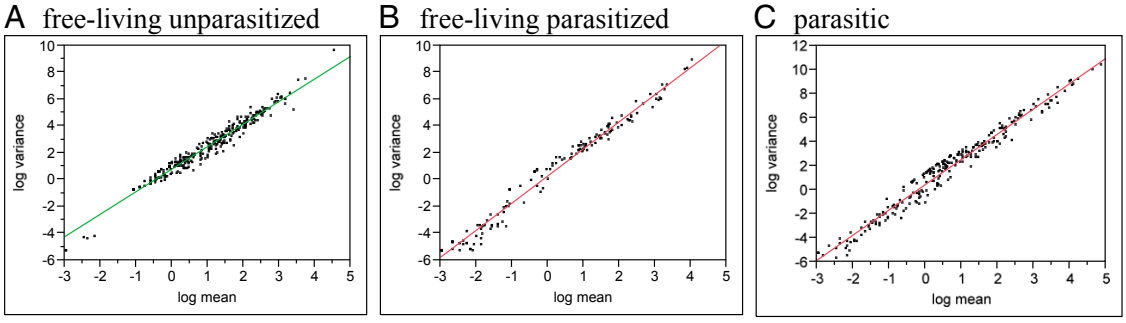

Fig. 1. Test of TL. Log variance of population density was an approximately linear function of the log mean of population density for (*A*) free-living unparasitized species, (*B*) free-living parasitized species, and (*C*) parasites. Each dot represents the log variance and log mean of population density of multiple samples of one life stage of one species at one lake in one season. The solid lines represent least-squares regressions. The estimated parameters and their 95% confidence intervals, the number of data points N (dots), and the adjusted R^2 are given in Table 2.

power of the linear model, which is TL, by approximately one part in a thousand. In the remaining analysis, we accepted TL as an adequate approximate description of the relation between variance and mean for parasites, as well as for free-living unparasitized and parasitized species. Future theoretical developments may perhaps lend scientific, not merely statistical, significance to the concave deviation from Taylor's law of (c) parasites. For now, we regard this deviation as a fluctuation.

The TL slope b differed significantly ($P < 0.0001$) among the three lifestyles, according to an analysis of covariance (ANCOVA), but the confidence intervals of b for free-living parasitized and parasitic species overlapped slightly (Table 2). A second ANCOVA excluding free-living unparasitized species rejected the null hypothesis that the slope was the same for free-living parasitized and parasitic species. Within this subset of 404 data points, the interaction between lifestyle and log mean of population density was statistically significant ($P < 0.0127$) in accounting for log variance of population density. To our knowledge, these results may represent the first demonstration that the parameters of TL depend on lifestyle within a given metazoan community.

The TL b was statistically significantly smaller than 2 for free-living unparasitized species, not statistically significantly different from 2 for free-living parasitized species, and statistically significantly larger than 2 for parasites. This difference cannot be a consequence of any monotonic function of body mass alone because the free-living unparasitized species were bigger than the parasites and smaller than the free-living parasitized species (Table 2).

For each lifestyle separately, the season (January, May, or September) in which the data were collected had no statistically significant effect on the slope of TL (ANOVA effect test $P > 0.8550$ for the season × log mean effect, for each lifestyle). For free-living parasitized and parasitic species, the lake from which the data were collected had no statistically significant effect on the slope of TL (ANOVA effect test $P = 0.8219$, $P = 0.2969$ for the lake × log mean effect, respectively). However, for free-living unparasitized species, relative to the slope of TL for data from the baseline lake Waihola, the slope of TL differed significantly for data from lakes Hayes ($P = 0.0197$) and Tomahawk ($P = 0.0016$). The effects of these two lakes on the TL slope had opposite signs and were both of small magnitude (<0.1), and lake Tuakitoto did not have a TL slope significantly different from that of Waihola. We have reported but do not make much of this small statistical heterogeneity among lakes for free-living unparasitized species only.

Density-Mass Allometry. The average body mass of a species was statistically significantly associated with that species' log mean of population density for each lifestyle separately, but the linear associations were not nearly as tight as those for TL (Fig. 2). The slope of DMA did not differ statistically significantly from −1/4 for free-living unparasitized species, from −3/4 for free-living parasitized species, and from −1 for parasitic species, but the confidence intervals of the slope overlapped considerably for the latter two lifestyles.

Log body mass, lifestyle, and their interaction (each effect with $P < 0.0001$) significantly affected the log mean population density (ANCOVA) when all three lifestyles were considered. As suggested by the confidence intervals in Table 2, ANCOVA for the free-living parasitized species and parasitic species (excluding free-living unparasitized species) showed statistically significant effects of lifestyle ($P < 0.0001$) and log body mass ($P < 0.0001$) on log mean population density, due to a difference between lifestyles in the intercept of DMA, but no statistically significant interaction between lifestyle and log body mass ($P = 0.2131$) (i.e., no effect of lifestyle on the slope of DMA).

For each lifestyle separately, the season (January, May, or September) in which the data were collected had no statistically significant effect on the slope of DMA (ANOVA effect test $P > 0.1158$ for the season × log body mass effect, for each lifestyle). Additionally, for each lifestyle separately, the lake from which the data were collected had no statistically significant effect on the slope of DMA (ANOVA effect test $P > 0.0590$ for the lake × log body mass effect, for each lifestyle).

Blackburn and Gaston (21), among others, criticized the use of ordinary linear regression for widely scattered data such as those in Fig. 2 and Fig. 3. In addition to ordinary least squares, we used quantile regression (22) to estimate a linear relation between log mean density and log body mass that lay above 90% of the conditional distribution of the vertical variable given each value of the horizontal variable (*SI Appendix*, Fig. S5 and Table S1). The intercepts for each lifestyle estimated by quantile regression unsurprisingly lay above the intercepts estimated by least squares regression, but the slopes estimated by the two methods differed little, with heavily overlapping confidence intervals (compare Table 2 and *SI Appendix*, Table S1). Both regression methods led to the same conclusions.

Variance-Mass Allometry. The average body mass was statistically significantly associated ($P < 0.001$) with the log variance of population density for species of each lifestyle separately. The linear associations were looser than those for TL (Fig. 3). The slope of VMA did not differ statistically significantly from −1/4 for free-living unparasitized species, from −7/4 for free-living parasitized species, and from −2 for parasitic species. The confidence interval of the slope for free-living parasitized species lay entirely within the confidence interval for parasitic species.

Log body mass, lifestyle, and their interaction significantly affected (each with $P < 0.0001$) the log variance of population density (ANCOVA) when all three lifestyles were considered. As

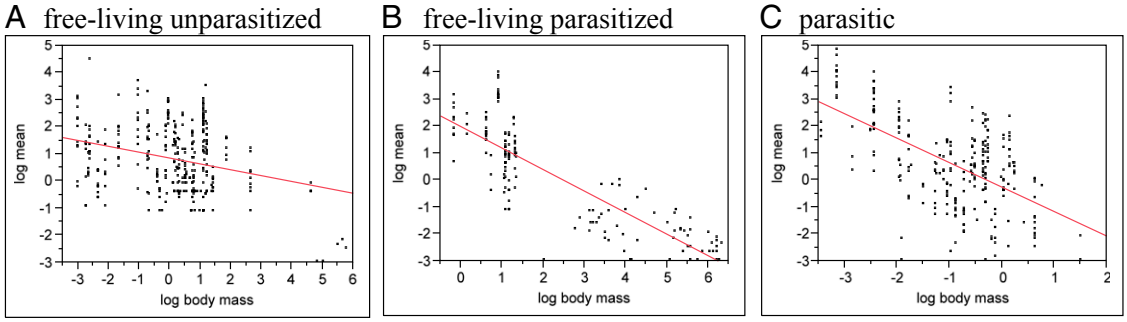

Fig. 2. Test of DMA. Log mean of population density was a linear function of the log mean body mass for (*A*) free-living unparasitized species, (*B*) free-living parasitized species, and (*C*) parasites. Plotting symbols are as in Fig. 1. The estimated parameters and their 95% confidence intervals, the number of data points N (dots), and the adjusted R^2 are given in Table 2.

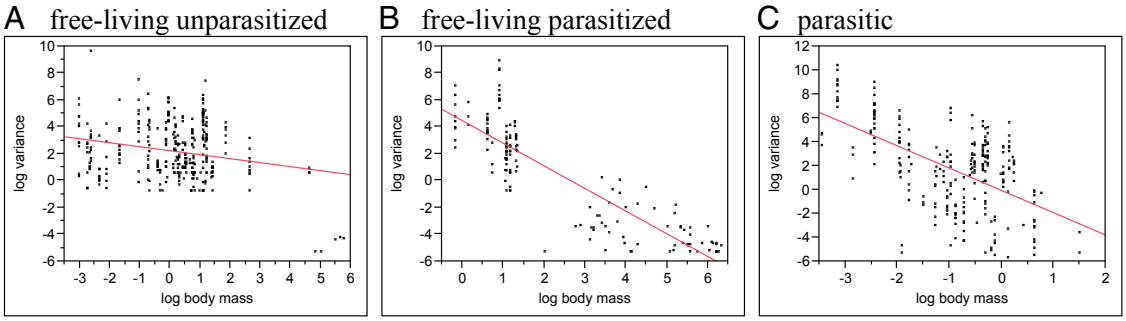

Fig. 3. Test of VMA. Log variance of population density was a linear function of the log mean body mass for (*A*) free-living unparasitized species, (*B*) free-living parasitized species, and (*C*) parasites. Plotting symbols are as in Fig. 1. The estimated parameters and their 95% confidence intervals, the number of data points *N* (dots), and the adjusted R^2 are given in Table 2.

suggested by the confidence intervals in Table 2, ANCOVA for the free-living parasitized species and parasitic species (excluding free-living unparasitized species) showed statistically significant effects of lifestyle ($P < 0.0001$) and log body mass ($P < 0.0001$) on log variance of population density, due to a difference between lifestyles in the intercept. As suggested by the confidence intervals of the slopes of VMA in Table 2, there was no statistically significant interaction between lifestyle and log body mass ($P = 0.3282$) (i.e., no effect of lifestyle on the slope). The VMA lines for the free-living parasitized species and parasitic species were not statistically distinguishable from being parallel, but both had slopes different from that of free-living unparasitized species.

To our knowledge, these results represent the first confirmation of VMA for any animal community, the first demonstration that VMA depends on lifestyle, and the first confirmation of VMA across a broad range of biological taxa. The only previous empirical confirmation of VMA was for oak trees (*Quercus*) in a temperate forest (9).

For each lifestyle separately, the season (January, May, or September) in which the data were collected had no statistically significant effect on the slope of VMA (ANOVA effect test $P > 0.1195$ for the season × log body mass effect, for each lifestyle). Additionally, for each lifestyle separately, the lake from which the data were collected had no statistically significant effect on the slope of VMA (ANOVA effect test $P > 0.0834$ for the lake × log body mass effect, for each lifestyle).

Quantile regression (22) was used to estimate a linear relation between log variance of density and log body mass that lay above 90% of the conditional distribution of the vertical variable given each value of the horizontal variable (*SI Appendix*, Fig. S5 and Table S1). As for DMA, for VMA the intercepts for each lifestyle estimated by quantile regression unsurprisingly lay above the intercepts estimated by least squares regression, but the slopes estimated by the two methods differed little, with heavily overlapping confidence intervals (compare Table 2 and *SI Appendix*, Table S1). Both regression methods led to the same conclusions.

Testing Whether TL and DMA Predict VMA. The form and the parameters of VMA were accurately predicted by the form and the parameters of TL and DMA according to formulas given by Marquet et al. (8) and Cohen et al. (9) (*SI Appendix*, *Theory*), for each lifestyle separately, and for both methods of estimating the parameters (ordinary least squares and quantile regression) (Table 2 and *SI Appendix*, Table S1). For example, for free-living unparasitized species, the intercept of VMA estimated by ordinary least squares was 2.2423, with 95% confidence interval (2.0228, 2.4618). From the coefficients of TL and DMA, the predicted value of the intercept of VMA was 2.2470, which fell within the 95% confidence interval of the actual intercept of VMA. In all cases, the predicted values of intercept and slope fell within the respective 95% confidence intervals.

The close relation between log mean and log variance of population density, given by TL, in combination with the looser DMA relation between log mean population density and log body mass, led to a looser VMA relation between log variance and log body mass. *SI Appendix*, Fig. S6 gives a way to see, with no equations, why this is so.

Discussion

Principal Findings. This study yielded several findings about species of different lifestyles (free-living unparasitized, free-living parasitized, and parasitic) in a metazoan community. First, free-living unparasitized species differed from free-living parasitized species in multiple ways, and both kinds of free-living species differed from parasitic species. Second, all three lifestyles were well described by three power-law relationships, although with different parameter values for different lifestyles. These relationships were a spatial TL (spatial variance in population density was a power-law function of the spatial mean population density); DMA (the spatial mean population density was a power-law function of mean body mass); and VMA (the spatial variance in population density was a power-law function of mean body mass). Third, TL and DMA, both classic relationships known for decades, accurately predicted the form and parameter values of VMA, a power-law relationship predicted only within the last decade (8, 9, 23), and previously tested empirically only once (9). To our knowledge, we provided here the first empirical confirmation of VMA for any animal community.

Free-Living Unparasitized Species Differed from Free-Living Parasitized Species in Multiple Ways. The three lifestyles differed in taxonomic distribution (Table 1) and in the distribution of average body mass (Table 2), notwithstanding some overlaps. The three lifestyles also differed (statistically significantly) in the parameter values of TL, DMA, and VMA, whereas all conformed to the form of these power-law relationships. In particular, free-living unparasitized species had a TL slope less than 2, whereas free-living parasitized and parasitic species had TL slopes of 2 or greater. The higher slope for the free-living parasitized taxa relative to the unparasitized taxa (i.e., the greater proportional increase in spatial variance in density for a given proportional increase in mean density) may be due to the additional influence of parasitism on the intraspecific variability in fecundity and mortality rates of hosts. The steeper slope for parasites than free-living unparasitized taxa may reflect the fact that parasite populations are driven by their own intrinsic dynamics superimposed on the dynamics of their host's population. Although they differ statistically, the TL slopes of free-living parasitized and parasitic species are similar. The TL relationship for parasites may to some extent be driven by the TL

relationship of their hosts. In support of this, there are significant, although not very tight, relationships between mean densities and variance in densities of parasites and those of their main host species (log mean density of parasites correlates with log mean density of their hosts, $R^2 = 0.53$; log variance in density of parasites correlates with log variance in density of their hosts, $R^2 = 0.59$). Overall, our findings confirmed the hypothesis that the interactions of free-living parasitized species and parasites added variability to the population dynamics of species of both lifestyles compared with free-living unparasitized species.

The differences among lifestyles in TL exponents do not mean that the variance in population density of free-living parasitized species and of parasites was larger than the variance in population density of free-living unparasitized species. The TL exponent is the proportional rate of increase of the variance of population density associated with a given proportional increase in the mean of population density. For example, if $b = 2$, then when the mean population density increases by 1% from one sample to another, on average one can expect that the variance of population density will increase by approximately 2% when those samples are compared. In our data, when the mean population density increased by 1% from one sample to another, the variance in population density increased by <2% (more precisely, 1.68%) for free-living unparasitized species and by >2% (more precisely, 2.10%) for parasitic species, and by approximately 2% (more precisely, 2.02%) for free-living parasitized species. Determining the causal basis for these differences and constructing a quantitative model that predicts them remain open challenges.

One possible approach is a model of stochastic multiplicative population growth that has been shown to predict TL and to provide an interpretation of the parameters of TL (24). In this model, population density changes from one discrete time (e.g., day or year) to the next discrete time as a result of multiplying the earlier population density by a random positive growth factor, which is assumed to be independently and identically distributed in time. In the model, by definition, if the growth factor exceeds 1, the population density increases from one time to the next; if the growth factor is smaller than 1, the population density decreases. If the mean value of the growth factor is M and the variance of the growth factor is V, then as time passes, the population density at large times satisfies TL with exponent $b = \log(V + M^2)/\log M$. If this model could be shown empirically to describe well the population dynamics of the taxa studied here, then the difference between taxa of different lifestyles in TL exponent b could be traced to differences between lifestyles in the values of the mean M or the variance V (or both) of their multiplicative population growth factors.

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Parasitism alters 3 power laws of scaling in a metazoan community: Taylor's law, density-mass allometry, and variance-mass allometry

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SUPPLEMENTARY MATERIALS: Supplementary text, 6 figures, 1 table

Theory: Taylor's law and density-mass allometry predict variance-mass allometry

TL may be written:

variance of population density = $a \times$ (mean population density)^b, where $a > 0$.

On logarithmic scales, TL becomes a linear relationship, assuming the variance and mean are positive:

log(variance of population density) = log(a) + $b \times$ log(mean population density).

This relationship holds for the logarithm to any base, and the value of b is independent of the base of the logarithms. We always used base 10. Because b appears as an exponent in the power-law form of TL and as the slope in the linear relationship, b is sometimes referred to as the exponent and sometimes as the slope of TL. The value of b is the same in either usage.

DMA may be written:

mean population density = $u \times$ (mean body mass per individual)^v, where $u > 0$.

Substituting DMA into TL predicts VMA:

variance of population density = $c \times$ (mean body mass per individual)^d,

where

$c = au^b > 0$, $d = bv$.

We tested whether the coefficients predicted for VMA from the estimated parameters of TL and DMA fell within the confidence intervals of the coefficients obtained by fitting VMA directly to the data.

Detailed methods

The four lakes (Hayes 44°58'59.4"S, 168°48'19.8"E; Tomahawk Lagoon 45°54'06.0"S, 170°33'02.2"E; Tuakitoto 46°13'42.5"S, 169°49'29.2"E; Waihola 46°01'14.1"S, 170°05'05.8"E) were sampled in three seasons (September 2012, January and May 2013). The four lakes were of modest sizes (2.76 km² surface area and 3.1 m mean depth for Lake Hayes; 0.096 km² and 1.1 m for Tomahawk Lagoon; 5.44 km² and 0.95 m for Lake Tuakitoto; 6.35 km² and 1.33 m for Lake Waihola).

In the combined samples of the four lakes, we found 22 taxonomic species of free-living parasitized species, 57 of free-living unparasitized species, and 35 of parasitic species. In this enumeration, we treated each life stage of parasite species (only) as a separate ‘species’. For example, we distinguished redia, metacercaria and adult of the trematode *Telogaster opisthorchis* as separate 'species'. For parasites, we measured density as individuals per square meter. This choice of metric made it possible to compare the variability of parasites with that of free-living parasitized and free-living unparasitized species.

The basic unit for which we calculated population density was a sample taken in one place at one time. Samples used different methods for different organisms (fish = seine nets, gillnets, fyke nets depending on the fish species; benthos = surber sampler; demersal species = standardized sweep net sampling; plankton = plankton net tows). All organisms were counted per sample, including metazoan parasites within their hosts, to give a density for each taxon.

In each lake and in each season (4 lakes × 3 seasons = 12 full sets of samples), we collected samples along four localities, i.e. four stretches of the littoral zone. The four sampled localities within each lake were not very distant from each other, although distances between sampling sites varied among lakes due to differences in lake size and shape (365 m minimum distance and 2680 m maximum distance along the shoreline between two sites in Lake Hayes; 100 m and 460 m in Tomahawk Lagoon; 420 m and 1550 m in Lake Tuakitoto; 1350 m and 3000 m in Lake Waihola). For fish, a single estimate of density was obtained for each locality. For benthic and demersal species we obtained 6 samples per locality and for plankton, 4 samples per locality. For each of the 12 lake × season combinations, means and variances were calculated across: 4 samples for the fish species (and for parasites within fish), 24 samples for benthic or demersal species (and for their parasites), and 16 samples for plankton species (which had no metazoan parasites).

Body mass was calculated differently for different types of organisms. Parasites were generally too small to be weighed and varied little in size within each life stage of each taxonomic species, so we averaged measurements of dimensions from a random subsample of individuals. We calculated the volume of one individual of average dimensions based on the most appropriate formula for its shape (e.g. adult nematodes and acanthocephalans = cylinder, adult trematodes = flattened ellipsoid, encysted juvenile trematodes [metacercariae] = spheres). Their volume was converted to mass assuming their density equaled that of water. Most free-living invertebrates

were large enough to be weighed individually (isopods, chironomids, odonates, large trichopteran larvae, adult hemipterans, mollusks, leeches), and we calculated the average mass of an individual. For small free-living invertebrates (amphipods, small trichopteran larvae, oligochaetes, planktonic crustaceans), which varied little intraspecifically, we pooled 5, 10 or 20 conspecific individuals (depending on the species) from random subsamples, weighed them as a group, and from the total mass calculated the average mass of one individual. For fish, each individual was weighed and we calculated average mass of an individual, giving equal weight to each individual. Consequently fish mass for a given species varied across lakes and seasons, while the mass of smaller organisms was treated as constant for each species (or life stage of parasites within a taxonomic species).

Statistics

The Supplementary data file (.txt format, comma-separated variables) gives the number of samples, the minimum sample size (minimum number of organisms), the maximum sample size (maximum number of organisms), and the total sample size (total number of organisms) for each estimate of the sample mean and the sample variance. The data column "Life stage" uses these abbreviations: Ad = adult, L = larva, C = cystacanth; Mc = metacercaria; Sp = sporocyst; Rd = redia.

In summary, of the 733 estimates of the mean and the variance of population density specific to species, life stage, lake, and season, 158 estimates were based on 4 samples each, 85 estimates were based on 16 samples each and 490 estimates were based on 24 samples each. The total number of samples was 13,752, giving an average of approximately 18.76 samples per estimate of mean and variance.

The total number of organisms was 1,037,058, of which 518,295 were free-living unparasitized, 144,384 were free-living parasitized, and 374,379 were parasites. The average number of organisms per sample was 75.41.

The five principal quantitative variables derived from the data were: number of samples, total sample size (number of organisms), average body mass, variance of population density, and mean of population density. The last four had highly right-skewed frequency distributions, hence these four variables were $\log_{10}$-transformed for further analysis. Scatterplot matrices displayed the bivariate relationships of each of these five variables as a function of each of the remaining four variables, for all species combined (SI Appendix, Figure S1), and separately for free-living unparasitized species (SI Appendix, Figure S2), free-living parasitized species (SI Appendix, Figure S3), and parasitic species (SI Appendix, Figure S4). These summary graphics provided a useful check for erroneous outliers and a visual impression of which variables were most closely associated.

For each lifestyle, by visual inspection the linear relationship between log variance and log mean density was much tighter than the linear relationship of any other pair of the five principal

quantitative variables (SI Appendix, Figures S2-S4). Log mean density clearly increased with log total sample size (log total number of organisms), as would be expected since log mean density is the total number of organisms per unit of area. Since log variance was very nearly linearly associated with log mean density, it was not surprising that log variance also increased with log total sample size.

Statistical calculations used JMP version 10 (1) and MATLAB version 8.3.0.532 R2014a (2). Analysis of covariance was used to test for differences of slopes. Analysis of variance was used to test for significance of effects. Quantile regression was used to estimate DMA and VMA. Quantile linear regression estimates the parameters of a straight line that lies above a certain percentage, in our case 90%, of the *y*-values conditional on each value of the predictor *x*-value. The MATLAB function quantreg.m (3) estimated each parameter of DMA and VMA with confidence intervals based on bootstrap sampling. As a check, the MATLAB function rq_fnm.m (http://www.econ.uiuc.edu/~roger/research/rq/rq.m , accessed 2014-09-12) was also run on the same data. The two programs gave estimates of the slope that generally agreed exactly to four decimal places but occasionally differed by 0.0001. They gave estimates of the intercept that generally agreed exactly to four decimal places but occasionally differed by 0.0001 or 0.0002. These differences in estimates are immaterial. Because rq_fnm.m gave no confidence intervals for the parameter estimates, we reported below only the estimates of parameters and confidence intervals from quantreg.m.

To test whether a putative linear relationship provided a statistically satisfactory description of a set of (x, y) observations, a quadratic relationship was fitted by ordinary least squares. If the coefficient of the quadratic term was statistically significantly different from zero ($P < 0.05$), then the nonlinearity was considered significant at the 0.05 level. For example, the quadratic extension of TL was

$$\log \text{variance} = \log(a) + b \times \log \text{mean} + c \times (\log \text{mean}) \times (\log \text{mean})$$

which is mathematically identical to (though differently expressed than) equation (14) of Taylor, Woiwod, and Perry (4). Here and in all calculations, log = $\log_{10}$.

Possibilities for future research

We measured the population density of parasitic species as individuals per square meter, as we did for all free-living species, and not as individuals per host, as in some prior studies of TL in parasitology (e.g., 5). Did the choice of measure materially affect the conclusions drawn? Do both measures satisfy TL? If so, is there a connection (theoretical or empirical) between the TL exponent using parasitic individuals per square meter and the TL exponent (if TL applies) using parasitic individuals per host individual?

Preliminary analyses not reported here indicated that the frequency distribution of parasites per host would be well described by the negative binomial distribution in many instances. But for

many parasites of fish, the prevalence of infection is 100% of hosts so the frequency distribution of parasites per host includes no zero counts, contrary to the negative binomial distribution. Relating the underlying distribution of parasites per host to the form and parameters of TL, if TL is satisfied, remains a challenge.

Mathematically, any two of the three power laws TL, DMA, and VMA predict the third, but statistically not all pairs of these power laws are equally useful in predicting the remaining power law. Specifically, in DMA (Figure 2) and VMA (Figure 3), for each value of body mass, the mean and variance, respectively, of population density range widely (by multiple orders of magnitude). Without additional information to connect particular values of mean density with particular values of the variance in density for a given value of body mass, it would not be possible to reconstruct the relatively tight association between the mean and the variance of population density in TL (Figure 1). However, given the similarities in the (rescaled) scatter of log mean and log variance of population density for a given average body mass (SI Appendix, Figure S6), it is not obvious whether the mechanisms underlying TL and DMA generate VMA or the mechanisms underlying TL and VMA generate DMA. This remains a question for future theoretical and empirical research.

Supplementary references

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Supplementary figures S1-S6

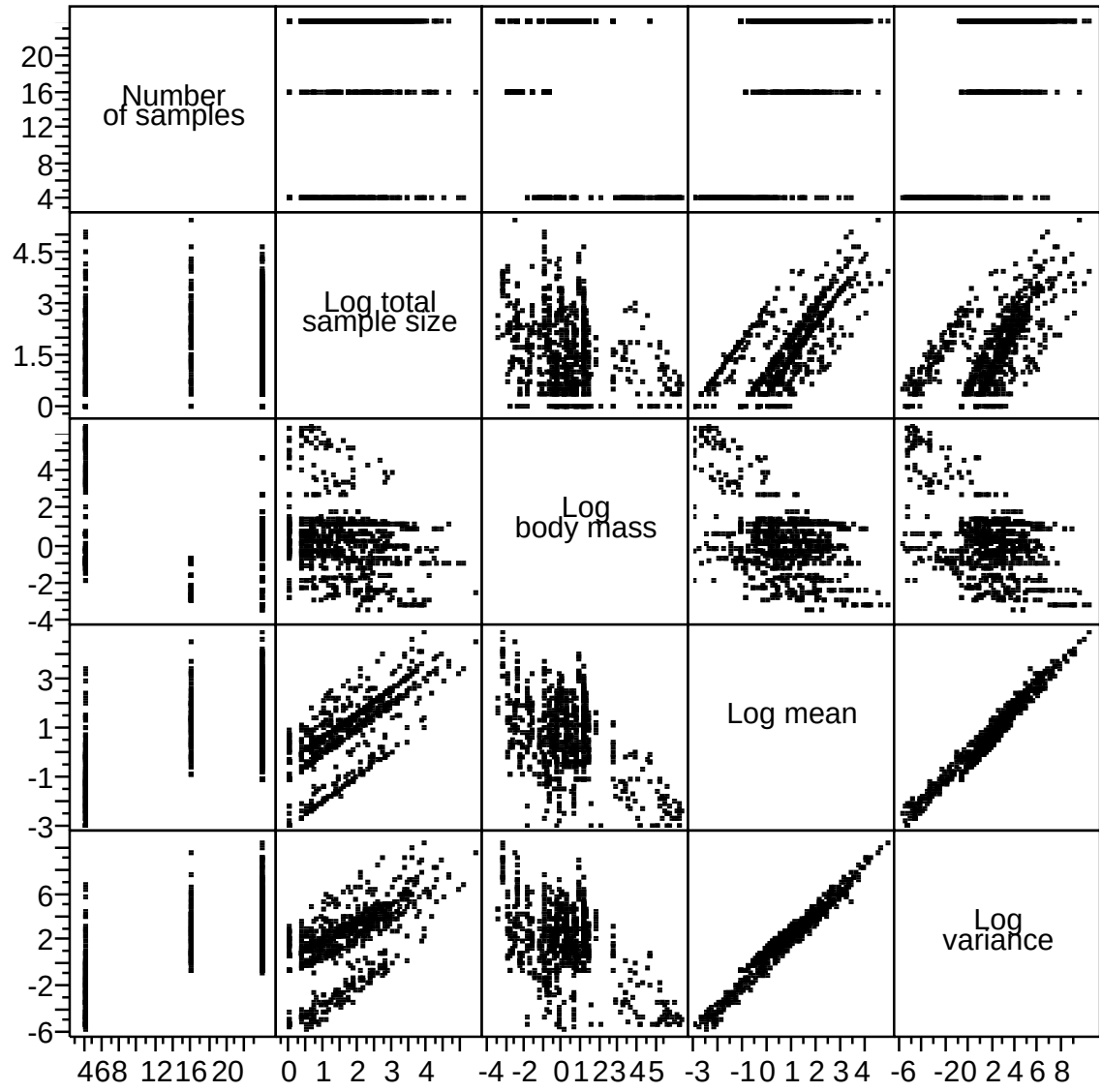

Figure S1. Scatterplot matrix of number of samples, log total sample size, log body mass, log mean of population density, and log variance of population density as a function of each of the other four variables, for species of all lifestyles pooled. For example, the scatterplot in the fifth row from the top and fourth column from the left displays log variance as a function of log mean, which is a test of Taylor's law. The scatterplot in the fourth row from the top and third column from the left displays log mean as a function of log body mass, which is a test of density-mass allometry. Each scatterplot has 733 points.

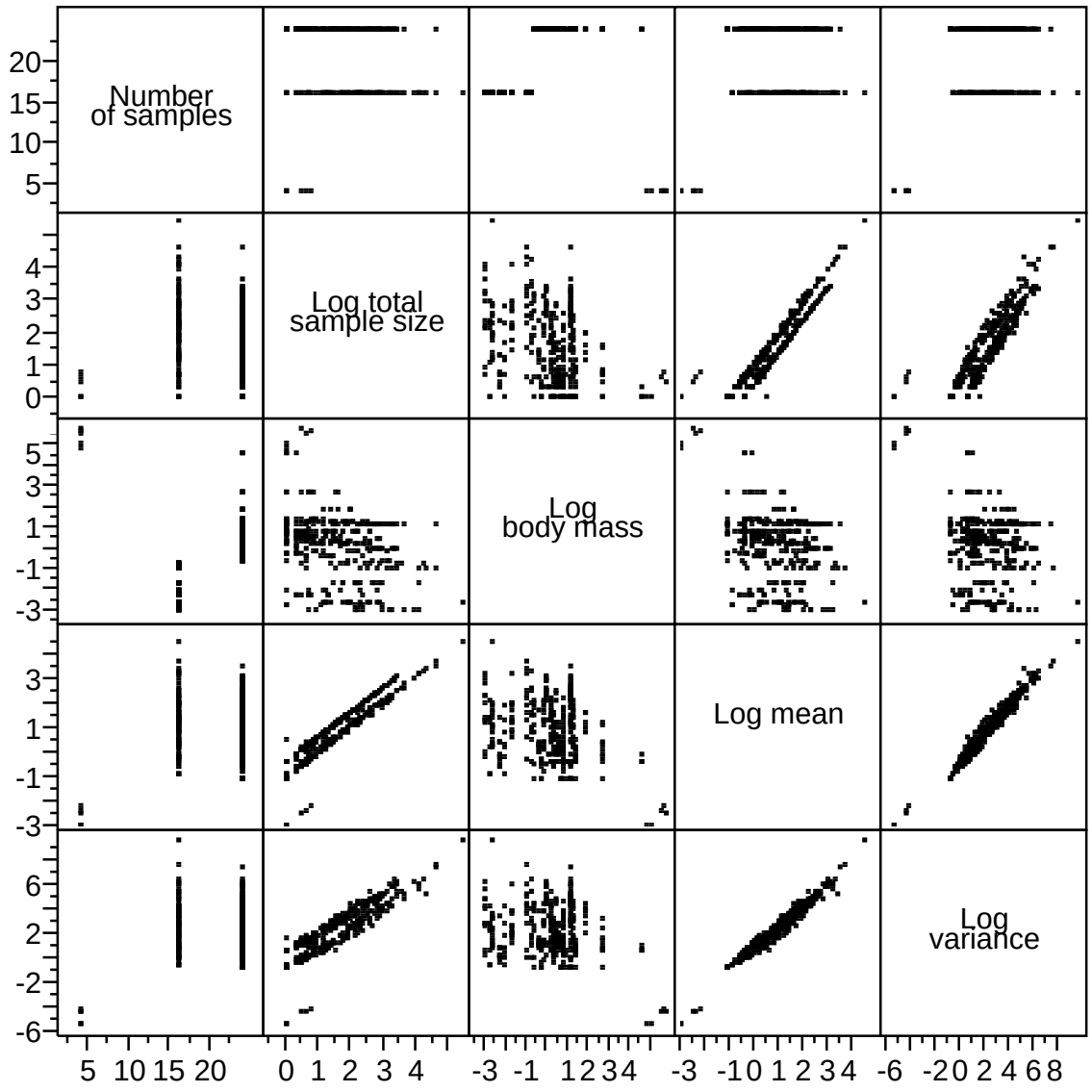

Figure S2. Scatterplot matrix of number of samples, log total sample size, log body mass, log mean of population density, and log variance of population density as a function of each of the other four variables, for unparasitized free-living species. The scatterplots are laid out as in Figure S1. Each scatterplot has 329 points.

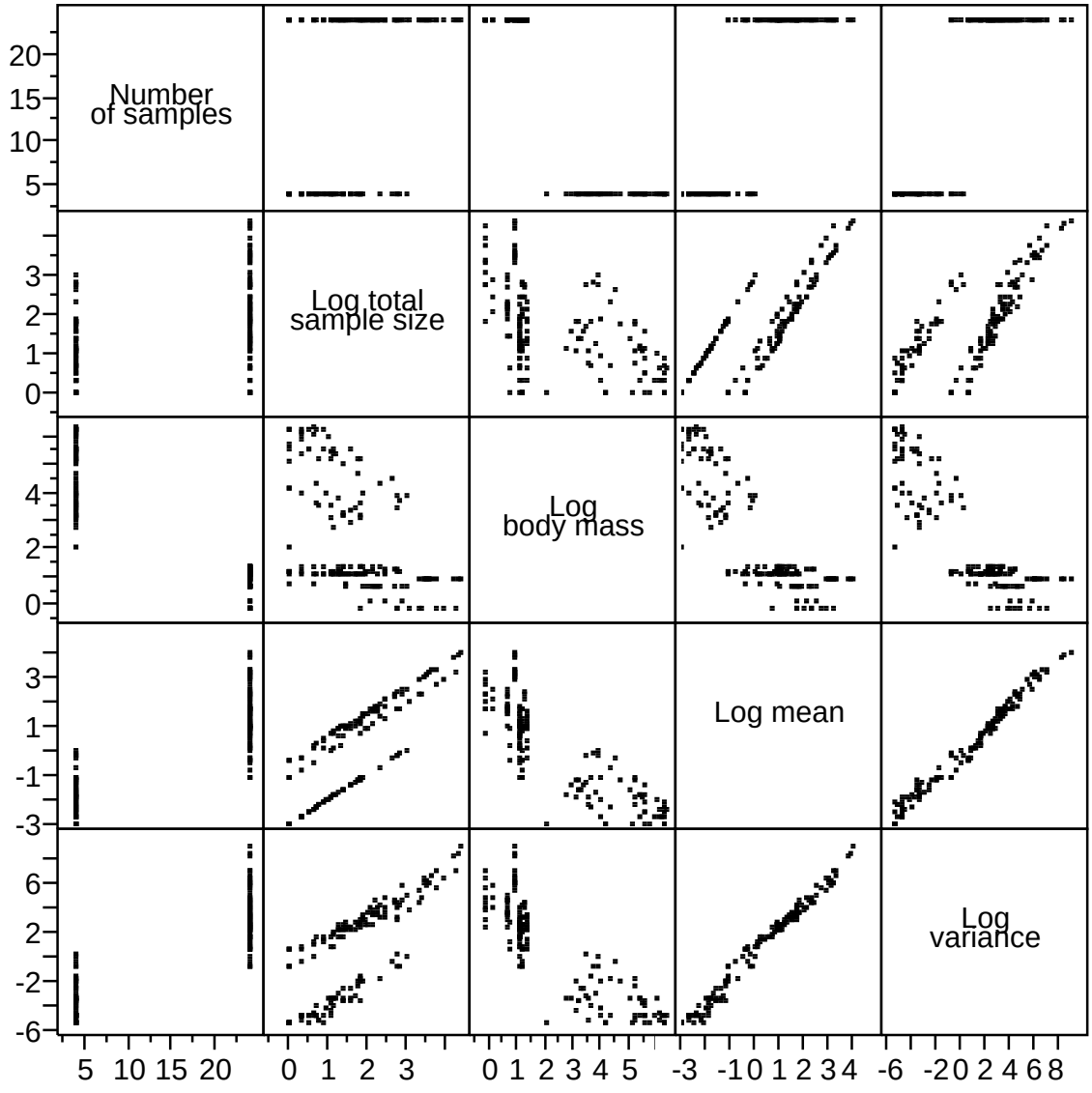

Figure S3. Scatterplot matrix of number of samples, log total sample size, log body mass, log mean of population density, and log variance of population density as a function of each of the other four variables, for parasitized free-living species. The scatterplots are laid out as in Figure S1. Each scatterplot has 151 points.

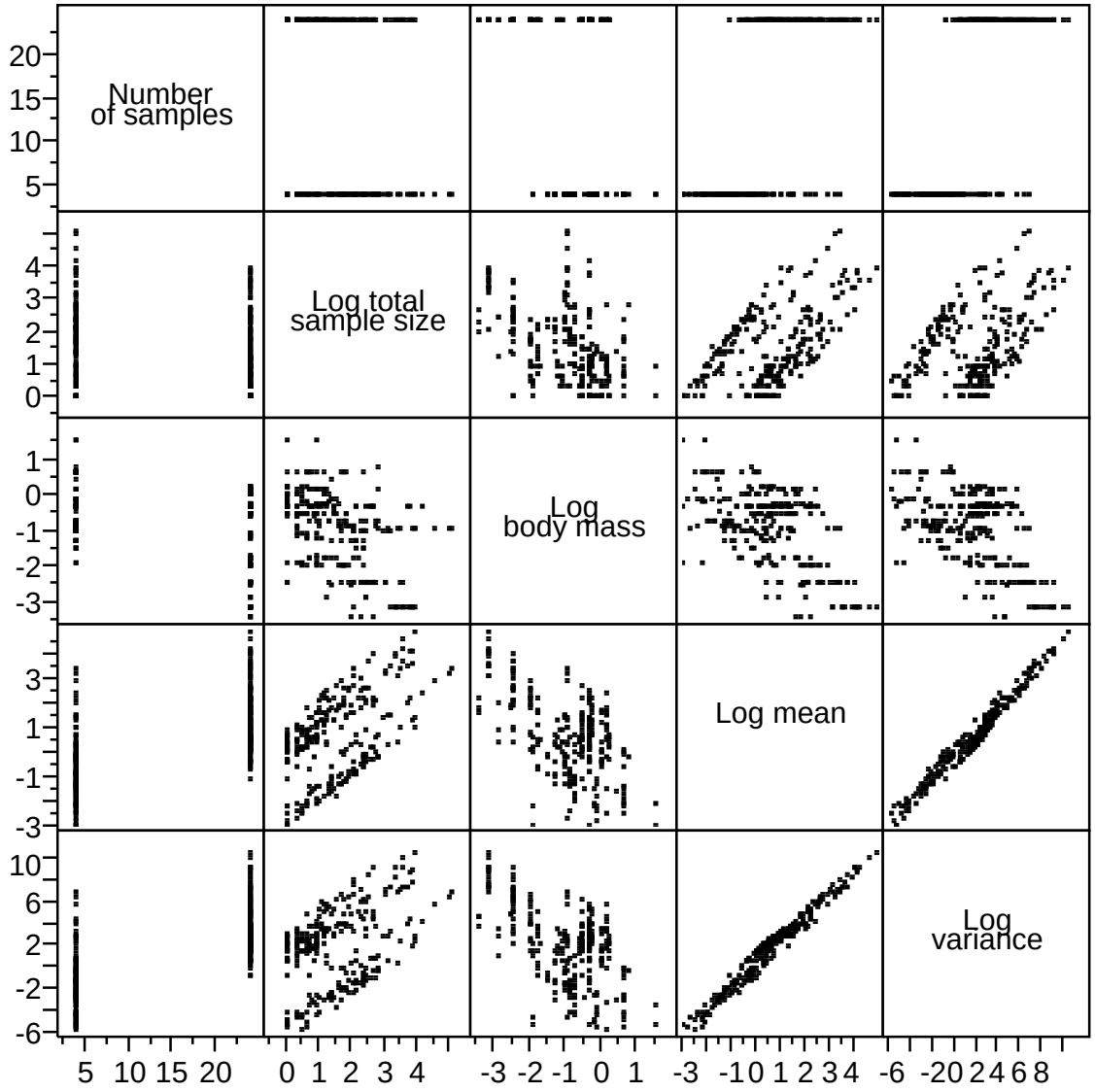

Figure S4. Scatterplot matrix of number of samples, log total sample size, log body mass, log mean of population density, and log variance of population density as a function of each of the other four variables, for parasitic species. The scatterplots are laid out as in Figure S1. Each scatterplot has 253 points.

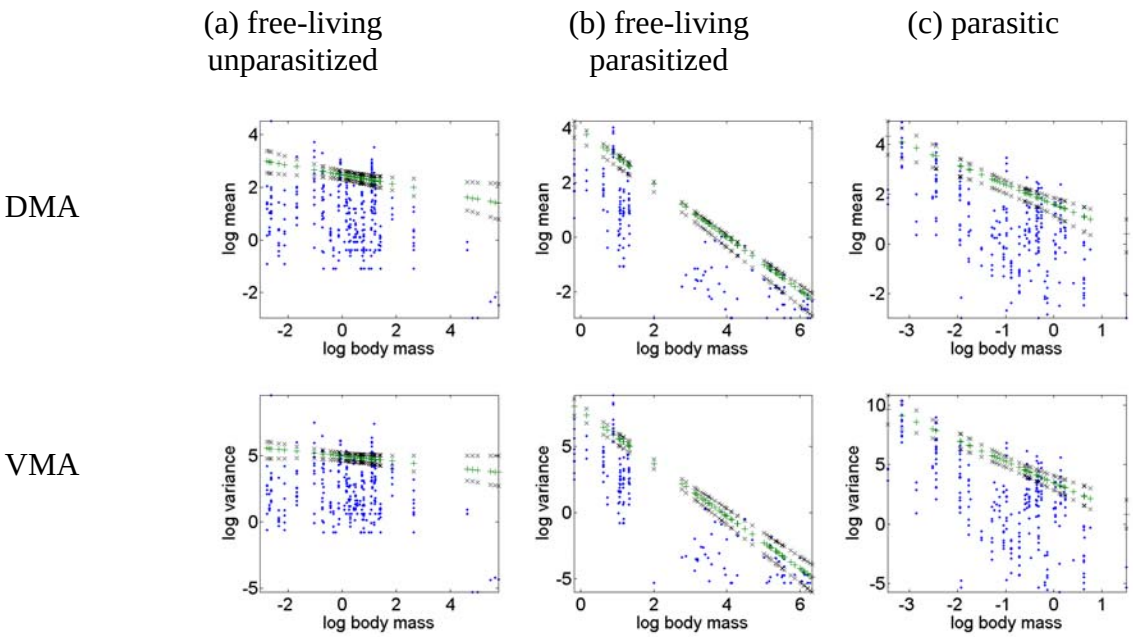

Figure S5. Quantile-regression estimation of density-mass allometry (DMA) and variance-mass allometry (VMA), for (a) free-living unparasitized species, (b) free-living parasitized species, and (c) parasites. The quantile-regression line (+ markers) is chosen to lie above 90% of the data points (small blue diamonds). The regression line is bounded above and below by its 95% confidence limits (x markers). The estimated parameters and their 95% confidence intervals are given in Table S1.

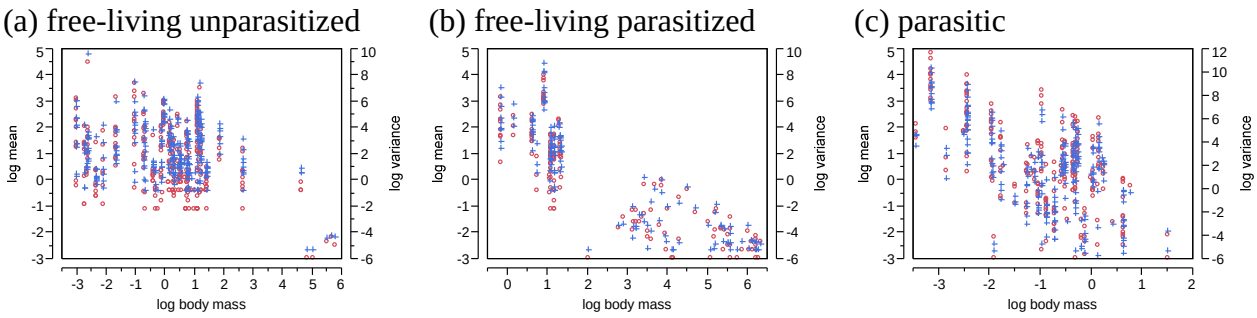

Figure S6. Log mean population density (left scales, open red circles o) and log variance of population density (right scales, blue plus signs +) as functions of log mean body mass, for (a) free-living unparasitized species, (b) free-living parasitized species, and (c) parasites, using independent vertical scales for the log mean (left, o) and log variance (right, +). The generally close pairing of data markers for the log mean (left, o) and log variance (right, +) reflects TL, and the general downward trend of both markers with increasing log body mass reflects DMA and VMA. In panels (a) and (b), the left scale runs from -3 to +5, while the right scale runs from -6 to +10, which is just 2 times the values in the left scale, because the slope of TL is not far from 2. In panel (c), the vertical scale on the right covers -6 to +12, which is a bit more than twice the range of the vertical scale on the left from -3 to +5, because the slope of TL slightly exceeds 2 for parasites.

Table S1. Parameter estimates using quantile regression to fit density-mass allometry (DMA) and variance-mass allometry (VMA) to log-transformed data on the spatial variation of population density (individuals per square meter) of free-living unparasitized species, free-living parasitized species, and parasitic species. The quantile-regression line is chosen to lie above 90% of the data points. For all three lifestyles, the intercept predicted for VMA, $\log_{10}(a)+b\times\log_{10}(u)$, fell within the 95% confidence interval of the intercept estimated for VMA, and the slope predicted for VMA, $b\times v$, fell within the 95% confidence interval of the slope estimated for VMA. Abbreviations: lo, Lower limit of 95% confidence interval, hi, Upper limit of 95% confidence interval

Lifestyle→	Free-living unparasitized	Free-living parasitized	Parasitic
Parameter ↓			
n: number of samples	329	151	253
DMA: mean density = $u\times(\text{mean body mass})^{v}$			
$\log_{10} u$	2.4784	3.9095	1.5903
Lo	2.3146	3.6055	1.2565
Hi	2.6422	4.2135	1.9242
v	-0.1849	-0.9784	-0.7903
Lo	-0.2995	-1.0744	-1.024
Hi	-0.0702	-0.8824	-0.5567
VMA: variance = $c\times(\text{mean body mass})^{d}$			
$\log_{10} c$	4.9852	7.6867	3.4812
Lo	4.6848	7.1332	2.91
Hi	5.2856	8.2403	4.0523
$\log_{10}(a)+b\times\log_{10}(u)$	4.9702	8.1848	3.7761
d	-0.2127	-1.9878	-1.788
Lo	-0.4109	-2.1769	-2.2269
Hi	-0.0144	-1.7987	-1.3491
$b\times v$	-0.3107	-1.9757	-1.6612