Allometric scaling of population variance with mean body size is predicted from Taylor's law and density-mass allometry

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Two widely tested empirical patterns in ecology are combined here to predict how the variation of population density relates to the average body size of organisms. Taylor's law (TL) asserts that the variance of the population density of a set of populations is a power-law function of the mean population density. Density–mass allometry (DMA) asserts that the mean population density of a set of populations is a power-law function of the mean individual body mass. Combined, DMA and TL predict that the variance of the population density is a power-law function of mean individual body mass. We call this relationship "variance–mass allometry" (VMA). We confirmed the theoretically predicted power-law form and the theoretically predicted parameters of VMA, using detailed data on individual oak trees (*Quercus* spp.) of Black Rock Forest, Cornwall, New York. These results connect the variability of population density to the mean body mass of individuals.

self-thinning | fluctuation scaling | Damuth's law | nonlinear least squares | spatial Taylor's law

Understanding how and why living populations, natural and engineered, vary in space and time is a core problem of ecology. When a population fluctuates to a low density, its risk of extinction may rise and its genetic diversity may pass through a bottleneck with enduring evolutionary consequences. In fisheries, forests, and agriculture, population fluctuations may directly affect human supplies of food, fiber, and timber and have economic consequences. Outbreaks of arthropod and molluscan vectors of diseases of humans and animals may raise risks of disease. These scientific and practical reasons make it important to understand how and why population densities fluctuate.

An important generalization about population variability is Taylor's law (1–3). Taylor's law (TL) is the subject of an estimated 1,000 papers (4) and has been confirmed for hundreds of species or groups of species in field observations and laboratory experiments (5, 6). The censused populations may include a single species, a single genus, or more loosely related organisms. TL asserts that

$$\begin{aligned}&\text{variance of population density}\\&\quad= a(\text{mean population density})^{b},\ a>0.\end{aligned}\qquad [1]$$

On logarithmic scales, TL becomes a linear relationship: log(variance of population density) = log(a) + b × log(mean population density). Typically, $b > 0$: The mean and variance of population density increase together. In many empirical examples, $1 \leq b \leq 2$.

Density–mass allometry (DMA) (7–13) asserts that

$$\begin{aligned}&\text{mean population density}\\&\quad= u(\text{mean body mass per individual})^{v},\ u>0.\end{aligned}\qquad [2]$$

Typically, bigger organisms are rarer and $v < 0$. DMA is sometimes called the self-thinning law (14). DMA applies to single species, collections of species (15–18), and foodwebs (19–23).

Substituting DMA, Eq. **2**, into TL, Eq. **1**, gives

$$\begin{aligned}&\text{variance of population density}\\&\quad= au^{b}(\text{mean body mass per individual})^{bv}.\end{aligned}\qquad [3]$$

We called this predicted relation variance–mass allometry (VMA). If $b > 0$ and $v < 0$, as is typical, then $bv < 0$: Increasing mean body mass will be associated with decreasing variance of population density. In particular, if $b \approx 2$ and $v \approx -1$, then $bv \approx -2$ is predicted.

Here we confirmed TL and DMA and tested the predicted power-law form and parameter values of VMA, using data from Black Rock Forest (24, 25). This 1,500-ha preserve in the Hudson Highlands region of New York State (41° 24′ N, 74° 01′ W) has been managed as a science field station with minimal human disturbance since 1928. We calculated the variance and mean of oak population density of subplots within each of 12 plots and then plotted the log variance as a function of the log mean with one point per plot. We carried out this analysis using data gathered before (in 2007) and after (in 2010) girdling of some of the trees in some plots (*Materials and Methods*). We used log = $\log_{10}$ throughout.

Results

In 12 plots each divided into 9 subplots (*Materials and Methods*), TL described well the observed relationship between the variance of oak (trees in the genus *Quercus*) population density (over subplots within a plot) and the mean of oak population density (over subplots within a plot) in 2007 before a 2008 girdling treatment [trunk incision to sever phloem and cambium (26)] and in 2010 after girdling (Fig. 1). The exponent b of TL significantly exceeded 0 but was not significantly different from 2.

DMA with exponent $v \approx -1$ described the relationship between mean population density and mean above-ground biomass per individual tree in plots and subplots in 2007 and 2010 (Fig. 2). The 95% confidence intervals (CIs) of v always excluded 0.

Before (in 2007) and after (in 2010) girdling (in 2008), the predicted VMA power law described well the changes in variance (over subplots within a plot) of oak population density as a function of the mean above-ground biomass of oak trees with diameter at breast height (dbh) ≥ 2.54 cm within the plot (Fig. 3). Substituting the quantitative estimate of DMA (Fig. 2) into the quantitative estimate of TL (Fig. 1) gave a quantitative prediction of the parameters of VMA.

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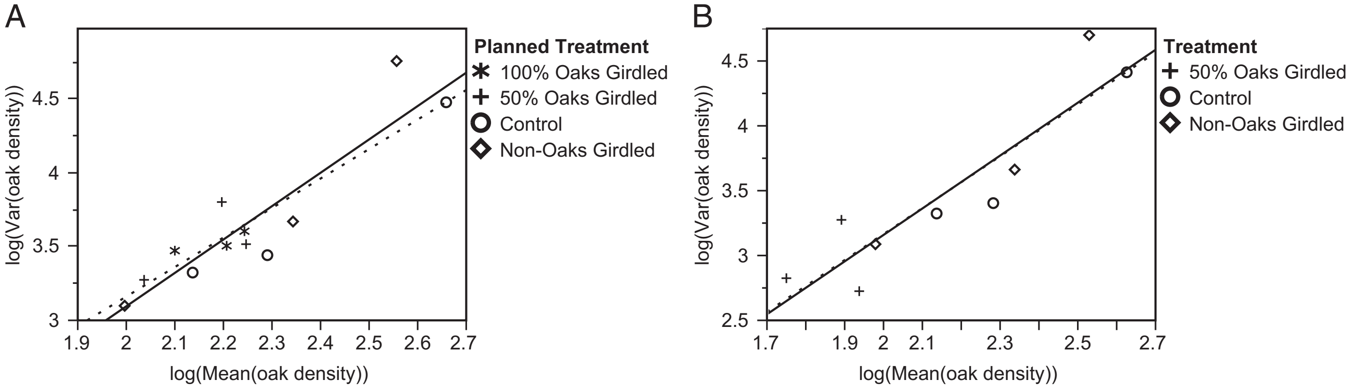

Fig. 1. Taylor's law held in plots in Black Rock Forest. The $\log_{10}$ variance of oak density (trees per hectare) increased linearly with the $\log_{10}$ mean of oak density, as predicted. The solid line is the least-squares regression line (on log–log coordinates). The 95% confidence intervals of each parameter of the regression line are given after the point estimates. The dotted line is the best-fitting line with slope 2. (*A*) $n = 12$ plots in 2007: log variance = −1.429 (−3.068, 0.211) + 2.262 (1.536, 2.988) × log mean. $R^2 = 0.828$, adjusted (adj.) $R^2 = 0.811$, root mean-squared error (RMSE) = 0.212. (*B*) $n = 9$ plots in 2010: log variance = −0.921 (−2.713, 0.872) + 2.040 (1.218, 2.861) × log mean. $R^2 = 0.831$, adj. $R^2 = 0.807$, RMSE = 0.295.

In 2007,

$$\begin{aligned}\log(\text{Variance of population density}) &= (-1.4286 + 2.2620 \times 5.1365) \\ &\quad - (0.9477 \times 2.2620) \cdot \log(\text{Mean(biomass)}) \\ &= 10.1902 - 2.1437 \cdot \log(\text{Mean(biomass)}).\end{aligned}$$

The predicted intercept 10.190 fell well within the 95% CI (7.634, 12.486) of the intercept estimated by log-linear regression. The predicted slope −2.144 fell well within the 95% CI (−2.896, −1.306) of the slope estimated by log-linear regression.

In 2010,

$$\begin{aligned}\log(\text{Variance of population density}) &= (-0.9205 + 2.0396 \times 5.8930) \\ &\quad - (1.2201 \times 2.0396) \cdot \log(\text{Mean(biomass)}) \\ &= 11.0989 - 2.4885 \cdot \log(\text{Mean(biomass)}).\end{aligned}$$

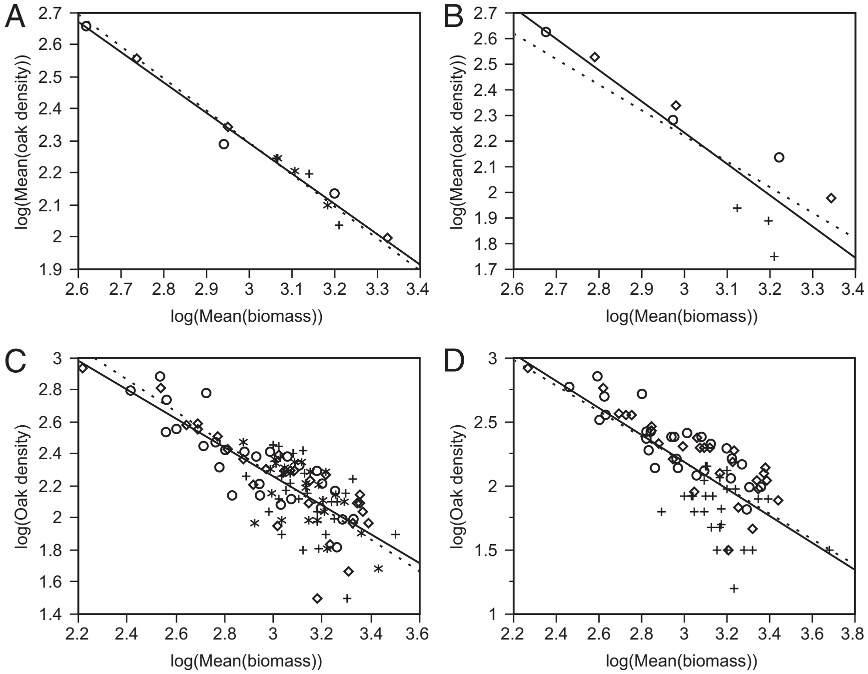

Fig. 2. Density–mass allometry held in Black Rock Forest. (*A*–*D*) The $\log_{10}$ mean of oak density decreased linearly with increasing $\log_{10}$ mean above-ground biomass of oak trees with diameter at breast height (dbh, cm) ≥ 2.54 cm, as predicted, in (*A* and *B*) plots and (*C* and *D*) subplots, in (*A* and *C*) 2007 (before girdling) and (*B* and *D*) 2010 (after girdling). In *A*–*D*, the dotted line is the best-fitting line with slope −1. Solid lines and markers are defined in Fig. 1. (*A*) $n = 12$ plots in 2007: log mean oak density = 5.136 (4.814, 5.459) – 0.948 (−1.053, −0.842) × log mean above-ground biomass. $R^2 = 0.976$, adj. $R^2 = 0.973$, RMSE = 0.032. (*B*) $n = 9$ plots in 2010: log mean oak density = 5.893 (4.192, 7.594) – 1.220 (−1.775, −0.665) × log mean above-ground biomass. $R^2 = 0.794$, adj. $R^2 = 0.765$, RMSE = 0.146. (*C*) $n = 108$ subplots in 2007: log oak density by subplot = 4.973 (4.544, 5.402) – 0.904 (−1.044, −0.764) × log mean above-ground biomass. $R^2 = 0.607$, adj. $R^2 = 0.604$, RMSE = 0.169. (*D*) $n = 81$ subplots in 2010: log oak density by subplot = 5.351 (4.699, 6.002) – 1.054 (−1.266, −0.842) × log mean above-ground biomass. $R^2 = 0.554$, adj. $R^2 = 0.548$, RMSE = 0.236. Only Fig. 2 shows subplots because the variance in Figs. 1 and 3 is not defined for a subplot.

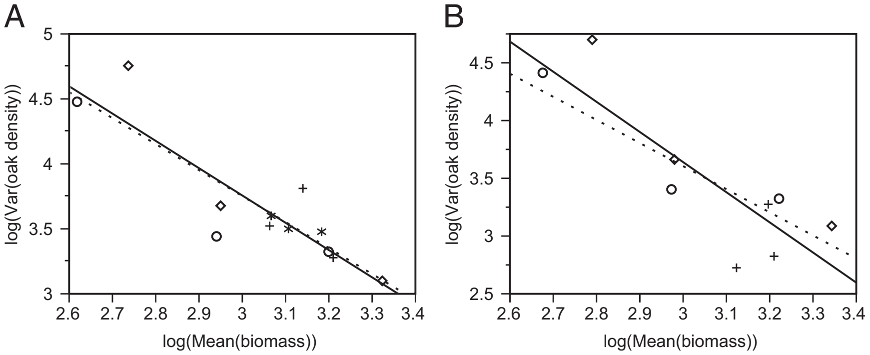

Fig. 3. Variance–mass allometry held in Black Rock Forest. The $\log_{10}$ variance of oak population density decreased linearly with increasing $\log_{10}$ mean above-ground biomass of oak trees with dbh ≥ 2.54 cm, as predicted. Solid lines and markers are defined in Fig. 1. The dotted line is the best-fitting line with slope −2. (*A*) $n = 12$ plots in 2007: log variance of oak population density = 10.060 (7.634, 12.486) − 2.101 (−2.896, −1.306) × log mean above-ground biomass. $R^2 = 0.776$, adj. $R^2 = 0.754$, RMSE = 0.242. (*B*) $n = 9$ plots in 2010: log variance of oak population density = 11.467 (7.071, 15.862) − 2.609 (−4.043, −1.174) × log mean above-ground biomass. $R^2 = 0.725$, adj. $R^2 = 0.686$, RMSE = 0.377.

Again, the predicted intercept 11.099 fell well within the 95% CI (7.071, 15.862) of the intercept estimated by log-linear regression. The predicted slope −2.489 fell well within the 95% CI (−4.043, −1.174) of the slope estimated by log-linear regression.

Fitting the original variables by nonlinear least squares to a power law in each year separately gave results that were very similar to those of fitting logarithmic variables by linear regression for TL (Fig. 4), DMA (Fig. 5), and VMA (Fig. 6). In each year, the 95% CI of the exponent in each nonlinear fit overlapped the 95% CI of the slope in the corresponding log-linear regression. In 2007,

$$\begin{aligned}&\text{Variance of population density}\\&\quad=\left(0.4351\times 148{,}420.5361^{1.8821}\right)\cdot(\text{Mean(biomass)})^{1.8821\times(-0.9593)}\\&\quad=2.3543\times 10^{9}\cdot(\text{Mean(biomass)})^{-1.8055}.\end{aligned}$$

The predicted coefficient 2.354×10^9 fell well within the 95% CI (-1.350×10^{10}, 1.717×10^{10}) of the coefficient estimated by nonlinear fitting. The predicted exponent −1.806 fell well within the 95% CI (−3.106, −0.430) of the exponent estimated by nonlinear fitting. In 2010,

$$\begin{aligned}&\text{Variance of population density}\\&\quad=\left(0.9500\times 739{,}140.6058^{1.7525}\right)\cdot(\text{Mean(biomass)})^{1.7525\times(-1.2066)}\\&\quad=1.8309\times 10^{10}\cdot(\text{Mean(biomass)})^{-2.1146}.\end{aligned}$$

Again, the predicted coefficient 1.831×10^{10} fell well within the 95% CI (-3.728×10^{10}, 4.336×10^{10}) of the coefficient estimated by nonlinear fitting. The predicted exponent −2.1146 fell well within the 95% CI (−3.927, 0.256) of the exponent estimated by nonlinear fitting.

In every comparison of the goodness of fit of each TL, DMA, and VMA power law before and after girdling, using linear regression of the logged variables or nonlinear fitting of the original variables, the root mean-squared error (RMSE) was smaller in 2007 before girdling than in 2010 after girdling (Figs. 1–6). Although the sample size was always greater before girdling than after (12 vs. 9 plots and 108 vs. 81 subplots), RMSE adjusted for this difference because RMSE is defined as the square root of the sum of the squared deviations between predictions and observations divided by the number of units of observation.

Discussion

Data on oak population density in Black Rock Forest confirmed TL, DMA, and the predicted relationship of VMA. Girdling loosened the agreement between the power laws and the data. If this consistent pattern in the Black Rock Forest data is confirmed elsewhere, it may suggest that badness of fit to these power laws is associated with, and may serve as an index of, natural or anthropogenic disturbance.

Marquet et al. (27, p. 1761) proposed that if TL described the variance over time in abundance as a function of the mean abundance over time with exponent between 1 and 2, and if the

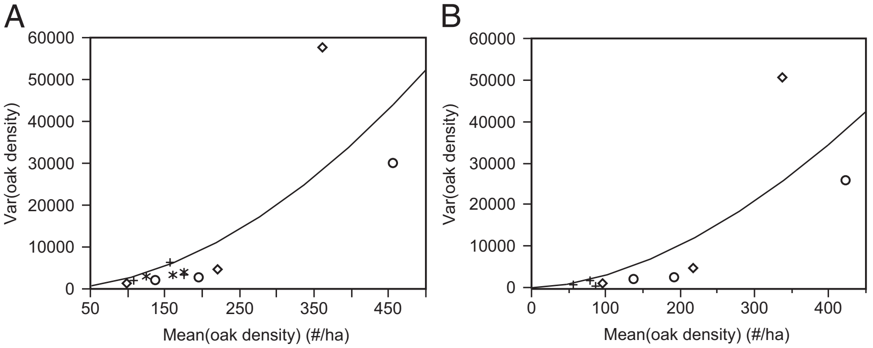

Fig. 4. Taylor's power law held in plots in Black Rock Forest. The variance of oak density (trees per hectare) increased as a power function of the mean of oak density, as predicted. The solid line is the least-squares power-law regression line. Markers represent treatments as in Fig. 1. (*A*) $n = 12$ plots in 2007: variance = 0.435 (−3.043, 3.913) × $(\text{mean})^{1.882\ (0.537,\ 3.227)}$. $R^2 = 0.625$, adj. $R^2 = 0.588$, RMSE = 10,841.269. (*B*) $n = 9$ plots in 2010: variance = 0.950 (−10.259, 12.159) × $(\text{mean})^{1.753\ (-0.249,\ 3.754)}$. $R^2 = 0.627$, adj. $R^2 = 0.574$, RMSE = 11,211.405.

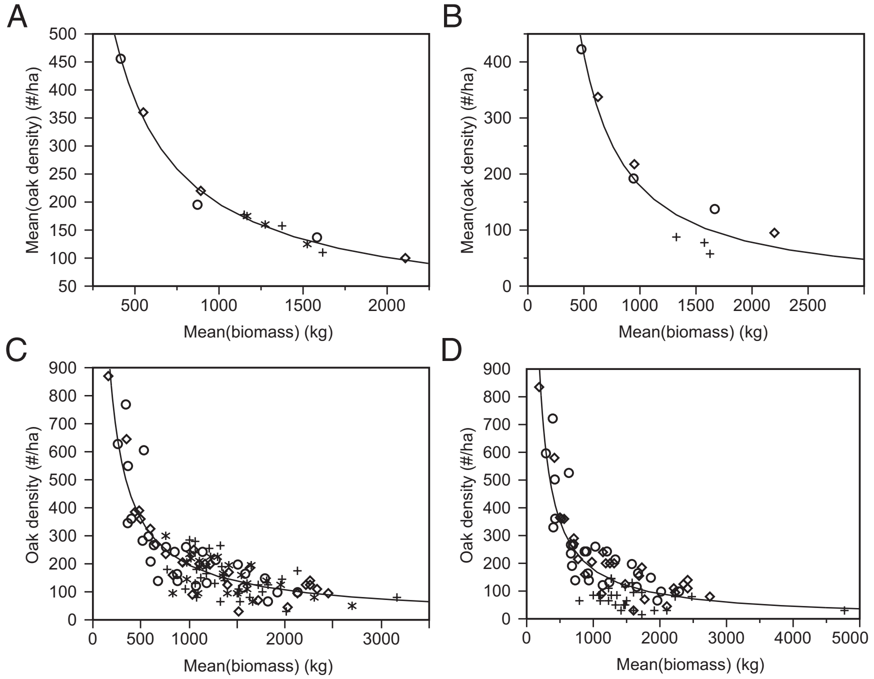

Fig. 5. Density–mass power-law allometry held in Black Rock Forest. (*A*–*D*) The mean of oak density in Black Rock Forest decreased as a power function with increasing mean above-ground biomass of oak trees with dbh $\geq$ 2.54 cm, as predicted, in (*A* and *B*) plots and (*C* and *D*) subplots, in (*A* and *C*) 2007 (before girdling) and (*B* and *D*) 2010 (after girdling). The solid line is the least-squares power-law regression line. Markers represent treatments as in Fig. 1. (*A*) $n = 12$ plots in 2007: mean oak density = 148,420.536 (78,082.585, 218,758.487) × (mean above-ground biomass)$^{-0.959\ (-1.033,\ -0.887)}$. $R^2 = 0.988$, adjusted $R^2 = 0.986$, RMSE = 12.390. (*B*) $n = 9$ plots in 2010: mean oak density = 739,140.606 (−715,789.482, 2,194,070.693) × (mean above-ground biomass)$^{-1.207\ (-1.509,\ -0.904)}$. $R^2 = 0.939$, adj. $R^2 = 0.930$, RMSE = 33.605. (*C*) $n = 108$ subplots in 2007: oak density by subplot = 84,915.578 (45,058.589, 124,772.566) × (mean above-ground biomass)$^{-0.880\ (-0.954,\ -0.805)}$. $R^2 = 0.781$, adj. $R^2 = 0.779$, RMSE = 67.441. (*D*) $n = 81$ subplots in 2010: oak density by subplot = 162,404.739 (58,526.777, 266,282.700) × (mean above-ground biomass)$^{-0.987\ (-1.090,\ -0.885)}$. $R^2 = 0.780$, adj. $R^2 = 0.777$, RMSE = 74.136.

mean abundance over time were a power-law function of body size with negative exponent −3/4, then "population variability should show a negative scaling relationship with body mass, taking values between −3/4 and −3/2. …[But] this relationship has not been tested explicitly in the literature …" We learned of this proposal only after submitting this work for publication. We confirmed the predicted VMA for variation in space of population density. Our point estimates of the scaling exponent of VMA before treatment, −2.101 (log-linear) and −1.768 (nonlinear), did not fall in the range Marquet et al. proposed, but our confidence intervals for the point estimates [(−2.896, −1.306) (log-linear) and (−3.106, −0.430) (nonlinear)] overlapped their suggested range.

VMA asserts that the variance in population density is a power-law function of the average body mass. VMA leads to testable predictions. For example, if self-thinning (14) of a stand increases average above-ground biomass per tree, VMA suggests that self-thinning should also reduce the spatial variance in density. In addition, if poor or harsh conditions limit average tree above-ground biomass compared with good growing conditions, then VMA predicts, all else being equal, that population density should also be more variable under poor or harsh conditions.

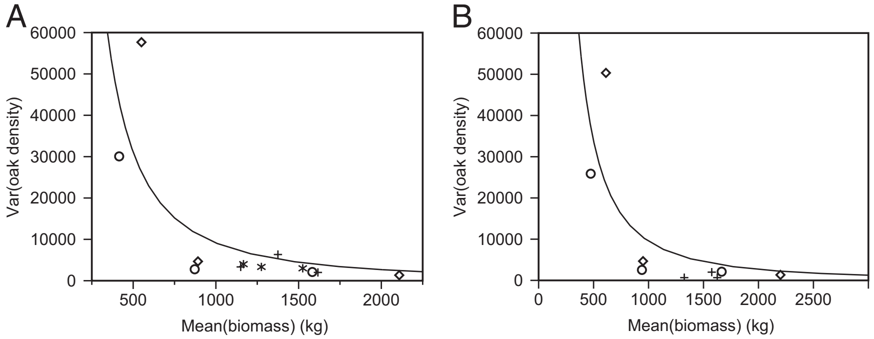

Fig. 6. Variance–mass power-law allometry held in Black Rock Forest. The variance of oak population density in Black Rock Forest decreased as a power function with increasing mean above-ground biomass of oak trees with dbh $\geq$ 2.54 cm, as predicted. The solid line is the least-squares power-law regression line. Markers represent treatments as in Fig. 1. (*A*) $n = 12$ plots in 2007: variance of oak population density = 1.835×10^9 (-1.350×10^{10}, 1.717×10^{10}) × (mean above-ground biomass)$^{-1.768\ (-3.106,\ -0.430)}$. $R^2 = 0.588$, adj. $R^2 = 0.547$, RMSE = 11,361.646. (*B*) $n = 9$ plots in 2010: variance of oak population density = 3.039×10^{10} (-3.728×10^{10}, 4.336×10^{10}) × (mean above-ground biomass)$^{-1.835\ (-3.927,\ 0.256)}$. $R^2 = 0.561$, adj. $R^2 = 0.498$, RMSE = 12,159.980.

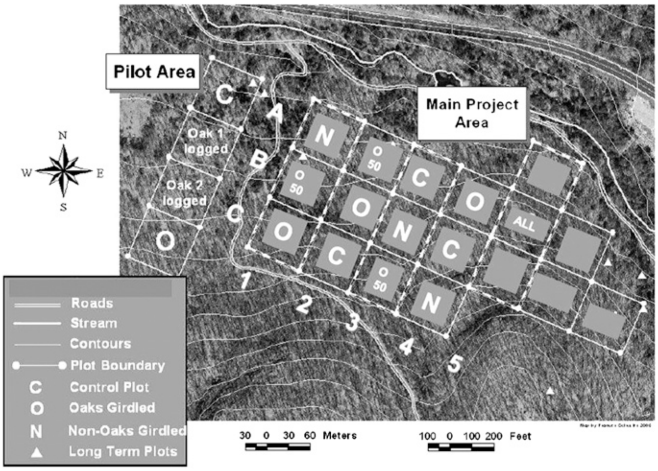

Fig. 7. Layout of 12 study plots in the main project area at Black Rock Forest. Plots were labeled by grid row (A, B, and C, corresponding to low, medium, and high elevation), column (1–4), and treatment in 2008: C, control (no intervention); N, nonoaks girdled; O, 100% oaks girdled; and O50, 50% of oaks girdled. Map by Frances Schuster, 2006.

TL takes multiple forms, depending on how space and time enter the calculation of the mean and variance. In a temporal form of TL, multiple spatially distinct populations are censused at multiple points in time, and the mean and the variance over time of each population are calculated. The logarithm of the variance is plotted as a function of the logarithm of the mean, with one point per spatially distinct population. One spatial form of TL considers the same underlying data but reverses the roles of space and time: For each census, the mean and the variance over distinct populations are computed, and then the log variance is plotted as a function of the log mean, with one point per census. Here we used a second spatial form of TL, in which population densities were recorded in a single census in subplots that were subdivisions of plots. The variance and mean of population density were calculated for the subplots within a plot. Then the log variance was plotted as a function of the log mean with one point per plot.

Additional data and analyses are required to test whether VMA is observed in other spatial and temporal forms corresponding to other spatial and temporal forms of TL. The existence, form, and parameters of VMA can be tested further using other datasets, especially those on tropical forests, and using other theoretical models, such as models of dynamic size spectra for fisheries (28, 29). A better understanding of how population dynamics and ecological mechanisms determine the parameters and forms of TL, DMA, and VMA requires further research.

Although the data here pertain to trees of a single genus, the components of the theory, TL and DMA, apply interspecifically (2, 11), and therefore VMA is predicted to apply interspecifically also. In marine and freshwater food webs where body sizes and species abundances have been reported (12, 19), and in the zoological portion of terrestrial food webs, smaller-bodied, more numerous species are generally consumed by larger-bodied, less numerous species. If VMA applied to such webs, population densities of smaller-bodied species should be expected to be more variable spatially or temporally than population densities of larger-bodied species. If VMA can be confirmed empirically for such webs, it could have theoretical and empirical consequences for their stability and management (27).

Materials and Methods

A rectangular field site on a slope dominated by oaks at Black Rock Forest was divided into 12 plots, each ~75 × 75 m, and each plot was subdivided into 9 subplots, each ~25 × 25 m (Fig. 7). The subplot in the middle of each plot was called the central subplot. In 2007 (before an intervention in 2008) and again in 2010 (after the intervention), the spatial coordinates and the dbh (in centimeters) of every individual oak tree were measured if dbh $\geq$ 2.54 cm. Species-specific biomass formulas (30) were applied to estimate each tree's above-ground biomass (AGB) (in kilograms) from its dbh.

The areas (hectares) of the 12 plots and 12 central subplots were measured. In the absence of direct measurement of the noncentral subplots, the remaining 8 subplots in each plot were assumed to have equal area, which was calculated as noncentral subplot area $=$ (plot area $-$ central subplot area)$/8$. The areas of the 108 subplots differed slightly from plot to plot because of differences among the plots in central subplot areas, but there was no change in areas of plots or subplots from 2007 to 2010. After the noncentral subplot areas were calculated, the areas of the central subplots of A3 and B3 were reduced by the surface area occupied by a stream.

In each subplot, oak density was calculated as the ratio of the number of oak trees over the subplot area. The mean and the variance of oak density were calculated over the subplots within each plot. For a plot or a subplot, the mean above-ground biomass of oak trees was calculated as the ratio of the sum of oak above-ground biomass over the number of oak trees.

Each plot was assigned one of four treatments applied in late June or early July 2008: control, no intervention (C); all nonoaks were girdled (N); 100% oaks were girdled (O); and every second oak tree encountered as a forester walked systematically through the plot was girdled (O50). Each grid row (A, B, and C) received all four treatments to avoid confounding treatment with elevation (grid row A was low, grid row B was medium, and grid row C was high) (Fig. 7).

In 2007, the five oak species in these plots were *Quercus rubra* L. Red Oak (59.4%), *Quercus prinus* L. Chestnut Oak (30.6%), *Quercus velutina* Lam. Black Oak (4.6%), *Quercus alba* L. White Oak (5.2%), and *Quercus bicolor* Willd. Swamp White Oak (0.2%). There were 1,319 living oaks in 2007 and 904 in 2010, and in 2007 oaks were 20.5% of all trees in the study site with dbh $\geq$ 2.54 cm. In 2010, 7 oaks survived girdling in the plots where all oaks were girdled (A4, B2, and C1). We excluded these three plots and these 7 surviving oaks from analyses of 2010 data. Hence the number of surviving oaks in the remaining nine plots in 2010 was 897. Using ANCOVA by species, we found that exponents in TL and VMA for red oaks did not differ significantly from the corresponding exponents in TL and VMA for chestnut oaks. The exponents for red oaks and chestnut oaks in DMA sometimes differed significantly according to ANCOVA and sometimes did not, depending on the year and whether plots or subplots were analyzed. The three other species constituted only 10% of the oaks, too few for meaningful comparisons of *b*. We pooled tree counts for all oak species.

Treatments and soil conditions—whether or not groundwater seeps were present at the soil surface—had no significant effects on *b*, the exponent of TL, in 2007 or 2010. Nine plots had no seep conditions in the soil (surface groundwater) and three plots (A1, A4, and B1) had seep conditions. Elevation of the plot grid did not affect *b* significantly before girdling, but after girdling, the higher the elevation, the bigger was *b*. These conclusions are based on ANCOVAs in which the number of plots being compared was very limited: three plots per treatment, four plots per elevation level, and three plots with seeps. We therefore omit the details.

Quadratic least squares were fitted to test for nonlinearity in the pairwise relationships between log-transformed variables. In both years, no significant nonlinear term was found for TL, DMA, or VMA.

Statistical calculations were performed using JMP version 9 (31). In calculating means and variances of population density for plots, subplots were weighted by their areas. In calculating log-linear and nonlinear regressions, plots were weighted equally and subplots were weighted equally. We fitted all power laws (TL, DMA, and VMA), using least-squares linear regression of the log variables ("log-linear regression") and nonlinear least-squares fitting of the original variables ("nonlinear regression"). For the nonlinear fitting, we used the analytic Gauss–Newton method of JMP version 9.

Data analyzed here are presented in Dataset S1 as a tab-delimited txt file. A blank cell in "Biomass in 2010 (kg)" means that the corresponding tree was dead in 2010.

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