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Robustness of Taylor's law under spatial hierarchical groupings of forest tree samples

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Abstract Testing how well Taylor's law (TL) describes spatial variation of the population density of a species requires grouping sampling areas (patches of habitat) into blocks so that a mean and a variance of the population density can be calculated over the patches in each block. The relationship between specific groupings and TL remains largely unknown. Here, using tree counts from a deciduous forest, we studied the effect of four biological methods of grouping sampling areas into blocks on the form and parameters of TL. Regardless of the method of grouping, the species-specific basal area densities obeyed TL, and the estimated slopes were not significantly different from one grouping method to another. Surprisingly, TL remained valid when four kinds of randomizations were performed to the biological groupings and tree census. These randomizations randomly assigned sampling areas to blocks, and/or randomized the species composition within or across sampling areas. We found that the form of TL was robust to different grouping methods and species randomizations, but its parameter values depended significantly on species compositions at sampling areas.

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Introduction

Quantifying and interpreting the spatial and temporal variations of the population size or density of species in nature is a central challenge in ecology (Hanski 1980, 1982, 1987). Studies of extinction (Schoener and Spiller 1992; Vucetich et al. 2000; Green 2003; Legendre et al. 2008), endangered species (McLaughlin et al. 2002), agricultural pest control (Dalin et al. 2009), and epidemic diseases (Isham 1991; Keeling and Grenfell 1999) all rely on the estimation of variations in species' population density.

Taylor's law (TL) is an empirical pattern quantifying variations of species' population densities. TL says that, in a set of samples, the variance of population density for a single (or a group of) species is a power-law function of the mean density (Taylor 1961): for all samples, approximately

$$(\text{variance of density}) = a \times (\text{mean of density})^b, \text{ with } a > 0. \quad (1)$$

Taking the logarithms of both sides of Eq. 1 yields a log–log form of TL: for all samples, approximately,

$$\log(\text{variance of density}) = \log(a) + b \times \log(\text{mean of density}). \quad (2)$$

Taylor (1961) confirmed Eq. 2 for 24 taxa, including zooplankton, insects, fishes, and viral lesions. During the last half-century, TL was confirmed for hundreds of biological taxa, such as annelids, beetles, molluscs, birds,

bacteria, viruses, plants, and humans (Taylor et al. 1978; Hanski 1980; Perry 1981; Keeling and Grenfell 1999; Ramsayer et al. 2011; Kaltz et al. 2012; Cohen et al. 2012, 2013a, b). TL was also verified for cell populations within organisms (Azevedo and Leroi 2001), hematogenous organ metastases (Kendal 2002), genes on human chromosome 7 (Kendal 2004a), and single nucleotide polymorphisms along domestic horse chromosome 1 (Kendal and Jørgensen 2011).

Because Taylor's discovery was confirmed by extensive empirical data, numerous attempts were made to explain the mechanisms underlying TL. Taylor (1984) and others (e.g., Arruda-Neto et al. 2012) proposed that TL resulted from behavioral interactions within species, and that the parameters of TL reflected species-specific characteristics. Hanski (1987) showed that large values of b could be generated by cross-correlation in the dynamics of local populations. Kilpatrick and Ives (2003) proposed that the parameters of TL reflected interspecific interactions. Jørgensen and his colleagues argued that TL has widespread descriptive success in ecology and other fields because it results from a statistical limiting process (Jørgensen 1987, 1997; Kendal 2004b; Jørgensen et al. 2009). Our recent analyses (Cohen et al. 2012; Cohen 2013) showed that stochastic multiplicative population dynamics in Markovian environments and linear birth-and-death processes (Jiang et al. 2014) led to TL. This is far from an exhaustive list of the mechanisms that have been proposed.

In the present paper, we do not attempt to establish a specific theory or any underlying mechanisms of TL. Instead, we study how different ways of grouping observations could affect the form, parameters, and interpretations of TL, using the basal area density data of trees in a deciduous forest in northeastern United States of America. Our motivation is that these empirical analyses would clarify the mysterious role of grouping methods and identify key biological factors to consider when interpreting TL.

Suppose that sampling areas are grouped into blocks according to some method and that the basal area density (defined below) of a tree species is known for each sampling area. Then by definition, a spatial hierarchical TL states that the logarithm of the spatial variance of basal area density of a tree species in the sampling areas of a given block is approximately a linear function of the logarithm of the spatial mean basal area density of that tree species in the sampling areas of that given block, when different blocks are compared (Taylor et al. 1978; Cohen et al. 2012). Basal area density of a sampling area was defined as the ratio of basal areas of trees to the area of land where the trees were sampled. This index is commonly used by forest managers to estimate a forest's timber

production. To test this TL, sampling areas of the forest were grouped into "blocks", and the means and variances of single tree species densities over all sampling areas within a block were calculated to test the linearity between the log mean and the log variance across blocks (TL, Eq. 2).

The goal of this work was to use tree basal area density data to study the effects, if any, on TL and its parameters of various methods of grouping sampling areas into blocks. In prior works on TL using forest trees, the most common grouping method assigned sampling areas that were spatially close to each other into a block (Taylor et al. 1978; Cohen et al. 2012). This method of grouping was often used in controlled experiments where sampling areas were artificially defined "patches" within the study area. It was convenient for sampling purposes but did not respect the biological heterogeneity of sampling areas within the same block. In a forest, spatially adjacent areas may differ biologically in soil condition, slope, altitude and aspect, which may directly or indirectly affect the growth and distribution of tree species.

Here, we analyzed the impact of 4 biologically distinct grouping methods on TL. If TL was confirmed under a biological grouping method, it was tested again using randomized grouping methods to check if the agreement was a statistical artifact or an ecological consequence of the biological method. Our findings are summarized at the beginning of the Discussion.

Materials and methods

Tree censuses and sampling method

The Black Rock Forest (BRF) (Schuster et al. 2008; Xu et al. 2012) is a 1,550 ha preserve located in the Hudson Highlands of Orange County, NY, USA (41°24′N, 74°01′W). In 1985, BRF had a total area of 1,416 ha and a forest-wide survey was used to divide a majority of the Forest into 71 stands according to the tree canopy characteristics and tree species composition. The size of a single stand ranged from 0.4 to 57.5 ha, with an average of 18.3 ha and a standard deviation of 18.6 ha. In each stand, at least 3 sampling points were designated randomly, based on the stand's shape (Avery and Burkhart 2002). Overall, 218 sampling points were located in the 71 stands (Electronic Supplementary Material (ESM) S1 and Fig. S1 give details).

The Bitterlich method was applied to count trees in a neighborhood (of variable physical size) of each sampling point (Bitterlich 1984) with a 10 basal-area-factor wedge prism. The Bitterlich method is not a plot-based sampling approach and does not generate sampling areas of fixed

size, since the sampling area varies depending on a tree's diameter at breast height (DBH). However each sampled tree contributed equally to the basal area relative to the sampling area. Therefore the counts of sampled trees at a sampling point measured (were proportional to) the basal area density at that sampling point (Gregoire and Valentine 2004). Sampled trees with DBH less than 2 inches (5.08 cm) were eliminated from the sample and each remaining tree (sometimes called a "stem") was identified to species. The count of each single tree species recorded at each sampling point was defined as the basal area density of that species in the corresponding sampling area. In total, 2,078 stems were located and identified to species at the 218 sampling points. Among all 35 identified tree species, three oak species (1,184 stems, 56.98 % of the total) illustrated the *Quercus*-dominated characteristic of the entire BRF (Schuster et al. 2008; Xu et al. 2012). The 9 most abundant species, *Quercus rubra* Linnaeus (red oak, RO), *Quercus prinus* Linnaeus (chestnut oak, CO), *Acer rubrum* Linnaeus (red maple, RM), *Quercus alba* Linnaeus (white oak, WO), *Tsuga canadensis* Carrière (eastern hemlock, EH), *Pinus resinosa* Aiton (red pine, RP), *Picea glauca* hort. ex Beissn (white spruce, WS), *Betula lenta* Linnaeus (black birch, BB), and *Acer saccharum* Marshall (sugar maple, SM) comprised 1,826 stems (87.87 % of the total), and were used in the data analysis. We eliminated the other 26 less common species from this work because their counts were mostly 0 (see Results, Descriptive statistics). Details about the forest classification and sampling method are included in the ESM S1.

Counts of individual tree species were arranged in a matrix of 218 rows and 9 columns (given in full in the on-line data file ESM S2). Each row corresponded to one sampling area and each column corresponded to one species. Columns were arranged in the descending order of species' summed counts from all 218 sampling areas (e.g., column 1 listed counts of red oaks in each of 218 sampling areas, column 2 listed counts of chestnut oaks in each of 218 sampling areas, etc.). The number in row i ($i = 1, 2, …, 218$) and column j ($j = 1, 2, …, 9$) represented the count in sampling area i of the jth most dominant species.

Grouping methods

Four biologically relevant methods were used to group sampling areas into blocks. First, Friday's method, designed by J. B. Friday, was based on a classification of stands in the 1985 forest inventory. Stands of the same canopy type were combined and sampling areas within those stands were grouped together as a block. Nine blocks were defined using the species composition and canopy height according to the following criteria: 80–100 % hardwood of height 20–40 feet, 80–100 % hardwood of height 40–60 feet, 80–100 % hardwood of height 60–80 feet, 80–100 % hardwood of mixed heights, 50–80 % hardwood of height 20–40 feet, 50–80 % hardwood of height 40-60 feet, 50–80 % hardwood of height 60–80 feet and mixed heights, 80–100 % softwood of height 20–60 feet, and 50–80 % softwood of height 40–80 feet.

Second, Schuster's method, designed by (coauthor) W. S. F. Schuster, grouped sampling areas by their community types. Community type was usually assigned based on the most common species of tree in the largest trunk size class in a sampling area. Community type nomenclature and designations followed closely the system developed by Reschke (1990) to describe the ecological communities of New York State. The nine community types, one for each block, were "sh" (successional hardwoods), "sm" (sugar maple woods), "os" (oak slope woods), "hc" (hemlock coves), "hw" (hilltop woods), "co" (chestnut oak woods), "rms" (red maple swamp), "cp" (conifer plantations), and "c + r" (cliff and rock).

Third, BRF was subdivided into first- and second-order watersheds based on stream order, using topographic divides as the boundaries between watershed areas. Each sampling area was categorized based on which first- or second-order watershed area contained it. This watershed method assigned each sampling area to one of 11 watersheds or sub-watersheds (in the cases of the largest watersheds). Each block was one watershed area. Resulting blocks were not necessarily the same or different in soil type, aspect, hydrologic regime and other attributes. The 11 watersheds (or sub-watersheds) were named "am" (Aleck Meadow, upper BRF watershed), "bm" (Bog Meadow), "lbrb" (Lower Black Rock Brook), "cas" (Cascade Brook), "ch" (Cat Hollow), "jp" (Jim's Pond), "lcb" (Lower Canterbury Brook), "lms" (Lower Mineral Springs Brook), "ucb" (Upper Canterbury Brook), "ums" (Upper Mineral Springs Brook), and "ur" (Upper Reservoir).

Fourth, the topography method assigned each sampling area to one of eight site moisture groups based on an ordinal (not quantitative) scale of moisture increasing from 1 (driest) to 8 (wettest). The moisture scale was based on the site aspect, topographic position, and slope steepness of each sampling area, and was the only grouping method with an ordinal scale. Sampling areas in the same moisture group were grouped together as a block. While the watershed and topography methods used physiographic rather than biological information of sampling areas, we referred for convenience to all four methods as biological grouping methods.

Randomizations of grouping methods and tree census

For each biological grouping method, we designed a random grouping method that randomly assigned sampling

areas into blocks, while keeping the numbers of blocks and numbers of sampling areas within a block the same as in the corresponding biological method. Then we tested TL under the biological grouping method and the associated random grouping method. The purpose of this random method was to test if the confirmation or violation of TL under any biological grouping was a statistical artifact. For each random grouping, sampling areas were randomly permuted and each sampling area appeared exactly once in exactly one randomly selected block. The species compositions and counts within each sampling area were preserved.

After testing TL under each biological grouping and corresponding random method, we examined the robustness of TL by testing it against randomized tree census data. The goal was to find out whether and how the composition of tree species within or among sampling areas affected TL and its parameters. Hence we designed 3 randomizations of the tree census.

First, within each sampling area, the counts of the 9 single tree species were randomly permuted among species. Each sampling area remained in the block to which the corresponding biological grouping assigned that sampling area. In this randomization, for each species, the distribution of its counts in the sampling areas differed from that in the original data. We called this procedure the *species randomization*.

Second, each sampling area was randomly assigned to a block and then the counts of single species within each sampling area were randomly permuted among the 9 species. This randomization preserved only the set of counts in each sampling area, not the species identity of those counts and not the block to which the sampling area was assigned. This method was called the *sampling area-species randomization*.

Third, all 1,962 (218 sampling areas × 9 species) counts of single species per sampling area were randomly permuted. This scrambling treated all 1,962 numbers as observations of a single hypothetical random variable, the count of one tree species per sampling area. This randomization procedure erased any association of species identity with counts in a sampling area and of sampling areas with blocks, and in addition altered the distribution of single species counts within a sampling area. We called it the *global randomization*.

Statistical and computational methods

We tested the spatial hierarchical TL under each biological grouping and the corresponding random grouping method. Then, for each biological method, we tested TL again using separately the three randomizations of the tree census data. Any block containing fewer than five sampling areas was

excluded from the analysis. Then a spatial mean and a spatial variance of single species counts per sampling area were calculated over all sampling areas within each block (including sampling areas with zero counts of the selected species) separately for each of the nine dominant species. Blocks with zero mean or zero variance were omitted later in the analysis as the logarithm of zero is undefined.

A linear regression and a quadratic regression were fitted separately for the dependent variable, log variance, as a function of the independent variable, log mean, pooling the (log mean, log variance) pairs from all nine dominant species. The null hypothesis that $b = 0$ (equivalent to the null hypothesis that there was no linear relationship between the log variance and log mean) was rejected if the linear regression coefficient was statistically significantly different from zero ($P < 0.05$).

Then a quadratic regression was used as an alternative to the linear regression model to test for the presence of a nonlinear relationship between log mean and log variance of the species counts. The nonlinearity was not statistically significant if the coefficient of the squared term (log mean)^2 in the quadratic regression was not significantly different from zero (Zar 2009).

TL was tested for each of the nine individual species, and its parameters were compared among the species (ESM S1, Sect. 2, Figs. S2–S5, Tables S1–S4).

Under each biological grouping method, 10,000 random groupings, 10,000 species randomizations, 10,000 sampling area-species randomizations, and 10,000 global randomizations of tree census data were generated to test TL. As in the data analyses, the log means, log variances, and linear and quadratic regressions were calculated for each randomized grouping and set of count data, and a set of 10,000 resulting regression coefficients and regression constants was obtained to find the point estimates (50 % quantile) and 95 % CIs (2.5 and 97.5 % quantiles) of the TL parameters and coefficients of the quadratic terms. Linear and quadratic regressions were performed using JMP 9 (SAS Institute 2010). Random permutations were carried out using MATLAB R2012b (MathWorks 2012). We always used log = log$_{10}$ and set the level of significance at 0.05.

Results

Numerical example

In the spatial-hierarchical TL, grouping methods determined the sample over which a spatial mean and a spatial variance of species densities were calculated, as various groupings assigned different sampling areas into a block. Here we give a simple artificial example to illustrate that

groupings could affect the values of means, variances, and parameters of spatial hierarchical TL. Suppose column 1 in the following matrix lists the population densities of a hypothetical species 1 in 8 hypothetical sampling areas, and column 2 does the same for a hypothetical species 2 in the same 8 sampling areas.

$$\begin{pmatrix} 251 & 126 \\ 134 & 204 \\ 56 & 462 \\ 169 & 401 \\ 271 & 316 \\ 84 & 450 \\ 68 & 197 \\ 627 & 264 \end{pmatrix}$$

We examined two hypothetical methods of grouping sampling areas into blocks and computed means and variance of each species within a block.

The first method defined block 1 as the group of sampling areas 1 and 2 (row 1 and row 2), block 2 as the group of sampling areas 3 and 4 (row 3 and row 4), block 3 as the group of sampling areas 5 and 6 (row 5 and row 6), and block 4 as the group of sampling areas 7 and 8 (row 7 and row 8). The resulting log means and log variances for species 1 (column 1) are (2.28, 2.05, 2.25, 2.54) and (3.84, 3.81, 4.24, 5.19) respectively. The resulting log means and log variances for species 2 (column 2) are (2.22, 2.64, 2.58, 2.36) and (3.48, 3.27, 3.95, 3.35) respectively. Applying simple linear regression to log means pooled from the two species (independent variable) and log variances pooled from the two species (dependent variable), the point estimate and 95 % confidence interval (CI) are 0.44 and (−2.56, 3.43) respectively for the slope, 2.86 and (−4.25, 9.97) respectively for the intercept.

The second method defined block 1 as the group of sampling areas 1 and 5 (row 1 and row 5), block 2 as the group of sampling areas 2 and 6 (row 2 and row 6), block 3 as the group of sampling areas 3 and 7 (row 3 and row 7), and block 4 as the group of sampling areas 4 and 8 (row 4 and row 8). The resulting log means and log variances for species 1 (column 1) are (2.42, 2.04, 1.79, 2.60) and (2.30, 3.10, 1.86, 5.02) respectively. The resulting log means and log variances for species 2 (column 2) are (2.34, 2.51, 2.52, 2.52) and (4.26, 4.48, 4.55, 3.97) respectively. Using the same regression procedure as method 1, the point estimate and 95 % CI are 3.15 and (0.62, 5.69) respectively for the slope, −3.70 and (−9.67, 2.27) respectively for the intercept.

The means, variances and parameters of TL all differed between the two methods. Compared to values under the first method, the estimated slope was larger and the

estimated intercept was smaller under the second method, although the difference was not statistically significant as corresponding CIs overlapped each other. This artificial example showed that the method by which sampling areas are grouped into blocks could strongly but not statistically significantly affect the parameters of TL. In the remaining sections we studied if such effect was significant using basal area density data from the 1985 Black Rock Forest survey.

Descriptive statistics

The maximum and minimum counts of any of the 9 single species per sampling area were 19 stems (once only) and 0 stems (more than 90 % of the 1,962 counts) respectively. More than 98 % of the 1,962 counts of a single species per sampling area were 8 stems or fewer. The mean counts per sampling area among the nine species was 0.9307 stems, with 95 % CI (0.8414, 1.0200), and the standard deviation was 2.0171 stems (almost twice the mean).

The numbers of sampling areas per block, in ascending order, were 6, 6, 9, 11, 12, 18, 21, 27, and 108 for Friday's method; 2, 2, 3, 8, 14, 15, 20, 39, and 115 for Schuster's method; 4, 10, 13, 14, 14, 15, 18, 23, 25, 41, and 41 for the watershed method; and 7, 7, 14, 18, 33, 39, 45, and 55 for the topography method. As in the analyses of randomizations, blocks with fewer than 5 sampling areas were eliminated from the analysis.

Taylor's law under biological groupings

Under all four biological methods of grouping sampling areas into blocks, the linear regression of log variances of tree counts per sampling area on log means, pooled from the nine most abundant tree species, had estimated slopes and intercepts that were significantly positive (Fig. 1). The slope b did not differ significantly from one grouping method to another: any slope between 1.1335 and 1.2887 fell within the 95 % CIs of all four biological groupings, and this interval contained all four point estimates of the slope from the different grouping methods. The 95 % CIs of the intercept from any two grouping methods overlapped (Fig. 1).

ESM S1, Sect. 2, fits TL to data from individual tree species one at a time. Analysis of covariance showed no statistically significant difference of slopes among the nine single species.

Quadratic least-square regressions showed that the coefficient of (log mean)^2 was not significantly different from zero in Friday's ($P = 0.6181$) and Schuster's ($P = 0.5206$) methods, but was significantly negative in the groupings by watershed ($P = 0.0273$) and topography ($P = 0.0212$), rejecting the null hypothesis that quadratic
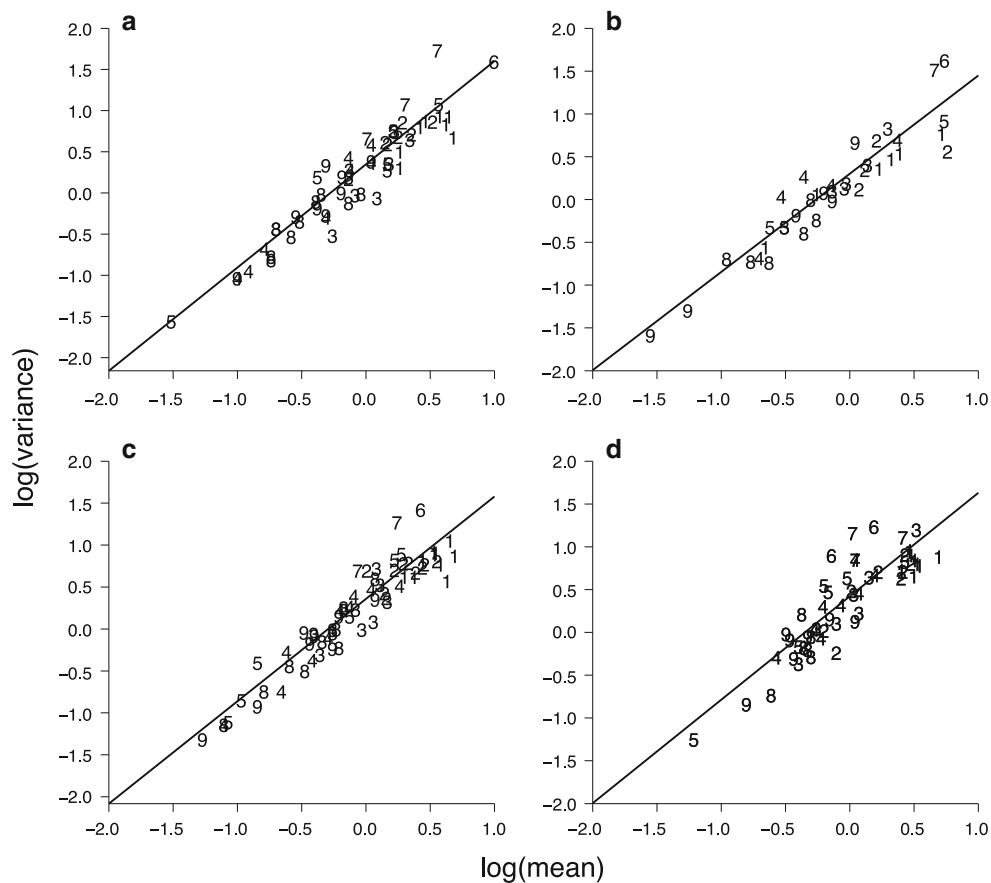
Fig. 1 Taylor's law held under each biological method of grouping sampling areas into blocks when the mean and variance of each species individually were plotted together for the nine most abundant species. Species are numbered in descending order of stem count in the whole study area. *1* red oak, *2* chestnut oak, *3* red maple, *4* white oak, *5* eastern hemlock, *6* red pine, *7* white spruce, *8* black birch, and *9* sugar maple. *Solid lines* are least-square linear regressions. In the following statements of the regression equations, 95 % CIs of the parameter estimates are given after the point estimates. *P* is the probability of the null hypothesis that the slope is 0. **a** Friday's grouping by species composition: log(variance) = 0.3480 (0.2881, 0.4079) + 1.2532 (1.1335, 1.3730) × log(mean). $P < 0.0001$, root mean square error (RMSE) = 0.2265, R^2 = 0.8832, adjusted (adj.) R^2 = 0.8812. **b** Schuster's grouping by species composition: log(variance) = 0.3012 (0.2200, 0.3823) + 1.1472 (1.0058, 1.2887) × log (mean). $P < 0.0001$, RMSE = 0.2332, R^2 = 0.8825, adj. R^2 = 0.8793. **c** Grouping by watershed: log(variance) = 0.3584 (0.3047, 0.4121) + 1.2197 (1.1114, 1.3280) × log(mean). $P < 0.0001$, RMSE = 0.2128, R^2 = 0.8861, adj. R^2 = 0.8844. **d** Grouping by topography: log(variance) = 0.4222 (0.3488, 0.4957) + 1.2085 (1.0240, 1.3930) × log(mean). $P < 0.0001$, RMSE = 0.2682, R^2 = 0.7650, adj. R^2 = 0.7606

regression was not better than linear regression for the watershed and topography groupings. However, for any grouping method, it was difficult to tell visually whether log variance was a nonlinear function of log mean (Fig. 1).

Taylor's law under randomized groupings and randomized species counts

On visual inspection, TL was confirmed again under each random grouping method (Fig. 2, left column). For each biological grouping, the corresponding random method yielded a 95 % CI of slope that overlapped the 95 % CI of the biological grouping. Random grouping did not significantly change the form or the slope of TL from the form or the slope of TL in the biological grouping. For Schuster's

and the watershed methods, the intercept of TL under the random groupings had a 95 % CI that lay entirely above the 95 % CI interval under the corresponding biological grouping. For Friday's and topography methods, the 95 % CIs of the intercept under biological and random groupings overlapped each other (Table 1). Despite the apparent linearity in Fig. 2, quadratic regressions for each random grouping method yielded a 95 % CI of the quadratic coefficients that lay entirely to the left of zero (Table 1), showing log variance as a slightly concave function of the log mean, consistent with the pattern under biological groupings.

For each biological method, randomizations of tree census data all yielded 95 % CIs of TL parameters that lay entirely above the 95 % CI estimated from the
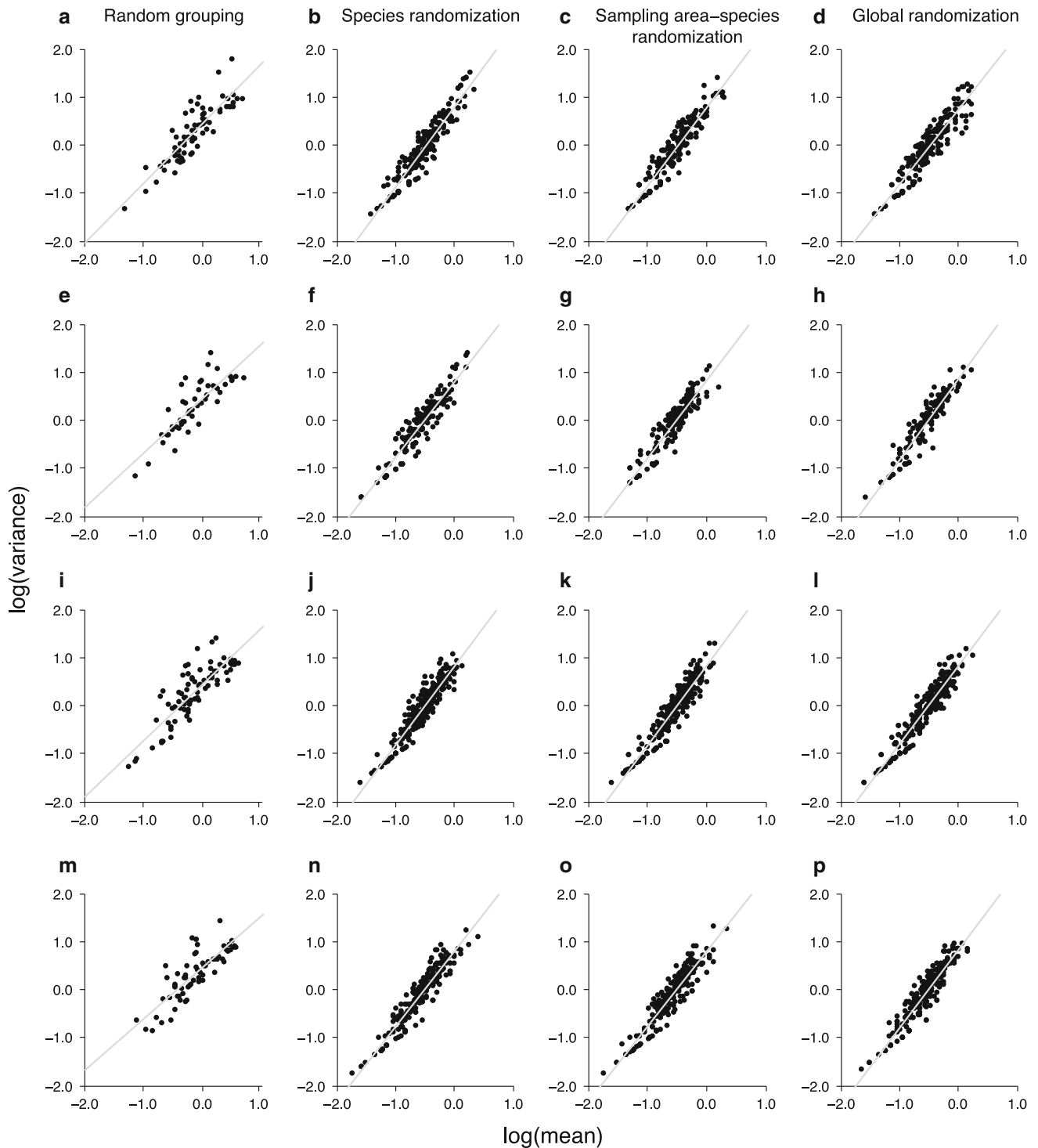
Fig. 2 Taylor's law holds using randomized groupings and random-ized tree censuses. Each *panel* shows one random realization. Each *solid circle* represented one pair, (log mean, log variance) of species-specific stem counts per block. The *solid grey lines* are least-square linear regression lines. Table 1 gives parameter estimates and CIs of corresponding biological and random groupings, except for the slope estimation under the topography method (Table 1), suggesting that the composition of the tree regressions. Rows 1–4 correspond to Friday's, Schuster's, watershed, and topography groupings respectively. Columns 1–4 correspond to random grouping, species randomization, sampling area-species randomization, and global randomization respectively

species within and among sampling areas influenced the values of TL parameters more than did any particular grouping method. Comparison between 95 % CIs from the

Table 1 Point estimates (medians) and 95 % confidence intervals (CIs) of log–log TL (Eq. 2) slope b and intercept log(a) from linear regressions, and quadratic coefficient from quadratic regressions using each randomized grouping method and tree-species count data

Regression parameters	Method	Random grouping		Species randomization		Sampling area-species randomization		Global randomization	
		Median	95 % CI	Median	95 % CI	Median	95 % CI	Median	95 % CI
Slope	Friday	1.2118	1.0903, 1.3107	1.6017	1.5042, 1.7156	1.5852	1.4595, 1.7121	1.5851	1.4523, 1.7190
	Schuster	1.1440	0.9891, 1.2627	1.6061	1.4781, 1.7594	1.5676	1.3869, 1.7427	1.5691	1.3811, 1.7528
	Watershed	1.1882	1.0951, 1.2662	1.4739	1.3608, 1.5808	1.5483	1.4306, 1.6724	1.5494	1.4273, 1.6743
	Topography	1.1245	0.9909, 1.2353	1.5006	1.3746, 1.6153	1.5852	1.4299, 1.7305	1.5851	1.4189, 1.7393
Intercept	Friday	0.4412	0.3909, 0.4869	0.5415	0.5145, 0.5663	0.5563	0.5207, 0.5894	0.5563	0.5243, 0.5875
	Schuster	0.4694	0.4159, 0.5181	0.5918	0.5676, 0.6124	0.5833	0.5469, 0.6189	0.5842	0.5504, 0.6175
	Watershed	0.4645	0.4342, 0.4917	0.5610	0.5455, 0.5741	0.5808	0.5591, 0.6011	0.5808	0.5603, 0.6003
	Topography	0.4669	0.4260, 0.5044	0.5704	0.5510, 0.5873	0.5798	0.5516, 0.6068	0.5804	0.5532, 0.6060
Quadratic Coefficient	Friday	−0.4671	−0.7921, −0.1904	0.0327	−0.2765, 0.2884	−0.1258	−0.5448, 0.1714	−0.1278	−0.5563, 0.1849
	Schuster	−0.5112	−0.9030, −0.1914	0.0979	−0.2393, 0.5359	−0.1409	−0.8055, 0.3169	−0.1320	−0.8169, 0.3294
	Watershed	−0.4673	−0.7288, −0.2670	−0.2243	−0.6711, 0.0265	−0.0518	−0.4614, 0.2407	−0.0511	−0.4621, 0.2335
	Topography	−0.4455	−0.8194, −0.1643	−0.3472	−0.7860, 0.0020	−0.2119	−0.7397, 0.1818	−0.2011	−0.7172, 0.1993

species randomization and sampling area-species randomization showed that, after species compositions were randomly permuted within a sampling area, random assignment of sampling areas to blocks did not significantly change the values of TL parameters, that is, that grouping methods had no additional effect on the values of TL parameters after species compositions were randomized. For each combination of biological methods and randomizations of the tree census, the 95 % CI of the quadratic coefficient from the quadratic regression contained zero, suggesting that the simple linear regression was sufficient to depict the relationship between log variance and log mean.

Discussion

We found that TL held for tree basal area densities under 4 biological methods of grouping sampling areas into blocks, and all 4 methods yielded statistically similar estimates of the slope b of TL. Thus the form (i.e., the linear relationship between log mean and log variance in Eq. 2) and the slope of TL were robust with respect to the method of grouping. To our surprise, none of the randomized groupings of sampling areas into blocks destroyed the form of TL or altered the slope of TL, but randomized groupings did increase the intercept of TL for Schuster's and the watershed grouping methods. These increases in intercept increased the variance by a constant factor for every mean density. These results implied that the form and the slope of TL cannot reflect the biological assumptions or details of the grouping methods.

However, when we randomly permuted tree census data within and among sampling areas, the slope parameter of TL changed significantly. This result showed that the species composition of sampling areas has a bigger impact on the slope of TL than does any particular grouping method. Overall, the robustness of the form of TL under various grouping methods suggested that TL must intrinsically relate to the shared or common frequency distribution of all observed basal area densities, since this frequency distribution was the only information left unchanged in the testing of TL after randomizations. Calculations elsewhere confirm this suggestion (J. E. Cohen and M. Xu, unpublished manuscript).

Our estimates of the parameters and goodness of fit of TL relied on the traditional method of linear regression of the log–log transformed power law, not least-squares fitting of the power law itself. This procedure has been criticized (McArdle 1988; McArdle et al. 1990; James and Plank 2007; Packard and Birchard 2008; Packard et al. 2011; Xiao et al. 2011) and defended (Smith 2009; Lai

et al. 2013). Xiao et al. (2011) found that the error distribution (the distribution of the residuals from the regression) determines which method is superior. After reviewing previous arguments, Lai et al. (2013) gave a compelling empirical example in favor of linear regression for fitting a log-transformed allometric relation of DBH to below-ground biomass of trees.

Using other data from Black Rock Forest, we compared the fitting of log mean and log variance to the log–log TL with non-linear least squares fitting of the untransformed mean and variance to the power-law TL (Cohen et al. 2012). We found that neither the parameter estimates nor the substantive conclusions were significantly affected by the method of fitting. Moreover, since here we were principally concerned with the methods of grouping sampling areas into blocks (means over which sampling areas? variances over which sampling areas?), we used the traditional (and consistent) method of linear regression for log transformed data.

The use of ordinary least squares here, rather than reduced major axis regression and its variants, is defensible because the variance of the sample mean is much smaller than the variance of the sample variance. Hence the log mean has much smaller sampling variation than the log variance, and the assumption of little variability in the horizontal coordinate compared to the variability in the vertical coordinate is more accurate than the alternative assumption in reduced major axis regression that the two variables are symmetrical (Smith 2009).

Taylor and his colleagues (Taylor et al. 1988) suggested that, when grouping sampling areas into blocks, the number of sampling areas per block should be at least 15 and the number of blocks in the regression should be at least five. These minima lacked theoretical explanations and depended on the specific data set. We followed Taylor's suggestions in part and required at least five sampling areas per block and at least five blocks per regression when testing TL.

Future research should investigate empirically and theoretically (following suggestive simulations by Sawyer 1989) whether and how the spatial scale (sizes of sampling units) influences the spatial hierarchical TL. Yamamura (1990), Figs. 1a, 2a; Table 1 therein compared the slope of TL using smaller and larger sampling areas in eight empirical examples of insect populations living on leaves. In all eight examples, the larger sampling area resulted in a larger slope of TL, but in four of those examples the increase in slope was not statistically significant (P of the F test was greater than or equal to 0.05). In analyzing the variability of human population density in the municipalities (smallest scale), counties (intermediate scale) and regions (largest scale) of Norway, Cohen et al. (2013b) "saw no clear relationship between the spatial scale of the unit of analysis (increasing from municipality to county to region) and the size of the regression slope or local slope …. However, when Oslo was excluded, the size of the regression slope or local slope was always smaller for municipalities than for counties …, reflecting perhaps lesser demographic divergence of municipalities than of counties." The effect of various spatial scales (sizes of sampling areas) on the parameters of TL was not tested using the present data, because the Bitterlich method did not produce sampling areas of fixed sizes and the data's spatial hierarchy did not contain sufficient levels (sampling area as the lower level and block as the higher level). Other ecological data sets with exactly defined sampling areas and multi-level (greater than two) spatial hierarchies are more suitable to be used to address this interesting question.

Taylor (1984) attempted to analyze how TL depends on underlying frequency distributions. He observed that the abundance of an insect species at progressively higher population densities conformed to different frequency distributions (e.g., Poisson, negative binomial, and lognormal) with identical slope parameter b. He used these distributions to characterize the increase of skewness and tail-length as population density increased. Taylor did not describe in detail how he fitted these distributions to his data, nor did he discuss any connection between TL and statistical distributions. Here we treated all observed basal area densities as a single distribution, and randomized the way species and sampling areas were grouped. The success of TL in describing the relation of log variance to log mean for randomized tree census data, whether biologically or randomly grouped, indicated to us that TL may arise as a statistical consequence of randomly sampling the frequency distribution of overall basal area densities. If this conjecture can be verified using other ecological data sets and confirmed using statistical theory, then we would have connected TL, a bivariate scaling pattern of variance and mean, with the univariate frequency distribution of species population density. To the extent, and under the conditions, that such a research agenda succeeds, then explanation of TL should be based on the theoretical understanding of observed frequency distribution. Future work on TL using BRF tree census data or other data sets should investigate the role of the underlying distribution of counts when interpreting TL.

The results of this work could easily be tested using available tree data from other forests. If our finding that TL's form and parameters do not depend on particular grouping methods were confirmed using other tree censuses, then the validity of a universal TL pattern would eliminate the need for a forest management team to classify sampling areas, and allows foresters to predict the

variations of basal area densities from the basal area densities directly. This could be extremely useful in monitoring the spatial variations in tree growth. The sampling method in our data was first applied by foresters for quick calculations of basal areas to predict tree production and growth rate. The confirmation of TL using basal area data therefore has practical implications for the timber industry, because it gives a guide to monitor spatial variability of timber species.

In ecology more broadly, our findings for deciduous trees should be tested using the rich stores of data available for other taxa. Are the form and parameters of TL always independent of the method of grouping sampling areas into blocks? Is the species composition of a sampling area always more influential on the parameter values of TL than the method of grouping sampling areas into blocks? Can the form and parameter values of TL always be explained by the underlying frequency distribution, without the need to group sampling areas? Future studies should address these questions.

Conflict of interest The authors state that they have no conflict of interest in this work.

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Robustness of Taylor's law under spatial hierarchical groupings of forest tree samples

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ELECTRONIC SUPPLEMENTARY MATERIAL

Section 1: Forest Classification and Sampling Design

In the 1985 inventory of the Black Rock Forest (BRF), 71 stands, with an average area of 18.31 ha, were delineated and classified according to canopy height ("2" = height 20-40 feet, "3" = height 40-60 feet, "4" = height 60-80 feet, or "6" = height mixed with short and tall trees), canopy cover ("A" = cover > 80 %, "B" = cover < 80 %, or " " = irregular cover due to mixed heights), and species composition ("H" = 80-100 % hardwood, "HS" = 50-80 % hardwood, "SH" = 50-80 % softwood, or "S" = 80-100 % softwood) (K. S. Friday and J. B. Friday, unpublished manuscript 1985, available from Black Rock Forest Consortium via coauthor W.S.F. Schuster). For example, a stand labeled with "H3A" was composed of 80-100 % hardwood of height 40-60 feet, with canopy cover greater than 80 %. Here canopy cover was defined as the percentage of ground area covered by the extension of plant foliage. Composition was defined by canopy cover (K. S. Friday and J. B. Friday, unpublished manuscript 1985), so a "> 80 % softwood" stand could mean that understory hemlock (a typical softwood) provided a great deal of cover, rather than that softwoods predominated in density, basal area or volume. Classifications of these stands (with a total area of 1,300 ha) were based on aerial photographs taken in 1981 and field checking carried out in 1985, when the Forest was smaller than at present.

To sample each stand, one or several axes were drawn on the map along the stand's "long axis" (or axes). As stands were often irregularly shaped, the axes were sometimes a straight

line and sometimes resembled a "Y", a "T", a "Z", or an "11" to sample irregular shapes or to skip over an inclusion.

Several sampling points were located within each stand and trees were censused at each sampling point. To designate sampling points, once the axes were drawn for a given stand, the "sampling point interval" was defined as the total length of the axes divided by three. A starting location was located one chain (66 feet or 20.12 m) along the axis from the northernmost end of the axis at the stand boundary. To find the distance along the axis from the starting location to the first sampling point, a random fraction between 0 and 1 was chosen from a random number table in Avery and Burkhart (2002) and multiplied by the sampling point interval. Thus the first sampling point was located along the axis that fraction of a "sampling point interval" from the starting location. Then the second and third sampling points were located further complete "sampling point interval" distances along that axis moving toward its southernmost end, or further along the axes when the axis was not a straight line. In this way, each sampling point was one "sampling point interval" distant from any neighboring sampling points. This method is described by Avery and Burkhart (2002).

The Bitterlich method was applied to sample trees at each sampling point. A 10 basal-area-factor wedge prism was used to tally trees with diameter at breast height (dbh) ≥ 2 inches (5.08 cm), called stems. dbh is the diameter of the trunk or bole of a tree measured 1.4 meters above ground, and is often used to characterize the tree body size (Burns and Honkala 1990). A wedge prism is a prism with a shallow angle between its input and output surface, here used as a device to count a stem "in" or "out" of a sampling area (Avery and Burkhart 2002).

Section 2: TL Analysis for Individual Tree Species

Simple linear regressions were applied to each of the nine dominant species, separately, if the corresponding species and grouping method yielded at least five pairs of well-defined log mean and well-defined log variance. Chestnut oak and eastern hemlock in Schuster's method, and red pine and white spruce in all methods contained fewer than five blocks and were therefore excluded, leaving 26 sets of blocks (for different methods of grouping and different species) to test the species-specific spatial hierarchical log-log TL (Eq. 2). In detail, $26 = (9$ species minus red pine and white spruce, i.e., 7 species) $\times$ 4 methods, minus chestnut oak and eastern hemlock in Schuster's method $= 7 \times 4 - 2$.

For the species-specific TL, point estimates of the slope and the intercept were positive in all 26 linear regressions (Tables S1-S4). In 22 of the 26 regressions, the 95 % CI of the slope lay entirely above zero, rejecting the null hypothesis of zero slopes. In 21 of the 26 regressions, the 95 % CI of the slope b included 1, which is the value of b for the Poisson distribution, but for only 6 of the 26 regressions did the 95 % CI of $\log(a)$ include 0, which is the value of $\log(a)$ for the Poisson distribution. In 5 of the 26 regressions, the 95 % CI of the slope b included 2, which is the value of b expected for distributions with a constant coefficient of variation. 23 of 26 linear regressions yielded a R^2 larger than 0.5. In quadratic regressions, the point estimate of the coefficient of the quadratic term (log mean)^2 was positive in 11 regressions and negative in 15, but was significantly different from zero in only two of 26 regressions. Thus the log variance of abundance increased (usually statistically significantly) as a linear function of the increasing log mean abundance for each tested combination of species and grouping method, as predicted by TL. In general, TL described acceptably the

relation between variance and mean, but neither a family of Poisson distributions nor a family of distributions with constant coefficient of variation was adequate to explain this agreement.

For each method of grouping, we tested the null hypothesis that the slope b of TL was the same among the nine species by analysis of covariance (ANCOVA) (Snedecor and Cochran 1989, pp. 374-393). For no method did the slope of TL differ significantly among the seven species which could be analyzed individually (P in ANCOVA ranged from 0.1902 to 0.6986 over different grouping methods). The intercept of TL differed significantly among these seven species only when sampling areas were grouped by topography ($P = 0.0231$). The two species with the highest intercepts, in descending order, were eastern hemlock and white oak. The intercept for red oak was the lowest and significantly smaller than that for eastern hemlock and white oak, but was not significantly different from that for sugar maple, red maple, black birch, and chestnut oak, in descending order.

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List of ESM figures and tables

Figure S1 Stands and sampling areas of Black Rock Forest in 1985.

Figure S2 TL under Friday's grouping for single dominant species.

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Figure S4 TL under the watershed grouping for single dominant species.

Figure S5 TL under the topography grouping for single dominant species.

Figure S6 Frequency distribution of number of trees per sampling area by species.

Table S1 Regression statistics of TL under Friday's grouping.

Table S2 Regression statistics of TL under Schuster's grouping.

Table S3 Regression statistics of TL under the watershed grouping.

Table S4 Regression statistics of TL under the topography grouping.

Figure S1
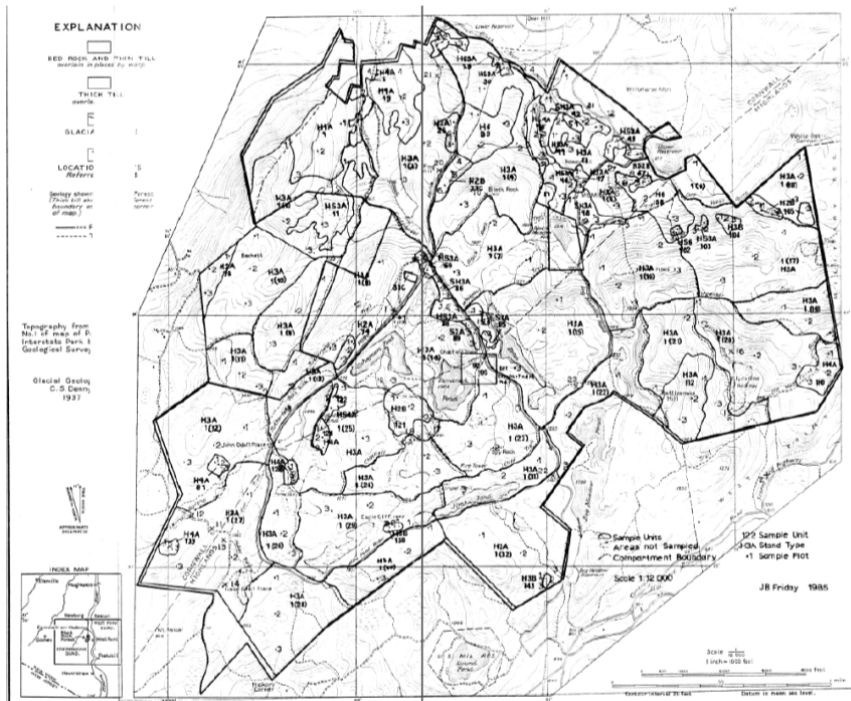
Fig. S1. Stands and sampling areas of Black Rock Forest in 1985. Map by James B. Friday, 1985, used by permission of the Black Rock Forest Consortium.

Figure S2

Fig. S2. Testing TL using counts of single tree species within a sampling area under Friday's grouping. (a) Red oak. (b) Chestnut oak. (c) Red maple. (d) White oak. (e) Eastern hemlock. (f) Black birch. (g) Sugar maple. Blocks are distinguished by numbers which have no biological implications. In all panels, the same number represents the same block. Solid line in each panel is the regression line. Statistics of each regression are listed in Table S1.

Figure S3

Fig. S3. Testing TL using counts of single tree species within a sampling area under Schuster's grouping. (a) Red oak. (b) Red maple. (c) White oak. (d) Black birch. (e) Sugar maple. Markers identify block: sh (successional hardwoods), sm (sugar maple woods), os (oak slope woods), hc (hemlock coves), hw (hilltop woods), co (chestnut oak woods), rms (red maple swamp), cp (conifer plantations), and c+r (cliff and rock). c+r is omitted from the tests because there are no trees in it. Statistics of each regression are listed in Table S2.

Figure S4

Fig. S4. Testing TL using counts of single tree species within a sampling area under the watershed grouping. (a) Red oak. (b) Chestnut oak. (c) Red maple. (d) White oak. (e) Eastern hemlock. (f) Black birch. (g) Sugar maple. Markers identify blocks: am (Aleck Meadow (Upper Black Rock Brook watershed)), bm (Bog Meadow), lbrb (Lower Black Rock Brook), cas (Cascade Brook), ch (Cat Hollow), jp (Jim's Pond), lcb (Lower Canterbury Brook), lms (Lower Mineral Springs Brook), ucb (Upper Canterbury Brook), ums (Upper Mineral Springs Brook), and ur (Upper Reservoir). Statistics of each regression are listed in Table S3.
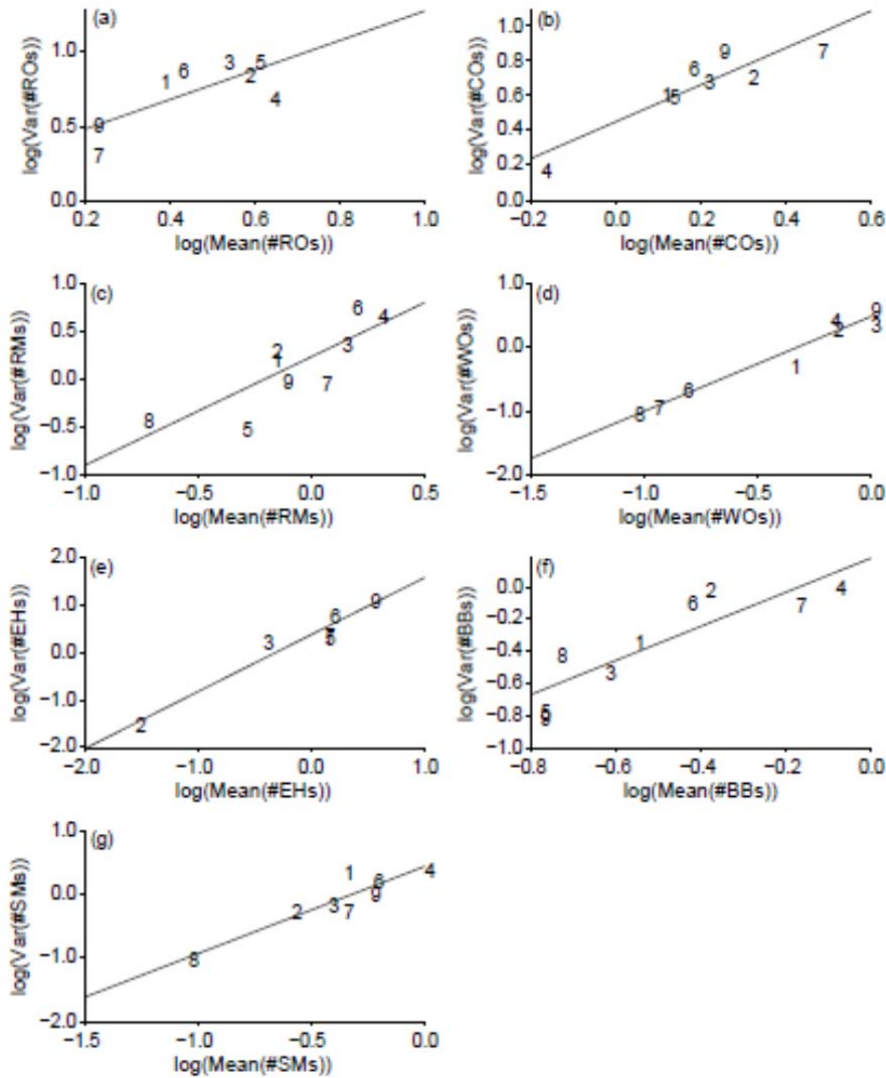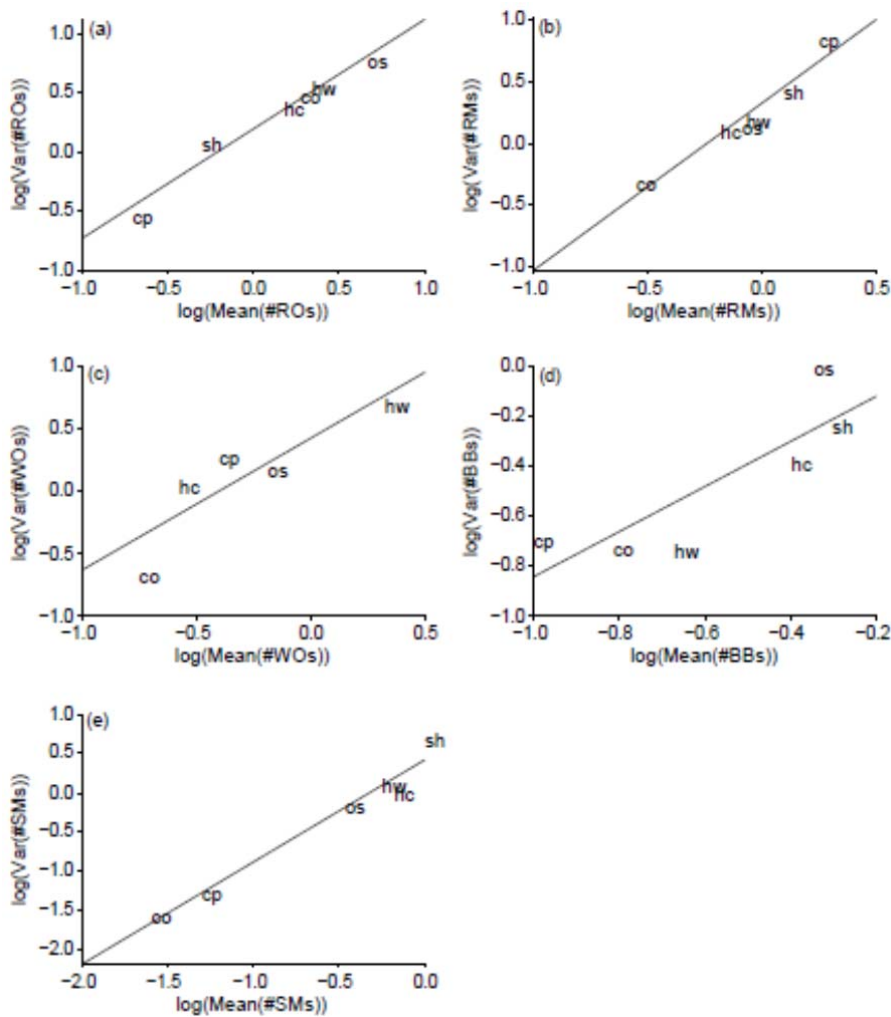
Figure S5

Fig. S5. Testing TL using counts of single tree species within a sampling area under the topography grouping. (a) Red oak. (b) Chestnut oak. (c) Red maple. (d) White oak. (e) Eastern hemlock. (f) Black birch. (g) Sugar maple. Markers identify block soil moisture scale (4 being driest and 11 being wettest) based on aspect, topographic position, and slope steepness. Statistics of each regression are listed in Table S4.

Figure S6
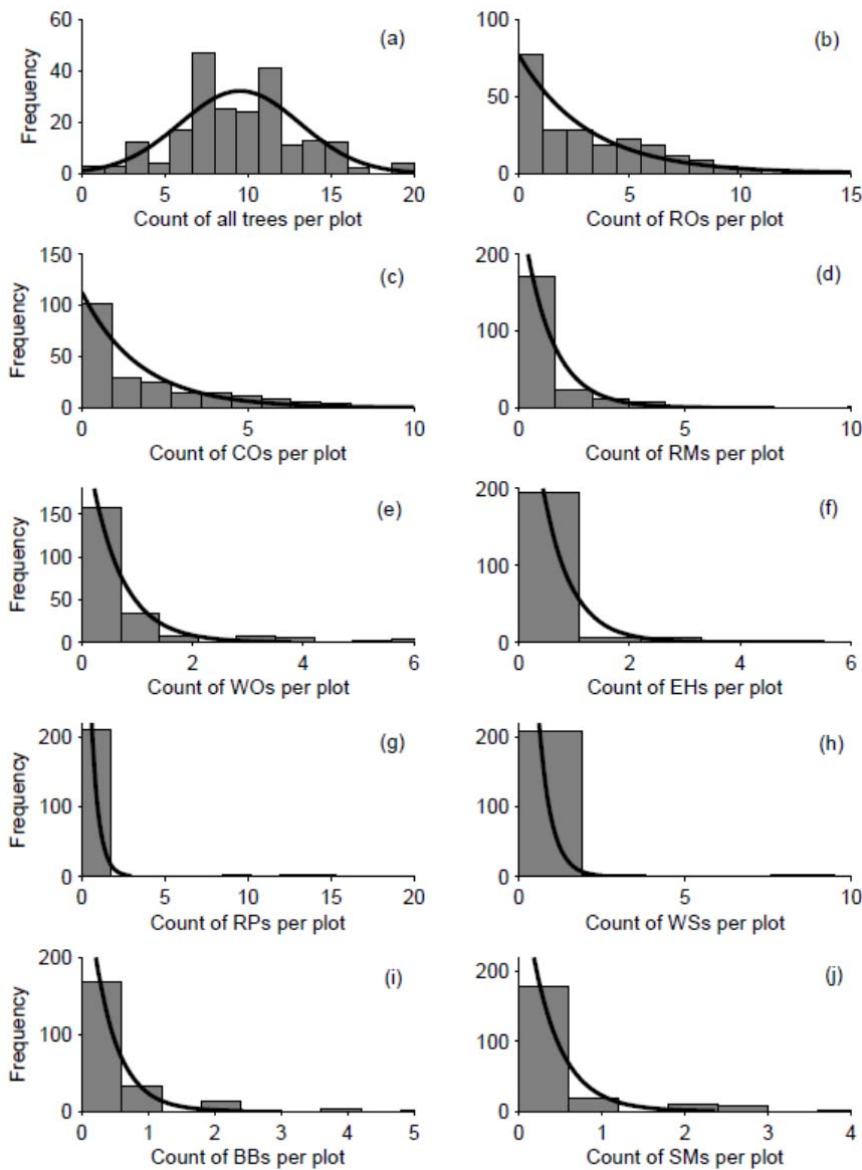
Fig. S6. Frequency distribution of number of trees per sampling area by species. (a) Trees of all 35 species summed, regardless of species. (b) Red oak. (c) Chestnut oak. (d) Red maple. (e) White oak. (f) Eastern hemlock. (g) Red pine. (h) White spruce. (i) Black birch. (j) Sugar maple. Solid lines represent fitted normal distribution for (a) and fitted exponential distributions for (b)-(j).

Table S1. Regression statistics of TL under Friday's grouping. Parameter point estimates and 95 % lower and upper bounds were obtained from normal theory using the original data. Species' abbreviations are given in main text

Species	Number of blocks	Linear regression						RMSE	R^2	Adjusted R^2	P	Quadratic regression squared term P	Sign
		Slope			Intercept								
		Estimate	Lower bound	Upper bound	Estimate	Lower bound	Upper bound						
RO	8	0.9854	0.0552	1.9156	0.2847	-0.1567	0.7262	0.1662	0.5282	0.4496	0.0411	0.0105	< 0
CO	8	1.0614	0.5619	1.5610	0.4569	0.3301	0.5837	0.1013	0.8184	0.7881	0.0020	0.0549	< 0
RM	9	1.1379	0.4139	1.8618	0.2330	0.0093	0.4568	0.2705	0.6637	0.6156	0.0075	0.3905	> 0
WO	8	1.4855	1.1575	1.8135	0.4854	0.2891	0.6817	0.1539	0.9534	0.9456	< 0.0001	0.6410	> 0
EH	6	1.2013	0.7963	1.6063	0.3857	0.1027	0.6688	0.2421	0.9443	0.9304	0.0012	0.6430	< 0
BB	9	1.0593	0.5340	1.5846	0.1814	-0.1133	0.4761	0.1616	0.7646	0.7310	0.0020	0.0478	< 0
SM	8	1.3641	0.7798	1.9485	0.4355	0.1464	0.7247	0.1952	0.8447	0.8188	0.0012	0.6373	< 0

Table S2. Regression statistics of TL under Schuster's grouping. Parameter point estimates and 95 % lower and upper bounds were obtained from normal theory using the original data. Species' abbreviations are given in main text

Species	Number of blocks	Linear regression										Quadratic regression squared term	
		Slope			Intercept			RMSE	R^2	Adjusted R^2	P	P	Sign
		Estimate	Lower bound	Upper bound	Estimate	Lower bound	Upper bound						
RO	6	0.9316	0.6940	1.1692	0.1945	0.0855	0.3035	0.0947	0.9673	0.9592	0.0004	0.1602	< 0
RM	6	1.3479	0.8619	1.8339	0.3337	0.2053	0.4622	0.1070	0.9368	0.9210	0.0015	0.0550	> 0
WO	5	1.0602	0.0037	2.1167	0.4242	-0.0908	0.9392	0.2765	0.7727	0.6970	0.0496	0.3805	< 0
BB	6	0.9061	0.1078	1.7044	0.0629	-0.4500	0.5757	0.1829	0.7129	0.6411	0.0345	0.1884	> 0
SM	6	1.3029	0.9925	1.6134	0.4243	0.1548	0.6939	0.1642	0.9714	0.9642	0.0003	0.3425	> 0

Table S3. Regression statistics of TL under the watershed grouping. Parameter point estimates and 95 % lower and upper bounds were obtained from normal theory using the original data. Species' abbreviations are given in main text

Species	Number of blocks	Linear regression										Quadratic regression squared term	
		Slope			Intercept			RMSE	R^2	Adjusted R^2	P	P	Sign
		Estimate	Lower bound	Upper bound	Estimate	Lower bound	Upper bound						
RO	10	0.6234	-0.2666	1.5133	0.4974	0.0536	0.9413	0.1434	0.2459	0.1517	0.1449	0.4592	< 0
CO	10	0.5242	-0.0850	1.1334	0.5352	0.3511	0.7192	0.1329	0.3298	0.2461	0.0825	0.5822	> 0
RM	10	1.1249	0.3117	1.9381	0.3144	0.1259	0.5029	0.2138	0.5598	0.5048	0.0128	0.9732	> 0
WO	10	1.3552	1.0371	1.6732	0.4084	0.2427	0.5742	0.1633	0.9235	0.9139	< 0.0001	0.5629	< 0
EH	6	1.3536	1.0103	1.6969	0.5366	0.2874	0.7857	0.1699	0.9677	0.9596	0.0004	0.9772	< 0
BB	9	1.3616	1.0347	1.6885	0.3570	0.1664	0.5475	0.1377	0.9327	0.9231	< 0.0001	0.1952	> 0
SM	6	1.3246	0.9881	1.6612	0.4131	0.2062	0.6200	0.1606	0.9252	0.9146	< 0.0001	0.5499	< 0

Table S4. Regression statistics of TL under the topography grouping. Parameter point estimates and 95 % lower and upper bounds were obtained from normal theory using the original data. Species' abbreviations are given in main text

Species	Number of blocks	Linear regression										Quadratic regression squared term	
		Slope			Intercept			RMSE	R^2	Adjusted R^2	P	P	Sign
		Estimate	Lower bound	Upper bound	Estimate	Lower bound	Upper bound						
RO	8	0.2603	-0.8830	1.4037	0.6922	0.1476	1.2369	0.1035	0.0492	-0.1093	0.5976	0.9385	> 0
CO	8	1.3387	0.6497	2.0277	0.2792	0.0729	0.4856	0.1997	0.7902	0.7552	0.0031	0.4000	< 0
RM	7	1.6282	1.1771	2.0793	0.3877	0.2618	0.5135	0.1282	0.9451	0.9341	0.0002	0.7591	> 0
WO	8	1.4165	0.7250	2.1081	0.5110	0.3252	0.7168	0.1808	0.8072	0.7751	0.0024	0.8928	> 0
EH	6	1.3702	0.7921	1.9483	0.5899	0.2542	0.9257	0.2524	0.9154	0.8943	0.0028	0.1971	< 0
BB	6	1.8885	-0.6623	4.4393	0.5814	-0.5242	1.6870	0.2425	0.5137	0.3921	0.1090	0.1489	< 0
SM	7	1.0893	0.3289	1.8496	0.3068	-0.0636	0.6771	0.1949	0.7306	0.6767	0.0143	0.0756	< 0