

Variant Scaling Relationship for Mass-Density Across Tree-Dominated Communities

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Abstract

The past few decades have seen a resurgence of interest in biological allometry. Specifically, a number of recent studies has suggested a $-4/3$ invariant scaling relationship between mass and density that is universally valid for tree-dominated communities, regardless of their phyletic affiliation or habitat. In the present study, we test this scaling relationship using a comprehensive forest biomass database, including 1 266 plots of six biomes and 17 forest types across China. The present study shows that the scaling exponent of the mass-density relationship varies across different tree-dominated communities and habitats. This great variability in the scaling exponent makes any generalization unwarranted. Although inappropriate regression methods can lead to flawed estimation of the scaling exponent, inconsistency of theoretical framework and empirical patterns may have undermined the validity of previous work.

Key words: allometry; mass-density; scaling relationship; trees.

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Allometric scaling has been one of the central topics in the development of modern ecology. A number of theoretical and empirical justifications for invariant scaling across terrestrial plant populations and communities has been given in the literature and the scaling exponent has been frequently claimed to be statistically indistinguishable from $1/4$ or its multiples (Enquist et al. 1998; Enquist and Niklas 2001, 2002; Niklas and Enquist 2001; Enquist 2003; Niklas et al. 2003). The recent burst of interest in the $3/4$ scaling “law” of metabolism with organism size has resulted in a series of generalizations (West et al. 1997; Enquist et al. 1998, 1999; West et al. 1999a, 1999b; Belgrano et al. 2002; Enquist 2002, 2003; Enquist and Niklas 2002; Ernest et al. 2003; Brown et

al. 2004; Savage et al. 2004b). One such generalization is that plant mass, M (i.e. aboveground biomass (M_{above}) or total mass (M_T) per individual) scales as the $-4/3$ power of the number of individuals, N , per unit area across tree-dominated communities, regardless of their phyletic affiliation, species attributes, and latitude (Enquist and Niklas 2001, 2002; Niklas et al. 2003).

However, lack of necessary explanations for contradictory conclusions and data preference de-emphasizes the importance of the above findings. The $-4/3$ scaling relationship for mass and density proposed by Enquist and Niklas (2001) related the average mass of trees, M_i , occurring in an i^{th} size class to the number of trees, N_i , in that class. The authors presented the empirical evidence for the -2 scaling power of N_i with the stem diameter of an i^{th} size class (D_i) only and reached their conclusion of $N_i \propto M_i^{-3/4}$ (i.e. $M_i \propto N_i^{-4/3}$) combining $N_i \propto D_i^{-2}$ with the $D_i \propto M_i^{3/8}$ prediction claimed from the “fractal volume-filling” theory of West et al. (1997, 1999; the WBE model). However, this $-4/3$ scaling relationship for M_i versus N_i for a size class is mathematically incompatible with the $-4/3$ scaling for M , the average individual mass, and N , the total number of individuals for a whole plot, because of the simple relationships that N is the sum of N_i and M is the sum of total biomass of different classes divided by N .

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Niklas et al. (2003) did show a direct validation for the $-4/3$ power of M_T to N for plots using the Cannell (1982) compendium data from tree-dominated stands. However, the criterion for the entry of data into the regression remains equivocal. For example, for the regression M_T versus N , the number of observations across angiosperm-dominated communities and across conifer-dominated tree communities is 668 and 325, respectively, but the regression of M_T to N for all communities was only based on 668 data points. Unfortunately, no justification for the selection of data was given. Compiling the Cannell (1982) data for tree plots with some small herbaceous plants, Enquist and Niklas (2002) show also a scaling exponent of -1.33 between M_T and N , but only 298 observations (less than 668) were put into the regression. In addition, because herbs tend to have smaller M_T and larger N than do trees, it can be expected that a value more positive than $-4/3$ is a reality for tree plots.

The statistical methodology also deserves scrutiny in the context of estimating the above scaling relationships. Two common regression methods, ordinary least square (OLS) and reduced major axis (RMA) were used in data analyses for deriving scaling exponents (Enquist and Niklas 2001, 2002; Niklas et al. 2003). The OLS method assumes there is no measurement error on independent variables and, thus, can be used if the purpose is only to predict one variable based on the other. However, RMA regression, treating the two variables in the same way, is more appropriate than OLS when the independent variable is measured with error (Sokal and Rohlf 1981; McArdle 2003). Both OLS and RMA assume a normal distribution of variables and estimate by minimizing the sum of squared residuals. Hence, estimators of the two methods are both sensitive to departures from the distributional assumption and outlying data points. Such limitations and lack of assumption test for the appropriateness of linear least squares methods undermine the reliability of the conclusions in the three above-mentioned papers.

In contrast, a semi-parametric approach without the assumption of normality, namely quantile regression (QR), also known as median regression given the quantile of 50%, could be far superior to least-squares methods under non-normal variable conditions (Neter 1996). The QR method estimates are based on minimizing sums of absolute residuals (Koenker and Bassett 1978) and, therefore, are free of normality assumption and also robust to the presence of outliers. Furthermore, several quantiles obtained with QR convey a more complete picture of the conditional distribution of the dependent variable than the single mean derived from a traditional least-squares approach using OLS or RMA. The $3/4$ scaling of M versus N was theoretically derived from the WBE model. The WBE model described vascular plants as a branching fractal object that fills space, so there should be an increasing efficiency of fractal networks in progressively larger trees. The model implies that different individuals that occupy the space of a stand as much as possible can be represented by their mass. Although there has been some skepticism about the accountability of fractal networks hypotheses in relationships of efficiency

versus size in large trees (Midgley 2001, 2003), nobody can deny the simple fact that the functional portion for space filling, indexed by its leaf area or the leaf mass, increased M_T with the development of a community (Osawa 1989, 1993; Weller 1989; Franco and Kelly 1998), which was quantified as leaf mass $\propto M^{3/4}$ (Enquist and Niklas 2002; Enquist 2003). Thus, M_T could be used as an approximate criterion for the degree of space filling in stands. Several scaling exponents of M_T versus N at the upper quantiles of M_T above the median could provide a comprehensive description of the scaling pattern for M_T versus N compared with a single value from either OLS or RMA. The above considerations stimulated us to introduce QR to the concerned calculation of scaling "laws".

Any relationship proposed as an ecological law or important inference should be thoroughly and carefully validated. Toward that end, herein we used the Chinese Forest Biomass Dataset (Luo, 1996), including 1 266 plots, six forest biomes and 17 main forest types across the entire country, to present an examination of the $-4/3$ of scaling exponent between M and N as claimed invariant across tree-dominated communities. We expediently follow the $-4/3$ scaling of M versus N as invariant in tree-dominated communities, as derived from Enquist and Niklas (2002) and Niklas et al. (2003), as our *a priori* expectation to evaluate whether these expectations can accord with our independent data. For a better comparison with the above papers, in addition to OLS and RMA, we used QR to compare results for consistency and to derive our conclusions. We calculate the scaling exponents of M_T versus N for each sub-dataset of six forest biomes types and the entire dataset by pooling all data. The aim of the present study was to determine whether there are invariant scaling relationships for mass and density at the stand level across tree-dominated communities with reference to diverse phylogenetic affiliation, latitude, and elevation.

Results and Discussion

As shown in Tables 1 and 2, there is no agreement on the expectation of $-4/3$ between the estimates for scaling exponent and confidence intervals (CI) by OLS and those by RMA. Because N compared with M_T within a given area can be counted more accurately in our dataset, the OLS results seemed to be preferred in this case (Niklas et al. 2003).

The OLS slopes vary from -0.938 to -1.34 across six biome types (Table 1). Among these, only for the result from boreal forest (-1.34) could the CI embrace $-4/3$, which contrasted with the six shallower slope estimates for the remaining datasets. In particular, the OLS slope estimate and the CI for the complete dataset could not meet our expectation of $-4/3$.

Compared with the OLS results, the observed exponents by RMA seem to be more favourable to $-4/3$ (Table 2). The expected exponent is supported by the estimates from three biomes, namely

Table 1. Observed scaling exponents for log₁₀-transformed data from the ordinary least squares regression statistics

| Biome type | Scaling exponent (SE) | 95% CI | Sampling size | <i>r</i> ² | Normality test | |
|--|-----------------------|----------------|---------------|-----------------------|-----------------------|----------|
| | | | | | <i>M</i> _T | <i>N</i> |
| Boreal forest | -1.340 (0.034) | -1.407, -1.273 | 248 | 0.864 | Failed | Failed |
| Temperate deciduous broadleaved forest | -0.938 (0.034) | -1.005, -0.872 | 301 | 0.723 | Passed | Passed |
| Subtropical evergreen broadleaved forest | -1.211 (0.038) | -1.286, -1.136 | 269 | 0.791 | Failed | Failed |
| Tropical rainforest and monsoon forest | -1.137 (0.205) | -1.588, -0.687 | 13 | 0.737 | Passed | Failed |
| Temperate coniferous forest | -1.025 (0.056) | -1.135, -0.915 | 154 | 0.691 | Passed | Failed |
| Subtropical coniferous forest | -1.169 (0.036) | -1.239, -1.099 | 281 | 0.794 | Failed | Failed |
| All data | -1.128 (0.022) | -1.171, -1.086 | 1 266 | 0.685 | Failed | Failed |

CI, confidence interval. SE, standard error; *M*_T, total biomass per individual; *N*, number of individuals per unit area.

Table 2. Observed scaling exponents for log₁₀-transformed data from the reduced major axis regression statistics

| Biome type | Scaling exponent (SE) | 95% CI | Sampling size | <i>r</i> ² | Normality test | |
|--|-----------------------|--------------------|---------------|-----------------------|-----------------------|----------|
| | | | | | <i>M</i> _T | <i>N</i> |
| Boreal forest | -1.441 (0.034) | -1.508, -1.375 | 248 | 0.864 | Failed | Failed |
| Temperate deciduous broadleaved forest | -1.103 (0.034) | -1.170, -1.037 | 301 | 0.723 | Passed | Passed |
| Subtropical evergreen broadleaved forest | -1.362 (0.038) | -1.437, -1.287 | 269 | 0.791 | Failed | Failed |
| Tropical rainforest and monsoon forest | -1.324 (0.205) | -1.774 9, -0.873 8 | 13 | 0.737 | Passed | Passed |
| Temperate coniferous forest | -1.234 (0.056) | -1.344, -1.124 | 154 | 0.691 | Passed | Passed |
| Subtropical coniferous forest | -1.312 (0.036) | -1.383, -1.242 | 281 | 0.794 | Failed | Failed |
| All data | -1.364 (0.022) | -1.406, -1.321 | 1 266 | 0.685 | Failed | Failed |

CI, confidence interval. SE, standard error; *M*_T, total biomass per individual; *N*, number of individuals per unit area.

subtropical evergreen broadleaved forest, temperate coniferous forest, and subtropical coniferous forest, as well as all data, but not by the estimates from the other three biomes. In particular, for boreal forest, the estimate of the scaling exponent by RMA (-1.441) and its CI (between -1.508 and -1.375) accord with -3/2, which was traditionally known as the exponent of the “-3/2 thinning law” (Yoda et al. 1963; Harper 1967; Gorham 1979; White 1985; Weller 1987a, 1989; Zeide 1987; Norberg 1988; Osawa 1989; Lonsdale 1990; Zeide 1991).

For tropical rainforest and monsoon forest, which have a limited distribution in China and, hence, the smallest sample size herein (Tables 1, 2), the CI estimated by either OLS or RMA contain both -4/3 and -3/2. Launching a correlation analysis shows that there is no significant relationship between sample size and slope estimate ($r^2 = 0.001$ and $P > 0.95$ for OLS; $r^2 = 0.020 2$ and $P > 0.79$ for RMA).

The values of scaling exponent estimated by RMA ranged from -1.103 to -1.441 (Table 2) over all the six tree-dominated community groups, with each value bigger than that determined by OLS. This is because the slope estimate of RMA is actually calculated by that of OLS divided by its corresponding correlation coefficient. We further performed a paired *t*-test to explore the effect of regression methods on the slope estimates of six independent datasets for biomes. As expected, the choice of different estimation methods (RMA or OLS) does make a significant difference in slope estimates (paired *t*-test $t = 10.428$, $P = 0.000 14$, $n = 6$,

normality satisfied). Thus, caution must be exercised when making inferences about the slope estimate from data using either RMA or OLS, particularly for those efforts over the validity of the invariant scaling exponents based on quite small differences in slope.

Both OLS and RMA have a limited suitability in our analysis because most of the bivariate data violated the normal distributional assumption. Among the seven listed datasets, only that of temperate deciduous broadleaved forest passed the normality test. However, the observed scaling exponents by OLS and RMA from this sole legitimate dataset (-0.938 and -1.103, respectively), as well as the related CI, both significantly contradict our expectation of -4/3.

The slope estimates by median regression fall between -1.324 and -0.936 across six biomes. Only the results from boreal forest can fit -4/3 well, whereas other datasets do not. Especially for across all 1 266 plots, the observed scaling exponent and its CI are significantly different from -4/3. A paired *t*-test for six pairs of slope values by different regression methods shows that the slopes estimated by median regression are significantly different from those estimated by OLS ($t = -7.33$, $P = 0.000 74$, $n = 6$, normality test passed), but not significantly different from the estimates obtained using RMA ($t = 0.454$, $P = 0.669$, $n = 6$, normality test passed). Without normality restrictions, median regression should have priority of consideration over OLS and RMA in the determination of the true value of slope. Therefore, so far there is no such

an invariant scaling relationship of $-4/3$ across six biomes that can be concluded by the above results and analysis.

Based on our datasets, are there other ways to reach the expected scaling of $-4/3$ for M_T versus N ? Our *a priori* expectation laid much predominant consideration on the “fractal volume-filling” theory of the WBE model (Enquist et al. 1998; Enquist and Niklas 2001, 2002; Niklas and Enquist 2001; Enquist 2003; Niklas et al. 2003). As its logical outcome, there should be an increasing efficiency of fractal networks in progressively larger trees (i.e. the bigger, the better). This has been quantified as the whole-plant resource use $Q \propto M_T^{3/4}$ (Enquist et al. 1998; Enquist and Niklas 2001, 2002; Niklas and Enquist 2001; Enquist 2003; Niklas et al. 2003). Therefore, herein we further take M_T to represent the degree of space filling in stands and use QR with quantiles of 0.75, 0.90, and 0.95 to explore the scaling relationships of M_T versus N at the higher M_T levels associated with the upper quantiles above the median (i.e. at above-average levels of community mass development; Table 4). Here, we are not trying to find the self-thinning or upper boundary line of M_T versus N (Osawa 1989; Weller 1990) or estimate effects of N as a limiting factor on different quantiles of M_T (Cade et al. 1999), but are simply trying to explore their scaling relationships for M_T versus N at the different

levels of M_T .

For six biomes and all data, estimates of slope for each quantile of M_T are statistically significant ($P < 0.001$). Among them, the slope estimates and 95% CI for 0.75 and 0.90 quantiles for boreal forest verified a $-4/3$ scaling exponent of M_T versus N . Combined with the result from median regression for the 0.5 quantile, the near parallelism of slope estimates seemingly suggests that the $-4/3$ scaling of M_T versus N exists at median and above-median levels of M_T and is kept consistent over the change of M_T that was caused by the community dynamics. However, it is also clear that for boreal forest the slope estimate and the CI with the 0.95 quantile of M_T accommodate both $-4/3$ and $-3/2$. Because the 0.95 quantile of M_T is close to the maximum (0.99), it seems to be supportive evidence for Midgley’s skeptic view on the WBE model’s prediction that large trees with a fully developed fractal system embody so much fractal essence such as $-4/3$ scaling (Midgley 2001, 2003). For subtropical coniferous forest, the slope estimate and CI of the 0.95 quantile contains only $-4/3$, but those at the 0.75 and 0.90 quantiles are significantly different from $-4/3$. For subtropical evergreen broadleaved forest, the estimates of the 0.90 and 0.95 quantiles could fit $-4/3$, but the 0.75 quantile estimate could not. For tropical rainforest and monsoon forest, the CI at the 0.75

Table 3. Observed scaling exponents for \log_{10} -transformed data from the median regression statistics

| Biome type | Scaling exponent (SE) | 95% CI | Sampling size | r^2 (pseudo) | P | Normality test | |
|--|--------------------------|----------------|------------------|-------------------|--------|----------------|--------|
| | | | | | | M_T | N |
| Boreal forest | -1.324 (0.039) | -1.400, -1.248 | 248 | 0.603 | <0.001 | Failed | Failed |
| Temperate deciduous broadleaved forest | -0.936 (0.050) | -1.034, -0.838 | 301 | 0.460 | <0.001 | Passed | Passed |
| Subtropical evergreen broadleaved forest | -1.227 (0.034) | -1.294, -1.161 | 269 | 0.555 | <0.001 | Failed | Failed |
| Tropical rainforest and monsoon forest | -1.234 (0.353) | -2.012, -0.456 | 13 | 0.437 | <0.001 | Passed | Failed |
| Temperate coniferous forest | -0.998 (0.065) | -1.126, -0.870 | 154 | 0.443 | <0.001 | Passed | Failed |
| Subtropical coniferous forest | -1.152 (0.041 4) | -1.234, -1.071 | 281 | 0.545 | <0.001 | Failed | Failed |
| All data | -1.156 (0.026) | -1.206, -1.106 | 1 266 | 0.428 | <0.001 | Failed | Failed |

CI, confidence interval. SE, standard error; M_T , total biomass per individual; N , number of individuals per unit area; r^2 (pseudo) indicates that it is not comparable with its least-square analogue because its calculation is based on median regression.

Table 4. Observed scaling exponents for \log_{10} -transformed data from quantile regression statistics

| Biome type | 0.75 Quantile | | 0.90 Quantile | | 0.95 Quantile | |
|---|----------------|----------------|-----------------|-----------------|----------------|----------------|
| | Slope estimate | 95% CI | Slope estimate | 95% CI | Slope estimate | 95% CI |
| Boreal forest | -1.273 (0.037) | -1.347, -1.200 | -1.314 (0.067) | -1.446, -1.182 | -1.256 (0.156) | -1.563, -0.949 |
| Temperate deciduous broadleaved forest | -1.008 (0.062) | -1.131, 0.886 | -1.019 (0.053) | -1.123, -0.916 | -1.047 (0.110) | -1.263, -0.832 |
| Subtropical evergreen broadleaved forest | -1.145 (0.065) | -1.274, -1.016 | -1.240 (0.1007) | -1.438, -1.0412 | -1.167 (0.161) | -1.485, -0.850 |
| Tropical rainforest and monsoon forest | -1.189 (0.106) | -1.423, -0.956 | -1.206 (0.043) | -1.301, -1.111 | -1.206 (0.028) | -1.267, -1.145 |
| Temperate coniferous forest | -0.993 (0.086) | -1.164, -0.823 | -0.885 (0.147) | -1.175, -0.595 | -1.061 (0.310) | -1.673, -0.450 |
| Subtropical coniferous forest | -1.152 (0.071) | -1.292, -1.012 | -1.170 (0.059) | -1.287, -1.053 | -1.148 (0.135) | -1.413, -0.883 |
| All data | -1.222 (0.027) | -1.274, -1.17 | -1.164 (0.035) | -1.233, -1.095 | -1.191 (0.062) | -1.313, -1.070 |

CI, confidence interval. SE, standard error; M_T , total biomass per individual; N , number of individuals per unit area.

quantile includes $-4/3$, whereas the CI at the 0.90 and 0.95 quantiles does not. For temperate coniferous forest, the 0.95 quantile estimate contains $-4/3$, but also $-3/2$, and the slope estimates at the 0.75 and 0.90 quantiles are significantly shallower than $-4/3$ (Table 4). Last, but not least, the slope estimates of all the regression quantiles for all data could not meet our *a priori* expectation of $-4/3$ scaling for M_T versus N .

The majority of QR results cannot validate the $-4/3$ scaling between M_T versus N . Because no assumption is violated and no information contained in the data is lost, the QR estimates can be more objective and more efficient than the commonly used methods of OLS and RMA. **If we assume $-4/3$ is an authentic scaling relationship across all the tree-communities investigated at the status called "equilibrium" (Enquist et al. 1998; Niklas et al. 2003), we have to admit our empirical results are very inconsistent and hard to explain according to the $-4/3$ scaling expectation and the relevant theory.**

This inconsistency mimics the long history of controversies over the validation of M versus $N^{-3/2}$ for the phrase termed "inter-specific size-density relationship" (White 1985; Weller 1989; Franco and Kelly 1998). This relationship between mass and density has long been a subject of intensive investigation over recent decades since Yoda et al. (1963) first formulated what they called "the $3/2$ power law of self-thinning" for a mono-specific population. Several early studies summarized that M versus $N^{-3/2}$ holds valid over seven orders of magnitude of N and almost 10 orders of magnitude of M (Gorham 1979; White 1981, 1985; Westoby 1984). A mathematical equivalent of M versus $N^{-3/2}$ is B versus $N^{-1/2}$ because $M = B/N$ (where B is total stand biomass per area). For logarithmic B versus logarithmic N , Gorham (1979) estimated a -0.49 slope from a diverse dataset for 65 plant stands including moss, ferns, and trees from angiosperms and gymnosperms, and gave a nearly ideal agreement with the hypothetical $-1/2$ value (Gorham 1979), whereas from the subset of 19 stands a less ideal slope of -0.43 was obtained. Both were not significantly different from the $-1/2$ value (Weller 1989). White (1980) reported the exponents for M versus N with the range between -1.8 and -1.3 (White 1980, 1985; Weller 1987a) considered examples of the same quantitative rule, although there was no objective basis to claim that -1.8 and -1.3 are close to -1.5 (White 1980, 1985; Weller 1987a). The $-3/2$ power rule was then regarded as the only law in plant ecology (Harper, cited in Hutchings 1983). However, it was later frequently relegated to a position where the fundamental validity of the rule itself was in suspension (Weller 1985, 1987a, 1987b, 1989, 1990, 1991; Zeide 1987, 1991; Lonsdale 1990). Several re-evaluations of this rule concluded that the exponent was much more variable than previous authors had claimed (Weller 1985, 1987a, 1987b, 1989, 1990, 1991; Zeide 1987, 1991; Lonsdale 1990). For example, Weller (1987a) once calculated 75 B versus N scaling exponents for mono- and multi-specific stands and found that in logarithmic plots the slope estimates ranged from -0.204 to -3.76 with a mean of -0.804 and that the slope

estimates differed significantly among plant groups, including herbaceous monocots, herbaceous dicots, temperate angiosperm trees, temperate gymnosperm trees, *Eucalyptus* trees, and tropical angiosperm trees (Weller 1985, 1987a, 1987b, 1989, 1990, 1991; Zeide 1987, 1991; Lonsdale 1990). Compiling the first database that was larger and more diverse than that of Gorham (1979), from 370 stands Weller (1989) presented an estimate of -0.326 for all data, which was significantly different from $-1/2$ but not from $-1/3$, whereas the subset of 154 stands gave -0.227 , significantly different from both $-1/2$ and $-1/3$, which was mostly cited as evidence to support objection to the idea of a single, ideal exponent for B versus N (Weller 1985, 1987a, 1987b, 1989, 1990, 1991; Zeide 1987, 1991; Lonsdale 1990). Using a more selective selection procedure for Weller's data to accommodate admissible 219 thinning stands, Lonsdale (1990) estimated a B versus N slope of -0.379 with a CI between -0.409 and -0.350 , which was afterwards regarded as supportive evidence for the $-4/3$ M versus N scaling exponent, although the CI did not include the expected $-1/3$ (Enquist et al. 1998; Enquist 2002; Niklas et al. 2003). Applying the criterion of a single data point for each species and selecting data of maximum B with maximum N as possible, Franco and Kelly (1998) claimed slope values for B versus N were consistent with $-1/3$ among four datasets used for independent contrasts (i.e. complete data, angiosperms only, dicots only, dicots without Asteridae) and a complete dataset by forcing and not forcing the intercept through the origins of axis. However, among the only four CI for the slope of $\log B$ versus $\log N$ (Franco and Kelly 1998, table 1), there are somehow two unbelievably large values, namely -0.35 ± 0.733 and -0.349 ± 0.166 , and, due to tiny sample sizes of less than 17, their claims were generally very weak. Compiling 251 data points from Yoda et al. (1963), Gorham (1979), Weller (1987, 1989), Lonsdale (1990) and some unknown studies, Enquist et al. (1998) developed an empirical finding of -1.341 that fit well with $-4/3$ for M versus N . Combined with the partial results from Weller (1987, 1989), and Lonsdale (1990), Enquist et al. (1998) was considered strong empirical evidence of a $-4/3$ scaling exponent for M versus N , the WBE model's derivation. In the wake of this, Belgrano et al. (2002), Enquist and Niklas (2002), and Niklas et al. (2003) consecutively showed their empirical validity favouring M versus $N^{-4/3}$.

Reviewing the published empirical evidence for M versus N exponents from the aforementioned individual studies, we found that the empirical patterns were highly subject to the vagaries of data choice, data quality, approaches of statistical analysis used, and theoretical basis. To give a complete and detailed description for this miscellaneous picture is beyond the scope of the present paper. In short, the variability of empirical evidence from different authors actually leaves considerable room for doubt that there is a universal exponent for M versus N or B versus N .

We would rather draw attention to a long-neglected methodological pitfall in which the aforementioned efforts for exponent validation have been trapped. There are two free parameters in

the regression equation of logarithmic mass-logarithmic density, namely slope and intercept. Two types of validating efforts, $-3/2$ from Euclidian geometric considerations and $-4/3$ from fractal space-filling theory, both focused on the slope to derive their explanations and generalizations. They both only expected data could fit with an exact value of slope and did not treat intercept in a like manner. However, in scatter plots and for the same data, just by swinging the intercept one could obtain a range of slopes that could fit data well. Based on our dataset for boreal forests, we demonstrate this problem through a contrived example using the popular regression method OLS. We obtained several slope values by changing intercepts. The results are presented in Table 5. Overall, we can see all the regression lines can fit the dataset well ($r^2 > 0.66$, usually $r^2 > 0.83$, and $P < 0.0001$). When the constrained intercept changed from 3 to 4, the corresponding slope estimates varied from -1.253 to -1.597 ($r^2 > 0.83$ and $P < 0.0001$). Among them, the -1.500 slope attained by forcing the intercept to be 3.717 presented an ideal agreement with $-3/2$, the -1.34 slope estimated by a constrained 3.253 intercept was consistent with $-4/3$, and the -1.253 slope corresponding to an intercept of 3.00 was indistinguishable from $-5/4$ (which is not unexpected if the fifth dimension, such as time or thought (He and Zhang 2004) is added into the four-dimensional models, such as in Blum (1977) or the WBE model). All three regression lines share a high correlation coefficient (r^2) at about the same level. We then launched Fisher's z transformation to compare the three concerned r^2 values. Between all the r^2 pairs, the absolute values of μ are less than $\mu_{(0.05, \text{two-tailed})}$ and exhibit no statistical differences (Table 6). Among the three lines with seemingly different slopes, there is no reason to infer that one fit the transformed data better than the rest. As expected, the t -test also showed that there is no statistical difference between the three slope values. Therefore, there is no reason to overinterpret the small difference of regression lines and slope estimates in this context. It may be worth noting that in the extreme case in Table 5, the regression equation with a much shallower slope (-0.221) attained by suppressing the intercept to zero could still satisfy the requirements for statistical significance ($r^2 = 0.663$ with $P < 0.001$). In a broader sense, if we take different measurements for goodness-of-fit there is no regression line of

best fit for the data (McGill 2003). Our results herein imply that most data cited previously in support of the overexpected exponent for M versus N ($-3/2$ or $-4/3$) could probably fit either of them "well".

We further analyzed Weller's independent datasets for intercepts and slopes from 27 tree species of 264 plots under thinning conditions (Weller 1987a, table 5) and found a very strong correlation between them (i.e. intercept = 0.920 4 slope + 5.148 3, with $r^2 = 0.829$, $n = 264$, and $P < 0.001$). This indicates that the intercept would be determined by a certain value of the slope in the cases concerned. If we take either $-4/3$ or $-3/2$ as a general rule applied to a variety of communities, we automatically obtain a certain intercept that varies little across these cohorts. Interestingly, Enquist and Niklas (2002) presented a regression line of M_T versus $N^{-1.33}$ with a discernable intercept of 3.7 or so (Enquist and Niklas 2002, fig. 5a), which roughly coincides with the prediction of the above equation of 3.9. The highly correlated relationship between intercept and slope implies that if we accept a unifying slope, at the same time we have to accept a fairly unifying intercept. Is it imaginable for so many diverse clades of tree-dominated communities to have a unifying equation in a real world?

The earliest, somewhat alternative, and strictly defined version for the relationship of $M \propto N^{-4/3}$ is N_{\max} , the maximum number of individuals that can be supported per unit area, scaled as the exponent of $-3/4$ to average mass of individuals within a given area (Enquist et al. 1998). Although N_{\max} was mainly derived from monospecific stands, it was, indeed, somehow cited as supportive evidence in other situations, such as considering size classes and communities, by Enquist and Niklas (2001) (see page 655 and page 656 in Enquist and Niklas 2001, pp. 655–656; Enquist 2002, p. 1056; Enquist and Niklas 2002, p. 1518). Following the WBE model's prediction, the whole-plant resource use for an i th individual, Q_i , scales as $3/4$ power for M_i , the mass for an i th individual and Enquist et al. (1998) showed empirical evidence in support of $Q_i \propto M_i^{3/4}$. The authors then related N_{\max} to Q , the average rate of resource use per individual, and R , the total rate of resource use of all individuals, using the equation $R \approx N_{\max} Q \propto N_{\max} M^{3/4}$, where M referred to average mass of individuals within a given area. At "equilibrium", when R is "constant", giving $R \approx N_{\max} Q$

Table 5. Slope estimates by constraining intercepts for the boreal forest subset

| Intercept statistics | | | Slope statistics | | | r^2 | N |
|----------------------|---------|----------|------------------|---------|----------|---------|-----|
| Value (forced) | SE | P | Value | SE | P | | |
| 0 | NA | NA | -0.221 | 0.010 | <0.000 1 | 0.663 5 | 248 |
| 3 | 0.098 9 | <0.000 1 | -1.253 | 0.034 3 | <0.000 1 | 0.861 | 248 |
| 3.253 | 0.097 6 | <0.000 1 | -1.340 | 0.033 8 | <0.000 1 | 0.864 | 248 |
| 3.717 | 0.102 | <0.000 1 | -1.500 | 0.035 4 | <0.000 1 | 0.852 | 248 |
| 3.783 | 0.103 3 | <0.000 1 | -1.523 | 0.035 8 | <0.000 1 | 0.848 | 248 |
| 4 | 0.108 6 | <0.000 1 | -1.597 | 0.037 7 | <0.000 1 | 0.832 | 248 |
| 5 | 0.148 1 | <0.000 1 | -1.941 | 0.051 4 | <0.000 1 | 0.688 | 248 |

NA, not applicable. SE , standard error; N , number of individuals per unit area.

Table 6. Significance test for the difference between r^2 values

| Statistics | Contrasts of r^2 values | | |
|-----------------------------------|---------------------------|----------------|----------------|
| | 0.861 vs 0.864 | 0.861 vs 0.852 | 0.864 vs 0.852 |
| Z | 1.643 vs 1.655 | 1.643 vs 1.609 | 1.655 vs 1.609 |
| $\mu_{(0.05, \text{two-tailed})}$ | 1.96 | 1.96 | 1.96 |
| μ | -0.133 | 0.376 | 0.509 |

$z=0.5 \ln(1+r/1-r)$, $|\mu| < \mu_{(0.05, \text{two-tailed})}$ indicates there is no significant difference between r^2 values.

$\propto N_{\max} M^{3/4}$, their expected result then yields $N_{\max} \propto M^{-3/4}$, as the authors stated (Enquist et al. 1998; Enquist 2002, 2003). They actually assumed $Q_i \propto M^{3/4}$ was equal to $Q \propto M^{3/4}$. However, Enquist et al. (1998), the most-cited original paper giving $Q_i \propto M_i^{3/4}$ among all, only showed an empirical result to validate $Q_i \propto M_i^{3/4}$, not that of $Q \propto M^{3/4}$. Confusing the two expressions and the relevant implications is not mathematically correct (Torres et al. 2001). Interestingly, Niklas and Enquist (2001) demonstrated an empirical example that the average value of biomass production rate for all individuals within a plot (G) scaled as $3/4$ power of M and G was assumed as "... a reasonable surrogate measure of the rate of resource use per individual Q ". If Enquist et al. (1998) did verify $Q_i \propto M_i^{3/4}$ and Niklas and Enquist (2001) verified $Q \propto M^{3/4}$, the two relationships are, in fact, not mathematically equivalent and cannot hold true together so the question then arises, which one is correct? The elusiveness of the question is not appropriate for the present paper focusing on the very subtle differences of an exponent burdened with heavy controversies with a unifying value of $2/3$ or $3/4$. Therefore, the semitheoretical derivation for $M \propto N^{-4/3}$ from $Q_i \propto M_i^{3/4}$ in Enquist et al. (1998) is highly questionable.

One of the most intriguing concepts in the context used to marry the two functions $Q \propto M^{3/4}$ and $R = N_{\max} Q = \text{constant}$ to reach the $-4/3$ scaling of M versus N is "equilibrium" (Enquist et al. 1998; Enquist 2003; Brown et al. 2004), which was assumed to be related to a constant R and N_{\max} and that can be supported per unit area and therewith rates of limiting resource supply R (Niklas et al. 2003). This imaginary concept is valuable for reasoning out a theoretical framework such as the so called "resource-based thinning theory" (Brown et al. 2004). Similar imaginary separations have proven to be fruitful in other branches of science. However, here it is not an operational and practicable standard for compiling a legitimate dataset to verify their theoretical prediction. Especially for survey data, there are no objective criteria to judge whether a real stand indeed arrives at N_{\max} by limiting resource supply. It is impossible to prove that the site quality of a given population is identical with that of a "equilibrium population density", a further concept introduced by Brown et al. (2004). As yet, the evidence of Enquist et al. (1998), Belgrano et al. (2002), Enquist and Niklas (2002), and Niklas et al. (2003) supporting $M \propto N^{-4/3}$ for terrestrial plants does not present explanations as to how the stands selected could be meet the requirement of "equilibrium". There is also no discernable information for the stands reaching N_{\max} in Cannell (1982), the datasource frequently cited by Enquist and

Niklas (Enquist et al. 1998; Enquist and Niklas 2001; Enquist 2002; Niklas et al. 2003).

Perhaps the fatal flaw of the logical framework leading to the $-4/3$ "law" or what is called "resource-based thinning theory" (Brown et al. 2004) is that, in different situations, they ambivalently input inconsistent meanings to free parameters in order to flex their model. In order to have $N_{\max} = \text{constant} M^{-3/4}$ and, hence, $N_{\max} \propto M^{-3/4}$, as the authors stated (Enquist et al. 1998; Enquist 2002, 2003), they first had $R \approx N_{\max} Q \approx N_{\max} C_B M^{3/4}$, where C_B was an allometric constant reflecting tissue-specific metabolic demand. However, they subsequently assumed $R = N_{\max} Q = N_{\max} C_B M^{3/4} = \text{constant}$ at "equilibrium" and reached $N_{\max} = (R/C_B) M^{-3/4}$, and, hence, $N_{\max} \propto M^{-3/4}$ because C_B was also constant for a certain monospecific stand. These analyses were typically conducted at the level of a single plot. Then, in Enquist (2002), the author found there was little variation in C_B that had been proved by previous studies (Niklas 1994; Enquist et al. 1999; Niklas and Enquist 2001) "... between forest trees and even across major plant taxa" (Enquist 2002). If R varies little between different cohorts too, then that means R/C_B , the intercept in the logarithmic plot of N_{\max} versus M , will be more close to constant, and $N_{\max} \propto M^{-3/4}$ will be tenable. However, Gillooly et al. further introduced the variable T , "biological relevant temperature", into the model (Gillooly et al. 2001; Savage 2004; Savage et al. 2004a) to flex C_B in the metabolic scaling relationship of $Q = C_B M^{3/4}$ (for a good understanding, note that the relevant authors used different symbols to express Q and C_B in the previous equation in their papers), giving $C_B = f(T) = i_0 e^{-E/kT}$, where i_0 , E , and k , but not T , were all constants and T was allowed to change between 0 and 40°C. In this case, only if $R = \text{constant} i_0 e^{-E/kT}$ would R/C_B be constant and $N_{\max} \propto M^{-3/4}$ could be still tenable. As yet, there has been no theoretical or empirical evidence supporting $R = \text{constant} i_0 e^{-E/kT} = \text{constant} C_B$; thus, the equation $N_{\max} = (R/C_B) M^{-3/4}$ becomes $N_{\max} = f(T) M^{-3/4}$ and then $N_{\max} \propto M^{-3/4}$ could not hold true. Furthermore, $N_{\max} = f(T) M^{-3/4}$ means T was an unmeasured variable in their earlier curve-fitting efforts for data between N_{\max} and M , either by OLS or by RMA in previous studies (Enquist et al. 1998; Belgrano et al. 2002; Enquist 2002, 2003; Niklas et al. 2003), and the relationship between N_{\max} and M would have been confounded with the effects of T on M and the slope estimate would have been biased, because least squares estimation based on mean function actually averages the effects of all the measured and unmeasured independent variables on the dependent variable (Rosenbaum 1995; Cade et al. 1999; Cade and Noon 2003). So, the supportive claim of a $-3/4$ exponent of N_{\max} versus M without considering the variable of T in previous studies (Enquist et al. 1998; Belgrano et al. 2002; Enquist 2002, 2003; Niklas et al. 2003) indicated just the opposite, that the true scaling pattern of N_{\max} versus M was not in accord with $-3/4$. Therefore, if the finding of Gillooly et al. (2001) of $C_B = f(T) = i_0 e^{-E/kT}$ and the attached strong evidence was true, then not only the underlying theoretical framework for derived from the WBE model, on which $N_{\max} \propto M^{-3/4}$ was based, but also the empirical evidence of Enquist

and Niklas (Enquist et al. 1998; Enquist 2002, 2003; Niklas et al. 2003) previously supporting $N \propto M^{-3/4}$ would probably not be valid.

Our *a priori* expectation of a 4/3 scaling between M versus N as invariant in tree-dominated communities now rests on shaky ground. Setting aside the implications burdened with ecological theory, this relationship is of great practical significance because it links the final product of forest management, namely biomass, with the most manageable stand variable, tree density, and facilitates the determination of attainable biomass. However, it cannot be hinged simply on a certain exponent. The analysis presented implies that it is impossible to describe such a variant relationship with the help of only two coefficients, one of which has been hard-pressed to be a universal constant. The persistence of the efforts to ascertain the existence of a universal constant probably reveals a typical mode of our thinking and its missettings: it seems that we are much more inclined to see constancy and unity, which provide immediate, if simplistic, solutions rather than the variability and diversity that need further exploration for achieving a more comprehensive understanding.

Conclusions

We have demonstrated the variant scaling relationships of M_T versus N for six biome types and for the complete dataset. Most of the estimated exponents and CIs, by median regression or QR, are inconsistent not only with $-4/3$, but also with $-3/2$. All the above analyses point to one conclusion: that the scaling exponent between N and M is not a unifying value across different tree-dominated communities and habitats. The present study shows that the scaling relationships of plant mass and density are quite different from $-3/2$ or $-4/3$. Inappropriate regression methods will lead to wrong conclusions on exponent estimation. Inconsistency of theoretical framework and empirical pattern undermine the reliability of extant results of the 4/3 power rule of mass and density. Therefore, it is almost impossible that a scale invariant property is universally valid for all plots, regardless of their phyletic affiliation or habitat.

Materials and Methods

Data source

The Chinese Forest Biomass Dataset for standing community biomass and productivity was originally extracted from the PhD dissertation of Luo (1996). Most of these data were obtained directly from inventories of the Forestry Ministry of China between 1989 and 1993. The rest of the data were collected from published forest reports, as well as from over 60 Chinese journals (including *Journal of Integrative Plant Biology* (formerly *Acta Botanica Sinica*), *Acta Phytocologica Sinica*, *Acta Ecologica Sinica*, *Chinese*

Journal of Ecology, *Forestry Science of China* etc.) covering the past 20 years. The dataset includes monospecific tree stands and communities composed of mixed tree species ranging between 18 and 53°N latitude, elevations of 10 and 4 240 m above sea level, and tree densities of 89 and 20 800 individuals per hectare. All these data are distributed among six biomes and 17 major forest types of China (Tables 1–4). For each community, the site name, latitude, longitude, elevation, tree density, total annual production, total biomass, and total aboveground biomass for trees (Luo 1996) are reported. We computed M_T for a representative (average) tree in each community by dividing the total standing biomass for trees by N . A detailed description on the methodology of biomass measurement and density estimate for the dataset can be found in Luo (1996), as well as in the English literature (Ni et al. 2001).

Protocol

We used STATA version 8.0 (4905 Lakeway Drive, College Station, Texas 77845, USA) for OLS and QR, whereas the RMA was performed using RMA version 1.14b (<http://www.bio.sdsu.edu/pub/andy/rma.html>). All data were \log_{10} transformed to ensure linearity and homoscedasticity. Because the measurement error for N was negligible compared with that for M_T , OLS was preferred for the exponent estimation of M_T versus N , whereas RMA was less efficient than OLS in this case (Sokal and Rohlf 1981; McArdle 2003). The unbiased estimates of OLS and RMA both depended on the assumption of normally distributed random variables, which was not tested when the two methods were applied in all relevant studies (Enquist and Niklas 2001, 2002; Niklas et al. 2003). For a wide range of non-normal data, QR is more appropriate than OLS and RMA because the conditional median is more efficient than the least squares estimator (Koenker and Bassett 1978). With these caveats in mind, and for the purposes of a well-put comparison, we used OLS, RMA, and median regression (QR with the 0.5 quantile) in the analysis of M_T versus N . We also conducted a Shapiro-Wilk normality test for the transformed data in order to evaluate the efficiency of estimation results. Statistical problems of artificially inflated correlations from using mean mass values against density would not bias our analysis because, the real measurement of the M_T of trees is more original than that of the total standing mass (Luo 1996; Ni et al. 2001). An alpha level of 0.05 was used to test the significance of all results.

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