Research

Tree size distributions in an old-growth temperate forest

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Despite the wide variation in the structural characteristics in natural forests, tree size distribution show fundamental similarities that suggest general underlying principles. The metabolic ecology theory predicts the number of individual scales as the −2 power of tree diameter. The demographic equilibrium theory predicts tree size distribution starting from the relationship of size distributions with growth and mortality at demographic equilibrium. Several analytic predictions for tree size distributions are derived from the demographic equilibrium theory, based on different growth and mortality functions. In addition, some purely phenomenological functions, such as polynomial function, have been used to describe the tree size distributions. In this paper, we use the metabolic ecology theory, the demographic equilibrium theory and the polynomial function to predict the tree size distribution for both the whole community and each species in an old-growth temperate forest in northeastern China. The results show that metabolic ecology theory predictions for the scaling of tree abundance with diameter were unequivocally rejected in the studied forest. Although these predictions of demographic theory are the best models for most of the species in the temperate forest, the best models for some species (*Tilia amurensis, Quercus mongolica* and *Fraxinus mandshurica*) are compound curves (i.e. rotated sigmoid curves), best predicted by the polynomial function. Hence, the size distributions of natural forests were unlikely to be invariant and the predictive ability of general models was limited. As a result, developing a more sophisticated theory to predict tree size distributions remains a complex, yet tantalizing, challenge.

Tree size distributions – the number of individuals that fall within each tree size class – vary considerably in forests (Hitimana et al. 2004, Coomes and Allen 2007). Various factors, such as competition for resources, regeneration patterns, disturbances, environmental conditions, irregular or seasonal climatic events account for the variation of tree size distributions in forests around the world (Denslow 1995, Coomes et al. 2003, Webster et al. 2005). Thus, tree size distributions have often been used in assessing the effect of disturbance within forests (Hett and Loucks 1976, Denslow 1995, Baker et al. 2005, Coomes and Allen 2007), in describing successional pathways and structural development (Goff and West 1975, Poorter et al. 1996, Zenner 2005), and in predicting future forest stand structure (Feeley et al. 2007).

Although tree size distributions vary widely among natural forests they show basic similarities that may suggest general underlying principles. For example, reverse-J shape diameter distributions (Hough 1932, Robertson et al. 1978, Kohyama 1986, Niklas et al. 2003) and approximate negative exponential distributions (Meyer 1952, Goff and West 1975, Manion and Griffin 2001, Hitimana et al. 2004) have often been ascribed as an emergent property of natural forests in the absence of disturbance, or on scales that average over a representative sample of disturbance. Early studies were mostly focused on describing these distributions without further consideration of underlying

generating mechanisms (Gates and Nichols 1930, Bailey and Dell 1973, West et al. 1981, Lorimer and Krug 1983, Kohyama 1986). Recently the metabolic theory has been used to explain the distributions based on the assumptions that individuals grow until they are limited by the resources supplied from the environment (Enquist et al. 1998, West et al. 1999, Brown 2004). The metabolic theory predicts the number of individuals scales with −2 power of tree diameter (Enquist and Niklas 2001). Although this relationship was found to hold true in several forests (Enquist and Niklas 2001), the reanalysis of the data of Enquist and Niklas (2001) shows inconsistent results at large tree sizes (Coomes et al. 2003).

In addition, other researchers consider the size distribution of a natural forest as a property that emerges from the demographics of individuals and therefore should be predictable from tree growth, mortality and recruitment processes (Kohyama et al. 2003, Muller-Landau et al. 2006, Coomes 2006, Coomes et al. 2007). They developed a demographic equilibrium theory to understand tree size distribution starting from the relationship of size distributions with growth and mortality. Muller-Landau et al. (2006) used the relationship to derive a variety of tree size distributions, such as negative exponential distribution, power distribution and Weibull distribution, based on various combinations of growth and mortality scaling functions. Although the negative exponential function,

Weibull function and power function, were well known in forestry for modeling tree size distribution (Bailey and Dell 1973, Leak 1975, Hett and Loucks 1976, Lorimer and Krug 1983, Nord-Larsen and Cao 2006), there has not been any serious theories proposed to explain their geneses. By comparing the fits of the metabolic ecology and demographic equilibrium predictions using data from 14 large-scale tropical forest plots, Muller-Landau et al. (2006) found that the observed tree size distributions dramatically deviated from the predictions of metabolic theory, but were often consistent with the demographic predictions. With respect to these demographic equilibrium predictions, negative exponential distribution and power distribution were almost always inferior to the Weibull function. Furthermore, some other statistical functions, such as the polynomial function, have been used to fit tree size distributions in different forests (Kohyama 1986, Zenner 2005). However, the applications of these functions are a purely phenomenological exercise, lacking theoretical basis.

Community-wide tree size distributions in forests are not sufficient to give a detailed understanding of forest structure. Many old-growth forests around the world are characterized by a multilayered structure and high variability in tree sizes among individual species. Muller-Landau et al. (2006) found that tree size distributions in some forests varied significantly in different canopy layers. In addition, the tree size distribution for individual species often differs from the whole-community size distribution (Lorimer and Krug 1983, Kohyama 1986). Relatively little is known about how or why these distributions vary within each species and whether the variations are dependent on life history traits (i.e. family and shade-tolerance characteristics) or other factors.

This study conducts an analysis of tree size distribution both for the whole community and each species in an old-growth temperate forest in northeastern China. Tree size is measured by the diameter at breast height (DBH). We attempt to test whether the metabolic ecology theory (power function with exponent −2), the demographic equilibrium theory (negative exponential, power, and Weibull function) and the purely statistical model (i.e. polynomial function) applied to trees growing naturally in the temperate forest, and to evaluate which function produces the best prediction with the observed tree size distributions. We also examine whether the tree size distributions for each species are dependent on their life history traits. This approach not only provides a relatively comprehensive understanding of the size distributions in old-growth temperate forests, but also a sound scientific basis for temperate forest management.

Study area and methods

Study area

The study site is located in the Changbai Nature Reserve, which was established along the border of China and North Korea extending from 127°42′ to 128°17′E and 41°43′ to 42°26′N. The reserve was first established in 1960 and is one of the largest biosphere reserves in China. It has been spared from logging and other severe human disturbances due to its remoteness and inaccessibility to the general public before establishment of the reserve. Changbai Nature Reserve joined the World Biosphere Reserve Network under the UNESCO Man and the Biosphere Programme in 1980. The reserve is about 200 000 ha in size with an elevation ranging from 740 m to 2691 m at the summit of Changbai Mountain on the Chinese side. Changbai Mountain is the highest mountain in northeastern China and is the head of three large rivers (the Songhua, Yalu and Tumen) in the northeastern provinces. Topographic features differ on the four slopes of the mountain, with the northern slope being relatively moderate (average slope <3%) and other slopes being relatively steep (average 10%). The area has a temperate, continental climate, with long, cold winters and warm summers. Annual mean temperatures vary from 7.3°C in the lowest reaches of the reserve to 2.8°C near Sky Lake (the volcanic crater lake) on the mountaintop, and annual mean precipitation varies from 750 to 1340 mm.

In 2004, a 25 ha old-growth temperate forest plot of 500 × 500 m was established in Changbai Nature Reserve (Fig. 1). Within the plot, all free-standing trees and shrubs at least 1 cm in DBH were identified, tagged and mapped, and their geographic coordinates were recorded following a standard field protocol (Condit 1998). At the study site, the terrain is relatively gentle. The elevation ranges from 791.8 m to 809.5 m, and mean elevation is 801.5 m. There were 38 902 stems, belonging to 52 species and 18 families (Hao et al. 2008, Wang et al. 2008a, 2008b). Species abundance varied greatly from 1 to 7381 individuals. Among the 52 species, there were 22 with more than 100 individuals, and 12 of 18 families were represented by more than 100 individuals. Vertically, the old-growth temperate forests are stratified into three vegetation layers and species occupy different canopy levels at maturity. Thus, the tree species guilds (groups) were easy to distinguished, such as overstory, midstory and understory tree species (Table 1).

Methods

Metabolic ecology theory
The theory assumes that resources consumed by all individuals in a community and the resources supplied from the environment are in balance (Enquist and Niklas 2001). The number of individuals scales as the −2 power of tree diameter:

$$f(D) = cD^{-2} \qquad (1)$$

where f(D) is the number of individuals in a given area, D is the individual diameter, and c is a normalization factor that may vary with organism type and communities.

Demographic equilibrium theory
The theory assumes that tree size distributions can be understood as the simple demographic consequence of size-dependent variation in growth and mortality (Coomes et al. 2003, Kohyama et al. 2003). The growth (g(D)), mortality (m(D)) and the tree size distribution (f(D)) are interrelated as:
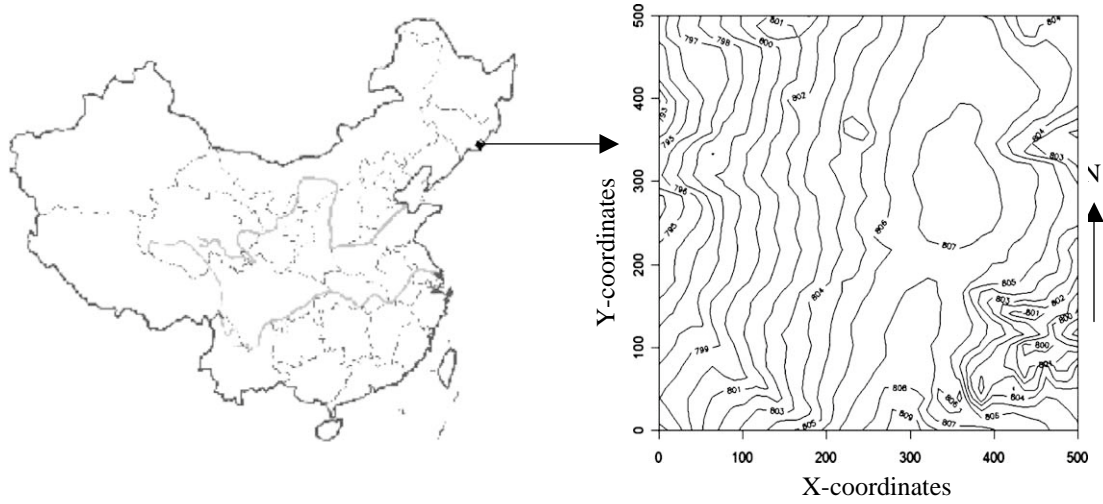
Figure 1. The location and contour map of the 25-ha (500 × 500 m) Changbai temperate plot.

$$f(D) = \frac{1}{Kg(D)} \exp\left[-\int_{D_0}^{D} \frac{m(D)}{g(D)} dD\right] \quad (2)$$

where g(D) and m(D) are functions of tree size, K is a normalization constant and D_0 is the size of individuals upon recruitment (Muller-Landau et al. 2006).

Negative exponential function

If the diameter growth rates and mortality rates are both constant with diameter and take values r and m respectively, the diameter distribution is a negative exponential function (Muller-Landau et al. 2006):

$$f(D) = K_n \exp(-\lambda D) \quad (3)$$

where K_n is normalization constant whose value depends on λ and D_0. $\lambda = m/r$.

Weibull function

If growth is a power function of diameter, following

$$g(D) = rD^{\alpha} \quad (4)$$

and mortality is constant at m, the diameter distribution will take a form of a Weibull function with shape parameter α and scale parameter $\beta = m/r(1-\alpha)$ (Muller-Landau et al. 2006):

$$f(D) = \frac{\beta(1 - \alpha)D^{-\alpha}\exp(-\beta D^{1-\alpha})}{\exp(-\beta D_0^{1-\alpha})} \quad (5)$$

Table 1. The life history traits and the best-fit function to the size distributions for each common species with individual >100 in the temperate forest.

| Species	No. of trees	Family	Canopy layer	Shade-tolerant
Corylus mandshurica	7834	Betulaceae	understory	shade-tolerant
Acer pseudo-sieboldianum	5984	Aceraceae	midstory	shade-tolerant
Acer barbinerve	3911	Aceraceae	understory	shade-tolerant
Pinus koraiensis	2468	Pinaceae	overstory	midtolerant
Syringa reticulata	1598	Oleaceae	midstory	light-demanding
Maackia amurensis	753	Leguminosae	midstory	midtolerant
Tilia mandshurica	410	Tiliaceae	overstory	shade-tolerant
Rhamnus ussuriensis	118	Rhamnaceae	midstory	shade-tolerant
Acer ginnala	108	Aceraceae	understory	shade-tolerant
Acer mono	6609	Aceraceae	midstory	shade-tolerant
Acer tegmentosum	846	Aceraceae	midstory	shade-tolerant
Prunus padus	515	Rosaceae	midstory	shade-tolerant
Philadelphus schrenkii	470	Saxifragaceae	understory	shade-tolerant
Acer triflorum	276	Aceraceae	midstory	shade-tolerant
Ulmus laciniata	192	Ulmaceae	midstory	midtolerant
Crataegus maximouwiczii	121	Rosaceae	understory	shade-tolerant
Malus baccata	106	Rosaceae	midstory	shade-tolerant
Ulmus japonica	1109	Ulmaceae	overstory	midtolerant
Acer mandshuricum	251	Aceraceae	midstory	shade-tolerant
Tilia amurensis	2927	Tiliaceae	overstory	shade-tolerant
Quercus mongolica	926	Fagaceae	overstory	light-demanding
Fraxinus mandshurica	681	Oleaceae	overstory	midtolerant
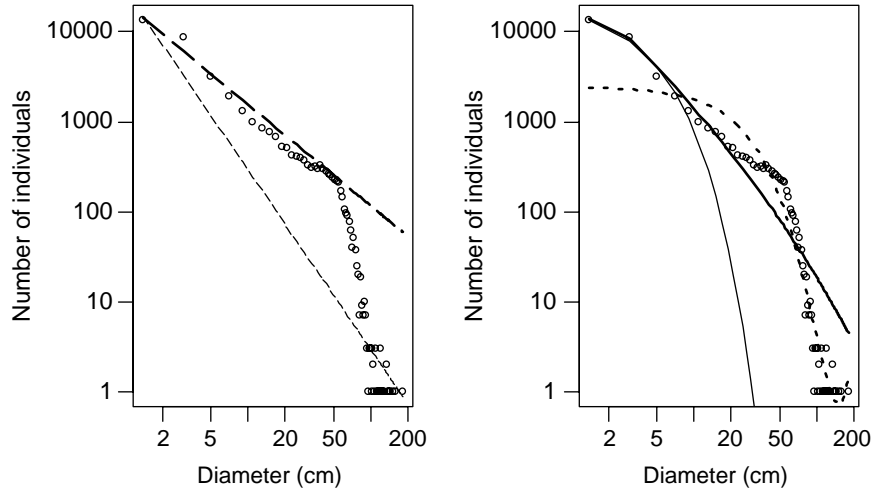
Figure 2. Observed tree size distribution for all individuals of the 25-ha temperate forest in northeastern China (circle) and the predications of the metabolic ecology (thin dashed line), power function (thick dashed line), negative exponential function (thin solid line), Weibull function (thick solid line) and polynomial function (dotted line).

Power function

If growth and mortality are both power functions of diameter, with growth following Eq. 4, and mortality following:

$$m(D) = mD^b \tag{6}$$

and if the scaling exponents are related such that $\alpha - b = 1$ (i.e. mortality is proportional to relative growth rate), the diameter distribution will be a power function with exponent $\theta = 1 + b + m/r$ (Muller-Landau et al. 2006):

$$f(D) = K_p D^{-\theta} \tag{7}$$

where K_p is normalization constant.

Polynomial function

No theory is proposed to explain the polynomial function and thus the polynomial function is purely statistical equation. Here, the semi-logarithmic transformed polynomial function is used to fit the relationship of the number of individuals and diameter:

$$\ln(f(D)) = a_1 D^4 + a_2 D^3 + a_3 D^2 + a_4 D + a_5 \tag{8}$$

where $a_1 \sim a_5$ are constants.

Model fits

We fitted negative exponential, Weibull, power, and semi-logarithmic transformed polynomial functions to the diameter distributions using maximum likelihood methods. We then used Akaike's information criterion (AIC) to compare the maximum likelihood fits of the different functions (Burnham and Anderson 2002). We separated fit distributions for the whole community, families, and each species in diameter. Depending on which mathematical

Table 2. Akaike information criteria for five models fit to the tree size distributions for all individuals, canopy layer and family.

	No. of trees	Metabolic model	Demographic model			Polynomial	Power function exponent, theta (SE)
			Power	Weibull	Negative exponential		
All	38 902	1187.4	1051.6	914.1	996.9	1322.5	−1.13 (0.03)
Canopy layer							
overstory	8575	902.8	800.4	769.8	723.6	811.2	−0.52 (0.04)
midstory	17 439	1050.4	840.1	720.3	859.3	1111.5	−1.21 (0.02)
understory	12 888	907.3	889.2	804.1	864.5	904.9	−1.10 (0.16)
Family with individual >100							
Aceraceae	18 024	1330.5	1074.3	954.0	1065.3	1422.2	−1.33 (0.02)
Betulaceae	7945	1123.6	1117.1	1124.4	1002.8	1443.8	−2.20(0.09)
Tiliaceae	3337	747.8	635.7	693.9	667.6	547.4	−0.63 (0.04)
Pinaceae	2475	832.2	771.3	447.0	734.0	491.0	−0.04 (0.00)
Oleaceae	2289	901.4	804.2	786.7	688.1	786.9	−1.05 (0.05)
Ulmaceae	1301	506.3	258.5	350.8	453.2	429.0	−1.22 (0.02)
Fagaceae	926	489.6	384.5	408.2	385.4	208.0	−0.32 (0.05)
Rosaceae	859	262.6	205.3	275.2	308.9	428.3	−1.67 (0.03)
Leguminosae	753	369.4	305.8	164.2	273.4	165.4	−0.41 (0.09)
Saxifragaceae	472	441.5	393.2	394.3	394.7	462.2	−6.24 (0.80)
Rhamnaceae	151	146.6	96.6	85.9	84.0	103.3	−0.87 (0.08)
Caprifoliaceae	112	55.0	5.1	14.9	0.8	14.4	−3.51 (0.17)

form is the best fit to these data, we will conclude which of the two theories is applicable and if the demographic theory is the best theory, then which of models 3, 5 and 7 is the best model.

Results

Tree size distribution for all individuals in our temperate forest approximated a power function for small and medium sized individuals (<60 cm DBH), and became ever more curvilinear on log–log scales at larger diameters (Fig. 2). However, the metabolic ecology prediction of power function size distribution with exponent −2 was a very poor fit, in large part because the deviations between predicted and observed are largest for trees of intermediate size (Fig. 2). Also, the fitted exponent of power function

was significantly different from −2 (Table 2). The negative exponential function only fit the tree size distribution well for very small individuals, whereas the polynomial function captured the curvature of the size distribution for relatively large individuals (Fig. 2). The Weibull distribution proved the best fit for the whole-community (all individuals), with the lowest AIC value (Table 2).

Similar to the size distribution for all individuals, the metabolic ecological theory gave very poor predictions for the distributions of the 12 families with more than 100 individuals (Table 2, Fig. 3). The demographic equilibrium theory was the best predictor for 10 families (negative exponential function 4, and the Weibull and power functions 3 each), but the semi-logarithmic transformed polynomial function was best for two families (i.e. Tiliaceae and Fagaceae). Thus, the demographic equilibrium theory was not the best predictor of the size distributions for all families.
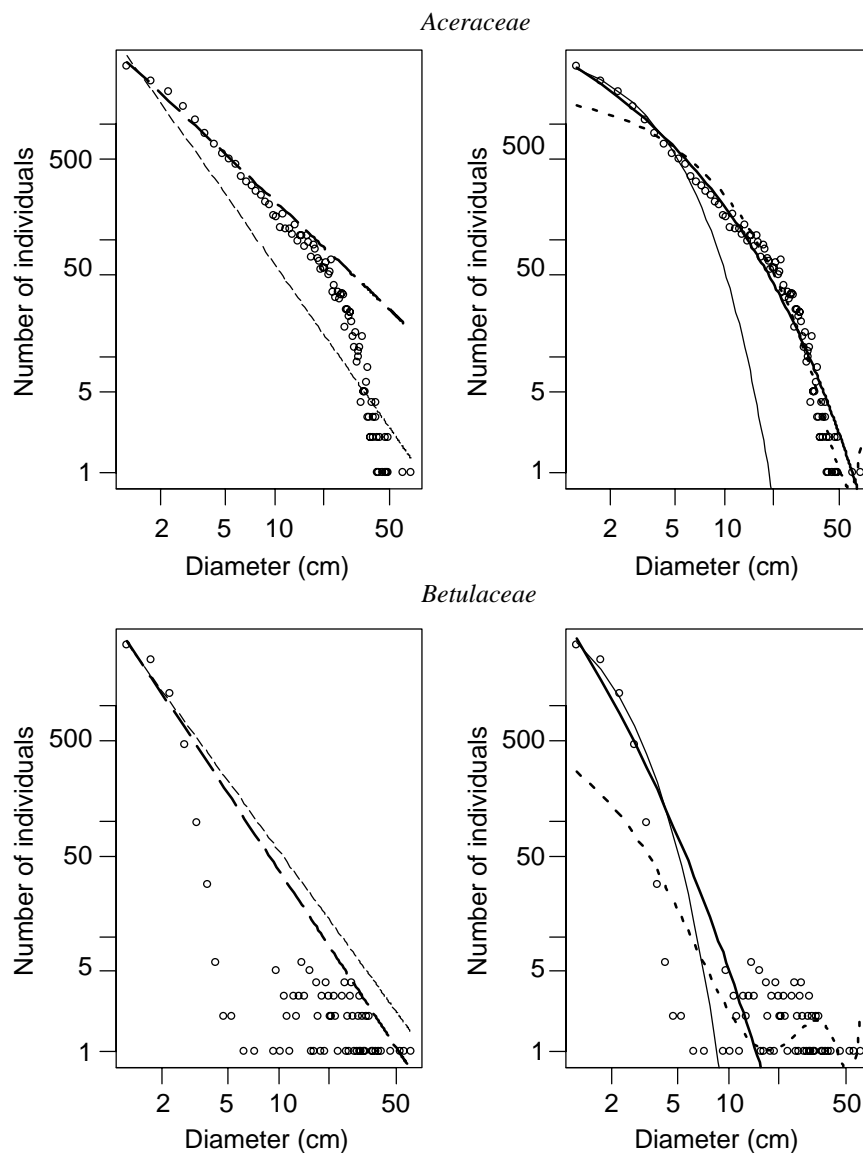

Figure 3. Observed tree size distribution for two families (*Aceraceae* and *Betulaceae*) of the 25-ha temperate forest in northeastern China (circle) and the predications of the metabolic ecology (thin dashed line), power function (thick dashed line), negative exponential function (thin solid line), Weibull function (thick solid line) and polynomial function (dotted line).

The metabolic theory also proved to be a poor explanatory process for the size distributions of all overstory, midstory and understory species, whereas the demographic equilibrium theory was best for all species, although the specific relationship varied somewhat (Table 2, Fig. 4). The size distribution for all overstory species was best predicted by the negative exponential function; and the Weibull function was the best predictor of the size distribution for all midstory and understory species, although the scale parameter (α) for midstory species was 0.3065 (± 0.0087), which differed significantly from a value of 0.1261 (± 0.0177) of understory species, reflecting a large change in the shape of the size distribution with canopy layer.

DBH distributions varied among species (Fig. 5–7). For the 22 common species with more than 100 individuals, the Weibull function was the best predictor for nine species, and the power function was best for eight species (Table 3). The negative exponential function was found best for only two species (*Ulmus japonica* and *Acer mandshuricu*). The polynomial function was best for the three major overstory species in the temperate forest of northeastern China (*Tilia amurensis*, *Quercus mongolica* and *Fraxinus mandshurica*)
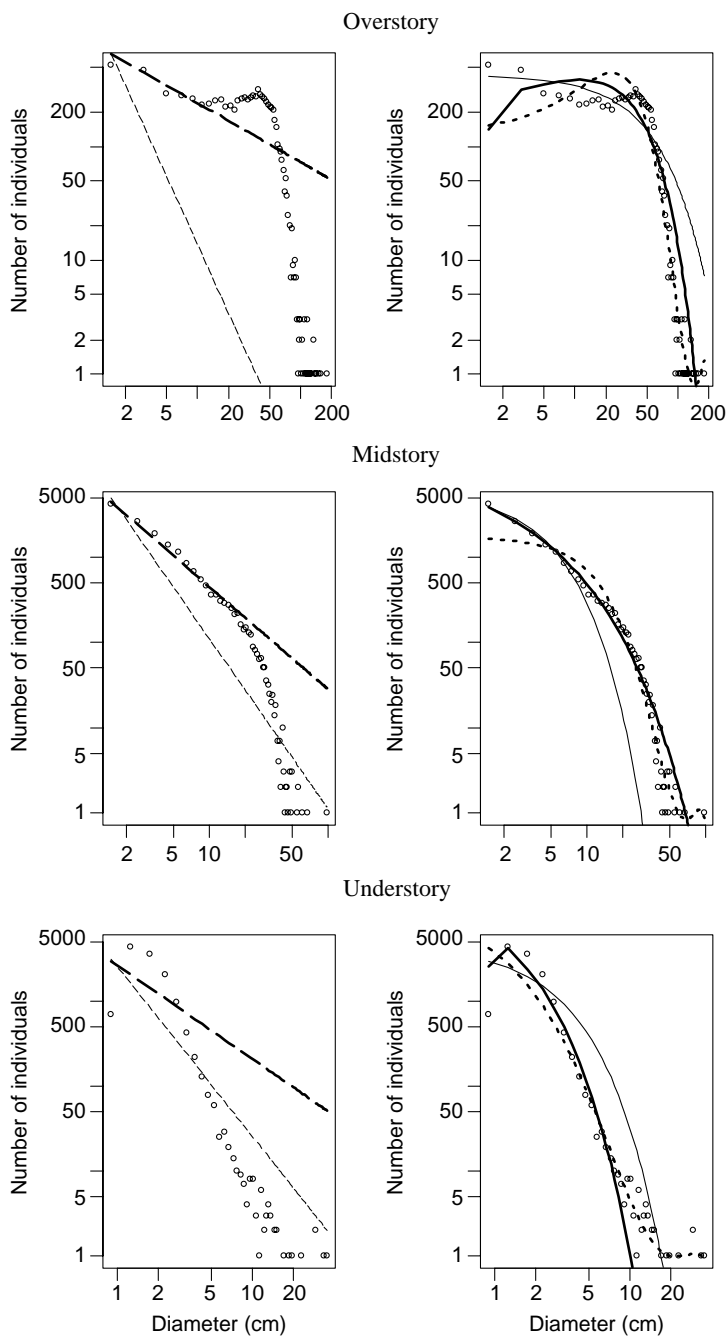

Figure 4. Observed tree size distribution for the three canopy layer (overstory, midstory and understory species) of the 25-ha temperate forest, northeastern China (circle) and the predications of the metabolic ecology (thin dashed line), power function (thick dashed line), negative exponential function (thin solid line), Weibull function (thick solid line), and polynomial function (dotted line).
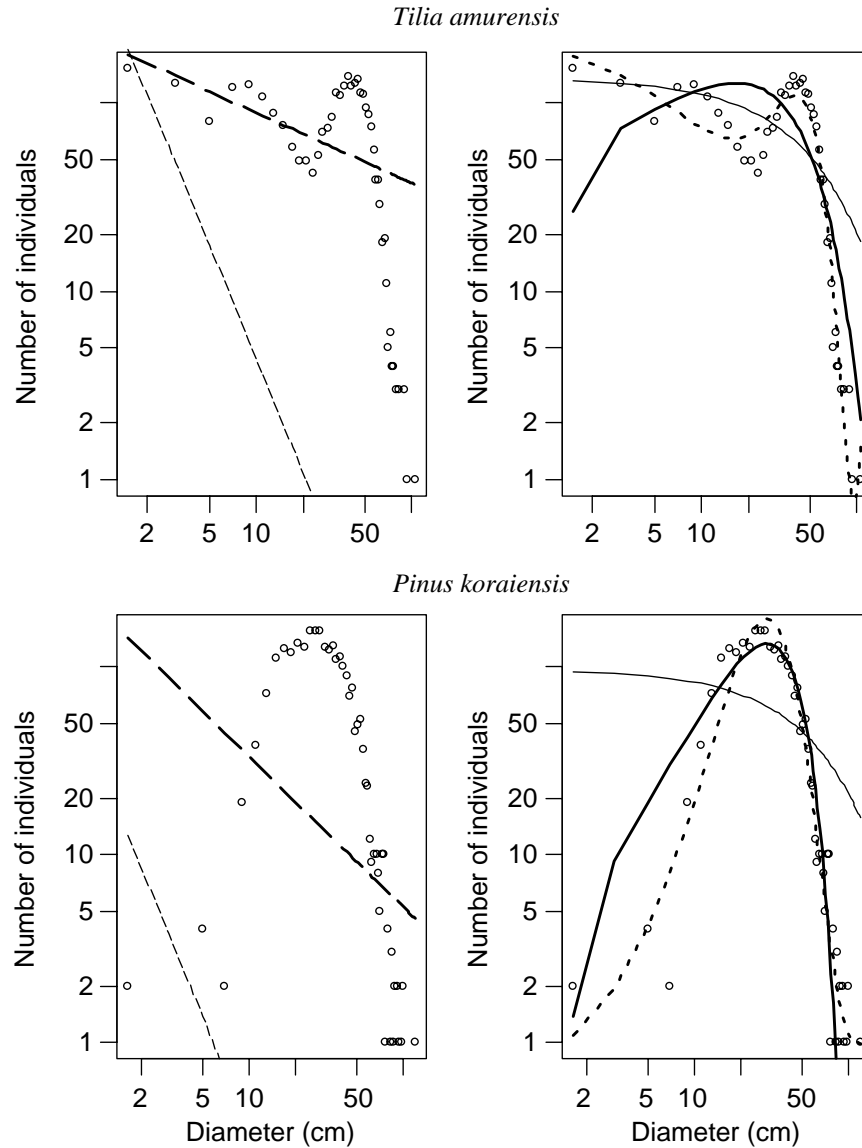
Figure 5. Observed tree size distribution for two overstory species (*Tilia amurensis* and *Pinus koraiensis*) of the 25-ha temperate forest in northeastern China (circle) and the predications of the metabolic ecology (thin dashed line), power function (thick dashed line), negative exponential function (thin solid line), Weibull function (thick solid line) and polynomial function (dotted line).

(Table 3). The shapes of the diameter distributions for each of the common species differed significantly from the power-function prediction of metabolic ecology. Moreover, the best-fit power-function exponents for the size distributions were significantly different from the predicted slope of −2 in seven of eight species, with the exception of *Crataegus maximouwiczii* (Table 3). Among the eight species with their size distributions best fitted by the power function, the exponents for five species differed significantly, whereas the exponents for the other three species – *Acer mono*, *Prunus padus* and *Malus baccata* – showed no significant difference (Table 3). Similarly, among the nine species with their size distributions best fitted by the Weibull function, some species showed no significantly different scale parameter, such as *Acer pseudo–sieboldianum*, *Rhamnus ussuriensis* and *Acer ginnala* (Table 3).

Discussion

Our results showed that the metabolic ecology theory predictions for the scaling of tree abundance with diameter were unequivocally rejected in the studied forest in northeastern China, consistent with the results of Coomes et al. (2003) and Muller-Landau et al. (2006). Moreover, the diameter distribution for both families and species in the forest did not resemble an invariant scaling function as the metabolic theory predicts (Table 2, 3). Although much evidence in support of the metabolic theory has come from comparisons of plants of vastly different sizes (Enquist et al. 1998, West et al. 1999, Enquist and Niklas 2001), it did not accurately predict what happens within particular forests (Coomes et al. 2003, Muller-Landau et al. 2006). The failure of the metabolic theory for predicting size
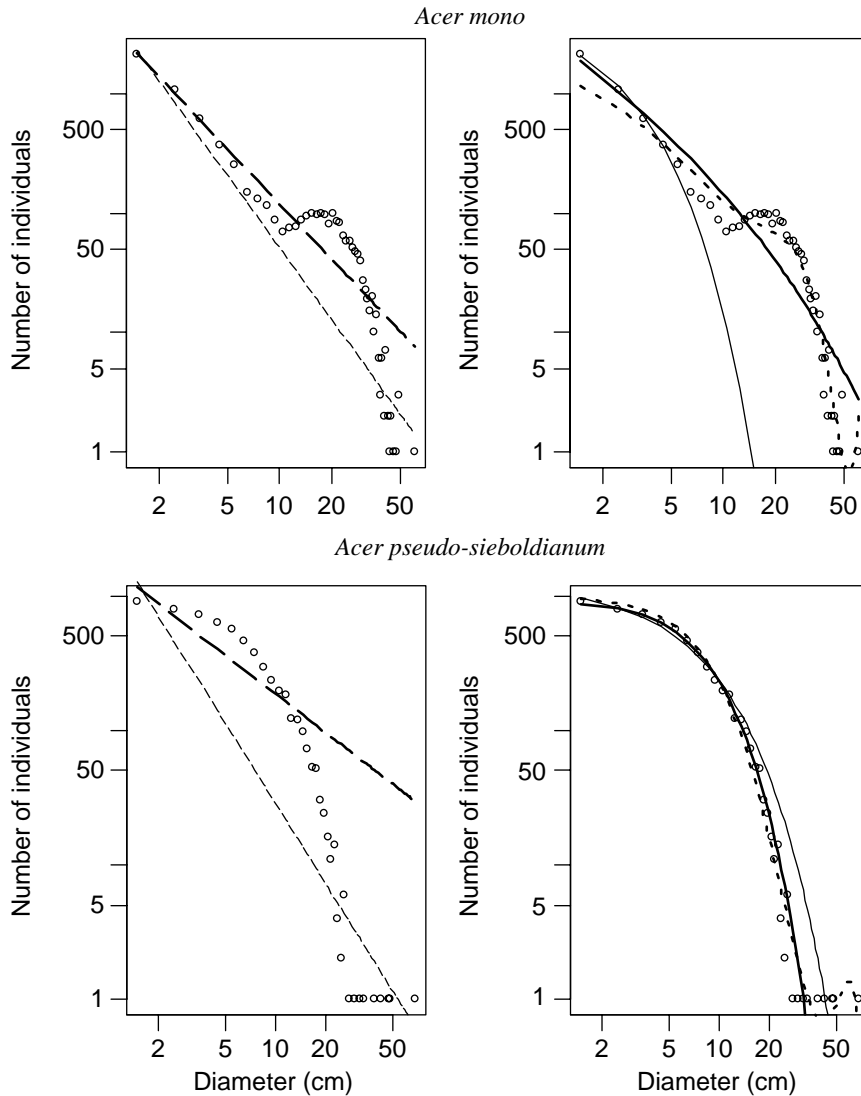
Figure 6. Observed tree size distribution for two midstory species (*Acer mono* and *Acer pseudo-sieboldianum*) of the 25-ha temperate forest in northeastern China (circle) and the predications of the metabolic ecology (thin dashed line), power function (thick dashed line), negative exponential function (thin solid line), Weibull function (thick solid line) and polynomial function (dotted line).

distributions of our forest might result from an untenable assumption that different size classes within a stand would receive (and use) the same amount of energy. This assumption was derived from previous work on self-thinning in even-aged forests. In even-aged forests, different stands of even age and size may have access to the same total resources, whereas this is not true of different size classes of trees within old-growth forests. There was strong vertical stratification in our old-growth temperate forest (Zheng and Luo 2003, Chen et al. 2004, Hao et al. 2008), resulting in uneven partitioning of energy (i.e. light), which affected the growth rates of trees and, consequently, violated the assumption made by the metabolic theory. Thus, the metabolic ecology prediction of power function size distribution with exponent -2 failed in the temperate forest in northeastern China.

The demographic equilibrium models assumed that the size distribution was a property that emerged from individual demographics based on relationships between growth and mortality rates and, provided that a system was

in dynamic equilibrium, could be estimated from size-specific growth and mortality curves (Muller-Landau et al. 2006). Our results showed that most size distributions in the temperate forest could be well predicted by these demographic models. A power function size distribution emerges as a special case when growth and mortality are themselves both power functions of size, with mortality proportional to the relative growth rate. Figure 2–4 show that some of the power function lines look like they were fit to only the smaller trees, which informs us of the approximate proportionality of relative growth and mortality in smaller trees, consistent with the results of Muller-Landau et al. (2006). Such proportionality may in turn reflect the dominant influence of resource availability and competition in determining both growth and mortality below the canopy (Coomes et al. 2003). However, the power-function relationship is not found among large individuals, probably because mortality is at least partly independent of resource availability and competition among large trees. Differences in growth and mortality
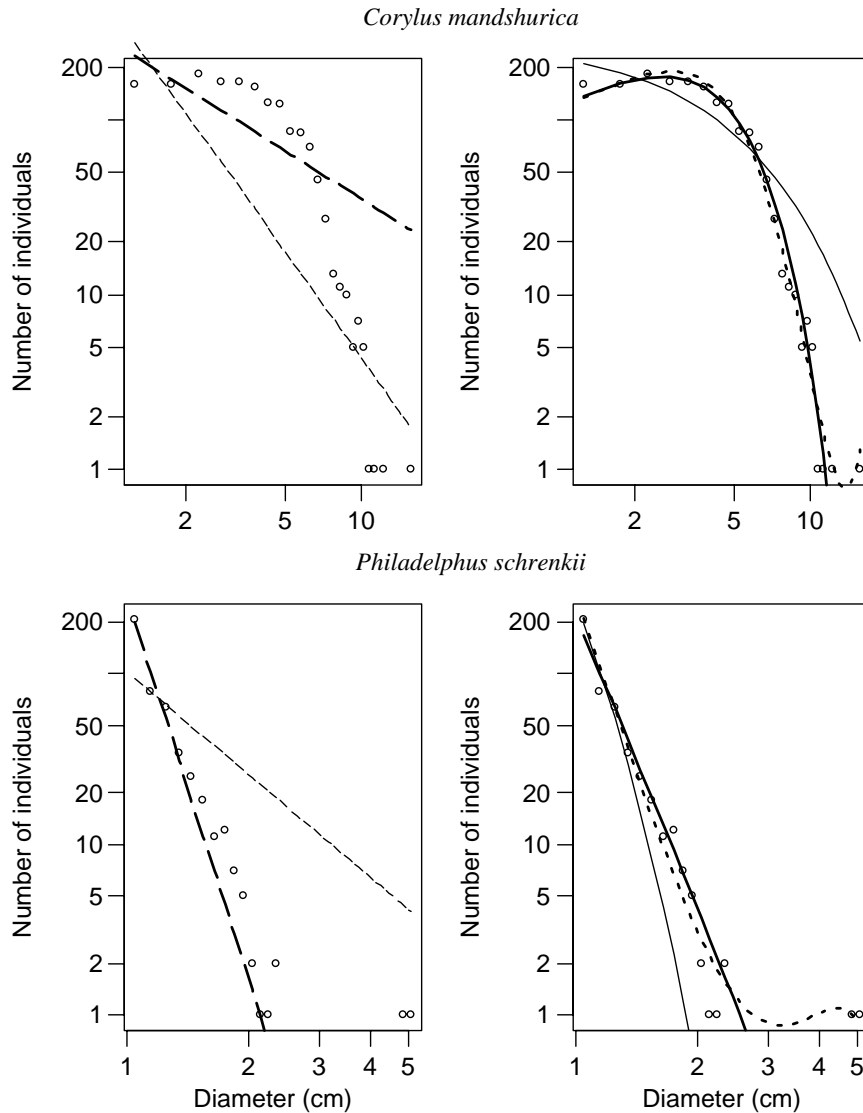
Figure 7. Observed tree size distribution for two understory species (*Corylus mandshurica* and *Philadelphus schrenkii*) of the 25-ha temperate forest in northeastern China (circle) and the predications of the metabolic ecology (thin dashed line), power function (thick dashed line), negative exponential function (thin solid line), Weibull function (thick solid line) and polynomial function (dotted line).

scaling between small and large individuals may also in part reflect differences in species composition and thus in life-history strategies and allocation patterns (Muller-Landau et al. 2006). In addition, tree size distributions varied with species even in the same family. For example, among the seven species with individuals more than 100 in the Aceraceae family, the size distributions for *Acer pseudo–sieboldianum*, *Acer barbinerve* and *Acer ginnala* could be well predicted by the Weibull function, similar to that for the whole Aceraceae family, the negative exponential function best predicted the size distribution for *Acer mandshuricum*, and the power function best predicted that of the other three species: *Acer mono*, *A. tegmentosum* and *A. triflorum*. Our results also shows that the size distributions varied considerably within the canopy layer. For example, among the nine species with the size distributions best fitted by the Weibull function, two, four and three species belonged to overstory, midstroy and understory species, respectively (Table 3). Moreover, the

power function could not predict the size distribution for overstroy species, and the exponential function could not predict the size distribution for the understory species. In addition, all of the three species with the size distribution best predicted by the polynomial function were overstory species. All these implied different demographic relationships among growth and mortality for species, independent of family and canopy layer.

Some previous studies showed that the size distributions were dependant on the life history traits of species (e.g. shade-tolerance). For example, shade-tolerant species were known to have steeply descending monotonic diameter distributions with a large number of suppressed small trees that could be approximated by the negative exponential and negative power functions (Leak 1975, Hett and Loucks 1976, Lorimer 1980). However, our study show that the diameter distributions for shade-tolerant species in the old-growth temperate forest did not always take the form of the descending, monotonic distribution. For instance, the

Table 3. The best-fit function to the size distributions and fitted parameters of the three demographic models for each common species with individual >100 in the temperate forest.

Species	Best-fit function	Weibull function parameters		Power function exponent (θ)	Exponential function parameter (λ)
		Shape (α)	Scale (β)		
Corylus mandshurica	Weibull	−0.93 (0.03)	0.46 (0.02)	−1.36 (0.17)	0.71 (0.09)
Acer pseudo-sieboldianum	Weibull	−0.2 (0.02)	0.12 (0.01)	−0.96 (0.06)	0.17 (0.003)
Acer barbinerve	Weibull	−0.39 (0.03)	0.43 (0.02)	−0.99 (0.18)	0.39 (0.08)
Pinus koraiensis	Weibull	−1.43 (0.04)	0.0002 (0.00)	−0.80 (0.25)	0.02 (0.004)
Syringa reticulata	Weibull	−0.81 (0.05)	0.08 (0.01)	−0.91 (0.13)	0.25 (0.03)
Maackia amurensis	Weibull	−0.93 (0.05)	0.01 (0.00)	−0.41 (0.09)	0.06 (0.01)
Tilia mandshurica	Weibull	0.51 (0.05)	0.6 (0.11)	−0.95 (0.05)	0.22 (0.02)
Rhamnus ussuriensis	Weibull	−0.14 (0.11)	0.11 (0.03)	−0.80 (0.11)	0.12 (0.02)
Acer ginnala	Weibull	−0.35 (0.17)	0.22 (0.07)	−1.02 (0.17)	0.35 (0.05)
Acer mono	power	0.58 (0.01)	0.99 (0.05)	−1.53 (0.03)	0.58 (0.02)
Acer tegmentosum	power	0.5 (0.01)	1.05 (0.16)	−1.81 (0.05)	0.99 (0.07)
Prunus padus	power	0.5 (0.06)	1 (0.19)	−1.57 (0.03)	0.6 (0.03)
Philadelphus schrenkii	power	0.89 (0.15)	40.49 (54.88)	−7.42 (0.31)	6.39 (0.34)
Acer triflorum	power	0.14 (0.07)	0.19 (0.04)	−1.05 (0.05)	0.28 (0.03)
Ulmus laciniata	power	0.48 (0.08)	0.43 (0.35)	−1.59 (0.03)	0.6 (0.03)
Crataegus maximouwiczii	power	−0.25 (0.22)	0.64 (0.22)	−1.89 (0.18)	1 (0.12)
Malus baccata	power	0.6 (0.11)	1.11 (0.47)	−1.48 (0.06)	0.56 (0.05)
Ulmus japonica	exponential	0.48 (0.03)	0.43 (0.05)	−0.87 (0.04)	0.15 (0.01)
Acer mandshuricum	exponential	0.59 (0.07)	1.05 (0.29)	−1.58 (0.09)	0.65 (0.05)
Tilia amurensis	polynomial	−0.47 (0.02)	0.01 (0.00)	−0.37 (0.06)	0.02 (0.003)
Quercus mongolica	polynomial	−0.58 (0.01)	0.002 (0.00)	−0.25 (0.07)	0.01 (0.003)
Fraxinus mandshurica	polynomial	−1.48 (0.08)	0.0001 (0.00)	−0.09 (0.20)	0.01 (0.005)

diameter distribution for *Acer barbinerve* was unimodal and rotated sigmoidally shaped for *Tilia amurensis*, indicating that a variety of curves types were present for these shade-tolerant species. Rotated sigmoidal distributions are concave in the smaller diameter classes and convex in the larger classes, which indicate a high mortality in small suppressed trees, low mortality in vigorous canopy trees and high mortality in large senescent trees. Some studies show that disturbance may cause the rotated sigmoid distributions and that the size distributions would progress toward descending, monotonic distribution (e.g. negative exponential or negative power distribution) in the absence of disturbance (Schmelz and Lindsey 1965, Parker et al. 1985, Leak 1996). In addition, Lorimer and Krug (1983) found that midtolerant species had almost unimodal distributions with few suppressed small trees. Although midtolerant species partly avoid suppression by rapid growth, considerable reduction in density by self-thinning occurs, and high mortality rates of suppressed small trees contribute to the relatively low numbers of suppressed trees. Our results show that the size distributions for these midtolerant species also had different curve types: descending for *Ulmus japonica* and *U. laciniata*, unimodal for *Pinus koraiensis* and binomial for *Fraxinus mandshurica*. As a result, the size distributions for each species might also be independent of shade-tolerant characteristics.

Although these predictions of demographic theory were the best models for most of the species in the temperate forest of northeastern China, the best models for some species (*Tilia amurensis*, *Quercus mongolica* and *Fraxinus mandshurica*) were compound curves (i.e. rotated sigmoid curves), best fitted by the purely statistically polynomial function. The failure of the demographic equilibrium models for these species might be because they predicted mortality to be constant or decline with size, and that

variation in growth and mortality due to local competition were negligible; this imposed limitations on the predictive ability of this approach. The situation in the temperate forest was more complex because large trees were often observed to have high mortality rates, perhaps because they were exposed to strong winds or were weakened by age (Wu 1997). The predisposition of large trees to disturbance and senescence might explain their dearth within the forests studied. As a consequence, mortality curves were often observed to be U-shaped. Some other studies have observed similar patterns (Lorimer et al. 2001, Coomes and Allen 2007), but others have observed a wide variety of patterns of mortality across diameter ranges (Runkle 2000, Woods 2000), which all violated the assumption of the demographic models. In addition, some species, especially *P. koraiensis*, seem to be demographically out of equilibrium. The size distribution for *P. koraiensis* shows that there is less than one 1–6 cm dbh sapling per ha, but more than 50 15–50 cm (age: 80–160 years; Wu and Han 1992) trees per ha, suggesting that most of these trees established following some past disturbance, but that few seedlings have established more recently. Because there were more than 300 old stumps and snags with basal diameter more than 50 cm in the 25-ha plot, we infer that many saplings of *P. koraiensis* began to establish following one large infrequent natural disturbance (e.g. wind storm) that occurred over the area of the plot in about 160 years ago. When these saplings had grown into large mature trees after 80 years, new saplings had high mortality because of unfavorable environmental factors (e.g. light), which caused fewer saplings in the plot now (Wu and Han 1988, Yang and Wu 1988, Xu 2001). Hence, the size (diameter)-distributions of natural forests were unlikely to be invariant and the predictive ability of general models was limited. As a result, developing a

more sophisticated theory to predict tree size distributions remains a complex, yet tantalizing, challenge.

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