

# A general quantitative theory of forest structure and dynamics

Geoffrey B. West<sup>a</sup>, Brian J. Enquist<sup>a,b,1</sup>, and James H. Brown<sup>a,c,1</sup>

<sup>a</sup>Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501; <sup>b</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721; and <sup>c</sup>Department of Biology, University of New Mexico, Albuquerque, NM 87131

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**We present the first part of a quantitative theory for the structure and dynamics of forests at demographic and resource steady state. The theory uses allometric scaling relations, based on metabolism and biomechanics, to quantify how trees use resources, fill space, and grow. These individual-level traits and properties scale up to predict emergent properties of forest stands, including size–frequency distributions, spacing relations, resource flux rates, and canopy configurations. Two insights emerge from this analysis: (i) The size structure and spatial arrangement of trees in the entire forest are emergent manifestations of the way that functionally invariant xylem elements are bundled together to conduct water and nutrients up from the trunks, through the branches, to the leaves of individual trees. (ii) Geometric and dynamic properties of trees in a forest and branches in trees scale identically, so that the entire forest can be described mathematically and behaves structurally and functionally like a scaled version of the branching networks in the largest tree. This quantitative framework uses a small number of parameters to predict numerous structural and dynamical properties of idealized forests.**

allometry | size spectra | metabolic scaling theory | plant ecology | competitive thinning

A long-standing goal of ecology has been to discover the mechanistic processes that underlie pervasive macroecological patterns (1–3). Body size distributions, in particular, have long been of interest (3–8), and one of the most prevalent is the inverse relationship between size and abundance (6, 8). In plant ecology and forestry, size–frequency distributions are perhaps one of the most general patterns (6, 9) and have been used to infer roles of competition and life history in structuring communities (for example, see refs. 10–12) and for estimating biomass content, wood yield, carbon fluxes, and productivity of ecosystems (13, 14). In perhaps the first attempt to quantify community size distributions, De Liocourt (15) suggested that many woody plant communities exhibit regular inverse relationship between size and number of individuals. Recently, it has been suggested that the pattern described by De Liocourt may be self-similar and that self-similarity may be a general property of forests across the globe (16).

Here, in the first of two articles, we develop a zeroth-order theory showing how tree size affects resource use, growth, and death, and how these individual-level processes determine the coarse-grained structure and dynamics of forests. The theory builds on previous approaches (17, 18) and is complementary, but yet different, to past work on “self-thinning” literature (19, 20) and “demographic theory” (21, 22) where, respectively, emphasis has been placed on the role of scaling plant architecture/geometry and demographic processes on the structure and dynamics in plant communities. Our theory provides a quantitative, predictive framework for understanding the structure and dynamics of an average idealized forest. Consequently, it provides a baseline for incorporating additional details and deviations due to site- and taxon-specific phenomena. The theory deliberately makes simplifying assumptions. In particular, the forest: (i) can be modeled as a stand with no recruitment

limitation, where recruitment begins with seedlings, and the size distribution is determined by the dynamics of growth and mortality (22); (ii) is in resource (23) and demographic steady state (22), so that, on average, the total rate of resource use equals the rate of resource supply, birth rates equal death rates, and a stable distribution of ages and sizes exists; (iii) comprises “allometrically ideal” individuals that obey previously derived quarter-power allometric scaling laws (24) that govern how they use resources, occupy space, and grow.

Given the above assumptions, the theory shows how scaling constraints at the individual level (23–26) determine rates of growth, mortality, and recruitment within the forest. As a consequence, phenomena such as size distributions and spacing patterns emerge at the population, stand, and ecosystem levels (23, 27–30). The generality of our theoretical approach can be attributed to its focus on two fundamental biological phenomena: metabolism and allometry. This framework differs from, but is not in conflict with, phenomenological “demographic theory” (12, 21, 31), in which structural and dynamical properties of forests are empirical manifestations of observed growth, mortality, and recruitment, rather than derived from general principles.

## The Model

We begin by considering a forest plot of area,  $A_{\text{Plot}}$ , containing a large sample of trees. The stand is characterized by a size distribution. This distribution can be visualized by apportioning individuals into  $(K + 1)$  size classes, where the  $k$ th class contains  $\Delta n_k$  individuals of similar size. Within each size class individuals are characterized by stem or trunk radius,  $r_k$ . Size classes range from the smallest,  $k = 0$ , to the largest,  $k = K$  (Fig. 1). In this theory, stem radius is the primary quantity characterizing size, because it is a major determinant of both biomechanical stability and the flux of resources from roots to leaves (24).

Since there is a functional relationship between size,  $r_k$ , and age,  $t$ , as determined by a growth equation for  $r_k(t)$ , the size distribution could also be expressed in terms of the age profile of the stand. Thus, the  $k$ th size class represents a time interval,  $\Delta t$ , of an average individual’s lifespan as determined by the growth equation. So  $\Delta n_k$  is the number of plants whose age is between  $t$  and  $t + \Delta t$  and whose size is between  $r_k$  and  $r_k + \Delta r_k$  where  $\Delta r_k$  is the size of the bin used to visualize the size distribution. Specifically,  $\Delta r_k \equiv r_{k+1} - r_k$  [see [supporting information \(SI\) Text and Tables S1 and S2](#)]. In steady state,  $\Delta n_k$  does not change with time so growth and death rates are not independent but inextricably linked (18). As individuals grow and transition from the  $k$ th to the  $(k + 1)$ th size class, an equal

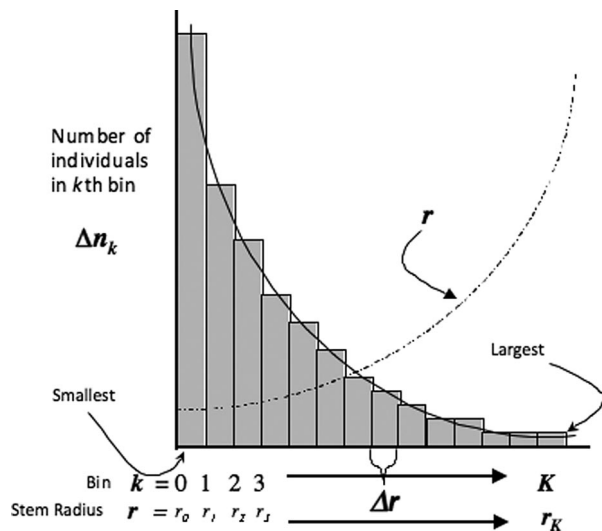
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<sup>1</sup>To whom correspondence may be addressed. E-mail: [benquist@email.arizona.edu](mailto:benquist@email.arizona.edu) or [jhbrown@unm.edu](mailto:jhbrown@unm.edu).

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**Fig. 1.** Summary diagram showing how several of the main parameters of our model are related to plant size and how the discrete size distribution is characterized in our model. Size distributions can be characterized as discrete or continuous functions. Here, the size distribution is visualized by binning the data into  $k$  discrete size classes. The size of each bin is  $\Delta r$ , where  $\Delta r = \Delta r_{k+1} - \Delta r_k$ . The stem radius increases as trees grow (dashed line) from the smallest sizes, where  $k = 0$  and the stem radius is  $r_0$ , to the largest size class,  $K$  with stem radius  $r_K$ . The predicted steady-state size distribution is  $\Delta n_k \propto r_k^{-2}$  (solid line function shown). Note that, here, bin size is chosen to be a constant, reflecting linear binning as discussed in ref. 54.

number in the  $(k + 1)$ th class must die, so we can define the change in the number of individuals per class as  $\Delta n_k = \Delta n_{k+1} = \Delta n_k^{\text{died}}$ . The steady-state assumption is consistent with dynamical data from several old-growth tropical forests (32, 33).

We assume that physiological and morphological characteristics of individuals obey allometric scaling relationships. These are typically expressed as

$$Y = Y_0 r^\phi, \quad [1]$$

where  $Y$  is a dependent variable such as metabolic rate or leaf area,  $Y_0$  is a normalization constant,  $\phi$  is the allometric exponent, and  $r$  is stem or trunk radius (26). Based on theoretical models and supporting empirical observations (23, 24), for simplicity, the following are assumed for within and between individual trees of radius,  $r_k$ : (i) Whereas leaf anatomy and physiology vary within and across individuals (34, 35), they are independent of plant size, so, for example, the surface area of an average leaf,  $a^L \propto r_k^0$ .\* (ii) The total number of leaves,  $n_k^L$ , and total leaf area per plant,  $a_k^L = n_k^L a^L$ , both scale as  $r^{1/a}$ . (iii) Individual rates of metabolism or energy use,  $B_k = B_0 r_k^{1/a}$ , where  $B_0$  is a normalization constant; so,  $B_k \propto n_k^L \propto a_k^L \propto r_k^{1/a}$  (36). (iv) The average total mass of a tree,  $m_k$  scales as  $m_k \propto r_k^{(2a+b)/a} \propto l_k^{a/b}$  so that  $r_k^a \propto l_k^{1/b}$ , where  $l_k$  is the length of the trunk that is proportional to the total tree height,  $h_k$  (see ref. 37). The values of  $a$  and  $b$  reflect biomechanics and the geometry of the plant branching network and their values may vary across taxa (see ref. 38).

Relationships *ii–iv* were previously derived by optimizing plant hydrodynamics and biomechanics subject to hierarchical space-filling geometry and the invariance of terminal units (24). Although the theory can be recast straightforwardly by using empirical values of  $a$  and  $b$  (24, 38, 39), for the idealized case (24)

we use  $a = 1/2$ ,  $b = 1/3$ , so that  $\theta \equiv 1/(2a + 2b) = 3/4$  and thus,  $B_k \propto n_k^L \propto a_k^L \propto m_k^\theta$  and  $l_k \propto r_k^{2/3}$  (37). The theory predicts, and empirical observations confirm, that typical trees in the size range considered here  $\theta \approx 3/4$  (see refs. 24, 38, and 40). Plants such as palms, seedlings, vines, etc., with architectures that do not conform to the above assumptions (24, 38, 39, 40) may have different values of  $a$  and  $b$  so their values of  $\theta$  and corresponding size distributions and growth and mortality rates will change accordingly. Violations of assumptions *i–iv* will also lead to calculable deviations from the idealized predictions. For example, parameters characterizing variation in leaf-level properties could be included in our model (36). We now show how these attributes of individuals scale up to the stand level to determine the structure and dynamics of forests.

**Scaling Canopy Dimensions and the Importance of Space-Filling.** We define the canopy of a tree as the smooth Euclidean surface enveloping all leaves and branches<sup>†</sup>—this to be contrasted with the actual fractal-like structure defined by the leaves and branches or the surface area of all of the leaves themselves. Combining an assumed isometric Euclidean scaling of the canopy with relationship *iv* above, we can equate the radius of the canopy to the trunk radius as  $r_k^{\text{can}} \propto l_k \propto h_k \propto r_k^{2/3}$ , where  $h_k$  is the height of the tree. Consequently the surface area of the canopy scales as  $a_k^{\text{can}} \propto r_k^{4/3}$ . These relationships are in general agreement with data (see figure 1c of ref. 41 and figure 3 in ref. 42).

Now consider how leaves are distributed within the canopy. The ratio of total leaf area ( $a_k^L \propto r_k^2$ ) to canopy area ( $a_k^{\text{can}} \propto r_k^{4/3}$ ) for an individual is  $a_k^L/a_k^{\text{can}} \propto r_k^{2/3}$  reflecting the greater than linear increase of the fractal-like surface area of all of the leaves relative to the Euclidean surface area of the canopy. Notice that, from our earlier work (24, 39, 40), the fractal-like leaf area,  $a_k^L$ , and the Euclidean canopy volume  $v_k^{\text{can}}$  scale identically,  $a_k^L \propto v_k^{\text{can}} \propto (r_k^{\text{can}})^3 \propto r_k^2$ . The number of leaves scales similarly,  $n_k^L \propto r_k^2 \propto v_k^{\text{can}}$ , so the average density of leaves in the canopy,  $n_k^L/v_k^{\text{can}}$ , is independent of tree size. The fractal-like space-filling branching vascular architecture that terminates in leaf surfaces confers an effective additional spatial dimension to the scaling properties of the network (43).

Space-filling implies that the total number of leaves of all individuals within any size class,  $\Delta n_k a_k^L$ , equally fills the same amount of area, independent of  $k$ . Specifically,

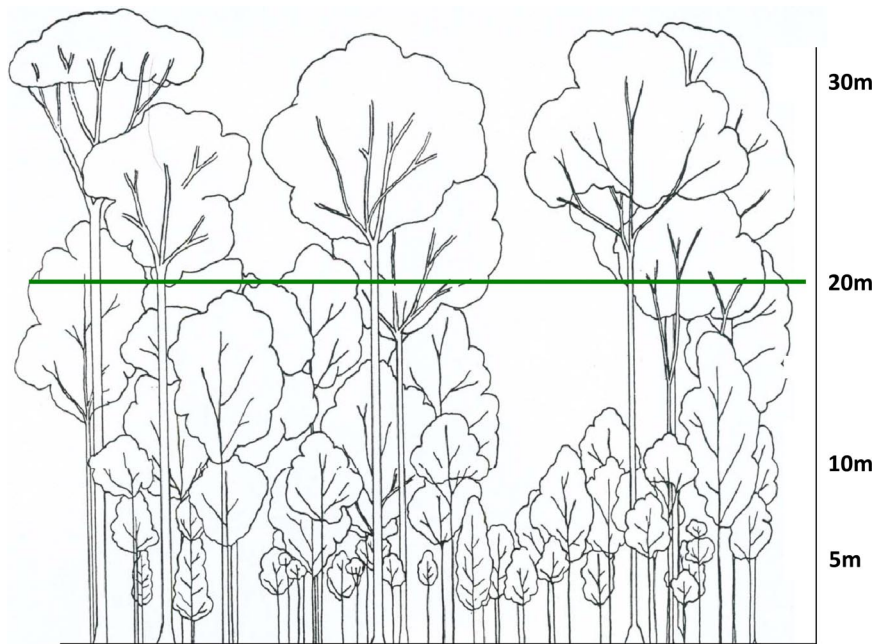
$$\Delta n_k a_k^L = \Delta n_{k+1} a_{k+1}^L \quad [2]$$

for any  $k$ . Consequently,  $\Delta n_k \propto 1/a_k^L \propto 1/r_k^2$ . The steady-state size distribution therefore approximates an inverse square law with many small individuals and few large ones (16). Assuming that individual leaf area,  $a^L$ , is invariant and that each leaf is supplied by an equal number of xylem elements, this implies that the total number of xylem elements of all individuals within each size class is approximately the same. Note that the concept of space-filling is expressed in terms of both leaf surface area and trunk cross-sectional area.

The above features have important and nonintuitive implications for the structure and function of the entire stand. It has been shown previously that the total hydrodynamic resistance of each microcapillary xylem “tube,” composed of sequential xylem elements running from root to leaf, is approximately independent of tube length (24). Consequently, the volume flow rate through any tube in any tree is approximately independent of tree size, so the total flux of fluid through all trees in each size class is approximately equal. The trunk of each tree and the total

\*For our notation we use superscript  $L$  to represent properties of a leaf and not an exponent.

<sup>†</sup>The surface area of the canopy,  $a^{\text{can}}$ , is essentially akin to the surface area that results from loosely wrapping the entire tree in a plastic sheet à la Christo and Jeanne-Claude (see [www.christojeanneclaude.net/wt.shtml](http://www.christojeanneclaude.net/wt.shtml)).



**Fig. 2.** Elevation of a tropical forest taken from Davis and Richards (45, p 368). The spatial position of each tree stem and canopy are shown. Note, as predicted by our model, the forest is characterized by a given distribution of tree sizes and spatial position of canopies. Specifically, our model predicts that, for a generic case, crown dimensions should overlap until they reach a certain size ( $\approx 20$  m) and then canopies should become increasingly separated as shown in this diagram. The horizontal line is the predicted tree height, based on observed scaling data for tropical tree crown dimensions, where, *on average*, canopies no longer overlap.

conducting tissue of the entire stand can therefore be viewed as composed of a very large number of elemental vascular tubes of varying length, each transporting water and nutrients at the same rate but to leaves at different locations in the canopy. Therefore, the size structure and spatial arrangement of trees in the entire stand are emergent manifestations of the way that functionally invariant xylem “tubes” are bundled together within trunks of individual trees, connecting them from the trunks, through branches, to the leaves.

**Stand Energetics, Size Structure, and Spatial Packing.** Since leaves are assumed to be invariant units, the fluid flux,  $Q_k$ , through any individual tree in the  $k$ th class is proportional to the number of leaves. Whole-plant metabolic rate is proportional to fluid flux, so  $B_k \propto Q_k \propto a_k^L \propto r_k^2$ . However, the number of individuals in a size class,  $\Delta n_k$ , decreases as  $r_k^{-2}$ . Consequently, all plants in a size class collectively use resources at the same rate,

$$B_k^{\text{tot}} = \Delta n_k B_k \propto r_k^0. \quad [3]$$

This prediction, reflecting the invariant number of vascular tubes in each size class, is the analog of the energy equivalence relation shown empirically for animal populations and parameterized in terms of mass by Damuth (4, 23). Furthermore, both the total canopy volume of all trees in a size class,  $\Delta n_k V_k^{\text{can}}$ , and their total leaf areas,  $\Delta n_k a_k^L$ , are also independent of size.

Building on our previous work (23), each individual is assumed to grow until it is resource limited. Consequently, trees compete for resources, and the total rate of resource use by all of the trees in the stand is equal to and limited by the total rate of resource supply,  $\dot{R}$ , so that  $B_{\text{Tot}} \propto \dot{R}_{\text{Tot}} = \dot{R} A_{\text{Plot}}$  (23). All of these stand-level “invariants” follow from general principles of space filling and optimal hierarchical branching operating jointly at both the individual and stand levels. From energy equivalence, the total rate of energy use for the entire stand,

$$B_{\text{Tot}} = \sum B_k^{\text{tot}} = (K + 1) B_k^{\text{tot}} = (K + 1) \Delta n_k B_k \quad [4]$$

valid for any  $k$ , where  $K + 1$  is the total number of size classes. The corresponding whole-community flux,  $B_{\text{Tot}}/A_{\text{Plot}} = (K + 1) \rho_k B_k$ , where  $\rho_k \equiv \Delta n_k/A_{\text{Plot}}$  is the population density. As we now show and further develop in our second article (42) these equations provide the basis for predicting the generic structure and dynamics of the entire stand and provide a basis for understanding deviations from predictions in terms of additional site- and taxon-specific details.

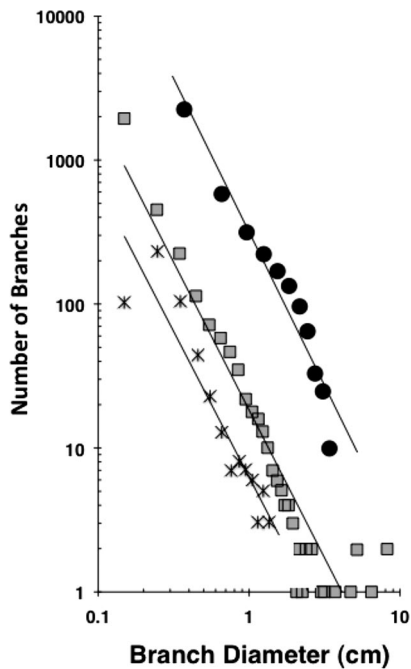
First, however, it is convenient to translate the above discrete formulation into a continuum notation (see *SI Text*). The distribution function representing the number of individuals per unit trunk radius,  $\Delta n_k/\Delta r_k$ , becomes, in the continuum limit,  $f(r) \equiv dn/dr$ . When size classes are characterized by linear binning of radii, corresponding to a constant infinitesimal  $\Delta r_k$ , independent of  $k$ , Eq. 4 gives

$$f(r) \propto \frac{1}{r^2}. \quad [5]$$

Since  $r \propto m^{3/8}$ , this is equivalent to  $f(r) \propto m^{-3/4}$  reflecting the  $3/4$  power scaling of metabolism (26). Note, however, that if the distribution is expressed in terms of mass, which is a derived quantity from a length measure,  $g(m) \equiv dn/dm$ , the number of individuals per unit tree mass rather than per unit trunk radius, then  $g(m) = f(r)(dr/dm) \propto m^{-11/8}$  leading to the curious  $-11/8$  exponent as recently reported (44). We discuss this result as well as issues of binning and viewing size spectra scaling in terms of discrete and/or continuous distributions in further detail in the *SI Text* (See Eqs. S7 and S8).

Our theory also makes explicit predictions for the spacings of individuals within the forest. Since the density of individuals in a size class,  $\rho_k$ , decreases as the square of stem radius,  $\rho_k \propto r_k^{-2}$  the average distance,  $d_k$ , between individuals of a given trunk radius is

$$d_k \propto \frac{1}{\rho_k^{1/2}} \propto r_k. \quad [6]$$



**Fig. 3.** Size distribution of branches or roots within a given tree. Shown are three trees, *Cryptomeria* sp. (black circles) *Picea* sp. (stars), and *Betula* sp. (gray squares) and the fitted OLS regression for each tree; the exponents are  $-2.13$ ,  $-2.03$ , and  $-2.05$  respectively. Data are taken from Shinozaki et al. (46). Because the exponent is essentially identical to the tree size distribution within a forest, the entire forest is, in a very real sense, a hierarchically branching resource supply network that can be described mathematically and behaves structurally and functionally like a scaled version of the branching network of the trees it contains.

Thus, the average distance,  $d_k$ , between the trunks of individuals of the same size scales linearly with radius:  $d_k = c_1 r_k$ , with  $c_1$  a scaling constant reflecting how individuals fill space.

Additionally, the theory predicts canopy overlap. The average distance separating the edges of canopies of trees of the same size is  $d_k^{\text{can}} = d_k - 2r_k^{\text{can}}$ . Since  $r_k^{\text{can}} = c_2 r_k^{2/3}$ , where  $c_2$  is a constant reflecting the geometry of the canopy,

$$d_k^{\text{can}} = c_1 r_k \left[ 1 - \left( \frac{2c_2}{c_1} \right) r_k^{-1/3} \right]. \quad [7]$$

This predicts that the canopies of larger trees overlap less than those of smaller trees, with the degree of overlap depending on the values of  $c_1$  and  $c_2$ . There is a critical value of  $r_k$  where canopies just touch,  $d_k^{\text{can}} = 0$ , given by  $r_k = (2c_2/c_1)^3$ . Therefore, Eq. 7 can be expressed as,

$$d_k^{\text{can}} = c_1 r_k [1 - (r_k/r_k)^{1/3}]. \quad [8]$$

In general, the canopies of smaller trees overlap until  $r_k = r_k$ . Thus, the values of  $c_1$  and  $c_2$  determine both the distance between trunks and the separation or overlap of canopies, thereby predicting the overall generic spatial configuration of the stand, as illustrated in Figs. 1 and Fig. S1. For example, for a Costa Rican forest where  $c_1 \approx 70$  and  $c_2 \approx 95 \text{ cm}^{1/3}$  (42) the theory predicts that, on average, only the canopies of trees larger than  $\approx 30 \text{ cm}$  in radius and  $20 \text{ m}$  in height are separated. Another tropical forest (45) exhibits qualitatively similar stand structure and canopy separation (Fig. 2).

### The Forest is the Tree

An interesting implication of our theory is that the distribution of sizes and resource fluxes among trees within a stand scales

**Table 1.** Similarity of predicted scaling relations for branches within a tree [quantities denoted by uppercase symbols and subscripts  $i$  (46)], and for trees within a forest (denoted by lowercase symbols and subscripts  $k$ )\*

Scaling quantity	Individual tree	Entire forest
Area preserving	$\frac{R_{i+1}}{R_i} = \frac{1}{n^{1/2}}$	$\frac{r_{k+1}}{r_k} = \frac{1}{\lambda^{1/2}}$
Space filling	$\frac{L_{i+1}}{L_i} = \frac{1}{n^{1/3}}$	$\frac{l_{k+1}}{l_k} = \frac{1}{\lambda^{1/3}}$
Biomechanics	$R_i^2 = L_i^3$	$r_k^2 = l_k^3$
Size distribution*	$\Delta N_i \propto R_i^{-2} \propto M_i^{-3/4}$	$\Delta n_k \propto r_k^{-2} \propto m_k^{-3/4}$
Energy and material flux*	$B_i \propto R_i^2 \propto N_i^2 \propto M_i^{3/4}$	$B_k \propto r_k^2 \propto n_k^2 \propto m_k^{3/4}$

\*The above theory is developed based on using radius as the primary measure of size. The dependences on mass, leading to quarter-power exponents, are derived expressions using the continuous distribution function  $f(r) \propto 1/r^2$  (Eq. 8 and SI Text, Eq. S3). The mathematical equivalence of these scaling relations shows that the entire forest behaves as if it were a hierarchically branching resource supply network that mimics the branching network of a single tree (see also Fig. 3).

identically to the distribution of sizes and resource fluxes of branches within a tree (24). Our model shows how the number of trees in a size class,  $\Delta n_k$ , decreases with trunk radius,  $r_k$ , as  $\Delta n_k \propto r_k^{-2} \propto m_k^{-3/4}$ , mimicking the decreasing number of branches within an individual tree,  $\Delta N_i$ , with increasing branch radius,  $R_i$ ;  $\Delta N_i \propto R_i^{-2} \propto M_i^{-3/4}$  (26), where,  $i$  is a branch size class within a given tree, so that, for example, Shinozaki et al. (46) measured the size distribution of branches and roots for 10 trees of 6 species and reported the discrete size distributions. Analysis of the branching size distribution reveals an exponent of  $-2.14$  (95% CI =  $-2.34$  to  $-1.95$ ) suggesting statistically indistinguishable from the predicted value of  $-2$  (Fig. 3).<sup>‡</sup> In addition to this inverse square law, quantities such as fluid flow rate and mass also scale identically in forests and trees (Table 1). In a very real sense, the entire forest is a hierarchically branching resource supply network that can be described mathematically and behaves structurally and functionally like a scaled version of the branching network of the largest tree.

### Discussion

This article presents the first part of our theory. A second article (42) makes additional predictions for, succession and whole-standard resource use and productivity, and provides detailed empirical tests. The theory builds on metabolic scaling theory, and is derived for the simplified case of a single species stand. It should also apply, however, to multispecies stands so long as all trees compete for the same limiting resources and obey the same allometric scaling relations. Our theory is complementary to the “self-thinning” literature because the geometry of a tree (as given by the plant branching networks governed by parameters  $a$  and  $b$ ) is fundamental in the scaling of forest structure and dynamics. However, our theory predicts that the exponent that characterizes the inverse relationship between size and density [i.e.,  $f(r)$  and  $g(m)$ ] is fundamentally different from the “self-thinning law” (6) in plant ecology where  $g(m) \sim m^{-2/3}$  but that  $f(r)$  is not explicitly derived. The core assumptions of our theory are well supported: (i) whereas co-occurring plants usually compete for a common resource such as light (47, 48), nutrients

<sup>‡</sup>Statistics are for binned data (histogram) for frequency and branch radius based on the original data plots from the 1964 Shinozaki et al. article (46). While reasonable, given that only the histogram data are available, a more accurate assessment of our model for branch distributions should use the more rigorous statistical approach based on the raw (un-binned) data as discussed in White et al. (54).

**Table 2. Summary of several prominent forest-level scaling predictions from this article and from Enquist and colleagues (42) when the forest is in resource and demographic steady state**

Stand property	Predicted stem radius, $r_k$ , based scaling function	Predicted mass, $m_k$ , based scaling function
Size class neighbor separation	$d_k \propto r_k$	$d_k \propto m_k^{3/8}$
Canopy scaling	$r_k^{\text{can}} \propto r_k^{2/3}$	$r_k^{\text{can}} \propto m_k^{3/4}$
Canopy spacing	$d_k^{\text{can}} = c_1 r_k \left[ 1 - \left( \frac{r_k}{r_k^{\text{can}}} \right)^{1/3} \right]$	$d_k^{\text{can}} = c_1 c m_k^{3/8} \left[ 1 - \left( \frac{m_k}{m_k^{\text{can}}} \right)^{1/4} \right]$
Energy Equivalence	$\Delta n_k B_k \propto r_k^0$	$\Delta n_k B_k \propto m_k^0$
Total forest resource use	$B_{\text{Tot}} \propto \sum \Delta n_k r_k^2 \leq \dot{R}$	$B_{\text{Tot}} \propto \sum \Delta n_k m_k^{3/4} \leq \dot{R}$
Mortality rate	$\mu_k \approx \bar{A} r_k^{-2/3}$	$\mu_k \approx -(3/4)(\bar{a} m_k^{-1/4})$
Size distribution	$N_k \approx \frac{\dot{R}}{(K+1)b_0} r_k^{-2}$	$N_k \approx \frac{\dot{R}}{(K+1)b_0 c} m_k^{-3/4}$

As discussed in the *SI Text*, the predicted functions are based on measuring plant size based on stem radius. The dependences on mass, leading to quarter-power exponents, are derived expressions using the continuous distribution function  $f(r) \propto 1/r^2$  (Eq. 8 and *SI Text*, Eq. S3 and Eq. S8). The value of  $c$  is from the allometric relationship linking stem radius to mass,  $r \approx c m^{3/8}$ .

(49), or water (50, 51); nonetheless, (ii) species in different taxonomic and functional groups (e.g., gymnosperms and angiosperms) exhibit similar scaling relations for structural dimensions and metabolic rates (25, 36, 37, 52); so that (iii) forests, and plant communities in general, tend to pack to fill space so that growth of some individuals must be matched by mortality of other individuals of similar size (6, 53). Consequently, the theory should be very general and apply to diverse forests (and possibly plant communities, in general) of coexisting tree species, irrespective of limiting resource, geographic location, and taxonomic or functional group. Furthermore, although derived for above-ground shoots, the model should also apply to below-ground roots, which exhibit similar scaling relations (46, 52).

In addition to providing a coarse-grained quantitative description of forests that reveals pervasive underlying regularities (see Table 2), the theory provides a unique way of viewing a forest community. Most intriguingly, we show that the forest can be viewed abstractly as an approximate uniform distribution of vascular “tubes” of equal length each transporting the same quantity of energy and resources. Furthermore, the mathematical structure and physical characteristics of the “virtual” network of interacting trees in the forest is essentially identical to the network of branches of an individual tree.

This zeroth-order theory deliberately makes simplifying assumptions and ignores ecological interactions that affect species composition. Consequently it does not address many traditional questions of plant community ecology: (i) How many and what kinds of species coexist? (ii) What are the ecological roles of different taxonomic or functional groups? (iii) What are the impacts of abiotic stress, disturbance, herbivores, and diseases? Nevertheless, the theory is directly relevant to these questions, because tree size is the single most important variable affecting resource use, population density, and stand dynamics. A major strength is that the theory endeavors to explain a lot with a little—it makes many quantitative predictions and unifies diverse features of forest structure and dynamics based on a small number of principles and parameters.

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