

Supporting Information

Simini et al. 10.1073/pnas.1000137107

SI Text

Discussion Scaling and Self-Similarity. Scaling and power law relationships are observed when the phenomenon being studied does not exhibit a characteristic length scale (S1–S5). Typically, there are both lower and upper cutoff scales for power law behavior and if these are well separated (say, by several orders of magnitude), scaling could hold in an intermediate range. In physical systems, one can discern the scaling regime by increasing the upper cutoff scale or the correlation length by adjusting the temperature or the pressure closer to its critical value. No such tuning is possible in an ecological community. The diameter distribution of trees in a forest has a lower cutoff scale set by the size of the plant upon recruitment whereas the upper cutoff is necessarily less than the typical diameter of the largest tree in the forest. Determining the scaling regime and even verifying that a scaling description is valid in an ecological community can be a challenge.

Finite-size scaling postulates that the PDF of tree diameters has the form $p_r(r|r_c) = r^{-\alpha} f_r(r/r_c)$ when r is larger than a lower (unspecified) cutoff value. This scaling form is a power law decay $r^{-\alpha}$ characterized by an exponent, α but modified by a scaling function $f_r(r/r_c)$, where r_c represents the upper cutoff. Over a range of r values, for which the scaling function is approximately constant, one obtains pure power law behavior. The scaling function $f_r(r/r_c)$ has the property that it decays to zero rapidly when its argument (r/r_c) becomes larger than 1 or when the tree diameter becomes larger than the cutoff value. In this regime, the PDF is dominated by a characteristic length, the cutoff scale, and pure power law behavior is lost. This ensures that the PDF appropriately vanishes when the tree diameter becomes larger than its cutoff value. Indeed, power law scaling is expected to hold only when the diameter is much smaller than its cutoff value. The exponent α is expected to be universal and depends only on certain essential attributes, whereas the scaling function f_r can depend on details such as the climate and the resource availability in a given forest. For another variable, such as the height h or the crown radius r_{cro} , the exponent α of the PDF has to be determined using the transformation rules described below. Such a scaling form can be used to describe the PDF of variables beyond the range over which they exhibit pure power law behavior.

When a scaling relation, $y \sim x^\omega$, exists between two random variables x and y (for example, x could be the height, h , and y could be the tree diameter, r), it is meant that the conditional probability distribution of y given x , $P_y(y|x)$, satisfies the relationship (we use P for the conditional probability of two random variables whereas we use p for PDF of a single random variable):

$$P_y(y|x) = 1/y \quad F_y(y/x^\omega). \quad [\text{S1}]$$

This is the correct generalization of the deterministic relation $y = x^\omega$ to a more general case in which the n th moment scales as $\langle y^n \rangle = c_n x^{\omega n}$, where the c_n s are constants. The deterministic case is obtained when $c_n = 1$. In the case, finite-size scaling holds for the PDF of random variable x , $p_x(x|x_c) = x^{-\alpha} f_x(x/x_c)$, the corresponding PDF for the random variable y , obeying Eq. S1, is $p_y(y|y_c) = y^{-(\alpha+\omega-1)/\omega} f_y(y/y_c)$ with the cutoffs transforming in the natural manner, i.e. $y_c = x_c^\omega$, and two scaling functions f_x and f_y related through an integral equation

involving the F_y that appears in Eq. S1. The power law exponent is the one it would be expected by the standard change of variable rule for PDF, i.e. $p_y(y) = p_x(x)|dx/dy|$ with $|dx/dy| = y^{(1-\omega)/\omega}$. As x varies, in principle, one would obtain independent curves $P_y(y|x)$ versus y . However, if Eq. S1 holds, all these curves can be collapsed on to a single curve if one plots $yP_y(y|x)$ (or equivalently the cumulative $P_y^>(y|x) = \int_y^\infty dy' P(y'|x)$) versus y/x^ω . In other words, for a given x , the characteristic scale of y is x^ω . Viewed in this manner, all curves appear the same. An example where Eq. S1 holds is shown in Fig. 2.

Derivation of Exponent α for Height PDF Using Finite Scaling. This is a derivation of the scaling exponent α for the PDF of the tree height, which is postulated to have the scaling form $p_h(h|h_c) = h^{-\alpha} f_h(h/h_c)$. We determine the exponent α by obtaining two different measures of the total volume of the forest and equating them. The first, Ah_c , is simply the product of the area of the forest and the characteristic height. The second measure is obtained by noting that the total number of trees with height in the range $(h, h + dh)$ is, according to hypotheses 3 and 4, given by $A p_h(h|h_c) dh$, and the volume of a tree of height h is given by h^{1+2H} . Thus, the total volume occupied by the forest in a plot of area A is given by:

$$Ah_c \propto A \int h^{1+2H} p_h(h|h_c) dh \propto h_c^{2H-\alpha} A. \quad [\text{S2}]$$

The last term is obtained using the assumed scaling form of $p_h(h|h_c)$, making the change of variable $x = h/h_c$, and including into the proportionality constant the integral $\int dx x^{1+2H} f_h(x)$. Equating the powers of h_c in the first and third terms of the above equation, one finds that, $\alpha = 1 + 2H$ or equivalently $p_h(h|h_c) \sim 1/h^{1+2H}$ for tree heights $h \ll h_c$.

Energy Equivalence. The total energy resources used in the forest is proportional to the total volume of the forest, Ah_c . This general result is independent of any scaling assumptions or the value of the H exponent. Thus the characteristic height of trees, h_c , is a measure of the average energy use per unit area or equivalently per tree. Therefore if we express the energy equivalence wrt a generic size variable $x \sim h^\gamma$, i.e. $p_x(x) \sim x^{-\frac{1+2H}{\gamma}}$ for $x < x_c \sim h_c^\gamma$, we obtain $E_{tot} \propto A \int x^{\frac{1+2H}{\gamma}} p_x(x|h_c^\gamma) dx \propto Ah_c^\gamma$ and this is in contrast with the scaling of energy per tree derived above, unless $\gamma = 1$.

Link Between Metabolic Ecology and Demographic Equilibrium Theory. Our approach allows one to bridge metabolic ecology (S6–S18) with demographic equilibrium theory (S19–S21).

On using the ontogenetic growth equation (S22–S24) with the generic finite-size scaling assumption (S2, S5), one gets the growth rate, $g(r) \sim r^c G(r/r_c)$ with $c = (2H - 1)/(2H + 1)$. The mortality rate, $m(r)$, can be obtained, following demographic equilibrium theory, and requiring that

$$\frac{\partial}{\partial r} [g(r)p_r(r|r_c)] + m(r)p_r(r|r_c) = 0. \quad [\text{S3}]$$

Inserting the finite size scaling equation for $p_r(r|r_c)$ in the previous equation leads to $m(r) \sim r^b M(r/r_c)$, with $b = c - 1 = -2/(1 + 2H)$ and $M(x) = 2G(x) - xdG(x)/dx - G(x)(x/f_r(x))(df_r(x)/dx)$. The choice $G, M = \text{constant}$ corresponds to the Muller-Landau et al. (S25) postulate of pure power law behavior, which is what happens here in the regime $r < r_c$, yielding

$M/G = 2$, independent of H . In ref. S25, this ratio was predicted to be $5/3$ based on the previous incorrect results of metabolic theory of refs. S8 and S15. When $H = 1$, $c = 1/3$ and $b = -2/3$ and are consistent with empirical data (S16) and agree with the predictions of refs. S8 and S15).

Derivation of Results Presented in Table 1. Here we present, as an example, the derivation of the probability distribution of metabolic rate B given the PDF of tree heights, as in Hypothesis 4, $p_h(h|h_c) = h^{-(1+2H)}f_h(h/h_c)$. As explained earlier, the scaling relation between B and h , $B \sim h^{1+2H}$, means that the conditional probability $P_B(B|h) = 1/BF_B(B/h^{1+2H})$. According to standard rules of combining probabilities one has

$$\begin{aligned} p_B(B|h_c) &= \int dh P_B(B|h) p_h(h|h_c) \\ &= \int dh \frac{1}{B} F_B(B/h^{1+2H}) h^{-(1+2H)} f_h(h/h_c) \\ &= B^{-\frac{1+4H}{1+2H}} f_B(B/h_c^{1+2H}). \end{aligned}$$

After performing the change of variable $z = B/h^{1+2H}$ in the last integral above, we find

$$f_B(x) = \frac{1}{1+2H} \int dz z^{-\frac{1+4H}{1+2H}} f_h[(xz)^{1/(1+2H)}] F_B(z).$$

1. Kadanoff LP (1966) Scaling laws for Ising models near Tc. *Physics* 2:263–272.
2. Fisher ME (1971) *Critical Phenomena*, eds Green MS (Academic, New York).
3. Widom B (1974) The critical point and scaling theory. *Physica* 73:107–118.
4. Wilson KG (1983) The renormalization group and critical phenomena. *Rev Mod Phys* 55:583–600.
5. Stanley HE (1999) Scaling, universality, and renormalization: Three pillars of modern critical phenomena. *Rev Mod Phys* 71:358–366.
6. West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.
7. Enquist BJ, Brown JH, West GB (1998) Allometric scaling of plant energetics and population density. *Nature* 395:163–165.
8. Enquist BJ, West GB, Charnov EL, Brown JH (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature* 401:907–911.
9. West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. *Nature* 400:664–667.
10. Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. *Nature* 410:655–660.
11. Niklas KJ, Enquist BJ (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc Natl Acad Sci USA* 98:2922–2927.
12. Enquist BJ (2002) Universal scaling in tree and vascular plant allometry: Toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiol* 22:1045–1064.
13. Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295:1517–1520.
14. Niklas KJ, Midgley JJ, Enquist BJ (2003) A general model for mass-growth-density relations across tree-dominated communities. *Evol Ecol Res* 5:459–468.

15. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
16. Enquist BJ, West GB, Brown JH (2009) Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proc Natl Acad Sci USA* 106:7046–7051.
17. West GB, Enquist BJ, Brown JH (2009) A general quantitative theory of forest structure and dynamics. *Proc Natl Acad Sci USA* 106:7040–7045.
18. West GB, Brown JH (2004) Life's universal scaling laws. *Phys Today* 57:36–42.
19. Coomes DA, Duncan RP, Allen RB, Truscott J (2003) Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. *Ecol Lett* 6:980–989.
20. Kohyama T, Suzuki E, Partomihardjo T, Yamada T, Kubo T (2003) Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *J Ecol* 91:797–806.
21. Muller-Landau HC, et al. (2006) Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. *Ecol Lett* 9:589–602.
22. West GB, Brown JH, Enquist BJ (2001) A general model for ontogenetic growth. *Nature* 413:628–631.
23. Banavar JR, Damuth J, Maritan A, Rinaldo A (2002) Ontogenetic growth (Communication arising) Modelling universality and scaling. *Nature* 420:626–626.
24. Stegen JC, White EP (2008) On the relationship between mass and diameter distributions in tree communities. *Ecol Lett* 11:1287–1293.
25. Muller-Landau HC, et al. (2006) Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecol Lett* 9:575–588.
26. Hubbell SP, Condit R, Foster RB (2005) *Barro Colorado Forest Census Plot Data*. Url: <http://ctfs.si.edu/datasets/bci>.

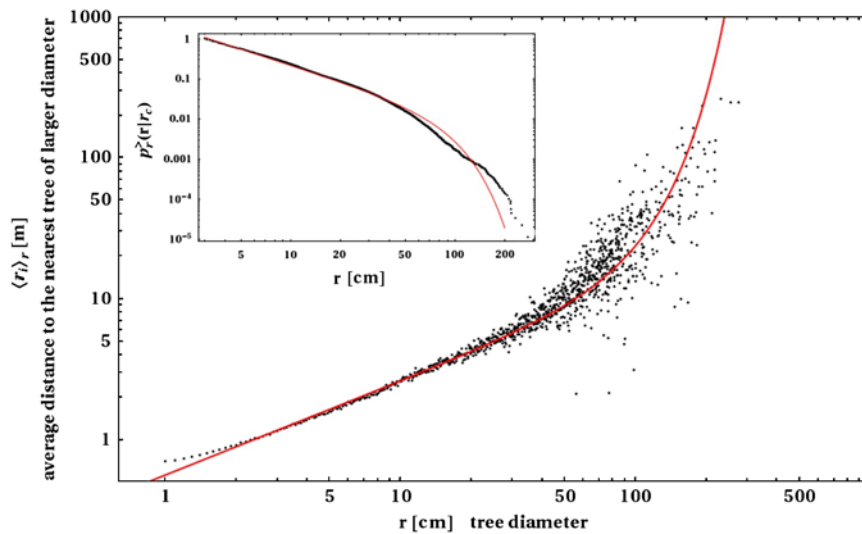


Fig. 51. Confirmation of the validity of finite-size scaling. The main panel shows a plot of the mean range of influence versus the stem diameter. The BCI diameter dataset were divided in 1 mm bin classes and for each class we measured the average distance to the nearest larger tree. The inset depicts the cumulative PDF of tree diameters for the BCI dataset (1995) (S26). $p_r^>(r/r_c)$ is the fraction of trees with diameter $\geq r$. The solid line shows a least squares fit with the function $p_r^>(r/r_c) = r^{-4/3}g(r/r_c)$, with $g(x) = \exp(-x^2/2)$. This functional form is consistent with our theory with a simple choice of a scaling function with r_c , the fitting parameter, equal to 86.6 cm. The precise fitting function g is somewhat arbitrary and we have chosen it to be a Gaussian. This choice is based on simplicity and merely serves to demonstrate how scaling can be used to interrelate two distinct patterns. r_c is the cutoff diameter and scaling is expected to hold for length scales much less than this cutoff value. This result is in accord with the direct determination of the scaling range (approximately 2.4–31.8 cm) obtained with the scaling collapse of $P_r^>(r_i|r)$ (see Fig. 2). The solid line in the main figure shows the average range of influence of trees of a given stem diameter, $\langle r_i \rangle_r$, using the estimate $\langle r_i \rangle_r \propto 1/\sqrt{p_r^>(r/r_c)} = 1.2r^{2/3}g(r/r_c)^{-1/2}$ with exactly the same $g(x)$ used in the inset and the value of r_c determined therein. The quality of the fit again demonstrates the validity of the scaling framework.