PRL **98,** 068104 (2007) PHYSICAL REVIEW LETTERS week ending 9 FEBRUARY 2007

Scaling in Ecosystems and the Linkage of Macroecological Laws

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(Received 12 July 2006; published 9 February 2007)

Scaling provides an elegant framework for understanding power-law behavior and deducing relationships between critical exponents. We demonstrate that scaling theory can be generalized to develop a framework for the analysis of diverse empirical macroecological relationships traditionally treated as independent. Our mathematical arguments predict links between the species-area relationship, the relative species abundance and community size spectra in excellent accord with empirical data.

DOI: 10.1103/PhysRevLett.98.068104 PACS numbers: 87.23.−n, 05.70.Jk, 87.23.Cc

There are many complex systems in nature which exhibit power-law behavior akin to those in critical phenomena. One of the most important of these are ecosystems [1,2]. Living organisms span 21 orders of magnitude in mass and there are many known algebraic relationships in ecology [3–12] (Fig. 1). Scaling [13] has proven to be a powerful tool in physics for unifying seemingly distinct phenomena and exploring relationships between apparently unrelated exponents. A physical system in the vicinity of a critical point is different from an ecosystem in several respects, and a straightforward application of scaling ideas in ecology is not possible for the following reasons: (i) there is a lack of knowledge of the Hamiltonian governing the dynamics of the ecosystem; (ii) in an ecosystem, there are no obvious dials similar to the temperature, pressure, and magnetic field in condensed matter physics to tune the system to or away from criticality; (iii) as a consequence there is no measure of how far from "criticality" an ecosystem is; and (iv) the scaling in an ecosystem involves quantities such as the number of species and their characteristic masses instead of standard variables such as temperature, pressure, and magnetic field, whose scaling is known from the singular behavior of physical quantities as the critical point is approached.

In this Letter, we generalize scaling in order to develop a unified framework for understanding ecological data. We connect seemingly distinct power-law relationships, we derive connections between apparently unrelated exponents, we derive bounds on the exponents, and in some cases we predict the exponent values. All our predictions are in excellent accord with empirical data, when available.

Consider an ecosystem of area A with S species [14]. A given species has a population abundance n and each individual is characterized by a mass m. The variables m and n will be treated as continuous variables, with nonzero lower bounds m_0 and n_0, respectively. Let us now introduce the joint probability distribution, $P(m, n|A)dm\,dn$, of finding a species with characteristic mass between m and $m + dm$ and population between n and $n + dn$ given that the ecosystem is in a stationary state in a region of area A. We make the following constructive hypotheses, the first of which is a scaling hypothesis, valid when power-law behavior is present, and the rest are based on empirical data or common sense:

$\mathcal{H}1$—This assumption postulates that:

$$P(m, n|A) = n^{-\Delta_1} m^{-\Delta_2} F\left(\frac{n}{A^{\Phi_1}}, \frac{m}{A^{\Phi_2}}\right). \qquad (1)$$

Note that m and n are *not* treated as independent variables

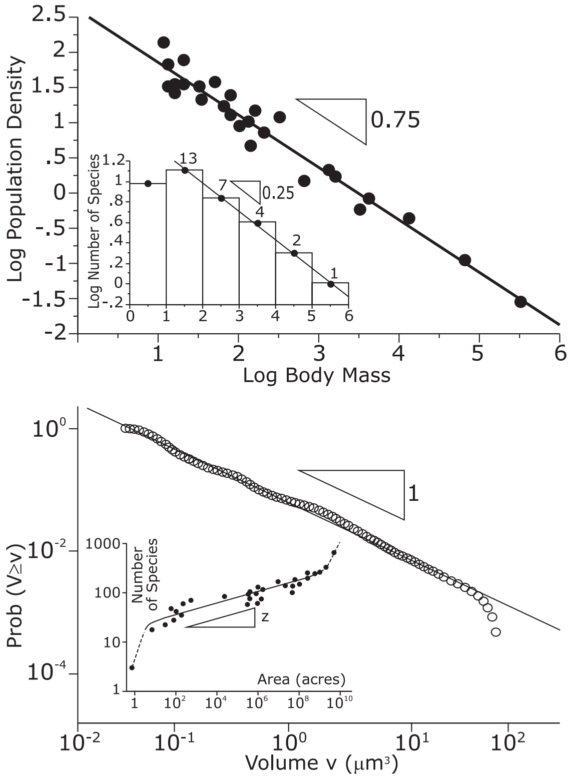

FIG. 1. Empirical evidence for scaling in ecology. Upper graph: population density regressed against mean body mass [7] (inset: scaling of the number of species [9]). Lower graph: size spectrum for marine microbial organisms [6] (lower inset: typical empirical evidence for species-area relationships [1,2]).

and the scaling function F does not necessarily have a separable form. Based on the vast empirical evidence, P is chosen to have algebraic dependencies on m and n and this power-law behavior gets cut off by requiring that F decays to zero sufficiently fast when at least one of the arguments becomes large (e.g., F could be zero if at least one of its arguments is above some threshold or goes to zero exponentially in both arguments). Furthermore $F(x_1, x_2)$ becomes a function of one variable $f_i(x_i)$ when the other variable $x_j \to 0$ with $j \neq i$, and $f_i(x_i) \to$ const when $x_i \to 0$. From Eq. (1) it follows that A^{Φ_1} (A^{Φ_2}) represents the characteristic scale for the maximum population (mass). Note that $\Phi_i > 0$ and, for self-consistency [see the normalization condition after Eq. (3)], $1 \leq \Delta_i$, $i = 1, 2$.

$\mathcal{H}2$—The total population N ought to be proportional to the area [9] A: $N \propto A$.

$\mathcal{H}3$—The total mass of all organisms M present in the ecosystem scales as the area, A, $M \propto A$. While a superlinear dependence of M on A might be viable over a small range of variation in A, it is not sustainable as A becomes large. On the other hand a sublinear dependence would not correspond to a fully developed ecosystem.

$\mathcal{H}4$—This assumption appeals again to the requirement of a fully developed ecosystem: the mass distribution of all organisms is as spread as possible, compatible with the previous hypotheses, having the effect of maximizing biodiversity. Our concern is with the comparatively simple situation of the steady state behavior in which, over evolutionary time, resources are exploited in full, individual and collective metabolic needs are met, and enough time has elapsed to produce a rough balance between speciation and extinction and ecological fluxes.

$\mathcal{H}5$—This assumption postulates that the threshold population for extinction does not depend on the characteristic mass of the species.

The simplified assumptions $\mathcal{H}2$, $\mathcal{H}3$, and $\mathcal{H}5$ can be readily generalized, if necessary for specific situations, by the introduction of nontrivial exponents for the scaling behavior of the total population and mass on the area and for the dependence of the extinction threshold on the species mass. It is straightforward to modify our analysis to incorporate such scaling.

The exponents Δ_i and Φ_i, $i = 1, 2$, are our concern here because, unlike the scaling function F, they are robust and typically fall into certain universality classes [13]. We will show that they are not independent within our framework, that they are related to observable power laws and to each other, and that self-consistency will constrain the ranges of values of these exponents.

We illustrate the mathematics involved in our analysis by considering the fraction of organisms with mass between m and $m + dm$, $P_m(m|A)$, where the mass m of an organism is assumed to be greater than or equal to m_0, the mass of the smallest sized organism, and less than or equal to M_A, the mass of the largest sized organism, which is assumed to scale as $M_A \sim A^{\Phi_2}$. The scaling hypothesis for this simpler case is

$$P_m(m|A) = m^{-\Delta_2} F_m\left(\frac{m}{M_A}\right),$$

with $F_m(x)$ approaching a constant when $x \to 0$ and zero sufficiently fast when $x \gg 1$. This scaling form will be derived below starting from Eq. (1). The qth moment of the distribution is defined as

$$\begin{aligned} I_q \equiv \langle m^q \rangle &= \int_{m_0}^{\infty} dm\, m^q P_m(m|A) \\ &= M_A^{1+q-\Delta_2} \int_{m_0/M_A}^{\infty} dx\, x^{q-\Delta_2} F_m(x). \end{aligned}$$

By splitting the integral into two parts, one integrated from m_0/M_A to, say, 1 and the other from 1 to ∞ (thus yielding a finite number independent of M_A), and using the assumption regarding the asymptotic behavior of F_m at small and large arguments one obtains

$$\begin{aligned} \langle m^q \rangle &= M_A^{1+q-\Delta_2}\{c_1 + c_2 M_A^{\Delta_2-1-q} + \text{less singular terms}\} \\ &\sim M_A^{\max(0,1+q-\Delta_2)}. \end{aligned}$$

The last step follows by noting that as $M_A \to \infty$, one has two possibilities. If $\Delta_2 - 1 - q < 0$, the dominant term is c_1 and the scaling is the same as the one following from naïve dimensional analysis, i.e., $\langle m^q \rangle \propto M_A^{q+1-\Delta_2}$. This result is what one would obtain from power counting in the integral $\int_{m_0}^{\infty} dm m^q P_m(m|A)$: the q arises from the m^q term, the 1 from the dm term, and $-\Delta_2$ from the scaling postulated above. If, on the other hand, $\Delta_2 - 1 - q > 0$, the dominant term of $\langle m^q \rangle$ is the second term. Thus $\langle m^q \rangle \sim$ const and naïve scaling analysis fails. The normalization condition $I_0 = 1$ implies that $\Delta_2 > 1$.

Using Eq. (1) and simple mathematics of the type illustrated above, we obtain an expression for a general moment of P at large areas A (see Ref. [15]):

$$\begin{aligned} I_{q_1,q_2} &\equiv \langle n^{q_1} m^{q_2} \rangle \\ &= \int_{n_0}^{\infty} \int_{m_0}^{\infty} dn\, dm\, n^{q_1} m^{q_2} P(m, n|A) \sim A^{\psi_{q_1,q_2}}, \end{aligned} \tag{2}$$

where

$$\begin{aligned} \psi_{q_1,q_2} = {} & \max\{0, (1 + q_1 - \Delta_1)\Phi_1\} \\ & + \max\{0, (1 + q_2 - \Delta_2)\Phi_2\}. \end{aligned} \tag{3}$$

The normalization condition $I_{0,0} = 1$ implies $\Delta_i \geq 1$. Several relationships follow from considering suitable choices of q_1 and q_2:

(i) *The species-area relationship* [1].—If N is the total number of organisms and S is the total number of species in the ecological system then their ratio is given by $N/S = I_{1,0} \propto A^{\psi_{1,0}}$. On using the previous results $\psi_{1,0} = \Phi_1(2 - \Delta_1)$ when $\Delta_1 < 2$, a self-consistency re-

TABLE I. Linked scaling relationships derived from Eq. (1). Summary of the main scaling relationships as a function of the proposed independent exponents Δ_1, Δ_2, Φ_1, Φ_2: S is the number of species within an ecosystem of area A; m and n denote the characteristic body mass and the numerical abundance, respectively, of a species; M_A denotes the largest body size; P_m is the community size distribution, the fraction of organisms in a given size class m, regardless of their species; P_S denotes the fraction of species in a given size class; $S(L|A)$ is the total number of species, whose organisms have a characteristic linear size L; and P_{RSA} represents the relative species-abundance relationship, the fraction of species with population abundance n. The scaling functions are inter-related (see text). Note that $F_m(x)$, $F_S(x)$, $\hat{F}_S(x)$, $F_{RSA}(x) \to 0$ as $x \to \infty$. All these functions, except $\hat{F}_S(x)$, approach a constant value as the argument approaches zero (see text). Pure power-law behavior is predicted to hold only when the scaling function is approximately constant over a range of its argument. This holds in all the cases except for $S(L|A)$, a quantity discussed in Ref. [10].

Derived relationship	Relation of exponents with Δ_1, Δ_2, Φ_1, Φ_2	Ideal values
$S \sim A^z$	$z = 1 - \Phi_1(2 - \Delta_1)$	$z = \frac{1}{4}$
$M_A \sim A^{\Phi_2}$	$\Phi_2 = 1/\Delta_2$	$\Phi_2 = \frac{1}{2}$ $\Delta_2 = 2$
$P_m(m|A) = m^{-\Delta_2} F_m(\frac{m}{A^{\Phi_2}})$		
$P_S(m|A) = m^{-\Delta_2} F_S(\frac{m}{A^{\Phi_2}})$		
$S(L|A) = L^{-\Delta_2'} \hat{F}_S(\frac{L}{A^{\Phi_2/3}})$	$\Delta_2' = \frac{3}{\Phi_2}[\Phi_2(\Delta_2 - 1) + \Phi_1(2 - \Delta_1) - 1]$	$\Delta_2' = \frac{3}{2}$
$P_{RSA}(n|A) = n^{-\Delta_1} F_{RSA}(\frac{n}{A^{\Phi_1}})$		$\Phi_1 = \frac{3}{4}$ $\Delta_1 = 1$

quirement imposed by the physically valid range of the species-area relationship exponent (see below). Using hypothesis $\mathcal{H}2$, one obtains

$$S \sim A^z \quad \text{with } z = 1 - \Phi_1(2 - \Delta_1). \tag{4}$$

Because the total number of species cannot grow faster than the total population one has $0 < z \leq 1$ leading to the constraint $\min\{1, 2 - 1/\Phi_1\} \leq \Delta_1 < 2$ where the bound $\Delta_1 \geq 1$, derived above, has also been taken into account.

(ii) *The scaling of total ecosystem biomass* [9].—A measure of the total mass of all organisms, M, is obtained by $I_{1,1} = M/S = A^{\psi_{1,1}}$. On using Eq. (4):

$$M \sim A^{1+\max[0,\Phi_2(2-\Delta_2)]} \tag{5}$$

Were $\Delta_2 < 2$, Eq. (5) would yield a superlinear growth of M with A. This may be viable over a small range of variation in A but is not sustainable as A becomes large. Hypothesis $\mathcal{H}3$ then leads to the inequality $\Delta_2 \geq 2$.

(iii) *The community size spectrum* .—The fraction of individuals in a given size class regardless of species, is given by (see Ref. [15]):

$$P_m(m|A) = \frac{S}{N} \int dnnP(n, m|A) = m^{-\Delta_2} F_m\left(\frac{m}{A^{\Phi_2}}\right), \tag{6}$$

where $F_m(x_2) = \int_0^\infty dx_1 x_1^{1-\Delta_1} F(x_1, x_2)$ and the lower limit of the integration interval has been safely extended to zero due to the hypothesis on the behavior of $F(x_1, x_2)$ at small x_1 and the fact that $\Delta_1 < 2$. Our assumption regarding the behavior of F at small x_2 leads to $F_m(x_2)$ approaching a constant value as x_2 approaches zero, thus yielding a pure power-law behavior of $P_m(m|A)$ in the large area limit. The largest possible spread of body size (m), which should characterize fully developed ecosystems, hypothesis $\mathcal{H}4$, results in Δ_2 approaching its lowest possible value consistent with the inequality derived by Eq. (5), i.e., $\Delta_2 = 2$, which is in excellent accord with pervasive empirical observations [5,6].

(iv) *The scaling of the mass of the biggest organism* [4].—In order to ensure the long term survival of a species, it is necessary that it exceed a threshold population [16], scaling according to hypothesis $\mathcal{H}5$. The population of the species of the largest body size must equal this number and is given by the product of the total population (which scales linearly as area A) and $P_m(M_A|A)$ (which scales as $M_A^{-\Delta_2}$) leading to $M_A \sim A^{1/\Delta_2} \sim A^{\Phi_2}$ and $\Phi_2 = 1/\Delta_2 = \frac{1}{2}$ [more generally from Eq. (5), $\Phi_2 \leq \frac{1}{2}$]. This prediction is consistent with recent analyses [3,4] of the maximum sizes of terrestrial herbivores and carnivores observed across ecosystem areas (A) spanning the range from small islands and isolated habitats up to whole continents. Note that Φ_2 could deviate from the predicted value if the size of the threshold population is dependent on body mass [3].

(v) *The species-mass relationship* [9].—Our theory predicts that the fraction of species in the mass interval (m, $m + dm$), i.e., $P_S(m, |A)dm$, has a scaling form similar to that of the community size distribution. The scaling hypothesis, Eq. (1), can be used to deduce that (see Ref. [15])

$$P_S(m, |A) = \int dnP(n, m|A) = m^{-\Delta_2} F_S\left(\frac{m}{A^{\Phi_2}}\right), \tag{7}$$

where $F_S(x_2) = f_2(x_2)$ (f_2 has been introduced in $\mathcal{H}1$) implying that $F_S(x_2)$ approaches a constant value at small arguments. The total number of species, whose organisms have a characteristic linear size $L \sim m^{1/3}$, in the logarithmic bin $d(\log L)$ is given by $S(L|A)d(\log L) \equiv A^z m P_S(m, A) d \log m$. From Eq. (7) we get

$$S(L|A) = L^{-\Delta_2'} \hat{F}_S\left(\frac{L}{A^{\Phi_2/3}}\right), \tag{8}$$

where $\Delta_2' = 3(\Delta_2 - \frac{z}{\Phi_2} - 1)$ and $\hat{F}_S(x) \propto x^{-3z/\Phi_2} F_S(x^3)$, which behaves as x^{-3z/Φ_2} at small argument. Note that, unlike $P_S(m|A)$ which at large areas converges to a pure power law m^{-2}, $S(L|A)$ scales as $L^{-3(\Delta_2-1)}A^z$, which is not only different from $L^{-\Delta_2'}$ but also has an A-dependent amplitude. Setting $z=\frac{1}{4}$, and noting that $\Delta_2 = 2$ and $\Phi_2 = \frac{1}{2}$, one obtains $\Delta_2' = 3/2$ in accord with a recent analysis [10] linking the scaling of the maximal body size, the species-area relationship and $S(L,|A)$.

(vi) *The relative species abundance* [11].—The fraction of species with population around n, is obtained as (see Ref. [15]):

$$P_{RSA}(n|A) = \int_{m_0}^{\infty} dmP(m,n|A) = n^{-\Delta_1}F_{RSA}\left(\frac{n}{A^{\Phi_1}}\right), \quad (9)$$

where $F_{RSA}(x_1) = f_1(x_1)$ (f_1 has been introduced in $\mathcal{H}1$). Note that $F_{RSA}(x_1)$ approaches a constant value as $x_1 \to 0$. A scaling form as in Eq. (9) has been shown to hold rigorously [17] for the self-similar model of Harte, Kinzig, and Green [12] with $\Delta_1 = 1$, which is our limiting value according to $\mathcal{H}1$. Using Eq. (4) one obtains in this case $\Phi_1 = 1 - z$.

Our main results are summarized in Table I. The scaling form for the relative species abundance holds exactly for the self-similar model of Harte, Kinzig, and Green [12]. In accord with empirical observations, the scaling analysis yields exponent values: $\Delta_2 = 2$ [5–8], $\Phi_2 = 1/2$ [3,4], and $\Delta_2' = \frac{3}{2}$ [10] on choosing the species-area relationship exponent $z = \frac{1}{4}$. Our results show that scaling theory provides a general framework for the analysis of macroecological data not only for establishing links between seemingly unconnected power-law relationships but also for assessing deviations from the idealized situation.

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[1] S. A. Levin, Ecology **73**, 1943 (1992); M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge University Press, Cambridge, 1995).

[2] J. H. Brown, *Macroecology* (University of Chicago Press, Chicago, 1995); J. H. Brown, G. B. West, and B. J. Enquist, in *Scaling in Biology*, edited by J. H. Brown and G. B. West (Oxford University Press, Oxford, 2000), pp. 1–24.

[3] P. A. Marquet and M. L. Taper, Evol. Ecol. **12**, 127 (1998).

[4] G. P. Burness, J. M. Diamond, and T. Flannery, Proc. Natl. Acad. Sci. U.S.A. **98**, 14 518 (2001).

[5] J. M. Blanco, F. Echevarria, and C. M. Garcia, Sci. Mar. **58**, 17 (1994).

[6] A. Rinaldo, A. Maritan, K. K. Cavender-Bares, and S. W. Chisholm, Proc. R. Soc. B **269**, 2051 (2002); K. K. Cavender-Bares, A. Rinaldo, and S. W. Chisholm, Limnol. Oceanog. **46**, 778 (2001).

[7] J. Damuth, Nature (London) **290**, 699 (1981); Biol. J. Linn. Soc. **31**, 193 (1987); Trends Ecol. Evol. **9**, 487 (1994).

[8] S. R. Kerr and L. M. Dickie, *The Biomass Spectrum: A Predator-Prey Theory of Aquatic Production* (Columbia University Press, New York, 2001).

[9] R. M. May, Science **241**, 1441 (1988); R. M. May and M. P. H. Stumpf, Science **290**, 2084 (2000).

[10] T. R. E. Southwood, R. M. May, and G. Sugihara, Proc. Natl. Acad. Sci. U.S.A. **103**, 6931 (2006).

[11] S. A. Levin, *Fragile Dominion: Complexity and The Commons* (Perseus Books, Reading MA, 1999); J. B. Plotkin *et al.*, Proc. Natl. Acad. Sci. U.S.A. **97**, 10 850 (2000).

[12] J. Harte, A. Kinzig, and J. Green, Science **284**, 334 (1999).

[13] B. Widom, J. Chem. Phys. **43**, 3898 (1965); M. E. Fisher, Rep. Prog. Phys. **30**, 615 (1967); L. P. Kadanoff *et al.*, Rev. Mod. Phys. **39**, 395 (1967); K. G. Wilson, Rev. Mod. Phys. **55**, 583 (1983); H. E. Stanley, Rev. Mod. Phys. **71**, S358 (1999).

[14] Our analysis is carried out in two dimensions. While a terrestrial ecosystem is manifestly two dimensional, marine systems can also be thought of as being two dimensional because the water depth “used” by the ecosystem does not vary significantly as the lateral extensions change. Plankton primarily exploit a relatively narrow layer of surface water because light attenuates rapidly in water.

[15] See EPAPS Document No. E-PRLTAO-98-053708 for supplementary material regarding the detailed mathematical derivation of the key results. For more information on EPAPS, see http://www.aip.org/pubservs/epaps.html.

[16] M. E. Soulé, *Viable Populations for Conservation* (Cambridge University Press, Cambridge, 1987).

[17] J. R. Banavar, J. Green, J. Harte, and A. Maritan, Phys. Rev. Lett. **83**, 4212 (1999).