

The fractal nature of nature: power laws, ecological complexity and biodiversity

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Underlying the diversity of life and the complexity of ecology is order that reflects the operation of fundamental physical and biological processes. Power laws describe empirical scaling relationships that are emergent quantitative features of biodiversity. These features are patterns of structure or dynamics that are self-similar or fractal-like over many orders of magnitude. Power laws allow extrapolation and prediction over a wide range of scales. Some appear to be universal, occurring in virtually all taxa of organisms and types of environments. They offer clues to underlying mechanisms that powerfully constrain biodiversity. We describe recent progress and future prospects for understanding the mechanisms that generate these power laws, and for explaining the diversity of species and complexity of ecosystems in terms of fundamental principles of physical and biological science.

Keywords: biodiversity; ecology; fractal; power law; scaling; self-similarity

1. BACKGROUND

The Earth's surface and the living things that inhabit it are incredibly diverse. The Earth presents an abiotic template of geology, physical oceanography and limnology, and climate that varies on a scale from the largest oceans, continents, lakes and rivers to the tiniest microsites. Billions of individual organisms belonging to millions of species are distributed over the Earth. They interact with each other and the abiotic environment on time-scales from microseconds to millennia and on spatial scales from a few micrometres to the entire globe. Underlying this enormous physical and biological diversity, however, are emergent patterns of ecological organization that are precise, quantitative, and universal or nearly so. Examples include the latitudinal, elevational and other gradients of species diversity, the way that species are aggregated into genera and higher taxonomic categories, the body sizes and relative abundances of coexisting species in ecological communities, the way that species diversity changes with sample area, and the successional changes in productivity, biomass and species composition and diversity following disturbance (Williams 1964; MacArthur 1972; Brown 1995).

These emergent general features of ecological systems provide powerful clues about the underlying mechanisms that constrain ecological complexity and regulate biodiversity. On the one hand, the emergent patterns represent the

outcome of the fundamental law-like processes of physics, chemistry and biology. Many of these mechanisms are well understood. They include thermodynamics, conservation of mass and energy, atomic particles and chemical elements, chemical stoichiometry, geological tectonics and erosion, laws of biological inheritance, evolution by natural selection, and many others. It is obvious that they must play a role in regulating biodiversity. On the other hand, it is far from clear how these fundamental processes act and interact to produce the emergent patterns of diversity. There remains the challenge of elucidating how these fundamental processes give rise to ecological systems that are simultaneously extremely variable and highly constrained. Most of the emergent ecological phenomena mentioned above have been recognized for decades and sometimes for centuries. Nevertheless, theoretical explanations in terms of basic physical and biological principles have remained elusive.

We focus on one restricted class of emergent ecological phenomena: scaling relationships that are self-similar or fractal-like over a wide range of spatial or temporal scales. These patterns can be characterized mathematically by an elegantly simple form, the power function:

$$Y = Y_0 X^b, \quad (1.1)$$

where Y is a dependent variable, Y_0 is a normalization constant, X is the independent variable, and the exponent b is another constant. Taking the logarithms of both sides of this equation gives the expression for a straight line:

$$\log Y = \log Y_0 + b \log X. \quad (1.2)$$

Thus, the statistics of linear regression can be used to fit power functions to data (figure 1).

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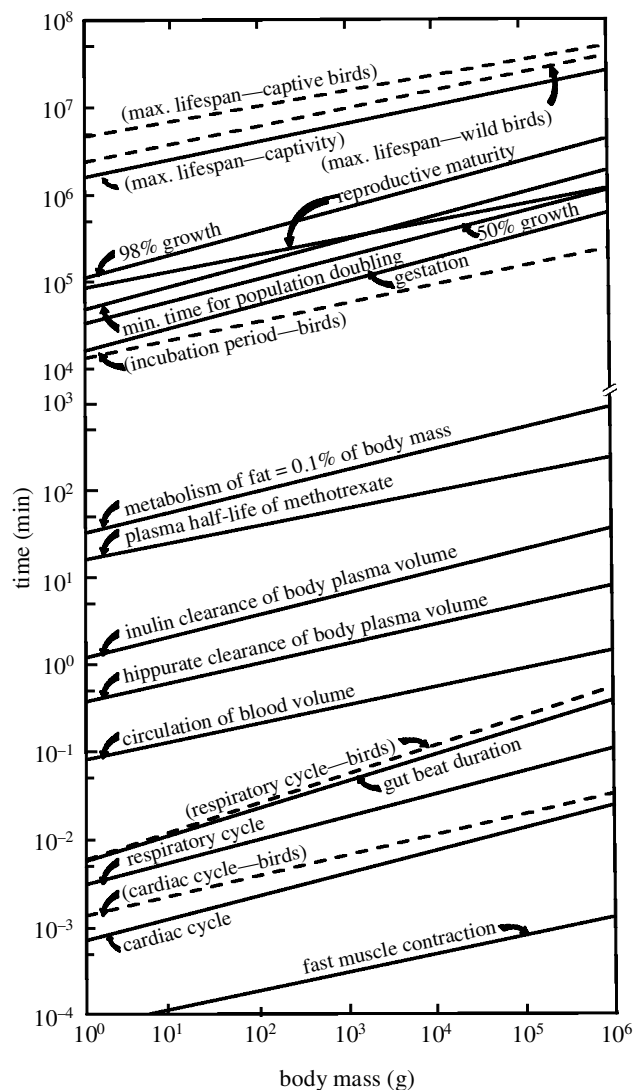


Figure 1. Examples of quarter-power allometries in biology: a wide variety of biological times, from twitch times of muscles measured in milliseconds to lifespans measured in years, all scale very close to the $1/4$ power of body mass, as indicated by the similar slopes of regression lines fitted to data for mammals (solid lines) and birds (dashed lines). From Linstedt & Calder (1981), with permission.

At least some of the documented power laws appear to be universal: they apply to plants, animals and microbes; to terrestrial, marine and freshwater habitats; and to human-dominated as well as 'natural' ecosystems. The self-similarity reflects powerful constraints on the organization of complex systems—constraints that are consequences of a few basic physical, biological and mathematical principles. Structures and processes that are self-similar over many orders of magnitude provide a means for extrapolating between scales: between the large scale of the globe, region, ecosystem or habitat where ecological relationships appear to be complex, and the small scale of the field or laboratory experiment where hypotheses can be tested and mechanisms can be studied. Most importantly, the study of scaling is one powerful way of simplifying ecological complexity and of understanding the physical and biological principles that regulate biodiversity.

2. A CRITICAL PERSPECTIVE ON SCALING RELATIONS

We develop two themes: (i) scaling relationships, power laws and fractals provide a powerful analytical framework for investigating universal principles that govern the structure and dynamics of complex ecological systems; (ii) scaling relationships offer clues to how the laws of physics and chemistry and the fundamental processes of organismal biology give rise to emergent features of biodiversity.

(a) Power functions

Power functions describe three classes of phenomena. Placing ecological scaling relationships into one of these classes clarifies the nature and domain of self-similar behaviour and facilitates the search for underlying mechanistic principles.

The first class includes those power laws whose constants exhibit a limited range of values. Of particular interest are values of the scaling exponent, b , which are often simple multiples of a number. For example, phenomena that exhibit Euclidean geometric scaling have exponents that are multiples of $1/3$ when the independent variable, X , is mass (M) or volume (V): i.e. linear dimensions scale as $V^{1/3}$ and surface areas as $V^{2/3}$. Biological allometries, in contrast, are the scaling of traits with respect to body mass, M . These power laws tend to have exponents that are multiples of $1/4$: whole organism metabolic rate scales as $M^{3/4}$; development time, lifespan and other biological times as $M^{1/4}$; and heart rate, maximum rate of population growth r_{\max} and other rates as $M^{-1/4}$ (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Charnov 1993; Brown & West 2000). The constrained values of the exponent can provide invaluable clues to the fundamental processes that govern the scaling behaviour. Thus, for example, the pervasive quarter-power scaling in biology apparently reflects the fractal-like designs of resource distribution networks (West *et al.* 1997, 1999*a,b*).

The normalization constants, Y_0 , also provide clues to underlying mechanisms. For example, in biological allometry, values of Y_0 often differ among taxa and environmental settings. The normalization constants appear to be related to fundamental constraints on the system: (i) differences among taxa in whole-organism power or production and in its differential allocation to maintenance, growth and reproduction; and (ii) differences among environments in the availability of energy, nutrients or other essential resources. For example, Y_0 for growth in diameter differs among coexisting tree species in a tropical forest, but much of this is due to variation in wood density, so that the rate of carbon allocation to growth is actually quite similar among species (Enquist *et al.* 1999). Thus, a seemingly general law of growth can be derived by relating the measured changes in diameter to the normalization constant via tissue density.

The second class of ecological power laws is not so constrained. In empirical equations the constants Y_0 and b take on a wide range of values. For example, a power function gives a close fit to the relationship between variances and means of the time-series for population densities of a single insect species at multiple, spatially separated, sites (Taylor *et al.* 1980; Taylor 1961, 1986). However, different species have statistically different values of Y_0 and b . Brian Maurer (1999 and personal communication)

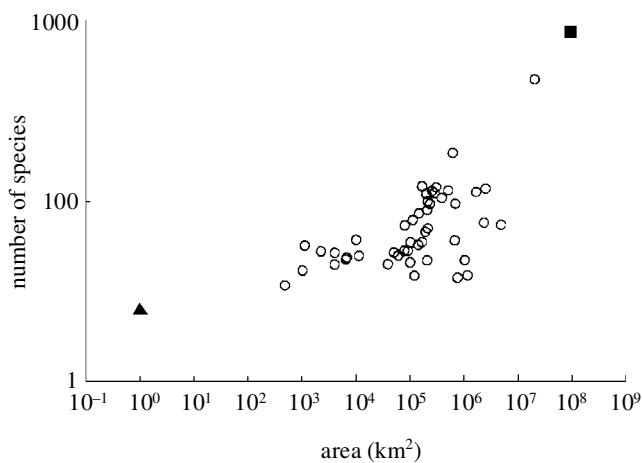


Figure 2. Species–area relationship for North American terrestrial mammals: (i) filled triangle, the average for 23 small patches of relatively homogeneous habitat; (ii) open circles, biomes; (iii) filled square, the entire continent. Although species–area relationships frequently appear linear when plotted on logarithmic axes, suggesting that they are scale-invariant, this is probably due to the fact that the sample areas vary by only a few orders of magnitude. As here, when data for a number of species are available for areas spanning many orders of magnitude, the relationship typically has this distinctively curvilinear, concave-upward shape. From Brown (1995).

obtains similar results for time-series of North American bird species. Scaling relationships that vary may reflect mixtures of lognormal distributions with different variances (Allen *et al.* 2001). Li *et al.* (1992) introduced a simple mathematical transformation based on weighted variances to form a stable distribution from combinations of such mixed distributions. Magnitudes of variation in species-specific parameters determine the values of Y_0 and b .

At first glance, such relatively unconstrained power functions may seem to offer few clues to specific physical and biological mechanisms. The possibility exists, however, that most of the variation is due to some key process, which can be characterized in terms of a parameter or combination of parameters. One example is the way that the Reynolds number can be used to reduce three key parameters of fluid flow (viscosity, path length and velocity) to a single key variable in studies of biomechanics and allometry (Koehl 1995, 2000).

The third class of ecological scaling relationships may not represent examples of self-similar behaviour over a wide range of scales. Examples may include species–area and species–time relationships and distributions of abundances or body sizes among species within a community. There is a long tradition of fitting species–area data with power functions (Willis 1922; Preston 1962; MacArthur & Wilson 1967; Hubbell 1995, 2001; Rosenzweig 1995; Scheiner *et al.* 2000). Some authors have suggested, however, that these relationships tend not to be self-similar over many orders of magnitude (figure 2; Williams 1964; Connor & McCoy 1979; Brown 1995; Rosenzweig 1995). There is also the question of whether exponents of species–area relationships vary widely or tend to take on a particular value, such as 1/4. In the case of species–abundance distributions, it is known that the data are

often at least as well fitted by other mathematical distributions as by power functions (see discussions in Whitaker 1970; May 1975; Tokeshi 1990).

(b) Physical and biological bases of biodiversity

One of the greatest challenges to modern science is to develop a unified theory of biodiversity. Can the variety of living things and ecological systems be explained in terms of relatively simple laws or principles? We are optimistic. We see evidence for such principles in the emergent general features of biodiversity, including the power laws that apply to biology and ecology. In our view, such ‘scaling laws’ are mathematical descriptions of important patterns in nature. But they are not scientific laws, because they do not describe the processes or mechanisms that give rise to the patterns. The spiral patterns of stars in a galaxy or water in a drain are not physical laws but the emergent outcomes of physical laws operating in complex systems containing many particulate interacting components. Similarly, we hypothesize that at least some ecological scaling relations reflect the outcome of underlying laws. The power laws can be used inductively, as empirical patterns that suggest how universal principles of ecology arise from the laws of physics, chemistry and biology.

3. RECENT PROGRESS

We can best illustrate how empirical power laws can lead to the formulation and testing of mechanistic hypotheses with a few well-chosen examples from allometry and river networks. Recent developments in allometric theory reinforce earlier studies by emphasizing that size is one of the major axes of biological variation. Living organisms range in body mass over an amazing 21 orders of magnitude, from 10^{-13} g bacteria to 10^8 g whales. For nearly a century biologists sought an explanation for the pervasive quarter-power allometric scaling, not only of metabolic rate, but also of many other anatomical, physiological, life history and ecological characteristics of plants and animals. West *et al.* (1997, 1999a,b) have developed models that explain these uniquely biological quarter-power scaling relationships in terms of organism-level structure and function, physical principles and geometric design. Because metabolism reflects both resource uptake from the environment and resource allocation to maintenance, growth and reproduction, it is possible to extend these models to account for the scaling of such ecological phenomena as population densities and growth rates of trees in forest stands (figure 1; Enquist *et al.* 1998, 1999). The allometric perspective guides the formulation of new theory for populations, communities and ecosystems based on the effects of body size and energetics.

A second example comes from research on river networks. A great deal of global biodiversity can be attributed to spatial variation in abiotic conditions and biotic interactions. The heterogeneity of terrestrial landscapes is due largely to tectonic and erosional processes that generate landforms and drainage basins. Classic scaling relations have been described for river networks (Horton 1945; Gupta & Waymire 1989, 1998a,b; Peckham & Gupta 1999). Variations of flows, velocities, depths, widths and

slopes take the general form $Y \propto Q^b$, where Y is the hydraulic-geometric variable, Q is stream discharge and related to size of a basin, and b is a scaling exponent (Leopold & Miller 1956; Ibbitt *et al.* 1998). The similarity of biological and river networks suggests that the three assumptions of West *et al.* (1997) might also be applied to river systems. For example, their assumption of a self-similar (fractal) vessel network corresponds exactly to the law of stream numbers described by Horton (1945) more than 50 years ago. Recent analyses of medium to large river networks find empirical bifurcation ratios, R_b , between 4.1 and 4.7 (Peckham 1995; Peckham & Gupta 1999), which are in contrast to the well-known random model where $R_b = 4.0$. A self-similar statistical theory can explain this feature (Veitzer & Gupta 2000). However, we hypothesize that an allometric derivation of R_b is also needed. The second assumption of invariant capillary diameter has its parallel in the well-known Horton relationship where drainage density, d , is independent of the contributing drainage area, A . However, d varies systematically with the P-E index of net moisture influx, which compares precipitation and evapotranspiration (Abrahams 1984). Since flow from the contributing area determines the size of first-order channels, we can infer that the size of first-order channels for regions of similar P-E index are invariant with respect to basin size. Finally, the assumption of minimum stream power for the entire network, similar to the assumption of West *et al.* (1997) of minimum hydrodynamic resistance, has been used to predict fractal scaling exponents for river networks (Rinaldo *et al.* 1992; Rigon *et al.* 1993; Sun *et al.* 1994). But Maritan *et al.* (1996) have shown analytically that this global minimization condition, by itself, does not explain the observed fractal exponents.

Implicit in these two examples is optimism that power laws describe emergent patterns of nature that can be understood in terms of basic physical, chemical and biological principles.

4. FUTURE PROSPECTS

Although some emergent ecological phenomena cannot be described by power laws, scaling relationships are widespread. Work on fractals is filled with examples from ecology, biology and the Earth sciences (Mandelbrot 1983). Examples of ecological data that have been fitted with power functions include numbers of species within genera or higher taxonomic categories (Burlando 1990, 1993), magnitudes of fluctuations in populations (Taylor 1986; Keitt & Stanley 1998), influence of body size on diet, life history, population density and species diversity (Yoda *et al.* 1963; Peters 1983; Calder 1984; Morse *et al.* 1985; May 1986; Reiss 1989; Lawton 1990; Charnov 1993; Enquist *et al.* 1998, 1999; Ritchie 1998; Ritchie & Olff 1999; Li & Charnov 2001), patterns of plant structure (Morse *et al.* 1985; Niklas 1994), properties of food webs (Ulanowicz & Wolff 1991; Martinez 1992), characteristics of stream networks and other landscape features (Gupta & Waymire 1989; Milne *et al.* 1992; Milne 1992, 1997, 1998_{a,b}; Rodriguez-Iturbe & Rinaldo 1997; Li 2000) and species-area and species-time relationships (MacArthur & Wilson 1967; Rosenzweig 1995; Harte & Kinzig 1997; Harte *et al.* 1999; Harte 2000).

Fitting these empirical relationships with power functions explicitly states the hypothesis that the organization of the system is fundamentally self-similar or fractal-like. It immediately suggests two lines of investigation.

(a) *Empirical characterization*

One line of investigation is better characterization of the empirical patterns. Are the relationships really self-similar? Over how many orders of magnitude has variation been analysed, and are there systematic deviations from self-similarity (i.e. from linearity in a log-log plot)? In theory, a perfect fractal is self-similar at all scales; it can be scaled up and down to infinity. Of course this is not true of any real biological or ecological system. The self-similarity is confined to a finite domain. West *et al.* (1997, 1999_b) call attention to the fact that many biological networks have terminal systems that are invariant, and this figures importantly in the quarter-power scaling. The terminal units may vary somewhat, but there is no consistent variation with respect to size. Examples of size-invariant units include the capillaries in mammals, leaves of plants, and zygotes (except for yolk content) of nearly all metazoan organisms. There is also a finite constraint at the other extreme. There is a limit to the maximum sizes of organisms, their parts, and the components of their abiotic environments. Because of these limits to self-similarity, it is preferable to refer to these systems as fractal-like.

It is also desirable, however, to ensure that scaling is indeed self-similar over many orders of magnitude before claiming that a system is fractal-like and proposing hypotheses that are based on some fundamentally fractal process. Examples are species-area and species-time relationships. A plot of number of species as a function of sample area on linear axes is usually curvilinear, but when the data are plotted on logarithmic axes the relationship is much more nearly linear. Power functions have customarily been used to fit such data (MacArthur & Wilson 1967; Rosenzweig 1995; but see Connor & McCoy 1979). Harte and colleagues (Harte & Kinzig 1997; Harte *et al.* 1999; Harte 2000) have assumed that species-area relations are self-similar, and have developed models to account for this feature. Typically, however, plots of species richness as a function of area encompass only a few orders of magnitude. When the data span a wider range of variation, the relationship is often curvilinear (see figure 2); this is especially apparent when the plots extend to very large spatial scales (Preston 1962; Williams 1964; Brown 1995; Rosenzweig 1995). This deviation from self-similarity raises questions about the number and kinds of mechanisms that need to be invoked to explain species-area and species-time relationships. It also suggests caution in extrapolating beyond the measured range of variation in using species-area or species-time scaling relations to make predictions about species diversity.

A more general issue is that other statistical distributions, such as lognormal and exponential, can appear quite linear on logarithmic plots, especially if the data include only part of the total distribution, or span only a limited range of variation (May 1975). This is an important distinction. If the data are better described by a lognormal or an exponential distribution rather than by a power law, this would imply different kinds of mechanistic hypotheses. In current applications of statistics to biologi-

cal or ecological data, there is often an unfortunate tendency to be satisfied with the 'model' or equation that gives a good fit. It is important, however, to consider the implications of the particular mathematical form of the equation.

(b) Mechanistic hypotheses

Self-similarity or fractality implies a particular kind of structural composition or dynamic behaviour. It implies that the fundamental features of the system exhibit an invariant, hierarchical organization that holds over a wide range of spatial scales (Gell-Mann 1994; Li 2000). Because only a few biological and ecological phenomena exhibit such self-similarity, and since special classes of processes are required to produce such fractality, empirical power laws suggest particular mechanistic hypotheses to explain the emergent characteristics of complex biological systems in terms of basic physical and biological principles.

Having said this, however, some qualification is required. There appears to be considerable variation in the kinds of processes that can give rise to power laws. On the one hand are very general phenomena that may not be very informative. For example, a wide variety of purely stochastic processes can give power-law distributions. One example is the widespread relationship between magnitude (G) and frequency (f), such that $G \propto 1/f$ or $G \propto f^{-1}$. Examples in biology include the frequency distributions of species among genera in taxonomic classifications (Burlando 1990, 1993; see also Williams 1964; Dial & Marzluff 1989; Solé *et al.* 2000) and perhaps of individuals among species in ecological communities (Williams 1964; Whittaker 1970; May 1975; Tokeshi 1990; Keitt & Stanley 1998). Famous examples from outside biology include the frequency distributions of sizes of earthquakes (Gutenberg–Richter law), of usage of words in written languages (Zipf's law) and of wealth among nations (Pareto distribution; Gell-Mann 1994). As mentioned above, combinations of lognormal distributions can give rise to power laws of this type (Allen *et al.* 2001). It seems an open question whether such widespread patterns reflect the operation of an interesting class of common mechanistic processes or just a large class of stochastic phenomena.

Somewhat similarly, power laws can emerge because of very general dimensional relationships among variables. In many examples of Taylor's power law for temporal fluctuations of animal populations, the variance in abundance, V , is related to the mean abundance, \bar{A} , as $V \propto \bar{A}^2$. This is expected, since it is the sum of the squared deviations from the mean: $V = \sum (A - \bar{A})^2$. Similarly, the fact that the connectance, C , of food webs seemingly scales with the number of species, S , as $C \propto S^2$ appears to be due to the simple dimensionality of food webs (Martinez 1992). Of course, the most familiar example of dimensionality is Euclidean geometric scaling, which characterizes the relationships between the three dimensions of length, l , area, A , and volume, V , so that in self-similar objects $A \propto l^2$, $V \propto l^3$, and $A \propto V^{2/3}$. This is not meant to imply that such simple dimensional scaling relationships are always uninteresting. For example, whereas many time-series of species abundances give Taylor power laws with the variance scaling as the square of the mean, some of

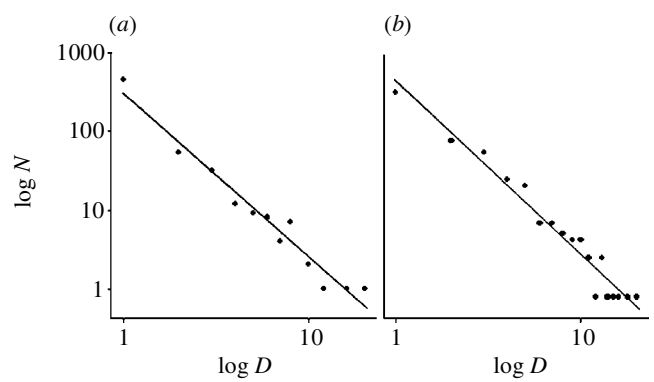


Figure 3. Relationships, plotted on logarithmic axes and fitted with power functions, for number of stems (N) as a function of trunk diameter (D) for all of the trees in two 0.1 ha plots of tropical rain forest in Colombia: (a) Tutunendo, Colombia, with 590 individuals of 271 species ($N = 316D^{-2.08}$, $r^2 = 0.96$), and (b) Baja Calima, Colombia, with 556 individuals of 263 species ($N = 501D^{-2.12}$, $r^2 = 0.96$). Note the goodness of fit of the power function (regression lines) and the similarity of the exponent to the predicted value of 2.0 (data: Gentry database; analysis: B. J. Enquist, J. H. Brown and G. B. West, unpublished data).

the variation in time and much of the variation over space exhibits different scaling exponents. These cases immediately raise unanswered questions about the underlying processes, such as the spatial scale of autocorrelations in important environmental variables and population responses.

Empirical power laws where the scaling exponents (b) and normalization constants (Y_0) take on a limited range of unusual values seem especially likely to lead to important insights into mechanisms. West *et al.* (1997, 1999a,b) hypothesize that the unique quarter-power exponents seen in the scaling of many biological traits with respect to body mass, M , has its origin in the fractal-like designs of distribution networks and exchange surfaces. The fractal geometry of these structures and functions endows them with a 'fourth spatial dimension' and causes them to scale with exponents that are simple multiples of 1/4 instead of multiples of 1/3 as would be expected from Euclidean geometric scaling. This theory raises many new questions about scaling of biological structure and function at levels of biological organization from molecules and cells to populations and ecosystems. For example, studies of plants by Enquist and collaborators have shown rates of whole-organism metabolism (respiration and production) scale as $M^{3/4}$ over 20 orders of magnitude, from single-celled algae to the largest trees (Niklas & Enquist 2001). As the metabolic rate sets the rate of resource demand that plants place on their environment, it is possible to develop resource-based models that predict the size structure, growth rates and life-history attributes of plants growing in single- and mixed-species stands (Enquist *et al.* 1998, 1999; West *et al.* 1999a). And these predictions are supported by data for the size distributions, productivity and biomass for a wide variety of forests from around the world (figure 3; Enquist *et al.* 2000; Enquist & Niklas 2001).

These applications to plants represent just a hint of the breadth of research still to be carried out. Until recently,

there was no widely accepted theory to explain the pervasiveness of quarter-power scaling in biology: in plants, animals and (probably) microbes; in terrestrial, freshwater and marine organisms; at levels of organization from molecules and cells to individual organisms to populations and ecosystems, and in traits from rates of biochemical reactions and durations of cell cycles, to rates of development and lifespans, to rates of population growth and times of ecological succession. Now, with a general theory of biological allometry, we have the potential to understand the pervasive role of size and scale in the diversity of life.

There is a similar potential to understand the mechanisms that underlie other emergent ecological phenomena that can be characterized by power laws. One promising candidate is the spatial and temporal heterogeneity of landscapes and the dynamics of ecological processes that play out on these templates. Features of landscapes often exhibit fractal-like properties (Milne 1991, 1992, 1998*b*; Li 2000), and these, in turn, affect the behaviour, abundance, distribution and diversity of organisms (Milne *et al.* 1992; Milne 1997; Ritchie 1998; Ritchie & Olf 1999). Perhaps the best example of an emerging theoretical basis for understanding the fractal-like properties of physical landscapes is the extensive work on stream networks (Horton (1945), Gupta & Waymire (1989), Rodriguez-Iturbe & Rinaldo (1997); and other references given above). What is still largely missing, but coming, is a synthesis that combines abiotic and biotic processes to characterize the structural and functional ecology of landscapes. For example, C. Restrepo, D. Kerkhoff and B. Milne (work in progress) have found that the distributions of the sizes of landslides on steep slopes of tropical mountains are well fitted by a power law. The size and frequency of landslides reflects strong feedback between ecological and geomorphic processes, including climate, geology, soil and vegetation. The wide variation in the sizes of patches undergoing succession in response to landslide disturbances probably affects species diversity and ecosystem productivity at local to regional scales.

5. CODA

Power laws are emergent general features of complex systems. Despite the complex and idiosyncratic features of organisms and the ecosystems where they occur, there are aspects of the structure and function of these systems that remain self-similar or nearly so over a wide range of spatial and temporal scales. Empirical power laws describe mathematically the hierarchical, fractal-like organization of these systems. Presumably these power laws reflect the outcome of simple rules or mechanisms. On the one hand, simple mechanisms that determine the structure and function of the fundamental components at the smallest scales constrain how these parts function when they are assembled in progressively larger subsets or hierarchies. On the other hand, simple mechanisms constrain the structure, and dynamics at the largest scales also place powerful limits on how the components interact and assemble in the large, complex system. Together, these bottom-up and top-down mechanisms give rise to power laws and other emergent features.

The twentieth century saw the triumph of reductionistic

science. Complex nature was pulled apart to reveal its fundamental parts, from subatomic particles in physics to genes and other molecules in biology. Powerful new tools provided unimaginable quantities of information. Enormous variety has been revealed. Now we are faced with the challenge of understanding the structures and dynamics of the complex systems themselves. We know that this cannot be done simply by assembling the parts in ever larger subsystems. There are just too many possibilities. Power laws and other emergent general features of these systems offer invaluable clues to the universal mechanisms that constrain the diversity of life and the complexity of nature.

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REFERENCES

- Abrahams, A. 1984 Channel networks: a geomorphological perspective. *Water Resources Res.* **20**, 161–186.
- Allen, A. P., Li, B.-L. & Charnov, E. L. 2001 Population fluctuations, power laws and mixtures of lognormal distributions. *Ecol. Lett.* **4**, 1–3.
- Brown, J. H. 1995 *Macroecology*. University of Chicago Press.
- Brown, J. H. & West, G. B. 2000 *Scaling in biology*. Oxford University Press.
- Burlando, B. 1990 The fractal dimension of taxonomic systems. *J. Theor. Biol.* **146**, 99–114.
- Burlando, B. 1993 The fractal dimension of evolution. *J. Theor. Biol.* **163**, 161–172.
- Calder III, W. A. 1984 *Size, function, and life history*. Cambridge, MA: Harvard University Press.
- Charnov, E. L. 1993 *Life history invariants*. Oxford University Press.
- Connor, E. F. & McCoy, E. D. 1979 The statistics and biology of the species area relationship. *Am. Nat.* **113**, 791–833.
- Dial, K. P. & Marzluff, J. M. 1989 Are the smallest organisms the most diverse? *Ecology* **69**, 1620–1624.
- Enquist, B. J. & Niklas, K. J. 2001 Invariant scaling relations across tree-dominated communities. *Nature* **410**, 655–660.
- Enquist, B. J., Brown, J. H. & West, G. B. 1998 Allometric scaling of plant energetics and population density. *Nature* **395**, 163–165.
- Enquist, B. J., West, G. B. & Brown, J. H. 2000 Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. In *Scaling in biology* (ed. J. H. Brown & G. B. West), pp. 167–198. Oxford University Press.
- Enquist, B. J., West, G. B., Charnov, E. L. & Brown, J. H. 1999 Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**, 907–911.
- Gell-Mann, M. 1994 *The quark and the jaguar. Adventures in the simple and the complex*. New York: Freeman.
- Gupta, V. K. & Waymire, E. 1989 Statistical self-similarity in river networks parameterized by elevation. *Water Resources Res.* **25**, 463–467.
- Gupta, V. K. & Waymire, E. 1998*a* Spatial variability and scale invariance in hydrologic regionalization. In *Scale dependence and scale invariance in hydrology* (ed. G. Sposito), pp. 88–135. Cambridge University Press.
- Gupta, V. K. & Waymire, E. 1998*b* Some mathematical aspects of rainfall, landforms, and floods. In *Advanced series in statistical sciences and applied probability*, vol. 7 (ed. O. E.

- Barndorff-Nielsen, V. K. Gupta, V. Perez-Abreu & E. C. Waymire), pp. 129–172. Singapore: World Scientific.
- Harte, J. 2000 Scaling and self-similarity in species distributions: implications for extinction, species richness, abundance, and range. In *Scaling in biology* (ed. J. H. Brown & G. B. West), pp. 325–342. Oxford University Press.
- Harte, J. & Kinzig, A. 1997 On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos* **80**, 417–427.
- Harte, J., Kinzig, A. & Green, J. 1999 Self-similarity in the distribution and abundance of species. *Science* **284**, 334–336.
- Horton, R. E. 1945 Erosional development of streams and their drainage basins; hydrophysical approach to quantitative morphology. *Bull. Geol. Soc. Am.* **56**, 275–370.
- Hubbell, S. P. 1995 Towards a theory of biodiversity and biogeography on continuous landscapes. In *Preparing for global change: a midwestern perspective* (ed. G. R. Carmichael, G. E. Folk & J. L. Schooner), pp. 171–199. Amsterdam: Academic Publishing.
- Hubbell, S. P. 2001 *The unified theory of biodiversity and biogeography*. Princeton University Press.
- Ibbitt, R. P., McKercher, A. I. & Duncaeri, M. J. 1998 Taieri River data to test channel network and river basin heterogeneity concepts. *Water Resources Res.* **34**, 2085–2088.
- Keitt, T. H. & Stanley, H. E. 1998 Dynamics of North American bird populations. *Nature* **393**, 257–260.
- Koehl, M. A. R. 1995 Fluid flow through hair-bearing appendages: feeding, smelling, and swimming at low and intermediate Reynolds number. In *Biological fluid dynamics, Soc. Exp. Biol. Symp.*, vol. 49 (ed. C. P. Ellington & T. J. Pedley), pp. 157–182. London: Company of Biologists.
- Koehl, M. A. R. 2000 Consequences of size change during ontogeny and evolution. In *Scaling in biology* (ed. J. H. Brown & G. B. West), pp. 67–86. Oxford University Press.
- Lawton, J. H. 1990 Species richness and population dynamics of animal assemblages. Patterns in body size: abundance and space. *Phil. Trans. R. Soc. Lond. B* **330**, 283–291.
- Leopold, L. B. & Miller, J. P. 1956 Ephemeral streams—hydraulic factors and their relation to the drainage net. US Geol. Surv. Prof. Paper 282A.
- Li, B.-L. 2000 Fractal geometry applications in description and analysis of patch patterns and patch dynamics. *Ecol. Model.* **132**, 33–50.
- Li, B.-L. & Charnov, E. L. 2001 Diversity-stability relationships revisited: scaling rules for biological communities near equilibrium. *Ecol. Model.* **140**, 247–254.
- Li, B.-L., Wu, Y. & Wu, J. 1992 Patchiness and patch dynamics: II. Description and analysis. *Chin. J. Ecol.* **11**, 28–37.
- Linstedt, S. L. & Calder, W. A. 1981 Body size, physiological time, and longevity of homeothermic animals. *Q. Rev. Biol.* **56**, 1–16.
- MacArthur, R. H. 1972 *Geographical ecology*. New York: Harper & Row.
- MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography*. Princeton University Press.
- Mandelbrot, B. B. 1983 *The fractal geometry of nature*. New York: Freeman.
- Maritan, A., Colaiori, F., Flammini, A., Cieplak, M. & Banavar, J. R. 1996 Universality classes of optimal channel networks. *Science* **272**, 984–986.
- Martinez, N. D. 1992 Constant connectance in community food webs. *Am. Nat.* **139**, 1208–1218.
- Maurer, B. A. 1999 *Untangling ecological complexity: the macroscopic perspective*. University of Chicago Press.
- May, R. M. 1975 Patterns of species abundance and diversity. In *Ecology and evolution of communities* (ed. M. L. Cody & J. M. Diamond), pp. 81–120. Cambridge, MA: Harvard University Press.
- May, R. M. 1986 The search for patterns in the balance of nature: advances and retreats. *Ecology* **67**, 1115–1126.
- Milne, B. T. 1991 Heterogeneity as a multi-scale phenomenon in landscapes. In *Ecological heterogeneity* (ed. J. Kolasa & S. T. A. Pickett), pp. 69–84. New York: Springer.
- Milne, B. T. 1992 Spatial aggregation and neutral models in fractal landscapes. *Am. Nat.* **139**, 32–57.
- Milne, B. T. 1997 Applications of fractal geometry on wildlife biology. In *Wildlife and landscape ecology* (ed. J. A. Bissonette), pp. 32–69. New York: Springer.
- Milne, B. T. 1998a Motivation and benefits of complex systems approaches in ecology. *Ecosystems* **1**, 449–456.
- Milne, B. T. 1998b Computation in ecological landscapes: multiscale nonequilibrium structure and dynamics. In *Proc. Escuela de Ciencia y Tecnología Comisión Atómico Constituyentes, Buenos Aires, Argentina*.
- Milne, B. T., Turner, M. G., Wiens, J. A. & Johnson, A. R. 1992 Interaction between the fractal geometry of landscapes and allometric herbivory. *Theor. Popul. Biol.* **41**, 337–353.
- Morse, D. R., Lawton, J. H., Dodson, M. M. & Williamson, M. H. 1985 Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* **314**, 731–733.
- Niklas, K. J. 1994 *Plant allometry: the scaling of form and function*. University of Chicago Press.
- Niklas, K. J. & Enquist, B. J. 2001 Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc. Natl Acad. Sci. USA* **98**, 2292–2297.
- Peckham, S. 1995 New results for self-similar trees with applications to river networks. *Water Resources Res.* **31**, 1023–1029.
- Peckham, S. D. & Gupta, V. K. 1999 A reformulation of Horton's law for large river networks in terms of statistical self-similarity. *Water Resources Res.* **35**, 2763–2777.
- Peters, R. H. 1983 *The ecological implications of body size*. Cambridge University Press.
- Preston, F. W. 1962 The canonical distribution of commonness and rarity. *Ecology* **43**, 185–215.
- Reiss, J. O. 1989 *The allometry of growth and reproduction*. Cambridge University Press.
- Rigon, R., Rinaldo, A., Rodriguez-Iturbe, I., Bras, R. L. & Ijjasz-Vasquez, E. 1993 Optimal channel networks: a framework for the study of river basin morphology. *Water Resources Res.* **29**, 1635–1646.
- Rinaldo, A., Rodriguez-Iturbe, I., Rigon, R., Bras, R. L., Ijjasz-Vasquez, E. & Mariani, A. 1992 Minimum energy and fractal structures of drainage networks. *Water Resources Res.* **8**, 2183–2195.
- Ritchie, M. E. 1998 Scale-dependent foraging and patch choice in fractal environments. *Evol. Ecol.* **12**, 309–330.
- Ritchie, M. E. & Olff, H. 1999 Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* **400**, 557–560.
- Rodriguez-Iturbe, I. & Rinaldo, A. 1997 *Fractal river networks*. Cambridge University Press.
- Rosenzweig, M. L. 1995 *Species diversity in space and time*. New York: Cambridge University Press.
- Schmidt-Nielsen, K. 1984 *Scaling, why is animal size so important?* Cambridge University Press.
- Scheiner, S. M., Cox, S. B., Willig, M. R., Mittelbach, G. G., Osenberg, C. W. & Kaspari, M. 2000 Species richness, species-area curves and Simpson's paradox. *Evol. Ecol. Res.* **2**, 791–802.
- Solé, R. V., Manrubia, S. C., Benton, M., Kauffman, S. & Bak, P. 2000 Criticality and scaling in evolutionary biology. *Trends Ecol. Evol.* **14**, 156–160.
- Sun, T., Meakin, P. & Jossang, T. 1994 The topography of optimal channel networks. *Water Resources Res.* **30**, 2599–2610.
- Taylor, L. R. 1961 Aggregation, variance and the mean. *Nature* **189**, 732–735.

- Taylor, L. R. 1986 Synoptic dynamics, migration and the Rothamsted Insect Survey: presidential address to the British Ecological Society. *J. Anim. Ecol.* **55**, 1–38.
- Taylor, L. R., Woiwod, I. P. & Perry, J. N. 1980 Variance and the large scale spatial stability of aphids moths and birds. *J. Anim. Ecol.* **49**, 831–854.
- Tokeshi, M. 1990 Niche apportionment or random assortment: species abundance patterns revisited. *J. Anim. Ecol.* **59**, 1129–1146.
- Ulanowicz, R. E. & Wolff, W. F. 1991 Ecosystem flow networks: loaded dice? *Math. Biosci.* **103**, 45–68.
- Veitzer, S. & Gupta, V. K. 2000 Random self-similar river networks and derivations of generalized Horton laws in terms of statistical simple scaling. *Water Resources Res.* **36**, 1033–1048.
- West, G. B., Brown, J. H. & Enquist, B. J. 1997 A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.
- West, G. B., Brown, J. H. & Enquist, B. J. 1999a A general model for the structure of plant vascular systems. *Nature* **400**, 664–667.
- West, G. B., Brown, J. H. & Enquist, B. J. 1999b The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* **284**, 167–169.
- Whittaker, R. H. 1970 *Communities and ecosystems*. New York: Macmillan.
- Williams, C. B. 1964 *Patterns in the balance of nature and related problems in quantitative ecology*. New York: Academic Press.
- Willis, J. C. 1922 *Age and area*. Cambridge University Press.
- Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. 1963 Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J. Biol., Osaka City Univ.* **14**, 107–129.