The Implications of Scaling Approaches for Understanding Resilience and Reorganization in Ecosystems

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Managing ecosystems for resilience—the capacity to maintain function in response to perturbation—is among the most pressing ecological and socioeconomic imperatives of our time. The variability of biological and ecological systems at multiple scales in time and space makes this task even more challenging, yet diverse ecological systems often display striking regularities. These regularities often take the form of scaling laws, which describe how the structure and function of the system change systematically with scale. In this article, we review recent work on the scaling of human settlement sizes and fertility as well as the size distributions of forests. We demonstrate that systematic departures from expected ecological scaling relationships may indicate particular structuring processes (e.g., fire) or the perturbation and reorganization of ecosystems. In sum, we argue that scaling provides a powerful tool for understanding resilience and change in ecological systems.

Keywords: allometry, forest structure, adaptive management, energetic equivalence rule, human ecology

s humans increasingly dominate the material and energetic dynamics of the biosphere, the growing ecological impact of our species compels us to manage the dynamics of natural systems on an unprecedented scale, in the face of great uncertainty (Hannah et al. 1994, Vitousek et al. 1997, Sanderson et al. 2002, Imhoff et al. 2004). Moreover, our dependence on the nonhuman biosphere is also global in scope-indeed, the estimated economic value of global ecosystem services is comparable to that yielded by all human economic endeavors (Costanza et al. 1997). Thus, understanding factors that contribute to the resilience of ecological systems-that is, the capacity of those systems to keep functioning in the face of disturbance-is critical for developing a sustainable global human population and ensuring human well-being (Gunderson 2000, Carpenter et al. 2001, Folke et al. 2002, Wackernagel et al. 2002, Diaz et al. 2006). However, ecological systems are remarkably dynamic, variable, and complex, and the formulation of a general, operational theory of ecological resilience, or even the delineation of common means of measuring resilience across systems, has proved difficult (Westman 1978, Holling and Allen 2002, Allen et al. 2005).

Understanding resilience in ecological systems requires an answer to the question, "Resilience *of* what *to* what?" (Carpenter et al. 2001). Empirically, this means identifying the relevant driving or structuring variables (e.g., phosphorus inputs, grazing pressures) that reinforce alternative states of the system of interest (e.g., oligotrophic versus eutrophic lake, grassland versus savanna), and the spatial and temporal scales over which those variables operate (Holling 1992, Peterson et al. 1998, Carpenter et al. 2001). The systemspecific nature of definitions of resilience stresses the inevitability of surprise in the dynamics of complex ecosystems, and much of the formative early work on resilience centered on the development of a coherent general framework for describing patterns (or cycles) of change and reorganization in systems that are viewed as complex and, in some sense, inherently unpredictable (Holling 1973, 1992, Westman 1978, DeAngelis 1980, Gunderson 2000, Carpenter et al. 2001). One of the hallmarks of the complexity of ecological systems, and one of the primary impediments to developing a generalized ecological theory, is the range of scales encompassed by ecological phenomena (Holling 1992, Levin 1992, Peterson et al. 1998).

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The importance of scale in ecology

Individual organisms span an amazing size range. The ratio of the mass of a redwood or a blue whale to that of a bacterium is approximately 10^{21} . To put this ratio into perspective, it is similar to the mass ratio of the moon to a typical human, that of a human to a single cytochrome oxidase molecule, or that of the known universe to our sun. The scales of ecological interactions are yet broader, spanning approximately 30 orders of magnitude in mass, from the smallest interacting microbes to the entire biosphere (~1.8 × 10¹⁹ grams). Thus, understanding biodiversity and ecological complexity is largely a matter of scale (Holling 1992, Levin 1992).

To a certain extent, the development of the conventional biological-ecological hierarchy, from cells through organisms, populations, communities, ecosystems, landscapes, and the biosphere, is an attempt to organize the dizzying diversity of ecological entities along an intuitive continuum, with different processes and constraints applying at different levels of organization. However, while the conventional levels of organization are to some extent nested (e.g., populations are made up of individuals, and the biosphere contains all landscapes), they are more properly defined as criteria for discerning the ecological entities and processes of interest, and thus do not readily map onto a physical scale (Allen and Hoekstra 1990, 1992). For example, the existence of communities of invertebrates participating in complex food webs within the leaves of pitcher plants (e.g., Sarracenia spp.; Buckley et al. 2003) challenges the traditional position of individual organisms (or in this case, plant organs) as "smaller" entities than populations, communities, or ecosystems. What makes the collections of invertebrates "communities" is not their size but the fact that they are relatively discrete groups of interacting species of interest to an ecologist.

The complexity of ecological systems thus results from the interactions of many qualitatively distinct entities (i.e., from different levels in the biological hierarchy) and processes across multiple scales in space and time (Holling 1992, Levin 1992, 1999, Peterson et al. 1998, Chave and Levin 2003). Furthermore, it is hypothesized that these structuring processes produce discontinuities in the structure of the system (e.g., in animal body-size distributions) that can be used both to identify relevant structuring processes and to diagnose system resilience (Holling 1992, Allen et al. 1999, 2005). However, despite their daunting complexity and variety, ecological systems appear to exhibit striking regularities that often take the form of scaling laws (Peters 1980, Brown and West 2000, Chave and Levin 2003, Ernest et al. 2003, Brown et al. 2004, Kerkhoff and Enquist 2006).

From scale to scaling laws

Scaling laws are simply empirical generalizations describing how some property of a system changes along one of the fundamental dimensions of the system. In the simplest case, this dimension may be a fundamental physical dimension, such as mass, length, or time. Alternatively, the dimension of interest may be more specifically biological, such as the mean population density of a species or the area of an island or habitat patch. The best-known scaling laws in ecology are the welldocumented species—area relationship (Rosenzweig 1995) and allometric relationships between organism size and various aspects of form, function, life history, and ecology (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Niklas 1994). In both of these cases, the scaling laws typically take the form of a power function,

$$Y = Y_0 M^b, \tag{1}$$

where *Y* is the property of interest (e.g., metabolic rate, species richness), M is the size of the observed entity along the dimension of interest (e.g., organism body mass, island or patch area), and Y_0 and b are the scaling exponent and coefficient, respectively, which may be fitted from data or drawn from theoretical expectations. Taking the logarithm of both sides produces the equation for a straight line, log(Y) = $\log(Y_0) + [b \cdot \log(M)]$. However, it is important to remember that despite the appearance of power laws as straight lines in logarithmic space, these relationships are generally nonlinear (except when the exponent is exactly 1). The logtransformation is appropriate not just in the statistical sense of normalizing variance; more important, it is necessary because most biological phenomena are fundamentally multiplicative processes, and it is their magnitude that matters. When it comes to body mass, metabolic rate, habitat area, or species richness, "How many times more?" is a more meaningful, or at least a more linear, question than "How much more?"

While power laws are often associated with complexity arising from critical phenomena in self-organizing systems (Milne 1998, Chave and Levin 2003), our treatment of scaling laws here is more pragmatic and concrete. Scaling studies begin with the premise that, at some level of analysis, ecological systems will exhibit strong, quantitative regularities, and that aspects of these regularities (e.g., the values of scaling exponents) will be predictable on the basis of theories describing the relevant underlying processes (Brown and West 2000). In general, ecological scaling relationships relate to entities at a single level of organization, and the measured variables are static, steady-state, or time averaged, rather than dynamical. However, the dimensions of the variables are context independent, continuous, and quantitative. Thus, more often than not the goal is to establish empirically, and sometimes to explain theoretically, how some variable of interest (e.g., metabolism, variance in population density) changes across entities (e.g., organisms, populations) that vary by orders of magnitude in scale (e.g., in body mass, in mean population density). Once established, scaling laws can be used to generate further predictions (Peters 1983) and hypotheses. Power laws are particularly interesting in this light because they are "scale invariant"; that is, a change in scale of the independent variable (e.g., *M* in equation 1) preserves the functional form and statistical properties of the original relationship. Thus, any particular example of the system of interest can then be seen as a rescaled version of any other (Milne et al. 1992, West et al. 2001).

Scaling and resilience

While researchers addressing questions of resilience have long acknowledged the importance of scale, effective communication between them and those who study scaling in ecological systems per se has arguably been limited. Likewise, scaling researchers often note the pragmatic implications of their highly generalized results (Brown and West 2000), but few have delved deeply into the problems of ecological resilience that face our species (Peters 1980, Levin 1999, Calder 2000). In this article, we seek the common ground between these two exciting research areas. Because our experience lies in the study of ecological scaling, we necessarily focus on how knowledge of scaling can inform the study of resilience. Obviously, to be most useful, the flow of information between the two fields must eventually become a two-way street (Allen et al. 2005).

Although studies of scaling and of resilience both highlight the importance of scale in the development of general-

ized, predictive ecological theory, their underlying goals are different. Resilience studies are largely concerned with the dynamics of particular systems, with how and why they change state. Scaling, on the other hand, describes properties that apply across ensembles of systems (generally in steady state), rather than any one system in particular. With its focus on the complex dynamics of the particular, resilience highlights the unpredictability of ecological systems, whereas scaling highlights the predictable characteristics that arise from a coarsegrained view of ensembles of such systems. The two approaches also differ in their concepts of scale. Studies of resilience generally treat scale in a discrete, hierarchical fashion, seeking to delineate the particular scales at which different ecological entities and processes influence the system. Scaling studies treat scale more continuously; the entities or processes are generally held constant, and attention is given instead to how their properties change with their magnitude (figure 1).

At first glance, it may appear that the resilience and scaling research programs have sought to answer different questions. However, they share a common interest in ecological theory and a common recognition that scale is a critical consideration for understanding ecological systems. Despite the differences described above, their common focus on scale provides an ample area of intersection and opportunities for cross-pollination between these two fields of study. Our thesis is that ecological scaling relationships may serve as baselines or attractors describing the steady-state structure and



Figure 1. A qualitative comparison illustrating subtly different views of scale. (a) Space-time diagram showing discrete domains of scale occupied by different vegetation entities in a forested landscape. In this perspective, qualitative variation in structuring processes across the boundaries is of primary concern (adapted from Holling 1992). (b) Because mass is proportional to volume (which is the cube of length), consideration of mass per unit area can put several scaling relationships into a similar space-time domain. Scaling studies are concerned primarily with quantitative aspects of variation within the entities (block arrows), here exemplified by the scaling relationship between leaf life span and leaf mass per area (data from Wright et al. 2004), and between stand turnover time and standing biomass per unit ground area (data from Cannell 1982). Both perspectives illustrate that the domain of ecological variation, while large (these are logarithmic scales), is in fact a highly constrained subset of the possible.

functioning of ecological systems; and, as a result, departures from scaling (i.e., the patterning or the magnitude of the residual variation) may serve as indicators of the disproportionate influence of particular structuring processes and their role in organizing, or reorganizing, the ecosystem.

To begin, we review some recent work highlighting the empirical existence, ecological importance, and theoretical basis for very general scaling properties in a variety of ecological systems, from plant communities to human populations. In the context of adaptive management, ecological scaling relationships could, in the absence of data, become valuable tools for estimating appropriately scaled ecosystem parameters. As an example, we focus specifically on the self-thinning or energetic equivalence rule (EER), which describes the remarkable regularity of plant community size structure, and the ability of this regularity to inform the study of resilience and reorganization in forest systems. The broad generality of the observed scaling relationships suggests that they are relatively robust to differences in the particulars of site history, plant life history, and environmental drivers. Here we explore the limits of this generality and their relationship to underlying theoretical assumptions. Successional trajectories following both natural and anthropogenic disturbances, as examples of ecosystem reorganization, provide support for the view that the EER size distribution across plant communities may act as an attractor, or at least a structural constraint, for forest ecosystems.

From 40-foot apes to forest dynamics: Ecological scaling in human and natural systems

The recent resurgence of interest in scaling has produced studies examining a variety of ecological and economic phenomena. These studies have been amply reviewed elsewhere (Stanley et al. 1996, Chave and Levin 2003, Brown et al. 2004). Here we discuss a few examples that highlight the potential interface between research on scaling and research on resilience. In particular, we focus on ecological scaling relationships related to properties of whole populations and communities in both human and natural systems.

Departures from scaling in human settlement size. Increasing anthropogenic impacts are frequently the basis for concern over ecosystem resilience (Folke et al. 1996, Levin 1999, Gunderson 2000). Thus, it is critical to understand whether and how regularities in human systems may constrain or determine the magnitude of environmental impacts across scales. Scaling approaches have proliferated in economics and geography in parallel with their resurgence in ecology and biology. In economics, global distributions of the size and economic performance of firms, as well as their variability, appear to follow power-law scaling relationships (Stanley et al. 1996, Axtell 2001, Gabaix et al. 2003), with the number of firms of size S (in either receipts or employees) falling off as a negative power of their size (i.e., $N_s = n_0 S^{-\alpha}$). Further, these scaling relationships appear to be universal, in the sense that they apply across firms despite enormous variation in the goods and services provided and the means of production employed.

If economic performance is indicative of environmental impact, this scaling relationship could be used to assess the proportional environmental impact of multinational corporations (which are enormous but relatively rare) versus small businesses (which are individually small but occur in huge numbers). The missing ingredient here is the scaling relationship, if one exists, between firm size and environmental impact (e.g., total net carbon release as a function of firm size). If such a relationship were to take the form of a power law—say, $I_s =$ $i_0 S^{\beta}$, where I_s is the impact of a firm of size S—then the total environmental impact of firms of size S is simply their number multiplied by their scaled impact: $N_{s}I_{s} =$ $n_0 i_0 S^{\beta - \alpha}$. Thus, if $\beta > \alpha$, the environmental impact increases more steeply with firm size than can be offset by the decrease in numbers, and larger economic entities produce disproportionately large impacts. Conversely, if $\beta < \alpha$, small firms, in aggregate, have a larger impact. This simple example, which uses scaling methods typical in studies of allometry, is only meant to illustrate the utility of exploring scaling relationships in socioeconomic systems to understand environmental impacts.

Similar power-law relationships have long been shown for the size distribution of human settlements. Indeed, it was proposed long ago that the size of cities should decay as the inverse of their rank within geopolitical regions, that is, $C = aR^{-b}$, where *C* is city size, *R* is its regional ranking, and the coefficient and exponent describe the shape of the rank-size distribution (Zipf 1949). Further, a simulation model of city growth has been shown to produce patterns in accordance with "Zipf's law" (Manrubia and Zanette 1998), which suggests that relatively simple processes of growth and migration may underlie this prevalent pattern. Still, it is important to note that very different underlying processes may in fact generate very similar macroscopic empirical patterns, which argues for caution in the interpretation of scaling patterns as diagnostic of particular processes (Keitt and Stanley 1998, Allen et al. 2001). In a study that explicitly considers both scaling and resilience, Bessey (2002) demonstrates that while a power law provides a good fit to aggregate data, especially for the largest cities, regionally partitioned data for the United States exhibit consistent departures from scaling (i.e., systematic residual variation), which Bessey attributes to hierarchical structuring processes that differentially affect cities over discrete ranges of scale. However, the identity of these differential structuring processes is not directly addressed (Bessey 2002).

The scaling of human fertility and energy use. Of course, the explosive growth of the human population is the fundamental process fueling anthropogenic global change. As a result, understanding the ecology of human fertility is arguably one of the most important directions for applied global change research. In an interesting recent contribution, Moses and Brown (2003) take a scaling approach to explaining the so-called demographic transition in which nations that attain a threshold degree of affluence exhibit a precipitous drop in domestic fertility. Their argument is based on the proposition that, while the ability to acquire and process energy is no longer a function of human physiological metabolic capacity, the resulting extrametabolic resource demands still exert a powerful influence on the life histories of industrialized humans. Based both on empirical data for mammals and on recent allometric and life history theory (Charnov 2001), fertility (F, births per female per year) should vary with metabolic rate (B, watts [W]) as $F = aB^{-1/3}$. Remarkably, this same relationship holds when the fertility of human societies is plotted as a function of per capita power consumption (Moses and Brown 2003). Moreover, not only is the exponent of the relationship indistinguishable from that of the relationship for mammals, but the extrapolated curve for modern nations accurately fits data for primate fertility based on metabolic power, including estimates for human hunter-gatherers and preindustrial agriculturalists (figure 2). Effectively, based on allometric expectations, a human in an energy-rich, affluent society (the United States, Canada, or western Europe) exhibits an energetic demand and fertility rate equivalent to that of a primate weighing in excess of 40,000 kilograms (kg)-roughly the size of a 40-foot gorilla. However, this theory does more than explain King Kong's attraction to Fay Wray, despite the presence of many Skull Islanders. It also illustrates how an apparently discrete and threshold-mediated change in the system (the demographic transition) can, under appropriate transformation, be usefully seen as a scaling continuum (figure 2). At the very least, visualizing each person in the United States, Canada, and the European Union as a 40,000-kg primate provides a powerful image for understanding the scale of our impact on the environment and the energy throughput that sustains it.

Implications of scaling in human systems for resilience and adaptive management. The study of resilience is fundamentally motivated by the concerns of natural resource management. As such, its system of concern does not stop at the wilderness boundary, but instead encompasses the coupled dynamics of natural systems and the human socioeconomic institutions that interact with them (Folke et al. 1996). The need for management strategies that are themselves resilient (i.e., strategies that protect the ecological system and are robust to large, sometimes surprising changes in the system) has led to the development of adaptive management (Gunderson 2000). In contrast with standard "command and control" methods of resource management, adaptive management views policies as hypotheses rather than answers, and thus management actions become experimental treatments that inform the rearticulation and improvement of new policies.

In the absence of sufficient hard data, adaptive management calls for the generation of hy-

potheses based on the best available science. Even at this most pragmatic level, scaling may inform the study of resilience. For example, Calder (2000) illustrates the use of scaling laws to derive surrogate values in the face of uncertainty as a powerful tool for adaptive management in species conservation. Specifically, he describes a three-step process: (1) derivation of the broadest possible scaling relationships from empirical data, (2) prediction from the empirical relationships, and (3) fine-tuning predictions on the basis of departures from scaling (Calder 2000). Calder illustrates this practice by predicting population recovery times for a threatened species. The allometric scaling of population doubling time is well established (step 1), and it can be used to predict the recovery time of a threatened species under protective management (step 2). These predictions can be significantly improved, however, if the manager takes into account how the species or its close relatives depart from scaling relationships (step 3). For example, simply knowing that the gestation time and time to maturity for a blue whale (Balaenoptera musculus) are 77% and 81% shorter, respectively, than expected from allometry (i.e., the species has a negative residual in both allometries) allows Calder to predict population doubling time to within 25% of estimates drawn from empirical harvest curves. Without taking departures from scaling into account, the allometric estimate of doubling time is approximately 85% too long. Fur-



Figure 2. Fertility rates for humans (modern nations; black circles), nonhuman primates (shaded triangles), and nonprimate mammals (open triangles) as a function of metabolic and, in the case of modern humans, extrametabolic power. Remarkably, nonhuman primates appear to fall along the same power–fertility continuum as modern humans in terms of per capita energy consumption (for humans, mostly fossil fuels; lower regression line, dashed where extended beyond the range of human data). This result has important implications for understanding the demographic transition, which is often described as a discontinuous process. The inset illustrates the demographic transition by plotting the same power–fertility data on arithmetic axes (data from Moses and Brown 2003).

thermore, such departures from scaling generate hypotheses about the underlying ecological and evolutionary forces at work. For instance, the reduced gestation time for *B. musculus* (335 days, as opposed to an allometric prediction of 1446 days) may be an adaptation to the Earth's orbital cycle.

Our thesis here echoes Calder's in the broader context of the management of wild and anthropogenically influenced ecological systems. The demographic transition described above provides interesting ground for exploring this thesis. Consider the oft-noted quandary: The management goal of zero population growth cannot be reached by raising the standard of living of populations in less-developed countries, because the energetic throughput of those populations would also rise, requiring the resources of a few more Earths (Vitousek et al. 1997, Wackernagel et al. 2002, Moses and Brown 2003, Imhoff et al. 2004). Thus, the demographic transition will not solve the problem of human population growth. While the ecological and economic processes underlying the demographic transition remain an open question, Moses and Brown's results suggest that any complete explanation must account for the energetic life-history tradeoffs inherent in a postindustrial lifestyle.

Here we put forward the notion that the scaling of fertility with energy use provides a baseline for understanding variation in human demography, and that residual variation around scaling law could prove to be quite useful information for the management of human impacts. In the context of adaptive management, useful socioeconomic policy guidelines (i.e., hypotheses) should not necessarily be sought in nations with low absolute fertility, but rather in those with low residual fertility, adjusted for per capita power consumption. Moreover, the largest positive outliers (the oilproducing states of the Middle East) may provide contrasting hypotheses regarding the social and economic factors that may cause reductions in fertility rates to lag behind rapid increases in energy consumption. These hypotheses could be tested by compiling more historical data, and then used to calibrate future population projections.

Of course, this incredibly complex problem cannot simply be reduced to the energetics of fertility. However, analyses of residual (energy-adjusted) fertility and other economic or social indicators (e.g., literacy, immigration and emigration rates, the Gini coefficient of income inequality, and other indicators of human well-being) could enable better understanding of changing human life histories in a rapidly industrializing and urbanizing world. At this point, such an approach is necessarily speculative, because with human systems, we are still largely at the first step of Calder's process: deriving robust scaling relationships for human systems and their environmental impacts. Still, we maintain that such scaling laws can usefully inform adaptive management of human impacts, just as allometric scaling laws can provide surrogate estimates for biological rates and times in the absence of available data.

Scaling in plant populations and communities. Like other taxa, land plants exhibit regular allometric variation in form and function with changes in size (Niklas 1994). The fundamental assumption underlying many ecological scaling approaches is that these allometric constraints at the level of the individual have critical implications for the structure and dynamics of populations, ecological communities, and ecosystems (Enquist et al. 2003, Kerkhoff et al. 2005, Kerkhoff and Enquist 2006). In this section, we ask whether (and how) strong regularities in plant population and community size structure can be used as diagnostic tools in the study of ecological resilience.

The long-acknowledged self-thinning law in plant populations describes the regular decrease in plant population density as its members increase in size (Yoda et al. 1963, Weller 1987). Enquist and colleagues (1998) proposed a simple model to explain how self-thinning patterns could emerge from individual plant allometries. They assumed, first, that all individuals share a common allometry of resource use, which is proportional to metabolic rate (*B*), where *B* is proportional to (\propto) mass raised to the 3/4 power ($M^{3/4}$); and, second, that all individuals in the population compete for limiting resources such that, in steady state, the rate of resource use approximates that of resource supply (*R*). It follows that the maximum number of individuals, N_{max} , that can be supported per unit area is related to the average whole plant size as $N_{max} \propto R(M^{-3/4})$. Traditionally, in studies of thinning, plant mass is plotted as a function of population density, so the prediction corresponds to $M \propto N_{\rm max}^{-4/3}$ (Enquist et al. 1998).

The inverse power-law scaling of population density with biomass (as $N \propto M^{-3/4}$) has also been widely documented in mixed-species communities of both plants and animals (Damuth 1981, Blackburn et al. 1993, Allen et al. 2002). This is particularly interesting because the scaling of density is the inverse of that of metabolic rate ($B \propto M^{3/4}$), which implies that the total energy consumed by a species per unit area is invariant with body size ($NB \propto M^{-3/4}M^{3/4} \propto M^0$), consistent with the EER. In fact, Allen and colleagues (2002) have gone so far as to estimate the average energetic flux density of a species as approximately 80 W per square kilometer, regardless of body size or phylogenetic affiliation.

Here we focus on forest communities, and as tree mass is impractical to measure, tree size generally refers to stem diameter (*D*). The plant allometric theory predicts, and empirical data broadly document, that plant mass is proportional to the 8/3 power of diameter (West et al. 1999). Thus, the EER size distribution becomes $N \propto D^{-2}$. This tight coupling between the size, abundance, and (through metabolism) productivity may offer considerable insights into the mechanisms structuring ecological communities in general (Enquist and Niklas 2001, Allen et al. 2002, Ernest et al. 2003, Kerkhoff et al. 2005, Kerkhoff and Enquist 2006).

If the shared values of allometric constants and exponents reflect fundamental similarities among plant taxa, they should provide a powerful constraint on community size-density distributions (Enquist and Niklas 2001, Niklas et al. 2003, Kerkhoff and Enquist 2006). It is important to note that in mixed-species communities, the EER $(N \propto D^{-2})$ size density distribution is only strictly expected for an "allometrically ideal" plant community at equilibrium (Kerkhoff and Enquist 2006). That is, all individuals must follow the same allometric rules, and total resource use must be in steady state with rates of supply, as in the case of the self-thinning model described above. Further, the community as a whole must be in a demographic steady state, with recruitment and growth continuously offset by mortality. Thus, many, if not most, ecologically interesting dynamics (e.g., competitive size hierarchies, episodic recruitment, or disturbance) should produce systematic deviations away from the EER size distribution (Coomes et al. 2003, Niklas et al. 2003, Kerkhoff and Enquist 2006). In accordance with our thesis, these deviations may be diagnostic of community reorganization and may thus be useful for understanding (and managing for) ecosystem resilience.

Enquist and Niklas (2001) examined within-site size distributions using macroecological data collected from more than 220 forest communities (Phillips and Miller 2002), ranging from near-monospecific stands to some of the most diverse forests on Earth. Although local size distribution exponents varied, they clustered around –2, in general agreement with the EER prediction (figure 3). Further, variation in the exponent was biogeographically structured; higher-latitude



Figure 3. Size distribution exponents for 226 0.1-hectare forest plots collected in the Gentry database (Phillips and Miller 2002), plotted as a function of species richness. The horizontal line is the energetic equivalence rule prediction of -2. Deviations at low richness are principally due to high-elevation and high-latitude sites.

forests with lower species richness tended to exhibit shallower (i.e., less negative) exponents (Enquist and Niklas 2001). Because many temperate and boreal forests regenerate through episodic recruitment of discrete cohorts, these forests would be expected to exhibit a dearth of small individuals and potentially reduced thinning in the larger cohorts, which could produce the shallower exponent characteristic of these communities (figure 3). Indeed, a more systematic analysis of variation in the size distributions (Niklas et al. 2003) revealed that the parameters of the size distributions (the coefficients and exponents) are significantly correlated with maximum stem diameter and total stem density. Specifically, the scaling exponent becomes shallower (less negative) as total density decreases and as maximum diameter increases (Niklas et al. 2003). A decrease in total density coupled with an increase in maximum size implies a community-level, successional thinning process, and the authors suggest that the shape of the size distribution (i.e., its exponent) may thus provide a general indicator of time since disturbance.

This scenario leads naturally to the hypothesis that if the processes limiting recruitment are somehow removed from the system, the forest size structure will converge toward the EER expectation. We tested this hypothesis using data from an old-growth Pinus ponderosa forest in northern Arizona that has been repeatedly measured since 1920 (Biondi et al. 1994). Before European settlement, this vegetation type was controlled by highfrequency, low-intensity ground fires, and stands were characterized by an open mosaic structure dominated by mature, fire-resistant trees, with little understory vegetation. With the introduction of grazing and active fire suppression in the early part of the 20th century, recruitment of P. ponderosa has been less sporadic, and the increased fuel load has led to a more catastrophic, crownfire disturbance regime (Savage and Swetnam 1990).

In accordance with our hypothesis, with the elimination of recruitment limitation by fire, the size structure of the forest appears to become steeper over time (figure 4). Interestingly, more qualitative aspects of the size distribution also appear to change in response to fire suppression. Specifically, in 1920, the distribution appears more discontinuous, possibly bimodal, with reduced numbers of individuals in the approximately 20- to 40-centimeter size range. Presumably, the gap in the distribution is related to the ground fire return interval over the extent of the study area. Under fire suppression, growth and recruitment appear to fill in the gap after 1920, resulting in a more continuous size distribution. Thus, systematic departures from scaling (both the shallow exponent and the structural size gap observed in 1920) appear to be the signature of a natural structuring process (ground fire), which in this case limits recruitment. This observation is in accordance with Holling's (1992) textural discontinuity hypothesis, but here we find a structural gap among individuals rather than among species.



Figure 4. Changes in the size distribution for a Pinus ponderosa forest in northern Arizona, from 1920 (at the dawn of active fire suppression) to 1990. With the suppression of fire, the size distribution exponent becomes steeper, approaching the energetic equivalence rule prediction of –2. Furthermore, the distribution shifts from clearly bimodal to more continuous, perhaps reflecting the relaxation of cohort dynamics that results from the typical fire return interval (data from Biondi et al. 1994).

The hypothesis that disturbance generates systematic deviations from allometrically derived size distributions provides a link between the dynamics of ecosystems and their scaling properties. While the analyses presented above are compelling, secondary successional trajectories provide another, more direct test of this hypothesis. We examined data for the mean tree size (D) and total stem density for disturbed and undisturbed plots of lowland forests in Nicaragua (Boucher et al. 2000) and Quercus-dominated forests in Costa Rica (Kappelle 1995). For reference, we also include data from a large compendium of forest plot data (Cannell 1982). For this comparative analysis, we plot stem density as a function of mean stem diameter. For such "cross-community" size distributions, stem density should vary inversely with mean diameter, but the shape of the relationship will depend on the largest and smallest sizes included in the samples, as well as on variation in the parameters of the size distribution among sites (Niklas et al. 2003).

Because sampling protocols most likely varied widely among the sites presented here, and because the parameters of the size distribution vary systematically with stem density, no quantitative expectation for the parameters of this relationship can be put forward at this point. However, it is interesting to note that the EER distribution appears to provide a reasonable upper boundary for the Cannell (1982) data, especially at higher mean diameters, which generally occur in more mature forests (figure 5). Forests from both locales support the hypothesis that disturbance is manifested in the



Figure 5. A cross-site comparison of stem density as a function of mean stem diameter, showing data from stands in Nicaragua (triangles; Boucher et al. 2000) and Costa Rica (diamonds; Kappelle 1995). Shading represents different degrees of disturbance (Nicaragua) or stages of succession (Costa Rica). Gray circles are reference data (Cannell 1982), and the line is the energetic equivalence rule (EER) prediction of -2, plotted here for reference. Note that more disturbed sites (white and gray symbols) tend to lie farther from the centroid of the data, for which the EER line appears to represent a reasonable constraint.

scaling properties of forest size structure. More disturbed sites lie farther from the mass of the Cannell data, and less disturbed sites appear to converge toward these data and toward the EER constraint line. The postagricultural sites in Nicaragua appear to be perturbed further from the undisturbed state than the posthurricane sites (figure 5), which implies that agricultural clearing is more thoroughgoing in its effects than hurricane disturbance (Boucher et al. 2000).

While further analyses of this kind are obviously necessary, these results suggest that the EER expectation may act as a steady-state attractor for the size structure across very different forest communities. Of course, whether this attractor represents a healthy, desirable state for the ecosystem (as in the Costa Rican and Nicaraguan examples) or a pathological one (as in the case of the Arizonan pine forests) depends on the system. However, in either case, the model may provide a useful framework for understanding ecosystem dynamics, because violation of various assumptions in the model should lead to systematic, quantitative deviations from the expected scaling relationship.

Implications for the resilience of ecosystems. Although these results are interesting, in the context of plant community resilience they may generate more questions than answers. In particular, we wish to highlight three critical open questions. The first has to do with the timescales and trajectory of community reorganization: If community-level scaling relationships do represent structural attractors to the system, what

determines the speed and direction of approach? Second, how can studies of scaling and resilience address variability, which is of critical concern for understanding ecological change? Many scaling studies deal only with the equilibrium, average state of the system of interest; what can they say about variance and covariance? Finally, echoing a question common to any attempt at generalized theory in ecology, if all of these different communities converge toward a similar structural state, what is the implication for biodiversity? Does scaling offer any insights on the role that species' ecologies play in the resilience of ecosystems? We do not seek to answer these questions here; instead, we bring them up as the basis for future work.

Ecological resilience measures the capacity of a system to maintain function in the face of disturbance, a dynamical property of ecosystems that depends on both the trajectory and the rate of change through time (Holling 1973, Westman 1978, DeAngelis 1980, Gunderson 2000, Carpenter et al. 2001, Holling and Allen 2002, Allen et al. 2005). In the secondary-succession examples discussed above (figure 5), the resilience of a system might be measured by the disturbance (e.g., tree removal) required for the system to be attracted to another part of the scaling law, or to an entirely different attractor. A distinct but related dynamical property of ecosystems, termed "engineering resilience," is the return time of the system to its steady, or equilibrium, state. The size structure of the forests in Costa Rica had recovered after only about 50 years (Kappelle 1995). Is this fast or slow? What determines the return time, and what would influence it in other systems (Westman 1978)?

While an enormous number of factors can easily come into play, variation in primary productivity is almost certainly relevant for plant communities. Because primary productivity is an integration of individual plant assimilation and growth, allometry suggests that the speed, and to some extent the trajectory, of system recovery will be very sensitive to the size structure of the surviving individuals immediately following disturbance, as well as the size structure of the system at its equilibrium (Niklas et al. 2003, Kerkhoff and Enquist 2006). Large individuals may provide a critically important source of propagules (Greene and Johnson 1994, Niklas and Enquist 2003) and may play a role in either competitively suppressing or ameliorating the environment of smaller individuals. However, the same amount of standing biomass distributed among smaller individuals is likely to generate much higher productivity per unit biomass. The EER size distribution itself presents an interesting case in this regard, because under the EER, productivity does not vary systematically with size. Thus, it results in a high degree of functional redundancy across size classes, which may enhance resilience (Peterson et al. 1998, Walker et al. 1999, Allen et al. 2005). From a management perspective, it would be particularly relevant to know whether extractive plant resource systems are more resilient when harvests thin the community but systematically maintain the size structure.

Because resilience is related to the degree of perturbation that is in some sense tolerable to a system, modeling the expected levels of ecological variance is critical (Carpenter and Brock 2006). One scaling approach to understanding variance, arising principally from the study of population dynamics, is known as Taylor's power law (Taylor 1961), which describes the scaling relationship between mean abundance (m) and its temporal (or spatial) variance (v) across populations: v =am^b. The value of the exponent is of particular interest, because when b < 2, relative variability (as indexed by the coefficient of variation) decreases with increasing mean; conversely, when b > 2, it increases. Across a wide variety of animal and plant taxa, mean-variance scaling exponents generally range between approximately 1 and 2 (Taylor 1961, Maurer and Taper 2002, Kerkhoff and Ballantyne 2003). Thus, mean-variance scaling relationships are interesting (and may be useful) because they provide a macroscopic summary of complex demographic processes that vary in space and time (Maurer and Taper 2002).

Understanding how variability in environmental drivers influences that of ecosystem structure and function is a critical challenge for global change research and ecological science in general. In this context, mean-variance scaling may be of interest well beyond the domain of population biology. Other ecological time series (e.g., productivity, species richness) may also exhibit scaling properties (Cottingham et al. 2001), as do many abiotic environmental drivers (e.g., precipitation; Knapp and Smith 2001, Davidowitz 2002). Mean-variance scaling relationships can be decomposed into individual variance and covariance components. For example, using a dynamical seed-output model (Satake and Iwasa 2000), Kerkhoff and Ballantyne (2003) showed that the mean-variance scaling exponent for seed output in a large collection of Northern Hemisphere tree species is determined by the relative values of the energetic cost of individual reproduction, which determines the variance in seed output of an individual tree, and by the degree of pollen limitation, which determines the reproductive covariance among trees in a stand. These insights suggest that if mean-variance scaling applies to the dynamics of ecosystem function, the parameters of the scaling relationship may be useful in diagnosing the relative importance of variance in the individual components of the system and the covariance among those components (Cottingham et al. 2001). Such knowledge is essential for any generalized understanding of the dynamical organization (and reorganization) of ecological systems (Carpenter and Brock 2006).

Many of the ecological scaling relationships we have discussed, from community size distributions to the scaling of population seed output, appear relatively insensitive to the diversity and taxonomic composition of the systems described. On the surface, it appears that ecological scaling may have little to say about the role of individual species in ecosystems. On the contrary, we argue that the generality of many scaling relationships provides an indispensable baseline for determining what is possible and predictable in ecological systems, and what apparently is not. Many scaling relationships demonstrate that the state space available to an ecosystem is highly constrained, relative to all permissible parameter values (see figure 1).

In plant communities, these regularities are the basis for several classification schemes that relate the traits of plant species to ecosystem organization and function (Grime 1979, Westoby 1998, Lavorel and Garnier 2002), and an explicit consideration of scaling may be very helpful in this area of research. In general, the traits that define functional diversity are chosen because they are easily measurable (making a classification scheme operational) and because of the informative scaling relationships that they share with many other plant traits (Wright et al. 2004). Communities can thus be considered combinations of traits, which are functionally informative and amenable to quantitative analysis, rather than combinations of species, which (as lists of names) are not (Westoby and Wright 2006). As such, the functional diversity of plant communities provides a quantitative basis for investigating community assembly and the link between composition and ecosystem function. The links between functional classification schemes and the scaling of plant community size structure are self-evident in the allometric relationships between plant size and many aspects of plant life history and

ecology (Niklas 1994). Further integration between allometric scaling and other approaches based on functional traits could prove useful for integrating the ecology of plant species and ecosystem processes (Diaz et al. 2004, Westoby and Wright 2006). In particular, examining how distributions of functional traits change across different strata or size classes within communities may provide important insights into community assembly and resilience (Weiher et al. 1998, Walker et al. 1999, Allen et al. 2005).

Conclusions

We have outlined what we believe to be the most important implications of scaling approaches for the study of resilience and reorganization in ecological systems. The regularities embodied by both empirically documented and theoretically derived scaling properties provide important baselines for understanding resilience and change in ecological systems. In the context of adaptive management, such baselines can be used to generate hypotheses and derive surrogate parameter estimates in the absence of more specific data. Further, ecological scaling relationships, which often (but not always) take the form of power laws, may describe attractors for, or constraints on, the structure and dynamics of ecosystems. Deviations from scaling relationships may be the signature of specific structuring processes or may indicate the transient reorganization of the system. Although we have focused on the scaling properties of human populations and forest communities, the concepts and research opportunities described here should apply to ecosystems more generally.

Most recent ecological scaling studies have focused largely on the documentation and explanation of generalized patterns across broad taxonomic and biogeographic domains. Here we argue that the time has also come to demonstrate the utility of these patterns for understanding and managing ecological systems, including those affected by humans. This path is not uncharted (Peters 1980, Calder 2000), but it has, of late, been the road less traveled. Scaling has been heralded as one of the major problems of ecology for more than a decade (Levin 1992). We argue that it also presents some of the most powerful scientific tools available to ecologists as they face problems that are unprecedented in both their scope and their stakes.

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References cited

Allen AP, Li BL, Charnov EL. 2001. Population fluctuations, power laws and mixtures of lognormal distributions. Ecology Letters 4: 1–3.

- Allen AP, Brown JH, Gillooly JF. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297: 1545–1548.
- Allen CR, Forys EA, Holling CS. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. Ecosystems 2: 114–121.
- Allen CR, Gunderson L, Johnson AR. 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. Ecosystems 8: 958–966.
- Allen TFH, Hoekstra TW. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. Journal of Vegetation Science 1: 5–12.
- ------. 1992. Toward a Unified Ecology. New York: Columbia University Press.

Axtell RL. 2001. Zipf distribution of US firm sizes. Science 293: 1818–1820. Bessey KM. 2002. Structure and dynamics in an urban landscape: Toward a multiscale view. Ecosystems 5: 360–375.

- Biondi F, Myers DE, Avery CC. 1994. Geostatistically modeling stem size and increment in an old-growth forest. Canadian Journal of Forest Research 24: 1354–1368.
- Blackburn TM, Brown VK, Doube BM, Greenwood JJD, Lawton JH, Stork NE. 1993. The relationship between abundance and body-size in natural animal assemblages. Journal of Animal Ecology 62: 519–528.
- Boucher DH, Vandermeer J, Grasnow de la Cerda I, Mallona MA, Perfecto I, Zamora N. 2000. Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. Plant Ecology 156: 131–137.
- Brown JH, West GB, eds. 2000. Scaling in Biology. New York: Oxford University Press.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. Ecology 85: 1771–1789.
- Buckley HL, Miller TE, Ellison AM, Gotelli NJ. 2003. Reverse latitudinal trends in species richness of pitcher-plant food webs. Ecology Letters 6: 825–829.
- Calder WA.1984. Size, Function, and Life History. Cambridge (MA): Harvard University Press.
- ———. 2000. Diversity and convergence: Scaling for conservation. Pages 297–324 in Brown JH, West GB, eds. Scaling in Biology. New York: Oxford University Press.
- Cannell MGR.1982. World Forest Biomass and Primary Production Data. London: Academic Press.
- Carpenter S, Walker B, Anderies JM, Abel N. 2001. From metaphor to measurement: Resilience of what to what? Ecosystems 4: 765–781.
- Carpenter SR, Brock WA. 2006. Rising variance: A leading indicator of ecological transition. Ecology Letters 9: 308–315.
- Charnov EL. 2001. Evolution of mammal life histories. Evolutionary Ecology Research 3: 521–535.
- Chave J, Levin S. 2003. Scale and scaling in ecological and economic systems. Environmental and Resource Economics 26: 527–557.
- Coomes DA, Duncan RP, Allen RB, Truscott J. 2003. Disturbances prevent stem size–density distributions in natural forests from following scaling relationships. Ecology Letters 6: 980–989.
- Costanza R, et al. 1997. The value of the world's ecosystem services and natural capital. Nature 387: 253–260.
- Cottingham KL, Brown BL, Lennon JT. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4: 72–85.
- Damuth J. 1981. Population density and body size in mammals. Nature 290: 699–700.
- Davidowitz G. 2002. Does precipitation variability increase from mesic to xeric biomes? Global Ecology and Biogeography 11: 143–154.
- DeAngelis DL.1980. Energy flow, nutrient cycling, and ecosystem resilience. Ecology 61: 764–771.
- Diaz S, et al. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15: 295–304.
- Diaz S, Fargione J, Chapin FS, Tilman D. 2006. Biodiversity loss threatens human well-being. PLoS Biology 4: 1300–1305. doi:10.1371/journal. pbio.0040277

- Enquist BJ, Niklas KJ. 2001. Invariant scaling relations across tree-dominated communities. Nature 410: 655–660.
- Enquist BJ, Brown JH, West GB. 1998. Allometric scaling of plant energetics and population density. Nature 395: 163–165.
- Enquist BJ, Economo EP, Huxman TE, Allen AP, Ignace DD, Gillooly JF. 2003. Scaling metabolism from organisms to ecosystems. Nature 423: 639–642.
- Ernest SKM, et al. 2003. Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecology Letters 6: 990–995.
- Folke C, Holling CS, Perrings C. 1996. Biological diversity, ecosystems, and the human scale. Ecological Applications 6: 1018–1024.
- Folke C, Carpenter S, Elmqvist T, Gunderson L, Holling CS, Walker B. 2002. Resilience and sustainable development: Building adaptive capacity in a world of transformations. Ambio 31: 437–440.
- Gabaix X, Gopikrishnan P, Plerou V, Stanley HE. 2003. A theory of powerlaw distributions in financial market fluctuations. Nature 423: 267–270.
- Greene DF, Johnson EA. 1994. Estimating the mean annual seed production of trees. Ecology 75: 642–647.
- Grime JP. 1979. Plant Strategies and Vegetation Processes. Chichester (United Kingdom): John Wiley and Sons.
- Gunderson LH. 2000. Ecological resilience—in theory and application. Annual Review of Ecology and Systematics 31: 425–439.
- Hannah L, Lohse D, Hutchinson C, Carr JL, Lankerani A. 1994. A preliminary inventory of human disturbance of world ecosystems. Ambio 23: 246–250.
- Holling CS. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4: 1–23.

——. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62: 447–502.

- Holling CS, Allen CR. 2002. Adaptive inference for distinguishing credible from incredible patterns in nature. Ecosystems 5: 319–328.
- Imhoff ML, Bounoua L, Ricketts T, Loucks C, Harriss R, Lawrence WT. 2004. Global patterns in human consumption of net primary production. Nature 429: 870–873.
- Kappelle M. 1995. Ecology of mature and recovering Talamancan montane *Quercus* forests, Costa Rica. PhD dissertation. University of Amsterdam, The Netherlands.
- Keitt TH, Stanley HE. 1998. Dynamics of North American breeding bird populations. Nature 393: 257–260.
- Kerkhoff AJ, Ballantyne F. 2003. The scaling of reproductive variability in trees. Ecology Letters 6: 850–856.
- Kerkhoff AJ, Enquist BJ. 2006. Ecosystem allometry: The scaling of nutrient stocks and primary productivity across plant communities. Ecology Letters 9: 419–427.
- Kerkhoff AJ, Enquist BJ, Elser JJ, Fagan WF. 2005. Plant allometry, stoichiometry and the temperature-dependence of primary productivity. Global Ecology and Biogeography 14: 585–598.
- Knapp AK, Smith MD. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291: 481–484.
- Lavorel S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Functional Ecology 16: 545–556.
- Levin SA.1992. The problem of pattern and scale in ecology. Ecology 73: 1943–1967.

———. 1999. Fragile Dominion: Complexity and the Commons. Reading (MA): Perseus Books.

- Manrubia SC, Zanette DH. 1998. Intermittency model for urban development. Physical Review E 58: 295–302.
- Maurer BA, Taper ML. 2002. Connecting geographical distributions with population processes. Ecology Letters 5: 223–231.

Milne BT. 1998. Motivation and benefits of complex systems approaches in ecology. Ecosystems 1: 449–456.

- Milne BT, Turner MG, Wiens JA, Johnson AR. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. Theoretical Population Biology 41: 337–353.
- Moses ME, Brown JH. 2003. Allometry of human fertility and energy use. Ecology Letters 6: 295–300.

- Niklas KJ. 1994. Plant Allometry: The Scaling of Form and Process. Chicago: University of Chicago Press.
- Niklas KJ, Enquist BJ. 2003. An allometric model for seed plant reproduction. Evolutionary Ecology Research 5: 79–88.
- Niklas KJ, Midgley JJ, Rand RH. 2003. Tree size frequency distributions, plant density, age and community disturbance. Ecology Letters 6: 405–411.
- Peters RH. 1980. Useful concepts for predictive ecology. Synthese 43: 257–269.
 . 1983. The Ecological Implications of Body Size. Cambridge (United Kingdom): Cambridge University Press.
- Peterson G, Allen CR, Holling CS. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1: 6–18.
- Phillips OL, Miller JS, eds. 2002. Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set. St. Louis (MO): Missouri Botanical Garden Press.
- Rosenzweig ML. 1995. Species Diversity in Space and Time. Cambridge (United Kingdom): Cambridge University Press.
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G. 2002. The human footprint and the last of the wild. BioScience 52: 891–904.
- Satake A, Iwasa Y. 2000. Pollen coupling of forest trees: Forming synchronized and periodic reproduction out of chaos. Journal of Theoretical Biology 203: 63–84.
- Savage M, Swetnam TW. 1990. Early 19th century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71: 2374–2378.
- Schmidt-Nielsen K. 1984. Scaling: Why Is Animal Size So Important? Cambridge (United Kingdom): Cambridge University Press.
- Stanley HE, et al. 1996. Scaling and universality in animate and inanimate systems. Physica A 231: 20–48.
- Taylor LR. 1961. Aggregation, variance and the mean. Nature 189: 732-735.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. Science 277: 494–499.
- Wackernagel M, et al. 2002. Tracking the ecological overshoot of the human economy. Proceedings of the National Academy of Sciences 99: 9266–9271.
- Walker B, Kinzig A, Langridge J. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2: 95–113.
- Weiher E, Clarke GDP, Keddy PA. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos 81: 309–322.
- Weller DE. 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecological Monographs 57: 23–43.
- West GB, Brown JH, Enquist BJ. 1999. A general model for the structure and allometry of plant vascular systems. Nature 400: 664–667.

. 2001. A general model for ontogenetic growth. Nature 413: 628–631.

- Westman WE. 1978. Measuring the inertia and resilience of ecosystems. BioScience 28: 705–710.
- Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199: 213–227.
- Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution 21: 261–268.
- Wright IJ, et al. 2004. The worldwide leaf economics spectrum. Nature 428: 821–827.
- Yoda K, Kira T, Ogawa H, Hozumi K. 1963. Intraspecific competition among higher plants, IX: Self-thinning in overcrowded pure stands under cultivation and natural conditions. Journal of Biology, Osaka City University 14: 107–129.
- Zipf GK. 1949. Human Behavior and the Principle of Least Effort: An Introduction to Human Ecology. Cambridge (MA): Addison-Wesley Press.

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