A Sense of Scale

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Books and articles discussed in this essay

West, G. 2017. *Scale: the universal laws of growth, innovation, sustainability and the pace of life in organisms, cities, economies, and companies*. Penguin Press, New York, New York, USA.

Farnsworth, K. D., L. Albantakis, and T. Caruso. 2017. Unifying concepts of biological function from molecules to ecosystems. *Oikos* 126:1367–1376.

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West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126.

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To judge from the accolades for, and paeans to, *Scale*, Geoffrey West's approach to generic scaling laws—"relationships that *quantitatively* describe how almost any measurable characteristic of animals, plants, ecosystems, cities, and companies *scales* with size" (p. 4; italics in original)—may be on a par with Galileo's cementing of the Copernican Revolution or the overthrow of Newtonian physics by quantum mechanics. Indeed, West himself argues that his way of thinking, developed over the last two decades with his colleagues at the Santa Fe Institute and including the well-known ecologists Jim Brown and Brian Enquist, represents

> *a way of thinking, about asking big questions, and about suggesting big answers to some of those big questions…how some of the major challenges and issues we are grappling with today, ranging from rapid urbanization, growth, and global sustainability to understanding cancer, metabolism, and the origins of aging and death, can be addressed in an integrated unifying conceptual framework. (p. 4)*

Yet ecologists who think, talk, and write about "scale"—and there are many of them, to judge from either a casual glance at the programs of our annual meetings, the pages of our journals, or a more formal citation analysis—including many who work on urban ecology, sustainability, or senescence, rarely think about scale in the same way that West does. This disconnection is the focus of this essay. It is not meant to be an exhaustive review of the literature (ecological or otherwise) on scale and scaling, nor is it meant to reify the concept of scale in ecology. Rather, this essay is a personal take on the last 30 years of how we view "scale," its importance in ecological systems and ecological thought, and what appear to be promising future directions in its understanding and application.

In his MacArthur Award lecture, delivered at the 1989 Annual Meeting of the Ecological Society of America, Simon Levin asserted that "the problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystem science, and marrying basic and applied ecology" (Levin 1992: 1943). He argued that there is no single natural scale at which ecological systems or phenomena should be studied; emphasized the different mechanisms that operate at different spatial, temporal, biological, or organizational scales; and focused attention on variability generated both by an investigator's perceptual bias (i.e., the scale at which we choose to observe a system) and the intrinsic variation that is part and parcel of evolution. Levin also suggested that patterns that are unique to a particular scale will have similarly unique causes and consequences.

In contrast, West, like many physical scientists, thinks of scale in terms of dimensionless ratios that characterize processes or mechanisms. For example, the Reynolds number, Re = uL/υ, where u is the velocity of a fluid (in m/s) with respect to an object, L is the characteristic length of the object (in m), and υ is the kinematic viscosity of the fluid (in m^2/s), can be used to predict when turbulent flow will occur in, over, or around objects such as pipes, boats, and wings. Because it is dimensionless, it can be applied to objects of any size, from molecules to large airplanes, and in anything that acts like a fluid, including water and air. The result is a scale-independent understanding of physical processes and mechanisms.

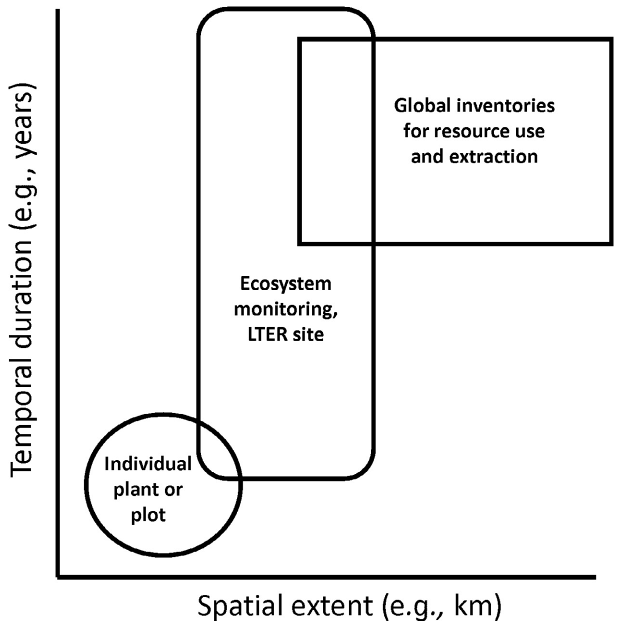

Fig. 1. Different ecological phenomena are measured most commonly at different spatial and temporal scales.

Illustrations that encapsulate Levin's approach to scaling are replete in the ecological literature. Whether conceptual or quantitative, these graphs usually have three axes (or two axes and the equivalent of contours of responses), of which two are "time" and "space", and third is a response, sampling program, model, or level of inference (Fig. 1; cf. Fig. 2 of Levin 1992).

In an informal poll that I conducted on Twitter (3 days, N = 75 respondents) in mid-December 2017, most (72%) ecologists conceptualized "scale" as illustrated in Fig. 1, and I am no exception. In my dissertation work in salt marshes and post-doctoral work in wet tropical forests, I worked primarily at the "patch" or "gap" scale, with a temporal resolution of days or weeks and duration of a few years. Longer-term professional stability has allowed me to work for longer times across larger spatial extents, including at LTER sites and with global models spanning millennia. But in moving one's research scale from the lower left to the upper right of Fig. 1, most ecologists also move through ecological subdisciplines (e.g., population, community, ecosystem, or landscape ecology), each with its own research cultures, journals, and meetings that interact less often than might be expected. These separate scales of inference and interactions reinforce the idea that there is no single or natural process, equation(s), or dimensionless number(s) with which to examine ecological phenomena or at which ecological processes operate. However, there might be characteristic equations *within* each of these scales that could be coupled *across* scales.

An alternative interpretation of scale, favored by 15% of the Twitter respondents and anticipated by Levin (1992), is one that describes the level of biological organization, *viz*. from gene and genome to physiology, organisms, populations, and ecosystems. This scale has both parallels and some overlap with the time-and-space scales of Fig. 1. The boundaries set by different scales of biological organization also are manifest in the structuring of academic departments and define in large measure the different programs, divisions, and directorates at the National Science Foundation. These structural constraints have made it more challenging to transcend boundaries of biological scales than have dif-

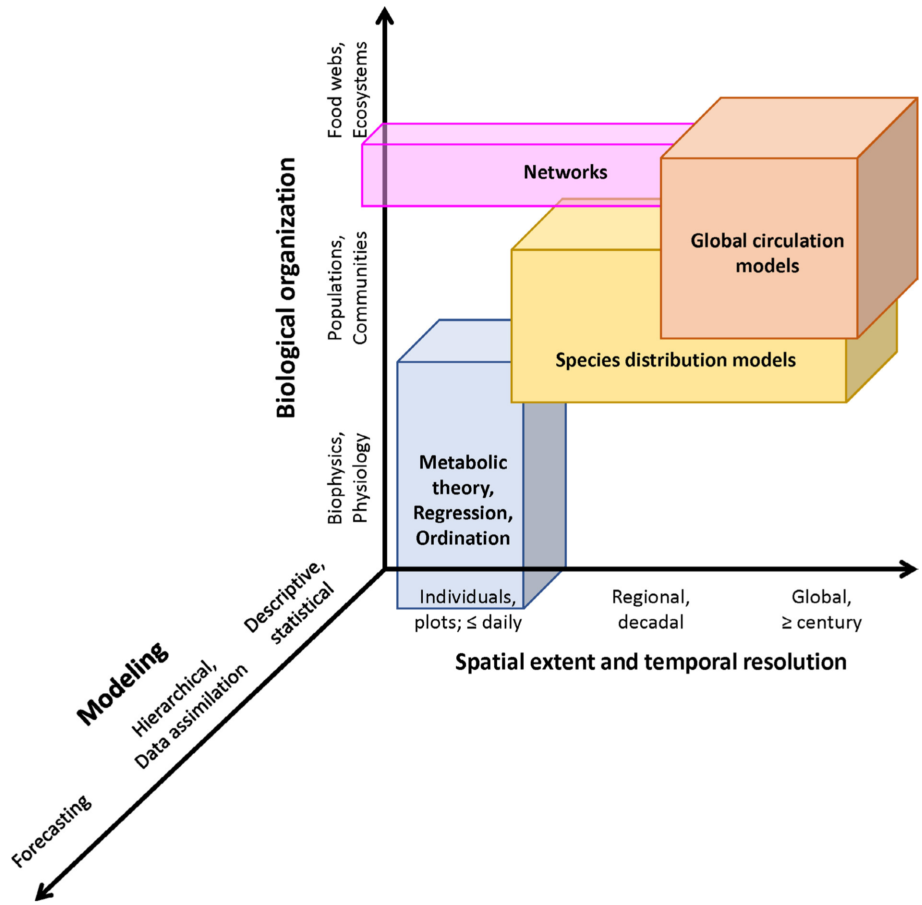

Fig. 2. Different types of models can cross scales of time, space, and biological organization. Figure inspired by a 2017 presentation of Scott Doney (University of Virginia) and concepts presented in N. Gruber and S. C. Doney. 2009. Modeling of ocean biogeochemistry and ecology. Pages 89–104 in J. Steele, K. K. Turekian, and S. A. Thorpe, editors. *Encyclopedia of ocean sciences,* second edition. Elsevier.

ferences in the technical skills, language, and conceptual frameworks (e.g., reductionism, holism, emergence) used to explore them. Yet, many ecologists have become adept at crossing biological scales; for example, "mechanisms" for observed ecological phenomena are often described at a biological scale once removed from the question of interest (e.g., selfish genes drive individual behavior, which in turn yields a mechanism for population-level dynamics).

Ecological modeling provides other ways to cross scales of time, space, and biological organization (Fig. 2). Although some models capture processes and dynamics of multiple scales of space, time, or biological organization, there is as yet no unified ecological process model that encompasses all of these scales. And perhaps there will never be. If, as Levin (1992) argued, there is no single natural scale at which ecological systems or phenomena should be studied, and if different mechanisms operate at different spatial, temporal, biological, or organizational scales, then our ecological approaches to studying or modeling scale-dependent phenomena are unlikely to unify population biology and ecosystem science, or basic and applied ecology.

West's focus in *Scale* on measuring one or more aspects of size (this type of scale was identified by

8% of Twitter respondents) and relationships between them is an alternative approach to scale that suggests the possibilities either of finding a general process equation for multiple ecological scales (sensu Fig. 1) or at least ways to link the processes within them. Twenty years ago, West et al. (1997) (re)-introduced ecologists to the ideas of allometry—the different growth rates of different body parts—and allometric scaling (*a.k.a.* power laws)—essentially a plot of the size of one thing to another, usually on a log-log scale. Allometry and allometric analysis long have been standard tools used to understand growth of organs and organisms, functional morphology (dating at least to D'Arcy Wentworth Thompson's 1917 classic *On Growth and Form*), and patterns of morphological evolution (popularized in the numerous technical and general works of Stephen Jay Gould), but their use had fallen out of favor among ecologists focused less on physiology or autecology, and more on populations, communities, and ecosystems.

West et al.'s (1997) starting point was the assertion that biological diversity is essentially a reflection of body size (mass), which ranges over more than 20 orders of magnitude from the smallest virus or prokaryotic cell to the largest organism. In *Scale*, West expands this range by yet another 10 orders of magnitude, stretching from metabolic molecules and DNA bases to ecosystems and cities (to put this into perspective, West points out that the mass of Earth differs from that of our entire galaxy by only 18 orders of magnitude, equivalent only to the difference between an electron and a mouse). West et al. (1997) subsequently used the general allometric (i.e., power law) equation, $Y = Y_0 M^b$, to relate body mass (M) to a diversity of physiological and metabolic variables (Y), including metabolic rate, lifespan, cross-sectional area of vessels, and the like. West et al.'s (1997) key observation was that the exponent b in the general allometric equation tended to be a multiple of $\pm\frac{1}{4}$; their fundamental scientific contribution was to propose a common mechanism for this quantitative pattern involving transport of materials through space-filling, fractal networks.

Scale is an extended meditation and disquisition on quarter-power scaling (i.e., $b \propto \pm\frac{1}{4}$), and especially on phenomenological differences between *sublinear* scaling ($b < 1$) and *superlinear* scaling ($b > 1$). Phenomena that scale sublinearly show efficiencies of scale—for example, larger animals need less calories day per unit of mass to survive, and have lower metabolic rates per unit of mass than do smaller ones—whereas phenomena that scale superlinearly are more productive at scale—for example, the number of patents produced in a city grows faster than its population. Although many allometric relationships are illustrated in *Scale*, a single underlying mechanism, such as that suggested by West et al. (1997) for physiological scaling, remains elusive for the broader set of patterns presented therein. Common patterns such as quarter-power scaling suggest common mechanisms, but West's vision of a grand unified theory of sustainability (p. 411*ff*) remains unfulfilled. Levin's terse observation that "simple statistical description of patterns is a starting point, but that correlations are no substitute for mechanistic understanding" (Levin 1992: 1960) serves as a useful counterweight to West's prolixity in *Scale*.

Others are making rapid progress at understanding scaling phenomena by following Levin's lead and targeting different mechanisms for different phenomena—even broad classes thereof. For example, Keith Farnsworth and his colleagues (2017) find unity across scales of biological organization by precisely defining and quantifying how different biological functions contribute to two essential biological processes: replication and growth. They start by using a common measure of biomass accumulation to characterize molecules, molecular networks, prokaryotic and eukaryotic cells, organisms and populations, ecological communities and meta-communities, and ecosystems (up to that of our entire planet). Farnsworth et al.'s (2017) key insight is to look for mechanisms (what they call a Cummins function) defined as the relationship between a system-level process and an essential function performed by one or more of its component parts. Except for ecosystem-level processes, functions at a lower level of biological organization (e.g., molecular level) are predicted to influence (cause) those at a higher level only when the functioning entity at the lower level is a part of the next level up (ecosystem functions and processes are a necessary exception, as there is no higher [emergent] level beyond the global ecosystem).

By defining function in terms of relationships between levels of organization, Farnsworth et al. (2017) highlight the role of interactions—and the importance of networks of interactions—as a proximate cause (i.e., a one-level-lower mechanism) of many ecological phenomena. They suggest that experimental manipulations that distinguish effects of network structure (emergent, community-level effects) from effects of traits (organism-level effects) could provide new insights into emergent properties of ecological communities and entire ecosystems. I suspect that a parallel experimental exploration of fractal networks of vessels contributing to metabolic scaling (West et al. 1997) would yield similar mechanistic insights.

Li et al. (2017) focus explicitly on scaling rules for cities, and develop a mechanistically simple model based on temporal aggregation of populations and exploration of new geographic areas. Li et al. (2017) model what they call the spatial distribution of "active populations," and use this model to predict scaling laws of road length, GDP, and city area as a function of population size. As with West et al. (1997) and Farnsworth et al. (2017), networks and interactions within them are critical controlling elements. Although both Li et al. (2017) and West (2017) find that road length and city area scale sublinearly with population size while GDP scales superlinearly with population size, Li et al.'s mechanistic model predicts scaling exponents that are multiples of ⅓ rather than ¼. Data from ten individual cities support their predictions.

The deviations from the general quarter-power scaling law predicted by West et al. (1997) and West (2017), such as those that were identified for a handful of cities by Li et al. (2017), have been found in many other organisms and systems (a salient review and critique is that of C. A. Price et al. [2012] Testing the metabolic theory of ecology. *Ecology Letters* 15:1465–1474). However, it is important to keep in mind that quarter-power scaling laws are thought to be applicable *across* scales of space and time and levels of biological and social organization. Counter-examples that emerge when looking *within* scales or levels—for example, different species of rodents or individual cities—tend to disappear, or at least regress to the mean, when aggregated data are plotted on a double-log scale.

In this light, Zaoli et al. (2017) have made an important advance by placing the differences in scaling exponents observed in different ecosystems or at different scales of biological organization into a coherent statistical framework. They link three power laws: the community size spectrum, $s(m) \propto m^{-\eta}$, where $s(m)$ is the fraction of individuals of body mass m in a species assemblage; the distribution of the average body masses, $P(m)$, of all species in an assemblage, $P(m) \propto m^{-\delta}$; and the average abundance n of a species given its typical body mass, $\langle n|m \rangle \propto m^{-\gamma}$. Zaoli et al.'s salient finding is that *within* a given community (assemblage, or ecosystem), the three exponents are not independent. Rather, they satisfy the relationship $\eta = \delta + \gamma$. In contrast, *among* communities (assemblages, or ecosystems), the exponents are independent. From some initial mathematics and an assumption of shared limiting resources, they derive a number of scaling laws familiar to ecologists, including the species-area relationship, scaling of total biomass or abundance, scaling of the mass of the largest organism, relative abundance distributions, and Taylor's law that links the mean and variance of the species abundance. In Zaoli's formulation, quarter-powers are but one of many possible allometric exponents, a result that has strong empirical support. A key practical conclusion from Zaoli et al.'s (2017) work is that the application of scaling laws, as has been done, for example, in using the species–area relationship to define reserve sizes to maintain biological diversity, should not be based either on a single power distribution applicable to all taxa or on a combination of, for example, average exponents measured in different systems.

For ecologists, a coherent sense of scale remains elusive. Perhaps this should not be surprising, as there are literally dozens of definitions of "scale" derived from homonyms and cognates rooted in Scandinavian, Germanic, and Romantic languages. The current (third) edition of the Oxford English Dictionary (OED Online: http://www.oed.com/) lists seven distinct meanings and roots of "scale" as a noun and three as a verb, all of which have many subsidiary definitions, ranging from bowls, husks, huts, and balances, through horny coverings of insects, fish, and plants, to ladders and the *scala naturae*. Most of our ecological senses of scale seem to be derived from the Latin *scāla* (a ladder or stairway) and entered English usage in the 17th or 18th centuries. Ecologists' senses of scale are easily as varied as the contemporary usages derived from *scāla* and reflect a "common-sense" usage of big, small, short, or long rather than the physicists' dimensional analysis. Although it is laudable, as Geoffrey West does in *Scale*, to seek a unified, process-based theory of scale, it may also be prudent to recall Cowper's assertion in his 1785 poem, *The Task* (Book III, stanza 221), that "God never meant that man should scale the heav'ns/ By strides of human wisdom."