

The Rise of the Concept of Scale in Ecology

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Recognition of the concept of scale occurred rapidly

Rin the 1980s, but the concept itself is far older. The last quarter of the 20th century witnessed major changes in the science of ecology, including increases in skill and rigor in the design of field experiments, the growth of mathematically based theory, computer-mediated advances in analytical capacity, and the accelerating capacity to acquire and retrieve data. These changes were accompanied by growing recognition of the problem of scale (Wiens 1989, Steele 1991, Levin 1992). The problem has three components. First, pressing problems in ecology often exist at the scale of decades and large ecosystems. Second, most variables can only be measured directly in small areas, over short periods of time. Relatively few variables, such as ocean color, can be measured at fine resolution over large areas via remote sensing. Most variables, and in particular most rates, can be measured only on site. Third, patterns measured at small scales do not necessarily hold at larger scales; nor do processes prevailing at small scales necessarily prevail at large scales. Consequently, pressing problems in ecology cannot be automatically addressed by scaling locally measured variables directly to larger areas and longer times.

The classic example of the problem of scale is loss of biodiversity. The causes of species extinction occur at the scale of ecosystems, whereas measurements are of necessity confined to smaller areas. Yet no biologist would try to address the problem by direct extrapolation from local samples, because it is well known that species number does not scale directly with area. It has become increasingly clear that the same principle applies to any ecological problem.

An example is research on recruitment variability in a major fishery such as that of cod, *Gadus morhua* (Figure 1). This fishery extended through the entire northeastern continental shelf of North America (Figure 1a) for centuries, until its collapse in the early 1990s. After the collapse, eggs and first-year juveniles were confined to coastal areas, where survival depends on suitable habitat. Habitat surveys can be made at the scale of coves or sections of coast (Figure 1b), but direct measurements of absolute density in relation to habitat can be made only by seine hauls in areas of a few hundred square meters (Figure 1c). Even within these small areas, habitat is highly heterogeneous (Figure 1d). Consequently, the ratio of area of interest (Figure 1a, b) to area surveyed

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(Figure 1c, d) cannot be used to estimate numbers and survival prospects at larger scales from direct measurements at smaller scales.

The three components of the problem of scale are illustrated in diagrammatic form (Figure 2) for the problem of monitoring pollution-induced variation in benthic invertebrate numbers against a background of natural variation in Manukau Harbour, New Zealand (Thrush et al. 1997). Pollutants are dumped at point sources (lower-left part of Figure 2a), but continued dumping and tidal mixing extend the problem to larger scales (upper-right corner, Figure 2a). Experiments and surveys to identify natural sources of variation in benthic populations are confined by costs to areas smaller than the scale of the problem (Figure 2b). At these smaller scales, movement rates exceed mortality rates (Figure 2c); hence an increase in mortality is difficult to detect because of organism movement across the boundaries of monitoring sites.

The concept of scale is now widely recognized as a central concern in ecology. How rapidly did this occur? What are the prospects that scaling concepts will lead to theoretical unification in ecology? This article reports on these questions at a convenient point in time, the end of the 20th century.

Definition of scale

The word *scale* has multiple meanings, contributing to its ambiguous usage in the ecological literature. The *Oxford English Dictionary* (Simpson and Weiner 1989) distinguishes 15 different meanings arising from two different roots. The Old

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Norse root in *skal* (bowl) gives rise to fish scales, the scales of justice, and hence, by extension, measurement by means of pairwise comparison of objects. Using an old-fashioned scale, one can assign a mass of 1 g to a beetle that balances a 1-g standard mass. The Latin root in *scala* (ladder) gives rise to musical scales, scaling a wall, and, by extension, measuring a length by counting steps or subdivisions. Using a ladder known to be 2 m in height, one can assign a height of half a ladder (1 m) to a bush.

In ecology, the word *scale* has acquired several common technical meanings. This diversity in acquired technical definition, added to the diversity in origin of the word, works against attempts at standard definition. A more productive approach is simply to ask that the word be used with an appropriate qualifier.

Common technical definitions of scale

The type of measurement scale (Stevens 1946) distinguishes variables quantified on a nominal scale (presence/absence), an ordinal scale (ranks), an interval scale (equal steps, such as degrees centigrade), and a ratio scale (equal steps and known zero, such as degrees kelvin).

Cartographic scale is the ratio of the distance on a map to the distance on the ground. A meter-wide map of the world has a scale of about 1:39,000,000.

Scale refers to the extent relative to the grain of a variable indexed by time or space (Wiens 1989, Schneider 1994a). Variables so indexed have a minimum resolvable area or time period (grain or inner scale) within some range of measurement (extent or outer scale). For example, a tree-coring device resolves annual changes over periods of thousands of years.

In *multiscale analysis*, the variance in a measured quantity, or the relation of two measured quantities, is computed with a series of different scales. This is accomplished by systematically changing either the separation (lag) between measurements or the averaging interval (window size) for contiguous measurements (Milne 1997).

Ecological scaling (Calder 1983, Peters 1983) refers to the use of power laws that scale a variable (e.g., respiration) to body size, usually according to a nonintegral exponent. Respiration typically scales as $\text{mass}^{0.75}$; hence, a doubling in body size increases oxygen consumption by $2^{0.75} = 1.7$, rather than by a factor of 2.

Powell (1989) defined *scale* as the distance before some quantity of interest changes.

Verbal expression of the concept: Paradigm shift or sustained growth?

The research literature suggests that recognition of the concept of scale occurred suddenly in the 1980s:

[1988] Kuhn's concept of a paradigm shift is a useful way to interpret the annual meeting of the ESA [Ecological Society of America].... Every symposium or session I attended featured, included, or was structured by the concepts of scale and spatial patterns. I left feeling I had observed one of those rare creatures of the intellectual bestiary, a paradigm shift (Golley 1989, p. 65).

[1997] We can no longer...cling to the belief that the scale on which we view systems does not affect what we see.... This is quite a different way of viewing the world than that which was in vogue a decade ago, and it is by no means yet widely embraced by everyone (Wiens 1999, p. 371).

Recognition of the importance of scale has been rapid, based on how frequently the word *scale* appears in the ecological research literature. In a digital version of the associated journals *Ecology* and *Ecological Monographs*, the term *spatial scale* made its first appearance in the early 1970s (Marten 1972, Wiens 1973). The term appears with increasing frequency in the late 1970s (Figure 3a). In the 1980s, frequency of appearance grew exponentially, at a pace 10 times the rate of growth in number of articles per yearly volume (Figure 3a). During that decade, the term appears to have been most commonly used in these two journals to qualify a result as being found at a particular spatial scale. The digital archive ends at 1996, so analysis was extended by reading abstracts. Frequency of use in abstracts (Figure 3b) paralleled that in the text, with some indication of decrease after 1996. The concept of scale currently is explicitly used in about 15% of articles each year in the two publications.

The sudden and exponential increase in explicit treatment of the concept of scale also occurred within a relatively old and specialized research area, the pelagic ecology of seabirds. In a comprehensive reference list on the topic (Schneider 1991), the two oldest articles were Collins (1884) and Murphy (1914). Publications that include reference to more than one space or time scale first appeared in 1980 (Schneider 1994b). The growth rate was exponential, at $18.9\% \text{ yr}^{-1}$ from 1980 to 1990.

In terrestrial ecology, hierarchical levels are used to express the concept of scale (Allen and Starr 1982). The concept of organizational level in biology (cell, tissue, organ, organism) was initially extended to populations and communities in the second edition of Odum's ecology text (1959). The concept of hierarchy in ecology (Allen and Starr 1982) refers to a focal level constrained by large-scale dynamics. O'Neill et al. (1986) developed the idea that levels beyond that of the organism arise during the course of energy dissipation in ecosystems. Because the idea that "scale matters" is central to hierarchy theory in ecology, the increasing frequency of

publication on the topic measures the rise in recognition of the concept of scale. A comprehensive list of 231 articles shows that the publication rate grew exponentially from 1969 to 1990 (Figure 3c). If the 63 nonecological publications in the list are removed, publication rate grew exponentially from 1973 through 1991, at 18.2% yr⁻¹.

The use of “hierarchy theory” and “spatial scale” indicates rapid recognition in the late 1970s and early 1980s, but the concept of scale in ecology is far older. For example, Johnstone ([1908] 1977) questioned whether catches from a limited area could be used to calculate the density of organisms for the entire Irish Sea. Greig-Smith (1952) quantified spatial patterns in plants and their environment at multiple scales. In a list of books and articles that use multiscale concepts (Schneider 1994a), publication occurs throughout the 20th century, with exponential growth in the 40-year period after World War II (Figure 3d). The drop after 1991 reflects the completion of the reference list in early 1992, with a few articles added during manuscript revisions in 1992 and 1993.

The increase in recognition of the concept of scale depends on how the search is defined. Sudden appearance followed by exponential growth was found when the term *spatial scale* or the concept of hierarchy theory was considered. Sustained growth over nearly a century (interrupted only by World War II) was found in a reference list from a review that aimed at comprehensive coverage of the concept of scale in ecology, regardless of whether the word *scale* was used (Figure 3d).

Graphical expression of the concept: Space–time diagrams

Figures with both space and time scales as axes first appeared in the ecological literature in 1978, when John Steele modified a diagram used in physical oceanography (Stommel 1963). Stommel’s three-dimensional diagram showed variability in sea level against both space and time scales. Steele used Stommel’s space and time axes to draw two different diagrams. Steele’s first diagram showed the space and time scales of patchiness of phytoplankton, zooplankton, and fish (Figure 4a). This space–time (ST) diagram was conceptual, showing the scales of named phenomena. A conceptual ST diagram first appeared in terrestrial ecology 5 years later (Delcourt et al. 1983). Steele’s second diagram compared the time and space scales of coverage by a single

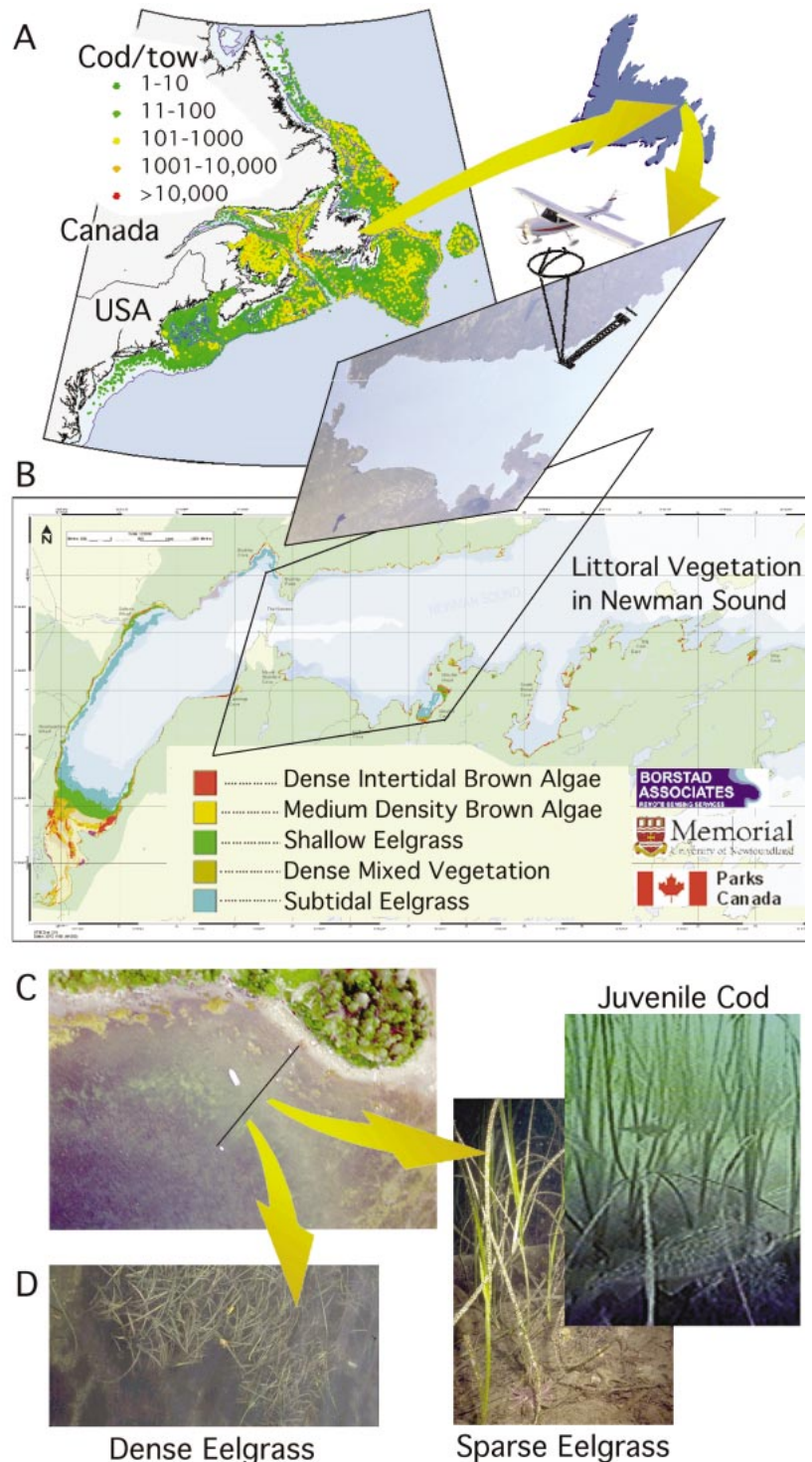


Figure 1. The problem of scale in ecology. Management of cod, *Gadus morhua*. (a) Variation in catch rates at the geographic scale of stocks in the northwest Atlantic Ocean. (b) Juvenile habitat variation at the scale of aerial surveys. (c) Habitat variation at the scale of direct measurement of juvenile cod density in 880 m² seine hauls. (d) Habitat variation at the scale of experimental investigation of juvenile survival.

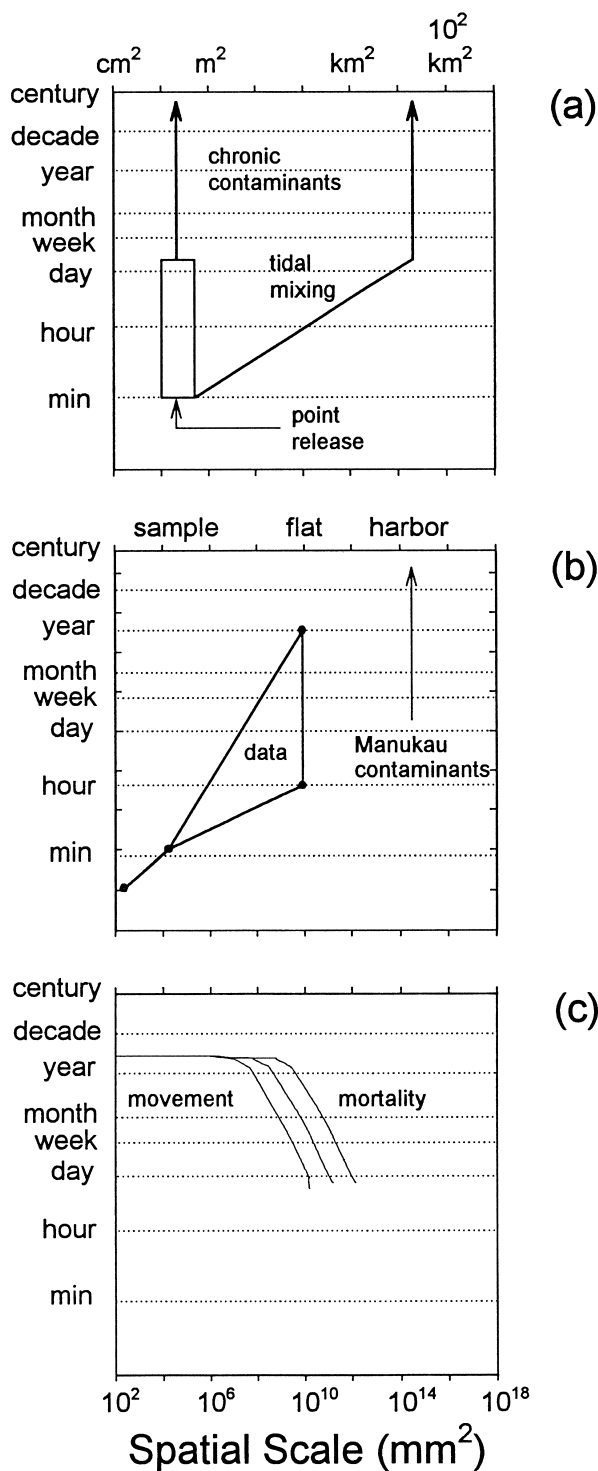


Figure 2. The problem of scale in ecology. Monitoring the impact of coastal pollutants on benthic invertebrates. (a) Point releases of contaminants are mixed throughout Manukau Harbour in Auckland, New Zealand. (b) Experimental data to separate the natural and contaminant-caused variation in benthic population densities are confined to limited areas (redrawn from Schneider et al. 1997). (c) At the scale of surveys and experiments, rates of movement exceed mortality rates in the bivalve *Macomona liliana*.

oceanographic research cruise with coverage by an oceanographic program using several ships (Figure 4b). This diagram was instrumental in that it showed the capacity of a particular instrument (research vessel in Figure 4b). An instrumental ST diagram first appeared in terrestrial ecology 13 years later (Firbank 1991).

ST diagrams are highly effective in comparing space and time scales of ecological questions to the capacity of research programs. In agricultural research, Firbank (1991) used an instrumental diagram to compare the space and time scales of experiments with those of surveys. In general, surveys extended beyond 10 km, with time scales of days to decades. Experiments were at the scale of a meter, with time scales ranging for 1 to 100 years. ST diagrams comparing phenomena to instrumental capacity have been published in research on disturbances in arctic ecosystems (Walker and Walker 1991) and on benthic experiments (Schneider et al. 1997).

The format used by Steele (1978) was modified by Horne and Schneider (1994) to show critical scales that mark change in prevailing dynamics. In these diagrams, a contour line marks the space and time scales at which two rates are of the same order of magnitude. At larger scales one rate prevails, while at smaller scales the other rate prevails. Figure 2c shows critical scales for movement versus mortality in the benthic bivalve *Macomona liliana*. Comparison with Figure 2b shows that experimental data occur in the “domain of scale” (Wiens 1999) dominated by kinematics (movement) rather than demographics (mortality).

A search of the literature turned up more than 60 diagrams with axes showing both space and time scales. The list excluded reprints of earlier diagrams, which were common, but did include modified versions of earlier diagrams. These graphical expressions of the concept of scale increased exponentially from 1980 to 1998 (Figure 3e). Conceptual ST diagrams (such as Figures 2a and 4a) were common during the 1980s, whereas critical-scale diagrams (such as Figure 2c) accounted for many of the plots after 1996. Instrumental ST diagrams (such as Figures 2b and 4b) appeared throughout the period.

Mathematical expression of the concept

Scope and power laws. In an instrumental ST diagram, the distance between two points is called the *scope*, or *ratio of extent to resolution*. In Figure 4b, the spatial scope of the multiship Fladen experiment is roughly 100 km / 0.8 km = 125, compared to a fish stock survey, with a spatial scope of roughly 1000 km / 20 km = 50. The idea of scope is widely applicable. The scope of a meter stick with a resolution of 0.001 m is 1 m / 0.001 m = 10³. The scope of a survey of 200,000 km² sampled with plots of 50 m by 100 m is 200,000 km² / 0.005 km² = 4 × 10⁷. A computational model representing population dynamics at half-day intervals for 3 years has a scope of 1095 days / 0.5 days = 2190. Halving the time step doubles the scope to 4380.

Scope as a quantitative concept leads naturally to power laws, which coordinate the scope of one measured quantity

with another according to an exponent (Schneider 1998). For isometric scaling, the exponent is, by definition, unity. An example is the scaling of volume to mass in large and small organisms:

$$\left(\frac{Volume_{large}}{Volume_{small}}\right) = \left(\frac{Length_{large}}{Length_{small}}\right)^1$$

This scaling relation applies to organisms that have the same specific gravity as water and are close to neutrally buoyant.

For euclidean scaling, the exponent is an integer or ratio of integers. The scaling of volume to length for a euclidean object is:

$$\left(\frac{Volume_{large}}{Volume_{small}}\right) = \left(\frac{Length_{large}}{Length_{small}}\right)^3$$

Organisms are often treated as euclidean in shape, but in fact they have convoluted or “fractal” (Mandelbrot 1977) surfaces and inhabit convoluted or fractal environments (Burrough 1981). For fractal scaling, the exponent relating the scope of one quantity to measurement is not an integer:

$$\left(\frac{LungArea_{coarse}}{LungArea_{fine}}\right) = \left(\frac{GridBox_{coarse}}{GridBox_{fine}}\right)^{-0.17}$$

The measured area of a lung depends in a systematic way on the size of the boxes used. Doubling the box size decreases the measurement of lung area by $2^{-0.17} = 89\%$ because detail is lost as the box size increases. The fractal dimension of the lung is $D_f = 2 - (-0.17) = 2.17$. The surface is more convoluted than a flat surface ($D = 2$), but not so convoluted as to completely fill a volume ($D = 3$).

Another example of fractal scaling is river length:

$$\left(\frac{River_{coarse}}{River_{fine}}\right) = \left(\frac{Ruler_{long}}{Ruler_{short}}\right)^{-0.3}$$

The fractal dimension of the river is $D_f = 1 - (-0.3) = 1.3$. It is more convoluted than a line ($D = 1$) but not so convoluted as to fill a plane ($D = 2$).

Power laws, which are common in biology, usually appear in forms that hide the underlying scopes. A power law equates one scope to another according to an exponent β :

$$\left(\frac{Q(M)}{Q(M_o)}\right) = \left(\frac{M}{M_o}\right)^\beta$$

This is shortened to

$$Q(M) = (M_o^{-\beta} \cdot Q(M_o)) \cdot M^\beta$$

then further shortened to the more familiar form

$$Q(M) = k \cdot M^\beta$$

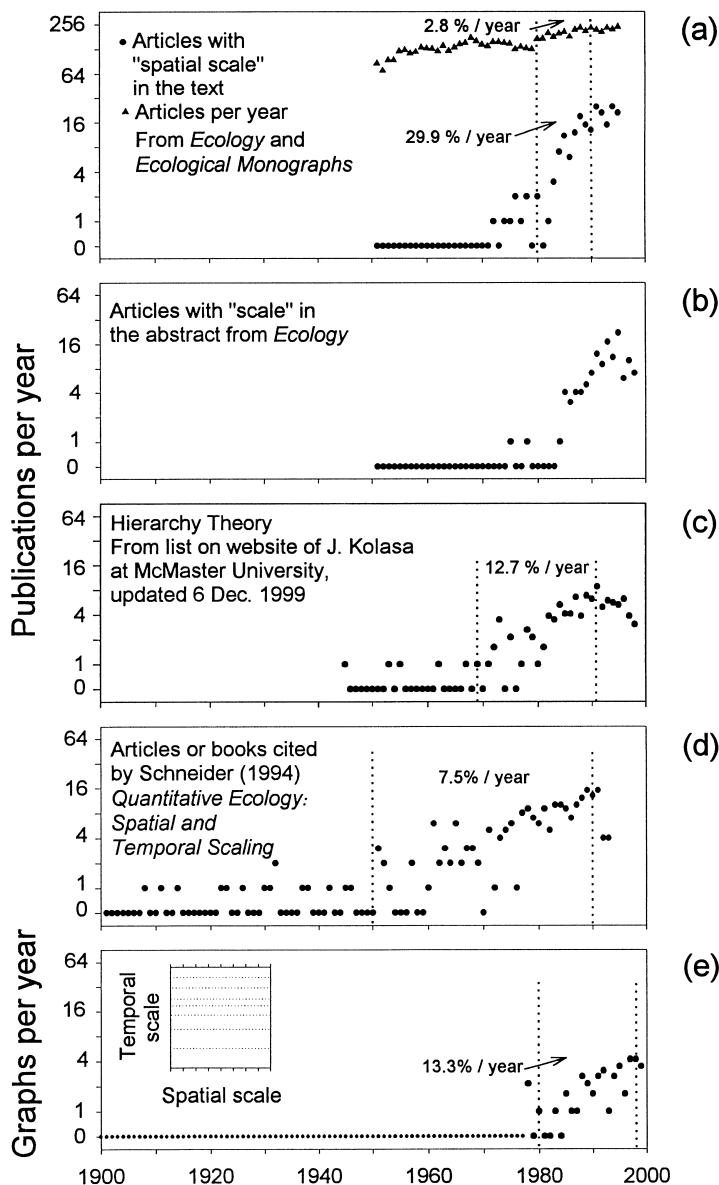


Figure 3. Increasing use of the concept of scale in ecology. Dotted lines bracket periods in which growth rate was exponential. (a) Articles with the term spatial scale in the text. (b) Articles with the word scale in the abstract. (c) Articles and books on hierarchy theory. (d) Articles and books that consider more than one space or time scale, whether or not the word scale is used. (e) Graphical expression of the concept of scale, as measured by publication of space-time diagrams with axes as shown.

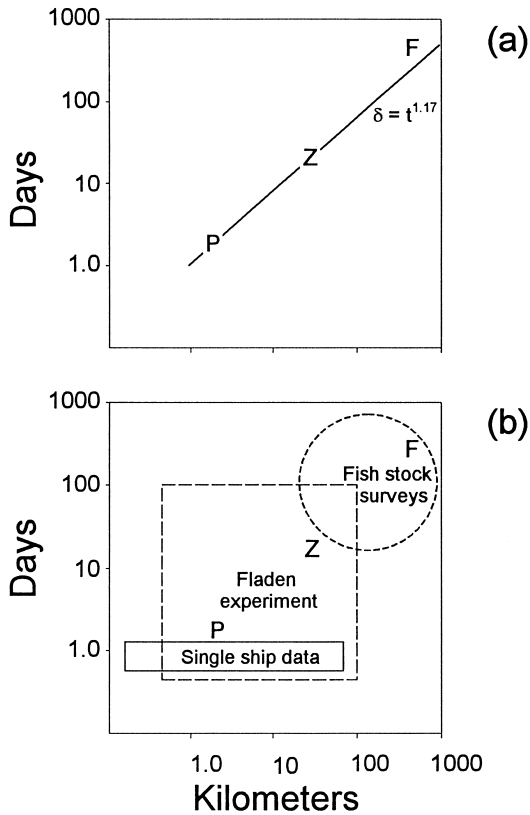


Figure 4. First use of space–time diagrams in ecology (redrawn from Steele 1978). (a) Conceptual space–time diagram showing life span (days) versus patch size (kilometers) in phytoplankton (P), zooplankton (Z), and fish (F). Line shows mixing scales, measured as power-law relation of dispersion of dye (δ , in km) with time (t , in days). (b) Instrumental space–time diagram showing space and time scales covered by various types of sampling programs.

The constant k contains all of the information about the scaling relation. It is more informative than the exponent alone (Gould 1979).

Until recently, power laws in ecology came mostly from the literature on species–area curves or body–size allometry. Rosenzweig (1995) discussed 48 articles that included species–area curves. In this list, the number of articles grew exponentially, at 4.8% yr^{-1} from 1920 to 1980. In organismal biology, Peters (1983) listed 251 articles containing 1050 power laws that scale organism form or function to body size. Growth in the number of articles (Figure 5a) was linear from 1950 to 1980. Growth in the number of power laws (Figure 5b) was exponential from 1930 to 1980.

Scaling theory. Power laws for species–area curves and body–size allometry (Figure 5) were not derived from theory. These scaling relations were empirical, estimated by regression rather than calculated from a set of theoretical statements. These empirical power laws do not meet Hempel’s criterion

(1964) that a theory must state the conditions leading to a result that can be tested against data.

Nevertheless, several scaling theories do meet Hempel’s criterion (1964). An example is the theory (Sarrus and Rameaux 1839, in Kleiber 1947) that respiration scales with euclidean surface area, which in turn scales as volume^{2/3} and, hence, mass^{2/3}. Another example is the theory that respiration scales with fractal surface area of the lung and hence scales as volume^{2.17/3} or mass^{0.72} (Pennycuik 1992, Schneider 1994a). More recently, West et al. (1999) theorized that supply rate in a branched network such as a vascular system scales with internal surface area $A = L^{2+\epsilon}$, and active tissue volume $V = L^{3+\epsilon+\zeta}$; hence delivery scales as $V^{(2+\epsilon)/(3+\epsilon+\zeta)}$. Delivery is maximized at $\epsilon = 1$ and $\zeta = 0$, hence delivery scales as volume^{3/4} or mass^{3/4}.

Another theory that meets Hempel’s criterion (1964) is that power laws arise from local interactions in disorganized physical systems when they near some critical state (Widom 1965, Wilson 1971). The appearance of a power law describing structure when dynamics are near a critical state is called *universal scaling* or *complexity theory* (Milne 1988). Spatially heterogeneous systems that tend to move toward critical states are called *self-organizing* (Bak et al. 1988). An example of self-organized criticality is the appearance of power law distribution of gaps in the rain forest at Barro Colorado Island in Panama (Solé and Manrubia 1995). Gaps develop at mul-

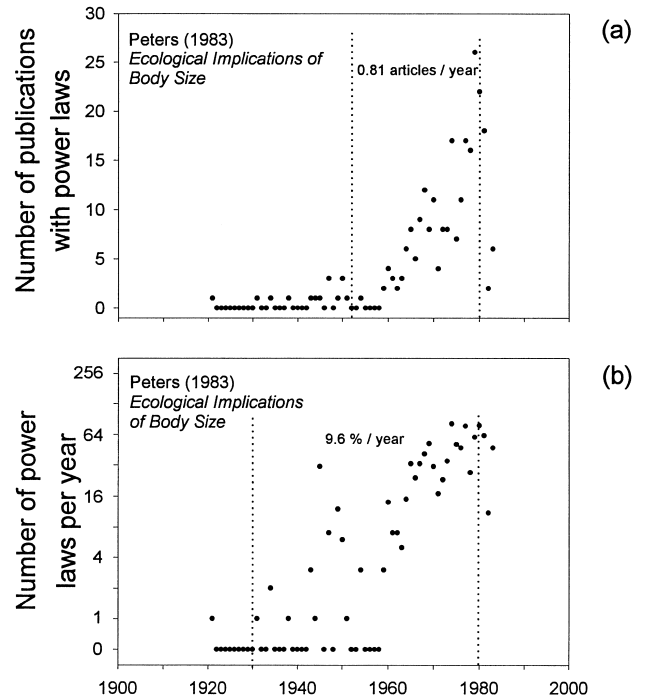


Figure 5. Increase in quantitative expression of the concept of scale by power laws that relate organism form or function to body size. (a) Number of articles with power laws listed by Peters (1983). (b) Number of power laws listed by Peters (1983).

tiple scales because vines bind trees, with the result being canopy collapse that propagates to scales larger than those of individual trees. In population biology, Levin and Pacala (1997) summarized examples of large-scale patterns emerging from locally coupled interactions, as in the spread of disease. In geomorphology, landscape structure at the scale of a watershed results from episodic erosion by rivers and streams. Power law (fractal) scalings in landscape data (Burrrough 1981) emerge when erosive dynamics exhibit self-organized criticality (Rodriguez-Iturbe and Rinaldo 1997).

What conditions must be met for power laws to emerge? In general, warring exponential rates result in power laws when loss acts on production at a lag, rather than simultaneously. An exponential production rate r acting on an initial quantity Q_0 yields an increase relative to Q_0 of

$$\frac{Q_{produced}}{Q_0} = e^{r \cdot t} \quad (1)$$

An exponential loss rate of z acting on Q_0 yields a decrease of

$$\frac{Q_{remaining}}{Q_0} = e^{-z \cdot t} \quad (2)$$

If loss acts with no lag on current stock of the quantity Q , then Q_0 in (1) is the same as Q_0 in (2), and hence:

$$Q = Q_0 \cdot e^{(r-z)t} \quad (3)$$

However, if loss acts on production at some time lag, then Q_0 in (1) is not the same as Q_0 in (2). For discrete time intervals:

$$\frac{1}{r} \cdot \ln\left(\frac{Q_{produced}}{Q_o}\right) = t = \frac{1}{-z} \cdot \ln\left(\frac{Q_{remaining}}{Q'_o}\right) \quad (4a)$$

$$\frac{Q_{produced}}{Q_0} = \left(\frac{Q_{remaining}}{Q'_0}\right)^{-r/z} \quad (4b)$$

Figure 6 shows the emergence of power-law behavior in a simple population model as the lag between production and

Scaling relation for chaotic population dynamics

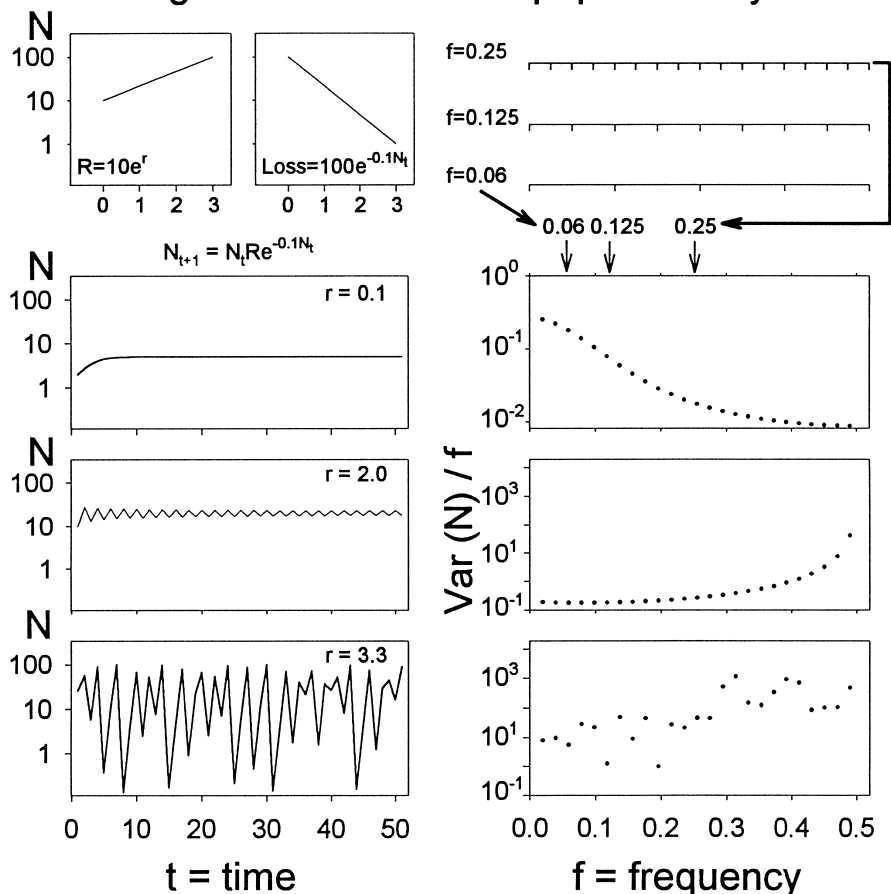


Figure 6. Emergence of power-law behavior from antagonistic exponential rates. In a discrete time population model with loss acting on recent production, time lags increase as the production rate increases from $r = 0.1$ (10% / time step) to $r = 3.3$ (330% / time step). In the bottom panel, the time series becomes chaotic, and Variance (N)/f scales as f (where f equals cycles per time step as shown in the top panel). The averaging interval increases from two steps to 50 steps as f decreases from 0.50 to 0.02.

loss increases. In this example, intrinsic differences in time scales of antagonistic rates delay removal relative to production (Steele 1995). As the delay increases, temporal variability spreads over multiple scales, diverging from any one scale. Figure 6 shows the appearance of scale-divergent dynamics in a discrete time model as the production rate increases, thus widening the lag between production and loss. A power-law relation of variance in number to temporal scale emerges (as a straight line on a log-log plot) as the time series becomes fully chaotic in the lowest pair of panels in Figure 6.

Potential applications. A few examples of the theory of scale-divergent dynamics certainly do not establish unifying theory in ecology. However, a large number of familiar problems in ecology are susceptible to analysis by this theory. A familiar and widely known example is the number of species in isolated systems (e.g., islands, lakes). The underlying dy-

namics meet the conditions for the emergence of power-law behavior if losses resulting from extinction act episodically on species that accumulate via colonization events or evolutionary change. Island biogeography (MacArthur and Wilson 1967) offers an equilibrium theory of loss versus colonization in isolated ecosystems. Scale-divergent dynamics offers a more inclusive theory, leading to either equilibrium or non-equilibrium behavior, depending on whether losses act on gains with a lag.

Metapopulation analysis (Levins 1969) focuses on the critical point at which recolonization offsets the probability of local extinction. With only slight refocus, the formalism underlying metapopulation analysis becomes a way of predicting the emergence of power-law behavior in semi-isolated patches of habitat.

Landscape ecology focuses on ecological processes against backgrounds of spatial structure such as ecotones. Fractal descriptions of habitat structures are becoming more frequent. Milne (1997) listed examples for eagles, woodpeckers, gophers, and rabbits. The power-law (fractal) structure of ecotones suggests that episodically warring rates are at work (e.g., gophers versus rabbits, grasses versus trees). In landscape ecology, one can expect to find antagonistic rates acting episodically whenever a power law (such as a fractal) describes habitat structure.

At evolutionary time scales, a change in species number can be analyzed as the outcome of extinction rates acting on the results of speciation. If, as seems likely, these antagonistic rates act episodically with respect to each other, then power-law behavior is expected in the record of species number through time.

From central concept to unifying theory?

[1992] 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, p. 1943).

[1999] Although the concept that “scale matters” is a central concern of landscape ecology, we have only fragments of a theory of scaling (Wiens 1999, p. 373).

Scaling has certainly become a central concept in ecology. Could it become a unifying concept? The question could not have been asked 25 years ago. The plenary sessions of the First International Congress of Ecology were reported in a book titled *Unifying Concepts in Ecology* (van Dobben and Lowe-McConnell 1975). Out of 28 contributions covering the major ideas in ecology at the time, only three touch on multiscale analysis. None uses the word *scale* explicitly or states that “scale matters.” Less than 20 years later, Allen and Hoekstra (1992) placed the concept of scale at the center of their book *Toward a Unified Ecology*.

Potential applications of the theory of scale-divergent dynamics easily exceed extant cases. It is not inconceivable that the concept of scale, and in particular the theory of scale-divergent dynamics (equations 1–4) will bring some theoretical

unity to ecology. In systems where loss and production act simultaneously, where there is no memory, and where history does not matter, classical equilibrium theory is expected to apply (equation 3). In systems where antagonistic rates act episodically, where there is memory, and where history does matter, scale-divergent dynamics are expected (equation 4).

Conclusion

Analysis of key phrases (“scale” and “hierarchy theory”) suggests that recognition of the problem of scale in ecology occurred as a sudden shift beginning in the late 1970s and early 1980s. The concept itself is far older. Verbal treatment of the concept, without the use of the word *scale*, began early in the 20th century. Graphical treatment employing both space and time scales began in 1978. Formal treatment based on power laws began around 1920 for the scaling of species number to area and for the scaling of organism form and function to body size. In physics, power laws describe complex behavior that arises from nonlinear interactions near critical points. In biology, power laws arise from scale-divergent dynamics when history matters and either exponential losses or production acts episodically. The theory of scale-divergent dynamics applies to a wide variety of phenomena. It has the potential to bring some theoretical unity to ecology.

Acknowledgments

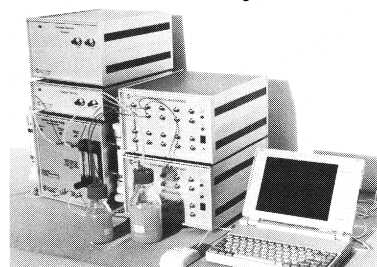
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References cited

- Allen TFH, Hoekstra TW. 1992. *Toward a Unified Ecology*. New York: Columbia University Press.
- Allen TFH, Starr TB. 1982. *Hierarchy*. Chicago: University of Chicago Press.
- Bak P, Tang C, Wiesenfeld K. 1988. Self-organized criticality. *Physics Review A* 38: 364–374.
- Burrough PA. 1981. Fractal dimensions of landscapes and other environmental data. *Nature* 294: 240–242.
- Calder WA. 1983. Ecological scaling: Mammals and birds. *Annual Review of Ecology and Systematics* 14: 213–230.
- Collins JW. 1884. Notes on the habits and methods of capture of various species of sea birds that occur on the fishing banks off the eastern coast of North America, and which are used as bait for catching codfish by New England fisherman. Report of the Commissioner of Fish and Fisheries for 1882 13: 311–335.
- Delcourt HR, Delcourt PA, Webb T. 1983. Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1: 153–175.
- Firbank LG. 1991. The implications of scale on the ecology and management of weeds. Pages 91–103 in Bunce RGH, Ryszkowski L, Paoletti MG, eds. *Landscape Ecology and Agroecosystems*. Boca Raton (FL): Lewis.

- Golley F. 1989. Paradigm shift: Editor's comment. *Landscape Ecology* 3: 65–66.
- Gould SJ. 1979. An allometric interpretation of species-area curves: The meaning of the coefficient. *American Naturalist* 114: 335–343.
- Greig-Smith P. 1952. The use of random and contiguous quadrants in the study of the structure of plant communities. *Annals of Botany* 16: 293–316.
- Hempel CG. 1964. *Philosophy of Natural Science*. Englewood Cliffs (NJ): PrenticeHall.
- Horne JK, Schneider DC. 1994. Analysis of scale-dependent processes with dimensionless ratios. *Oikos* 70: 201–211.
- Johnstone J. [1908] 1977. *Conditions of Life in the Sea: A Short Account of Quantitative Marine Biological Research*. New York: Arno.
- Kleiber M. 1947. Body size and metabolic rate. *Physiological Reviews* 27: 511–541.
- Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.
- Levin SA, Pacala SW. 1997. Theories of simplification and scaling of spatially distributed process. Pages 271–295 in Tilman D, Kareiva P, eds. *Spatial Ecology*. Princeton (NJ): Princeton University Press.
- Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237–240.
- MacArthur RH, Wilson EO. 1967. *Theory of Island Biogeography*. Princeton (NJ): Princeton University Press.
- Mandelbrot BB. 1977. *Fractals: Form, Chance, and Dimension*. San Francisco: Freeman.
- Marten GG. 1972. Censusing mouse populations by means of tracking. *Ecology* 53: 859–867.
- Milne B. 1997. Applications of fractal geometry in wildlife biology. Pages 32–69 in Bissonette JA, ed. *Wildlife and Landscape Ecology: Effects of Pattern and Scale*. New York: Springer-Verlag.
- . 1988. Motivation and benefits of complex systems approaches in ecology. *Ecosystems* 1: 449–456.
- Murphy RC. 1914. Observations on birds of the south Atlantic. *Auk* 31: 439–457.
- Odum HT. 1959. *Fundamentals of Ecology*. 2nd ed. Philadelphia: W. B. Saunders.
- O'Neill RV, DeAngelis DL, Waide JB, Allen, TFH. 1986. *A Hierarchical Concept of Ecosystems*. Princeton (NJ): Princeton University Press.
- Pennyquick CJ. 1992. *Newton Rules Biology*. Cambridge (UK): Cambridge University Press.
- Peters RH. 1983. *The Ecological Implications of Body Size*. Cambridge (UK): Cambridge University Press.
- Powell TM. 1989. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. Pages 157–176 in Roughgarden J, May RM, Levin SA, eds. *Perspectives in Ecological Theory*. Princeton (NJ): Princeton University Press.
- Rodriguez-Iturbe I, Rinaldo A. 1997. *Fractal River Basins: Chance and Self-Organization*. Cambridge (UK): Cambridge University Press.
- Rosenzweig ML. 1995. *Species Diversity in Space and Time*. Cambridge (UK): Cambridge University Press.
- Schneider DC. 1991. The role of fluid dynamics in the ecology of marine birds. *Oceanography and Marine Biology Annual Review* 29: 487–521.
- . 1994a. *Quantitative Ecology: Spatial and Temporal Scaling*. San Diego: Academic Press.
- . 1994b. Scale-dependent patterns and species interactions in marine nekton. Pages 441–467 in Giller P, Raffaelli D, Hildrew A, eds. *Aquatic Ecology: Scale, Pattern, and Process*. London: Blackwell.
- . 1998. Applied scaling theory. Pages 253–269 in Peterson DL, Parker VT, eds. *Ecological Scale*. New York: Columbia University Press.
- Schneider DC, Walters R, Thrush S, Dayton PK. 1997. Scale-up of ecological experiments: Density variation in the mobile bivalve *Macomona liliana*. *Journal of Experimental Marine Biology and Ecology* 216: 129–152.
- Simpson J, Weiner E, eds. 1989. *Oxford English Dictionary*. 2nd ed. Cambridge (UK): Oxford University Press.
- Solé RV, Manrubia SC. 1995. Are rainforests self-organized in a critical state? *Journal of Theoretical Biology* 173: 31–40.
- Steele JH. 1978. Some comments on plankton patchiness. Pages 11–20 in Steele JH, ed. *Spatial Pattern in Plankton Communities*. New York: Plenum.
- . 1991. Can ecological theory cross the land-sea boundary? *Journal of Theoretical Biology* 153: 425–436.
- . 1995. Concepts and models: An overview. Pages 90–92 in Levin SA, Powell TM, Steele JH, eds. *Patch Dynamics*. New York: Springer-Verlag.
- Stevens SS. 1946. On the theory of scales of measurement. *Science* 103: 677–680.
- Stommel H. 1963. The varieties of oceanographic experience. *Science* 139: 572–576.
- Thrush SF, et al. 1997. Scaling-up: Where to next? *Journal of Experimental Marine Biology and Ecology* 216: 243–254.
- van Dobben WH, Lowe-McConnell RH, eds. 1975. *Unifying Concepts in Ecology: Report of the Plenary Sessions of the First International Congress of Ecology*. The Hague (Netherlands): Dr. W. Junk B.V. Publishers.
- Walker DA, Walker MD. 1991. History and pattern of disturbance in Alaskan arctic terrestrial ecosystems: A hierarchical approach to analyzing landscape change. *Journal of Applied Ecology* 28: 244–276.
- West GB, Brown JH, Enquist BJ. 1999. The fourth dimension of life: Fractal geometry and allometric scaling of organisms. *Science* 284: 1677–1679.
- Widom B. 1965. Surface tension and molecular correlations near the critical point. *Journal of Chemical Physics* 43: 3892–3898.
- Wiens JA. 1973. Pattern and process in grassland bird communities. *Ecological Monographs* 43: 237–270.
- . 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.
- . 1999. The science and practice of landscape ecology. Pages 371–383 in Klopach JM, Gardner RH, eds. *Landscape Ecological Analysis*. New York: Springer-Verlag.
- Wilson KG. 1971. Renormalization group and critical phenomena. *Physics Review B* 4: 3174–3205.

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