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ESSAY REVIEW

Spatial scaling in ecology[1]

J. A. WIENS
Department of Biology and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, USA

'The only things that can be universal, in a sense, are scaling things'

(Mitchell Feigenbaum[2])

Introduction

Acts in what Hutchinson (1965) has called the 'ecological theatre' are played out on various scales of space and time. To understand the drama, we must view it on the appropriate scale. Plant ecologists long ago recognized the importance of sampling scale in their descriptions of the dispersion or distribution of species (e.g. Greig-Smith, 1952). However, many ecologists have behaved as if patterns and the processes that produce them are insensitive to differences in scale and have designed their studies with little explicit attention to scale. Kareiva & Andersen (1988) surveyed nearly 100 field experiments in community ecology and found that half were conducted on plots no larger than 1 m in diameter, despite considerable differences in the sizes and types of organisms studied.

Investigators addressing the same questions have often conducted their studies on quite different scales. Not surprisingly, their findings have not always matched, and arguments have ensued. The disagreements among conservation biologists over the optimal design of nature reserves (see Simberloff, 1988) are at least partly due to a failure to appreciate scaling differences among organisms. Controversies about the role of competition in structuring animal communities (Schoener, 1982; Wiens, 1983, 1989) or about the degree of coevolution in communities (Connell, 1980; Roughgarden, 1983) may reflect the imposition of a single scale on all of the species in the community. Current ecological theories do little to resolve such debates, because most of these theories are mute on scale – they can be applied at any scale on which the relevant parameters can be measured.

Recently, however, ecologist studying a wide range of topics have expressed concern about scaling effects (see Dayton & Tegner, 1984; Wiens *et al.*, 1986a; Giller & Gee, 1987; Meetenmeyer & Box, 1987; Frost *et al.*, 1988; Rosswall, Woodmansee & Risser, 1988). 'Scale' is rapidly becoming a new ecological buzzword.

Scientists in other disciplines have recognized scaling issues for some time. The very foundation of geography is scaling. In the atmospheric and earth sciences, the physical processes that determine local and global patterns are clearly linked (e.g. Schumm & Lichty, 1965; Clark, 1985; Dagan, 1986; Ahnert, 1987) and their importance is acknowledged in hierarchies of scale that guide research and define subdisciplines within these sciences. Physical and biological oceanographers often relate their findings to the spectrum of physical processes from circulation patterns in oceanic basins or large gyres to fine-scale eddies or rips (e.g. Haury, McGowan & Wiebe, 1978; Steele, 1978; Legrende & Demers, 1984; Hunt & Schneider, 1987; Platt & Sathyendranath, 1988). Physicists and mathematicians studying fractal geometry, strange attractors, percolation theory, and chaos address scaling as a primary focus of their investigations (Nittman, Daccord & Stanley, 1985; Orbach, 1986; Grebogi, Ott & Yorke, 1987; Gleick, 1987).

Why have ecologists been so slow to recognize scaling? Ecologists deal with phenomena that are intuitively familiar, and we are therefore more likely to perceive and study such phenomena on anthropocentric scales that accord with our own experiences. We have also been somewhat tradition-bound, using quadrats or study plots of a particular size simply because previous workers did. Unlike the physical and earth sciences (and many laboratory disciplines of biology), where our perceptual range has been extended by technology, few tools have been available to expand

[1] Adapted from the first Katharine P. Douglass Distinguished Lecutre at the Rocky Mountain Biological Laboratory, Gothic, Colorado, 23 July 1987.
[2] Quoted in Gleick, 1987, p. 186.

our view of ecological phenomena (but see Platt & Sathyendranath, 1988; Gosz, Dahm & Risser, 1988).

My thesis in this paper is that scaling issues are fundamental to all ecological investigations, as they are in other sciences. My comments are focused on spatial scaling, but similar arguments may be made about scaling in time.

The effects of scale

Some examples

The scale of an investigation may have profound effects on the patterns one finds. Consider some examples:

● In hardwood forests of the north-eastern United States, Least Flycatchers (*Empidonax minimus* Baird & Baird) negatively influence the distribution of American Redstart (*Setophaga ruticilla* L.) territories at the scale of 4-ha plots. Regionally, however, these species are positively associated (Sherry & Holmes, 1988). Apparently the broad-scale influences of habitat selection override the local effects of interspecific competition. Similar scale-dependency has been found in the habitat relationships of shrubsteppe birds (Wiens, Rotenberry & Van Horne, 1986b), interspecific associations among plant species (e.g. Beals, 1973) or phytoplankton and zooplankton (Carpenter & Kitchell, 1987), and the patterns of coexistence of mosses colonizing moose dung (Marino, 1988) or of ants on mangrove islands (Cole, 1983).

● In the Great Barrier Reef of Australia, the distribution of fish species among coral heads at the scale of patch reefs or a single atoll may be strongly influenced by chance events during recruitment and the species composition of local communities of fish may be unpredictable (Sale, 1988; Clarke, 1988). At the broader scales of atolls or reef systems, community composition is more predictable, perhaps because of habitat selection, niche diversification, or spatial replacement of species within trophic guilds (Ogden & Ebersole, 1981; Anderson *et al.*, 1981; Green, Bradbury & Reichelt, 1987; Galzin, 1987).

● On the basis of experiments conducted at the scale of individual leaf surfaces, plant physiologists have concluded that stomatal mechanisms regulate transpiration, whereas meterologists working at the broader scale of vegetation have concluded that climate is the principal control (Jarvis & McNaughton, 1986; Woodward, 1987). In a similar manner, most of the variation in litter decomposition rates among different species at a local scale is explained by properties of the litter and the decomposers, but at broader regional scales climatic variables account for most of the variation in decomposition rates (Meentemeyer, 1984).

● Domestic cattle grazing in shortgrass prairie use elements of local plant communities quite nonrandomly on the basis of short-term foraging decisions, but use of vegetation types is proportional to their coverage at the broader scale of landscape mosaics (Senft *et al.*, 1987).

● The distribution of phytoplankton in marine systems is dominated by horizontal turbulent diffusion at scales up to roughly 1 km (Platt, 1972; Denman & Platt, 1975). At somewhat broader scales, phytoplankton growth, zooplankton grazing, and vertical mixing override these local effects (Denman & Platt, 1975; Lekan & Wilson, 1978; Therriault & Platt, 1981). At scales of >5 km, phytoplankton patchiness is controlled largely by advection, eddies, and local upwelling occurring over areas of 1–100 km (Gower, Denman & Holyer, 1980; Legrende & Demers, 1984). The same controls operate in lakes, although the transitions occur at finer scales (Powell *et al.*, 1975).

These examples could easily be extended. The salient point is that different patterns emerge at different scales of investigation of virtually any aspect of any ecological system.

Linkages between physical and biological scales

In the marine phytoplankton and other aquatic systems, physical features may be primary determinants of adaptations of organisms, and physical and biological phenomena may scale in much the same way. However, in many terrestrial environments, atmospheric and geological influences may often be obscured by biological interactions (Clark, 1985). The relationships between climate and vegetation that are evident at broad scales, for example, may disappear at finer scales, overridden by the effects of competition and other biological processes (Greig-Smith, 1979; Woodward, 1987). Local biological interactions have the effect of decoupling systems from direct physical determination of patterns by introducing temporal or spatial lags in system dynamics or creating webs of indirect effects. However, at broader scales, physical processes may dominate or dissipate these biological effects (Levin, 1989). There are exceptions: plant distributions on fine

scales may be controlled by edaphic or microtopographic factors, and vegetation may influence climate at regional scales.

System openness and the scale of constraints

Ecological systems become closed when transfer rates among adjacent systems approach zero or when the differences in process rates between adjacent elements are so large that the dynamics of the elements are effectively decoupled from one another. In open systems, transfer rates among elements are relatively high, and the dynamics of patterns at a given scale are influenced by factors at broader scales. However, 'openness' is a matter of scale and of the phenomena considered. At the scale of individual habitat patches in a landscape mosaic, for example, population dynamics may be influenced by between-patch dispersal, but at the broader scale of an island containing that landscape, emigration may be nil and the populations closed. The same island, however, may be open with regard to atmospheric flows or broad-scale climatic influences.

The likelihood that measurements made on a system at a particular scale will reveal something about ecological mechanisms is a function of the openness of the system. The species diversity of a local community, for example, is influenced by speciation and extinction, and by range dynamics at regional or biogeographic scales (Ricklefs, 1987). Changes in population size at a location may reflect regional habitat alterations, events elsewhere in a species' range, or regional abundance and distribution rather than local conditions (May, 1981; Väisänen, Järvinen & Rauhala, 1986; Roughgarden, Gaines & Pacala, 1987; Wiens, 1989). Habitat selection by individuals may be determined not only by characteristics of a given site but by the densities of populations in other habitats over a larger area (O'Connor & Fuller, 1985). den Boer (1981) suggested that small local populations may frequently suffer extinction, only to be reconstituted by emigrants from other areas. The fine-scale demographic instability translates into long-term persistence and stability at the scale of the larger metapopulation (Morrison & Barbosa, 1987; DeAngelis & Waterhouse, 1987; Taylor, 1988).

Ecologists generally consider system openness in the context of how broad-scale processes constrain finer-scale phenomena. This is one of the primary messages of hierarchy theory (Allen & Starr, 1982) and of 'supply-side' ecology (Roughgarden *et al.*, 1987) and it is supported by studies of the temporal dynamics of food webs as well (Carpenter, 1988). However, the ways in which fine-scale patterns propagate to larger scales may impose constraints on the broad-scale patterns as well (Huston, DeAngelis & Post, 1988; Milne, 1988). Ecologists dealing with the temporal development of systems (e.g. forest insect epidemics: Barbosa & Schultz, 1987; Rykiel *et al.*, 1988) recognize this sensitivity to small differences in fine-scale initial conditions as the effects of historical events on the subsequent state of the system.

Extent and grain

Our ability to detect patterns is a function of both the *extent* and the *grain*[1] of an investigation (O'Neill *et al.*, 1986). Extent is the overall area encompassed by a study, what we often think of (imprecisely) as its scale[2] or the population we wish to describe by sampling. Grain is the size of the individual units of observation, the quadrats of a field ecologist or the sample units of a statistician (Fig. 1). Extent and grain define the upper and lower limits of resolution of a study; they are analogous to the overall size of a sieve and its mesh size, respectively. Any inferences about scale-dependency in a system are constrained by the extent and grain of investigation — we cannot generalize beyond the extent without accepting the assumption of scale-independent uniformitarianism of patterns and processes (which we know to be false), and we cannot detect any elements of patterns below the grain. For logistical reasons, expanding the extent of a study usually also entails enlarging the grain. The enhanced ability to detect broad-scale patterns carries the cost of a loss of resolution of fine-scale details.

Variance, equilibrium and predictability

When the scale of measurement of a variable is changed, the variance of that variable changes. How this happens depends on whether grain or extent is altered. Holding extent constant, an increase in the grain of measurement generally decreases spatial variance. In a perfectly homogeneous area (i.e. no spatial autocorrelation among

[1] This use of 'grain' differs from that of MacArthur & Levins (1964), who considered grain to be a function of how animals exploit resource patchiness in environments.

[2] Note that what is a fine scale to an ecologist is a large scale to a geographer or cartographer, who express scale as a ratio (e.g. 1:250000 is a smaller scale than 1:50000).

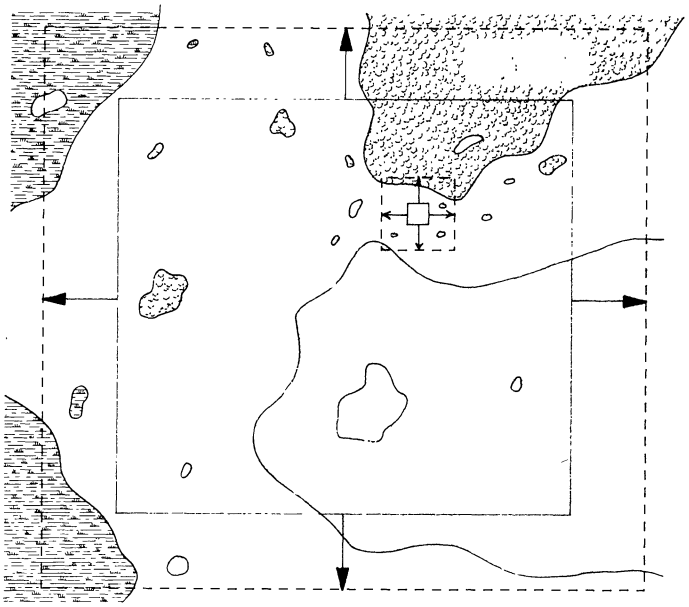

Fig. 1. The effects of changing the grain and extent of a study in a patchy landscape. As the extent of the study is increased (large squares), landscape elements that were not present in the original study area are encountered. As the grain of samples is correspondingly increased (small squares), small patches that initially could be differentiated are now included within samples and the differences among them are averaged out.

sample locations), the log-log plot of variance versus grain (or N) has a slope of −1 (Fig. 2a). In a heterogeneous area, this slope will generally be between −1 and 0 (O'Neill *et al.*, unpublished), although the relationship may be curvilinear (Fig. 2a; Levin, 1989). As grain increases, a greater proportion of the spatial heterogeneity of the system is contained within a sample or grain and is lost to our resolution, while between-grain heterogeneity (= variance) decreases (Fig. 2b). If the occurrence of species in quadrats is recorded based on a minimal coverage criterion, rare species will be less likely to be recorded as grain size increases; this effect is more pronounced if the species are widely scattered in small patches than if they are highly aggregated (Turner *et al.*, unpublished). If the measurement criterion is simply the presence or absence of species in quadrats, however, more rare species will be recorded as grain increases, and diversity will increase rather than decrease with increasing grain. Exactly how variance changes with grain scale thus depends on the magnitude and form of the heterogeneity of an area (Milne, 1988, unpublished; Palmer, 1988) and on the type of measurement taken.

Spatial variance is also dependent on the extent of an investigation. Holding grain constant, an increase in extent will incorporate greater spatial heterogeneity, as a greater variety of patch types or landscape elements is included in the area being studied (Fig. 1). Between-grain variance increases with a broadening of scale (extent) (Fig. 2b).

These considerations also relate to the patterns of temporal variation or equilibrium of ecological systems. Ecologists have often disagreed about whether or not ecological systems are equilibrial (e.g. Wiens, 1984, in press; Chesson & Case, 1986; DeAngelis & Waterhouse, 1987; Sale, 1988). Whether apparent 'equilibrium' or 'nonequilibrium' is perceived in a system clearly depends on the scale of observation. Unfortunately, current theories provide little guidance as to what we might expect: models in population biology (e.g. May & Oster, 1976; Schaffer, 1984; May, 1989) and physics (Gleick, 1987) show that order and stability may be derived at broad scales from finer-scale chaos *or* that fine-scale determinism may produce broad-scale chaos, depending on circumstances. Perhaps ecological systems follow principles of universality, their final states at broad scales depending on general system properties rather than fine-scale details (cf. Feigenbaum, 1979). Brown (1984) has championed this view, but we still know far too little

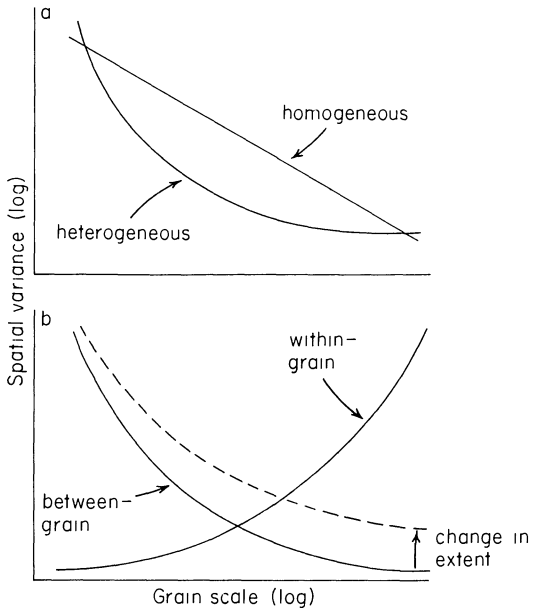

Fig. 2. (a) As the grain of samples becomes larger, spatial variance in the study system as a whole decreases, albeit differently for homogeneous and heterogeneous areas. This is related to the within- and between-grain (sample) components of variation. (b) With increasing grain scale, less of the variance is due to differences between samples and more of the overall variation is included within samples (and therefore averaged away). An increase in the extent of the investigation may increase the beween-grain component of variance by adding new patch types to the landscape surveyed (Fig. 1), but within-grain variance is not noticeably affected.

about the scaling behaviour of ecological systems to consider universality as anything other than an intriguing hypothesis.

Predictability and space-time scaling

Because the effects of local heterogeneity are averaged out at broader scales, ecological patterns often appear to be more predictable there. Whether or not the predictions are mechanistically sound depends on the importance of the fine-scale details. The Lotka-Volterra competition equations may predict competitive exclusion of species that in fact are able to coexist because of fine-scale spatial heterogeneity that is averaged away (e.g. Moloney, 1988). These predictions are not really scale-independent but are instead insensitive to important scale-dependent changes.

Our ability to predict ecological phenomena depends on the relationships between spatial and temporal scales of variation (Fig. 3). With increased spatial scale, the time scale of important processes also increases because processes operate at slower rates, time lags increase, and indirect effects become increasingly important (Delcourt, Delcourt & Webb, 1983; Clark, 1985). The dynamics of different ecological phenomena in different systems, however, follow different trajectories in space and time. An area of a few square metres of grassland may be exposed to ungulate grazing for only a few seconds or minutes, whereas the temporal scale of microtines in the same area may be minutes to hours and that of soil arthropods days to months or years. There are no standard functions that define the appropriate units for such space-time comparisons in ecology. Moreover, the continuous linear scales we use to measure space and time may not be appropriate for organisms or processes whose dynamics or rates vary discontinuously (e.g. 'physiological time' associated with diapause in insects; Taylor, 1981).

Any predictions of the dynamics of spatially broad-scale systems that do not expand the temporal scale are *pseudopredictions*. The predictions may seem to be quite robust because they are made on a fine time scale relative to the actual dynamics of the system (Fig. 3), but the mechanistic linkages will not be seen because the temporal extent of the study is too short. It is as if we were to take two

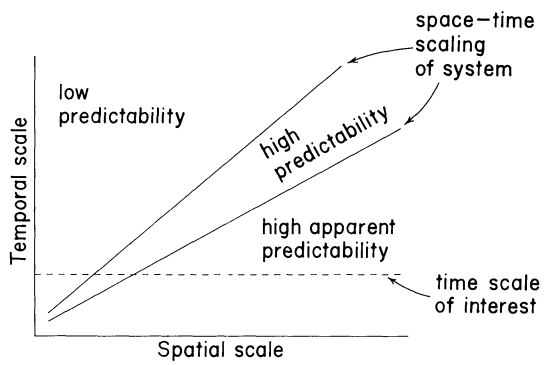

Fig. 3. As the spatial scaling of a system increases, so also does its temporal scaling, although these space-time scalings differ for different systems. Studies conducted over a long time at fine spatial scales have low predictive capacity. Investigations located near to the space-time scaling functions have high predictive power. Short-term studies conducted at broad spatial scales generally have high apparent predictability (pseudopredictability) because the natural dynamics of the system are so much longer than the period of study. Often, ecologists and resource managers have been most interested in making and testing predictions on relatively short time scales, regardless of the spatial scale of the investigation.

snapshots of a forest a few moments apart and use the first to predict the second. This problem may be particularly severe in resource management disciplines, where the application of policies to large areas is often based on very short-term studies.

Detecting patterns and inferring processes

The characteristics of ecological systems at relatively fine scales differ from those at relatively broad scales (Table 1), and these differences influence the ways ecologists can study the systems. The possibilities for conducting replicated experiments vary inversely with the scale of investigation. The potential for sampling errors of several kinds are greater at finer scales, although the intensity of sampling is generally lower at broader scales. Fine-scale studies may reveal greater detail about the biological mechanisms underlying patterns, but generalizations are more likely to emerge at broader scales. Because the time-frame of ecological processes tends to be longer at broader scales (Fig. 3), long-term investigations are more often necessary to reveal the dynamics of the system. The scale of investigation thus determines the range of patterns and processes that can be detected. If we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale. Because we are clever at devising explanations of what we see, we may think we understand the system when we have not even observed it correctly.

Dealing with scale

Scale arbitrariness

The most common approach to dealing with scale is to compare patterns among several arbitrarily selected points on a scale spectrum. In his analysis

Table 1. General characteristics of various attributes of ecological systems and investigations at fine and broad scales of study. 'Fine' and 'broad' are defined relative to the focus of a particular investigation, and will vary between studies.

	Scale	
Attribute	Fine	Broad
Number of variables important in correlations	many	few
Rate of processes or system change	fast	slow
Capacity of system to track short-term environmental variations	high	low
Potential for system openness	high	low
Effects of individual movements on patterns	large	small
Type of heterogeneity	patch	landscape mosaic
Factors influencing species' distribution	resource/habitat distribution, physiological tolerances	barriers, dispersal
Resolution of detail	high	low
Sampling adequacy (intensity)	good	poor
Effects of sampling error	large	small
Experimental manipulations	possible	difficult
Replication	possible	difficult
Empirical rigor	high	low
Potential for deriving generalizations	low	high
Form of models	mechanistic	correlative
Testability of hypotheses	high	low
Surveys	quantitative	qualitative
Appropriate duration of study	short	long

of reef-fish communities, for example, Galzin (1987) compared distributions within a single transect, among several transects on the same island, and among five islands. Roughgarden *et al.* (1987) compared the dynamics of rocky intertidal barnacle communities and assemblages of *Anolis* lizards on islands at 'small', 'medium', and 'large' spatial scales. Senft *et al.* (1987) examined herbivore foraging in relation to vegetation patterns at the scales of the local plant community, the landscape, and the region. Multiscale studies of birds have considered patterns at three to five scales, and Wiens *et al.* (1986a) recognized four scales of general utility in ecological investigations.

In these examples, the definition of the different scales makes intuitive sense and the analyses reveal the scale-dependency of patterns. Casting the relationships in the context of hierarchy theory (Allen & Starr, 1982; O'Neill *et al.*, 1986) may further sharpen our focus on scaling by emphasizing logical and functional linkages among scales. The scales chosen for analysis are still arbitrary, however: they tend to reflect hierarchies of spatial scales that are based on our own perceptions of nature. Just because these particular scales seem 'right' to us is no assurance that they are appropriate to reef fish, barnacles, anoles, cattle, or birds. We need nonarbitrary, operational ways of defining and detecting scales.

Dependence on objectives and organisms

What is an 'appropriate' scale depends in part on the questions one asks. Behavioural ecologists, population ecologists, and ecosystem ecologists, for example, all probe the relationship between resources and consumers, but differences in their objectives lead them to focus their investigations at different scales (Pulliam & Dunning, 1987). Conservation of key species or habitats may target particular patches or landscape fragments for management, whereas programmes emphasizing species richness or complexes of communities may concentrate on preserving broader-scale landscape mosaics (Noss, 1987; Scott *et al.*, 1987).

Differences among organisms also affect the scale of investigation. A staphylinid beetle does not relate to its environment on the same scales as a vulture, even though they are both scavengers. What is a resource patch to one is not to the other. The scale on which an oak tree 'perceives' its environment differs from that of an understorey bluebell or a seedling oak (Harper, 1977). Local populations of vagile organisms may be linked together into larger metapopulations and their dynamics may be less sensitive to the spatial configuration of local habitat patches than more sedentary species (Morrison & Barbosa, 1987; Fahrig & Paloheimo, 1988; Taylor, 1988). Chronically rare species may follow different dispersal and scaling functions than persistently common species. Consumers that use sparse or clumped resources are likely to operate at larger spatial scales than those using abundant or uniformly distributed resources, especially if the resources are critical rather than substitutable (Tilman, 1982; O'Neill *et al.*, 1988).

Such scaling differences among organisms may be viewed in terms of 'ecological neighbourhoods' (Addicott *et al.*, 1987) or 'ambits' (Hutchinson, 1953; Haury *et al.*, 1978); areas that are scaled to a particular ecological process, a time period, and an organism's mobility or activity. The ecological neighbourhood of an individual's daily foraging may be quite different from that of its annual reproductive activities. The ecological neighbourhood of the lifetime movements of a tit in a British woodland may comprise an area of a few square kilometres whereas a raptor may move over an area of hundreds or thousands of square kilometres; a nomadic teal of ephemeral desert ponds in Australia may range over the entire continent. Incidence functions (Diamond, 1975) or fragmentation response curves (Opdam, Rijsdijk & Hustings, 1985) depict the ecological neighbourhoods of species with respect to colonization and persistence of populations in areas of different sizes (scales).

To some extent, differences in ecological neighbourhoods among taxa parallel differences in body mass. This raises the possibility of using allometric relationships (e.g. Calder, 1984) to predict scaling functions for organisms of different sizes. On this basis, for example, one might expect the scale of the home range of a 20-g lizard to be approximately 0·3 ha, whereas that of a 20-g bird would be in the order of 4 ha; the parallel scale for a 200-g bird would be 92 ha. Although such an approach ignores variation in allometric relationships associated with diet, age, season, phylogeny, and a host of other factors, it may still provide an approximation of organism-dependent scaling that is less arbitrary than those we usually use.

Because species differ in the scales of their ecological neighbourhoods, studies of interactions among species may be particularly sensitive to scaling. The population dynamics of predators and of their prey, for example, may be influenced

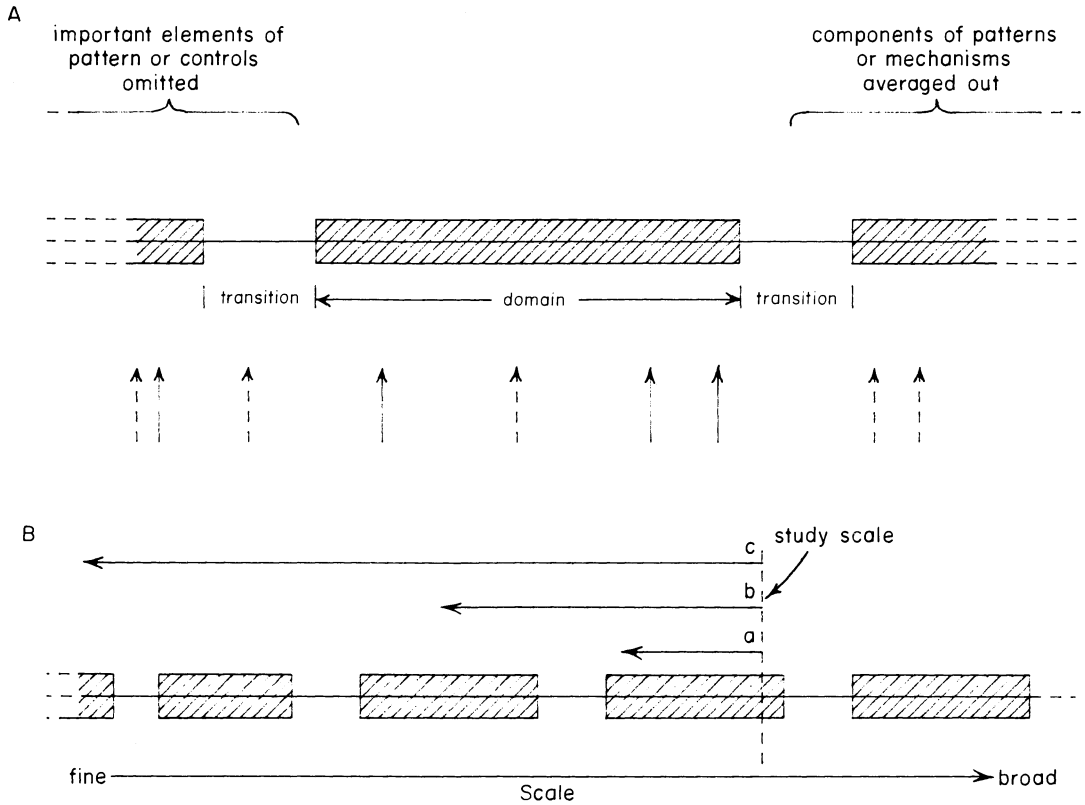

Fig. 4. (A) The domain of scale of a particular ecological phenomenon (i.e. a combination of elements of a natural system, the questions we ask of it, and the way we gather observations) defines a portion of the scale spectrum within which process-pattern relationships are consistent regardless of scale. Adjacent domains are separated by transitions in which system dynamics may appear chaotic. If the focus is on phenomena at a particular scale domain, studies conducted at finer scales will fail to include important features of pattern or causal controls; studies restricted to broader scales will fail to reveal the pattern or mechanistic relationships because such linkages are averaged out or are characteristic only of the particular domain. Comparative investigations based on sampling the scale spectrum at different points in relation to the distribution of scale domains and transitions (solid and dashed vertical arrows) will exhibit different patterns. (B) If a reductionist approach is adopted to examine patterns found at a particular scale of study, the findings (and inferences about causal mechanisms) will differ depending on how far the reductionism is extended toward finer scales and how many domains are crossed (compare a, b, and c).

by factors operating on different scales (Hengeveld, 1987), and attempts to link these dynamics directly without recognizing the scale differences may lead to greater confusion than enlightenment. The competitive interactions among species scaling the environment in similar ways may be more direct or symmetrical than those between organisms that share resources but operate on quite different scales. If we arbitrarily impose a particular scale (e.g. quadrat size) on a community of organisms that operate on different scales, we truncate the interactions to different degrees for different species.

Domains of scale

Scale-dependency in ecological systems may be continuous, every change in scale bringing with it changes in patterns and processes. If this is so, generalizations will be hard to find, for the range of extrapolation of studies at a given scale will be severely limited. If the scale spectrum is not continuous, however, there may be *domains* of scale (Fig. 4a), regions of the spectrum over which, for a particular phenomenon in a particular ecological system, patterns either do not change or change monotonically with changes in scale. Domains are separated by relatively sharp transitions from dominance by one set of factors to dominance by other sets, like phase transitions in physical systems. Normally well-behaved deterministic systems may exhibit unpredictable behaviour at such transitions (Kitchell *et al.*, 1988), and nonlinear relations may become unstable (O'Neill, personal communication). The resulting chaos makes translation between

domains difficult (Heaps & Adam, 1975; May, 1989). The argument over the relative merits of linear versus nonlinear models in ecology (e.g. Patten, 1983) may reflect a failure to recognize the differences in system dynamics within versus between domains.

How may we recognize domains of scale in a way that avoids the arbitrary imposition of preconceived scales or hierarchical levels on natural variation? Several statistical approaches are based on the observation that variance increases as transitions are approached in hierarchical systems (O'Neill *et al.*, 1986). If quadrats in which plant species abundances have been recorded are aggregated into larger and larger groupings, the variance of differences in abundance between pairs of contiguous groups fluctuates as a function of group size (scale). Peaks of unusually high variance indicate scales at which the between-group differences are especially large, suggesting that this may represent the scale of natural aggregation or patchiness of vegetation in the communities (Greig-Smith, 1952, 1979), the boundary of a scale domain. Similar techniques may be used to analyse data gathered on continuous linear transects (Ludwig & Cornelius, 1987). Coincidence in the variance peaks of different features of the system (e.g. plants and soil nutrients, seabirds and their prey) may indicate common spatial scalings and the possibility of direct linkages (Greig-Smith, 1979; Schneider & Piatt, 1986). For a series of point samples, the average squared difference (semivariance) or the spatial autocorrelation between two points may be expressed as a function of the distance between them to estimate the scale of patchiness in a system (Sokal & Oden, 1978; Burrough, 1983). Other investigators have used spectral analysis (Legrende & Demers, 1984) or dimensional analysis (Lewis & Platt, 1982). Obviously, the degree to which any of these methods can reveal scales of spatial patterning is sensitive to grain and extent.

Another approach involves the application of fractal geometry (Mandelbrot, 1983; Peitgen & Saupe, 1988) to ecological patterns. In many physical systems, such as snow crystals, clouds, or flowing fluids, the configuration of patterns differs in detail at different scales but remains statistically 'self-similar' if the changes in pattern measurements are adjusted to the changes in measurement scale (Burrough, 1983; Hentschel & Procaccia, 1984; Nittman *et al.*, 1985). The way in which detail differs with scale is characterized by a fractal dimension, D, which indexes the scale-dependency of the pattern. Statistical self-similarity of patterns (constant D) occurs when processes at fine scales propagate the patterns to broader scales, although self-similar patterns may also arise from the operation of different but complementary processes (Milne, 1988). A change in the fractal dimension of a pattern, on the other hand, is an indication that different processes or constraints are dominant. Regions of fractal self-similarity of pattern may therefore represent domains of scale, whereas rapid changes in fractal dimension with small changes in measurement scale (e.g. the landscape patterns analysed by Krummel *et al.*, 1987 or Palmer, 1988) may indicate transitions between domains. There is a relationship between the sizes and movement patterns of organisms and the fractal dimensions of their habitats (Morse *et al.*, 1985; Weiss & Murphy, 1988, Wiens & Milne, in press), so it may be possible to define ecological neighbourhoods or domains using functions that combine allometry and fractals.

Domains of scale for particular pattern-process combinations define the boundaries of generalizations. Findings at a particular scale may be extrapolated to other scales within a domain, but extension across the transition between domains is difficult because of the instability and chaotic dynamics of the transition zone. Measurements made in different scale domains may therefore not be comparable, and correlations among variables that are evident within a domain may disappear or change sign when the scale is extended beyond the domain (as in the examples of species associations given on p. ?). Explanations of a pattern in terms of lower-level mechanisms will differ depending on whether we have reduced to a scale within the same domain, between adjacent domains, or across several domains (Fig. 4b). The peril of reductionism in ecology is not so much the prospect that we will be overcome by excessive detail or distracted by local idiosyncrasies but that we will fail to comprehend the extent of our reduction in relation to the arrangement of domains on a scale spectrum.

Of course, not all phenomena in all systems will exhibit the sort of discontinuities in scale-dependence necessary to define domains. Some phenomena may change continuously across broad ranges of scale. The boundaries of even well-defined domains may not be fixed but may vary in time, perhaps in relation to variations in resource levels. The notion of domains, like other conceptual constructs in ecology, may help us to understand nature a bit better, but it should not become axiomatic.

Developing a 'science of scale' in ecology

Recently, Meentemeyer & Box (1987) have called for the development of a 'science of scale' in ecology, in which scale is included as an explicitly stated variable in the analysis. I think that we must go further, to consider scaling issues as a *primary focus* of research efforts. Instead of asking how our results vary as a function of scale, we should begin to search for consistent patterns in these scaling effects. How does heterogeneity affect the size of scale domains? Are the ecological neighbourhoods of organisms in high-contrast landscapes scaled differently from those in areas where the patch boundaries are more gradual? Are there regularities in the transitions between orderly and seemingly chaotic states of ecological systems with changes in scale, in a manner akin to turbulence in fluid flows? Do selective forces influence how organisms scale their environments, so that particular life-history traits are related to responses to particular scales of environmental patchiness? If one adjusts for the size differences between organisms such as a beetle and an antelope that occur in the same prairie, can they then be seen to respond to the patch or fractal structure of the 'landscapes' they occupy in the same way? Are differences between them interpretable in terms of differences in their physiology, reproductive biology, or social organization? Does the spatial heterogeneity of soil patterns at different scales have different effects on how forest ecosystems respond to climatic changes? Is the spread of disturbances a function of the fractal structure of landscapes? Does nutrient redistribution among patches at fine scales lead to instability or stability of nutrient dynamics at broader scales?

To address such questions, we must expand and sharpen the ways we think about scaling. Our ability to detect environmental heterogeneity, for example, depends on the scale of our measurements, whereas the ability of organisms to respond to such patchiness depends on how they scale the environment. Proper analysis requires that the scale of our measurements and that of the organisms' responses fall within the same domain. Because of this, however, the 'proper' scale of investigation is usually not immediately apparent. Moreover, the ecological dynamics within a domain are not closed to the influences of factors at finer or broader domains; they are just different. Ecologists therefore need to adopt a multiscale perspective (Legrende & Demers, 1984; Clark, 1985; Wiens *et al.*, 1986a; Blondel, 1987; Addicott *et al.*, 1987). Studies conducted at several scales or in which grain and extent are systematically varied independently of one another will provide a better resolution of domains, of patterns and their determinants, and of the interrelationships among scales.

We must also develop scaling theory that generates testable hypotheses. One particular focus of such theory must be on the linkages between domains of scale. Our ability to arrange scales in hierarchies does not mean that we understand how to translate pattern-process relationships across the nonlinear spaces between domains of scale, yet we recognize such linkages when we speak of the constraining effects of hierarchical levels on one another or comment on the openness of ecological systems. Perhaps there is a small set of algorithms that can serve to translate across scales. Discovering them requires that we first recognize that ecological patterns and processes are scale-dependent, that this scale-dependency differs for different ecological systems and for different questions that we ask of them, that ecological dynamics and relationships may be well-behaved and orderly within domains of scale but differ from one domain to another and become seemingly chaotic at the boundaries of these domains, and that an arbitrary choice of scales of investigation will do relatively little to define these scaling relationships.

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