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"Pattern, Scale, and Variability:
An Ecological Perspective"

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CHAPTER 1

Pattern, Scale, and Variability:
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I. INTRODUCTION

One of the fundamental challenges of ecological science is to blend population and community theory, to examine the relationships among phenomena occurring on different scales and the dynamic processes underlying the emergence of pattern. It is a challenge incompletely met; yet community ecology, in its search for integration, is leagues ahead of ecosystems ecology. There, the need and desire for synthesis are at least as great, but the gap separating the subject from population biology remains virgin territory. In each of these quests, reductionistic and holistic approaches must be wedded; in each, the goals are to understand system structure and function in relation to the dynamics at lower levels of organization, and to understand how changes at higher levels may filter down to influence lower levels.

II. PATTERN

The search to understand any complex system is a search for pattern, for the reduction of complexity to a few simple rules, principles to abstract the signal from the noise. As oceanographers long have recognized, pattern can be found at any level of investigation; and like the sound of the tree falling in the forest, community pattern makes little sense without consideration of the observer. Nietsche (1901) said "There are no facts, only interpretations." Much of the literature on ecological pattern emphasizes equilibrium and homogeneity, reflecting a perspective shaped by historical tradition. When we examine the system in other ways, we find new patterns whose importance is obscured by the classical approach.

In the early twentieth century, as the attention of ecologists turned to community organization, Gleason's emphasis on individualistic and stochastic considerations lost out to Clements' more holistic notion of the climax stable state, and his perception of the community as a superorganism whose characteristics were determined by the local properties of the physical environment (McIntosh 1985). The mathematical theory that emerged from this approach emphasized equilibrium, constancy, homogeneity, stability, and predictability.

A broader perspective, however, makes clear that these attributes are not absolutes, but vary in degree depending on the scale of observation. Systems develop simultaneously on

many different scales. On any one scale, one may regard some variables as changing so slowly that in effect they are constant, or so rapidly that only their statistical properties are relevant. But the situation is much more complicated than that, and recognition of the interrelationships among scales is one of the fundamental steps in understanding the development of structure and pattern.

III.   THOUGHTS ON THE DEVELOPMENT OF PATTERN

How does pattern form in the absence of a detailed blueprint? Can simple, localized, contextual rules account for the emergence of pattern at more global scales? This is a pervasive problem in biology, in cosmology, in chemistry, in geology, and indeed in almost any branch of knowledge. In developmental biology, in linguistics, and elsewhere, a central question has been how a few basic rules, largely local in nature, reliably can give rise to recognizable entities at higher levels of organization. Turing (1952) showed how symmetry could be broken through local autocatalysis, reinforcing random or otherwise insignificant inhomogeneities. But the breaking of symmetry is just the first step in the development of pattern; without some mechanism to retard its spread on nonlocal scales, that initial inhomogeneity will give rise to a new homogeneous pattern, simply displacing its predecessor.

What is implicit in Turing's original model (see Levin and Segel 1976, 1984) and in alternative models of pattern generation (see Gierer and Meinhardt 1972; Murray and Oster 1984) is that local activation, as expressed in the enhancement of differences, is in opposition to longer—range inhibition that eventually stabilizes pattern and retards the spread of disturbance. The various models proposed for development differ drastically in their underlying mechanisms, but all successful ones have these two basic features: short—range activation and long—range inhibition (Meinhardt 1982). Indeed, the fact that these two characteristics are all that are needed to produce a very wide range of patterns makes clear the impossibility of discovering process from pattern: quite distinct underlying processes can give rise to identical sets of patterns.

Pattern involves the coexistence of different elements or states, and some regularity in their arrangement. In the theory of population genetics, the first ingredient of pattern is expressed as polymorphism: the coexistence of alleles and of distinct genotypes. The simplest case of allelic coexistence, that of balanced polymorphism, arises because of the superiority of the heterozygote; this may be thought of as gene—level frequency dependence favoring the rare allele, since the rare allele (in contrast to the common one) occurs primarily in the heterozygous form. More generally, whether at the genetical or at the ecological level, frequency dependence favoring rare types, whatever its underlying basis, can play the dual role of catalyzing the spread of local inhomogeneities (short—range activation) and retarding its growth when the inhomogeneities are no longer localized (long—range inhibition). This by itself may not be sufficient to constitute pattern, since no obvious regularities in distribution are expressed; but the essential ingredients are present. This frequency dependence, when

coupled with a delay in its operation, can lead to periodic dynamics, clear manifestations of temporal pattern, or to more complicated temporal patterns that at least exhibit statistical regularity. The delay can be explicit, in which case temporal pattern can arise even in a single—variable system, or implicit, operating through the interaction of two or more factors (e.g., predator and prey, or different age classes). In the single—variable case, the concept of selection for rare types is replaced by that of a compensatory mechanism that results in a decreasing per capita population growth rate as population density increases.

The role of the delay in the above example is to assure that activation and inhibition are expressed on different time scales, a central feature of temporal pattern. Similar considerations and mechanisms underlie the generation of patterns in space, a problem that has been studied widely in diverse fields. Because geometrically similar patterns are observed whether one is interested in landscape patterns, animal coat markings, chemical mixtures, thin films of fluids heated from below, or a variety of other situations, it is natural to try to abstract those features that are common to those situations and to develop models that ignore inessential detail. The central aspects of the mechanisms underlying spatial pattern development are some set of rules for local growth or kinetics, and some scheme for redistribution of materials or communication among local environments. The most familiar model systems incorporating these features are those for the diffusion and reaction of chemicals, although the standard models extend easily to more general and nonlocal redistribution regimes. Whatever the context, these models lead to similar consequences.

In the discrete (island) version of this model, pattern can arise as a result of the existence of multiple stable states in the underlying dynamics. The presence of multiple stable states means that the local asymptotic dynamics are influenced by small changes in initial conditions, and hence small differences among local environments become exaggerated due to positive feedback. Thus, we have the first ingredient necessary for pattern to arise: a mechanism for breaking symmetry through short—range activation. In the case of population biology, the initial differences that become enhanced may arise from nothing more than the vagaries of colonization episodes, and the phenomenon usually is described as the "founder effect" (Mayr 1942). Longer—range inhibition is provided by the discrete geometry, which places information exchange among patches on a longer time scale than the instantaneous mixing that is assumed to hold within them, introducing a dichotomy of scales both in space and in time.

In spatially continuous environments, the stabilization mechanism associated with long—range inhibition is lacking, and for the simplest environments no stable non—uniform patterns can result. However, as Matano (1979) has shown, this result, which holds true in convex environments, breaks down in complex geometries that, by forcing materials to flow through bottlenecks, create environments that are quasi—discrete (Fig. 1). Similarly, it need not hold even in convex regions if the diffusion coefficients are spatially non—uniform; such

nonuniformity may be determined extrinsically, or may arise through dependence on the local state. In the latter case, an initially homogeneous diffusion regime can become heterogeneous as a result of symmetry–breaking through local activation, and this then may give rise to the quasi–discrete environment necessary to provide longer–range activation (Levin 1979; Fife and Peletier 1980).

Fig. 1: A geometry that can support non–uniform spatial patterns through the existence of multiple stable states. The key is the existence of bottlenecks.
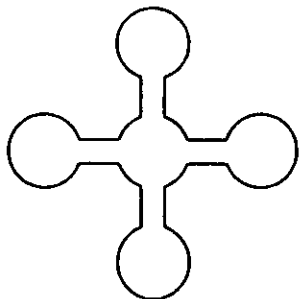
A more explicit way to get short–range activation and long–range inhibition is to assume that there are two separate agents, e.g., chemical morphogens, that specifically fill the roles of activators and inhibitors. In the model of Turing, and the related work of Gierer and Meinhardt (1972), Murray (1981), and others, one assumes that the system has two components: an activator species, whose diffusion is spatially limited, and an inhibitor that diffuses over broader scales. Because symmetry–breaking depends in this case upon the differences in diffusion rates, the phenomenon has been called diffusive instability; the resultant nonuniform pattern is sometimes called a dissipative structure (Glansdorff and Prigogine 1971; see also Levin and Segel 1984). Applications to ecological situations, in which a prey species serves as activator and a predator as inhibitor, are discussed in Segel and Jackson (1972), Levin (1974), Levin and Segel (1976, 1984), and Segel and Levin (1976).

In two–dimensional systems, the mechanisms of activation and inhibition need not be so clearly separable that each resides in a particular species. Levin and Segel (1984), in considering the role of apostatic selection (the tendency of predators to concentrate on common prey types) in fostering diversity, show that nonuniform distributions of character types may arise and be maintained. In this system, symmetry is broken in two ways: initial monomorphic assemblages cannot be maintained, as apostasis provides a mechanism favoring rare types. At the other extreme, completely equitable distributions of competing types may become unstable due to the focusing effects of prey (assortative) mating and reproduction. More generally, activation and inhibition can arise in higher dimensional systems through

feedback loops involving many species, or can arise even in one dimension when different phenomena are manifest at different spatial or other scales (Levin and Segel 1984).

IV. ASYNCHRONIZED LOCAL DISTURBANCE

The above discussion relates to the development of stable patterns, but such considerations leave out an important class of patterns, those that are transient or are dynamic with some underlying regularity, including chaotic and spatio–temporal patterns.

Following A.S. Watt's prescient presidential address (Watt 1947) to the British Ecological Society in 1947, appreciation grew for the importance of variability in space and time as a factor structuring communities, and as a key to coexistence and coevolution. As Watt's work and a growing body of later work (e.g., Levin and Paine 1974, 1975; Paine and Levin 1981; Pickett and White 1986) have shown, natural biotic and abiotic disturbance recycles limiting resources, developing mosaics of successional change that allow species to subdivide resources temporally. The explicit incorporation of disturbance, variability, and stochasticity as part of the description of the normative community is thus an imperative if one is to capture the essential nature of such systems. For many and perhaps most species, local unpredictability globally is the most predictable aspect of these systems (Levin and Paine 1974).

Work examining the importance of gaps and mosaic phenomena has demonstrated the inseparability of the concepts of equilibrium and scale. As one moves to finer and finer scales of observation, systems become more and more variable over time and space, and the degree of variability changes as a function of the spatial and temporal scales of observation. Such a realization long has been part of the thinking of oceanographers, who observe patchiness and variability on virtually every scale of investigation. A major conclusion is that there is no single correct scale of observation, and that the insights one achieves from any investigation are contingent on the choice of scales. Pattern is neither a property of the system alone nor of the observer, but of an interaction between them.

The importance of scales also becomes apparent from an examination of population models, both in terms of their general dynamic properties and in terms of their applicability to real populations. Much recent mathematical work has demonstrated that even the simplest models of populations can exhibit oscillatory and even chaotic behavior; and that, as a consequence, it is impossible to predict accurately the precise dynamics of populations governed by such equations (e.g., May 1974).

To some extent, such investigations render moot the classical debate over whether populations are controlled by density–dependent or density–independent factors. Close to the theoretical equilibrium, the dynamics of such populations may be indistinguishable from those of appropriately chosen stochastic density–independent models; near the equilibrium, density dependence is very weak, and will be obscured by any overriding density–independent

variation. On the other hand, far from equilibrium, density–dependent factors assume more importance because the nonlinearities are stronger. Thus, density dependence is the primary mechanism constraining major excursions in population density and keeping populations within bounds; but within those bounds, density–independent phenomena predominate. Concepts of stability that rely on asymptotic return to an equilibrium state are seen to be irrelevant on many scales of interest, and more general concepts such as boundedness and resiliency replace them (Levin 1987).

The increasing recognition that ecological systems are dynamically changing spatiotemporal mosaics has spurred interest in the development of measures that allow comparisons of the importance of disturbance and patchiness across systems and across scales. Hastings et al. (1982) suggest that one approach is to examine the cumulative frequency distribution of patches of various sizes. Their investigation of patch distributions for various successional classes, based both on field data and on the output of simulation models, produces a hyperbolic form (above some threshold patch size) for the cumulative distribution of patch area greater than a given amount. Thus, one has a distribution of the form

$$\text{prob } (A > a) = (\text{const}) \times a^{-B}, \tag{1}$$

where A is patch area for a given successional class. Hastings et al. (1982) transform B by the relation $H=2-2B$ (following Mandelbrot 1977; see also Mandelbrot 1983) to produce a measure that they term "the fractal exponent ... of successional stage." B typically is larger early in succession.

The measure described above is a static one, a snapshot of the system at a particular point in time. As such, it joins a distinguished set of measures of patchiness that community ecologists have used for a long time (see, for example, Greig–Smith 1964, Southwood 1978). But the importance of system dynamics is lost in such measures, and thus there is a need for approaches that look across time as well as across space. In oceanography, the Stommel diagram (Stommel 1963, 1965; Haury et al. 1977) is one means for representing the variability of a system both in space and in time; in geostatistics, various schemes for stratified random sampling achieve the same objective (Bras and Rodriguez–Iturbé 1985). The application of such approaches to ecological systems holds the potential for producing fundamentally new perspectives on these systems, ones that emphasize the changes in the perception of processes across different spatial and temporal scales. Ultimately, these methods can be extended to the consideration of phenomena across organizational scales, and give us powerful new tools for understanding systems.

With my colleague Linda Buttel, I have begun the analysis of successional systems by using this methodology, building on a general successional model that can be tailored to forests, to grasslands, or even to intertidal communities (Levin and Buttel 1986). We have

developed a model incorporating disturbance, colonization, and local competition, and investigated its dynamics on the Cornell PSF Supercomputer. In this approach, disturbances of various sizes are superimposed on a grid composed of 10,000 cells, according to a set of stochastic rules that depend on the local states of the system. Disturbances are centered in particular cells, and their size and frequency distribution is conditional upon the current status of the cell (for example, late successional cells are more likely to give rise to larger disturbances through their effects upon neighboring cells); the disturbance then is allowed to radiate outward to adjacent cells. In one version of the model, edge–related disturbances are incorporated; that is, in analogy with systems such as the balsam fir forests studied by Sprugel (1976), trees on exposed edges of disturbances are more susceptible to damage than are more protected trees.

Once a gap is formed, that space is available for recolonization. We assume that colonization comes from a pool, and that different species have different probabilities per unit time of arriving at a site. It is straightforward, although computationally more complicated, to extend the colonization model to include nearest neighbor effects. Competitive ability is assumed to be inversely related to probability of arriving at a site. In the simplest version of the model, a site is occupied by a single individual, selected randomly from among those in the highest competitive class arriving at the site. In more complicated versions, a local growth simulator apportions the local resource (space within a cell) according to a set of rules that allows local coexistence and that implicitly incorporates the time delays that are associated with local competitive displacement.

It is clear that, in this model, the observed temporal variability of any state variable will be a function of the scale of observation. In particular, if one averages a particular measure, such as the percent occupancy of space by a particular species, over a square block of n cells, then the expected temporal variance of that average ($y_n = (x_1 + x_2 + \cdots + x_n)/n$) is given by

$$S_n^2 = E((y_n - E(y))^2 = E((y_n - E(x))^2) = \sigma^2/n + ((n-1)/n)\text{cov}_n, \tag{2}$$

where σ^2 is the variance of x and cov_n is the covariance of the values of x for two points drawn at random from the square block of n cells. The difficulty is that cov_n depends on n in a complicated way, and thus it is difficult to derive analytically the relationship between S^2 and n.

Clearly, were there no spatial correlation, the variance would fall off inversely with n. More generally, the relationship between S_n^2 and n depends on the relationship between cov_n and n, a relationship that may be very complicated. The empirically derived

relationship is somewhat surprising: for every measure that we examined, the relationship between the variance and n was remarkably well approximated on a log–log plot by a linear model (see, for example, Fig. 2). That is, our examination of the temporal variability of nested spatial averages led to the discovery of hyperbolic relationships between variance and scale. For example, for each species examined, the temporal variance of the n–point spatial average (the spatial average for n equally spaced and symmetrically arrayed points) approximately satisfied the relationship

$$S_n^2 = (\text{const}) \times n^{-z},$$

where the exponent z is a measure that reflects the degree of spatial correlation. In general, z varies with successional stage, and is closest to unity for those stages where small–scale patchiness is most important. The deviation from unity is a measure of the spatial scale of disturbance and recovery.

The significance of the above relationship is that, over a broad range of spatial scales, log of the variance of a spatial average is related approximately linearly to the logarithm of the area sampled. Because attention is focused on the slope of this line, the expected value should be independent of the mesh size used; that is, it should be independent of the scale of investigation, facilitating comparisons across systems and across scales. The model on which this relationship is based is a fairly simple one, but the existence of the relationship is very suggestive: if the system is structured according to a single underlying dynamic, then although the observed variance in general will be a function of scale, the slope of the log of variance versus the log of area may represent an invariant, one that is relatively independent of the scale of investigation. If significantly different slopes are found in the investigation of different systems, or of the same system studied on different scales (as we have found for more complicated models), then this suggests that different mechanisms or rates apply in determining those different system structures. More generally, even if a simple relationship hadn't emerged from our investigations, the results would emphasize the importance and value of quantifying the relationship between variability and scale as opposed simply to measuring variance at a single scale.

V.   SUMMARY

The recognition of what organizes and characterizes a system is a recognition of the manifold patterns the system exhibits. But pattern manifests itself differently on different scales, and the description of system pattern is interwoven with the observer's choice of scales of interest. On any scale, pattern arises from the interplay between order and disorder, between mechanisms upsetting the monotony of homogeneity and those maintaining heterogeneity against the forces of conformity.

Fig. 2:   The relationship between variability and scale. See text for discussion.

LOG–LOG PLOT OF VARIANCE VERSUS SCALE

SUCCESSIONAL CLASS 1

SLOPE = -0.712
r² = 0.9993

LOG OF SPATIAL SCALE

LOG OF CLASS 1
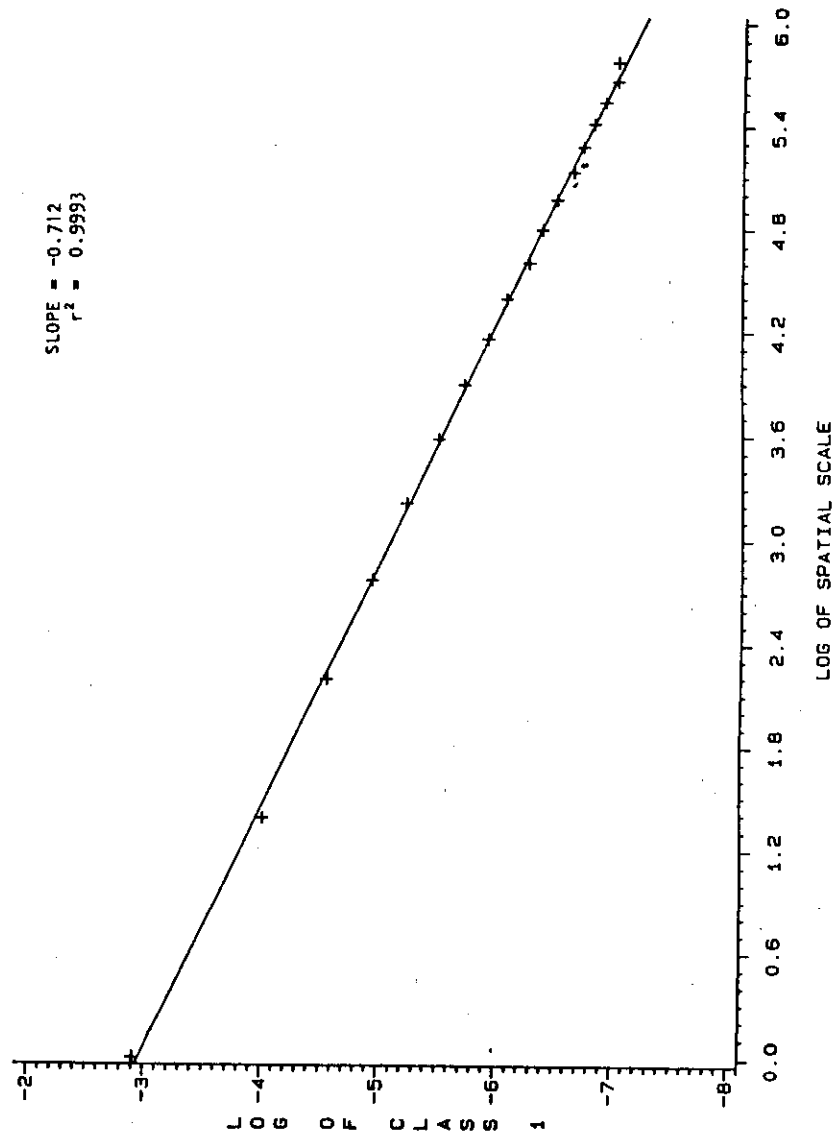
That pattern forms on multiple scales makes evident that focusing on only one scale will give a distorted picture of a system, a single frame in a multi-dimensional motion picture. It emphasizes the importance of examining phenomena across scales rather than conducting a futile search for the true scale of the system. Our study of a model of successional dynamics, and our analysis of the dynamics of that system over a variety of spatial and temporal scales, has led us to discover a number of surprising insights concerning the relationship between variability and scale.

It is clear that these investigations just scratch the surface of what can be learned from examining systems on multiple scales. The escape from single scale studies will provide us with fundamentally new perspectives on the hierarchical dynamics of ecosystems, and may bring some basis for order to the cross-system examination of community and ecosystem structure.

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