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PATTERN, PROCESS AND MECHANISM - THE FUNDAMENTALS OF SCIENTIFIC INQUIRY APPLIED TO VEGETATION SCIENCE

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Abstract. Vegetation science is concerned with a search for patterns, the discovery of processes giving rise to these patterns, and the uncovering of the mechanisms which ultimately cause such patterns and processes. The distinction between pattern, process and mechanism is rarely explicit in accounts of vegetation study, albeit always implied. I stress the need for a clear distinction of these three concepts as a pre-requisite for clarity in studying vegetation.

Most studies of vegetation dynamics deal with either describing pattern, or modelling process, but many fail to connect the two. It is even more rare to see patterns and processes predicted from underlying mechanisms. When such is attempted, it usually includes ambitious assumptions and far-fetched syntheses. This can be traced to the difficulty of the task. I examine vegetation science in terms of its components, namely, pattern recognition, process definition and mechanism isolation, and identify the sources of difficulty. In doing so, I sketch the evolution of thought and methods in, reflecting upon the works of some major contributors.

The critical phase is, of course, pattern recognition, which itself is at the mercy of the analytical tools, and, inherently, of perception. Once a pattern has been recognized, process and mechanism are inferred. The reliability of this is limited by the amount of observation that can be made on the system. The method of inference is also critical. In addition, scale effects complicate the picture. Consequently, the connections between pattern, process and mechanism may be blurred. I emphasize the importance of scale and review some approaches to its study. Although establishing the relationships between pattern, process and mechanism through inference thus entails several practical difficulties, it may be that the fundamental challenge lies in the theoretical complications.

Stability and uniqueness are properties characteristic of simple systems and induce facility in the establishment of cause-effect relationships. Vegetation, however, is a complex system owing mainly to instability (small inputs leading to large and/or divergent outcomes), and plurality of causes and effects in its dynamics. It is likely that, as a consequence, the relationships between causes and effects (pattern, process and mechanism) are also complex. In essence, the problems identified may be ill-posed, rendering them more difficult to solve than previously thought. I illustrate these points and show that the search for understanding of these relationships predominates scientific inquiry.

Introduction

The recognition of patterns, processes and mechanisms in vegetation is the way in which we attempt to understand our environment. The general environment has no limits and is thus cannot be defined. However, there must exist some method of limiting environment so that it can be studied. Billings (1974) defines a "specific" environment as "the whole of all influences, energy exchanges, and material exchanges through time between the universe and a particular living or non-living system". Significantly in this, the biota can provide the framework for environment definition. A community of organisms and its environment are usually treated together as a functional system of complemetary relationships. This is the definition of an ecosystem (Whittaker 1970). In ecosystems, living beings are distributed neither uniformly nor at random. In fact, Van Leeuwen (1966) realized that "ecology is possible and pregnant partly by the fact that life circumstances are not equal everywhere as well as by the fact that an organism cannot live under all circumstances." Indisputably, pattern is ubiquitous.

Many (e.g., Odum 1962; McCormick et al. 1974) claim that a chief goal of ecology is to identify and quantify relationships between structure and function in ecosystems. This is the study of pattern, processes and mechanisms. The medium, however, is extremely complex (Orlóci 1993). As a result, the science of ecology is fragmented and the greater task is almost always partitioned into smaller ones, relying upon inference as the basis of conclusions.

The diagnostic character of vegetation in any ecosystem is unquestionable. The understanding of patterns, processes and mechanisms in vegetation is thus elemental in the advancement of the science of ecology. More importantly, it is a way in which we can generate models and make decisions enhancing our ability to postdict past events and to predict the future. The application of models is particularly relevant to imminent environmental problems such as the effects of atmospheric carbon dioxide levels (e.g., Allen 1990; Dahlman 1993) and pollution (Marx 1975), on global climate change (e.g., Schlesinger 1993), biodiversity and the survival of species (Pimm 1991), and sustainable development (Nebel and Wright 1993).

Pattern, process and mechanism in ecology

Pattern is defined in Webster's dictionary as "a discernible coherent system based on the intended interrelationship of component parts." While comprehensive, this definition is unsatisfactory due to the infinite ways in which 'discernible' and 'coherent' may be interpreted and themselves defined. Furthermore, patterns may exist regardless of the 'intention' of interrelationships. Clearly, if a useful definition of pattern is desired, it cannot be such a general one. In application, pattern must be defined specifically, that is, with a particular purpose in mind. Pattern so defined, process can be defined, following Webster's, as "a series of operations or actions conducting to an end or pattern", and mechanism is the "fundamental physical or chemical process involved in or responsible for action, reaction, or other phenomenon."

While there are obvious connections, it is very important to distinguish between the concepts of pattern, process and mechanism. Process is sometimes referred to as simply pattern in time. This suggests an important link between the two, however, they are not equivalent. Furthermore, often the terms process and mechanism are (incorrectly) used interchangeably, thus it is crucial to understand exactly what is meant and then to decide which term is appropriate. Often only two of the three terms are even recognized. In most cases all three are implicit. For example, McCook (1994) states that "the goals of successional ecology are to describe the similarities and differences in both the pattern and the process: to extract generalizations, and to identify the bases for differences in process." Clearly, while only two of the terms are used, namely *pattern* and *process*, the third, *mechanism*, is implied and distinguished as the "bases".

Generally, and most simply put, in a given system, patterns are *what* we perceive, processes describe *how* these patterns come about, and the mechanisms provide explanations as to *why* these patterns occur. When considered in this manner, the concepts of pattern, process, and mechanism appear to be universal in life. In fact, van Leeuwen (1966) claims that these are what constitute life itself. But an investigation of these concepts, free of metaphysical entanglement, requires the specification of an application. The concepts of pattern, process and mechanism are nicely exhibited in the process of any scientific, and in particular, ecological investigation. A classic illustration of this framework was Darwin's (1859) recognition of a pattern in the distribution of species which led to the conception of the process of evolution and the mechanism of natural selection. In a syntactic context, Dale (1980) and Orlóci (1988) suggest that pattern recognition is the "primitive", while function or process is the "grammar", and structure is the "message" or information content.

Of course, it would be ideal to be able to study all of pattern, process and mechanism in a system, however, this is not practical. Instead, usually the simplest and most apparent of these, namely pattern, is studied and then an attempt is made to infer one or both of the other two. This method is based upon inductive reasoning. A set of non-experimental observations is made, and patterns (or the lack of them) are discovered. From these patterns, theories and generalizations are induced to explain processes. "Customarily, work begins with the contemplation and collection of data from some part of the biosphere. The ecologist then tries to argue back, inductively, from observed effects to hidden processes" (Scheiner and Gureritch 1993). Inductive inferences are by nature probabilistic. Pielou (1977) realizes this when she states that "the mathematics used is usually statistical". What is actually desired, in the end, is the proximate or ultimate causes or mechanisms.

Thus, of the three, it is pattern recognition which can be regarded as a precursor or limiting factor in the pursuit of understanding. May (1986) suggests that the search to understand any complex system is primarily the search for pattern. Southwood (1980) sees the function of pattern recognition as a fundamental prerequisite to the development of theory. In particular, pattern recognition often leads to the formulation of specific, testable hypotheses, which attempt to explain the observed patterns.

Legendre and Fortin (1989) summarize the importance of spatial or temporal pattern, as a key element of many ecological theories. They claim that recognition of such patterns is the basis of several theories such as those related to species diversity, parasitism, population growth, and predator-prey interactions. In addition, the contribution of spatial pattern to ecosystem stability has been established (May 1974). Root (1975) suggests that pattern in vegetation is adaptive and thus could aid in the study of natural selection.

Pattern in vegetation

Vegetation science is defined by Austin and Smith (1989) as the study of those processes which determine the patterns of composition and emergent properties observed in vegetation. The study of vegetation dynamics is essentially the study of the total changes in vegetation structure. Clearly, a definition of structure or pattern with application to vegetation is necessary. Hutchinson (1953) defined pattern as structure which includes both order and arrangement. Whittaker (1970) suggested that community structure and composition involved vertical structure, horizontal pattern, time relations and niche differentiation. Patterns are detected on the basis of variation in the texture, diversity, abundance or, most commonly, the distribution of species or plant communities.

When we speak of pattern in vegetation dynamics, we may be referring to either pattern in space, or pattern in time (processes). "Nature forms patterns. Some are orderly in space but disorderly in time, others orderly in time but disorderly in space" (Gleick 1987). While the relative importance of each of these types of patterns is difficult to establish, both are present in the vegetative environment. Definitions of spatial and temporal pattern may vary, again usually depending on the particular application. While temporal patterns ideally reveal movement in vegetation, in most cases, spatial patterns are more obvious and thus easily detected.

Greig-Smith (1961a) defined pattern as departure from randomness of arrangement in relation to a defined area. Similarly, ver Hoef et al. (1993) define pattern as the non-random horizontal spatial abundance of organisms. This approach of definition by exclusion is rather attractive, however, it does not provide any extraordinary insight into the meaning of pattern itself. More specifically, pattern is "the zero-dimensional characteristic of a set of points which describes the location of these points in terms of the relative distances of one point to another" (Upton and Fingleton 1985), where points are individual plants, patches, or communities.

To attempt to give meaning to many of the definitions of pattern, it appears that the concept of randomness must be first defined. Although the preceding definitions suggest that randomness is some type of anti-pattern, Pielou (1977) allows for a 'random pattern'. Zar (1974) defines a random pattern (or distribution of objects in space) to be one in which each portion of the space has the same probability of containing an object and the occurrence of an object in any portion of the space in no way influences the occurrence of any other object in any portion of space (independence). Pielou (1977) defines random pattern as one which results from individuals having been assigned independently and at random to the available units. The Poisson distribution is used to describe randomness, in the sense that it would be expected to find that the number of individuals per unit is a Poisson variate (Upton and Fingleton 1985). It seems useful to recognize randomness as a unique 'pattern', and to realize that the number of non-random patterns may be infinite.

Ver Hoef et al. (1993) point out that very few organisms exhibit complete spatial randomness at all scales, and thus attention must naturally be focused toward the description of non-random patterns. Though random changes undeniably occur in ecosystems, they are of much less interest than those changes which are not random (Goodall 1977). Departures from randomness can be analyzed using several classical distributions (e.g., generalized Poisson, compound Poisson), but they rely upon the assumption of independence of events, which in many cases is highly unrealistic. More appropriate, yet sophisticated, methods can be used in pattern analysis and will be discussed later. Some examples of spatial patterns are presented in Fig. 1. In such point patterns, transformations such as enlargement or rotation do not change a pattern, but distortion (stretching or folding) does.

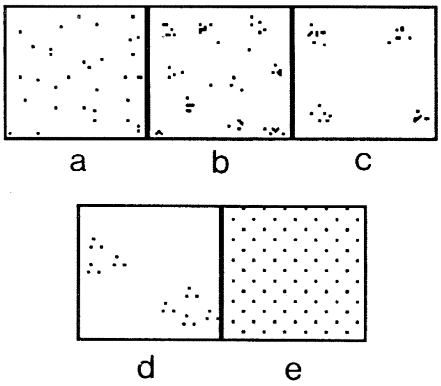

Figure 1. Five kinds of spatial pattern: a. random or Poisson. b. clumped. c. regularly clumped. d. clumps of regular points. e. regular. (modified from Whittaker (1970) and Upton and Fingleton (1985).

Temporal patterns (or processes) are revealed when areas are observed repeatedly over time. At any discrete point in time, these patterns are simply spatial (time-static) patterns. It is in essence the change in pattern which represents temporal pattern. Such patterns can be made analogous to spatial ones by considering distances between points or objects to be measured in time rather than space. One way of distinguishing (spatial) pattern from process is to once again consider the random pattern. The random *pattern* is defined by the Poisson *process*. The Poisson process is a function given by two parameters, which, when iterated, generates the random pattern. In these terms, the pattern is called the descriptor and the process is the function. Temporal patterns have been given the general term 'successions' in ecology. The use of analog patterns is common practice in vegetation studies, attempting to gain insight into the nature of possible long term compositional changes in a community (Orlóci 1981). Under the influence of Watt (1947), many ecologists came to regard spatial pattern in plant communities as a manifestation of processes which are cyclical in time though coherent in space (Hill 1973). This was important in realizing the relationship between (spatial) pattern and process (temporal pattern).

Watt (1947) insists that the descriptions of plant communities (pattern) provide information of some, but not critical, value to an understanding of them. It is the dynamic behaviour (processes) of how the individuals and the species are put together, and what determines their relative proportions and their spatial and temporal relations to each other which requires much more study.

How can pattern be detected?

Some types of pattern are quite visible, while others may require unmasking through more elaborate observation. "If a large area, including widely differing habitats, is examined, pattern is evident on casual inspection, and, if the range of habitats and corresponding vegetation are great enough, different plant communities will be recognized in different parts of the area" (Greig-Smith 1961b). In such a case, pattern detection is simple. However, even if vegetation is visually homogeneous (i.e., there are no obvious patterns), pattern may still exist. Detection of pattern may however require sensitive methods of analysis. Probing analytical (geometric or theoretical) space (Orlóci 1988) for patterns may be useful (Whittaker 1970). Orlóci (1988) quotes Benzecri (1969) who claims that such an approach is necessary as he sees pattern as a property which should emerge "from a sea of data, not through a priori nominalistic postulates or axioms or by unduly fragmentary measurements of isolated facts...but through the simultaneous synthesis... of putting together a number of elementary facts...". Pattern recognition in itself has become an extensive field of research (e.g., Bouxin 1991; Kissov et al. 1990; Kuncheva 1993).

The detection and quantification of pattern in vegetation has been studied by many (e.g., Greig-Smith 1952, 1961a, 1961b 1970; Kershaw 1973; Hill 1973; Usher 1975). The function of pattern analysis is to summarize data in a way such that those features which are not apparent are appreciated (Hill 1973). Greig-Smith (1952) invented an analytical technique which essentially compared observed variances in data grouped into larger and larger size units, and facilitated pattern detection at various scales. His method has been widely used and has sparked new and (arguably) improved methods of pattern detection (Kershaw 1957; Usher 1975; Carpenter and Chaney 1983; Ford and Renshaw 1984; Dale and MacIsaac 1989; Dale and Blundon 1990).

As multivariate methods became more accessible, they became an essential tool for pattern detection in vegetation ecology (Orlóci 1978,1988; Digby and Kempton 1987). Detection of pattern in vegetation ecology is often done through the multivariate methods of ordination (e.g., Ludwig and Reynolds 1988), classification (e.g., Gauch and Whittaker 1981) and multiple regression (e.g., Scheiner and Gureriter 1993). Often this is done to reduce complexity, by eliminating unnecessary 'noise', without losing any critical information. Olsvig-Whittaker (1988) sees the primary conceptual problem as that of reducing high-dimensional pattern to a more recognizable (i.e., 2 or 3) dimension. However, to be effective, pattern analysis must allow for the derivation of the general community pattern, and relate the patterns of individual species to the general pattern. Furthermore, it must be possible to relate both species and community pattern to the pattern of environmental variation, in order to study plant-environment relationships. Geostatistics (Robertson 1987; Halvorson 1994) and fractal geometry (Palmer 1988) have recently been applied to pattern detection in vegetation.

With so many different tools and methods of pattern detection, it is reasonable to ask, how is perception of pattern affected by the method of analysis? From his studies of real and artificial data, Usher (1975) found that no single analysis yielded complete information on pattern. That is, it appears that each method provides some unique insight into pattern detection. He suggests that several different analyses should be performed and some consensus of results accepted. Podani (1989) provides a comparison of ordination and classification methods and attempts to provide a decision framework to help determine which methods are most appropriate for the types of patterns requiring detection.

Processes and mechanisms in vegetation dynamics

Vegetation ecology, as it exists today, has clearly evolved through the recognition of patterns and processes and the subsequent suggestion of mechanisms governing them. These elements, in particular processes, define the study of vegetation dynamics. The evolution of vegetation dynamics can be sketched through mention of the work of some original contributors.

Although the study of vegetation dynamics began sooner (e.g., Kerner Von Marilaun 1863; Warming 1895), one of the first to formalize the dynamical nature of vegetation was Cowles (1899). He stressed the existence of a constant dynamic interaction between plant formations and the underlying geological formations. This view considered vegetation to be continuously-changing. Through the recognition of spatial patterns related to geological and other environmental factors, he realized that it was important to "endeavor to discover the laws which govern the panoramic changes"(mechanisms) and that "ecology, therefore, is a study of dynamics" (processes).

Later, Clements (1916) demonstrated that the distribution of vegetation in space required consideration of vegetation processes in time, and the capacity of vegetation to modify the environment. His work incited immense controversy and he was repeatedly criticized for his implications that design, purpose and unity were functioning in vegetation processes. One of the tenets of Clements' theory was that vegetation change was a directional process, eventually leading to a final, more or less stable climax community. While his insights into the *processes* of vegetation change were valued, the *mechanisms* he suggested to explain these processes were debated.

His fiercest contender was Gleason (1926) who asserted dispersal was the governing *process* in distribution of vegetation. To this end, Roberts (1987) credits Gleason with introducing stochasticity in vegetation dynamics. Gleason also pursued the individualistic hypothesis of succession, which, in complete contrast to Clement's holistic view, emphasized the importance of adaptations of individual species as a functioning *mechanism*, independent of any transcendental properties of the whole community. Gleason thus provided a slightly more complicated picture about the *processes* involved in vegetation dynamics.

Cooper (1926) and Tansley (1935) combined and modified the ideas put forth by Clements and Gleason. They introduced the importance of scale in the perception of vegetation dynamics, and the possible existence of several climaxes (polyclimax). This suggested that vegetation dynamics could follow more than one pathway or *process*, leading to possibly different *patterns*. Tansley emphasized that the vegetation change was continuous. Both also stressed the importance of an ecosystem approach to vegetation dynamics, such that plant-animal interactions were included as potential *mechanisms* of change.

These pioneer vegetation scientists, along with many others, brought forth some of the issues in the study of processes and mechanisms in vegetation dynamics. Their ideas remain of contemporary importance (Burrows 1990), and it was through these that vegetation scientists would attempt to synthesize a theory (Roberts 1987). Van der Maarel (1988) provides a classification of the processes identified, to date, in vegetation dynamics. He suggests eight kinds of changes in vegetation: fluctuations, gap dynamics, patch dynamics, cyclic succession, regeneration succession, secondary succession, primary succession, and secular succession. His classification is based on temporal scale, the degree of isolation of the vegetation (spatial pattern) and the 'level-of-integration' at which vegetation is actually studied (spatial scale).

Although some contention still exists with respect to the level at which ecosystems function, and the mechanisms that are involved, the theory of vegetation dynamics has progressed. The present theory of vegetation dynamics recognizes that the distribution of vegetation in time and space must be considered concurrently, and that "the composition and subsequent development of vegetation is partly stochastic and partly determined by the self-modifying properties of a dynamical system" (Roberts 1987). Much of the work in vegetation ecology still focuses on the recognition of patterns and processes (e.g., Silvertown and Wilson 1994). While these have been essential towards theory formulation, perhaps more importantly, several mechanisms have been identified.

While processes are the agents of change, mechanisms are the causes of change in vegetation structure (pattern). Recognition of some basic mechanisms responsible for pattern dates at least as far back to Cowles (1899) who proposed such principle factors as light and heat, wind, soil, and water. With respect to the distribution of organisms, Hutchinson (1953) suggested five types of pattern, which were defined by their underlying mechanisms: 1) Vectorial patterns are those which are determined by environmental factors. 2) Reproductive pattern is the product of processes such as dispersal. 3) Social pattern results from signaling of various kinds leading to spacing or aggregation. 4) Coactive pattern, he defined as the product of interspecific competition. 5) Finally, there is also stochastic pattern, which depends solely on random forces.

These broad categories of mechanisms have more or less served as a basis for explanation of pattern in vegetation ecology. For example, Kershaw (1963) names the three major causes of pattern as morphological, environmental, and sociological. These causes of pattern resemble very much Whittaker's (1970) reasons for the occurrence of patches (pattern) in vegetation. He attributes pattern to dispersal, differences in environment and species interrelations. More importantly, he recognizes that these three causes will certainly interact. He also suggests that differentiation in time could be related to rhythms of environment caused by cycles in time. Similarly, Greig-Smith (1979) outlined some of the major causes of vegetation spatial heterogeneity (pattern). These were: environment, animals, interrelations between plants, disturbance and fire, reaction of the whole vegetation, inefficiency of dispersal, historic causes, and chance. Mueller-Dombois and Ellenberg (1974) explain that these mechanisms can occur in space, or they can be time-dependent as in the cases of successions.

Spatial mechanisms can further be divided into what have been termed endogenous and exogenous causal factors (Webb et al. 1972), or autogenic and allogenic concepts of vegetation change (see Odum 1971). The former involve characteristics within the vegetation itself, whereas the latter are environment-related. Time-dependent mechanisms (those involved in successions) must also be considered. It is critical to realize that it is extremely difficult to isolate these two mechanisms in vegetation dynamics, since they occur simultaneously and will be co-dependent.

The relative importance of causal factors remains debatable. It still remains a very difficult task to determine which mechanisms are dominant behind patterns and processes. However, interaction of vegetation with the physical environment is agreed to be one of the most important mechanisms functioning in spatial and temporal patterns (Scott 1974; van Hulst 1978; White 1979).

The problem of scale

Pattern, process, and their causes can only be defined within specified limits. These limits are in space and time, and they may not even be conscious. The concepts of pattern or process are clearly useful only in relation to a defined limits (Greig-Smith 1961a), commonly referred to as scale. Scale becomes important both in the selection of points or units in pattern identification, and in the overall space or time span allowed in pattern or process recognition. Scale is definitive of pattern.

Allen and Starr (1982) define scale as "the period of time or space over which signals are integrated or smoothed to give the message." Scale is thus defined by perception, but at the same time it may influence perception. Clearly, the perception of pattern is dependent not only on inherent presuppositions and biases (which are often necessary and inevitable), but also on the perspective from which a system is viewed. Tauber (1994) quotes Nietsche : "There are no facts, only interpretations." "The notion that a numerical result should depend of the relation of object to observer is in the spirit of physics in this century and is even an exemplary illustration of it" (Mandelbrot 1982). Allen and Starr (1982) go so far as to suggest three types of scales in any scientific observation: the scale of transmission, the scale of acquisition, and the scale assumed in observation (perception). The effect of the space-time scale on observation is critical since it has importance in sampling, model design and inference. Issues of perception and the role of the observer may provide philosophical contention, however, it can be safely concluded that pattern independent of scale is meaningless.

Pattern recognition may only be possible in the first place at a particular scale. That is, given more or less area or time, patterns may disappear, or be missed. When the lower or upper limits of the quantities of area and time are undefined, it becomes extremely difficult to decide on the appropriate scale. Furthermore, pattern occurs at several scales in vegetation. It thus also becomes difficult to interpret the relative importance of large scale patterns and their underlying component patterns. Due to the effect of scale, perceived patterns may only represent a snapshot of a long-term trend. Often, this can be misleading and result in a misidentification of patterns. A particular pattern observed at one scale may appear different (or not appear at all) at other scales. For example, Orlóci (1981) suggests that it is obvious that there is a time constraint on the interpretation of successional evidence, since changes which are actually cyclic in the long run may appear linear in the short run. It must be noted, however, that practical difficulty in deciding on the sufficiency of scale for interpretation of pattern formation lies in the reality that patterns will perceived at any scale.

Scales and levels in vegetation science

Whittaker (1970) defines some common scales in vegetation studies. He does this by posing three questions which, in essence, he sees as three scales. First, how are species populations distributed in relation to one another and communities along an environmental gradient? Second, how are kinds of communities in an area related to patterns of more than one environmental gradient (ecocline)? Third, how should world-wide relations of communities to climatic gradients be interpreted (biome)? He regards succession as an ecocline in time, which he referred to as a coenocline.

Greig-Smith (1979) suggests that obvious large-scale pattern is well-documented and can be generally attributed to environmental or biotic factors, however, less obvious large and intermediate scales of pattern must be correlated with less obvious environmental differences. As the scales become smaller, it becomes more difficult to identify environmental correlations, and other explanations must be sought.

Palmer (1988) suggests that vegetation displays detail at all spatial scales of interest (and is thus a prime example of a fractal). He gives the example that, on a small scale, patterns are defined by the spacings and interactions of individual plants. On a larger scale, vegetation consists of patches, and on a yet larger scale, vegetation patterns are influenced by geomorphological features of the environment. His studies reveal that the fractal dimension (see Barnsley 1988) of vegetation varies as a function of scale. He thus finds vegetation not to be self-similar statistically (objects need be strictly self-similar to be classified as fractals (Mandelbrot 1982)).

However, perspective considerations of space need not be limited by Euclidean measurements such as length, depth, thickness, etc.. Mandelbrot (1982) introduced the idea of fractal geometry as a basis for pattern recognition. Palmer (1988) has successfully applied Mandelbrot's fractal geometry to the description of spatial patterns of vegetation.

While scale can be critical in pattern resolution, it must be recognized that the *level* at which patterns are sought is equally important. Levels in vegetation ecology refer to the units at which measurements or observations are made. Many levels have been suggested (e.g., Odum 1977; Levins and Lewontin 1980). Wiegleb (1989) suggests six levels: individual, population, species, community, vegetation unit and vegetation complex. These levels s encompass those most commonly used in population and community ecology. Wiegleb (1989) further suggests that some levels are 'real' (individuals, species, vegetation), and others are 'abstract' (community, ecosystem, flora). It has been suggested that as the units increase in scope, information is lost through the accumulation of what they have termed 'aggregation error' (Cale and Odell 1980; Gardner et al. 1982; Cale et al. 1983). This is based on the idea that ecological studies often deal with aggregate variables, which attempt to summarize the seemingly infinite components of ecosystems. In general, it has been found that aggregate behaviour is different from the sum of the behaviours of the components (Cale and Odell 1980).

The critical importance of scale of observation in ecological studies has been recognized by many, leading towards a search for an appropriate theoretical framework (e.g., Kershaw 1960; Levin 1988; Allen and Hoekstra 1990). Kershaw (1963) claims that scale is important because it aids in the understanding of causal mechanisms. For example, he suggests that if some pattern is observed at a scale of 10 cm, an explanation can be sought which is based on the morphology of the plant. Conversely, if the scale of pattern is of the order of several meters, the causal factors are more likely to be related to topography, drainage or soil composition. Delcourt et al. (1983) employ a hierarchical model to suggest methods of spatial and temporal scale resolution which is promising.

The role of models

A theory of vegetation, as all theories, must include a model of some shape and form. Jeffers (1982) identifies the need for models to reduce ambiguity, and to describe complexity with maximum parsimony. Models would seem particularly useful when the purpose is to describe processes and their outcomes, namely patterns, which may indeed be complex. In fact, Pickett and Kolasa (1989) define models as "conceptual constructs that indicate the objects and phenomena of interest, show the relationships and causal interactions between them, and specify the states the system may take." Hill (1973) claims that the function of modelling, and a major aim of vegetation science, is to describe data in a way which is suggestive of their underlying structure.

Attempts towards modelling vegetation dynamics implies predictability, which in turn, asserts the presence of some non-random pattern. Whether the assumption of predictability is plausible can be questioned, however, it is a requirement for modelling attempts of any kind. Goodall (1977) states that knowledge of the changes is in some degree generalizable, thus predictable. If this condition is not satisfied modelling could hardly claim to be a part of science. Modelling is usually the basis for decisions (Goodall 1972). Once a model is formulated, it can be tested and re-tested to see if a reproducible property (pattern) of the behaviour (processes) of the system (vegetation) emerges.

The recent trend has been towards mathematical models, since they are testable (Goodall 1972). Pielou (1981) defines (mathematical) modelling as "mentally constructing a plausible symbolic representation of the functioning of an (eco)system in the form of mathematical equations." There also exists, however, a group of non-mathematical models which are simply descriptive in nature (e.g., Connell and Slayter 1977).

But can vegetation be modelled mathematically? The first question we must ask if we are to attempt any mathematical applications is whether vegetation is quantifiable and whether hypotheses can be generated. Goodall (1972) suggests that these are possible. Collection of data is usually done in sample areas (usually quadrats) within which the quantity of each species is recorded. This quantity can be density (the number of individual plants per unit area), biomass per unit area, cover abundance or basal area. Leps and Hadincova (1992) propose that some more accurate method of vegetation quantification be found as the present methods are highly variable. However, vegetation units can almost always be reduced to a pattern of points (Ripley 1977).

Hill (1973) suggests three major types of inferences which can be drawn from pattern data: (i) relating differences in the local environment to differences in the vegetation; (ii) determining the approximate scale of an autogenic mosaic; (iii) suggesting or checking theories about the competition and establishment of plants in the community. Scott (1974) outlines the four major plant community hypotheses dealing with vegetation-environment relations, which have been developed based on spatial pattern. Patterns can also suggest testable hypotheses about causes of species diversity and species coexistence with the plant community (Olsvig-Whittaker 1988). Pattern establishment can thus allow us to formulate and, more importantly, test hypotheses through models. Pickett and Kolasa (1989) list several models which have been important in the study of vegetation dynamics. Some of these include models of gap dynamics (Shugart 1984), dispersal (McDonnell 1988), and competition (Tilman 1982).

One of the major criticisms of mathematical models is their reliance upon assumptions which may not be valid. Assumptions, however, are necessary for models to maintain parsimony. One may even argue that, if the function of a model is to provide predictive power, and this is achieved, then, such a model is valid, regardless of the assumptions. But this goes against the idea that predictability and knowledge are synonymous (Peters 1991). Furthermore, Slobodkin (1974) argues that it is unreasonable to suggest that one does not need a correct set of assumptions for a theoretical formulation if the conclusions are valid. He maintains that if there exists a theory based on erroneous assumptions which lead to valid conclusions, there also must exist a theory based on valid assumptions which lead to correct conclusions. Finding this, he warrants, may take more ingenuity, effort and intelligence and is thus a greater challenge. Wiens (1984) also acknowledges the possibility of obtaining the ""right" patterns for the wrong reasons."

Models are useful and necessary (Pielou 1981), however, they must be recognized for their limitations so that unreasonable expectations are not held. It must be stressed that they primarily test our perceptions of pattern and process, and rarely give insight into causes. In this respect, early attempts were considered a colossal failure (Yockey et al. 1958). At most, models can suggest possible mechanisms through the description of processes giving rise to patterns. This limitation exists because often mechanisms are treated as a black box, and only the output of the model are examined (McCook 1994). For example, Horn's (1981) Markov model of succession suggest the nature of the process of succession and the resulting pattern, but makes no claim to explaining the mechanisms at work.

However, there does exist a class of 'mechanistic' models which attempt to directly link mechanisms to patterns. They are often mathematical in nature, however, the difference is that mechanisms *define* the model. These mechanistic models are usually not true causal models. Many still rely on the inference of a cause from a pattern. In particular, there is a tendency to consider the correlations between certain life history traits, such as growth form or growth rate, and shade tolerance. Assuming this correlation to be high, life history traits are then used as surrogates for the mechanism of competition. Tilman (e.g., 1982) supports the explanation that correlations in life history traits can explain successional patterns. Botkin et al. (1972) and Huston and Smith (1987) construct simulation models which attempt to incorporate such causal concepts. While they may provide a closer approximation of the mechanisms driving the processes which could account for the observed patterns, correlation cannot be equated to causality. The development of modelling of vegetation processes has been reviewed by many (e.g., Fekete 1985; McCook 1994).

Unsolved problems in the pattern, process, mechanism complex

To this point, the search for pattern, process and mechanisms in vegetation has been described. Furthermore some of the links between these concepts have been suggested. It is through these links that processes and mechanisms are widely inferred from pattern. Wiens (1984) sees the scenario as beginning with the discovery of a pattern. Then a process is identified by inference through logic and realistic evidence, or the premises behind a theoretical model are accepted in order to provide explanation. It can be shown, however, that the relationships are not simple. Often processes are not deducible from pattern (Cale et al. 1989), and rarely are mechanisms deducible from pattern (Kershaw 1963). Much of this can be attributed to the complexities of vegetation and its interactions with the rest of the biosphere. Furthermore, there may exist inherent properties of the system which further complicate the picture. In particular, the relationships between pattern, process and mechanism may not be simple or predictable.

The inverse problem

Complications become apparent when the *direction* of the relationships between pattern, process and mechanism is considered. There are two directions of interest. On one hand, knowledge of relationships may allow the prediction of observed data (usually pattern or process) from a model (usually process or mechanism). This gives rise to the *direct* problem. Conversely, a model may be inferred from observed data. This becomes the *inverse* problem.

Since one can only record limited amounts of data, and since one can only fit a limited number of parameters into a model, it suffices in practice to consider model space and data space to be finite dimensional Cartesian spaces (Scales and Gersztenkorn 1988). Consider the following simplistic formalization of the mechanism-pattern problem (in which the relationship between mechanism and pattern is chosen as an example):

$$Am=p \tag{1}$$

where $\boldsymbol{m}$ is a given mechanism in **M** (Mechanism space), $\boldsymbol{p}$ is a member of **P** (Pattern space) and **A** is some (linear or non-linear) operator representing the mapping from model space (**M**) to data space (**P**) Perhaps the mapping could represent a process (see Fig. 2). Then, given a mechanism ($\boldsymbol{m}$), the pattern ($\boldsymbol{p}$) could be predicted. For example, if we know how the mechanism of competition ($\boldsymbol{m}$) works (**A**) then, the composition or distribution of vegetation ($\boldsymbol{p}$) will always be determined through (1). The calculation of Am with given $\boldsymbol{m}$ is the direct problem. There is no question that in practical applications a critical step is modelling the process, resulting in the symbolic description of **A**.

Now, suppose we were interested in just the opposite. Given a pattern, we would want to infer the mechanism. This would require the definition of the inverse of **A**, (A^{-1}), and could be represented by:

$$A^{-1}p=m \tag{2}$$

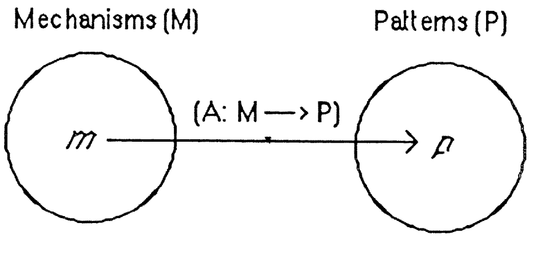

Figure 2. Formal mapping A from model space M to data space P.

This is the *inverse* problem (the determination of $\boldsymbol{m}$ given $\boldsymbol{p}$ and the relation in (1)). By definition two problems are inverses of one another if the formulation of each involves all or part of the solution of the other (Keller 1976). Inverse problems concern the determination of properties of some inaccessible regions from observations on the boundary or outside the boundary of that region (Anger 1993). Clearly this is applicable to the problem of pattern and mechanism in ecology. Knowledge about mechanisms is not always accessible. All we have to work with are patterns. These patterns are then used to infer mechanism.

The establishment of the nature of A^{-1} is critical because it will determine the nature of the inverse problem. In particular, depending upon the nature of A^{-1}, the inverse problem may be properly-posed, or ill-posed. Moritz (1993) points out the conditions (originally introduced by Hadamard (1902)) which must be satisfied for a mathematically properly-posed problem to correspond to reality:

1. The solution must exist (existence).

2. The solution must be uniquely determined by the data (uniqueness).

3. The solution must depend continuously on the data (stability).

In the case of our application, the first requirement implies that for every $\boldsymbol{m}$ in **M**, there exists a solution $\boldsymbol{p}$ in **P**. The second requirement implies that **A** be a one-to-one mapping, in which case A^{-1} is also one-to-one. The third requirement implies stability of the problem on the spaces (**P**, **M**).

If one or more of these conditions is violated, then the problem is ill-posed. Most direct problems are properly posed, however, it turns out that most inverse problems are ill-posed (Moritz 1993). To concern ourselves with the violation of the existence requirement at first seems rather absurd. It seems intuitive that every cause will have an effect and thus a solution will always exist. But it is entirely possible that a mechanism has no apparent effect (more familiarly, a rejection of the null hypothesis). In this case m would not be considered a member of M. This would then lead to the reformulation of the problem.

It is much more interesting to examine violations of uniqueness and stability. It turns out that these violations lead to some very interesting questions about the relationship between pattern, process and mechanism. While many claim that such ill-posed problems are difficult or nearly impossible to solve (e.g., Anger 1985) others (e.g., Tikhonov and Arsenin 1977) are optimistic.

Uniqueness

If uniqueness is the case, that is, for every perceived pattern it is known *a priori* that there exists a unique mechanism proceeding to its formation, then inference is valid. Given a mechanism, pattern could be predicted with certainty. Given a pattern, the mechanism could be inferred. However, this power relies on the presupposition that, not only is it known that there exists a unique relationship between mechanism and pattern, but also that the relationship is *known*. It may

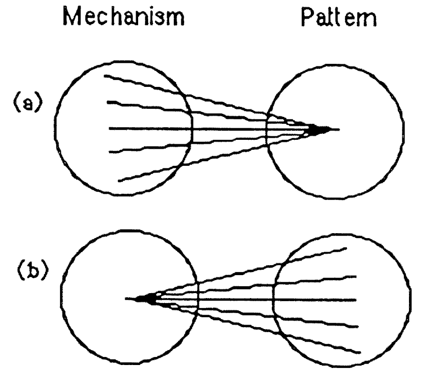

Figure 3. Non-uniqueness of the Mechanism-Pattern relationship. (a) plurality of causes (b) plurality of effects.

very well be that the problem of finding these relationships is not simple.

But is anticipation of unique relationships realistic? Is it not reasonable to believe that certain patterns could be achieved through several *different* mechanisms? Similarly, could one mechanism not lead to several *different* patterns? These relationships are sketched in Figure 3. Copi's (1978) logic is useful in evaluating these situations, especially in the case of different mechanisms leading to the same pattern, what he terms 'plurality of causes' (Fig. 3a). He makes use of the idea that *every difference must make a difference.* That is to say, if the effects of two mechanisms are not different, then the mechanisms themselves must not be different. In other words, differences in effects are really the basis upon which mechanisms are distinguished. But to accept that every difference makes a difference may not always be prudent in practice.

Copi (1978) argues against the doctrine of 'plurality of causes'. He suggests that this predicament is often the result of the insufficient resolution of the effect. Thus, as an effect is more and more precisely specified, the number of possible causes is reduced. Eventually, the effect is defined such that only one possible cause remains. Hence the doctrine of uniqueness of cause becomes the product of inductive reasoning. These arguments, while rather convincing, do not solve the problem at hand. Namely, it may be impossible to reduce a given pattern to the desired level. How should one assess relative success? Are relationships discovered at those levels even desired? Does this mean that generalization becomes impossible? Surely this is not in line with general experience. Finally, it is still conceivable that two or more very different mechanisms could result in *exactly* the same pattern, which tempts one to believe that every difference *does not* need to make a difference. The observation of evolutionary convergence actuates such a suspicion.

Plurality of causes clearly questions the ability to infer mechanisms from a given pattern. What about predicting pattern from a given mechanism? In particular, how is this possible if a given mechanism can result in several different patterns (Fig. 3b)? Of course if one assumes the "*every difference ...*" doctrine, then this is not an issue. However, plurality of effects may exist, especially, if the impact of omnipresent stochastic inputs is not known. It is also possible that while effects may be *apparently* different, they may all in fact be part of the same process or causal link. This is typically the case when effects are perceived at different (temporal or spatial) scales. It remains a challenge to incorporate scale effects into the problem of pattern, process and mechanism.

Stability

If the third condition of properly-posed problems is not met, then the problem is unstable. This implies that small fluctuations in the initial specification of the initial conditions (data) may have a large effect on the outcome (model). In essence, for a problem to be stable, the solution must depend continuously on the data. Deterministic processes, as considered in classical mechanics, depend uniquely and continuously on the initial data, and, in fact, this is the essence of causality. Modern theory of nonlinear dynamical systems, however, has revealed that even classical systems can show the property of instability. This has also been referred to as 'sensitive dependence on initial conditions' or 'The Butterfly Effect" (Lorenz 1963) in the terms of the newly developed chaos theory.

Sensitive dependence on initial conditions has some interesting consequences with respect to the classical views of pattern, process and mechanism. For example, it seems intuitive that complex patterns are the result of equally complex processes or mechanisms. "This is true in many cases, but at the same time the long standing paradigm is far from being true in general. Rather, it seems, and this is one of the major surprising impacts of fractal geometry and chaos theory, that in the presence of a complex pattern there is a good chance that a very simple process is responsible for it. In other words, the simplicity of a process should not mislead us into concluding that it will be easy to understand its consequences" (Peitgen et al. 1992).

Chaos theory yields interesting relationships where the nature of the effects cannot be predicted by knowing the nature of the causes. But it must be remembered that chaos is only one subset of complexity. The relationship between complexity (see Lewin 1992) and chaos theory is presented in Fig. 4. Clearly, in attempting to predict or infer in a system

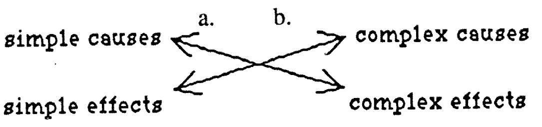

Figure 4. The relationship between complexity and chaos. Path a. is how complexity arises. Path b. is an implication of chaos.

of patterns, processes and mechanisms, one would be limited by conventional logic.

Some would argue that the implications of chaos theory render complex systems unpredictable and thus it is futile to attempt to study them (Mullin 1993). But while chaos theory implies unpredictability, chaotic systems are deterministic (Kellert 1993). Chaos theory could still help to provide explanations for apparent chaotic patterns, that is, suggest some order in chaos.

Closing remarks

Many patterns, processes and mechanisms have been identified in the practice of vegetation ecology. While some insight into the relationships between these concepts has been gained, there is as yet no general theory that links vegetation patterns to basic plant processes (Smith and Huston 1989). This is not surprising due to the elaborate nature of the task. Efforts are complicated by ambiguities in pattern recognition, process definition, and mechanism isolation. Many of these ambiguities are related to the problem of scale influencing perception.

Vegetation dynamics is complex due to instability and plurality of causes and effects. It is thus a challenge to study and model such systems, especially in the case when unusual, namely chaotic, behaviour is observed. In such a case, practical progress seems hindered as much by theoretical obstacles as by the lack of methodologies. Much investigation is still needed with respect to the relationship between the concepts of pattern, process and mechanism in vegetation. This is essential in order to justify the ambitious inferences which are being made on the basis of incomplete information. However, this will be difficult, and arguably not completely possible due to the seemingly immeasurable complexities. But this difficulty does not rule out inference as the main objective of scientific inquiry. The importance of understanding these relationships lies in clarifying and linking together usually limited observations which can be made on a system. Furthermore, inference is important to the public at large since it provides the foundation for decision-making in attempts to deal with arising crises.

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References

Allen, L. H. and T. B. Starr. 1982. Perspectives for Ecological Complexity. Univ. Chicago Press, Chicago.

Allen, L. H. 1990. Plant responses to using carbon dioxide and potential interactions with air pollutants. J. Environ. Qual. 19:15-34.

Allen, T. F. H. and T. W. Hoekstra. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. J. Veg. Sci. 1: 5-12.

Anger, G. 1985. On the relationship between mathematics and its application: a critical analysis by means of inverse problems. Inverse Problems. 1: L7-L12.

Anger, G. 1993. Basic principles of inverse problems. In: G. Anger, R. Gorenflo, H. Jochmann, H. Moritz, W. Webers. (eds.), Inverse Problems: Principles and Applications in Geophysics, Technology, and Medicine. Akademie Verlag, Berlin.

Austin, M. P. and M. P. Smith. 1989. A new model for the continuum concept. Vegetatio. 83: 35-47.

Barnsley, M. 1988. Fractals everywhere. Academic Press, Inc., Boston.

Benzecri, J. P. 1969. Statistical analysis as a tool to make patterns emerge from data. In: S. Watanabe (ed.), Methodologies of pattern recognition. Academic Press, New York.

Billings, W. D. 1974. Environment: Concept and Reality. In : B. R. Strain and W. D. Billings (eds.), Handbook of Vegetation Science: Vegetation and Environment. Dr. W. Junk b. v. Publishers, The Hague.

Botkin, D. B., J. F. Janak and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60: 849-872.

Bouxin, G. 1991. The measurement of horizontal patterns in vegetation: a review and proposals for models. In: E. Feoli and L. Orlóci (eds.), Handbook of Vegetation Science: Computer assisted vegetation analysis. Kluwer Academic Publishers, Dordrecht.

Burrows, C.J. 1990. Processes of Vegetation Change. Unwin Hyman Ltd., Boston.

Cale, W. G. and P. L. Odell. 1980. Concerning aggregation in ecosystem modeling. In: E. Halfon (ed.), Theoretical systems ecology.Academic Press, New York.

Cale, W. G., R. V. O'Neill, and R. H. Gardner. 1983. Aggregation error in non-linear ecological models. J. Theor. Biol. 100: 539-555.

Cale, W. G., G. M., Henebry and J. A. Yeakley. 1989. Inferring process from pattern in natural communities. Bioscience. 39: 600-605.

Cannon, J. R. and U. Hornung. 1986. Inverse Problems. Birkhäuser Verlag, Basel.

Carpenter, S. R. and J. E. Chaney. 1983. Scale of spatial pattern: four methods compared. Vegetatio. 53: 153-160.

Case, T. and R. Sidell. 1983. Pattern and chance in the structure of model and natural communities. Evolution. 37: 832-849.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Publ. 242. Carnegie Inst., Washington, D.C.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Cooper, W. S. 1926. The fundamentals of vegetation change. Ecology. 7: 391-413.

Copi, I. M. 1978. Introduction to Logic. Macmillan Publishing Co., Inc., New York.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Part. I. -- geographical relations of the dune floras. Bot. Gaz. 27: 95-117.

Dahlman, R. C. 1993. CO_2 and plants: revisited. Vegetatio. 104/105: 339-355.

Dale, M. B. 1980. A syntactic basis of classification. Vegetatio 42: 93-98.

Dale, M. R. T. and D. A. MacIssac 1989. New methods for the analysis of spatial pattern in vegetation. J. of Ecol.. 77: 78-91.

Dale, M. R. T., and D. J. Blundon. 1990. Quadrat variance analysis and pattern development during primary succession. J. of Veg. Sci. 1: 153-164.

Darwin, C. 1859. On the origin of species. Murray, London.

Delcourt, H. R., P. A. Delcourt and W. Thompson III. 1983. Dynamic plant ecology: the spectrum of vegetational change in space and time. Quat. Sci. Rev. 1: 153-175.

Digby, P. G. N. and R. A. Kempton. 1987. Multivariate analysis of ecological communities. Chapman and Hall, London.

Fekete, G. 1985. Succession of terrestrial vegetation: theory, model and reality. (in Hungarian) In: G. Fekete (ed.), Paradigms of Coenological Succession. Akadémiai Kiadó, Budapest.

Ford, E. D. and E. Renshaw. 1984. The interpretation of process from pattern using two-dimensional spectral analysis: modelling single species patterns in vegetation. Vegetatio. 56: 113-123.

Gardner, R.H., W. G. Cale, and R. V. O'Neill. 1982. Robust analysis of aggregation error. Ecology. 63: 1771-1779.

Gauch, H. G. and R. H. Whittaker. 1981. Hierarchical classification of community data. J. Ecol. 69: 537-557.

Gleason, H. A. 1926. The individualistic concept of the plant association. Am. Midl. Nat. 21:92-108.

Gleick, J. 1987. Chaos: Making a New Science. Penguin Books, New York.

Goodall, D. W. 1972. Building and testing ecosystem models. In: J. N. R. Jeffers (ed.), Mathematical models in ecology. Blackwell Scientific Publishers, Oxford.

Goodall, D. W. 1977. Dynamic changes in ecosystems and their study: the roles of induction and deduction. J. Envir. Manag. 5: 309-317.

Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. Ann. Bot.Lond. 16:293-316.

Greig-Smith, P. 1961. The use of pattern analysis in ecological investigations. Recent Advances in Botany. University of Toronto Press, Toronto.

Greig-Smith, P. 1961. Data on pattern within plant communities. II. *Ammophila arenaria* (L.) Link. J. Ecol. 49: 703-708.

Greig-Smith, P. 1970. Statistical plant ecology. Ann. Rev. Ecol. Sys. 1:99-124.

Greig-Smith, P. 1979. Pattern in vegetation. J. of Ecol.. 67: 755-779.

Hadamard, J. 1902. Sur les problèmes derivées partielles et leur signification physique. Princeton Univ. Bull. 20:49-52.

Halvorson, J. 1994. Geostatistics and ecology. ESA Bulletin. 75: 36-38.

Hill, M. O. 1973. The intensity of spatial pattern in plant communities. J. Ecol. 61: 225-235.

Horn, H. S. 1981. Some causes of variety in patterns of secondary succession. In: D. C. West, H. H. Shugart, and D. B. Botkin (eds.), Forest Succession: Concepts and Application. Springer-Verlag, New Yourk, pp. 24-35.

Huston, M. and T. Smith. 1987. Plant succession: life history and competition. Am. Nat. 130: 168-198.

Hutchinson, G. E. 1953. The concept of pattern in ecology. Proc. Acad. Nat. Sci. 105: 1-12.

Jeffers, J. N. R. 1982. Modelling. Chapman and Hall, London.

Keller, J.B. 1976. Inverse problems. American Mathematical Monthly: 83: 107-118.

Kellert, S. H. 1993. In the wake of chaos. Univ. of Chic. Press, Chicago.

Kerner von Marilaun, A. 1863. Das Pflanzenleben der Danauländer. 348 pp. Innbruck, Wagner. (Trans. by Conard, 1951).

Kershaw, K. A. 1957. The use of cover and frequency in the detection of pattern in plant communities. Ecology. 38: 291-299.

Kershaw, K.A. 1960. The detection of pattern and association. J. of Ecol.. 48:233-242.

Kershaw, K. A. 1963. Pattern in vegetation and its causality. Ecology. 44: 377-388.

Kershaw, K. A. 1973. Quantitative and dynamic plant ecology. Edward Arnold. Limited, London.

Kissov, V., S. HadjitodovoV and L. Kuncheva. 1990. Using key features in pattern classification. Pat. Rec. Let. 11:1-5.

Kuncheva, L. 1993. 'Change-glasses' approach in pattern recognition. Pat. Rec. Let. 14: 619-623.

Legendre, R. and M. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio. 80: 107-138.

Leps, J. and V. Hadincova. 1992. How reliable are our vegetation analyses? J. Veg. Sci. 3: 119-124.

Levin, S. A. 1988. Pattern, scale, and variability: an ecological perspective. In: A. Hastings (ed.), Community Ecology. Springer-Verlag, Berlin.

Levins, R. and R. Lewontin. 1980. Dialectics and reductionism in ecology. Synthese. 43: 47-78.

Lewin, R. 1992. Complexity: life at the edge of chaos. Macmillan Pub. Co., New York.

Lorenz, E. N. 1963. Deterministic nonperiodic flow. J. Atm. Sci. 20: 130-141.

Ludwig, J. A. and J. F. Reynolds. 1988. Statistical ecology: a primer on methods and computing. Wiley, New York.

McCook, L. J. 1994. Understanding ecological community succession: causal models and theories, a review. Vegetatio. 110: 115-147.

McCormick J. F., A. E. Lugo, and R. R. Sharitz. 1974. Experimental analysis of ecosystems. In: B. R. Strain and W. D. Billings (eds.), Handbook of Vegetation Science: Vegetation and Environment. Dr. W. Junk b. v. Publishers, The Hague.

McDonnell, M. J. 1988. Landscapes, birds and plants: Dispersal patterns and vegetation change. In: J. Downhower (ed.), Biogeography of the Island Region of western Lake Erie. Ohio State Univ. Press, Columbus.

Mandelbrot, B. B. 1982. The Fractal Geometry of Nature. W. H. Freeman and Co., San Francisco.

Marx, J. L. 1975. Air pollution effects on plants. Science. 187: 731-733.

May, R. M. 1974. Stability and complexity in model ecosystems., 2nd ed. Princeton Univ. Press, Princeton.

May, R. M. 1986. The search for patterns in the balance of nature: advances and retreats. Ecology. 67: 1115-1126.

Moritz, H. 1993. Basic principles of inverse problems. In: G. Anger, R. Gorenflo, H. Jochmann, H. Moritz, W. Webers (eds.), Inverse Problems: Principles and Applications in Geophysics, Technology, and Medicine. Akademie Verlag, Berlin.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods in vegetation ecology. John Wiley & Sons, New York.

Mullin, T. 1993. The nature of chaos. Claredon Press, Oxford.

Nebel, B. J. and R. T. Wright. 1993. Environmental science. Prentice-Hall, Inc., New Jersey.

Odum, E. P. 1962. Relationship between structure and function in the ecosystem. Jap. J. Ecol. 12:108-118.

Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders, Philadelphia.

Odum, E. P. 1977. The emergence of ecology as a new integrative discipline. Science. 195:1289-1293.

Olsvig-Whittaker, L. 1988. Relating small-scale vegetation patterns to the environment. In: H. J. During, M. J. A. Werger, and J. H. Willems (eds.), Diversity and pattern in plant communities. SPB Academic Publishing, The Hague.

Orlóci, L. 1978. Multivariate methods in vegetation research. Dr. W. Junk, The Hague.

Orlóci, L. 1981. Probing time series vegetation data for evidence of succession. Vegetatio. 46: 31-35.

Orlóci, L. 1988. Detecting vegetation patterns. ISI Atlas of Science. 1:173-177.

Orlóci, L. 1993. The complexities and scenarios of ecosystem analysis. In: G. P. Patil and C. R. Rao (eds.), Multivariate Environmental Statistics. North Holland, Amsterdam.

Palmer, M.W. 1988. Fractal geometry: a tool for describing spatial pattern of plant communities. Vegetatio. 75:91-102.

Peitgen, H. O., H. Jurgens, and D. Saupe. 1992. Chaos and Fractals. New Frontiers of Science. Springer-Verlag, New York.

Peters, R. H. 1991. A critique for ecology. Cambridge University Press, Cambridge.

Pickett, S. T. A. and J. Kolasa. 1989. Structure of theory in vegetation science. Vegetatio. 83: 7-15.

Pielou, E.C. 1977. Mathematical Ecology. John Wiley & Sons, Inc., New York.

Pielou, E. C. 1981. The usefulness of ecological models: a stocktaking. Quart. Rev. Bio. 56:17-31.

Pimm, S. L. 1992. The Balance of Nature? The University of Chicago Press, Chicago.

Podani, J. 1989. Comparison of ordinations and classifications of vegetation data. Vegetatio. 83: 111-128.

Ripley, B. D. 1977. Modelling spatial patterns (with discussion). J. Roy. Stat. Soc., Series B. 39: 172-212.

Roberts, D. W. 1987. A dynamical systems perspective on vegetation theory. Vegetatio. 69: 27-33.

Robertson, G. P. 1987. Geostatistics in ecology: interpolating with known variance. Ecology. 68: 744-748.

Root, R. B. 1975. Some consequences of ecosystem texture. In: S. A. Levin (ed.), Ecosystem Analysis and Prediction. SIAM, Philadelphia.

Scales, T. A. and Gersztenkorn, A. 1988. Robust methods in inverse theory. Inv. Prob. 4: 1071-1091.

Scheiner, S. M. and J. Gureriter. 1993. Design and analysis of ecological experiments. Chapman and Hall, New York.

Schlesinger, W. H. 1993. Response of the terrestrial biosphere to global climate change and human perturbation. Vegetatio. 104/105: 295-305.

Shugart, H. H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlag, New York.

Scott, D. 1974. Description of relationships between plants and environment. In: B. R. Strain and W. D. Billings (eds.), Handbook of Vegetation Science: Vegetation and Environment. Dr. W. Junk b. v. Publishers, The Hague.

Silvertown, J., and J. B. Wilson. 1994. Community structure in a desert perennial community. Ecology. 75: 409-417.

Slobodkin, L. B. 1974. Comments from a biologist to a mathematician. In: S. A. Levin (ed.), Ecosystem Analysis and Prediction. SIAM, Philadelphia.

Smith, T. and M. Huston. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio. 83: 49-69.

Southwood, T. R. E. 1980. Ecology- a mixture of pattern and probabilism. Synthese. 43: 111-122.

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology: 284-307.

Tauber, A. I. 1994. A typology of Nietzsche's biology. Biol. Phil. 9:25-44.

Tikhonov, A. N., and V. Y. Arsenin. 1977. Solutions of Ill-posed Problems. John Wiley & Sons, New York.

Tilman, D. 1982. Resource competition and community structure. Princeton Univ. Press, Princeton.

Upton, G. and B. Fingleton. 1985. Spatial Data Analysis by Example. Vol.I. John Wiley & Sons, Ltd., Chichester.

Usher, M. B. 1975. Analysis of pattern in real and artificial plant populations. J. Ecol. 63: 569-586.

van der Maarel, E. 1988. Vegetation dynamics: patterns in time and space. Vegetatio. 77: 7-19.

van Hulst, R. 1978. On the dynamics of vegetation: patterns of environmental and vegetational change. Vegetatio. 2: 65-75.

van Leeuwen, C.G. 1966. A relation theoretical approach to pattern and process in vegetation. Wentia. 15: 25-46.

Ver Hoef, J. M., N. A. C. Cressie, and D. C. Glenn-Lewin. 1993. Spatial models for spatial statistics: some unification. J. Veg. Sci. 4: 441-452.

Warming, E. 1895. Plantesamfund. Grundtraek of den kologiske Plantegeografi. 335. pp. Kjbenhavn, Philipsens.

Watt, A. S. 1947. Pattern and process in the plant community. J. Ecol. 35: 1-22.

Webb, L. J., J.G.Tracey, and W. T. Williams. 1972. Regeneration and pattern in the subtropical rain forest. J. Ecol. 60: 675-695.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev.. 45: 229-299.

Whittaker, R.H. 1970. Communities and Ecosystems. The Macmillan Company, Collier-Macmillan Limited, London.

Wiegleb, G. 1989. Explanation and prediction in vegetation science. Vegetatio. 83: 17-34.

Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In: D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), Ecological Communities. Princeton University Press, Princeton.

Wilbur, H. M. and J. Travis. 1984. An experimental approach to understanding pattern in natural communities. In: D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), Ecological Communities. Princeton University Press, Princeton.

Yockey, H. P., R. L. Platzman, and H. Quastler (eds.) 1958. Information Theory in Biology. Pergamon Press, New York.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliff, New Jersey.

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