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The Template: Patterns and Processes of Spatial Variation

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Abstract

Ecosystem processes are inherently variable in space and time, in part because they occur on a spatially heterogeneous template or landscape. For many purposes, the patterns of heterogeneity can be characterized as gradients, patchworks, or networks—or some combination of these fundamental patterns. Each class of landscape pattern implies that it has been generated by certain kinds of abiotic or biotic mechanisms, which can be described by particular mathematical formulations. We illustrate these points with a few selected, ecologically relevant examples. Quantitatively characterizing the patterns of variation in the template and understanding their causes, correlates, and consequences are important steps in investigating the influence of spatial heterogeneity on the structure and function of ecological systems at all scales from molecular to global.

Introduction

Before getting too far into the consideration of the spatial heterogeneity of ecological processes, it is usually necessary to ask: How and why is the landscape heterogeneous? To understand how ecological processes play out on an underlying template of abiotic and biotic environmental variation, it is first necessary to understand that variation. At any given time, this template sets the initial conditions for the subsequent structural development and dynamic interactions of the system. So how is the template structured, why is it organized this way, and how does it change over time? These are big, complicated questions. The answers draw from many disciplines and remain incomplete.

Nevertheless, we will attempt to provide a conceptual framework to characterize some of the fundamental features of spatial environmental heterogeneity. We should make it clear from the outset that we do not consider ourselves to be either ecosystem or landscape ecologists. We hope to offer an outsider's perspective on characterizing and understanding heterogeneity.

What we have done is to collect in one place ideas stretching from physics and the earth sciences to biology and ecology and to suggest that we can use these concepts and mathematical tools to begin to characterize heterogeneity in a more general framework. We define heterogeneity simply as spatial variation in the environment. We suggest that this environmental variation can be characterized as a combination of gradients, patches, and networks. We discuss how these patterns can be characterized mathematically, how they are formed, and some of the consequences for the ecological processes that play out on these templates. Finally, we attempt to illustrate the potential utility of a centralized approach to dealing with heterogeneity by providing several examples from the literature.

Patterns and Their Causes

We recognize three categories of patterns: gradients, patchworks, and networks. We do this with some trepidation. We are well aware of the pitfalls of dividing the natural world, and the frameworks that we use to study it, into compartments that may be artifactual human constructs. Nevertheless, such a classification seems appropriate in this case for several reasons. First, the processes that usually create these patterns are often distinct and operate at different scales. Second, the qualitative differences in the patterns and their causal processes mean that different mathematical and analytical methods are necessary to characterize them. Third, some degree of simplification is appropriate, even desirable, to study ecological processes on complex landscapes. The search for syntheses and mechanistic explanations based on first principles will require some simplifications, but ones that capture the essence of the phenomena.

Gradients

We define gradients as patterns of continuous variation, typically of a single focal variable. Under this definition, there can be no more independent variables than there are Euclidean dimensions of the system. For two-dimensional space, therefore, there can be only two gradients of orthogonal variation. If more than two gradients occur on the earth's surface, there will be some degree of correlation among them. This can make gradients difficult to disentangle, especially because several gradients can simultaneously influence an observed pattern. In practice, we are often concerned with one-dimensional gradients: for example, with patterns such as temperature varying with latitude or elevation, temperature and pressure varying with water depth, and time of exposure varying with height in the intertidal. As in most of these examples, the pattern of variation itself may be curvilinear, just as long as it is continuous.

Gradients are fairly common. They tend to occur whenever there are strong polar differences in one or more correlated variables with some kind of averaging, homogenizing process operating in between. They are most apparent at large spatial scales where physical factors operate over substantial distances to generate relatively continuous variation in temperature, light, pressure, solute concentrations, and other important features of the biosphere. For example, the latitudinal gradient of temperature is due to the position of the earth in relation to the sun, and to the homogenizing effects of air and water movement. The elevational gradient of temperature is due to adiabatic heat exchange in response to variation in air pressure and again to the homogenizing effects of air movement. The gradient concept is fundamental to ecology and has been well developed for some time (Whittaker 1967). Where the process generating the gradient is known, it should be possible to use first principles to describe the quantitative pattern of variation.

Gradients tend to be best behaved at relatively large scales where the generating process dominates the variability in the observed values. As one "zooms in" to smaller scales within the gradient, additional processes become dominant, and the continuous gradient pattern becomes swamped by the now dominant local processes. Examined in detail on sufficiently small scales, temperature does not vary smoothly and monotonically with either latitude or elevation. An example is a thermal inversion in air temperature with elevation, a fairly common phenomenon. Nevertheless, a gradient described by a simple monotonic function usually captures most of the variation of temperature with respect to latitude, elevation, and water depth, at scales over which the impacts of the major process (solar incandescence, adiabatic cooling, and solar penetration) operate. At smaller scales, other processes dominate, and the previously smooth relationship appears increasingly patchy.

Patches

Patches are the pattern that most biologists consider when talking about spatial heterogeneity. In principle, patches can be defined as discrete units of area that are more similar to one another in one or more variables than to their neighbors (Kotliar and Wiens 1990). For example, a patch type could be defined by an area of some size either containing or lacking nitrogen-fixing plants. In practice, many patch types must be based on artificial cutoffs (e.g., high nitrogen *vs.* low nitrogen, lowlands *vs.* highlands), and resulting arbitrary boundaries. Sometimes, the borders between patch types are effectively steep gradients, more continuous than discrete (Gustafson 1998).

Much of this type of discrete spatial heterogeneity is, at its core, due to the three-dimensional complexity of the earth's surface. If the earth were a simple plane or a perfectly smooth sphere, environmental variation would likely be characterized by simple gradients, with a maximum of two truly independent axes. However, the real landscape is heterogeneous and discontinuous because of geological and biological processes. The geological processes of tectonics and erosion have created a crumpled, dimpled, and layered surface, which interacts with the predictable gradients of solar energy input, air and water pressure, tidal exposure, and other factors to create a complex discontinuous abiotic template.

Biological processes modify this already complex template in several ways. First, as discrete entities with unique combinations of variables, individual organisms serve as patchy environments for other organisms. The most obvious example of this is hosts serving as patchy environments for parasites and symbionts. However, this phenomenon is actually much more general. Gradients and topographical features influence local climate and soil conditions. This patchy local abiotic environment determines the flora that can inhabit the area, and the flora, which is patchy as a result of the climate and soils, combines with the abiotic template to influence the abundances and distributions of animals at the site. Feedbacks between the animals, plants, and the abiotic environment can then occur, causing additional variation. For example, organisms can act as engineers, moving materials or altering flows to create new patches or alter existing ones (e.g., Jones et al. 1994). Examples include plant canopies creating unique microenvironments by altering the flows of energy, water, and nutrients. Burrowing animals can alter soil properties and create unique structures that are used by still other organisms (e.g., Reichman and Seabloom 2002).

Given the enormous variety of patch types, and of the processes that produce them, can we draw any generalizations about their properties? Patchy environments have traditionally proven difficult to describe quantitatively and thus to model. Perhaps the most promising approach is based on the application of fractal geometry (Mandelbrot 1983). Interestingly, it appears that many different kinds of patches have self-similar or fractal-like distributions. This means that, over at least some substantial range of scales, patterns of covariation can be characterized by power laws of the form

$$Y = Y_0 X^b, \tag{3.1}$$

where Y is some variable that can be considered the dependent variable, Y_0 is a normalization constant, X is the independent variable, and b is another constant, the scaling exponent. Power laws have the useful property of being linearized by taking the logarithms of both sides of Equation (3.1),

$$\ln(Y) = \ln(Y_0) + b \ln(X), \tag{3.2}$$

such that a plot of $\ln(Y)$ as a function of $\ln(X)$ is a straight line with a slope of b and an intercept of $\ln(Y_0)$. The slope, b, can take on a wide range of values that produce a wide variety of curves when plotted on linear axes. These curves can be increasing ($b > 0$), decreasing ($b < 0$), or invariant ($b = 0$), and the increasing curve can be concave up ($b > 1$), concave down ($0 < b < 1$), or linear ($b = 1$; Figure 3.1). The variation described by Equation (3.1) is

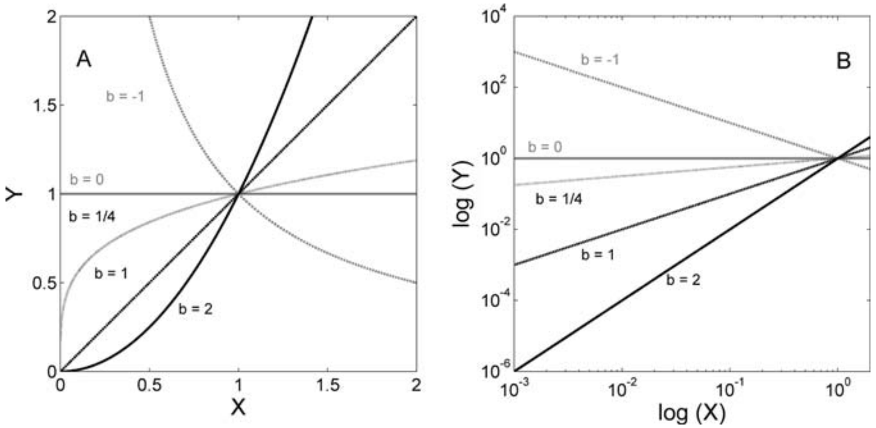

FIGURE 3.1. Example plot of power functions with different exponents, b (A, linear axes; B, logarithmic axes). For all functions, $Y_0 = 1$. Note that except when $b = 1$, relationships are curvilinear when plotted on linear axes, but all are linear when plotted on logarithmic axes.

called self-similar or fractal, because the ratios of variables at any scale have a constant relationship to each other. That is

$$Y_1/Y_2 = (X_1/X_2)^b, \tag{3.3}$$

where Y_1, Y_2, X_1, and X_2 represent measurements of Y and X at two different scales, 1 and 2, respectively.

Multiple approaches to characterizing the shape and distribution of patches based on fractal-like behavior of particular features have been proposed (Milne 1991b). These approaches include the standard box counting and mass fractal dimensions (approximations of the Hausdorff dimension), the perimeter-area fractal dimension, and many others. These different fractal dimensions characterize different aspects of the patchy environment (Milne 1991b).

Many patches in nature, although they may be characterized in a variety of different ways, appear to have fundamentally fractal-like properties. This is true of patches and other landforms created by abiotic geological processes. The classic case is that of a coastline, which appears self-similar over a wide range of scales so long as the geological parent material and formative process is essentially the same (Richardson 1961; Mandelbrot 1983). As the length of the ruler used to measure the coastline gets smaller, the total length of the coastline increases ($coast\ length \propto ruler\ length^{-D}$, where D is the fractal dimension). Although the coastline is continuous and therefore not necessarily patchy in a traditional sense, it is "patchy" in a mathematical sense when compared to a straight line (i.e., it is not smooth). More obvious patchiness occurs when a complex geological landscape is partially filled with water, creating either lakes on land or islands in water.

One characterization of the fractal nature of patches that we find particularly intriguing is the scaling of frequency *versus* magnitude. It is well established that, for earthquakes, the area involved in a seismic event is approximately inversely proportional to the number of those events observed (i.e., there are more smaller events). This is called the Guttenberg-Richter law and it is the basis for measuring the magnitude of earthquakes on a logarithmic Richter scale. This relationship between frequency and the area involved is described by a power-function relationship, with a slope of approximately -1. This general pattern between frequency and magnitude has been observed in other systems, in particular forest fires (Malamud et al. 1998) and financial markets (Mandelbrot 1997). Although relatively poorly studied in ecological systems, there is some evidence that ecological patches may follow a similar power-function distribution. In particular, lakes, islands, and vegetation patches have frequency-magnitude distributions with $b \approx -1$ (Figure 3.2; see also Korcak 1938; Hastings et al. 1982; Wetzel

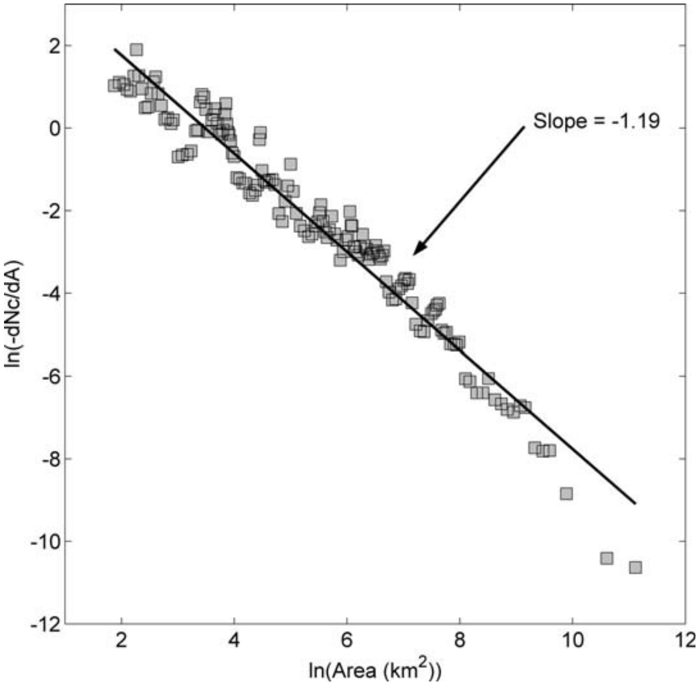

FIGURE 3.2. Plot of the frequency of the Southwest Pacific and Moluccan islands by island area. Binning method (linear or logarithmic) and bin size complicate estimation of the precise underlying distribution. Thus, we generate the inverse cumulative distribution function (cdf) for the observed data and then estimate the underlying probability density function (pdf) by calculating the slope of the cdf using a sliding window with a 5-point width (Malamud et al. 1998). This approach provides equivalent results to those based entirely on the cdf (Hastings and Sugihara 1993). Data on island area was taken from Flannery (1995).

1991; Hastings and Sugihara 1993). This slope is approximately the same as that for earthquakes and implies that the total magnitude of all events in any given logarithmic magnitude class is approximately equal. For example, for the islands in Figure 3.2, the total area of small islands (1 to 10 km^2 in area) should be approximately equal to the total area of large islands (100 to 1000 km^2 in area). Similar slopes have been observed for forest fire frequency (Malamud et al. 1998). Peninsulas (Milne 1991b) and forest patches (N. Baum, unpublished data) also appear to have a power-function relationship between frequency and area, though the reported exponents are closer to -2. This suggests that the general form of the power-law relationship holds for different landscape features but that the specific exponent depends on the particular feature being observed. Consequently, differences in exponents may suggest important differences in the processes generating the patterns and in their effects on biological systems. Lakes, islands, vegetation patches, peninsulas, and burns all represent heterogeneously distributed ecological patches that have important consequences for ecological processes at scales of organization from the individual to the ecosystem.

Organisms are the source of additional patchiness. And again, some of the patterns may be fractal-like. For example, most deserts can be characterized as a mosaic of two patch types: vegetation and bare soil. Figure 3.3 shows the pattern of perennial vegetative cover on Brown's long-term study site in the Chihuahuan desert. Analysis of these patches using the box-counting method reveals a fractal-like distribution, similar to that for coastlines, with the area of occupied grid cells increasing as larger cells are used to characterize patches (Figure 3.3B, inset). This relationship is traditionally presented as a negative relationship between the number of cells occupied with vegetation and the size of the cells (Figure 3.3B). In addition to broad taxonomic groups like plants, individual species exhibit similar patterns of presence and absence (e.g., Virkkala 1993; Kunin 1998; Lennon et al. 2002; Olff and Ritchie 2002; Green et al. 2003).

Many other power laws are related to plant and animal body size. They are the subject of the large literature on biological allometry (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown and West 2000; Brown et al. 2002). Within functional groups, such as trees in a forest or animals in a habitat, total population density or number of individuals per unit area, N, often appears to scale with body mass, M, as

$$N = N_0 M^{-3/4}, \tag{3.4}$$

a power-law scaling relation that appears to reflect the scaling of whole-organism metabolic rate and hence per-individual resource requirements (e.g., Damuth 1981; Enquist et al. 1998; Li 2002). In pelagic lake and marine ecosystems, there are somewhat different scaling relations that hold across an enormous range of organisms, from unicellular phytoplankton and prokaryotes to the largest fish and whales. Total density scales as M^{-1}, so that total biomass is invariant or scales as M^0 (e.g., Sheldon et al. 1972; Cyr et al. 1997; Kerr and Dickie 2001). It is interesting to note that the scaling of

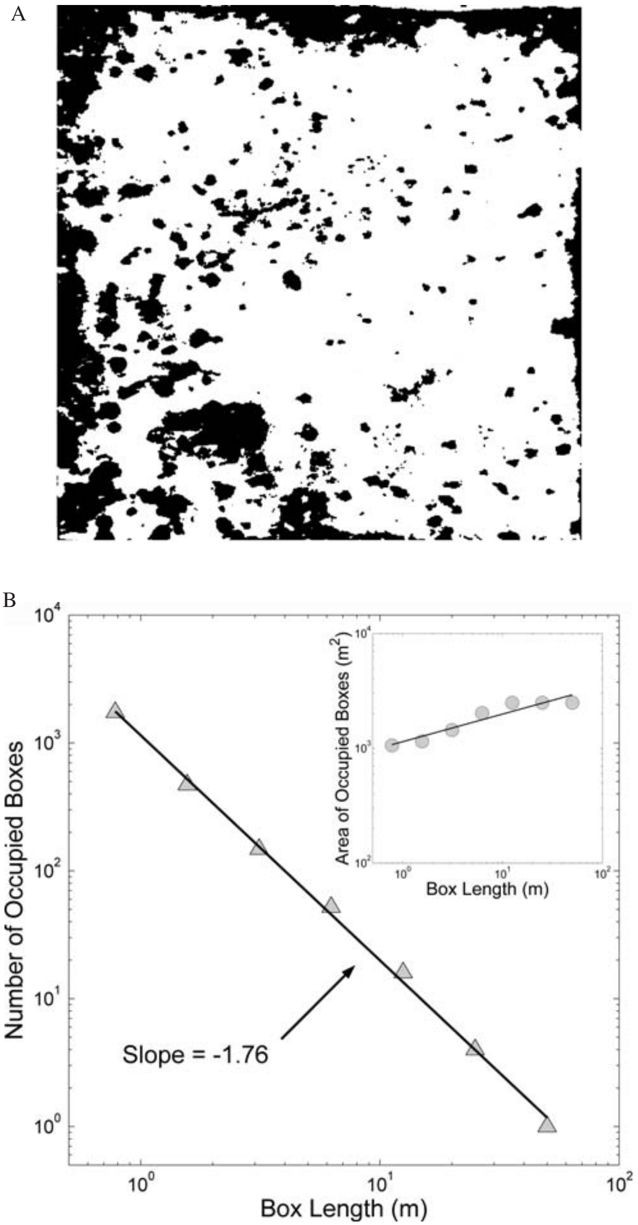

FIGURE 3.3. Fractal-like pattern of vegetation patchiness at Brown's long-term research site near Portal, AZ. (A) Map of the vegetation cover (black) on a 50 × 50 m plot. (B) Fractal dimension plot, using the box-counting method, of the number of grid cells on the map occupied by vegetation as a function of the length of the edge of a grid cell. Insert shows the same data plotted in a different way, with the total area of occupied grid cells replacing the number of occupied grid cells.

population density could be considered to be a form of frequency-magnitude scaling. These scaling relations mean that organisms are distributed on the landscape with predictable relationships among density, size, and other correlated variables, such as nearest neighbor distance, stem diameter, canopy height and radius, and water, mineral, and energy flux for plants; and nearest neighbor distance, home range size, movement distance, food requirement, and excretion rate for animals. So, to the extent that organisms constitute patchy environments or resources for other organisms, these scaling relations can be used to predict important characteristics of patch structure and dynamics. In addition, these patterns (e.g., home range size $\propto M^1$) suggest that organisms of different size interact with the environment at different scales (e.g., Morse et al. 1985). This should have important consequences for the scales at which heterogeneity impacts organisms.

We have listed but a few of the possible patchy distributions in ecological systems. It is clearly important to begin to catalogue and understand how other attributes of the geological and biological templates scale and to integrate these patterns into ecological research. For example, what are the relations among perimeter, area, and elevation for islands or comparable dimensions of perimeter, area, volume, and depth for lakes? What is the nature of the distribution of distinctive soil patches, such as serpentine or gypsum, and, if they can be described as fractal-like, how do the normalization constants and scaling exponents change across different geological settings? Some of the answers to these questions are probably available in the geological literature, but they have not generally been picked up and used by ecosystem and landscape ecologists.

Another important question is how these varied fractal-like patterns are related to one another. We stated earlier that there are different fractal dimensions that characterize different features of patchy environments. These different fractal dimensions each appear to describe multiple phenomena. It may be that the components of this diverse assemblage of self-similar relationships are connected to one another in much the same way as has recently been shown for hydrologic networks and biological allometries (see "Networks," below; some relationships between dimensions are understood, e.g., Hastings and Sugihara 1993). If this is true, then the confusing labyrinth of fractal landscape metrics might condense to a small number of important underlying variables.

Networks

Our final pattern is the network, which we define as a system of connected, hierarchically branching elements of structure and function. Networks represent combinations of both relatively continuous and discrete variation. Along the direction of flow, when measured at coarse scales, the variation appears relatively continuous. For example, the variation in stream properties from headwaters to mouth are the basis of the river continuum concept (Vannote et al. 1980). On the other hand, when viewed at a smaller scale, the variation is more discrete. So, for example, the properties of a stream change abruptly when two similar-sized branches join.

The application of networks to heterogeneity is twofold. First, the properties of a network determine the values of important parameters within that network. For example, the width, depth, and nutrient loading of a stream network depend on the order of the stream (Rodriguez-Iturbe and Rinaldo 1997). This creates predictable heterogeneity for processes and organisms operating within the network. Second, networks often flow over non-network templates (e.g., streams over land), and in doing so they create a particular distribution of the materials that they are fluxing across the landscape (water, nutrients, sediments, etc.). It is believed that many natural networks are produced by some process of self-organization, and many of them seem to be fractal-like, at least over some range of scales (Rodriguez-Iturbe and Rinaldo 1997). Given this self-similarity we can begin to describe patterns in the network quantitatively.

Some of these natural networks are abiotic. The classic examples are streams and related networks such as river deltas, desert alluvial fans, and tidal drains. These branched hierarchies are formed by the physical forces generated by flowing water, and the resulting continuous reconfiguration of the channel due to erosion of substrates and deposition of sediments during both extreme flood events and more usual flows. Geologists and hydrologists have studied stream networks and their self-organizational formation. The famous Horton-Strahler system of characterizing the order of branches was developed for streams (Horton 1945; Strahler 1957). This system describes the hierarchy of the network and can be illustrated most simply by thinking about pruning the source (outermost) branches of the stream network sequentially. First prune the source branches. By definition, these are the first-order branches. Using the pruned network, prune the terminal branches again. These branches become second order and so on until only the trunk remains (Melton 1959).

Ordered in this way, networks exhibit fractal-like properties. Examples include Horton's ratios (Horton 1945)

$$\begin{aligned} n_{w+1}/n_w &= R_n \\ l_{w+1}/l_w &= R_l \\ a_{w+1}/a_w &= R_a, \end{aligned} \tag{3.5}$$

where n_w is the number of streams of order w, l_w is the average length of those streams, a_w is the average area of those streams, and R_n, R_l, and R_a are constant ratios between those values at order $w + 1$ and order w (invariant ratios across hierarchical levels are characteristic of self-similar patterns). Another example is Hack's law (Hack 1957),

$$L \propto A^h, \tag{3.6}$$

which characterizes the relation between the length of the main channel in a drainage basin, L, and the area of that basin upstream, A, in terms of a scaling exponent, h. For a visual description and a complete list of stream network scaling relationships, see Dodds and Rothman (1999).

The numerous patterns in streams have recently been shown to be related to one another, thus simplifying the description of multiple empirical scaling relations to two simple quantitative descriptors: the fractal dimension of individual streams (D similar to that of the coastline example) and the ratio of the logarithms of R_l and R_n (Dodds and Rothman 1999). These patterns may be explained mechanistically based on the stream networks minimizing their global energy expenditure (Rodriguez-Iturbe and Rinaldo 1997; Rinaldo et al. 1998), providing a more process-oriented explanation for these observed patterns. For an in-depth treatment of river network scaling, see Rodriguez-Iturbe and Rinaldo (1997) and references above.

Organisms also form hierarchically branching networks. The most obvious are the fractal-like architectures of both the roots and shoots of most land plants (Morse et al. 1985; Tatsumi et al. 1989; Fitter and Strickland 1992; Neilson et al. 1997). Structural and functional properties of some of these networks are described by scaling laws, which have been used to characterize their self-similar organization and the relationships between structural and functional variables. Most of the work to date has focused on plant architecture and vascular systems (e.g., McMahon and Kronauer 1976; Niklas 1994; Neilson et al. 1997; West et al. 1997, 1999; Horn 2000). These networks form fractal-like habitat for terrestrial and subterranean organisms that use plants (e.g., Morse et al. 1985).

Why a Quantitative Framework?

So far, we have suggested that environmental variability can be divided into three major categories, and that each of them can, at least in some cases, be described using a relatively simple quantitative framework. One great advantage of a having such a quantitative framework for studying heterogeneity is that these characterizations can be incorporated into models for ecological processes (e.g., Ludwig et al. 2000). Consequently, it should often be possible not only to predict whether heterogeneity is important for the question being studied, but also to understand precisely how the organization of spatial variation affects ecological processes. This provides the potential to move beyond purely correlative studies to understand the operation of different processes at different spatial scales (Milne 1991a). It should be useful in determining which habitat variables, and their associated patterns of heterogeneity, are important for a particular process. Such a framework may eventually answer a question that we have been asked to address: At what scale does heterogeneity become unimportant (i.e., when can it be ignored)? The answer will surely be that this scale depends on the question of interest, the type of heterogeneity considered, and the inherent scale of the units and processes. Gradients, patches, and networks at the scale of micrometers are important for microbes but probably unimportant for elephants and whales (e.g., Addicott et al. 1987; With and Crist 1996). The way to define this scale for a particular process may be through a combination of quantitative modeling and empirical analysis. Determining this scale is simply a special case of using these descriptors of heterogeneity to make quantitative predictions about their effects on ecological systems. There are several good examples of these quantifications being used to model and understand ecological processes.

Examples

An example of the use of a quantified gradient for studying patterns of species coexistence is provided by Yamamura (1976), who used a theoretical gradient to explore patterns of the spatial distribution of plant communities. He showed that by introducing simple continuous gradients into basic population dynamics models (through the influence of spatial position on the growth rate and competition parameters), he could generate patterns of species distributions reflecting different combinations of competitive exclusions and coexistence. Studies of diversity maintenance based on spatial and/or temporal variability in environmental conditions have benefited from taking a similar quantitative approach (e.g., Chesson 2000). Patterns of compositional change along a gradient can be explained by combining the relatively continuous change in one or more key environmental variables with the impacts of those changes on important population variables for the species involved. An example of this is provided by Arris and Eagleson (1994), who used the response of tree species productivity to changes in the length of the growing season, photosynthetic capacity, potential evapotranspiration, and soil moisture availability along a latitudinal gradient to predict the location of the ecotone transition between boreal and deciduous forests in the eastern United States. By quantifying the gradients, they were able to show that through their influence on the rates of production, the gradients should lead to a transition in the dominant forest type at approximately the latitude observed. This suggests that the broad-scale heterogeneity in the environment (i.e., the gradients) produced the ecotone pattern through influences of abiotic environmental variables on net primary production.

An excellent example of the use of the fractal-like nature of patches to describe model ecological systems is provided by Ritchie and Olff (1999). They suggest that due to the fractal-like clustering of resources (Milne 1992, 1997), herbivores of different sizes will see the patchiness of landscapes differently and thus respond differently to the patchy pattern of resource. Small, dense patches can be used by small species, whereas large, less concentrated patches are more appropriate for large species. Because resources are patchily distributed and the different patches are used differently by different body sizes, these relationships can be used to predict body size distributions of coexisting herbivorous mammals and to help understand how variation in body size facilitates the maintenance of biodiversity (Hutchinson 1959; Hutchinson and MacArthur 1959). The authors use the observed fractal-like nature of resource distributions to make specific quantitative predictions about the frequency distribution of body sizes and the number of species that can be supported by a habitat. This example illustrates how a quantification of heterogeneity can provide explicit predictions about its impacts on ecological systems.

We are less familiar with the use of networks for characterizing ecological heterogeneity. They have proved useful in understanding and quantifying the effects of resource distribution networks on metabolic rates of animals and plants, and these effects cascade through ecological systems, having effects at scales from individuals to entire ecosystems (Enquist et al. 2003; Brown et al. 2004). One area where networks will likely prove important for characterizing heterogeneity is in aquatic and riparian ecology. The increasingly well quantified and mechanistically understood scaling relations for stream networks have many obvious ecological implications.

One effort in aquatic ecology is to understand how stream properties, and hence ecological patterns and processes, vary from source streams to the main channel. Geologists and hydrologists have developed a solid understanding of abiotic variation as a function of stream order through a quantitative approach that uses scaling laws to characterize the hierarchical self-similarity of river networks (see "Networks," above). This approach does not explain all of the important patterns, but it does provide robust, quantitative characterizations of a suite of important variables (e.g., flow rate, stream length and width, etc.), thereby providing a first-order model of abiotic heterogeneity from headwaters to main channels. The next challenge for stream ecologists is to begin to understand how these abiotic patterns influence biotic processes. The river continuum concept (Vannote et al. 1980) and the flood pulse concept (Junk et al. 1989) attempt implicitly to understand how the regular abiotic scaling properties of streams affect the ecology of riverine and riparian ecosystems. These concepts would seemingly benefit from the explicit incorporation of the quantitative framework describing the changes in the abiotic template as a function of stream order.

Conclusions

The emphasis of this book and of the Cary Conference that spawned it is on the extent to which, and the mechanisms by which, spatial heterogeneity affects ecosystem function. We define ecosystem function as the fluxes and transformations of energy, materials, and information (and of organisms containing those currencies) that occur within and between ecosystems and other ecological subsystems. These flows and transformations are inherently heterogeneous. They occur in specific places on the landscape, and they are driven by abiotic and biotic processes that are heterogeneously distributed. These fluxes and transformations are also inherently heterogeneous at all spatial scales. Some processes, such as biotic weathering of rock surfaces and microbial uptake of organic compounds, occur at the molecular level of organization and at the scale of nanometers to micrometers. Other processes, such as the circulation of the atmosphere and oceans, occur at regional to global levels of organization and on the scale of 10^n kilometers. The structure and dynamics of these flows are governed largely by the geometric, physical, and biological characteristics of the spatial template.

An essential task for understanding how habitat heterogeneity affects ecosystem processes is to characterize the patterns of heterogeneity and to understand the processes underlying those patterns. A useful framework is to recognize that patterns of environmental variability across landscapes can generally be separated into three major categories: gradients, patches, and networks. Each of these categories can often be described using a relatively simple quantitative framework. By incorporating these quantifications into the study of biological systems, it should be possible to predict not only if heterogeneity will have an effect on ecosystem function, but also precisely what the nature and magnitude of the effect should be. Progress toward increased understanding, precision, and predictability will also benefit from incorporating advances from other disciplines, including physics, chemistry, biology, and the earth sciences, on the laws, principles, and factors that generate the gradients, patches, and networks and that govern the flows and transformations of energy, materials, information, and organisms within and between these heterogeneous landscape elements.

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