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Challenges in Understanding the Functions of Ecological Heterogeneity

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Abstract

Ecological systems usually are heterogeneous, and this heterogeneity has important functional consequences. Nevertheless, it is not always necessary for ecologists to explicitly include this heterogeneity in their studies and models of ecological systems. Heterogeneity may be safely ignored if its grain size is much smaller than the spatial extent over which measurements are integrated or much larger than the spatial extent of the study area. Heterogeneity may be functionally unimportant if the vectors connecting patches are small or slow relative to the time span of the study or if the system is governed by processes with linear dynamics. Further, the heterogeneity expressed by some ecological systems may be amenable to analysis using simplified models. Finally, it may not be efficient to include heterogeneity in study designs or models, even if including heterogeneity would improve the study performance. Despite these considerations, ecologists will need to address heterogeneity explicitly in many cases to achieve a satisfactory understanding of ecosystem functioning, particularly for regional to global scales.

Several other general issues concerning the functional consequences of heterogeneity arose at the Tenth Cary Conference. Human-caused heterogeneity probably has different characteristics and functional consequences than heterogeneity arising from other sources and therefore needs special attention. Models of heterogeneity developed in other disciplines that deal with heterogeneous, reactive systems (e.g., economics) may have application in ecology. At least some heterogeneous ecological systems appear to evolve in predictable ways because the functional consequences of heterogeneity feed back onto the structure of the system; these feedbacks need further study.

Introduction

All models are wrong, but some are useful.
—G.E.P. Box

The subject of ecological heterogeneity encompasses a diverse collection of scientific, management, and policy issues, many of which are important to ecology and difficult to address. The diversity of issues and rapid pace of conceptual and empirical progress on ecological heterogeneity make it difficult to summarize the current state of the field, and I will not try to provide such a summary based on the Tenth Cary Conference. Instead, I will offer brief impressions of some interesting issues that arose at the conference, lay out research challenges, and, where possible, suggest directions in which answers might lie.

A Model of Heterogeneity

It may be useful to introduce a simple conceptual model of a functionally heterogeneous system to provide a context for a discussion of the issues that arose at the conference. Consider a system (shown as two-dimensional in Figure 20.1 but more often three-dimensional in ecological contexts) consisting of a series of patches (Figure 20.1A) with different functional attributes (such as denitrification rate, prey abundance, leaf area index,

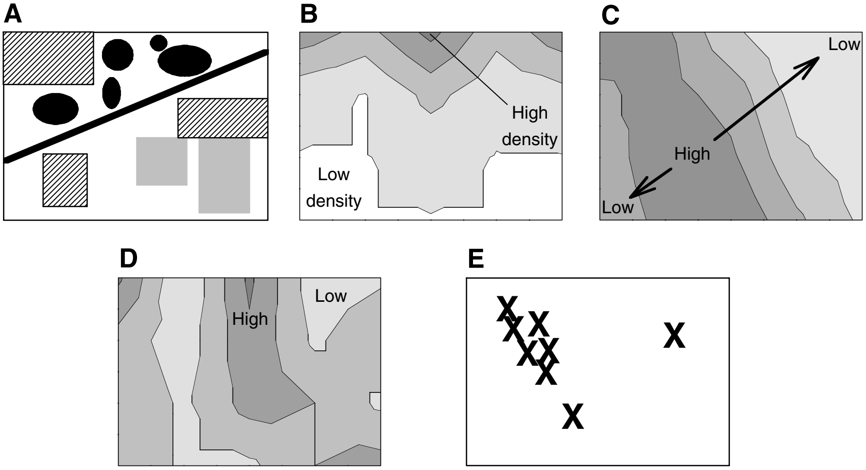

FIGURE 20.1. General model of a heterogeneous system, emphasizing five aspects of heterogeneity occurring in the same hypothetical geographical area. (A) Patch structure, (B) vector mass-density, (C) potential field, (D) resistance, (E) location of externally driven disturbances.

permeability, etc.). The system might be conceived of as continuous rather than discrete, although discrete models are more often used by ecologists and are easier to describe by simple drawings.

The patches are connected by vectors that move across this heterogeneous landscape. The vectors carry reactive objects (material, energy, information) across the landscape, where these objects interact differentially with the different patches. Ecological systems contain many kinds of vectors; familiar examples include wind, the flow of water, diffusion, and the movement of animals. Reiners (this volume; see also Reiners and Dreise 2001) described and categorized the kinds of vectors that are important in ecological systems. The flux rate (direction and magnitude) of a vector is jointly determined by the mass density of the vector (e.g., the amount of water, the density of animals moving nutrients; Figure 20.1B), differences in the potential field that drives vector movement (e.g., the movement of water downhill or down hydraulic gradients; the movement of air down pressure gradients; the movement of animals from areas of low food abundance to high; Figure 20.1C), and resistance to vector movement through the various patches (Figure 20.10). Often, more than one substance (e.g., water, nitrogen, and organic matter) or vector (water and animals) needs to be considered simultaneously to satisfactorily understand the process or function of interest (Fisher and Welter this volume).

Finally, the system may be affected by forces arising from outside the system (e.g., lightning strikes, inputs of water from streams and precipitation) whose influence typically is spatially heterogeneous (Figure 20.1E).

This model thus identifies five essential components of heterogeneity: (1) the patch structure, (2) the spatial pattern of vector mass-density, (3) the potential field, (4) the spatial pattern of resistance to the vector, and (5) the spatial distribution of external influences on the system. Typically, ecological systems contain heterogeneity over a very wide range of spatial scales, so that maps of heterogeneity at any given scale mask heterogeneity that occurs at finer scales. It may be a daunting task to describe adequately all of these components of heterogeneity and then construct a model that mimics the behavior of the system at one time. But of course, we often are interested in the behavior of the system over a period of time, not just at a single time. Therefore, we must add to our already complicated conceptual model the possibility that the function of the system feeds back to change the patch structure, vector mass, potential field, and resistance over time. Likewise, external influences on the system (such as disturbances) may be affected by the patch structure. Explicit consideration of heterogeneity presents three formidable difficulties: (1) conceptualizing such a complicated system, (2) gathering the spatially referenced data to describe adequately the system, and (3) building and evaluating models of the function of dynamic, heterogeneous systems.

Of course, there are alternative ways to conceptualize heterogeneous systems (e.g., Reiners and Dreise 2001). It is not necessary to accept the particular conceptualization of Figure 20.1, though, to appreciate the difficulty of conceptualizing, describing, understanding, and modeling the behavior of temporally dynamic, heterogeneous, reactive systems like ecosystems.

When Does Heterogeneity Matter?

The central question of the conference was "When and how does spatial heterogeneity matter for ecosystem processes and functions?" This question can be interpreted in two ways. The first interpretation might be phrased as, "When and how does heterogeneity affect processes and functions in real ecosystems?" Briefly, whether considered in the abstract (Strayer et al. 2003) or through empirical studies (below, and elsewhere in this volume), heterogeneity nearly always affects processes and functions in ecosystems, and in diverse ways. All five aspects of heterogeneity identified in Figure 20.1 may affect ecosystem function, although only two have received much attention. There are many compelling examples showing that the patch structure of the ecological system may have important consequences for its function. Turestky et al. (this volume) showed that different parts of the boreal ecosystem accumulate carbon at very different rates, and even transient patchiness in the apparently homogeneous open ocean may substantially increase nitrogen uptake by phytoplankton and reduce phytoplankton-zooplankton encounters (Mahadevan this volume). Many other examples presented at the conference (e.g., Fisher and Welter this volume; Tague this volume; Tongway and Ludwig this volume) and elsewhere show that heterogeneity in patch structure often affects ecosystem function. Likewise, the effects of external disturbances may be distributed heterogeneously in ecosystems, either because the disturbance is heterogeneous in occurrence or because it is propagated unevenly through the system. Fires in forests in the western United States are patchy in occurrence and have different ecosystem effects because ignition sources are patchy (e.g., Gosz et al. 1995), because the different parts of the ecosystem are differentially susceptible to the initiation and propagation of wildfires, and because the nature and severity of fire's effects vary across ecosystems (Romme this volume). Presumably, spatial variation in the mass-density of vectors, potential fields, or resistance may affect ecosystem function as well, although these seem not to have been studied much. Regardless of the details, the importance of heterogeneity to ecosystem function is indisputable.

The second interpretation of "When and how does spatial heterogeneity matter for ecosystem processes and functions?" is "When should we explicitly consider heterogeneity when we study, model, or manage processes and functions of ecosystems?" If we accept that heterogeneity nearly always affects the functioning of ecological systems, it might seem obvious that we should nearly always explicitly incorporate that heterogeneity in our studies and models. However, as we have seen, it may be exceedingly difficult to incorporate fully the multiple heterogeneities that occur in ecological systems into our research. Therefore, we must carefully consider when it is

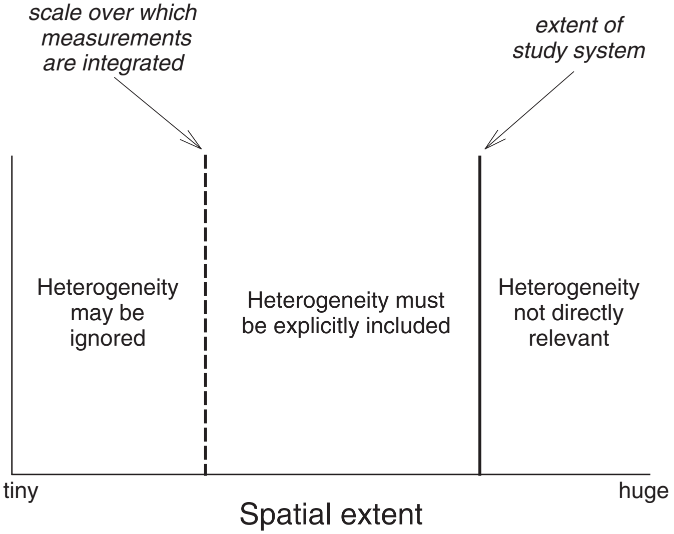

FIGURE 20.2. The relative spatial scales of ecological heterogeneity, measurements, and the extent of the study area determine whether spatially explicit studies or models are required. See text for discussion.

really helpful or necessary to explicitly include heterogeneity in our studies of ecological systems. Given the ubiquity and importance of functional heterogeneity in ecological systems, it probably is simplest to begin by listing the conditions under which it is *not* helpful or necessary to explicitly consider heterogeneity.

First, heterogeneity may safely be ignored if its grain size (or dominant length scale, Mahadevan this volume) is much smaller than the spatial extent over which measurements are integrated or much larger than the spatial extent of the study area (Figure 20.2). This recommendation follows the conclusion of hierarchy theorists (e.g., O'Neill et al. 1986) that processes operating at levels higher than the scale of observations change slowly and may be treated as constants, whereas processes operating at a level lower than the scale of observation change so rapidly that they may be treated as averages. All ecological measurements integrate over some spatial (and temporal) scale. The net functional effects of all heterogeneity finer than this scale of integration are implicitly included in any measurement we make and need not be further considered in our analysis of the system. Thus, a typical pH measurement measures the average pH in several cubic centimeters of water, a free-water estimate of stream metabolism integrates the net functional effects of a large area (perhaps 10^2–10^4 m^2) of patchy streambed, and gas flux measurements from a soil chamber integrate the function of the heterogeneous system enclosed in the chamber. As long as our focus is on the stream ecosystem rather than the patches it contains, free-water productivity measurements allow us to ignore the fine-scale interactions that occur among the various parts of the streambed and together determine the productivity of the stream ecosystem. Of course, a scientist may choose for various reasons to study these fine-scale interactions (by using finer-scale techniques that integrate over smaller spatial scales), but it is not necessary to engage in reflexive reductionism by including finer and finer heterogeneity merely because we know it exists.

The scale of measurements may deliberately be chosen to minimize problems in dealing with heterogeneity. Consider the problem of estimating nutrient loss from a patchy forest. We could measure nutrient losses from a series of lysimeters placed in the different habitats of the forest and then try to integrate these measurements by studying the interactions among patches that govern nutrient cycling. Alternatively, we could measure nutrient losses at a weir on a stream that drains a large section of forest. This latter measurement already implicitly includes the results of interactions among patches and probably would provide simpler, less expensive, and more accurate estimates of nutrient losses from the forest than the lysimeter study.

Any influence of heterogeneity much larger than the study area will be expressed through external inputs to the study system and need not be considered explicitly. Again, the extent of the study area may deliberately be chosen to minimize problems with heterogeneity. Indeed, many classic studies of ecosystem function were based on study areas deliberately defined to exclude large-scale heterogeneity (e.g., lakes, relatively homogeneous watersheds).

It is no longer always possible for ecologists to choose relatively small, homogeneous study areas, though. Regional- and global-scale management issues have increasingly forced ecologists to work on large, heterogeneous study areas (e.g., Possingham et al. this volume), thereby moving the solid line in Figure 20.2 to the right. At the same time, the rapid rise of landscape ecology (Turner et al. 2001) has provided the intellectual impetus to understand large, heterogeneous landscapes. Indeed, the move by ecologists to embrace regional and global problems has probably been one of the important motivations for bringing the subject of the functional consequences of heterogeneity to the fore.

Second, we may safely disregard heterogeneity in our studies if that heterogeneity truly has small effects on ecosystem function. There are at least three classes of circumstances in which heterogeneity is most likely to have small functional effects. If the vectors connecting patches are small or slow (relative to the time span of the study), then the mosaic or quasidistributed approach described by Turner and Chapin (this volume) and Tague (this volume) may be adequate, especially over short timescales. Note that vectors will be small if the contrast across patches is small (or equivalently, if gradients in a continuous system are short or shallow). If the system is governed by nearly linear dynamics, then models based on the mean values of variables (rather than the spatial distribution of variables) will adequately predict the function of the system (Strayer et al. 2003). This result follows because the mean of a linear function evaluated at a series of values of independent variables gives the same value as that function evaluated at the mean values of the independent variables. Nevertheless, truly linear ecological systems probably are rare, in part because interactions among controlling variables produce nonlinearities. Finally, we can disregard the heterogeneity we measure across patches if it has no functional significance. That is, heterogeneity in sulfate in a strongly light-limited wetland will probably have little effect on primary production even if we can readily measure variations in sulfate concentrations. Kolasa and Rollo (1990) made a similar distinction between functional and what we might call measurable but functionally neutral heterogeneity.

Third, there are special cases in which a greatly reduced model of heterogeneity may be adequate to capture the behavior of a functionally heterogeneous system. For example, if a single patch or element of the landscape strongly dominates system function, then it may be permissible to study only the properties of this master element and ignore the heterogeneity elsewhere in the system. If we are studying vertical water movement through a layered aquifer and a layer of clay has hydraulic conductivity several orders of magnitude lower than that of the other materials in the aquifer, we can concentrate our attention on the properties of that clay layer and disregard heterogeneity above that layer. Systems with regular heterogeneity (which are discussed below in more detail) may also be amenable to simplified approaches.

Fourth, even if the explicit consideration of heterogeneity improves our abilities to predict or understand the function of an ecological system, it may not be *efficient* to explicitly include that heterogeneity in our studies. It may not be parsimonious to add a lot of detailed information describing the heterogeneity of a system if that information improves only slightly our understanding or predictive power. In cases where models are fitted to data (i.e., the number of data points is much larger than the number of parameters), information theoretic criteria can be used formally to choose the most parsimonious of several competing models (Burnham and Anderson 2002). Smith (this volume) described the application of this approach to epidemiological models. Such an approach can help ecologists in some circumstances to decide whether it is efficient to include heterogeneity.

In cases where models cannot be statistically fitted, increasing model complexity to account for heterogeneity may introduce serious problems with error propagation and model selection. It has long been recognized that errors associated with parameterizing a complex model may outweigh those associated using aggregated parameter estimates (O'Neill 1973; Rastetter et al. 1992). Further, as the number of variables rises, the number of possible (or even likely) functional connections among variables rises sharply. The investigator must then choose among a large number of competing model structures by intuition or by somehow testing the various parts of the model. Thus, it may be preferable to accept a simple model, even if it is biased and incomplete, than to build a complicated model whose structure and accuracy must either be accepted on faith or subjected to extensive testing [see further debate by DeAngelis (2003) and Hakanson (2003) about whether complex models are prone to error amplification].

Finally, it may not be efficient from a cost/benefit perspective to explicitly include heterogeneity, even if its inclusion undeniably improves understanding or predictive power (Figure 20.3). In science, we often think our goal is to maximize predictive power, but other goals probably are closer to our actual needs. For instance, our goal may be to achieve some fixed level of predictive power (say the coefficient of variation of a prediction <20%) at minimum cost (lines P_1 and P_2 in Figure 20.3). Alternatively, we may want to maximize predictive power for a given fixed cost (lines C_3 and C_4 in Figure 20.3). In both of these cases, it may be desirable to disregard heterogeneity in the frequent situations in which simpler approaches initially cost less per unit understanding than explicitly heterogeneous approaches (Figure 20.3), especially if our predictive needs or available budgets are modest (lines P_1 and C_3). Many ecologists believe that spatially explicit approaches will ultimately allow us to achieve greater understanding by giving us the mechanistic understanding needed to extrapolate across sites and scales (Turner and Chapin this volume), so if our predictive needs are great or if we have a large budget, spatially explicit approaches may be preferable.

Despite these considerations, which allow ecologists to ignore heterogeneity in many studies of ecological function, it seems clear that it will be necessary to address heterogeneity explicitly in many cases if we are to achieve a satisfactory understanding of ecosystem functioning. This is particularly true for regional to global studies, in which the grain size of functionally important heterogeneity is larger than the scale of measurement but smaller than the size of the study area. The increasing importance of understanding the functioning of these large ecosystems means that ecologists will have to learn to incorporate heterogeneity into their studies and models of ecosystems, however knotty the problem.

How Do We Best Include Heterogeneity in Studies of Ecosystem Function?

Reaching the conclusion that heterogeneity often will need to be included explicitly in studies and models of ecosystem function immediately raises the question of how best to do so. I expect that a large effort will be devoted to answering this question in the near future. Already at the conference there were discussions of technical issues such as the use of discrete *versus* continuous models (Turner and Chapin this volume), the use of network

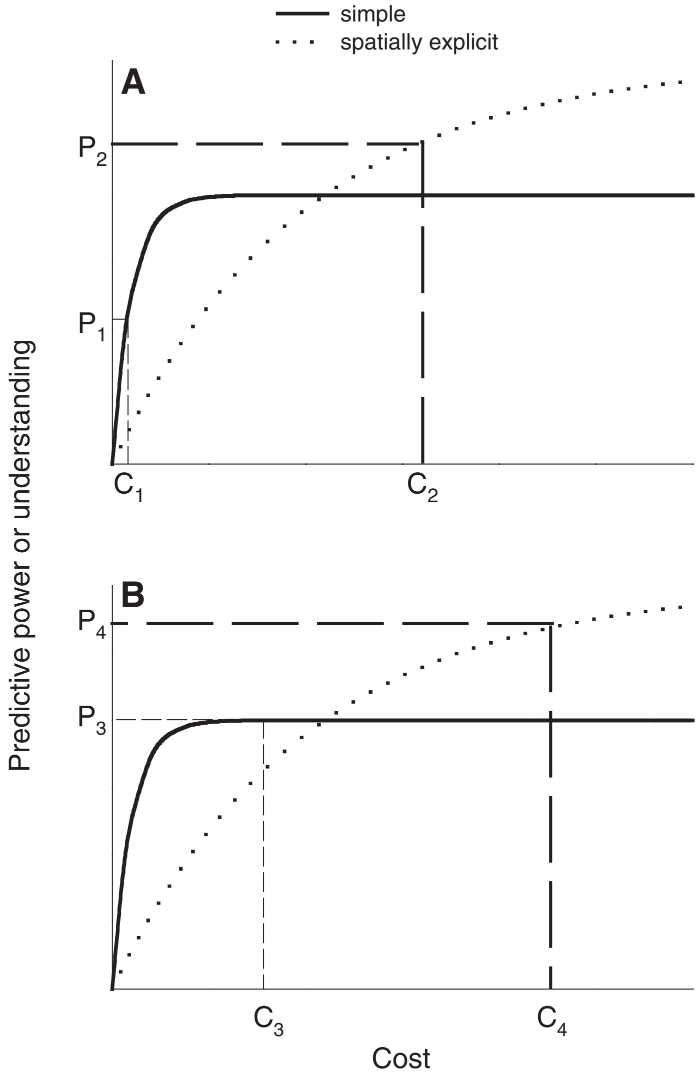

FIGURE 20.3. Hypothetical cost-benefit curves for simple and spatially explicit approaches. (A) Minimizing cost to achieve some predetermined level of predictive power in cases where predictive needs are modest (P_1) or stringent (P_2). (B) Maximizing predictive power for a given fixed cost where the budget is small (C_3) or large (C_4). If available funds are low (C_3) or requirements for understanding are modest (P_1), then simple approaches will be preferable. If more funds are available (C_4) or if more complete understanding is needed (P_2), the spatially explicit approach will be preferable.

models (Swanson and Jones 2003), the adequacy of mosaic *versus* interactive models (Fisher and Welter this volume; Tague this volume; Turner and Chapin this volume), and the best mathematical and statistical approaches to describe and analyze heterogeneity (Fortin et al. 2003; Mahadevan this volume; Possingham et al. this volume; Reiners this volume; Reiners and Dreise 2001; Smith this volume; Tague this volume). Here, I will raise just a few general issues about approaches to understanding the functional consequences of ecological heterogeneity.

Careful selection of study systems can speed up progress in understanding the functional consequences of ecological heterogeneity. The heterogeneity contained in many ecological systems is more regular (and therefore simpler to study) than that shown in Figure 20.1. For example, ecological heterogeneity often is *directional*, in which conditions change monotonically across the study area (Figure 20.4); *periodic*, in which the units of heterogeneity are predictably repeated; or *fractal* (Brown and White this volume). All of these kinds of regular heterogeneity are common in nature. Soil catenas and elevational gradients are familiar examples of directional heterogeneity; sediment waves and the kind of patterned vegetation described by Tongway and Ludwig (this volume), Aguiar and Sala (1999), and Armesto et al. (2003) represent periodic heterogeneity; and forest patches, Minnesota lakes, and shrub patches in New Mexico have fractal-like properties (Brown and White this volume). Systems can contain more than one kind of regular heterogeneity: streams combine the periodic heterogeneity of the repeated riffle-pool sequence with the directional heterogeneity of headwaters-to-mouth succession. The ability to detect and describe regularity in heterogeneity depends on the study extent and grain; if the spatial components are large, for example, the regularity will not be detected unless the study area is very large.

It should be much easier to model and design studies of systems with regular heterogeneity than those with irregular heterogeneity. As Tongway and Ludwig (this volume) showed, studies of relatively simple, regularly heterogeneous systems can give rise to general hypotheses about heterogeneity that can be extended to or tested in other systems.

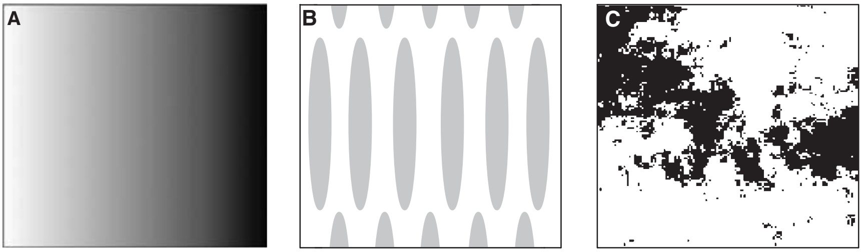

FIGURE 20.4. Examples of regular heterogeneity. (A) Directional heterogeneity, (B) periodic heterogeneity, (C) fractal heterogeneity in a simulated landscape (from Hargrove et al. 2002).

Also, it will be useful to choose study systems whose actual integrated function is measurable, so that we can test our models of the functional consequences of heterogeneity. If we do not have an independent measure of the function of the entire heterogeneous system, it will be difficult to assess how well our models work or to compare the performance of competing models. As a result, systems such as watersheds, whose actual integrated function is readily measurable, will continue to be valuable.

There are many kinds of heterogeneous reactive systems other than ecological systems. Scientists working on these nonecological systems have developed models and methods for understanding their systems that may be helpful to ecologists. For example, discussions of the functional implications of economic and cultural heterogeneity in human societies (e.g., Löfgren and Robinson 1999; Sen 2004) are reminiscent of the discussions at the Tenth Cary Conference. The formal models used to analyze this economic heterogeneity (e.g., Löfgren and Robinson 1999; Vargas et al. 1999; Devarajan et al. 2004) may be inspirational to or usable by ecologists. Likewise, chemical engineers (e.g., Smith 1981; Oran and Boris 1987) have developed models to describe the function of solid catalysts, which formally resemble some kinds of ecological boundaries, and their models of multiphase flow may have ecological counterparts. There must be many other examples of disciplines that have to deal quantitatively with the function of heterogeneous systems. In view of the widespread occurrence of heterogeneous, reactive systems outside of ecology, we might ask if there is even such a thing as a separate theory of ecological heterogeneity, as distinguished from a general theory of heterogeneity. If so, what characterizes such a distinctively ecological theory? That is, to what extent must ecologists develop their own body of knowledge about the functional consequences of heterogeneity, as opposed to using or adapting theories from other disciplines or working jointly with scientists from other disciplines to develop and test truly general theories of heterogeneity? I would guess that ecologists and scientists in other disciplines could benefit from closer communication about the functional consequences of heterogeneity.

Does Anthropogenic Heterogeneity Have Distinctive or Strong Functional Consequences?

Human activities are among the many sources of heterogeneity in ecological systems. With the increasing focus on humans as parts of ecosystems, we might ask if anthropogenic heterogeneity has the same functional consequences as heterogeneity arising from other sources or is distinctive in some way. I suggest that anthropogenic heterogeneity may both have different actual consequences for ecosystem functioning and be harder to ignore than heterogeneity arising from other sources, for three reasons.

On one hand, humans often create and maintain sharp boundaries and high-contrast landscapes through heavy subsidies of material and energy. For instance, Band et al. (this volume) noted that lawn watering, leaky pipes, and an intensive drainage network give cities and suburbs high hydrologic contrast, where wet and dry areas may be closely juxtaposed. Such high contrast and steep gradients should lead to strong interactions among patches, one of the key conditions under which heterogeneity has strong functional consequences. On the other hand, humans create nearly impermeable barriers (e.g., highways and dams that block animal movement) or patches that are entirely inhospitable to certain ecological processes (e.g., pavement that supports no primary production or denitrification), which would reduce patch interactions below natural levels. As a result, landscape interactivity may vary over a wider range in human-dominated landscapes than in landscapes without humans.

Management issues involving humans often occur at regional or subregional scales (>100 km^2), so that study areas are necessarily large. This leads to a large range over scales for which heterogeneity must be considered explicitly (Figure 20.2).

Finally, although anthropogenic heterogeneity occurs across a range of spatial scales, it is my impression that humans create a lot of heterogeneity at a scale of 0.1–1000 ha (i.e., housing lots, farm fields, parking lots), and often obliterate heterogeneity at smaller scales (Cumming 2003; Fraterrigo et al. 2005). This scale is larger than the scale of integration of many ecological measurements but smaller than that of many kinds of study areas—just the scale most likely to force us to consider explicitly heterogeneity in our studies. These considerations suggest that ecologists who are interested in the ecological roles of humans will need to consider explicitly heterogeneity more often than other ecologists.

How Do the Functional Consequences of Heterogeneity Feed Back into the Temporal Dynamics of Heterogeneous Systems?

Because the functional consequences of heterogeneity can feed back onto the structure of the ecological system, the structure or function of heterogeneous systems can evolve over time in a predictable way. Such feedbacks could affect any of the five aspects of heterogeneity (Figure 20.1), and in complex ways.

At least some heterogeneous ecological systems do appear to evolve in predictable ways as a result of these feedbacks. For example, Meinders and van Breemen (this volume) described several examples of ecological systems in which strong positive feedbacks result in self-organizing heterogeneity. Thus, interactions between litter quality, soil nutrients, and the nutrient-driven growth and survival of trees may reinforce or alter spatial patterning of tree species in forests of the northeastern United States over time (e.g., Bigelow and Canham 2002). Likewise, patches may move across a landscape in a predictable way. There are many examples of regular patch movement driven by physical forces (e.g., dunes, sediment waves), but ecological interactions may also drive such regular patch movement, as in the case of forested patches moving across the patterned landscape of Fray Jorge (Armesto et al. 2003). Naiman et al. (this volume) showed that interactions between a stream channel and the surrounding riparian forest produce debris jams, which initiate a predictable development of channel form and vegetation. It would be interesting to know how general such cases are and whether there are simple rules for identifying systems whose spatial structure changes predictably over time.

Conclusions

It is apparent even from this brief survey that the subject of ecological heterogeneity encompasses a diverse collection of scientific, management, and policy problems in ecosystem science, some of which are difficult. These problems are likely to become increasingly important in the future, as ecologists strive to address regional- to global-scale problems and incorporate humans into their studies of ecosystem functioning. Ecologists must learn both to develop effective solutions to these difficult problems and to know when to avoid the problem of explicitly including heterogeneity in their studies and models. Presentations at the conference showed that there is a broad front of progress on understanding the importance of ecological heterogeneity to ecosystem functioning, as well as many promising avenues to follow into the future.

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