22 Spatial Heterogeneity: Past, Present, and Future

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Abstract

Explanation and interpretation of spatial heterogeneity in nature have been central concerns in ecology since long before the word *ecosystem* was first defined. As ecological knowledge has developed during the past century, it has become clear that the problems of heterogeneity are diverse and can be studied as a number of component issues; together, the chapters of this book represent a state-of-the-art summary of current understanding. Simplifying assumptions of spatial homogeneity and temporal stability are still used widely in ecological research and will continue to be used for the foreseeable future, but long-term, global understanding requires a multiscale approach in which homogeneity and heterogeneity are parts of one continuum and change never stops. Future priorities for research include dynamic approaches to heterogeneity in complex spatial networks, the search for broad patterns in heterogeneity across spatial scales, and reconciling the goal of environmental sustainability with the fact that we live in a patchy, constantly changing world.

Introduction

A central goal of ecology is to explain the causes and interpret the implications of spatial variability and spatial patterns in nature. Spatial heterogeneity is inevitable and unavoidable at all levels of ecological organization, because no two places on Earth can have exactly the same chemical, physical, and biological environment and no two organisms can occupy exactly the same place at the same time. Although the search for generality and the need to simplify often lead to assumptions of homogeneity in ecological processes or patterns in particular instances or at a particular spatial scale, any global understanding must acknowledge the importance of spatial heterogeneity.

A reassessment of the current state of the art in understanding of spatial heterogeneity, as summarized in the chapters of this book, is both timely and

highly appropriate. As the scale and complexity of human domination of the earth's ecosystems increase, simple models that assume homogeneity over large areas or constant environments over long periods are less and less useful to understanding or management. New techniques and new conceptual models are also being developed at a rapid rate and show great promise for major advances. The aim of this brief chapter is to provide a personal response to the state of the art, as presented at the Tenth Cary Conference on "Ecosystem Function in Heterogeneous Landscapes" (Lovett et al. this volume). The response is organized around four questions that might be asked by a student, a nonspecialist, or an outsider approaching the issues of spatial heterogeneity with the aim of catching up on current knowledge and future directions.

Is a Concern for Spatial Heterogeneity New to Ecology and Ecosystem Science?

Spatial variation and spatial patterns in nature were a dominant concern of early ecologists, but they lacked both the long history of empirical studies and the rich array of conceptual and mathematical models described in this book. This was particularly true in early studies of ecological succession, in which ecologists like Henry Chandler Cowles (1899) tried to explain spatial patterning and temporal change in vegetation as the result of a dynamic interaction among plants, soils, and the physical environment. The classic debate between Gleason and Clements (e.g., Gleason 1926; Clements 1936) was largely about spatial patterns in vegetation and the factors that cause them. Early studies of niche differentiation in both plants and animals also commonly focused on spatial differences in species distributions, often in relation to resource availability; Weaver's (1919) descriptions of rooting patterns in grasses and Grinnell's (1917) studies of bird distributions are examples.

At the ecosystem level, it is true that spatial heterogeneity has often been ignored in practice, at least within the particular ecosystem under study. This occurred despite the fact that Tansley's (1935) original definition of the word *ecosystem* came as a contribution to the same global discussion of vegetation succession and spatial variation that dominated plant ecology in the early twentieth century. The classic "black box" approach to biogeochemistry of ecosystems, in which the difference between inputs and outputs is analyzed as a means of inferring how the whole system works, does not necessarily require recognition of any internal spatial structure (Likens and Bormann 1972). On the other hand, the simple fact that outputs differ from inputs in a "black box" ecosystem model means that ecosystem processes *generate* spatial heterogeneity at the landscape scale. The overwhelming importance of the spatial context in which ecosystems lie led Swanson and Sparks (1990) to define "The Invisible Place" to reflect the fact that what we know about ecosystem function depends strongly on spatial interactions with neighboring systems.