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Spatial Pattern and Ecosystem Function: Reflections on Current Knowledge and Future Directions

JERRY F. FRANKLIN

Abstract

Relationships between spatial patterns and ecosystem function are briefly reviewed with regard to the current state of the science and its application and some important challenges. Ecosystem functions that are affected by heterogeneity include maintenance of species diversity (habitat) as well as material and energy cycles. Structural diversity and spatial heterogeneity play an important role in all of these functions and require increased attention. Spatial pattern or heterogeneity is important to ecosystem function at all spatial scales from centimeters to kilometers, not just the larger scales. The relevance of spatial patterns to ecosystem function, including the statistical patterns and significance of the relationships, depend on the function or parameters chosen and the spatial and temporal scales of interest. As a consequence, few, if any, general principles exist for interpreting the effects of landscape heterogeneity on ecosystem function. For example, heterogeneity does tend to increase the number of niches available and, hence, the diversity of environmental conditions that are present. Whether the effects of this increased diversity are positive or negative depends on the processes or organisms of interest. One important conceptual challenge in studying landscape heterogeneity is to move beyond the classic patch-corridor-matrix model to approaches that incorporate networks and gradients.

Introduction

Spatial patterns—in resources, in populations of organisms, and in structure—play crucial roles in ecosystem functioning. We have known this for a long time, although we often have chosen to ignore the effects of heterogeneity. Indeed, field biologists traditionally have been trained to avoid complex or heterogeneous circumstances in selecting study sites for reasons of simplification and reduced variance. At other times, heterogeneity is present but is not at a relevant spatial scale (Strayer this volume). Despite

the tendency to ignore it, we have known intuitively that heterogeneity is important over a very broad range of spatial scales—not just at the larger, landscape level—and that interpreting the effects of heterogeneity depends largely on the ecosystem processes of interest. This is why heterogeneity is emerging today as a topic of major interest!

My objective here is to provide some general observations on the relationships between spatial heterogeneity and ecosystem function and to identify challenges for scientists and managers in extending the frontiers of this topic. The scientific literature, including papers in this volume, provide a wealth of diverse viewpoints, concepts, and examples. My observations will draw on these sources as well as my own experiences in research on ecosystems and landscapes and the application of this knowledge to management of natural resources. I will also consider the effects of spatial heterogeneity on ecosystem functions at scales smaller than landscapes—such as environmental and structural heterogeneity within forest stands.

In lecturing students and general audiences, I generally find that most important general ecological concepts are so obvious in retrospect as to appear trivial—akin to such profound discoveries as "water runs downhill" (except when it doesn't, of course). Consequently, I always feel a bit like the village idiot when attempting generalizations about ecological topics, such as relationships between spatial heterogeneity and ecosystem function. Note that these represent the viewpoint of a forest ecologist who has learned such profound things during his career as:

- All forest patches are not created equal (as habitat or anything else), and much of the inequality is related to structural, including spatial, complexity;
- Dead trees and down boles have important ecological functions;
- Forests and streams are highly integrated; and
- Landscape (larger spatial scale) perspectives are imperative!

So, at risk of appearing simplistic, my commentary follows.

General Observations

Habitat Is an Ecosystem Function and Structure as Its Measure

I want to begin by commending ecosystem scientists that consider "maintenance of species diversity" an ecosystem function on a par with more traditional functions, such as material cycles (Lovett et al. 2005). This is an important extension of the list of recognized ecosystem functions, one not yet adopted by many ecosystem scientists—traditionally generally limiting ecosystem functions to the nature of and controls on energy and material cycles. Yet, much of the "ecosystem management" underway today is focused