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Causes and Consequences of Spatial Heterogeneity in Ecosystem Function

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Abstract

Understanding the causes and consequences of spatial heterogeneity in ecosystem function represents a frontier in both ecosystem and landscape ecology. Ecology lacks a theory of ecosystem function that is spatially explicit, and there are few empirical studies from which to infer general conclusions. We present an organizing framework that clarifies consideration of ecosystem processes in heterogeneous landscapes; consider when spatial heterogeneity is important; discuss methods for incorporating spatial heterogeneity in ecosystem function; and identify challenges and opportunities for progress. Two general classes of ecosystem processes are distinguished. *Point processes* represent rates measured at a particular location; lateral transfers are assumed to be small relative to the measured response and are ignored. Spatial heterogeneity is important for point processes when (1) the average rate must be determined over an area that is spatially heterogeneous or (2) understanding or predicting the spatial pattern of process rates is an objective, for example, to identify areas of high or low rates, or to quantify the spatial pattern or scale of variability in rates. *Lateral transfers* are flows of materials, energy, or information from one location to another represented in a two-dimensional space. Spatial heterogeneity may be important for understanding lateral transfers when (1) the pattern of heterogeneity influences net lateral transfer and potentially the behavior of the whole system, (2) the spatial heterogeneity itself produces lateral transfers, or (3) the lateral transfers produce or alter patterns of spatial heterogeneity. We discuss homogeneous, mosaic, and interacting element approaches for dealing with space and identify both challenges and opportunities. Embracing spatial heterogeneity in ecosystem ecology will enhance understanding of pools, fluxes, and regulating factors in ecosystems; produce a more complete understanding of landscape function; and improve the ability to scale up or down.

Introduction

Understanding the causes and consequences of spatial heterogeneity in ecosystem function represents a frontier in both ecosystem and landscape ecology (Turner et al. 2001; Chapin et al. 2002), and it is recognized as important in a variety of other disciplines; for example, biological oceanography (Platt and Sathyendranath 1999), limnology (Soranno et al. 1999), soil ecology (Burke et al. 1999), conservation (Pastor et al. 1999), and global change studies (Shugart 1998; Canadell et al. 2000). Ecosystems do not exist in isolation, and interactions among patches on the landscape influence the functioning of individual ecosystems and of the overall landscape. Efforts to estimate the cumulative effect of ecosystem processes at regional and global scales have contributed to the increased recognition of the importance of landscape processes in ecosystem dynamics (Chapin et al. 2002). Transfers among patches, representing losses from donor ecosystems and subsidies to recipient ecosystems, are important to the long-term sustainability of ecosystems (Polis and Hurd 1996; Naiman 1996; Carpenter et al. 1999; Chapin et al. 2002).

Ecology lacks a theory of ecosystem function that is spatially explicit, and there are few empirical studies from which to infer general conclusions. Ecosystem ecology focuses on the flow of energy and matter through organisms and their environment. As such, it addresses pools, fluxes, and regulating factors. Spatially, ecosystem ecology encompasses bounded systems like watersheds, spatially complex landscapes, and even the biosphere; temporally, it crosses scales ranging from seconds to millennia (Carpenter and Turner 1998). From its initial descriptions of the structure and function of a diverse variety of ecosystems, ecosystem ecology moved toward increasingly sophisticated analyses of function; for example, food web analyses, biogeochemistry, regulation of productivity, and so forth (Golley 1993; Pace and Groffman 1998; Chapin et al. 2002). Typically, ecosystem studies are conducted within a single ecosystem, such as a lake or a forest stand, and homogeneous sites are generally chosen to minimize the complications associated with spatial heterogeneity. From ecosystem studies, ecology has gained an excellent understanding of the mechanisms underlying many processes and of temporal dynamics in function. However, understanding patterns, causes, and consequences of spatial heterogeneity in ecosystem function remains a frontier.

Landscape ecology explicitly addresses the importance of spatial configuration for ecological processes (Turner et al. 2001), and, in North America, landscape studies were strongly promoted by ecosystem ecologists (Risser et al. 1984). Landscape ecology often, but not always, focuses on spatial extents that are much larger than those traditionally studied in ecosystem ecology. Early research in landscape ecology emphasized methods to describe and quantify spatial heterogeneity, spatially explicit models to relate pattern and process, and understanding of scale effects. Indeed, there