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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.