4
Thoughts on the Generation and Importance of Spatial Heterogeneity in Ecosystems and Landscapes

John Pastor

Abstract

Landscapes are spatially dynamic because materials and energy spread over them and change the distribution of ecosystem properties. This heterogeneity of the distribution of ecosystem properties can either be random or patterned. The landscape becomes patterned when the spread of materials and energy correlates an ecosystem property in one local neighborhood with that at another. When the spread of materials and energy does not correlate properties of different neighborhoods, then the landscape can still be heterogeneous but random. Various processes that result in spatial heterogeneity include physical disturbances (e.g., fire, erosion, etc.) that spread across neighborhoods and remove materials but whose spread is partly determined by previous disturbances; directional gradients in the flow of materials, energy, or information; and different diffusion rates of coupled ecosystem components combined with positive feedbacks, otherwise known as diffusive instability. Examples of these processes will be given from other papers in this conference and elsewhere.

Introduction

The living world is not all green slime or a big leaf; things are different from place to place. This variety of the living world is what makes it a stunningly beautiful and interesting place to live. It is also what makes understanding ecological systems difficult.

Spatial heterogeneity of the distribution of ecosystem processes across the landscape can be random or patterned (or a combination of both). A heterogeneous spatial distribution of ecosystem properties is random if, given the value of an ecosystem property at a point, the value of that property at adjacent points cannot be predicted. In contrast, a heterogeneous spatial distribution is patterned if, given the value of an ecosystem property at a point, the value at adjacent points and possibly points further away can

be predicted with some confidence. Because the spread of materials and energy across the landscape correlates values of an ecosystem property between adjacent local neighborhoods, this spread can therefore result in patterned heterogeneity.

For the most part, we know how to analyze spatially homogeneous distributions through analysis of variance and general linear statistical models. We know how to model their dynamics through coupled ordinary differential equations that depict energy and material flows between ecosystem components and whose parameters do not depend on position in space. In contrast, we are only beginning to learn how to describe the origin and dynamics of spatial heterogeneity. These require new mathematical, experimental, and observational tools for their description and analysis.

Physical disturbances create and sustain heterogeneities by removing materials from ecosystems or transferring materials from one ecosystem or ecosystem component to another. Physical disturbances often have a large random element, but they also may depend on underlying heterogeneity, which is often caused by previous disturbances. The spread of a disturbance correlates values of an ecosystem property at a given point with those at its neighbors and beyond to the boundary of the patch created by the disturbance.

Transport of energy and materials along a directional gradient, such as movement of water and suspended sediments or dissolved compounds downhill, also creates patterned heterogeneity. The transport of energy and materials along a directional gradient correlates ecosystem properties along the gradient. Ecosystem properties will therefore be similar for long distances along transects in the direction of the gradient but become less similar more rapidly along transects perpendicular to the gradient.

Spatial heterogeneities can also be generated by positive feedbacks between ecosystem components, such as soil, vegetation, and higher trophic levels (Meinders and van Breemen this volume). Such patterned heterogeneity can arise even in the absence of gradients and physical disturbances and can create patterned heterogeneity from homogeneity or random heterogeneity. This generation of pattern from homogeneity or randomness in the environment via positive feedbacks between ecosystem components is sometimes called "self-organized complexity" (Kauffman 1993; Bak 1997; Meinders and van Breemen this volume).

If two interacting ecosystem components also diffuse or spread across the landscape, new and surprising heterogeneities can arise even without any underlying heterogeneity in the physical environment (Okubo and Levin 2002). Under some circumstances, such heterogeneities could be stable. This seems to be especially prevalent in herbivore-vegetation systems where both the herbivore populations and the plant species that support them are diffusing across the landscape. For example, the spatial dynamics of balsam fir is coupled to the spatial dynamics of spruce budworm populations during an outbreak. In turn, the changes in the spatial distribution of balsam fir affect the fate of the outbreak (Holling 1978).