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Flowpaths as Integrators of Heterogeneity in Streams and Landscapes

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Abstract

Streams are heterogeneous in both space and time. Hydrologic flowpaths along which biogeochemical processing occurs integrate different patches of the stream. Disturbance events (flood and drying) change these patches, alter connectivity, and reinforce spatial heterogeneity. Heterogeneity within patches (surface stream, hyporheic zone, sand bars, and riparian zone) is generated by the interaction of nitrogen (the limiting nutrient) in transport and organisms such as algae and bacteria. These organisms store nitrogen as they grow, alter N forms and concentrations in transport, and in some cases (e.g., denitrification) export it to the atmosphere. Changes in nitrogen in transport can be large, as are community responses to nitrogen availability, thus reinforcing spatial heterogeneity in successional time. Flowpaths connect patches as well and generate changes in recipient patches as a function of nitrogen delivery rate. This is especially evident at patch boundaries. In streams, flow is markedly linear and inexorably downstream in orientation; however, landscapes are drained by coalescing, dendritic networks that intimately connect stream channels with terrestrial flowpaths over and beneath soils. We propose that a unified theory of landscapes will require a focus on spatial linkage, a consideration of both spatial and temporal heterogeneity, and a blurring of distinctions between terrestrial and aquatic elements.

Introduction

The concept of heterogeneity has been used variously in stream ecology to describe habitat variability (e.g., sediments) and effects on invertebrate communities (Palmer et al. 1997) or more broadly as patch structure and dynamics at multiple scales (Pringle et al. 1988). Poff et al. (1989) considered heterogeneity of forcing variables such as flood and drought in shaping stream function, again with an emphasis on invertebrates. Dent and Grimm

(1999) considered spatial heterogeneity of nutrient concentration using spatial autocorrelation analysis in a desert stream and applied this approach at three scales to deduce scale-specific causation of resultant patterns (Dent et al. 2001). Results of this approach lend insight into stream structure and function and permit an objective determination of operant hierarchical scales. Fractal analysis has been used to determine patterns of algal distribution in streams (Sinsabaugh et al. 1991) and to infer causes of spatial heterogeneity of invertebrate communities resulting from biotic interactions (Cooper et al. 1997).

Many stream ecologists have acknowledged that streams are spatially variable and have considered how these subsystems interact. Stanford and Ward (1993) have shown how the stream channel interacts with flood plains and how this variability and connectivity are central to stream function and biodiversity. Poole (2002) used a hierarchical approach adapted from Frissell et al. (1986) to examine longitudinal changes in solutes and community organization in streams and to thereby define an integrative approach to fluvial landscape ecology. Fisher et al. (1998a) developed a model of lateral interaction of stream elements in disturbance time to show how subsystem interactions shape whole system function, in that case, in terms of nutrient retention and spiraling.

Although these efforts represent substantial progress in understanding streams as spatially complex ecosystems, the field is still struggling with the challenge of linking heterogeneity with whole ecosystem functioning (Palmer and Poff 1997), determining how and when heterogeneity, in all its manifestations, matters.

Objectives

The purpose of this paper is to examine the consequences of heterogeneity for ecosystem function using streams as an example; in particular, results of our work in Sycamore Creek in Arizona. We will attempt to develop a concept of patch integration to determine when heterogeneity generates higher order properties by virtue of patch interaction. Several terms are essential to this discussion. First, *structure* refers to the configuration of the ecosystem in space. *Patch structure* refers to a situation in which variance changes abruptly at boundaries that enclose patches that are themselves relatively homogeneous. Gradients may occur within patches or may characterize entire ecosystems wherein boundaries do not exist (although they may be arbitrarily imposed). Patch *integration* refers to an interaction among patches and may take several forms (hydrology, organismal movements, wind action) and involve several distinct *currencies* such as nitrogen, caribou, bird song, pheromones, and visual images (Reiners et al. this volume). We think of *integrator* as the mode of connection among patches and currency as the entity moved by the integrator. More broadly, an integrator can be viewed as