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## Origins, Patterns, and Importance of Heterogeneity in Riparian Systems

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### Abstract

Riparian systems epitomize heterogeneity. As transitional semiterrestrial areas influenced by water, they usually extend from the edges of water bodies to the edges of upland terraces. Riparian systems often exhibit strong biophysical gradients, which control energy and elemental fluxes, and are highly variable in time and space. These attributes contribute to substantial biodiversity, elevated biomass and productivity, and an array of habitats and refugia. Focusing on riparian systems of medium-sized floodplain rivers, we describe heterogeneity at multiple space and time scales, illustrate interactions among scales, and propose a conceptual model integrating major system components. We show how climatic and geologic processes shape an array of physical templates, describe how disturbances redistribute materials, and illustrate how soils and subsurface processes form and are sustained. Collectively, these processes strongly influence plant productivity and fluxes of channel-shaping large woody debris (LWD). Ultimately, riparian ecosystem function integrates climate (past and present), geologic materials and processes, soil development and attendant microbial transformations, subsurface characteristics, plant productivity, animal activities, and LWD—and the active, continuous and variable feedbacks between the individual components.

### Introduction

Riparian communities respond continuously in time and space to a complex array of hydrologic (e.g., water regimes, hydraulic shear stress, sediment deposition, erosion, deposition of large woody debris) and biotic (e.g., animal activities, plant production, microbially mediated nutrient cycling) influences. The resulting mosaic of riparian subcommunities are composed of species with contrasting life history strategies that moderate downstream fluxes of water, materials and energy—and fundamentally influence nutrient

and organic matter dynamics. Collectively, the biophysical processes support numerous types of aquatic, semiaquatic, and terrestrial food webs, resulting in high biodiversity. Indeed, riparian systems appear to be sites of focused storage and dissipation of materials and energy within the larger, regional landscape. They are likely “hotspots” for regional heterogeneity owing to the inherently dynamic and nonlinear processes linking the flux and retention of water and materials to interactive landscapeforming processes (Benda et al. 1998; Naiman et al. 1998).

Riparian systems provide an unusually rich array of lessons on the origins, patterns, and ecological importance of biophysical heterogeneity. Heterogeneity is manifested in a diverse array of landscape elements and processes operating on several spatial and temporal scales. These include longitudinal, lateral, and vertical gradients in geomorphic features (e.g., gravel bars, terraces, islands), surface and subsurface flows of water and nutrients, and disturbance regimes (e.g., floods, drought, fire, wind). Fluvial actions (e.g., erosion, transport, deposition) are the dominant agents of riparian change and constitute one suite of the natural disturbance processes primarily responsible for sustaining the high level of heterogeneity (Poff et al. 1997; Ward et al. 2002). It is the hydrologic connectivity—the flux of matter, energy, and biota via water—in combination with animal activities (Naiman and Rogers 1997), microbial processes, and vegetation dynamics that largely sustain riparian heterogeneity. Although individual features such as a specific vegetative patch type may exhibit dynamic transitions fueled by interactions between fluvial dynamics and plant succession, their relative abundance within a catchment tends to remain in quasiequilibrium over decades to centuries. In general, riparian systems are highly heterogeneous, as well as central nodes for biodiversity, for energy and elemental fluxes, and for elevated biomass and productivity. Throughout a catchment, riparian systems exhibit strong biophysical gradients, high variability in time and space, and provide a diversity of habitats and refugia (Naiman and Décamps 1997; Naiman et al. 2005).

This chapter describes riparian heterogeneity at multiple scales of space and time, illustrates interactions among the scales, and offers a conceptual model integrating the major ecosystem components. We accomplish our objectives by showing how climatic and geologic processes shape physical templates, and by illustrating how soils and subsurface processes form and are sustained on the major physical templates. We then discuss how the latter processes influence biodiversity and plant productivity and, ultimately, the generation of channel-shaping large woody debris (LWD) and the disturbances driving fluxes of LWD from the forest to streams. Integration at the ecosystem scale is accomplished through a conceptual model relating climate, geology, soils, subsurface characteristics, plant productivity, and LWD with the active, continuous, and variable feedbacks between the individual components. Examples herein draw heavily on lessons we have learned from mid-sized alluvial rivers draining the rainforests of the North American