

Why does heterogeneity matter?

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Heterogeneity is a popular “buzzword” in ecology, especially landscape ecology. It reminds us that in real systems we do not have the luxury to speak in terms of mean fields or homogenous processes. Heterogeneity does not imply randomness. As Turner & Chapin point out in Chapter 2, when heterogeneity is a manifestation of some process or patterning-agent, we can study it at one scale to help us understand the patterns at a different scale. As we incorporate ideas of scale into ecological analyses, we are often examining heterogeneous processes that at some smaller scale break-down into more predictable continuous processes.

Ecosystems Function in Heterogeneous Landscapes is an edited volume from the 10th Cary conference held in 2003. The Cary conference series has been running biennially since 1985; participants are selected due to their substantial contributions to a particular topic and are brought together to synthesize the state of the science for the particular topic. In the five sections of this volume, the authors seek to lay out the sources of heterogeneity in different systems and evaluate

how they contribute to our understanding of patterns and processes with regards to system function.

Section one contains four chapters outlining some of the challenges arising from heterogeneous landscapes as well as the conceptual approaches for dealing with them. Turner and Chapin discuss heterogeneity in terms of point processes and interacting flows of resources. They start with first principles like Jenny’s theory of soil generation and continue through some of the major heterogeneity generating mechanisms such as current flows, biotic feedbacks, and how the variation they generate promotes new flows within the heterogeneous system. White and Brown, in Chapter 3, pick up on some of these themes by describing the physical template and suggest characterizing landscapes quantitatively as systems of gradients, patches and networks. They describe briefly the primary methods by which these structures are explored: gradient models, scaling laws, and fractals. They also remind us of the fundamental fact that appropriate scale is always relevant to the organisms and processes under consideration. Pastor (Chapter 4) again deals with flows and patches in the context of coupled differential equations to show how Lotka-Volterra dynamics can instill stable heterogeneous states in the absence of a heterogeneous environment and Reiners (Chapter 5) goes so far as to name ten transport mechanisms as an

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organizing framework to study the generation of heterogeneity.

Section two examines heterogeneity from perspectives other than those of landscape ecologists. Fahrig and Nutton (Chapter 6) speak for population ecologists and contrast the situations in which either landscape configuration or composition matter to biota. In Chapter 7, Tague discusses heterogeneity in hydrologic systems by examining heterogeneity in watershed size, precipitation events, the density of rain gauges, topography, the slope-aspect energy balance, and the difficulty in spatially estimating parameters.

Epidemics are one of the archetypical spatial processes; they move from host to host, spreading as those hosts move and mingle. In Chapter 8, epidemiologist David L. Smith applies these notions to ecosystem functioning by examining how a variable environment can give rise to patchy host distributions and mixing. A different sort of mixing is explored in Chapter 10 caused by the differential rates of mixing in the ocean's surface, namely fast horizontal flow versus slow vertical mixing. Here Mahadevan explores the generation and dissipation of heterogeneity in remotely sensed temperature and chlorophyll. Patchiness results from the differences in these rates.

The seven chapters in section three constitute examples of heterogeneity formation in different systems, including: deserts, soil-vegetation interactions, carbon storage in boreal systems, urban systems, riparian areas, streams as area integrators and dynamic lakes. A common theme in these chapters considers flows of some kind, be they water, nutrients, wind, wood or landscapes themselves and how variation in flow sets up feedbacks leading to heterogeneity. The breadth of these chapters is impressive and they will be enlightening to many ecologists as they cover quite dissimilar areas including arid vegetation patterns (Tongway and Ludwig Chapter 10.), boreal peat bogs (Meiners and van Breeman Chapter 11) and urban ecosystems (Band et. al. Chapter 13).

Water is shown to play an extremely important role in transport leading to heterogeneity, as one would expect. Much of the initial heterogeneity in

landscapes derives from water's dual importance as terrestrial organizer and ecosystem requirement. It moves soil and nutrients from high points to low and in so doing allows plants to root and grow and inhibit its own flow. Chapters 14 and 15 provide primers on the many ways water and soil/topography interact to carry nutrients through a system, sort sand, silt and clay, change the direction of rivers, and turn over habitat. Chapter 15 highlights the theoretical separation of aquatic and terrestrial landscapes and argues that they can be considered as an integrated system connected by hydrology and that this may form part of a broad theory of landscapes (a suggestion repeated in Chapter 18). Chapter 16 delves into lakes and points out how heterogeneous even a potentially well mixed environment can become and how systematic differences can form within and across lakes in a landscape.

Section four looks at how landscape heterogeneity is incorporated into three different management contexts: fire, water, and conservation. In Chapter 17, Romme covers one of the other archetypical spatial processes, wildland fire, and how not only local heterogeneity, but large-scale heterogeneity must be taken into account for effective management. One of the most important sources of variation is the pattern of fire regimes across the western US and the need to incorporate different management strategies in each; for instance, consider fire management in dry ponderosa pine versus moist northeastern forests. In Chapter 18, Steinman and Denning review water as a manageable resource and how waterways and hydrologic flow integrate landscape attributes and how their configuration needs to be addressed within management contexts. In the last management Chapter (19), Possingham and his colleagues examine the reserve design debate from the standpoint of capturing heterogeneous areas in such a way as to support their continued existence.

Section five, the synthesis section, begins with a chapter by Strayer covering two major issues. He first summarizes heterogeneity into five generating phenomena and then revisits how scale of inquiry dictates those forms of heterogeneity which require study or rather how to ignore those that do not. Franklin then highlights some areas

of knowledge deficiency, particularly regional scale below-ground sensing capability. He urges a move from the homogenous patch-based view, to a more continuous variability view and urges a greater focus on ecosystem structure in addition to the usual focus on community structure. The editors penned the final chapter and attempt to form a structure out of the many preceding pieces. In doing so, they postulate several well-defined rooms in their construct, but, they admit there is no roof, no overlying framework under which to organize “heterogeneity”.

This volume attempts to cover a lot of topics and will be particularly relevant to graduate students of Landscape Ecology trying to grasp some of the landscape to regional organizing

frameworks that may provide fruitful avenues of research. It may also be helpful to researchers and managers when trying to fit their system/jurisdiction into the hierarchy of systems. Much of the book is either theoretical or anecdotal; each chapter has different authors and they were not specifically written in sequential order. Sections one and five certainly give the broadest overviews and could be considered the theoretical underpinnings of the volume. I especially liked section three for the variety of specific examples of heterogeneity forming within different systems. Ultimately the reader will be led to other sources for more in depth treatments, but I think this could prove valuable for providing direction and broad theoretical understanding.