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Edited by A.J. Hansen and F. di Castri

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# Landscape Boundaries

## Consequences for Biotic Diversity and Ecological Flows

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## Preface

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The emergence of landscape ecology during the 1980s represents an important maturation of ecological theory. Once enamored with the conceptual beauty of well-balanced, homogeneous ecosystems, ecologists now assert that much of the essence of ecological systems lies in their lumpiness. Patches with differing properties and behaviors lie strewn across the landscape, products of the complex interactions of climate, disturbance, and biotic processes. It is the collective behavior of this patchwork of ecosystems that drives pattern and process of the landscape.

This realization of the importance of patch dynamics is not an end point in itself, however. Rather, it is a passage to a new conceptual framework, the internal workings of which remain obscure. The next tier of questions includes: What are the fundamental pieces that compose a landscape? How are these pieces bounded? To what extent do these boundaries influence communication and interaction among patches of the landscape? Will consideration of the interactions among landscape elements help us to understand the workings of landscapes?

At the core of these questions lies the notion of the *ecotone*, a term with a lineage that even predates *ecosystem*. Late in the nineteenth century, F.E. Clements realized that the transition zones between plant communities had properties distinct from either of the adjacent communities. Not until the emergence of patch dynamics theory, however, has central significance of the ecotone concept become apparent. As transition zones, eco-

tones actually define the patches composing the landscape, much as abrupt changes in color define the forms, and hence, the essence, of an abstract painting. Moreover, ecotones bound landscape elements, raising the question as to whether ecotones control the flows of materials and interactions among patches. Studying landscapes without consideration of ecotones may be as fruitless as trying to understand cellular behavior without knowledge of cell membranes.

Will an expanded ecotone theory help us to understand and manage landscapes? In the mid-1980s, a small group of ecologists concluded that the answer was "yes." They proceeded to organize a coordinated set of international programs on ecotones. The Scientific Committee on Problems on the Environment (SCOPE) and the UNESCO's Man and the Biosphere Program (MAB) introduced in 1988 (Di Castri F, Hansen AJ, Holland MM [eds] [1988]. A new look at ecotones: Emerging international projects on landscape boundaries. *Biology International* [Special Issue 17]) the rationale and design of two related efforts on ecotones. The MAB program focuses on land-inland-water ecotones and involves a coordinated set of field studies around the world. Two recent books (Naiman RJ, Decamps H [1990] *The Ecology and Management of Aquatic-Terrestrial Ecotones*. Parthenon Publishing Group, Paris; and Holland MM, Risser PG, Naiman RJ [in press] *Ecotones: The Role of Landscape Boundaries in Management and Restoration of Changing Environments*. Routledge, Chapman and Hall, New York) develop the conceptual underpinnings of the program.

The SCOPE project is a 4- to 6-year effort to synthesize current information and to advance theory and management of ecotones. A Scientific Advisory Committee under the Chairmanship of one of us (Francesco di Castri) and including Paul Risser, Josef Rusek and Aleksey Armand offered direction on the project. Specifically, the project focuses on the influence of ecotones on biodiversity and ecological flows, particularly under the influence of global land use and climate change. The first of the projects' three planned workshops was held in Paris, France, in December of 1988. Approximately 30 scientists explored the role of ecotones in influencing biological diversity and the flows of energy, materials, and organisms. A second workshop on ecotones under global change was held at the Kellogg Biological Station, Hickory Corners, Michigan, in April, 1991. A final meeting on the management of ecotones is being planned for a location in the Soviet Union in late 1991 or 1992.

This book has evolved from the first of these three workshops. Our purpose in the book is to better integrate consideration of ecotones into landscape theory and, more specifically, to examine the influence of ecotones on ecological flows and biodiversity. The movements of energy, materials, and organisms among ecosystems are critical to landscape functioning, and the chapters of this book explore the role of ecotones in con-

trolling those flows. The effect of ecotone patterning and landscape fragmentation on genetic, species, and community diversity is a subject of great interest. Here, we examine this subject in the context of landscape theory. The objectives of the book are to (a) synthesize existing theory on these topics, (b) evaluate central hypotheses relative to empirical data and results of simulation models, and (c) put forth any new hypotheses that emerge from our analyses.

The chapters are organized into five parts. Part I deals with the significance of ecotones, their ecological characteristics, and methods for studying them. In Chapter 1, we attempt to provide a context for the book by explaining the socioeconomic forces that ultimately drive landscape pattern and the relevance of landscape management to human welfare. Delcourt and Delcourt (Chapter 2) and Gosz (Chapter 3) examine pattern and process in ecotones across a range of temporal and spatial scales, with particular reference to past and possible future climate change. Lepart and Debussche (Chapter 4) offer an account of linkages between human populations and landscape patterns in southern France over the past 2 millennia. In Chapter 5, Johnston et al. present quantitative methods of studying landscape boundaries.

Part II, on biodiversity, is introduced by Neilson et al. (Chapter 6), who examine the hierarchy of factors that constrain structural and species diversity. The interactions between landscape fragmentation and population dynamics are evaluated by Merriam and Wegner (Chapter 7). Hansen et al. (Chapter 8) suggest that both landscape dynamics and the life history characteristics of communities are strong determinants of patterns of species diversity. The section is concluded by Rusek (Chapter 9), who analyzes the diversity of soil invertebrates across ecotones of differing spatial scales.

Part III, on ecological flows, opens with a theoretical model of the factors that control movements across landscapes by Wiens (Chapter 10). Forman and Moore draw an analogy between ecotones and the structure and functioning of cell membranes in Chapter 11. In Chapter 12, Gardner et al. model flows across landscapes, using percolation theory. Ryszkowski (Chapter 13) and Küppers (Chapter 14) synthesize diverse studies on the energetics, nutrient cycling, and plant physiology across shelterbelts in agricultural landscapes. Swanson et al. (Chapter 15) develop and test some novel hypotheses on the role of geomorphology in directing ecological flows and structuring landscape boundaries.

Empirical evidence from diverse systems is presented in the form of case studies in Part IV. Topics include desert vegetation stripes (Cornet et al., Chapter 16); treeline dynamics (Slatyer and Noble, Chapter 17; and Armand, Chapter 18); vegetation response to climate change (Weinstein, Chapter 19; and Fu, Chapter 20); and coastal ecotones (Ray and Hayden, Chapter 21).

Part V comprises the Epilogue (Chapter 22), which evaluates central hypotheses of the book and considers implications for future research and management.

It is not our intent in this volume to offer a complete and tidy theory of ecotones. Indeed, we have much yet to learn about the role of ecotones in landscapes. We will feel successful if this volume and others emerging from the SCOPE and MAB projects on ecotones stimulate the thinking and research that are necessary to build a satisfying theory of landscapes.

We thank the many people and organizations that made this book a reality. We are indebted for continuing support and encouragement to SCOPE, to the A.W. Mellon Foundation, to the Commission of European Communities and to UNESCO. Our salaries were provided by the Mellon Foundation; the SCOPE Executive Board; the National Center for Scientific Research (CNRS) in Montpellier, France; and the COPE Program, College of Forestry, Oregon State University, Corvallis, Oregon. Veronique Plocq, Executive Secretary of SCOPE, oversaw the administration of the project, with the assistance of Susan Greenwood, and hosted the Paris workshop in December 1988. Technical reviewers of one or more chapters in the book include A. Cornet, Gary Cunningham, Richard Forman, Robert Gardner, James Gosz, Gordon Grant, Carol Johnston, John Lehmkuhl, Jacques Lepart, Joe Means, Gray Merriam, Carlos Montana, Ron Neilson, Ian Noble, Paul Risser, Fred Swanson, Dean Urban, David Weinstein, Dennis White, and John Wiens. Finally, Marcy Berg helped with correspondence among authors during the editing phase.

Andrew J. Hansen  
Francesco di Castri

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