

Introduction: Questions of Scale

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I. Scaling from Ecophysiology

Predicting and analyzing the structure and function of ecological systems on large spatial and long temporal scales are research challenges of rare potential but daunting difficulty. The potential derives from both practical need and scientific opportunity. The difficulty reflects the diversity and nonlinearity of ecological responses. This book explores aspects of both the potential and the difficulties, using paradigms and approaches from plant ecophysiology as starting points for capitalizing on opportunities and managing problems.

The traditional focus of plant ecophysiology, understanding how plants cope with often stressful habitats, is organism centered (Mooney *et al.*, 1987a; Mooney, 1991). The questions and approaches focus on diversity in the levels of environmental factors, implications of plant functional diversity for mass and energy exchange, and influences of mass and energy exchange on plant persistence, growth, and reproduction. This organism-centered approach provides a useful framework for predicting the characteristics of organisms likely to be successful in any given habitat and for assessing ecological consequences of physiological mechanisms and morphological characteristics.

In the past, few ecophysiologicalists emphasized extending these capabilities to problems involving many individuals. However, many of the same individual-level characteristics that determine persistence, growth, and reproduction are primary components of ecosystem-level fluxes of matter and energy, which are, in turn, critical determinants of the biogeochemical cycles of carbon, water, and nutrients. Ecophysiology is, in a sense,

preadapted for large-scale problems. This preadaptation is, however, far from complete. Ecophysiology traditionally lacks many of the technical tools for large-scale analyses, and the evolutionary perspective that is so useful at the organism level does not necessarily extend to higher scales.

The clear role of the terrestrial biosphere in global change, including feedbacks on climate (Shukla and Mintz, 1982; Dickenson, 1991), the composition of the atmosphere (Mooney *et al.*, 1987b), and the fate of anthropogenic CO₂ (Tans *et al.*, 1990), generates a critical need for large-scale assessments that are both accurate and generalizable outside the envelope of existing conditions. Because of its focus on the responses of underlying mechanisms to variation in environmental factors, ecophysiology offers the promise of generalization. The accuracy will depend on the effectiveness with which ecophysiological concepts can be integrated with large-scale measurement techniques, global databases, and models from atmospheric sciences, hydrology, biogeochemistry, and population dynamics.

As much as ecophysiology hopefully will contribute new perspectives to large-scale analyses, contributions in the reverse direction are also likely. Global and regional patterns traditionally have provided important stimuli for new hypotheses in ecophysiology. Convergent evolution (Cody and Mooney, 1978) and plant life zones (Woodward, 1987) are clear examples of concepts developed from a geographic perspective. Increasingly quantitative assessments of large-scale patterns are likely to stimulate other advances in ecophysiology. Evidence for the striking generality of the efficiency with which light is used in growth (Goward *et al.*, 1985) already is leading to new research in ecophysiology. The localization of terrestrial sources and sinks of carbon, using global analysis (Tans *et al.*, 1990; Enting and Mansbridge, 1991), almost certainly will lead to intensive ecophysiological studies in the putative source and sink areas.

II. The Art of Scaling

Combining quantitative mechanisms understood precisely at small scales into synthetic assessments appropriate over larger scales of space and time can be a grand expression of scientific confidence, or it can be a sobering warning that information is still missing. Scaling is perhaps most useful between these extremes, when applied as a tool for testing hypotheses and identifying missing components of interpretations.

The need for synthetic assessments based on quantitative mechanisms integrated across scales extends across the sciences. In fields related to ecophysiology, issues of scale are very explicit; the treatment of scale is very sophisticated in landscape ecology (Dale *et al.*, 1989; Turner, 1989), hydrology (McNaughton and Jarvis, 1991), and global change (Rosswall

et al., 1988). The chapters in this book take no single approach to scaling. Because they start with the mechanisms underlying the biological processes, the chapters emphasize different aspects of the scaling problem. As a group, they may not present a definitive answer to the general problem of scaling, but they clearly demonstrate that ecophysiology can make major contributions to analysis of ecosystems on large spatial and long temporal scales.

III. Some New Dimensions

This book is a collection of chapters based on presentations and discussions at a meeting in Snowbird, Utah, in December 1990. Some chapters are based on presentations at the workshop that were discussed extensively, and were modified to incorporate concepts and syntheses that emerged from the discussions. For selected topics that are recognized broadly as representing new frontiers, but in which progress will be critically dependent on input from a range of perspectives, the chapters started from discussions at the workshop. The final form of each discussion chapter reflects the enthusiasm of a number of participants and the dedication of one or a few discussion leaders who not only kept the discussions focused, but also built chapters around the concepts covered in the discussions.

The book begins with two chapters that consider conceptual and formal tools for spatial integration. The next two sections address scaling from the two ends of the spatial spectrum: from the bottom up and from the top down. The “bottom-up” chapters develop conceptual frameworks for complex mechanistic models but also assess the quantitative impacts of a number of simplifications. The “top-down” discussions develop general approaches to using global-scale information to constrain smaller scale interpretations.

The fourth section of the book addresses the interface between physiological processes and biological diversity. Two chapters consider scaling of population and community phenomena and two others assess prospects for managing complications of biodiversity by collecting species into functional groups. The three chapters in Part V consider technologies for scaling—stable isotopes, remote sensing, and canopy-flux measurements.

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I

Integrating Spatial Patterns

Questions of spatial and temporal scale are unavoidable in biological systems, particularly when one is interested in understanding processes and the implications of interactions among processes. This first section begins with a theoretical consideration of pattern and scaling issues by Levin. In this chapter, he points out that, although there is no correct choice of scale, there may be paradigms or laws that can be used to address the phenomena of interest at higher levels of organization. He provides us with the relevance of such approaches through an examination of spatiotemporal mosaics. Although part of his presentation on patchiness and patch dynamics is for a marine system, he argues that the same principles will apply to terrestrial studies.

Subsequently, Schimel, Davis, and Kittel present an examination of FIFE, a large scale study of ecological processes that spanned leaf-level to landscape-level components. FIFE, First ISLSCP Field Experiment (ISLSCP is International Satellite Land Surface Climatology Project) was an effort to understand ecological and physical processes that regulate gas exchange between the surface and the atmosphere. The project represented a combined effort of different disciplines and approaches (e.g., modeling, remote sensing, geographical information systems), many of which are discussed in later chapters of this volume.

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