

COMPLEX ADAPTIVE SYSTEMS

Use and Analysis of Complex Adaptive Systems in Ecosystem Science: Overview of Special Section

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INTRODUCTION

Ecological systems are complex assemblages of interacting organisms embedded in an abiotic environment. Complexity arises from interspecific and intraspecific interactions among individuals or agents, interactions across trophic levels, and the interactions of organisms with the abiotic environment over space and time. In addition, interactions can range from strong and direct to weak and diffuse and are modified by both positive and negative feedback with the environment. In our effort to understand pattern formation at the community or ecosystem level, we are confronted with the daunting array of processes that function across different spatial and temporal scales. We are thus forced to address the question of how these different levels of organization can be integrated, or how mechanisms and patterns at one level of organization can be understood in terms of processes operating at a different level of organization.

The goal of this *Ecosystems* Special Section is to provide an overview of the relatively new approach of analyzing ecosystems using complex adaptive systems (CAS) theory. CAS theory is an extension of traditional systems theory [for example, see von Bertalanffy (1968)] but addresses one of the omissions of systems theory—namely, adaptation—by specifically modeling how individual variation and

changes in that variation lead to system-level responses. To introduce this Special Section, we distinguish systems theory and complex adaptive systems theory, outline the articles in this Special Section, and suggest new ecological insights that could emerge from CAS-based approaches.

SYSTEMS THEORY

Systems theory is an analytical approach that represents the natural world as a set of stocks and flows regulated by a variety of feedback processes. These representations are subjected to a variety of mathematical analyses in order to gain insight into system behavior. Systems theory has been widely applied in ecology. For example, early work on processes organizing community dynamics and patterns, such as predator-prey interaction, used systems concepts. These early analyses were generally deterministically and analytically based. Even so, relatively simple models were able to produce complex dynamics [for example, see May (1976)]. With increasingly powerful computers, researchers have had the opportunity to increase model complexity, and analyze and replicate simulations at larger spatial and temporal scales, or conduct simulations with greater spatial and temporal resolution. Explicitly representing space in models, for instance, leads to significantly different model behaviors and outcomes than those resulting from a nonspatial or homogeneous model (Huffaker 1958; Turner 1989; Levin 1992; Durrett and Levin 1994; Tilman and Kareiva 1997; Hartvigsen and Levin 1997; Kinzig and Harte 1998).

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One of the main limitations with the traditional systems approach to analyzing ecological dynamics is that it omits the influential process of adaptation. Clearly, the ability of species to adapt to changing environmental conditions is likely to be important. The ability of ecologists to incorporate adaptation in models has in the past been limited by the inherent difficulty of including variability and selection within the aggregated stocks and flows used in systems analysis. Recent advances in both theory and computing ability have, however, increased our capacity to incorporate individual-level variability and adaptation. These advances have enabled ecologists to create simple models of adaptive and selective processes in ecological systems.

COMPLEX ADAPTIVE SYSTEMS

Complex adaptive systems theory builds upon systems theory by explicitly representing the diversity and heterogeneity that systems theory tended to aggregate within homogeneous stocks and flows. In other fields, CAS approaches have been particularly useful in analyzing situations in which individuals in a population are governed by nonlinear dynamics (Rodríguez-Iturbe and Rinaldo 1997). Treating such a population as an aggregate—rather than an interacting and heterogeneous set of individuals—may hide a rich set of dynamics, or even lead to incorrect predictions or insights regarding probable population-level and community-level behavior. Nonlinearity and individual heterogeneity are ubiquitous in ecology, and we must find ways to capture their importance in our analysis of ecological systems; the use of CAS offers methods and approaches for capturing heterogeneity.

CAS differs from traditional systems theory because it explicitly incorporates the role of adaptation in governing the dynamics and responses of these now heterogeneous reservoirs. One increasingly common and powerful CAS approach to incorporating individual-level or agent-level variability and adaptation in models involves using genetic algorithms (Goldberg 1989; Mitchell 1996). The CAS approach enables ecologists to analyze how processes at lower levels of organization (for example, genes) produce patterns at higher levels of organization (for instance, ecosystems). Hartvigsen and Levin (1997) developed a model of plant–herbivore interactions that incorporated individual-level genetic variability in plant defense and herbivore response to investigate the influence of adaptation on population and community dynamics. Their work suggests that large-scale population and community dynam-

ics (that is, numbers of individuals and the relative abundance of species over time) can be extremely sensitive to variability among individuals and that this response depends on the spatial structure of the interacting populations (Hartvigsen and Levin 1997). This Special Feature is intended to provide a general introduction to this and other CAS approaches to ecology.

The incorporation of variability and adaptation in CAS allows for a greater understanding of how patterns and processes emerge and interact across levels of biological organization, and across spatial and temporal scales. In addition, other systems, such as economies, also function as complex adaptive systems (Arthur and others 1997a; Brock forthcoming). These systems share the property that self-organization produces macroscopic patterns that emerge through local, small-scale interactions. Our understanding and ability to predict large-scale ecosystem dynamics have been and continue to be dependent on our understanding of small-scale properties that we are able to test experimentally; CAS offers a method for using the insights and data from small-scale experimental manipulations to understand and predict larger-scale patterns and processes.

AN INTRODUCTION TO COMPLEX ADAPTIVE SYSTEMS IN ECOLOGY

Recently, the Australian ecologist Brian Walker observed that CAS appeared to have a lot to offer with respect to improving our understanding of the dynamics of ecological systems, but he had yet to see a demonstration of what that offering might contain. He suggested that *Ecosystems* develop a Special Section on complex adaptive systems, to explain how this approach could be applied to understanding and managing ecological systems. We solicited the following articles in an attempt to provide a stimulating and diverse overview on the use of CAS in the field of ecology.

Simon Levin (in this issue) provided the first article, which outlines the structure of complex adaptive systems and provides guidance for applying our understanding of such systems to ecological problems. He defines complex adaptive systems to be systems with interacting individuals that vary, are spatially discrete, and change in response to selection. This definition is a simplification from previous work (Arthur and others 1997b) and facilitates our identification of those systems that exhibit emergent properties from small-scale processes. CAS do not depend, per se, on the presence

of genetic-level variability. They do, however, depend on a population of interacting agents that varies either due to their intrinsic attributes, their environmental context, or their pattern of interactions with other agents.

Bonabeau (in this issue) discusses the formation and maintenance of self-organized patterns in colonies of social insects, with particular reference to ant colonies. Social insect colonies are composed of hundreds to millions of genetically similar individuals. These individuals interact locally yet collectively produce large-scale patterns of colony dynamics. Researchers since at least Darwin have been fascinated by how large colonies appear to have organized collective behavior. Reintroducing the concept of "stigmergy," Bonabeau discusses ant-colony behavior as an emergent property of self-organization based on local communication among individual ants. Through his discussion of ant-colony behavior, he illustrates the role of self-organization as a defining property of CAS and how this approach to understanding self-organization can be applied to other dynamic, interacting populations.

Large-scale patterns also emerge in human societies from the interaction and cooperation of individual people. Specifying only the rules governing interactions among individuals can produce societal-level patterns of behavior (Axelrod 1984, 1997). Karl Sigmund (in this issue) uses game theory to discuss the role of reciprocity in the interactions among individuals and makes the important point that cooperation can be adaptive in the formation and maintenance of groups or societies.

Complexity also arises at the community and ecosystem levels. Bruce Milne (in this issue) discusses the application of integrative analysis techniques such as renormalization group analysis, borrowed from physics, to understanding pattern formation at the landscape level. He suggests that the use of these types of approaches may lead to a synthesis within ecology to understand scaling patterns across hierarchical levels of organization.

The final article discusses the application of CAS to the management of interacting and coevolving social and ecological systems. Janssen (in this issue) uses genetic algorithms to model adaptation in two management situations: how the evolution of drug resistance alters malaria dynamics, and how individual-level variability in human perspectives alters group responses to elevated atmospheric carbon dioxide. These cases illustrate how relatively simple CAS techniques can produce novel perspectives of complex management problems that are difficult to address with traditional ecological models.

THE POTENTIAL OF COMPLEX ADAPTIVE SYSTEMS APPROACHES

Complex adaptive systems offer ecologists tools to analyze how large-scale organization arises and is maintained and reorganized by processes occurring at smaller scales of organization. This understanding should improve our ability to manage complex ecological systems. For example, management of salmon in the Pacific Northwest has focused on the absolute number of salmon rather than the heterogeneity within salmon populations, despite the well-known importance of this behavioral and genetic heterogeneity (Gross 1991). While maintaining some populations, this policy has led to the extinction of many stocks and the endangerment of hundreds of others. CAS-based management models that explicitly consider variability among and across salmon populations have the potential to improve salmon management greatly (Volkman and McConaha 1993; Jager and others 1997; Policansky and Magnuson 1998).

The ability of ecosystems and the biosphere as a whole to respond to perturbations such as changes in climate, declines in biodiversity, and disruption of regional and global biogeochemical cycles is difficult to predict. Understanding how change at one level of biological organization will alter emergent patterns or mechanisms at another level of biological organization is one of the most pressing problems in ecology. CAS approaches offer insights into these cross-scale interactions and enable analysis of the role of adaptation in governing system dynamics and response to novel situations. An extension and challenge is to use our understanding of ecosystems as complex adaptive systems in our management efforts. Clearly, our ability to manipulate and rehabilitate damaged ecosystems rests with our understanding of how these complex systems adapt, respond, and change over time.

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