SPECIAL FEATURE

Paradigms in Ecology: Past, Present, and Future[1]

Ecologists generally discover early in their scientific careers that there are certain fundamental principles, or ''paradigms,'' that can be useful in conceptualizing biological patterns and processes. Whether one uses paradigms in an attempt to make generalizations about nature, as a starting point for scientific discussion, or to teach ecological concepts, it is clear that paradigms play an essential role in the advancement of ecology. Realizing that some pioneering paradigms are as important to modern research as they were during their inception, we convened a symposium at a recent meeting of the Western Society of Naturalists to discuss the significance of historical contributions to the evolution of modern ecology. Our theme was ''How do ecological breakthroughs really happen? And, what can the past tell us about useful future directions in ecology?''

This Special Feature consists of overviews of several popular, fruitful, and contentious issues, showing in each case how an historical context provides valuable insights into the development of key ideas in ecology. These articles are not simply reviews of specific paradigms, but rather focus on how paradigms have contributed to the development and advancement of ecology. Our goal is to provoke interested students to revisit central constructs from an historical perspective. We make no pretense of being all-inclusive. Rather, we have explored selected paradigms hoping that readers will do the same for their specific questions of interest. Our perspective is one of active practitioners of ecology—rather than bona fide philosophers of science—making observations and drawing conclusions relevant to the philosophy and practice of our science.

In the introductory paper, Graham and Dayton discuss how Kuhn's concept of paradigms (Kuhn, T. S. 1962. The structure of scientific revolutions. University of Chicago Press, Chicago, Illinois, USA) is useful for studying the evolution of ecological ideas. They consider how ecological theories are developed, tested, accepted, and eventually attain paradigm status, and they examine various processes leading to ecological progress. They ultimately realize that ecological advances can also serve as impediments to future progress. Increasing specialization, formation of ecological subdisciplines, and a mounting literature are clear signs of progress, yet make it increasingly difficult for researchers to track and exploit recent ecological discoveries, especially among seemingly distant subdisciplines. Thus, progress inherently focuses attention on contemporary research, potentially erasing the memory of previous contributions. They stress that increased appreciation of historical contributions in ecology is necessary to sustain scientific momentum and impede the recycling of ideas.

It is clear that natural populations do not grow unchecked, yet if, when, and how population regulation occurs was a protracted issue during the past century. Hixon, Pacala, and Sandin review the contentious history of the population regulation paradigm and explore current empirical and theoretical issues. They report that progress in studying population regulation was impeded by repetitious debates that questioned fundamental principles, such as whether demographic density dependence is required for population regulation (it is), and whether population regulation occurs solely due to competitive interactions (it does not). Although such debates were vital to the conceptual development of the population regulation paradigm, their contentious nature often led some ecologists to conclude wrongfully that population regulation does not exist. Furthermore, the authors argue that advances in studying population regulation in demographically open systems have recently stalled due to an inability of current fieldwork and theory to grasp fully the inherently different scales over which density dependence can act. They conclude that an appreciation of how density dependence is differentially expressed over broad scales from individuals to metapopulations is key to further advances in understanding population regulation.

That organismal life-history traits may evolve in response to density or fluctuating environmental

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conditions may seem self-evident, but as Reznick, Bryant, and Bashey demonstrate in their reexamination of the now unfashionable theory of *r*- and *K*-selection, the path to such a realization has been circuitous. Since its origination, the *r*- and *K*-selection paradigm has been the subject of heated debate, due primarily to the initial theory's failure to incorporate important aspects of selection and to the occurrence of apparently anomalous data. However, drawing from the theoretical development of the field and their own guppy research, the authors reveal how the paradigm's original concepts were crucial to identifying the roles of density dependence, resource availability, and environmental fluctuations as selective agents in the evolution of life-history patterns. While contemporary research has outgrown the confines of the original *r*- and *K*-selection paradigm, the authors conclude that the early ideas and debates were vital to defining the subdiscipline. The key to future advances lies in how researchers reconcile inconsistencies between paradigmatic ideas and empirical data, while taking advantage of historical conceptual developments.

The rocky intertidal zone has long been a wellspring of ecological theory. In their paper, Robles and Desharnais examine the origin and development of predation theory as it attempts to explain one of the most conspicuous phenomena of rocky shore communities, intertidal zonation. They describe shifting perspectives of the causes of intertidal zonation: from an emphasis on physical stresses alone, to the hypothesis that zones are static refuges from predation, to the current synthesis depicting dynamic processes, in which an equilibrium between prey production and predation set the lower boundaries to prey zones. The contemporary synthesis is presented as a spatially explicit population model, illustrating how this new approach employs spatial information to understand the dynamic processes shaping natural communities. They conclude by arguing for the reliance of contemporary ecological advances on insights of earlier research, and they highlight ways by which paradigms evolved to accommodate new, sometimes contradictory data, often facilitated by technological advances.

The papers in this Special Feature testify to the fundamental role of debate in propelling to paradigm status some of the most important and influential ideas in ecology. Accordingly, Naeem's review of the contested role of biodiversity in ecosystem functioning provides a contemporary example of the ecological dialectic that pits thesis against antithesis, drives periodic debates within ecology, and spurs the emergence and decline of paradigms. He discusses how the disputed concepts of ''ecosystem'' and ''community'' are vital to understanding the significance of biodiversity and the consequences of its loss; and he argues that, without these concepts, ecologists lack the necessary framework for relevant theoretical, observational, and experimental findings. He urges that students not be distracted, dismayed, or dissuaded by debate in ecology, but rather that they seek to evaluate critically the deeper causes of debate, which requires underlying familiarity with the history of ecology.

In the final paper, Paine asks whether or not advances in ecology occur by the process proposed by Kuhn in which old belief systems are overturned by upheaval. Unlike the physical systems on which Kuhn's ideas were based, biological systems are impelled by many processes that interact in often unpredictable ways. As such, ecological paradigms are rarely fixed upon single binary (yes/no) models that, when rejected, negate all prior advances. Instead, Paine argues that the pluralistic nature of ecology buffers the discipline from revolution, with advances in ecological understanding coming as a continued refinement of pre-existing models and ideas. The most significant recent advances in ecology have not been driven by theoretical revolution, but rather have resulted from methodological and technological innovations that have improved our ability to test new hypotheses, to revisit old ones, and to explore uncharted territory.

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