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What Is the Role of Ecology in Understanding Ecosystem Resilience?

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In the article that begins on page 489 of this issue of *BioScience,* Andrew J. Kerkhoff and Brian J. Enquist make an important synthesis from two hitherto largely separate fields of biological inquiry. One is the conceptually well-established, although not uncontentious, area of allometric scaling laws. The other is the less-established area known as resilience.

The concept of resilience, as applied to an ecosystem, is loosely defined as the ability of the system to maintain its function when faced with novel disturbance. The concept is related to stability, but with its focus on maintenance of function and novel disturbance, resilience uniquely encompasses aspects of society's reliance on ecosystem services and increasing anthropogenic change. Thus, scientists from many different backgrounds recognize the societal importance of resilience and are intellectually intrigued by resilience concepts.

While ecologists generally seem to share this perspective, many are also frustrated by the diversity of definitions for resilience and the complex role of ecology in this area. These issues arise partially from the history of resilience research, which has been performed by very different groups of scientists, and partially from the inherent difficulties of integrating interdisciplinary research. Indeed, resilience is still an evolving concept. Since resilience research is not driven solely by ecology, the challenge for ecologists is to understand resilience perspectives from multiple fields in order to better integrate traditional ecology with modern perspectives and research on resilience.

A brief history of resilience

Holling (1973) and Pimm (1984) used a mathematical approach to illustrate resilience concepts in ecology. Parallel development of resilience concepts by these two researchers and others resulted in two dominant paradigms. Engineering resilience (Pimm 1984) is the length of time that a system takes to return to equilibrium following perturbation (i.e., disturbance). Ecological resilience (Holling 1973) is the amount of perturbation a system can withstand before it moves into a different basin of attraction or stability domain; there are several variations on this general theme, including the idea of system "flips" (Scheffer et al. 2001), which may make it hard to return a system to a stability domain that it has left. These paradigms of resilience are now seen primarily as analogies, at least partially because of the difficulties in interpreting these mathematical models clearly in an empirical, ecological context.

Much of the current research on resilience relevant to ecosystems has broadened to include multiple fields and moved to a complex adaptive systems (CAS) approach. Complex adaptive systems are composed of diverse components with localized interactions and a selection process (Levin 1998). Scientists from many fields, interested in the response of CAS to novel disturbance, define resilience as maintenance of system function when confronted with some perturbation that exceeds the historical range of variation. Two main types of research outside of traditional ecology comprise much current resilience research. First, researchers taking a CAS approach in engineering, computer science, physics, and other fields look for commonalities among their systems to elucidate which characteristics of CAS enhance resilience (often termed "robustness" in the CAS context). These general principles can be applied to ecosystems. The robustness projects carried out at the Santa Fe Institute (*www.santafe.edu*) are a clear example of this type of research. Second, researchers interested in sustainable development and adaptive management use a CAS approach in studying coupled social–ecological systems (SES). The SES approach differs from that of traditional ecology by placing equal weight on the human and ecological dimensions of ecosystem function and maintenance. The Resilience Alliance (*www.resalliance.org*) has spearheaded much of this SES research.

Differences in approaches among traditional ecology, SES, and CAS in nonecological fields, though rarely articulated, may dissuade ecologists from working with the resilience concept. In part, these differences have developed because researchers from different fields highlight the facets of resilience that are most important for their primary field, thus contributing to the vagueness of the resilience concept as perceived by ecologists. In addition, researchers comparing CAS across fields or working within SES frequently are problem driven and use a case study approach. In contrast, traditional ecology is dominated by hypothetico–deductive reasoning and experimentation. These differences make it difficult for ecolo-

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gists to reconcile current ecological knowledge and approaches with current progress in understanding resilience.

Ecology's relevance to resilience

Some resilience researchers argue that only an SES perspective makes sense for ecosystem resilience, because every ecosystem is affected by humans. However, in many ecosystems, the level of human impact has been relatively small over the long timescales that affect the development of ecosystem structure and characteristics. In addition, most ecosystems have a long history of nonanthropogenic disturbance that may remain more influential than human impacts. In any case, scientists clearly must understand ecological processes and how they cohere despite a range of stressors in order to gain an a priori expectation of ecosystem response to novel disturbances. Focusing on how basic ecological characteristics and processes respond to novel disturbance will contribute to understanding how society might develop sustainably, but it does not necessarily require ecologists to consider explicitly the human origins of novel disturbance at the level of hypothesis generation and experimental design.

Ecology's unique contribution to resilience

Ecology is already beginning to incorporate CAS approaches that contribute to the broader picture of resilience. Several well-developed areas of ecology are closely related to mechanisms thought to be important in CAS resilience, particularly the biodiversity–stability debate, the study of ecosystem flips and hysteresis, and analyses of the structure–stability relationship of ecological networks (e.g., food webs). However, traditional ecology studies still differ from those using the CAS resilience concept when they do not explicitly incorporate novel disturbance or maintenance of system function. For example, studies of biodiversity and stability frequently do not focus on truly novel disturbance.

Ecologists also have unique perspectives that can contribute to the concept of resilience. Community and ecosystem ecologists appreciate the role of natural selection and evolution in shaping ecological response to disturbance, which is largely missing from the current discussion on resilience. Long-term data on ecosystem responses to the historical environmental regime form the basis of many ecological studies, and these data are particularly relevant to understanding resilience when a system is faced with a novel disturbance. With increasing anthropogenic change, this situation is becoming more familiar to ecologists as their long-term plots are affected (e.g., Vandermeer et al. 2004), and it presents an opportunity for ecologists to think about how their work can be informative in a resilience context.

For example, Kerkhoff and Enquist apply the idea of scaling laws from ecology to the problem of identifying and measuring loss of resilience in ecosystems. The underlying logic is that all organisms are subject to the same allometric rules that underlie scaling laws, resulting in constraints on the ecosystem. Thus, resource use and community demography must be in a steady state in undisturbed systems. Ecosystems that deviate from scaling laws represent deviations from these assumptions and so point to the possibility of there being an underlying community reorganization, a well-recognized phenomenon in the study of resilience. Kerkhoff and Enquist further develop this method by presenting strong evidence that this approach is realistic for systems that can be studied in practice. Their data show that disturbed forest systems with known disturbance and recovery trajectories deviate from scaling laws, while undisturbed systems comply with them.

The remaining barriers to a larger representation of traditional ecology within current resilience research are largely those of communicating among different groups interested in resilience and of framing ecological results in a resilience context. In 2003, I helped organize a workshop cosponsored by the Resilience Alliance and the Santa Fe Institute's robustness project in order to bring these groups together, along with several traditional ecologists, to discuss these issues. The article by Kerkhoff and Enquist in this issue of *BioScience* is one outcome of this workshop.

Like many other traditional ecologists, I initially had difficulty appreciating the diversity of viewpoints and research surrounding the idea of resilience. However, after completing a traditional ecology and evolution graduate program and postdoctoral training on resilience, I now appreciate these better and see the potential for a merging of the different scientific approaches and disciplines within this area. I also see the potential for a strong ecological contribution to resilience in the form of a better understanding of how ecological processes affect the response of ecosystems and SES functions to novel disturbance. Other foreseeable contributions from ecology might be greater clarity about the importance of selection in CAS, and long-term studies that address how systems function before and after novel disturbances. Moreover, work like that of Kerkhoff and Enquist and other ecologists shows that the synergy and complementary insights gained from integrating current views on resilience is worth the intellectual investment required to bridge different scientific approaches.

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