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The 21st century is an exciting time for biological scientists and other researchers interested in complex systems. Relating biodiversity to ecological function and sustainability, understanding the dynamics of coupled human and natural systems, and unraveling functional genomics at scales ranging from organisms to community assemblages—to provide just a few examples—are challenging research opportunities that portend exciting and significant breakthroughs for science and society. Biological scientists and their colleagues from physical, social, mathematical, and other disciplines are poised to explore many of these complex issues.

In response to the need to address questions of increasing breadth and complexity, the study of "biocomplexity" has emerged and continues to develop as both a research focus and a research program, funded through the National Science Foundation. Because biocomplexity has so rapidly developed, it seems appropriate to define biocomplexity, examine some of the characteristics of biocomplexity, and speculate on the future of biocomplexity studies. The objective of this article is to address these three issues in the context of both the scientific and funding environments that gave rise to biocomplexity.

Defining biocomplexity

Biocomplexity is a term that does not yet reside in most dictionaries and spell-checkers. Although difficult to define precisely, it is nevertheless a concept that many scientists and engineers can intuitively grasp. All of us have, at one time or another, been struck by the emergent complexities of biological phenomena under investigation, particularly as time or space scales change and as underlying mechanisms or external forcing functions confound or amplify one another. Despite this intuitive understanding of biocomplexity, the term has most frequently been associated with the recent National Science Foundation program solicitations for "Biocomplexity" and "Biocomplexity in the Environment."

Editor's note: This article was derived from a panel discussion at the AIBS annual meeting in March 2001.

Because biocomplexity has been an explicit topic of study for only 2 years, any current definition of the term is probably inadequate and will most likely change dramatically as our scientific understanding of this concept grows. Despite this caveat, we will define biocomplexity as *properties emerging from the interplay of behavioral, biological, chemical, physical, and social interactions that affect, sustain, or are modified by living organisms, including humans.*

Characteristics of biocomplexity

To better elucidate the meaning of biocomplexity through some examples, we will first emphasize what biocomplexity is not. Biocomplexity is not a synonym for reductionist science and it cannot be addressed without using highly integrative approaches. Furthermore, a single investigator cannot

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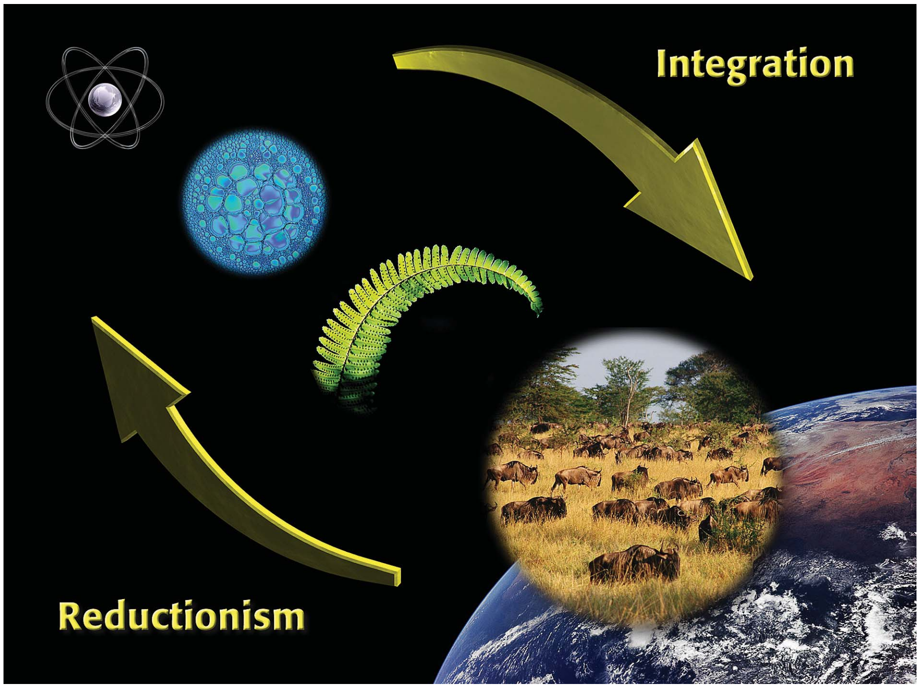

Figure 1. Understanding of biocomplexity requires much more emphasis on the synthesis and integration of information from across temporal, thematic, and spatial scales. This new perspective recognizes the interactions in biological systems, the connectedness between biological systems and their physical environments, and the complex properties that emerge from the interplay among the biological and environmental components. Photographs: Earth, wildebeest, fern, and cells from Corbis Corporation (www.corbis.com)*; atom, courtesy of Dirk Brandts, National Center for Ecological Analysis and Synthesis, University of California–Santa Barbara. Figure illustrated and provided by Dirk Brandts.*

typically address biocomplexity questions, which by their very nature are complex and interdisciplinary. Often, because of time and monetary constraints, scientists have worked very hard to reduce complexity in their field and laboratory studies. This is accomplished through carefully controlled experiments and observational programs in which the number of independent variables is reduced to a manageable size and significant effort is made to minimize "interference" from external factors, as well as interactive and feedback effects that are difficult to identify and quantify. Such efforts are designed to enable the identification of causal mechanisms and are viewed by many as being the hallmark of reductionist science. There can be no doubt about the value of this approach—it has led to much of our knowledge base to date.

On the other hand, it is also true that the time and monetary constraints that have forced us to tease apart underlying mechanisms for a small and manageable piece of the puzzle often yield results that are not robust in real-world situations with myriad confounding factors operating at different temporal and spatial scales. Phenomena in the environment can be understood most effectively through the synthesis and integration of information across relevant temporal, spatial, and thematic scales (Figure 1). Two particularly salient features of biocomplexity are that (1) it arises as temporal, conceptual, and spatial "boundaries" are breached and (2) the system may exhibit emergent or unexpected properties (i.e., behavior of the whole is often not predictable based on a study of the component parts). Thus, biocomplexity can be understood only through the combined efforts of scientists from many disciplines who are equipped (and supported) to work at the relevant spatial and temporal scales. Among the questions that underlie biocomplexity research are the following:

- How do systems with living components respond and adapt to stress?
- Are biological adaptation and change predictable in a changing environment?
- How will climate change affect species' ranges across multiple trophic levels?
- Can we forecast the combined effects of climatic and socioeconomic change?
- How does diversity (species, genetic, cultural) affect system sustainability?

It may not be readily apparent that these examples fully encompass biocomplexity as previously defined. However, several characteristics of these issues set them apart from typical research questions. First, these biocomplexity questions are relevant for organisms ranging from microbes to humans. Second, they are relevant for a wide range of environments, from polar regions to volcanic vents to tropical forests to agricultural lands to urban centers. Implicit in these first two points is the recognition that biocomplexity may cross multiple hierarchical scales of biological organization (e.g., gene, cell, individual, community, ecosystem, biosphere) and environments. Third, biocomplexity may be reflected in nonlinear, chaotic, or even unpredictable behaviors. Thus, highly innovative and quantitative (that is, mathematical, statistical, and simulation) approaches are often essential for elucidating biocomplexity. Fourth, biocomplexity may be typified by interactions that are likely to span multiple hierarchical levels as well as several spatial and temporal scales. Advances in geometry, graph theory, topology, control theory for chaotic systems, and novel approaches for managing and modeling uncertainty are just a few examples of how fundamental mathematics may enhance our understanding of "biocomplex" systems.

Examples of biocomplexity research

Three recently published research studies exemplify many characteristics of biocomplexity in the environment. First, Niklas and Enquist (2001) demonstrated that the relationship between the growth rate (annualized biomass production) and the body size of plants is scale-invariant over 20 orders of magnitude in body size (Figure 2). This study exemplifies the predictive power that can result from the assembly and analysis of complex data sets representing biological and physical interactions across many scales of resolution. The scaling relationship was indifferent to habitat and phylogenetic affiliation (consistently applying to single-celled algae, aquatic ferns, aquatic and terrestrial herbaceous dicots, and arborescent monocots, dicots, and conifers, including the giant sequoia). That a seemingly simple linear relationship exists to explain such a fundamental relationship in plants is truly a remarkable discovery—one that can be useful to scientists and resource managers in myriad ways.

Second, Pascual and colleagues (2000) showed that outbreaks of cholera in Bangladesh closely track Pacific warming, which is largely associated with El Niño–Southern Oscillation (ENSO) weather patterns. Their integrative work required sophisticated mathematical modeling and combined research from disciplines as disparate as oceanography and human epidemiology.

Third, Parmesan and colleagues (1999) also demonstrated that weather patterns—in this case, long-term patterns reflecting global warming—can affect the distribution of species across space and time. They combined natural history accounts with decadal temperature fluctuation data to show that the species ranges of several nonmigratory butterflies in Europe have shifted poleward over the last 50–100 years. Their work revealed previously undiscovered, broad-scale, and consistent changes in the distributions of many species. Project success depended on data sharing and collaboration among a large team of international scientists focused on elucidating these broad-scale patterns. All three examples exhibit characteristics of biocomplexity research. They addressed

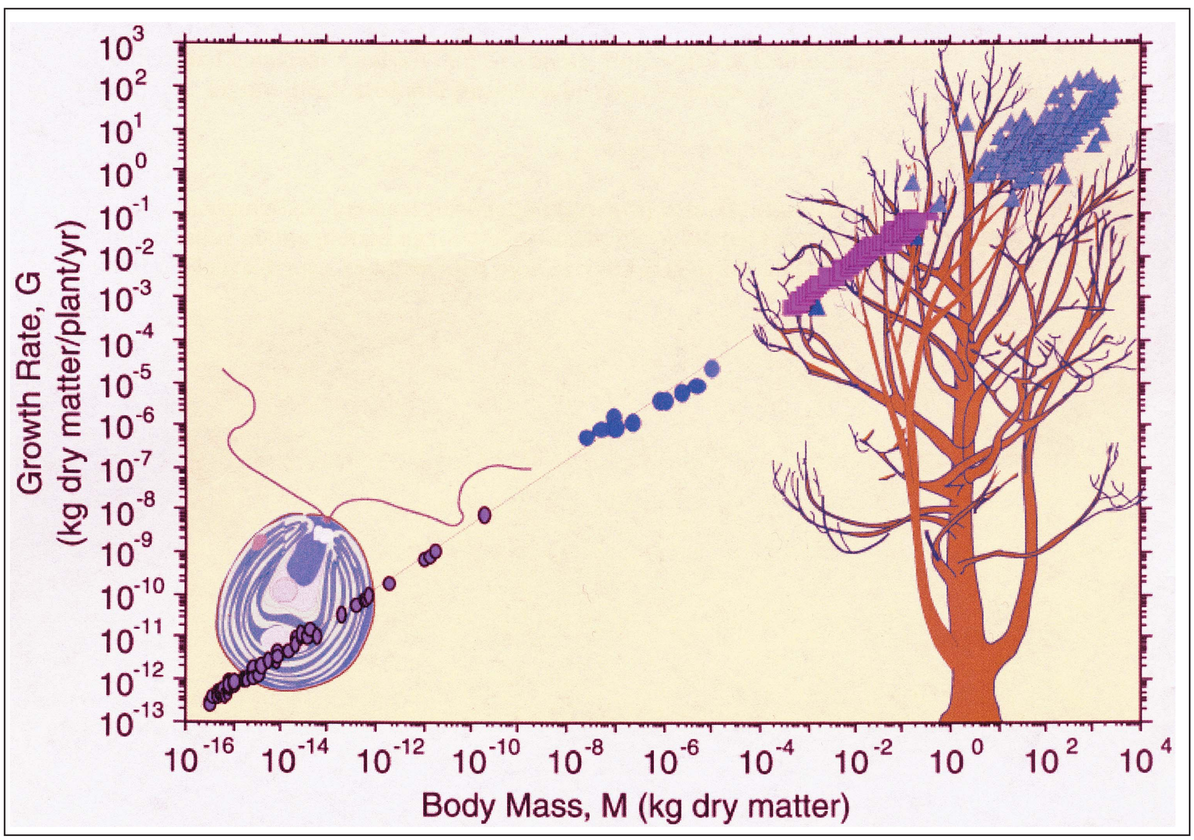

Figure 2. Annualized biomass production (growth) rate, G, of unicellular and multicellular plants plotted against body mass, M. Adapted from Niklas KJ and Enquist BJ (2001). Figure drawn and provided by K. J. Niklas (Cornell University).

fundamental questions in new, integrative, and innovative ways; they required collaboration among scientists from wide-ranging backgrounds; and they addressed broad-scale patterns and processes.

In a recent assessment of the state of ecological research, Thompson and colleagues (2001) identified four principal research frontiers that were deemed paramount for understanding the ecological dynamics of biocomplexity:

- dynamics of coalescence in complex communities—that is, seeking to understand how species availability, physical environment, evolutionary history, and the temporal sequence of assembly interact to develop complex ecological communities from a regional species pool
- ecological memory—that is, documenting how "past environmental conditions and subsequent selection on populations—[are] encoded in the current structure of biological communities and reflected in the genetic structure of species" (p. 17)
- emergent properties of complex systems, such as determining "whether first principles of physics, chemistry, and evolution by natural selection can successfully predict the composition, structure, and functioning of ecosystems" (p. 20)
- ecological topology—that is, identifying "rules" and evaluating how these rules, each of which operates over different spatial and temporal scales, interact to define ecological patterns and processes

Clearly, past research success, as well as future success in addressing "frontier" biocomplexity issues, such as those identified for the ecological sciences by Thompson and colleagues (2001), presupposes a new era of interdisciplinary collaboration, increased access to large research and monitoring databases, greater emphasis on integration, and enhanced technological sophistication and innovation.

Biocomplexity as an NSF program

Biocomplexity has existed as a program at NSF since 1999. Annual program solicitations illustrate phases in the evolution of our conceptual understanding and present different approaches to the study of biocomplexity.

Biocomplexity Phase I. The first program announcement for biocomplexity appeared in 1999 (NSF 1999). Phase I of the competition focused on the functional interrelationships between microorganisms (prokaryotes, including archaea and eubacteria, and unicellular eukaryotes, including algae, protozoa, and fungi) and biological, chemical, geological, physical, and social systems. The announcement particularly encouraged projects that sought to understand the ways that microorganisms structure or control complex systems.

This first program announcement was significant in several respects. First, biocomplexity was defined as "a dynamic property of life [that] emerges from the functional interrelationships between biological entities, at all levels of organization, and the biological, chemical, geological, physical and social environment, at all levels of aggregation." Second, there was an explicit focus on sophisticated research approaches that could integrate across conceptual, spatial, and temporal boundaries. Third, there was also explicit recognition that new types of collaborations were required, especially those that transcended institutional, departmental, and disciplinary boundaries. Fourth, although the program announcement did not establish criteria for "research sophistication," it did offer a list of the types of questions appropriate for the biocomplexity competition, which focused on highly quantitative concepts such as feedbacks, resiliency, fractal analysis, chaos, and nonlinear dynamics.

Response to this first competition was extremely positive. NSF received 118 preproposals; 34 groups were encouraged to submit full proposals. A total of almost $18 million (considerably more than the planned $11 million) was awarded to five teams of scientists; awards ranged in size from $2.2 million to $4.8 million. The successful projects focused on

- interacting roles of mycorrhizal fungi, plants, and soil resources in carbon and nutrient transfers
- oceanic nitrogen fixation and global climate
- integration of genomic and ecologic analysis of symbiotic bacteria that mediate insect herbivory
- bacterial and computational experiments to identify general principles that govern the evolution of complexity
- factors affecting, and impact of, diazotrophic microorganisms in the western equatorial Atlantic Ocean

Characteristics of these projects included the interdisciplinary and interinstitutional (up to six institutions) nature of the research teams, the focus on nonlinear dynamics and feedback loops, the incorporation of sophisticated modeling and computationally intensive analytical approaches, and the high dimensionality of the systems under study.

Biocomplexity Phase II. Phase II of the competition (NSF 2000) was much broader in scope than Phase I and focused on integrated research to better understand and model complexity among biological, physical, and social systems. This program announcement particularly encouraged projects that would "directly explore nonlinearities, chaotic behavior, emergent phenomena or feedbacks within and between systems and/or integrate across multiple components or scales of time and space in order to better understand and predict the dynamic behavior of systems." In addition to full research proposals, the program announcement specified that 10 percent of the budget ($5 million of $50 million) would be set aside for smaller proposals, termed *incubation activities*, that would enable new groups of individuals to develop biocomplexity projects via workshops and other development activities.

In addition to the expansion in scope, Phase II was different in that many of the criteria for successful biocomplexity projects, particularly those related to research approaches, were explicitly stated. In particular, competitiveness was related to the extent to which a systems-level approach was adopted, meaning those projects involving the holistic, "explicit and a priori integration across multiple components of time and space and...[using] a conceptual, mathematical or computational model, computer simulation, or artificial intelligence techniques to direct the research." There was specific emphasis on the need to estimate uncertainty in model predictions, the need for sufficient sample size and statistical power, and, moreover, the requirement that at least one quantitative expert be part of the research team.

Response to the Phase II competition was overwhelming. Approximately 300 full and 165 incubation activity proposals were submitted, from which 16 research projects and 57 incubation activities were funded by NSF ($52.5 million total). Successful research projects were highly quantitative and dealt with complex phenomena across multiple conceptual, spatial, and temporal scales. Research themes included the following:

- universal scaling laws for biodiversity
- mathematical and biological modeling of cell polarization
- dynamics of introduced and invasive species, including diseases
- self-organization in planktonic ecosystems
- complex human–environmental interactions, including the basis for land-use decisionmaking

Incubation activities covered a similarly broad spectrum and included a diverse mixture of pilot proof-of-concept studies, actual and virtual workshops, tests of simulation and mathematical models, and related activities.

Biocomplexity Phase III. Phase III of the competition (NSF 2001), "Biocomplexity in the Environment," is expected to support about 110 awards ($55 million total), of which 70 will be for research projects and 40 will be for conference, planning, or exploratory activities. Instead of a single competition, Phase III and subsequent competitions will focus on four areas:

1. dynamics of coupled natural and human systems
2. coupled biogeochemical cycles
3. genome-enabled environmental science and engineering
4. instrumentation development for environmental activities

Phase III places biocomplexity directly in an environmental context and, like the prior year's competition, emphasizes research with a high degree of interdisciplinarity and a focus on biotic interactions in complex environmental systems and on systems with high potential for exhibiting nonlinear or tightly coupled behavior with other systems. Holistic and highly quantitative approaches continue to be emphasized in Phase III. For example, the development of probabilistic models, novel algorithms, and statistical techniques to comprehend the effects of multiple stressors or threshold effects on environmental systems should greatly enhance researchers' ability to develop ecological forecasting tools. In addition, two other integrative elements are considered essential in all activities. First, formal educational activities from precollege to faculty levels, or informal education for the public via science centers, aquaria, museums, and similar facilities, are expected to be integrated with all research. Second, investigators are strongly encouraged to adopt a global perspective and, if appropriate, identify international research partners.

Future of biocomplexity research

We anticipate that the study of biocomplexity will yield significant new knowledge. In particular, emerging results from biocomplexity projects should enable us to

- add to knowledge about the environment, ranging from the genetic diversity of microorganisms to global climate change
- gain better understanding of the role of living organisms in the global, regional, and local chemical and water cycles
- learn about human influences on natural processes and of natural processes on human behavior
- develop new methods and computational strategies to model and manage complex systems
- use biologically or biocomplexity-inspired design strategies to discover new materials, sensors, engineering processes, and other technologies

Most important, biocomplexity represents an increasingly important way of doing science. Funds are being provided to build comprehensive projects that address biocomplexity questions at *relevant* conceptual, spatial, and temporal scales. Instead of decomposing a complex problem into small, manageable pieces that can each be addressed over the long term via several multiyear projects, scientists are being encouraged to address problems from a holistic and integrative perspective (Figure 1). Also on the horizon is a new program to move the interdisciplinary culture in an increasingly quantitative direction. The NSF's proposed Mathematical Sciences Initiative was envisioned as a comprehensive program that will stimulate interdisciplinary research through mathematical innovation and that will enhance biocomplexity research by providing funding to foster collaboration among mathematicians, scientists, and engineers. If Congress approves this initiative, funds will be available to support work that enhances the use of existing mathematical and statistical approaches and work that leads to new mathematical advances of relevance to complex systems. As a result, it is expected that scientists will begin to understand the emergent properties of complex systems as the scale and levels of aggregation within these systems change—that is, to understand phenomena as they occur in the real world.

The results of the projects funded through NSF's biocomplexity programs are expected to have significant and direct impact. More important, however, biocomplexity research may lead to a paradigm shift, whereby scientists routinely address complex problems at the appropriate spatial and temporal scales in an integrative fashion, and collaborate with colleagues from all relevant disciplines. This type of approach will support understanding of complex phenomena and emergent properties, as well as the discovery of universal laws.

Such a paradigm shift would naturally necessitate a new generation of researchers who are accustomed to broaching conceptual, disciplinary, and institutional boundaries. The critical role of collaboration in understanding biocomplexity has been emphasized by Rita Colwell (2000), NSF director, who pointed to the need to collaborate on all fronts and across all disciplines and scales. Ultimately, biocomplexity research will benefit not only from collaboration among multiple disciplines but also from the development of truly interdisciplinary teams of scientists.

Current research and technology capabilities are frequently inadequate for the comprehensive examination of the environment at the multiple conceptual, spatial, and temporal scales that are the foundation for understanding biocomplexity. Alan Covich (2000) noted that "examining the self-organization, hierarchical structure, and dynamics of communities and ecosystems over time and space requires new approaches and a new generation of nonlinear modeling, designed by collaborators in the natural, social, and computational sciences" (p. 1035). Moreover, holistic examination of complex biological phenomena necessitates the synoptic collection and integration of data representing scales ranging from the genome to the globe. Few, if any, biological field stations or marine laboratories are equipped to study phenomena at these scales. Such research ultimately requires a new research platform, such as the National Ecological Observatory Network (NEON), which has been proposed to fill this void (Mervis 1999).

Conclusion

Although we have attempted to define biocomplexity, this definition must be considered tentative at best. The ultimate definition rests on those studies that are under way, new studies to be funded in competitions this year and in future years, and on a new cohort of biologists and other scientists who will be increasingly better prepared to elucidate biocomplexity. These studies have enormous repercussions for both science and society. No one has better emphasized this point than Rita Colwell (1998) who, in a plenary address for the 49th annual meeting of the American Institute of Biological Sciences, expounded upon what it means to understand biocomplexity: "It is not enough to explore and chronicle the enormous diversity of the world's ecosystems. We must do that—but also reach beyond, to discover the complex chemical, biological, and social interactions in our planet's systems. From these subtle but very sophisticated interactions and interrelationships, we can tease out the principles of sustainability" (p. 786).

Acknowledgments

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