The Sustainable Biosphere Initiative: An Ecological Research Agenda: A Report from the Ecological Society of America

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THE SUSTAINABLE BIOSPHERE INITIATIVE: AN ECOLOGICAL RESEARCH AGENDA

A Report from the Ecological Society of America[1,2]

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Key words: biological diversity; biosphere; ecological research; environmental decision-making; global change; research agenda; research funding; research priorities; sustainability; sustainable ecological systems.

PREFACE

This preface introduces a document that is unprecedented in its scope and objectives. In August 1988 the Ecological Society of America initiated an effort to define research priorities for ecology in the closing decade of the 20th Century. Several independent factors motivated this endeavor. First, within the academies of science, the halls of government, and the institutions that fund research, it had become increasingly clear that scientists must order their priorities and make hard judgments concerning the research directions that hold the greatest promise for advancing our base of knowledge and for improving the human condition. Responding to this need, Frank Press, the President of the National Academy of Science, challenged all scientists to define their priorities. Financial resources are finite. Competing national demands range from national security to social services, and various major priorities vie for attention and funding. Consequently, it is not feasible to support all scientific research. If we as scientists do not set our own priorities, others will do so for us.

Second, the need to ameliorate the rapidly deteriorating state of the environment and to enhance its capacity to sustain the needs of the world's population has become paramount. We will increasingly require ecological knowledge to utilize and sustain the Earth's resources. Although the needs for new knowledge and for the application of existing knowledge are increasing, the means to accomplish these goals are decreasing due to the limitation of available funds. Tough decisions need to be made concerning what to fund and what not to fund.

Against this background it is essential to make clear that basic research is the foundation on which informed environmental decisions must rely: the greater are the applied needs, the more important becomes basic research. If this point is not made clear, narrowly based applications will carry the day. Unless the science of applied ecology is based on a sound foundation, attempts to manage the environment are bound to fail. The greatest advances in ecological understanding have come from the creative fertility of investigators, carrying out basic research motivated by intellectual curiosity. It is critical to examine how best to nurture the development of this basic substructure, and to train the ecologists of tomorrow.

The dilemma of increasing needs in the face of decreasing means, and the challenge to identify priorities, set the stage for the Ecological Society of America to lead its members into a period of introspection, in which the whole realm of ecological activities would be examined. The present study is the centerpiece of that analysis. It identifies those endeavors that were deemed most ur-

[1] The authors listed serve as members of the Ecological Society of America's Committee for a Research Agenda for the 1990's. Institutional affiliations can be found on page 405.

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gent in terms of both the advancement of the field and the potential for improving the human condition.

In order to accomplish this monumental task, one of us (HAM) established a broadly representative committee, under the leadership of Jane Lubchenco, then Vice-President and now Second President-Elect. This committee, composed of ecologists representing a wide array of ecological subdisciplines, met intensively over a period of more than a year. They undertook to identify the most exciting and relevant areas of ecological research and to submit their conclusions to the critical evaluation of the Society's membership and other interested parties. Their efforts included consideration of research priorities, needs in education and outreach, and strategies for implementing the recommendations.

The process of review and revision has been one of the most thorough any document has ever received. Although this effort was led by committee, the document itself truly represents input from the entire Ecological Society of America, and from a broader community as well. Early on and throughout the process, calls were made through the *Bulletin* of the Society, through the Public Affairs Office newsletter, and through workshops and seminars for input on the document and the process itself. These calls resulted in the involvement of large numbers of people, and the incorporation of their ideas. In August of 1990, at the annual meeting of the Society, a presentation of the draft document was made to nearly a thousand members. There was widespread support for its sense and structure. Questions from the floor provided further input as did a subsequent workshop, also attended by a large number of Society members. Following the annual meeting more than 150 letters were received from members giving further suggestions. This new input was incorporated by the committee into the document that follows. Although individual Society members undoubtedly would not agree with every detail of this report, the iterative review and revision have resulted in a document that is a community-wide effort of which we can all be proud. The Executive Committee of the ESA has enthusiastically endorsed this report. We cannot rest too long on the success that we have achieved. The challenge that faces us is to make the program outlined here a reality, and to include our international colleagues and those in related disciplines as partners in this bold undertaking, to provide the scientific basis for a sustainable biosphere.

The committee is pleased to acknowledge the Andrew W. Mellon Foundation, the Ecological Society of America, and Oregon State University for support for conceptual development of the SBI, and the Andrew W. Mellon Foundation, the National Science Foundation, the U.S. Environmental Protection Agency, the National Aeronautics and Space Administration, and the U.S. Department of Energy for support of publication costs. We (HAM and SAL), gratefully acknowledge the leadership efforts of Jane Lubchenco, and thank the committee for its remarkable efforts.

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President 1988–1989
Ecological Society of America

and

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President 1990–1991
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EXECUTIVE SUMMARY

In this document, the Ecological Society of America proposes the Sustainable Biosphere Initiative (SBI), an initiative that focuses on the necessary role of ecological science in the wise management of Earth's resources and the maintenance of Earth's life support systems. This document is intended as a call-to-arms for all ecologists, but it also will serve as a means to communicate with individuals in other disciplines with whom ecologists must join forces to address our common predicament.

Many of the environmental problems that challenge human society are fundamentally ecological in nature. The growing human population and its increasing use and misuse of resources are exerting tremendous pressures on Earth's life support capacity. Humankind must now develop the knowledge required to conserve and wisely manage Earth's resources. Citizens, policy-makers, resource-managers, and leaders of business and industry all need to make decisions concerning the Earth's resources, but such decisions cannot be made effectively without a fundamental understanding of the ways in which the natural systems of Earth are affected by human activities. Investigator-initiated, peer-reviewed basic research is the foundation on which informed environmental decisions must be based. Ecological knowledge and understanding are needed to detect and monitor changes, to evaluate consequences of a wide range of human activities, and to plan for the management of sustainable natural and human-dominated ecological systems.

In response to these national and international needs, the Ecological Society of America has developed the Sustainable Biosphere Initiative (SBI), a framework for the acquisition, dissemination, and utilization of ecological knowledge which supports efforts to ensure the sustainability of the biosphere. The SBI calls for (1) basic research for the acquisition of ecological knowledge, (2) communication of that knowledge to citizens, and (3) incorporation of that knowledge into policy and management decisions.

Research Priorities

This document focuses primarily on the acquisition of ecological knowledge. It identifies the ecological research programs of highest priority and recommends the steps required to pursue

research objectives. The document also lays the groundwork for improving the communication and application of ecological knowledge.

The criteria used to evaluate research priorities were (1) the potential to contribute to fundamental ecological knowledge, and (2) the potential to respond to major human concerns about the sustainability of the biosphere. Based on these criteria, the SBI proposes three Research Priorities:

- **Global Change,** including the ecological causes and consequences of changes in climate; in atmospheric, soil, and water chemistry (including pollutants); and in land- and water-use patterns
- **Biological Diversity,** including natural and anthropogenic changes in patterns of genetic, species, and habitat diversity; ecological determinants and consequences of diversity; the conservation of rare and declining species; and the effects of global and regional change on biological diversity
- **Sustainable Ecological Systems,** including the definition and detection of stress in natural and managed ecological systems; the restoration of damaged systems; the management of sustainable ecological systems; the role of pests, pathogens, and disease; and the interface between ecological processes and human social systems.

Research Recommendations

Each of these research priorities requires a different type of action. Existing national and international initiatives address aspects of the first two priorities. However, the success of these programs will require increased emphasis on key ecological topics.

RESEARCH RECOMMENDATION #1: Greater attention should be devoted to examining the ways that ecological complexity controls global processes.

Within the topic of global change, insufficient attention has been paid to the ways in which ecological complexity controls global processes. Such key factors as species and habitat diversity, patterns of distribution of ecological assemblages, and differences in the productivity and storage capabilities of different types of ecosystems all influence how the biosphere functions in the Earth system.

RESEARCH RECOMMENDATION #2: New research efforts should address both the importance of biological diversity in controlling ecological processes and the role that ecological processes play in shaping patterns of diversity at different scales of time and space.

Within the topic of biological diversity, much of the current effort is devoted to enumerating the species in various habitats and to preserving biotically significant sites. These important efforts lay the groundwork for the research proposed here and must be continued, but two vitally important topics must also be addressed. First, it will be necessary to discover to what extent patterns of biological diversity are important in determining the behavior of ecological systems (e.g., responses to climate change, rates of nutrient flow, or responses to pollutants). Only when these relationships are known will it be possible to develop management strategies for maintaining natural and human-dominated ecological systems. Second, it will be necessary to understand how ecological processes interact with physical and chemical factors to control or determine biological diversity. Doing so will require investigation of the manner in which individual species interact with and are modified by the abiotic environment on both ecological and evolutionary time scales.

RESEARCH RECOMMENDATION #3: A major new integrated program of research on the sustainability of ecological systems should be established. This program would focus on understanding the underlying ecological processes in natural and human-dominated ecosystems in order to prescribe restoration and management strategies that would enhance the sustainability of the Earth's ecological systems.

Plans for comprehensive programs in the areas of global change and biological diversity are more advanced than those in the area of sustainable ecological systems. Research programs exist to develop specific sustainable natural resources (e.g., sustainable forestry or sustainable agriculture). However, current research efforts are inadequate for dealing with sustainable systems that involve multiple resources, multiple ecosystems, and large spatial scales. Moreover, much of the current research focuses on commodity-based managed systems, with little attention paid to the sustainability of natural ecosystems whose goods and services currently lack a market value. Addressing the topic of sustainable ecological systems will require integration of social, physical, and biological science.

IMPLEMENTATION

Successful implementation of the SBI will require a significant increase in interdisciplinary interactions that link ecologists with the broad scientific community, with mass media and educational organizations, and with policy-makers and resource-managers in all sectors of society. This document recommends specific actions that will begin to develop such links and initiate the first steps of the SBI. The action items that follow will be initiated by the Ecological Society of America, but will require broad support and participation by other groups and individuals, ranging from federal and state funding agencies and other scientific societies to policy-makers, leaders of business and industry, and concerned citizens.

Research component of the SBI

Initiation of the research component of the SBI will involve coordination with ongoing programs as well as initiation of new programs. A series of workshops is proposed to bring ecologists together with experts from related disciplines in the natural and social sciences and with resource-managers and environmental policy-makers to develop projects for immediate action.

ACTION ITEM #1: During the coming year, an organizing committee of the Ecological Society of America will plan workshops with the goal of coordinating the SBI with current research efforts on global change and increasing research on the role of ecological complexity in global processes.

ACTION ITEM #2: During the coming year, an organizing committee of the Ecological Society of America will plan workshops with the goal of developing an initiative on biological diversity that focuses on the ecological causes and consequences of patterns of biological diversity.

ACTION ITEM #3: During the coming year, an organizing committee of the Ecological Society of America will plan workshops with the goal of initiating a comprehensive program on sustainable ecological systems, emphasizing the underlying ecological processes that affect the sustainability of natural and managed systems.

Education component of the SBI

The environmental conditions that have mandated the Sustainable Biosphere Initiative also demonstrate the need for ecological education among citizens of today and tomorrow. Understanding and managing the biosphere requires ecological information. There are many strategies for addressing educational needs, such as working with the mass media to increase public awareness of ecological concepts and issues, making ecological literacy a goal of undergraduate curricula, and developing more interdisciplinary graduate degree programs that involve topics necessary for understanding the biosphere. The following action items represent the first steps in addressing these needs.

ACTION ITEM #4: During the coming year, the Research Agenda Committee of the Ecological Society of America will oversee the preparation and publication of a non-technical, public education document that articulates the importance of ecology and ecological research to society.

ACTION ITEM #5: During the coming year, the Education Section of the Ecological Society of America will develop systematic, short- and long-term strategies for enhancing ecological knowledge among students and the public.

Moreover, the Ecological Society of America should determine the human resources needed to conduct the ecological research proposed by the SBI and should develop specific vehicles to address the identified needs, including training grants and career development awards.

Environmental decision-making component of the SBI

Thousands of ecologically based decisions are made annually by policy-makers and regulatory agencies, land- and water-use planners, resource-managers, business and industry, consulting firms, and conservation groups. To be useful to decision-makers, ecological information must be both accessible and relevant to their mandates and responsibilities. Therefore, the application of ecological knowledge will require better communication between ecologists and decision-makers in all sectors of society. The experience of management-oriented professional societies in setting environmental priorities will be essential to open new avenues of communication.

ACTION ITEM #6: During the coming year, an organizing committee of the Ecological Society of America will begin to explore ways in which ecologists can become more responsive to and bring their expertise more fully to bear on critical environmental problems. This committee will work closely with management-oriented professional societies, resource-managers, and other environmental decision-makers.

International dimensions of the SBI

The framework for this Initiative was developed in North America, but the research priorities and the environmental problems related to them are important world-wide.

ACTION ITEM #7: During the coming year, the Ecological Society of America will organize a meeting of leading ecologists from many nations of the world to evaluate the SBI and to begin construction of an operational framework for international cooperation.

At the same time there will be efforts to interact with governmental (e.g., UNESCO) and non-governmental (e.g., the International Council of Scientific Unions, ICSU) international bodies that have programs closely related to the research agenda of the SBI.

Funding the SBI

Meeting the financial needs of the SBI will require significantly increased funding from both public and private sources. Because of the broad importance of this Initiative, creative approaches to funding research will be required. Typically, public agencies such as the National Science Foundation fund basic research, mission agencies fund research that applies to problems of specific interest to the agency, businesses fund research to answer pressing industry questions, and foundations fund topics or themes of particular interest. The SBI encompasses all of these missions, and as a result, must be planned and funded by a range of agencies and organizations.

Current administrative structures are insufficient to coordinate and fund the range of activities envisioned by the SBI. Consequently, it will be necessary to develop a new administrative structure that allows many agencies to support the integrated research program. To accomplish the needed coordination and funding, a variety of vehicles should be considered, including a new or existing interagency committee, a new national institute, or other administrative arrangements. This new organization would further develop research priorities within the SBI, coordinate funding strategies, and establish and implement procedures for evaluating the research progress of the Initiative.

In constructing new interdisciplinary and interagency approaches, it will be particularly important to preserve the opportunity for creativity and innovation. The cornerstone of the SBI should be investigator-initiated, peer-reviewed research conducted by individual investigators or multidisciplinary research teams.

ACTION ITEM #8: During the coming year, the Ecological Society of America will initiate discussions to develop an innovative framework to coordinate and fund the SBI. Emphasis will be placed on enhancing opportunities for investigator-initiated, peer-reviewed research in the context of coordinated programs that would fund both individual investigators and multidisciplinary research teams.

The ecological research agenda proposed in this document begins with the assumption that advances in understanding basic ecological principles are required to resolve many urgent environmental problems, continues with the identification of three priority areas for intense research efforts, and concludes with actions to be initiated by the Ecological Society of America to strengthen and expand research efforts in these key areas. The success of the Sustainable Biosphere Initiative will depend upon (1) the willingness of individual ecologists to participate in the proposed activities, to disseminate the vision of the SBI, and to plan and execute subsequent phases, and upon (2) the vision and abilities of policy-makers, funding agency administrators, government officials, business and industry leaders, and individual citizens to support, amplify, and extend the actions we have initiated. At present, neither the funding nor the infrastructure in this country is sufficient to address the research needs described in this document. Moreover, achievement of a Sustainable Biosphere will require not only the acquisition of ecological knowledge via research, but also the communication of that information and understanding to all citizens and the incorporation of that knowledge into environmental, economic, and political decisions. Although there are formidable barriers to accomplishing these tasks, achieving a Sustainable Biosphere is one of the most important challenges facing humankind today. Time is of the essence. New technologies, widespread appreciation for the magnitude of environmental problems, and an increasing appreciation for the relevance of basic ecological research combine to provide an unprecedented opportunity to make significant progress in achieving a sustainable biosphere.

I. INTRODUCTION

Environmental problems resulting from human activities have begun to threaten the sustainability of Earth's life support systems. Among the most critical challenges facing humanity are the conservation, restoration, and wise management of the Earth's resources. Citizens, policymakers, resource-managers, and leaders of business and industry all need to make informed decisions concerning these resources. Ecological knowledge is one critical facet of the information required for making complex environmental decisions. Ecological understanding and knowledge are urgently needed to detect and monitor environmental changes, to evaluate consequences of a wide range of human activaties, and to plan for the management of sustainable ecological systems. New interdisciplinary connections will be required to conduct the needed research, to educate scientists and the public, and to ensure that the special expertise of ecological science is available to environmental decision-makers in all sectors of society. In response to these national and international needs, the Ecological Society of America proposes the **SUSTAINABLE BIOSPHERE INITIATIVE (SBI)**, a framework for the acquisition, dissemination, and utilization of ecological knowledge to ensure the sustainability of the biosphere. In this document, we define the scope of, and develop the rationale for, this Initiative.

Many of the environmental problems that challenge human society are fundamentally ecological in nature. The human population now numbers 5.2 billion, and is increasing at a rate approximating 1.8% each year. The growth of this population and its increasing resource use are exerting tremendous pressure on Earth's ecological systems. As a result, Earth's life support systems are changing, and their ability to sustain human society is being degraded rapidly. The sustained productive capacity of the Earth is at risk, as evidenced by the increasing difficulties in managing solid and toxic wastes, rapid rates of deforestation and watershed destruction throughout the world, high rates of species extinction caused by human activities, and changes in the atmosphere, such as increases in tropospheric trace gases and depletion of stratospheric ozone. Many environmental problems, particularly those involving hunger, disease, and sustainable resource use involve patterns of resource allocation as well as total resource availability. As the world's population expands, as demands for the reallocation of scarce resources continue, and as developing nations' standards of living change, the effects of human activities on the Earth's resources will grow at even faster rates.

Ecological understanding of complex phenomena is essential if society is to anticipate and ameliorate the environmental effects of human activities. Human activities may have unanticipated or indirect effects on parts of the Earth's life support systems, often at considerable distances from the site of the activity. For example, tropical deforestation may affect global climate by altering the global carbon balance. The introduction of irrigated agriculture may affect the productivity of marine fisheries by the alteration of water quality and flow regimes due to damming. In such

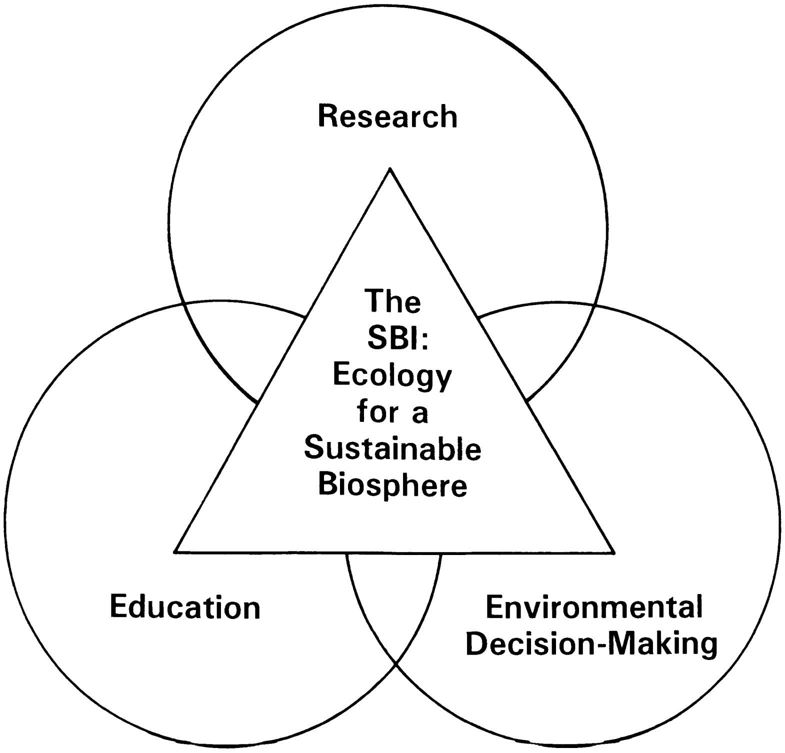

FIG. 1. Interdisciplinary interactions called for by the Sustainable Biosphere Initiative (SBI).

cases, ecological research can elucidate the links among populations, communities, and ecosystems, and between the abiotic and biotic realms.

The establishment of new interdisciplinary connections will facilitate the advancement of ecological understanding and help make ecological knowledge more accessible to the public and to environmental decision-makers (Fig. 1). Advances in the physical, chemical, biological, or social sciences are interdependent. Just as fundamental discoveries in ecology may depend on data or techniques derived from other scientific disciplines, information on the role of ecological processes in the physical or chemical environment, or in social systems, can contribute to advances in other fields. However, the acquisition of new ecological knowledge will be insufficient to address the Earth's environmental problems unless that information can be disseminated and used. In addition to improved programs for teaching ecology in the traditional educational context, increased interaction between ecologists and the media is needed to enhance public awareness and understanding of ecological approaches and principles. Moreover, interactions with environmental decision-makers in the public, private, and non-profit spheres must be facilitated. A forum is needed for discussion of the ecological information most critically needed to solve specific environmental problems and of how best to disseminate ecological information to decision-makers.

Within the field of ecology, the SBI calls for advances in research, improvements in education, and enhanced application of fundamental ecological knowledge in environmental decision-making (Fig. 2). This document focuses primarily on the research component of the SBI. In it we identify the ecological research programs of highest priority and recommend the steps required to pursue the research objectives. The educational and environmental decision-making components of the SBI require further development to identify needs, set priorities, and make recommendations for the communication and application of ecological knowledge.

THE SUSTAINABLE BIOSPHERE INITIATIVE

The research component of the SBI is the primary focus of this document. The criteria used to evaluate priorities for this research were (1)

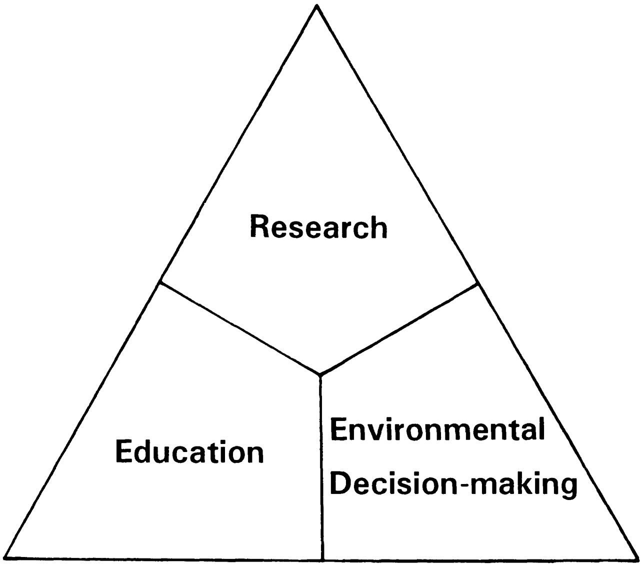

FIG. 2. Components of the Sustainable Biosphere Initiative: the acquisition, communication, and utilization of ecological knowledge.

the potential to contribute to fundamental ecological knowledge, and (2) the potential to respond to major human concerns about the sustainability of the biosphere (Fig. 3).

Based on these criteria, the SBI proposes three Research Priorities:

- **Global Change,** including the ecological causes and consequences of changes in climate; in atmospheric, soil, and water chemistry (including pollutants); and in land- and water-use patterns.
- **Biological Diversity,** including natural and anthropogenic changes in patterns of genetic, species, and habitat diversity; ecological determinants and consequences of diversity; the conservation of rare and declining species; and the effects of global and regional change on biological diversity.
- **Sustainable Ecological Systems,** including the definition and detection of stress in natural and managed ecological systems; the restoration of damaged systems; the management of sustainable ecological systems; the role of pests, pathogens, and disease; and the interface between ecological processes and human social systems.

The last of these three priorities—the sustainability of ecological systems—is one of the greatest challenges facing human society, yet it is the one that has received the least attention to date. We strongly endorse efforts already under way to address problems of global change and biological diversity. Moreover, we call for a greatly accelerated and expanded effort toward developing sustainable ecological systems.

Although ecologists have unique knowledge and skills that allow them to conduct research on these topics, interactions with other disciplines are necessary for a truly comprehensive approach to urgent environmental problems. Studies of global change, for example, cut across many fields, including ecology, atmospheric chemistry and physics, oceanography, hydrology, and geology, as well as human demography and economics. Likewise, to address issues of biological diversity, ecologists must collaborate with taxonomists and conservation biologists, policy-makers, planners, political scientists, and economists. Finally, sustainable human use of Earth's resources will require new alliances between ecology and other disciplines, such as resource management; agronomy, forestry, soil science, and other environmental sciences; epidemiology and demography; economics and planning. Ecology, in many ways an interdisciplinary science itself, will play a critical role in accelerating the development of new interdisciplinary approaches to the study of these environmental problems.

An initiative of the magnitude we envision will transcend traditional institutional boundaries and will involve innovative new collaborative pro-

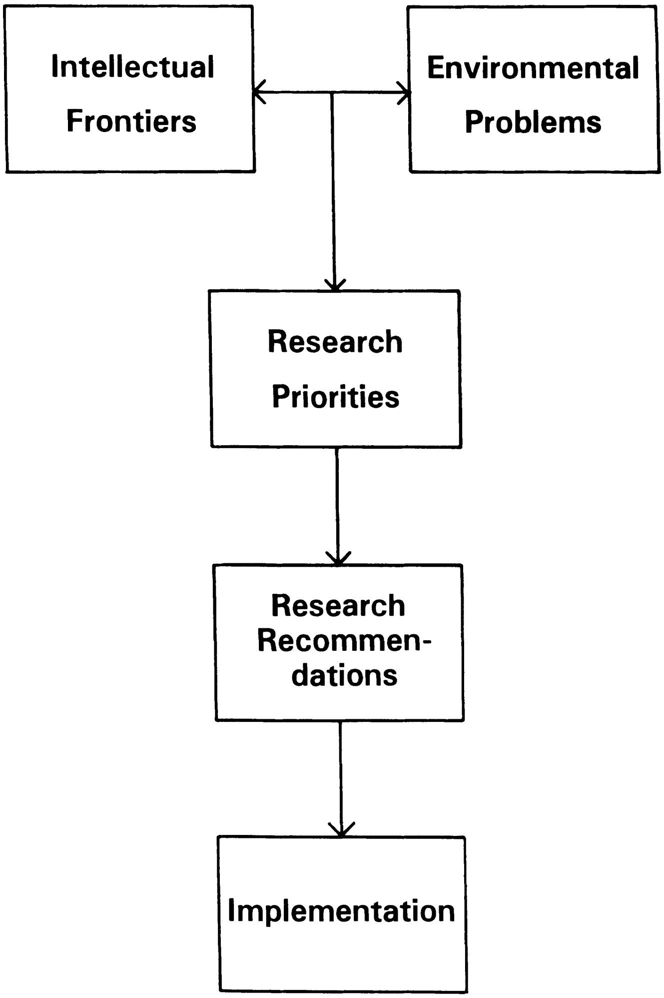

FIG. 3. Relationships among sections of this document. Intellectual frontiers and environmental problems are dual criteria used to establish research priorities. Essential components of research in the priority areas have received insufficient attention. These key components form the basis of the research recommendations. Implementation of the recommendations will require specific actions by the Ecological Society of America and by other supporting institutions (Section VI).

grams. In constructing expanded interdisciplinary and interagency approaches, it will be particularly important to preserve the opportunity for creativity and innovation. Thus, the cornerstone of the SBI should be investigator-initiated, peer-reviewed research. The SBI is not the work for a single agency; interagency cooperation, perhaps through a coordinating committee or a new institute, will be essential to achieving the objectives. Moreover, coordination with national and international agencies and institutions outside the United States will ultimately be required.

The primary message of the SBI is that advances in understanding basic ecological principles are required if environmental problems are to be resolved. The three seemingly distinct priorities—understanding the consequences of global change, understanding and conserving biological diversity, and assuring a sustainable future—share a common, ecological foundation, i.e., an understanding of the structure, functioning, and resiliency of natural systems. This document shows these links and indicates the fundamental ecological research needed to address the priorities. In this document, we explore the ecological principles and questions from which the priorities were selected, i.e., intellectual frontiers in ecology (Section II), and ecological knowledge required to help solve environmental problems (Section III). Subsequent sections highlight the research priorities and key research topics needed to address the priorities (Section IV), the major research recommendations of the SBI (Section V), and an action plan for further developing the SBI (Section VI).

II. INTELLECTUAL FRONTIERS IN ECOLOGY

Intellectual frontiers serve as one starting point (Fig. 3) for identifying research priorities. These frontiers are firmly grounded both in those ecological problems that are linked to specific levels of biological organization (Appendix A), and in those problems that cut across these levels (Appendix B).

Ecology has developed from a largely descriptive science to one that also includes analytical, experimental, and comparative approaches, and employs sophisticated laboratory, field, and remote sensing techniques. A growing body of ecological theory addresses the principles that govern the regulation and organization of populations and communities in space and time, and the interaction of biotic and abiotic components of the environment. New tools, including remote sensing, computational approaches, molecular and isotope analyses, and global-scale models, afford the opportunity to discover new ecological phenomena and to study known phenomena at previously inaccessible spatial and temporal scales. (See National Research Council 1989*c* for a more comprehensive treatment of new opportunities in ecology.)

In this section, we present an overview of interesting, exciting questions in ecology, arranged from individual- and evolutionarily based questions to those involving the interplay between the biotic and abiotic components of ecosystems. Several criteria were used in the decision to highlight these specific research questions. First, these questions are synthetic. They involve a search for general principles that can unite disparate studies and provide the basis for extrapolation and prediction. Second, these questions represent frontiers in ecology, because new empirical results, new conceptual advances, and new research tools hold the potential for clarifying general ecological principles. Although we have identified these intellectual frontiers based on their potential to advance the science of ecology, we also point out their obvious applications in the solution of environmental problems.

- **What are the patterns of diversity in nature, and what are their critical ecological and evolutionary determinants?** Understanding the diversity of nature is, in various forms, a fundamental problem of ecological research. New techniques have extended the temporal and spatial scales over which patterns of diversity can be detected. Modern molecular techniques permit systematists to construct phylogenies based on genetic material or population biologists to analyze the fine-scale genetic characteristics of existing populations. These techniques open new possibilities for describing the evolutionary history of diversity and elucidating the mechanisms that regulate genetic variation in modern-day populations. Remote sensing technologies are increasingly used to describe large-scale patterns of diversity at the community, ecosystem, and landscape levels. Characterizing patterns of diversity is a critical first step in preserving that diversity, hence providing the foundation for conservation biology. In community ecology, one of the most active areas of empirical research and conceptual synthesis is the elucidation of how abiotic and biotic factors interact to generate patterns of diversity. There is a growing need to conduct theoretical and empirical studies aimed at integrating mechanistic explanations with large-scale patterns of diversity. Understanding what regulates diversity is central to guiding strategies for habitat preservation, and for restoration ecology.

- **How do morphological, physiological, and behavioral traits of organisms interact?** Much of classical biology is concerned with the relationship between structure and function. The relationship of the morphology of organisms to the tasks they perform—how they resist physical stresses, how they capture prey, or how they attract mates—is at the core of the study of nature. In the growing field of biomechanics, novel applications of physics and engineering principles and use of new technology have permitted significant advances in understanding the functional costs and benefits of morphological variation in organisms. New applications of stable isotope analyses in plant ecology have the potential to link physiological and environmental processes in new ways.

Modern approaches have succeeded in placing traditional questions within a proper evolutionary framework (e.g., Jacob 1977). Recognition of the importance of frequency dependence has led to numerous recent advances in the application of game theory to behavioral and evolutionary problems. Such perspectives have motivated the development of more sophisticated theories that link systematics, autecology, and evolutionary biology. The next decade should witness the successful application of these approaches to a wide array of problems.

• **How plastic are the morphology, physiology, and behavior of organisms in the face of environmental stresses? What are organisms' proximal limitations?** Understanding the extent to which the genotype of an organism determines its phenotype and the degree to which environmental factors can modify the expressed phenotype is a classical problem (i.e., nature vs. nurture) in biology and psychology. Separation of the sources of variance among genetic and environmental factors was one of the first great conceptual advances of the theory of population genetics. Analysis of plasticity is critical to understanding the capacity of organisms to respond to anthropogenic changes and predicting whether environmental changes will cause genetic shifts within populations and taxonomic shifts within communities.

• **What are the determinants and consequences of dispersal and dormancy?** Dispersal and dormancy are two of the most basic life history responses to environmental variability. They govern the persistence of the majority of species within communities because disturbances of various kinds create colonization opportunities. They also hold the key to the recovery of damaged ecosystems, to the spread of species following climate change, and to the spread of introduced species, including genetically engineered organisms.

• **What factors explain the life history adaptations of organisms? What are the population-level consequences of these adaptations?** The theory of life history evolution is one of the richest branches in evolutionary ecology. Its relation to population-level phenomena (including reproductive tactics, dispersal, dormancy, phenology, resource allocation, and other traits) has been the focus of active research since Lamont Cole's landmark paper (Cole 1954). Game theory and related approaches described earlier have given us a new set of tools to address these problems. The importance of understanding how populations will respond to environmental change has given us new motivation to find answers. Life history theory should be an active area of investigation in the next decade.

• **What factors control the sizes of populations? How are changes in population size related to processes mediated at the level of the individual?** Understanding what controls population dynamics is a central question in ecology and one that also lies at the core of a remarkable diversity of applied issues. These include the management of harvested populations (e.g., fisheries), the spread of agricultural pests and human disease, the persistence of endangered species, the success of deliberate introductions of exotic or genetically engineered organisms, the possible accidental and undesirable spread of those organisms, and restoration ecology.

The mathematical theory of population dynamics, involving periodic and chaotic behavior, threshold behavior, and multiple equilibria, has seen great advances in the past 15 yr. Theories abound, and the challenge is to link these theories to data by relating individual performance and population dynamics. Considerable work is under way on individual-based models aimed at replacing classical phenomenological approaches with mechanistic models that will allow a basis for extrapolation beyond historical experience.

• **How does the internal structure of a population affect its response to various stresses?** The dynamics of a population are affected fundamentally by its internal structure, including its age, stage, and genetic structure, and its spatial distribution. Classical population dynamic theories have tended to view populations as lumped aggregates of identical units, except for the explicit treatment of genetic structure in evolutionary theory. Yet other aspects of population structure have been shown to be critical in understanding coexistence of species, population fluctuations, the spread of disease, and other critical phenomena. In recent years, attention has turned to developing methods to incorporate demographic and spatial structure into population models, setting the stage for important advances.

• **How does fragmentation of the landscape affect the spread and persistence of populations?** Natural and human-induced patterns of disturbance interact with species' traits and interspecific relationships to affect the patterns of spread, persistence, and abundance of species. Understanding these influences has been a problem of fundamental theoretical interest for nearly half a century (Watt 1947). Today, the study of land mosaics plays a key role in efforts to link processes in local populations, communities, and ecosystems with those at the level of the biosphere. Human land use has modified patterns of fragmentation. Because the extinction of desirable species or the spread of undesirable ones may depend in part on landscape patterns, studying these problems has become increasingly urgent.

• **What factors govern the assembly of communities and ecosystems and the ways those systems respond to various stresses? What patterns emerge from cross-system comparisons?** The analysis of patterns of community structure—including description of the trophic network—is a central focus of ecological theory. Numerous theoretical approaches have been used to develop an understanding of the key factors that generate and maintain that structure across a range of temporal and spatial scales. Studies in island biogeography have made a useful contribution by blending theoretical and experimental approaches to the processes governing assembly of communities. Work on these questions must be given increased attention, both for its fundamental theoretical importance and because of its relevance to problems of restoration and recovery of ecosystems following major damage.

Experimental studies have examined how particular ecosystems respond to different classes of perturbations, ranging from nutrient or pollutant additions to the removal of species. Multifactor experimental studies have been instrumental in understanding how biotic and abiotic factors interact to shape communities. These studies have led to an increased appreciation for the role of indirect effects in species' interactions. Such studies form the foundation of community and ecosystem theory. Their scope must be expanded. It is necessary to compare and synthesize the ways different ecosystems respond to a particular class of stresses and the ways a particular ecosystem responds to different stresses. Such studies, in addition to their obvious theoretical importance, can lay the basis for a functional taxonomy of ecosystems and guide research in ecotoxicology, restoration, and management.

• **What are the feedbacks between the biotic and abiotic portions of ecosystems and landscapes? How do climatic, anthropogenic, and biotic processes regulate biogeochemical processes?** Work on this topic must include studies of the exchanges of energy and materials among ecosystems and of atmospheric–biospheric and land–sea interactions. Furthermore, although numerous studies have described the biogeochemical cycles and patterns of energy flow within ecosystems (in some cases across a range of spatial and temporal scales), few mechanistic theories exist to explain how those cycles and flows are regulated. How robust are they in the face of disturbance? What is the role of biota in regulating climate and ecosystem processes? Research on the linkages between the biotic and abiotic portions of ecosystems and between population biology and ecosystem approaches is essential to understanding how those systems will respond to global change, and comprise one of the greatest of challenges facing ecologists.

• **How do patterns and processes at one spatial or temporal scale affect those at other scales?** Recent developments in remote sensing and Geographic Information System (GIS) technologies permit examination of ecological patterns at spatial scales larger than was previously possible. At the same time, there has been increased appreciation for the importance of processes at small spatial sales (e.g., dispersal and recruitment) in the structure of populations and communities. Long-term ecological studies and the development of new techniques to reconstruct past communities and environments have extended the temporal scale of ecological studies, while continuous or frequent sampling has highlighted the importance of small-scale temporal variation. In addition, experimental and observational studies suggest that temporal and spatial scales interact (e.g., rare events may have profound effects on spatial pattern). The increasing availability of data across temporal and spatial scales and the urgency of solving large-scale environmental problems have stimulated theoretical and empirical studies

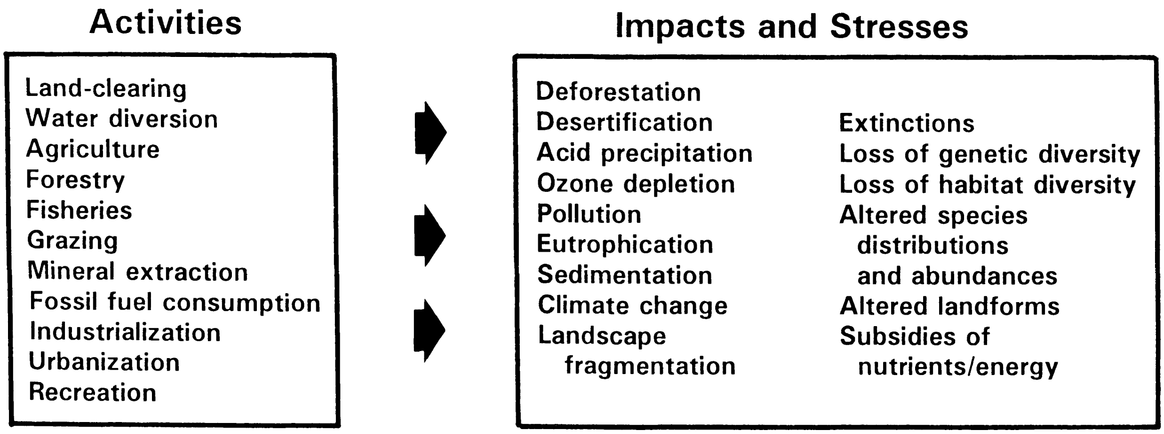

FIG. 4. Human activities affecting sustainability of the biosphere.

that attempt to integrate pattern and process across scales.

• **What are the consequences of environmental variability, including natural and anthropogenic disturbance, for individuals, populations, or communities?** A fundamental concept in ecology states that environmental variation can promote coexistence among genotypes or species. Recent theoretical and empirical results have refined this concept and identified conditions that relate environmental variation to long-term community stability or change. These results have directed attention to the specific ways environmental fluctuations affect populations; the effect of environmental variability upon species interactions; and intra- and interspecific differences in response to environmental variation and to biotic factors such as competition, predation, or mutualism.

III. ECOLOGICAL KNOWLEDGE REQUIRED FOR A SUSTAINABLE BIOSPHERE

Urgent environmental problems and their consequences for human well-being serve as a second starting point (Fig. 3) for identifying ecological research priorities. Human population growth and human activities have profound effects on the environment (Fig. 4); they contribute to global change, loss of biological diversity, and environmental degradation. Many anthropogenic environmental changes have deleterious consequences for human health and well-being. Because the science of ecology is devoted to understanding interactions between organisms and their environments, it is particularly appropriate for ecologists to focus on the complex relationships between humans and the biosphere (National Research Council 1989*c*, Roughgarden et al. 1989, Raven 1990, Edmondson 1991). In this section, we consider some of the ecological knowledge needed to understand and to ameliorate the ecological impacts of human activities.

Among the many environmental problems facing humanity, three are particularly critical, and their solutions require ecological knowledge: global change, the maintenance of biological diversity, and the sustainability of natural and managed systems. These three topics represent different facets of ecological knowledge needed to achieve a sustainable biosphere, yet there is considerable overlap among them. For example, human activities and their ecological consequences alter processes of global change and, at the same time, have immediate local and regional effects on the sustainability of natural and managed systems. Biological diversity is affected by processes occurring at local, regional, and global scales. The SBI recognizes that common ecological processes govern the response of the biosphere to human activities. Therefore, common ecological principles are likely to be involved in the solution of environmental problems.

We discuss large-scale changes in land use, environmental chemistry, and climate in Section A (Ecological Aspects of Global Change), where we focus on interactions between the biosphere and the abiotic realm. In Section B (The Ecology and Conservation of Biological Diversity), we em-

Box 1. Ecological Causes and Consequences of Global Climate Change

The biosphere both regulates and responds to the climate system through physical and chemical feedback mechanisms. An important challenge for ecologists is to understand processes that link species and ecosystems with climate and to predict ecological responses under climates that do not presently exist.

Ecological processes control the release and uptake of many greenhouse gases. Biological systems also exert control over hydrology and surface-energy balances, which are critical determinants of global climate. Albedo, evapotranspiration, soil moisture, and surface roughness are affected by the characteristics of terrestrial and marine biota. For example, certain groups of marine phytoplankton generate sulfate aerosols that act as cloud condensation nuclei. These may increase the extent of high-albedo cloud cover, altering the global radiation balance. Consequently, the composition of phytoplankton assemblages and the physical factors (e.g., upwelling) and biotic factors (e.g., competition or herbivory) that regulate the abundance and distribution of phytoplankton may play an as yet undetermined role in the global climatic system (Keller et al. 1989). Likewise, changes in vegetation canopy characteristics and evapotranspiration may influence regional and even global climate (Shukla et al. 1990). Thus, ecological studies that explicitly link biological and climatic processes will be useful in reducing the uncertainty in global climate models and in predicting the climatic consequences of human activities that alter ecological systems.

Ecological responses to climate change are complex. An important contribution of the paleoecological approach has been to document the relationship between climate change and biological communities of the past. Temperatures predicted for the next century (Jaeger 1988) are higher than any experienced by the Earth's biota during the last several million years, and the projected rates of change may be more than an order of magnitude faster than any global change in the past 2 million years. Major impacts will result from alterations in precipitation and disturbance regimes and in temperature extremes, as well as from changes in mean temperature (Dobson et al. 1989). Geographic shifts in climatic regime may occur faster than some species can disperse to new locations with suitable conditions (Davis 1986, 1989, Graham 1986). Quaternary pollen records show that the compositions of plant communities have continuously changed in response to long-term climatic variations. Changes in animal ranges have occurred for many but not all species, leading to the formation of new species assemblages (Graham 1986). Recent research in population and community ecology suggests that changes in community composition are likely to result not only from direct abiotic limits to species' dispersal, establishment, or persistence, but also from alterations in complex interactions between species and their mutualists, competitors, predators, or pathogens. Prediction of the consequences of climate change will be improved by integrating studies of the current and past distributions of species with mechanistic studies of abiotic and biotic interactions.

Another likely long-term consequence of global climate change is modification of the genetic composition of populations and species. It is difficult to predict the effect of evolved resistance to particular stressors on overall stress-resistance of organisms. Many organisms that can rapidly evolve resistance to environmental toxins (Bishop and Cook 1982) are also likely to evolve rapidly in response to changes in climate and concentrations of greenhouse gases (Holt 1990). Selection for tolerance to heat or desiccation can quickly lead to the evolution of general stress-tolerant genotypes that are resistant to a variety of environmental stressors and that may have altered life history traits (Huey and Kingsolver 1989, Parsons 1989). In contrast, tolerance of certain stresses may increase the sensitivity of organisms to other stresses (Weis and Weis 1989). Ecological studies that predict how climate change might alter population size and migration would contribute to understanding the consequences of global change for genetic variability, genetic drift, and hence evolution, within populations and species.

phasize the processes that affect biological diversity at several scales. Finally, we address local- and regional-scale issues of sustainability in Section C (Strategies for Sustainable Ecological Systems), where we focus on environmental assessment, restoration, and management, including the interface between ecological processes and human populations. In each section, we define the scope of the issues and the significance of ecological knowledge for addressing the problems. In the boxes, we highlight immediate research needs that also suggest the key research topics discussed in Section IV (Research Priorities for a Sustainable Biosphere).

A. Ecological Aspects of Global Change

Human activities are currently leading to unprecedented changes in the Earth's atmospheric, terrestrial, freshwater, and marine environments. Land-clearing, agriculture, fossil fuel consumption, and industrialization add a variety of trace gases and pollutants to the atmosphere. The potential consequences of altered atmospheric composition range from climatic warming and depletion of stratospheric ozone to enhanced biological productivity through CO_2- and nitrogen-enrichment, with subsequent alterations in population, community, ecosystem, and landscape processes. Human activities also divert and deplete surface and groundwater supplies and add toxic substances, wastes, and pollutants to lakes, rivers, and oceans, thus altering the productivity and biological diversity of freshwater and marine ecosystems. Although global change is often equated with greenhouse warming, it is clear that an ecological definition of global change also must include large-scale alterations in patterns of land and water use and anthropogenic changes in environmental chemistry, in addition to climate change.

Box 2. Direct Ecological Causes and Consequences of Changes in Atmospheric, Soil, Freshwater, and Marine Chemistry

The Earth's biota is both a source and a sink for many trace materials that have potential direct effects on ecological systems. Increasing concentrations of CO_2 can directly influence terrestrial, freshwater, and marine systems. Effects of acid deposition on lake and river systems have been well-documented. Potential effects of nutrient loadings, pesticides, and industrial wastes on ecological processes in soils and estuaries have become an important research issue in recent years. Such effects are destined to become more important as human populations grow.

Studies are needed on the ecological factors controlling material fluxes on land and in freshwater and marine systems, as well as on the feedbacks and consequences of such changes to the functioning of ecological systems. For example, to address questions of the local impact of ozone generated by urban activities in temperate regions and by biomass burning in tropical areas (Andreae et al., *in press*), ecological studies are needed that link the effects of elevated ozone levels at physiological, population, community, and ecosystem scales. To predict the effect of high ozone levels on plant distributions, for instance, an interdisciplinary approach could link physiological studies on the relative sensitivities of plant species to ozone with ecological studies on how differential tolerance alters competitive relationships and susceptibility to herbivores or pathogens.

To address larger scale impacts of regional air, soil, and water pollution on ecological systems, multidisciplinary studies are needed of the effects of human activities on microbial processes, whole-ecosystem biogeochemical cycling, and emission of CO_2 and trace gases to the atmosphere. Ecologists must address a variety of questions in collaboration with scientists from other disciplines to understand the fundamental processes controlling fluxes of materials and their effects on terrestrial, freshwater, and marine systems.

Changes in the Earth's ecosystems are both a cause and a consequence of altered global environmental conditions. To understand the complex feedbacks that link biota with air and water, ecological research is needed on the role of biotic and abiotic factors in controlling population dynamics, community structure, and biogeochemical cycles. The anthropogenic causes of global change in the hydrosphere, atmosphere, and climate lie in processes occurring at regional scales (e.g., water-diversions, burning of fossil fuels, deforestation, release of chlorofluorocarbons or other pollutants). However, the ecological consequences of global change may be felt first at the individual, population, and community levels. For example, changes may occur in individual organisms (e.g., in altered photosynthetic rates, changed behavior, altered microbial activity) and in community structure, due to altered disturbance regimes and species interactions. Changes in both individual function and community structure may ultimately be expressed as changes in ecosystem function. Thus, biotic and abiotic interactions must be understood across different levels of biological organization and across different spatial and temporal scales.

Three interrelated, immediate needs exist for fundamental ecological research concerning global change:

- the ecological causes and consequences of global climate change (Box 1)
- the ecological causes and consequences of changes in atmospheric, soil, freshwater, and marine chemistry (Box 2)
- the impact of land- and water-use change on global and regional processes (Box 3).

Significance of ecological knowledge to understanding global change

Land-use change and other human activities have caused massive changes in the biosphere. Deforestation, soil depletion, contamination of air and water resources, and depletion of biological diversity have resulted in dramatic global change over the last century. The threat of climate change adds a new dimension to existing global problems resulting from human activities. The consequences of human activities directly and indirectly affect and are affected by ecological complexity—the diversity of species and habitats, the patterns of ecological assemblages on the landscape, and differences in the productivity and storage capabilities of ecosystems. Better ecological information will improve predictions of global changes that might result from continued alterations in land and water use and industrial activity. It will also better enable ecologists to predict the long-term consequences of global change for the Earth's resources and populations, providing a basis for better management choices.

Research on the ecological aspects of global change will contribute to basic ecological understanding of processes regulating the Earth's biota. Two fundamental ecological questions lie at the center of this research: What regulates the large-scale dynamics of plant and animal populations? What regulates the fluxes of energy and materials (including nutrients and pollutants) within and between ecosystems? Answering these questions requires ecological studies of fundamental interactions among systems at different levels of biological complexity. New ecological understanding of these interactions will be significantly advanced by more collaborations between ecologists and scientists in other disciplines, including atmospheric science, soil science, oceanography, and environmental toxicology. Answering fundamental ecological questions and extending the scope of ecological knowledge will better enable ecologists to assist decision-makers in devising policies to anticipate, ameliorate, or respond to global change.

Advances in ecological science can contribute to societal decision-making by improving predictions of the global consequences of human activities that alter ecological systems. Ecological studies can elucidate biological processes that regulate ecosystem or climatic processes. The effects of biota on albedo or trace-gas emissions, for example, are not currently well understood. Accordingly, the predictive ability of global climate models would be improved by incorporation of more realistic ecological feedback mechanisms (Schneider 1988).

Ecological advances will also contribute to improved prediction of the responses of the biosphere to the novel conditions expected as a result of global change. Improved understanding of how specific environmental changes affect species and alter species' interactions will better enable ecologists to predict how the distribution of species and communities and the magnitude of productivity will change as a result of natural or human-caused global change.

Theoretical and empirical studies are needed to understand the links among ecological responses at various levels of biological organization. For instance, information gained from physiological studies must be used to couple local and meso-scale models with large-scale climate models. Large-scale and longer term experiments, remote-sensing techniques, and large-scale data sets offer new opportunities for ecologists to synthesize their work at regional and global scales and to cooperate among disciplines.

Most of the needs for research on global change identified in the SBI have been considered in the planning documents of the International Geosphere–Biosphere Program (IGBP) (National Research Council 1988), the U.S. Global Change Research Program (USGCRP) (Earth System Sciences Committee 1988, Committee on Earth Sciences 1990), the Global Ocean Ecosystem Dynamics Research Program (GLOBEC) (1988), the Long-Term Ecological Research Network Office (LTER) (1990), and the Joint Oceanographic Institutions (1990). Some of these issues have also become focal points for research in the IGBP core projects (e.g., tropical land-use change and atmosphere–biosphere interactions; International Global Atmospheric Chemistry Program [IGAC], Glabally 1989). Each of these research plans makes clear the need for strong participation by ecologists in studying the local, regional, and global implications of the changing Earth. However, the relative research effort devoted to ecological and biological questions has been drastically underrepresented in many global change research programs.

Building on these earlier efforts, the SBI calls for increased participation by ecologists in planning and research in on-going programs, especially emphasizing the importance of ecological complexity in global processes and linking studies of global change with efforts to understand biological diversity and the sustainability of local and regional ecological systems.

Box 3. Ecological Consequences of Land- and Water-Use Changes

Over the past century, changes in land and water use have converted natural systems to a variety of managed systems (e.g., agriculture, grazing, urban and industrial uses, or intensive forestry), changing the Earth's atmospheric chemistry and altering the fluxes of materials into freshwater and marine systems. Throughout the world, major diversions of freshwater for agriculture, hydroelectric power, and residential use have severely altered flow regimes and chemistry in major rivers and have destroyed fisheries. The effects of some land- and water-use changes can be detected regionally and globally, and they can alter population, community, and ecosystem processes at substantial distances from the initial change.

Examples of land-use effects on emissions of greenhouse gases are plentiful. Deforestation in the tropics alone has been estimated to contribute a net CO_2 flux to the atmosphere of around 1–2.5 Pg/yr (Detweiller and Hall 1988, Houghton 1990) and may also be a significant cause of the increasing concentration of atmospheric NO_x (Luizao et al. 1989). The use of fertilizers has led to increased fluxes of nitrogen trace gases in temperate ecosystems and may have an even greater impact in the tropics. Growing populations of livestock (Cicerone and Oremland 1988) and increasing rice paddy extent and production may represent substantial sources of the global increase in CH_4. At the same time, water diversions, removal of native vegetation, and conversion to human land uses have increased sediment and nutrient fluxes to surface waters, altering the hydrologic regimes and chemistry of lakes, rivers, estuaries, and near-shore marine systems in much of the world. Consequently, there is an urgent need to understand how the land–water–atmosphere system responds to land-use change.

Multidisciplinary studies at a variety of spatial and temporal scales will be necessary to address the effects of land-conversion and water-diversion on (1) microbial processes in the soil, sediments, and water column; (2) physical characteristics of soils and sediments; and (3) the roles of physiological and ecological processes in the exchange of materials within and among the atmosphere, soils, and water (see Box 2). Such studies will be needed to evaluate the biotic and abiotic consequences of alternative land uses, including the relatively new sustainable approaches and the ever-increasing use of fertilizers.

B. The Ecology and Conservation of Biological Diversity

The diversity of life on Earth constitutes a unique resource for future generations. The 1.4 million species of organisms identified and catalogued to date are only a small fraction of the 5 to 50 million species thought to exist. Human activities have profound consequences for biological diversity at many levels. Habitat destruction is the chief cause of the global extinction rate estimated to be approximately 17 500 species per year, or almost 0.1% of the extant species per year (Wilson 1990). Regionally, species introductions and altered disturbances rates may favor increased local diversity, but habitat loss or modification, outbreaks of introduced or native species, and management of exploitable systems tend to decrease species richness and heterogeneity.

Because only a small fraction of the earth is protected in parks and reserves, and the human population is growing, the accelerated extinction of species and destruction of habitats will continue. Current efforts to conserve biological diversity have focused on diversity at the species level and on prevention of extinction. However, an ecological definition of diversity also must include both the genetic diversity necessary to maintain each species, and the diversity of communities and ecosystems that support them. The goal of preserving diversity at all levels—genes, species, and ecosystems—requires a better understanding of how ecological processes operating on different spatial and temporal scales interact. To resolve the most pressing issues concerning biological diversity, ecologists must

- describe the global distributions of species and their associations and determine the factors that affect rates at which diversity changes (Box 4)
- accelerate research on the biology of rare and declining species (Box 5)
- determine the effects of global and regional change on biological diversity (Box 6).

Animal and plant populations continually face changes in climate, environmental chemistry, water- and land-use patterns, and fragmentation of habitats. Destruction of habitat leads directly to reductions in the size of breeding populations and loss of local genetic variability, both of which increase the likelihood of local extinction. However, these effects may be mitigated if landscape configurations permit the local loss of species or genetic diversity to be offset by immigration from nearby areas. Additionally, water diversion and increased pollution and sedimentation in streams, lakes, and estuaries often leads to degradation of valuable aquatic habitat and the consequent loss of biological diversity. Changes in land-use patterns also cause the natural and semi-natural habitats that harbor most biological diversity to be contiguous with intensely managed agricultural and industrialized urban areas. Although natural areas function as buffers around such managed ecosystems (Goselink et al. 1974), the proximity of natural and managed areas also means that natural populations are necessarily affected by agricultural, industrial, and other urban waste and by demand for resources (e.g., water). Thus, global and regional patterns of human activities need to be linked with descriptions of the abundance and distribution of species and communities and with intensive studies of the ecological processes that regulate diversity.

Synthesis of results from many subdisciplines of ecology will be needed to describe global and regional patterns of biological diversity, to determine the processes that maintain diversity, and to contribute to the conservation of biological diversity at all levels. Ecology has been characterized by numerous approaches and several distinct subdisciplines, such as physiological, evolutionary, community, ecosystems, or landscape ecology. Such variety is healthy and necessary for understanding the processes operating at different spatial and temporal scales that account for patterns of biological diversity. However, particularly challenging collaborative tasks lie ahead; for example, (1) fine-scale individual-based models (i.e., those that emphasize aspects of physiology, behavior, development, and genetics) must be integrated into more coarse-scale ecological models (i.e., those that emphasize population and meta-population structure, species assemblages, community structure, and ecosystem function), and (2) physical aspects of the environment must be incorporated into traditional biologically based studies of populations and species interactions.

Significance of ecology to the conservation of biological diversity

The challenges posed by global change, habitat loss and fragmentation, and species extinctions have the potential to stimulate significant advances in fundamental understanding of ecological processes. For instance, the primary focus of population and community ecology has been to elucidate the manner in which biotic and physical factors interact to account for the distribution and abundance of species. The threat of global change (see Section III A, Ecological Aspects of Global Change) now demands that ecologists extend theoretical and empirical studies in order to predict how populations and species will respond to the anticipated large-scale changes in climate and environmental chemistry. Changes in land and water use and fragmentation of habitat give impetus to studies on the interaction between landscape configuration (including aspects of the size, shape, isolation, and persistence of patches) and patterns of genetic and species diversity. The need to halt the extinction and decline of species directs attention to questions regarding the genetics of small population size; movement, colonization, and invasion dynamics; and the persistence of small populations when interacting with multiple competitors and predators or when establishing new mutualistic relationships. The search for solutions to such problems will stimulate the development of every facet of fundamental ecological science.

Ecologists are increasingly asked to justify the benefits of biological diversity compared to the human benefits that might be derived from economic development. Ecologists will be challenged over the coming decades to evaluate the functional significance of genetic diversity, species diversity, and ecosystem diversity. The ability of ecologists to influence the debate on biological diversity will depend greatly on advances in understanding the functioning of natural systems and the significance of individual species in ecosystem processes. Because human resources are limited, society will weigh the costs of conserving diversity against the long- and short-term costs of its loss. Thus, there is also an urgent need (1) to forge new theory that explicitly incorporates economic as well as ecological principles, and (2) to conduct research on the economics of exploitation and conservation.

Advances in ecological research can contribute to the conservation of biological diversity. Studies of rare and declining species have immediate application in the design of natural areas and the development of management plans for their preservation. Although there is an obvious need to set aside and manage relatively undisturbed areas as preserves, the conservation of the vast majority of species must take place within the "semi-natural matrix" of forests, grazing lands, rivers, and estuaries (Brown 1988). Thus, ecological studies of the effect of land-use change and landscape fragmentation on biological diversity will play an increasingly important role in (1) designing urban and agricultural landscapes that include natural and semi-natural areas, and (2) developing management practices that conserve biological diversity and meet the complex needs of a modern society.

Needs for research on biological diversity have been considered in Congressional and agency initiatives and in various national and international planning documents (e.g., National Research Council 1989*b*, National Science Board 1989, Reid and Miller 1989, Soulé and Kohm 1989, di Castri and Younes 1990, Elswerth 1990, and McNeely et al. 1990). Building on these earlier efforts, the SBI calls for new research programs that focus on (1) the role of biological diversity in controlling eco-

Box 4. Biological Inventory

An ambitious program of biological inventory is needed not only to catalog and map the world's major distributions of species and species associations, but also to link the pattern of distribution of species and habitats with natural and anthropogenic processes that affect biological diversity (Soulé and Kohm 1989). This effort will require coordination among ecologists, systematists, and natural-resource biologists working across very different spatial and temporal scales—from ecosystem ecologists using remote sensing and broad-based landscape analysis to population biologists working on locally endemic, rare forms and genetic varieties. Such investigations will require the establishment of new and perhaps more finely tuned habitat-classification schemes based on multiple aspects of individual species, complex associations of species, and interactions between biotic and abiotic factors. Particular attention must be paid to associations between ecotones and patterns of global and regional biological diversity. An inventory of the world's biological diversity should also incorporate the work of systematists and population geneticists detailing phylogenetic relationships and that of paleoecologists describing the past distribution of species and communities and their responses to environmental change.

Analysis of speciation patterns offers clues to ecological processes that account for changes in biological diversity across broad geographic areas. For example, world-wide distributions often show "centers of endemism," local regions that are particularly rich in endemic species. Approximately 15% of the species in Costa Rica are endemic compared with only 1% in West Germany (Reid and Miller 1989). Remote oceanic islands, such as the Hawaiian and Ascension Islands, show unique constellations of endemic flora and fauna. Patterns of endemism are important to study because endemic species are often rare and subject to higher probabilities of extinction. Accounts of the biological processes that lead to the formation of new species will help in establishing conservation and management programs for rare species.

Box 5. The Biology of Rare and Declining Species

A major focus of conservation biology is the ecological and evolutionary study of rare and declining species.

Rare species. The study of rare species may yield different insights into ecological processes than would studies of more common species. Ecological studies have focused primarily on very common species, but most species are relatively rare. Geographically widespread species may be very uncommon locally. Alternatively, some species may be endemic to a very restricted locale, but may be quite abundant there. The Hawaiian silver sword, *Argyroxyphium macrocephalus,* for instance, is a plant that occurs only in the crater of Haleakala volcano, but is represented there by over 47,000 individuals (Rabinowitz et al. 1986).

Although rare or endemic species are in greater danger of extinction than are widespread, common species, many rare species show prolonged periods of stable persistence. Furthermore, many of today's common species were rare during the past. The ability of species to persist when rare depends on the interaction between species' life history traits and environmental conditions. The life history phenomena that underlie rare species' population growth and, consequently, the likelihood of long-term persistence are thought to be quite different from those of common species. Studies are needed to understand how life history patterns and other traits associated with different forms of rarity interact with environmental factors.

Declining species. The decline of widespread, common species potentially reflects large-scale or long-term environmental changes and is likely to have a large impact on the communities in which they occur. The decline of amphibian species has been associated with local habitat destruction, the introduction of predators, and consumption by humans. However, population declines have also occurred in the absence of these factors, suggesting that other factors such as pesticide pollution, acid rain, low-level increases in ultraviolet exposure, or climate change may be implicated in some cases (Blaustein and Wake 1990). Natural fluctuations may also account for the decline of some species. Because amphibians are major consumers of invertebrates and are eaten by many vertebrates and invertebrates, a decline of amphibians could have ecological consequences that extend throughout many ecosystems. A global inventory (Box 4) is needed to provide the long-term data and the comparisons with other taxa that are required to evaluate the status of declining species.

Evolutionary responses. Long-term evolutionary responses in species that are rare or declining depend upon the underlying genetic structure of constituent populations. Rare or declining species may often exist only as small, locally isolated populations that are subject to increased inbreeding. The determination of breeding structure, effective population size, and inter-population movement is essential for understanding the potential for persistence or recovery of such populations.

Strategies for preserving endangered species also will require information on the genetic and demographic constraints to adaptation in individual species. Evolutionary change depends on the pattern of variance in important traits and the covariance among essential traits, as well as on the rate of environmental change and the population size and age structure. New developments in the genetic theory of life history phenomena will be important in understanding whether populations can adapt to environmental change.

Colonization. Conservation programs may ultimately rely upon introducing endangered species into new habitats, necessitating increased research on the dynamics of colonization and invasion. What features of a species enable it to succeed as an invader or as a colonist? How does success as an invader depend on the network of interactions with species already present in the community? What conditions promote the establishment of early colonists? Ecological studies of the processes and factors that regulate both the number of species in a community and the dynamics of species replacements will help provide answers to these questions.

logical processes, and (2) the complex suite of ecological processes that shape patterns of diversity. Such ecological studies would also contribute to understanding the processes underlying global change and the principles necessary for sustainable use of the biosphere.

C. Strategies for Sustainable Ecological Systems

Humans depend on natural and managed ecological systems for food, shelter, clothing, and clean air and water. As demands for the goods and services of the biosphere increase, so does the need to understand the complex array of interactions between humans and the biosphere. Ecological approaches to understanding environmental change increasingly will include the roles of humans both as agents of change and as populations responding to change.

Virtually every ecosystem on Earth has been influenced, to some extent, by the activities of humans. Effects range from the indirect influences of globally distributed pollutants on remote, uninhabited areas to the direct influence of activities that remove species, alter their distributions, or restructure entire landscapes. In addition, large areas of the Earth's surface are covered by ecosystems, such as agroecosystems and forest plantations, that have been designed and maintained by humans. Hallmarks of these managed systems are low species diversity; the infusion of large quantities of energy and nutrients to maintain them; and the extraction of additional energy, biomass, and nutrients. Many ecosystems are also used for recreation, for watershed management, or as reserves to maintain biological diversity.

As the human population continues to grow, it will place additional heavy demands on the earth's ecosystems. Even if the world's population equilibrated today, the pressure to increase the quality of the lives of existing people would tax the Earth's resources. To prevent or reverse the degradation of the resources of the biosphere, human use of those resources must be made sustainable. Advances in the political, social, and economic spheres, in agronomy and resource management, as well as in ecology are needed to work toward the goal of sustaining the biosphere (Brown 1989). The current generation of humans must accept the challenge to develop methods for deriving needed resources from the environment, and for making use of it in other ways, without compromising the ability of future generations to maintain themselves and to sustain their quality of life.

Box 6. Effects of Global and Regional Change on Biological Diversity

Ecologists are now being asked to predict the impact of climate change and changing land-use patterns on biological diversity (Soulé and Kohm 1989). How do changes in environmental chemistry, global temperature, patterns of precipitation and wind stress, or oceanic circulation affect population dynamics and global species diversity? What are the implications of increasing fragmentation of once large and continuous habitats? Ironically, most ecological models of population growth and species interactions focus almost solely on biotic rather than on physical factors such as temperature, precipitation, atmospheric or aquatic turbulence, or landscape configuration.

A renewed focus on the role of abiotic forces in structuring biotic assemblages is in order. Although nutrient concentrations and ratios have been included in models of both terrestrial and aquatic plant communities, these models often do not incorporate other factors such as solar radiation, temperature, and soil moisture. However, models of crop and forest production explicitly consider the influence of daily temperature and precipitation patterns on crop growth. These models could be used to predict the impact of climate change on short-term plant growth by incorporating the temporal patterns of temperature and precipitation derived from climate models. One of the great challenges will be to integrate similar fine-scale models with community and ecosystem models (e.g., forest-gap models) to predict the long-term consequences of climate change on biological diversity (Huston et al. 1988).

Human activities turn natural landscapes into mosaics of croplands, forests, and abandoned areas in different stages of succession. Many animal and plant species occupy a range of different habitat types in these complex landscapes and may exhibit different demographic characteristics in different habitat types. Greater attention must be paid to habitat-specific demography and life history phenomena as well as local adaptive changes in reproductive biology. We need to better understand the effects of landscape pattern (i.e., the sizes, shapes, and arrangement of habitat patches) on population size, dispersal, and diversity at the local landscape level. When suitable habitat is fragmented, the intervening habitat may impede dispersal to varying degrees. Therefore, the matrix between habitat patches, as well as the distance between the patches, may greatly influence the regional stability of populations, establishment of new populations, and long-term persistence of mobile species. Such matrix-dependent processes require ecologists to focus more attention on how the specific geometry of landscapes influences biological diversity (articles in Burgess and Sharpe 1981, Turner 1987).

Box 7. Indicators of Ecological Responses to Stress

Human activities induce stress in ecological systems by introducing pollutants, by altering landforms, and by directly adding or removing organisms. These activities indirectly affect species composition and alter interspecific interactions within the affected communities, ultimately changing the flux of natural and anthropogenic materials through the system (Levin et al. 1989). To understand and ameliorate the effects of anthropogenic stresses on natural systems, research is needed on how different stresses affect the behavior and physiology of individuals, population and community processes, and ecosystem function within particular systems and among systems (Westman 1985). In addition, the potential for interactions among multiple stressors requires further explication (e.g., Sheehan et al. 1984). Required research includes detecting and quantifying patterns in space and time and explicating underlying mechanisms.

Indicators. A major empirical problem is the definition and measurement of ecological responses to various stresses. The lack of sensitive indicators of environmental stress limits detection of the early stages of ecological change, and this seriously impedes understanding and effective management of ecological systems (Barrett and Rosenberg 1981). In some ecosystems, functional measurements of ecosystem processes (such as productivity and nutrient cycling) are often less sensitive indicators of ecosystem stress than are structural properties such as species composition (Schindler 1987). Sometimes extensive degradation has already occurred by the time ecosystem-level functions change. Thus, individual populations or attributes of communities are likely to be better indicators of ecosystem response to stress (Karr 1991).

Ideally, indicators would be chosen on the basis of the speed of their response or their sensitivity to specific stresses (Cairns 1977, National Research Council 1986). Because unperturbed populations, communities, and ecosystems may be quite variable through time, it is essential to know the baseline variability of the physical environment and of the selected biological indicators in order to determine whether undesirable change has occurred (Sheehan et al. 1984). It remains to be seen whether indicators that optimize the ratio of sensitivity to variability can be developed.

A great deal of basic research is needed before indicators of environmental change can be used with confidence. The development and testing of environmental indicators requires (1) long-term studies to establish baseline variability; (2) field perturbation experiments of appropriate spatial scale, intensity, and duration to test the sensitivity and specificity of indicators (Likens 1985, Schindler 1987); and (3) comparisons of systems exposed to stresses of different types and magnitudes (Steele et al. 1989, Cole et al. 1990). Access to long-term research sites and data bases (Strayer et al. 1986, Likens 1987), which may be shared by many projects (Kitchell et al. 1988), offers ecologists opportunities to develop and test ecological indicators in interdisciplinary settings.

Test systems. To assess the environmental consequences of particular human activities, test systems and rules for extrapolating from test systems to natural or managed systems must be developed. The problem of extrapolation is central to the development of test systems (Levin et al. 1989), involving basic principles of scale in ecology. The spatial scale or organizational complexity of an ecological system, and the type, duration, and frequency of anthropogenic stresses may affect the response of the system to a particular stress. Verification of rules for extrapolation requires experimental and observational tests at a number of scales (Frost et al. 1988), involving collaboration among scientists and agencies (Mooney et al. 1991). Thus, ecological research is needed at scales commensurate with restoration and management of entire natural systems.

To promote a sustainable biosphere, ecological science must

- determine patterns and indicators of the responses of ecological systems to stress (Box 7)
- provide guidelines and techniques for the restoration of ecological systems (Box 8)
- develop and apply ecological theory to the management of ecological systems (Box 9)
- further develop our ecological understanding of introduced species, pests, and pathogens (Box 10), and apply ecological theory to the management of infectious diseases (Box 11)
- develop interdisciplinary and multi-disciplinary approaches that integrate ecology, economics, and other social sciences (Box 12).

Although the exact meaning of "sustainability" is actively debated (Shearman 1990), we use the term to imply management practices that will not degrade the exploited systems or any adjacent systems (Turner 1988). Achievement of sustainability often requires both minimal subsidization of managed systems so they are relatively self-sufficient, and restoration of damaged systems whose goods and services are essential to human well-being. Because unchecked growth of the human population and misuse of natural resources degrades the biosphere, sustainability also implies "consumption standards that are within the bounds of ecological possibility and to which all can aspire" (World Commission on Environment and Development 1989).

Natural systems provide a point of reference for defining and detecting environmental degradation (Box 7) and creating models for environmental restoration and management (Boxes 8 and 9). In addition, significant interactions link managed and natural systems at many scales. For instance, managed systems are often critically affected by "wild" species. They may be pests or pathogens that reduce productivity (Box 10), or they may play a beneficial role, serving as sources for recruitment in restoration projects, as essential symbionts of harvestable species (e.g., as pollinators or mycorrhizae), or as agents of biological control (e.g., as predators, pathogens, or competitors of pest species). Using knowledge gained from natural systems to generalize about processes in managed systems depends on ecological research that explicitly compares processes in natural and managed systems and that focuses on interactions at their interface.

Box 8. Restoring Ecological Systems

Restoration has been called the "acid test for ecology" (Bradshaw 1987) and the "ultimate test for ecological theory" (Ewel 1987). Numerous attempts have been made, with varying degrees of success, to restore degraded ecological systems (Holdgate and Woodman 1986, Ashby 1987, Kline and Howell 1987). Improving the success rate and cost-effectiveness of restorations requires a better understanding of such fundamental ecological processes as nutrient cycling, succession, competition, and predation, and of the interaction of biotic and abiotic factors.

Effects of abiotic factors on the biota have a long and distinguished history in ecological research. Many of the problems associated with restoration involve a poor understanding of how physical factors in degraded systems limit the establishment and growth of species. Physical factors may affect recovering populations directly. For example, attempts to restore mining spoil sites have been retarded because, following initial preparation, the soil collapses to a dense medium through which roots cannot easily penetrate (Rimmer 1982). Physical factors may also affect species indirectly through their effects on interspecific interactions. Exposure to stress, for example, may alter the susceptibility of recovering plant populations to herbivory (Louda 1988).

In addition, population and community processes may have potent effects on ecosystem processes. Fluctuations in certain populations may reverberate throughout all trophic levels, causing changes in productivity, nutrient cycling, and fluxes of contaminants and pollutants. It is now apparent that the biogeochemical heterogeneity of continents has been structured significantly by animal population dynamics (Naiman 1988). Ecologists also recognize that animal population dynamics are coupled at continental and intercontinental scales (Brown and Maurer 1989, Holling 1988).

Basic research on the couplings between community processes and ecosystem functions is fundamental to progress on ecosystem restoration. Ecological research can provide a conceptual framework to guide ecological restoration projects and increase their effectiveness. To facilitate the development of such a framework, financial and institutional support is needed for research on a broad scope of community and habitat types and on all ecological aspects of restoration, from population genetics to ecosystem function.

Significance of ecological science to the development of sustainable ecological systems

Research aimed at developing ecological strategies for a sustainable biosphere will advance fundamental understanding of ecological processes. As in the past, applied ecological studies in human-affected systems will continue to make significant contributions to understanding basic ecological phenomena (e.g., population dynamics,

Box 9. Developing and Applying Ecological Theory to the Management of Ecological Systems

Managed and natural ecosystems form a continuum from monocultures of row crops to pristine, unexplored sites. Intermediate degrees of management are applied to semi-natural systems such as fisheries, grazing and forest lands, and national parks. Managed systems generally have lower genetic and species diversity than natural systems, with genotypes or species adapted to relatively constant environmental regimes. Relatively open nutrient cycles in managed systems often result in significant impacts on surrounding systems. Managed systems are usually subjected to frequent, severe, intentional perturbations (i.e., management) that interfere with long-term ecological processes.

Because human well-being depends upon ecological systems, managed systems must be characterized by stability or by resiliency as environmental change occurs. Lessons from natural systems suggest that the sustainability of managed systems may be enhanced by closed nutrient cycles (Coleman and Hendrix 1988), increased species and genetic diversity, and decreased negative influences on surrounding areas (Cox 1984). In a sense, "designer" ecosystems must be constructed with natural ecosystems serving as the model (see Coleman 1989).

Experiments. The science of ecology has much to contribute to ensure the sustainbility of ecological systems in the face of human exploitation. In addition, the advance of ecological science will greatly accelerate if management actions can be structured as large-scale experiments. Large experimental perturbations have a distinguished history of contributions to ecosystem ecology (Likens 1985), and are essential for rapid evaluation and comparison of alternative management strategies (Walters 1986). Every major development project or management intervention is a learning opportunity if adequate baseline and follow-up data are collected, and a proper statistical approach is employed. By linking such large experiments with studies in smaller scale test systems, non-linear effects, interactions among factors, and the roles of covariates can be understood. Collaborations among ecologists, statisticians, and managers offer the prospect of developing powerful new experimental tools for evaluating the consequences and effectiveness of management options (Matson and Carpenter 1990).

Modeling. Ecological modeling is undergoing rapid advances and improvement. A new generation of models will incorporate the effects of physicochemical factors and community-level interactions to analyze the dynamics of managed populations or ecosystems. Management experiments offer the opportunity to develop, test, and improve models at scales ranging from individual organisms to ecosystems (Kitchell 1991). Strong manipulations at the scale of management force "informative failures" of management models and lead to rapid identification of the models that perform best in a management context (Walters 1986).

Today, the discipline of ecology faces the challenges of enlarging ecological perspectives to include human values and needs and to identify the major ways in which managed and natural ecosystems affect each other's long-term well-being. If managed ecosystems are viewed as integrating a local community with farm, non-farm, and natural resource (forest, wetland, aquatic) sectors, then research is needed to examine interactions beyond the farm, forest, or park gate and the impact of social and economic forces (National Research Council 1990). A world so altered by human activity offers the opportunity and the challenge to expand the scope of the discipline of ecology.

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succession, predator–prey systems, and ecosystem processes). Increasingly, the need for extrapolation and generalization of ecological principles at scales similar to those of environmental assessment, restoration, and management will promote the development of theoretical and empirical approaches that link processes across scales. In addition, ecologists will be challenged to integrate human-induced perturbations (with their characteristic type, frequency, duration, intensity, and extent) into models of the effects of stress and disturbance on populations, species interactions, and ecosystem processes.

Ecological science can provide some of the tools needed to assess, restore, and manage Earth's life support systems. To define and detect environmental degradation, and to guide the restoration of ecological systems, studies are needed to link population- and community-level processes with ecosystem function. In addition, ecological studies are necessary to elucidate the role of biota in mediating the transport, fate, and effects of pol-

THE SUSTAINABLE BIOSPHERE INITIATIVE
RESEARCH PRIORITIES

- ♦ Global Change
- ♦ Biological Diversity
- ♦ Sustainable Ecological Systems

FIG. 5. Research priorities: understanding the role of ecological complexity in global processes, the ecological causes and consequences of biological diversity, and the underlying ecological processes that affect the sustainability of natural and managed ecological systems.

lutants and toxicants in the environment. Ecological approaches to sampling, statistical analysis, and experimental evaluation of underlying mechanisms will be useful in improving tests of the environmental consequences of restoration and management strategies.

In all of this work, it will be essential to combine studies of human populations with those

Box 10. Introduced Species, Pests, and Pathogens

The importance of introduced species, pests, and pathogens cannot be overlooked, whether we are restoring ecosystems, creating new ones, or trying to predict changes in existing systems. Many anthropogenically altered ecosystems have been characterized by problems associated with pests. In the future, as species are introduced or move in response to environmental changes, some of today's desirable species may become pests in their new environmental contexts, while some pests may become more pernicious.

Control of agricultural pests can depend on cultural practices (Phillips et al. 1980), the introduction of biological control agents (Batra 1982), the use of chemical pesticides, or combinations of these and other methods. Building on a long history of study of pest-control techniques, ecological research is needed to improve understanding of the biological basis of control. For example, research is needed to resolve controversies over the nature of predator–prey population dynamics (Hassell et al. 1989) in successful and unsuccessful biological control (e.g., Murdoch et al. 1985, 1989); the number of species of natural enemies and biological attributes of such species to be used in biological control programs (e.g., Crawley 1987, Myers 1987, Myers et al. 1989); and the source area for introduced natural enemies and the degree of their prior evolutionary exposure to the pest (Hokkanen and Pimentel 1989, Pimentel and Hokkanen 1989). Additionally, the degree of synergistic or antagonistic interactions of pests (Allen and Bath 1980, Haynes et al. 1980) under changing scenarios (Pimentel 1977) requires further explication.

Introduced species and genetically altered organisms are potential "pests" that deserve ecological consideration. "Designer" ecosystems may include introduced or altered species (Whalen 1986, Gasser and Fraley 1989). Will any of these forms "escape" and become pests (Ellstrand and Hoffman 1990)? What is their potential if introduced into relatively unmanaged systems (Doebley 1990)? Critical ecological experiments are needed to test specific hypotheses posed by these questions (e.g., Regal 1987, Regal et al. 1989, Tiedje et al. 1989, Hoffman 1990).

The spread of infectious diseases is an ecological phenomenon—essentially a host–parasite interaction. This point is often ignored in epidemiological studies, although the earliest epidemiological models (e.g., those for malaria) were explicitly ecological. More recently, viral and other diseases have been examined within the same framework that has been used for epizootics (Anderson and May 1979, May and Anderson 1979). Melding techniques from epidemiology and ecology, this approach considers disease-induced mortality and variable population size, non-homogeneous mixing, and other ecological factors. Evolutionary considerations, such as the evolution of reduced or increased virulence, also provide a wealth of research questions and may suggest possible ecological approaches to disease management.

that examine changing patterns of resource use, air and water quality, or global and regional climates. Some of the most important research topics of the coming decade will be at the interface of the social, economic, and ecological sciences. These topics include both the effects of humans on the environment and the consequences of environmental change for human populations and human well-being.

The task of assessing, restoring, and managing sustainable ecological systems can only be addressed by a comprehensive, organized research effort. Current efforts to assess and restore specific ecosystems (e.g., wetlands, mining sites) or to manage sustainable systems (e.g., agricultural, forest, or fisheries resources) represent initial, necessary steps toward the goal of sustaining the biosphere. However, these efforts are not presently united in a comprehensive research framework. Such a framework is needed because ecological processes link natural and managed populations to ecosystems and because common ecological principles underlie effective management strategies. A comprehensive approach is also needed to link studies of sustainable management practices to issues of global change and biological diversity.

The foundations of a more comprehensive approach to research on sustainable ecological systems have been laid by scientists working in the fields of conservation biology (e.g., Soulé and Kohm 1989, Raven 1990) and sustainable resource use (National Research Council 1989*a*, 1990). The SBI proposes the formulation of an integrated research framework to coordinate existing research efforts and to initiate new research programs devoted to enhancing the sustainability of the biosphere.

IV. RESEARCH FOR A SUSTAINABLE BIOSPHERE: PRIORITIES AND KEY TOPICS

After considering intellectual frontiers in ecology and the ecological knowledge required to help solve urgent environmental problems (Fig. 3), we have identified three research priorities (Fig. 5)—**global change**, **biological diversity**, and **the sustainability of ecological systems**. These three priority areas are developed in Section III, where we define their scope, discuss their significance, and identify research needs. In the present section, we introduce key research topics that ad-

Box 11. The Ecology of Disease Spread

Recent efforts to refine ecologically based models of disease transmission are yielding new insights that will improve efforts to control human disease (Anderson 1989). These models, and related empirical studies, have identified several factors that have complex consequences for the transmission of disease in human populations (Hassell and May 1989).

The frequency and nature of contact between infected and susceptible individuals largely determines the spread of disease. Rural–urban migration, for instance, affects the probability of contact by changing both the movement patterns of individuals and population densities. Patterns of behavior may also influence the rate of spread of certain diseases (e.g., the number of partners in sexually transmitted disease). Interdisciplinary studies linking ecology, human demography, and social sciences can contribute to a better understanding of the role of migration and behavior in disease transmission.

Disease transmission often involves multiple hosts with complex life history patterns, as in schistosomiasis. Ecological life history analysis coupled with modern techniques for sensitivity analysis can identify sensitive links in the transmission cycle, resulting in better programs for eradication and control.

Disease transmission may also be regulated by intrinsic and extrinsic factors affecting the susceptibility of individuals. Susceptibility to infectious disease may vary with age, gender, race, genotype, or other intrinsic traits of individuals. Furthermore, extrinsic factors, such as malnutrition, exposure to toxic chemicals, or migration-induced stress may alter susceptibility to disease. By taking such ecological factors into account, the reliability of epidemiological models as tools for the management of public health will continue to improve (Anderson 1989). Additionally, the ecological perspective—with its emphasis on population and evolutionary processes—increasingly will be integrated into immunological, human genetic, and environmental health perspectives on the spread of human disease.

dress the three priority areas and show the links among them. Research in each of these areas has the potential to advance the discipline of ecology and to produce essential information for solving environmental problems.

The three priority areas are interrelated. Because elements of the biosphere are naturally linked by ecological processes, a given human activity may have implications for all three areas. For example, deforestation may alter regional climates by affecting the hydrological cycle, may reduce local species diversity by removing habitats and inhibiting dispersal, and may threaten the sustainability of fisheries by increasing sedimentation in streams within the watershed.

Moreover, the three priorities pose common challenges to the discipline of ecology. For example, implementation of each of these priorities

Box 12. Ecological Processes and Human Populations

No discussion of the Earth's environmental problem is complete without explicit consideration of the growth and shifting demographic patterns of the human population. As the world's population continues to expand, and as developing nations move toward standards of living that imitate those of the more developed nations, the effects of human population growth on the Earth's resources will accelerate. It is essential to consider the impact of increased economic demands for renewable and nonrenewable resources on ecological systems, and to recognize that humans are essential elements of the ecosystem we study.

The issues associated with population growth are broad, involving such factors as changes in per capita income and resource distribution; increasing pollution and environmental degradation; problems of health and poverty; the effects of urban, industrial, and agricultural expansion; and especially the integration of ecological and socioeconomic considerations. Even those factors that are primarily economic will have substantial environmental effects.

The human population now numbers 5.2 billion, and is increasing at the rate of approximately 1.8%/yr. The average growth rate, however, masks disparities among populations of different regions and different nations. The change in demography from a situation of high birth rates and high death rates to one of low turnover, termed "demographic transition," has occurred in most of the developed world but has not occurred in most of the developing world. In much of the developing world, death rates greatly declined after World War II; however, birth rates in many cases increased and have only recently begun to decline. The ecological implications of demographic transition in a large number of developing nations have not been explored fully.

Today, many developed countries have replacement total fertility rates (TFR) of about 2.1, corresponding to the average number of surviving children a woman will have in her lifetime. Such a replacement pattern generates a stable population size. However, many developing countries have TFR's of 4 or more, implying rapid population growth. Efforts to reduce birth rates will require more information and expertise on interactions among human populations and resources. The social and economic constraints that prevent the appropriate and effective use of resources must also be understood.

The effects of human population growth on human health and welfare cannot be treated independently from issues of resource distribution and availability. Often increasing levels of poverty and disease in specific geographic locations can be attributed more to shifting patterns of agricultural production than to strict increases in population size. For example, in some regions of Central America shifts from domestic to export crop production contribute more to poverty and malnutrition than does increasing population growth (Durham 1979). An ecological analysis of human demographic patterns must incorporate the long-term effects of shifting patterns of resource availability and distribution along with the socioeconomic implications of these changing patterns.

There is a real need to bring ecological techniques, especially methods from population biology, to bear on the problems of human population growth. Such studies would require detailed investigations of human demographic structure, variation in growth patterns across different regions, implications of migrational patterns, and shifting age structure. These investigations must be related to studies on changing patterns of energy use, resource production and distribution, disease spread, and urban-industrial expansion. To fully understand how human populations affect and are affected by ecological processes, the complex interfaces between ecology and social and economic sciences and policy analyses must be developed to a much greater extent.

TABLE 1. Key research topics that cut across the three priority areas.*

Key Research Topics
Examples of Research Questions

1. Determine the ecological causes and consequences of global climate change by quantifying and modeling the links between biospheric and global change.
   - What are the differences among biomes and among species within biomes in regulating interactions between the biosphere and the abiotic realm (i.e., the atmosphere, hydrosphere, and lithosphere)? How does community composition affect ecosystem function?
   - How do canopy- and ecosystem-scale energy, water, and gas exchange processes interact with the physical climate system?
   - How do the direct and indirect effects of changing physical and chemical environments alter ecological communities and the population dynamics of component species?
   - To what extent are species' ranges determined by the direct effects of climate or other physical factors, as opposed to biological interactions?
   - How would changes in rainfall distribution affect food supply? How would this affect human population dynamics?
   - How does climate change affect plant and animal dispersal and colonizing abilities?
   - To what degree does the paleoecological record permit prediction of future ecological and evolutionary responses to global change?

2. Determine the ecological causes and consequences of changes in atmospheric, soil, freshwater, or marine chemistry, using fundamental models of how ecological systems regulate the chemistry of the biosphere and models for the ecological consequences of changes in these processes.
   - What are the consequences of increasing CO_2 for biotic interactions in terrestrial ecosystems?
   - What are the relative sensitivities of animal and plant species to regional air pollution?
   - Is the ocean an effective buffer for increased atmospheric CO_2 inputs and, if so, what are the consequences of enhanced oceanic productivity?
   - How do elevated levels of nutrients affect plant–herbivore interactions? How are those changes transmitted through higher trophic levels?
   - How are community composition and species diversity affected by persistent toxic substances?
   - How does chronic exposure to pollutants affect human susceptibility to disease? What are the consequences for rates or patterns of disease transmission?

3. Determine the ecological consequences of land- and water-use change through a functional understanding of how land conversion and water diversion affect ecological processes.
   - How do individuals, populations, and ecosystems respond to the scale, frequency, pattern, and type of disturbance?
   - How do the alterations in species composition that accompany land-use changes affect nitrogen and carbon trace gas emissions to the atmosphere?
   - How do land-use changes and water diversions affect river-basin and other water-body processes and terrestrial–aquatic interactions?
   - What are the relationships between land-use patterns and various measures of water quality?
   - What is the effect of landscape fragmentation on local and regional patterns of diversity?
   - How do land-use change and land conversion affect biogeochemical processes and trace-gas emissions?
   - How does land-use change affect human population structure?
   - What roles do wetlands of various types play in the production of wildlife and fisheries?

4. Determine the evolutionary consequences of anthropogenic and other environmental changes.
   - Under what conditions should new genotypes evolve in response to environmental changes, including climate changes and new sets of species interactions?
   - How does the relative likelihood of evolutionary response vs. extinction change with the rate of climate change?
   - How are demographic parameters of species and interspecific interactions affected by evolutionary changes in physiological tolerance?
   - What are the evolutionary consequences of stage- or age-specific toxicity effects?

TABLE 1. Continued.

- What are the ecological and evolutionary consequences of long-term, intense exploitation of natural populations?

5. Inventory the patterns of genetic, species, habitat, and ecosystem diversity. Determine the rates of change of biological diversity and the subsequent effects on community structure and ecosystem processes. Accelerate research on factors determining diversity at all levels.
   - What are the distributions in the world of species and community types?
   - What are the rates of loss of biological diversity across different habitats and taxonomic groups?
   - What are the key species whose presence or absence can critically alter the composition of local communities?
   - What processes account for the patterns in biological diversity across broad geographic ranges? Do speciation patterns serve as clues to those processes?
   - How are life history traits, reproductive success, evolution, and genetics coupled through reciprocal constraints?

6. Accelerate research on the biology of rare and declining species and develop the scientific information necessary to sustain populations of potentially valuable rare and declining species.
   - What are the evolutionary responses of rare species to environmental change and to long-term conservation strategies?
   - What factors control the dynamics of colonization and invasion by recovering populations?
   - How do the reproductive biology and behavior of individuals of rare species respond to stress?
   - How does genetic structure affect the long-term evolutionary responses of populations that are becoming rare?
   - What role do ecological processes play in the social, political, and economic trade-offs of different conservation or management strategies?
   - What common features distinguish species that have persisted over long periods in the past?

7. Determine patterns and indicators of ecological responses to stress, leading to technologies necessary to assess the status of ecological systems, to forecast and assess stress, and to monitor the recovery of damaged ecological systems.
   - What are early indicators of stress, and what is the ecological significance of changes in such indicators?
   - Can model systems be designed to adequately test the consequences of proposed human activities?
   - What are the empirical scaling rules for extrapolating from model to natural systems?

8. Accelerate the basic science of restoring damaged and degraded ecological systems, by developing, testing, and applying principles of restoration ecology.
   - How is the structure within biological communities (e.g., genetic structure, composition, or species diversity) linked with the functional aspects of ecosystems (e.g., productivity, nutrient cycling, or sequestration and release of contaminants)?
   - How can ecological and evolutionary principles provide a framework to guide restoration projects?
   - What are the separate and combined effects of physical and biotic factors in limiting the establishment and growth of recovering species in degraded systems?
   - How do species' life history traits affect population and community structure?
   - What are the economic and social trade-offs for different restoration options?
   - Under what conditions is mitigation an ecologically defensible policy?

9. Advance, test, and apply ecological principles for the design and use of sustainable, managed ecological systems at appropriately large scales.
   - How do physical factors and community-level interactions affect the productivity of populations of exploited species?
   - Is there a "minimum mix" of species, guilds, and life forms that would result in sustainability of a particular system?
   - Will native animals and microbes persist and participate in sustainable ecosystems composed of novel combinations of plant species?
   - What are the mechanisms allowing or preventing the coexistence of species?

TABLE 1. Continued.

10. Determine the principles that govern outbreaks and patterns of spread of pest and disease organisms.
    - What are the effects of climate change scenarios on the redistribution of pests (including human disease vectors), potential pests, and their host organisms?
    - Why do pest populations vary in their abundance, environmental impact, and susceptibility to extinction?
    - Are multiple-predator, multiple-parasite combinations more effective than single agents in the control of target species?
    - Will parasite and predator species switch to different host species when the population of the target species becomes so low that a residual population cannot be maintained?
    - How do specific environmental changes (e.g., deforestation, drought) alter transmission of infectious diseases in human populations?

* The key research topics listed in this table are derived from the research needs discussed in the various boxes in Section III. Research on each topic may address needs discussed in several boxes.

will require a better understanding of the interactions between the biotic and abiotic components of ecological systems; better integration of population biology with ecosystem science; better synthesis of ecological with evolutionary approaches; and new theoretical and empirical studies that relate patterns across disparate spatial, temporal, and organizational scales.

Recognizing the interrelatedness and common ecological foundations of the three priority areas, we have identified 10 key research topics (Table 1) that further define the three priority areas. The order of presentation of the research topics does not reflect differences in their importance. Instead, each topic represents an integral part of the SBI—fundamental research needed to help solve environmental problems. For each research topic, we have listed examples of the types of research questions that might be addressed. These lists are not intended to be exhaustive, but to suggest the range of ecological research approaches required to address each research topic.

V. RESEARCH RECOMMENDATIONS

Three specific research recommendations emerge from unmet research needs in the three priority areas of the SBI (Fig. 3).

RESEARCH RECOMMENDATION #1: Greater attention should be devoted to examining the ways that ecological complexity controls global processes.

Within the topic of global change, insufficient attention has been paid to the ways in which ecological complexity controls global processes. Such key factors as species and habitat diversity, patterns of distribution of ecological assemblages, and differences in the productivity and storage capabilities of different types of ecosystems all influence how the biosphere functions in the Earth system. The role of this ecological complexity must be incorporated if we are to understand global processes.

RESEARCH RECOMMENDATION #2: New research efforts should address both the importance of biological diversity in controlling ecological processes and the role that ecological processes play in shaping patterns of diversity at different scales of time and space.

Within the topic of biological diversity, much of the current effort is devoted to enumerating the species in various habitats and to preserving biotically significant sites. These important efforts lay the groundwork for the research proposed here and must be continued, but two vitally important topics must also be understood. First, it will be necessary to discover to what extent patterns of biological diversity are important in determining the behavior of ecological systems (e.g., responses to climate change, rates of nutrient flows, or responses to pollutants). Only when these relationships are known will it be possible to develop management strategies for maintaining natural and human-dominated ecological systems. Second, it will be necessary to document how ecological processes interact with physical and chemical factors to control or determine biological diversity. Doing so will require investigation of the manner in which individual species interact with and are modified by the abiotic environment on both ecological and evolutionary time scales.

RESEARCH RECOMMENDATION #3: A major new integrated program of research on the sustainability of ecological systems should be established. This program would focus on understanding the underlying ecological processes in natural and human-dominated ecosystems in order to prescribe restoration and management strategies that would enhance the sustainability of the Earth's ecological systems.

Plans for comprehensive programs in the areas of global change and biological diversity are more advanced than those in the area of sustainable ecological systems. Research programs exist to develop specific sustainable natural resources. However, current research efforts are inadequate for dealing with sustainable systems that involve multiple resources, multiple ecosystems, and large spatial scales. Moreover, much of the current research focuses on commodity-based managed systems, with little attention paid to the sustainability of natural ecosystems whose goods and services currently lack a market value. Addressing the topic of sustainable ecological systems will require integration of social, physical, and biological sciences.

These Research Recommendations are made to ecologists, to researchers in related disciplines, and to funding agencies whose interests encompass one or all of the research priority areas. Immediate and long-term research programs and funding for research in these areas is vital to the success of the SBI.

VI. IMPLEMENTATION: AN ACTION PLAN FOR THE ECOLOGICAL SOCIETY OF AMERICA

The Sustainable Biosphere Initiative identifies the research needed to provide the ecological knowledge required for a sustainable biosphere. Successful implementation of the SBI will require a significant increase in research in the three priority areas. Successful implementation will also require interdisciplinary interactions that link ecologists with the broad scientific community, with mass media and educational organizations, and with decision-makers in all sectors of society (Fig. 1). Obtaining the ecological knowledge needed for a sustainable biosphere necessitates interdisciplinary projects involving collaboration between ecologists and scientists in the natural and social sciences. In addition, achieving a sustainable biosphere will require dissemination and application of ecological knowledge.

Achieving the goals of the SBI will require separate and coordinated activities by scientists and administrators in academia, in government agencies and private organizations, and in business and industry. In this section, we identify specific activities planned by the Ecological Society of America to address the research recommendations and to further develop the educational and environmental decision-making components of the SBI. We also consider the international dimensions of the SBI and the funding needed to implement it. In addition to these activities planned by the Ecological Society of America, implementation of the SBI will require complementary actions by individuals and institutions (Fig. 6). Individual principal investigators, program managers within Federal agencies, policymakers in governmental and non-governmental organizations, and private foundations hopefully will identify special opportunities within their purview to address the objectives of the SBI.

Research

It is crucial that modern science preserve a pluralistic approach to solving scientific problems. The research opportunities described herein demand new combinations of scientific disciplines and the application and expansion of recently developed research tools. To address these research priorities most effectively, it is important to draw on a broad base within the research community, permitting ecologists to incorporate new ideas and reevaluate research priorities.

ACTION ITEM #1: During the coming year, an organizing committee of the Ecological Society of America will plan workshops with the goal of coordinating the SBI with ongoing research efforts on global change and increasing research on the role of ecological complexity in global processes.

ACTION ITEM #2: During the coming year, an organizing committee of the Ecological Society of America will plan workshops with goal of developing an initiative on biological diversity that focuses on the ecological causes and consequences of patterns of biological diversity.

ACTION ITEM #3: During the coming year, an organizing committee of the Ecological So-

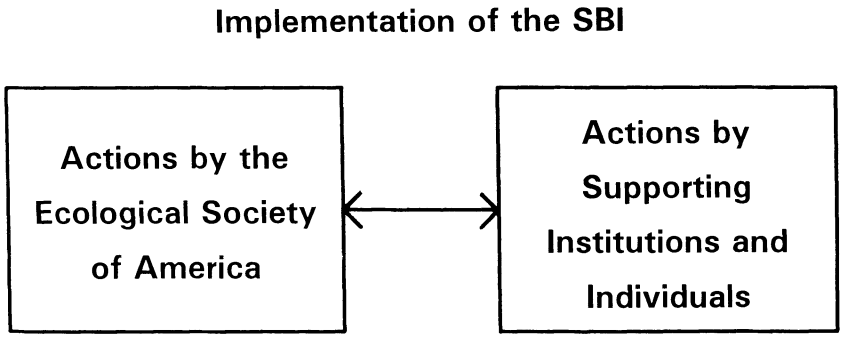

FIG. 6. Implementation of the Sustainable Biosphere Initiative will require a wide range of activities by many organizations (see text).

ciety of America will plan workshops with the goal of initiating a comprehensive program on sustainable ecological systems, emphasizing the underlying ecological processes that affect the sustainability of natural and managed systems.

These workshops will bring ecologists together with experts from related disciplines in the natural and social sciences and with resource-managers and environmental policy-makers to develop projects for immediate initiation.

EDUCATION

The environmental conditions that have mandated the Sustainable Biosphere Initiative also demonstrate the need for ecological education among citizens of today and tomorrow. Understanding and managing the biosphere requires ecological information. There are many strategies for addressing educational needs, such as working with the mass media to increase public awareness of ecological concepts and issues, making ecological literacy a goal of undergraduate curricula, and developing more interdisciplinary graduate degree programs that involve topics necessary for understanding the biosphere. Ecologically literate citizens should know not only the key concepts and principles of ecology, but also the basic processes by which ecological knowledge is acquired and the ways in which science and culture interact.

ACTION ITEM #4: During the coming year, the Research Agenda Committee of the Ecological Society of America will oversee the preparation and publication of a non-technical, public education document that articulates the importance of ecology and ecological research to society.

A diversity of strategies should be employed to address the educational needs of students, teachers, the general public, and decision-makers. These include: building ecology into pre-college curricula and teacher-training programs; making ecological literacy a goal of undergraduate education; and working with the mass media to increase public awareness of ecological concepts and issues. Educational efforts for fostering ecological understanding should build on and work with existing programs and initiatives in science and environmental education. Likewise, such efforts must be systematic and sustained.

ACTION ITEM #5: During the coming year, the Education Section of the Ecological Society of America will develop systematic, short- and long-term strategies for enhancing ecological knowledge among students and the public.

The Ecological Society of America should determine the human resources needed to conduct the ecological research proposed by the SBI and should examine specific vehicles to address the identified needs, including training grants and career development awards. Innovative professional education programs will be needed at the undergraduate, graduate, and post-doctoral levels to break down social and intellectual boundaries to interdisciplinary research, facilitate students' exposure to diverse biotic and professional environments, introduce students to conceptual advances in subdisciplines of ecology, and promote the incorporation of new technologies in students' emerging research programs. Finally, more opportunities are needed for established ecologists and other scientists to pursue interdisciplinary interactions, learn new techniques, and synthesize ecological knowledge.

Environmental Decision-making

Thousands of ecologically based decisions are made annually by policy-makers and regulatory agencies, land- and water-use planners, resource-managers, business and industry, consulting firms, and conservation groups. To be useful to decision-makers, ecological information must be both accessible and relevant to their mandates and responsibilities. The research component of the SBI is directed toward acquiring the ecological information (i.e., conceptual approaches, methods and tools, and data) needed to assess the status of ecological systems; to anticipate the impacts of management decisions and development options; and to conserve, restore, or manage ecological systems.

The application component of the SBI calls for the development of new institutional structures that will make ecological information more accessible to decision-makers. For example, collaborative programs between management agencies and academic ecologists offer benefits beyond the solution of important applied questions. Agencies benefit from the enthusiasm and innovative ideas of students and postdoctoral fellows; academics are challenged by urgent, complex problems. Training of students in both basic and applied realms will have long-term benefits for the development of ecology. Even the largest scale management projects involve mechanistic experiments and modeling studies that yield the short-term publications needed for career advancement within academia. Thus, the alliance of basic and applied ecology can invigorate academic ecology and strengthen the scientific basis of environmental assessment, rehabilitation, conservation, and management.

Application of ecological knowledge will require better communication between ecologists and decision-makers in all sectors of society. Knowledge transfer must be expedited and interdisciplinary barriers overcome. The experience of management-oriented professional societies in setting environmental priorities will be essential to open new avenues of communication.

ACTION ITEM #6: During the coming year, an organizing committee of the Ecological Society of America will begin to explore ways in which ecologists can become more responsive and bring their expertise more fully to bear on critical environmental problems. This committee will work closely with management-oriented professional societies, resource-managers, and other environmental decision-makers.

International Dimensions of the Sustainable Biosphere Initiative

The framework for this Initiative was developed in North America, but the research priorities and the environmental problems related to them are important world-wide. What is needed now is an extension of this initiative into an operational program of global scope.

ACTION ITEM #7: During the coming year, the Ecological Society of America will organize a meeting of leading ecologists from many nations of the world to evaluate the SBI and to begin construction of an operational framework for international cooperation.

At the same time there will be efforts to interact with governmental (e.g., UNESCO) and non-governmental (e.g., the International Council of Scientific Unions) international bodies that have programs closely related to the research agenda of the SBI.

Funding the Sustainable Biosphere Initiative

Meeting the financial needs of the SBI will require significantly increased funding from both public and private sources. Although there is a wide array of important and rewarding research questions, the SBI has identified those that are of the highest priority for the development of required knowledge and its application to conserving and wisely managing the Earth's resources.

Because of the broad importance of this Initiative, creative approaches to funding research will be required. Typically, public agencies such as the National Science Foundation fund basic research, mission agencies fund research that applies to problems of specific interest to the agency, businesses fund research to answer pressing industry questions, and foundations fund topics or themes of particular interest. The Sustainable Biosphere Initiative encompasses all of these missions, and as a result, must be planned and funded by a range of agencies and organizations.

Current administrative structures are insufficient to coordinate and fund the range of activities envisioned by the SBI. Consequently, it will be necessary to develop a new administrative structure that allows many agencies to support the integrated research program. To accomplish the needed coordination and funding, a variety of vehicles should be considered, including a new or existing interagency committee, a new national institute, or other administrative arrangements. This new organization would further develop research priorities within the SBI, coordinate funding strategies, and establish and implement procedures for evaluating the research progress of the Initiative.

ACTION ITEM #8: During the coming year, the Ecological Society of America will initiate discussions to develop an innovative framework to coordinate and fund the SBI. Emphasis will be placed on enhancing opportunities for investigator-initiated, peer-reviewed research in the context of coordinated programs that would fund both individual investigators and multidisciplinary research items.

Concluding Remarks

The ecological research agenda proposed in this document begins with the assumption that advances in understanding basic ecological principles are required to resolve many urgent environmental problems, continues with the identification of three priority areas for intense research efforts, and concludes with actions to be initiated by the Ecological Society of America to strengthen and expand research efforts in these key areas. The success of the Sustainable Biosphere Initiative will depend upon (1) the willingness of individual ecologists to participate in the proposed activities, to disseminate the vision of the SBI, and to plan and execute subsequent phases, and upon (2) the vision and abilities of policy-makers, funding agency administrators, government officials, business and industry leaders, and individual citizens to support, amplify and extend the actions we have initiated. At present, neither the funding nor the infrastructure in this country is sufficient to address the research needs described in this document. Moreover, achievement of a Sustainable Biosphere will require not only the acquisition of ecological knowledge via research, but also the communication of that information and understanding to all citizens and the incorporation of that knowledge into environmental, economic, and political decisions. Although there are formidable barriers to accomplishing these tasks, achieving a Sustainable Biosphere is one of the most important challenges facing humankind today. Time is of the essence. New technologies, widespread appreciation for the magnitude of environmental problems, and an increasing appreciation for the relevance of basic ecological research combine to provide an unprecedented opportunity to make significant progress in achieving a sustainable biosphere.

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IX. APPENDICES

Appendix A. Ecological Problems at Different Levels of Organization

Although many ecological problems cut across levels of biological organization, it is convenient to organize important ecological questions according to the appropriate level of organization. In listing the following questions, we have drawn extensively on the report of the Committee on the Application of Ecological Theory to Environmental Problems (National Research Council 1986).

Level of organization Ecological topic	Questions
Individuals	
Functional Morphology	What explains morphological variation within and among species? How does function follow form?
Physiological Ecology	How do physiological constraints limit the responses of organisms to their biotic and abiotic environments? What determines the physiological limits of an organism's response to stress?
Behavioral Ecology	How do individuals respond to information on the physical environment, resources, competitors, predators, or mates?
Ontogenetic Factors	What determines variation in the response of organisms at different stages of their life histories?
Individual Variability	How does the genotype of an individual affect its ecological interactions? What is the relative importance of genotypic and plastic variation in the response of individuals to environmental variation?
Populations	
Population Regulation	What processes have the most effect on population growth rate? Which of these are density dependent? How do density-dependent processes interact with other important processes?
Population Stability	What is the pattern of temporal variation in population size? Does the population density tend to return to some equilibrial level when displaced? Are there multiple stable points? Is there a minimal population size necessary to avoid extinction?
Dispersal and Migration	What regulates population dispersion and migratory behavior? How do populations respond to the frequency, scale, intensity, type, and duration of disturbance?
Population Structure	How do elements of population structure (i.e., genetic and age structure; patterns of variation in life history traits, physiology, and phenotypic plasticity) affect the ecological responses and interactions of a population? How does exploitation affect population structure?
Among Populations	
Predation, Parasitism, and Disease	To what extent do consumers or pathogens control a population? What is the relative importance of consumers or pathogens and extrinsic factors (e.g., stress, disturbance)? What is the role of fixed or inducible natural defenses?
Competition	What is the role of competition in the evolution and ecology of populations?
Mutualism	How do mutualistic interactions affect the response of a population to perturbations?
Indirect Effects	What are the potential indirect interactions in a food web? What is the relative strength of direct and indirect effects? How do higher order interactions and non-linearities in interaction equations affect the predictability of population responses to perturbation?

Level of organization Ecological topic	Questions
Communities	
Community Structure	How does community structure affect individual species embedded within the community? To what degree are some species interchangeable without affecting community processes? What do the collective properties of communities, including various community indices, tell us about their functioning? How is community structure affected by population dynamics of component species?
Biotic Diversity	What are the patterns, causes, and consequences of spatial and temporal variation in species diversity? What is the role of diversity of genetic composition, phenotypes, functional groups, demic structure, habitats, landscapes, and biogeochemical processes in ecological communities?
Succession	How do population interactions and other processes at the level of the individual organism combine to produce the relatively predictable sequences in community composition during colonization or re-colonization of an open habitat? What processes retard or accelerate the rate of succession in ecological communities?
Community Stability	How well do communities resist environmental forces that may perturb them? What properties of communities lead to resilience in the face of environmental change? How rapidly do communities return to their initial state, and what factors determine the rate of recovery? To what degree are communities resistant to invasion by alien species? How might we predict the ability of a new species to become established in a given community?
Ecosystems	
Flux of Energy and Matter	How does variation in energy and material fluxes affect ecosystem structure? What mechanisms account for the flux of energy and matter within an ecosystem? How does resource availability interact with other limiting biotic and abiotic factors to influence biogeochemical cycling?
Diagnostic Indices of Function	What ecosystem features serve as indices of ecosystem stress or "health?"
Cross-system Comparisons	How do ecosystems differ in structure, function, or response to perturbation or management? How does climate mediate ecosystem structure and function?
Ecosystem Mediation of Climate, Wastes	How do ecosystems mediate climate? What is the role of a given ecosystem in processing or sequestering anthropogenic wastes?
Among Ecosystems	
Landscape Ecology	How do land-use patterns influence the ecology of component systems, including all levels of ecological organization up to the scale of the landscape itself?
Responses to Environmental Change	What are the feedbacks between ecosystem and atmospheric processes, both within and among separate ecosystems, extending to a global scale? How does vegetation affect climate? What is the response of terrestrial, aquatic, and marine ecosystems to variation in CO_2? What are the effects of changing climate, atmospheric composition, sea level, ocean circulation, and ultraviolet insolation on ecosystem processes, including biogeochemical cycling?

Appendix B. Cross-cutting Issues in Ecology

A few general ecological issues are common to many specific ecological questions. This list identifies issues critical to elucidating ecological processes and enhancing the usefulness of ecology for solving practical environmental problems.

Interactions among levels of ecological organization. Virtually all questions in ecology explore how phenomena at one level are related to processes operating at other levels. Even if not explicitly identified, this issue must be considered in most ecological investigations. For example, responses at the level of the population, community, and ecosystem must be related to processes at the level of the individual organism, the level at which natural selection acts.

The effects of spatial and temporal scales. Processes and events at one scale in space and time have serious implications for, and may even control, processes and patterns at other scales. For example, intense competition for a limited resource could occur very rarely, yet dictate many characteristics of the competing species over long intervals of time.

The importance of heterogeneity or diversity at all levels of biological organization. Here we include questions concerning the role of genetic diversity, species diversity, and habitat heterogeneity at several nested scales; landscape-scale complexity; and many other aspects of ecological systems. For example, patchiness and heterogeneity of the environment may affect life history evolution, the coexistence of species, and the maintenance of ecosystem processes.

How multiple factors combine to affect ecological systems. It is critical to assess the cumulative impact of numerous factors at all levels of ecological organization. Physical and biological factors interact to influence ecological processes; a better understanding of this interaction would help to address larger problems. For example, organisms already stressed by crowding and the consequent intense competition for resources may often be more susceptible to mortality when subjected to additional stress. Multiple disciplines must be incorporated into ecological research as a means to understanding how multiple factors combine. Understanding the role of atmospheric processes, geochemistry in the soils, and the physics of the transfer of matter, heat, and momentum in water are all critical to developing the science of ecology.

The role of environmental variability. Ecological theory and empirical study alike have demonstrated the vast differences between systems at equilibrium and nonequilibrial systems. Consequently, priorities in ecological research include the magnitude and specific action of natural and authropogenic disturbance and the interaction of disturbance with other biotic and abiotic factors. Such research includes the issue of the ecological responses to environmental stress and the question of how structure and function of ecological systems at all levels reflect stress. Implicit in this general problem is also the question of how to detect change in ecological systems against a background of substantial variability.

Appendix C. List of Boxes