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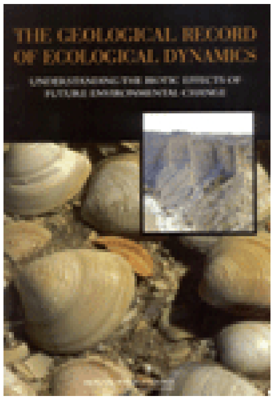

The Geological Record of Ecological Dynamics: Understanding the Biotic Effects of Future Environmental Change

Committee on the Geologic Record of Biosphere Dynamics, National Research Council

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THE GEOLOGICAL RECORD OF ECOLOGICAL DYNAMICS

UNDERSTANDING THE BIOTIC EFFECTS OF FUTURE ENVIRONMENTAL CHANGE

Committee on the Geologic Record of Biosphere Dynamics
Board on Earth Sciences and Resources
Board on Life Sciences
Division on Earth and Life Studies
NATIONAL RESEARCH COUNCIL
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Cover: Background photograph shows mollusk shells on the Colorado River delta in Mexico, which record the biotas and environmental conditions prior to upstream diversion of freshwater. Radiocarbon, amino acid, and growth line analyses of the shells, together with oxygen and carbon stable isotope analyses, provide detailed chronologies of temperature, salinity, productivity, and other environmental parameters. Photo courtesy Karl W. Flessa. Outcrop photograph shows rhythmically bedded Late Cretaceous (~87 Ma) limestones and shales in the Terlingua Creek canyon of West Texas. The geologic record can be used as an ecological laboratory when rocks preserve a near-continuous sequence of repeated environmental and biotic change; photo courtesy Brad Sageman.

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COMMITTEE ON THE GEOLOGIC RECORD OF BIOSPHERE DYNAMICS:
THE KEY TO UNDERSTANDING THE BIOTIC EFFECTS OF FUTURE ENVIRONMENTAL CHANGE

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Preface

The economic and environmental security of the United States and the world depends on the ecosystem services and functions provided by natural and managed biotic systems. It is vital therefore that we learn how these systems respond to both natural and anthropogenic change. Predicting and managing the biotic response to future environmental change require a sound scientific understanding of the rate and character of past biotic responses to environmental perturbations. The converse also applies—biotic systems, through their effects on the characteristics of the earth's surface and on biogeochemical cycles, affect the climate system. Understanding this feedback is a crucial requirement for predicting both future climate and the response of the biosphere to climate change. The geologic record is vital for understanding the complex interactions between environmental and biotic change; the last 200 years of direct scientific observations is too short a time period to allow direct observation of the range of environmental conditions we are likely to encounter in the future, too short to expose the nature of long-term ecological processes, and too short to fully reveal the ecological legacy of past events. The geologic record also provides critical insight into the character of biotic systems unaffected by human activities.

Recent technological and conceptual advances in the earth and life sciences make analyses of the geologic record of past biotic change especially powerful and relevant. Ecological studies are now revealing the importance of past events, long-term environmental change, and evolutionary processes in the structure and function of living ecosystems. Significant improvements in dating geological materials and correlating events among sites now allow the resolution of rates of environmental and biotic change, as well as the identification of short-term events and their effects over large areas. Two decades of intense research on the processes of fossilization and on analytical methods to detect and compensate for incomplete and biased records now allow scientists to discern true ecologic patterns in fossil assemblages and true evolutionary signals in the fossil record. The development of precise biogeochemical indicators of past environmental and biotic conditions now permits high-resolution reconstructions of past biotas and their variability. The power of these developments has been greatly increased by the development of large databases and tools for data dissemination, integration, and visualization. Such databases and database tools provide the foundation for regional and global syntheses to assess the ecological and evolutionary impacts of environmental changes across a range of timescales. These advances set the stage for collaborative efforts among earth scientists and life scientists for innovative and integrative examinations of the geological record of past environmental and biotic change.

In light of these advances—and the potential for collaborative, interdisciplinary research on the nature of biotic response to future environmental change—the National Science Foundation and the U.S. Geological Survey requested that the National Academies assess the scientific opportunities provided by the geologic record of biosphere dynamics, and recommend how academic and agency scientists could best exploit those opportunities for the nation's benefit. The committee, composed of both life scientists and earth scientists, met three times as a group to review existing agency and academic research efforts, to hear testimony solicited from expert scientists, to formulate its recommendations, and to write key components of the report.

The concept of biosphere dynamics encompasses any and all changes in the earth system that involve living organisms, regardless of temporal or spatial scale. Environmental changes, including climate change, tectonic activity, and sea level changes, have driven evolutionary and ecological dynamics at timescales ranging from thousands to hundreds of millions of years. Evolutionary novelties, ranging from the origin of oxygenic photosynthesis to the origin of our own species, have led to a broad range of environmental and ecological responses. Faced with the vast array of phenomena that could be subsumed under the term "biosphere dynamics," and recognizing the basic scientific and applied resource management issues facing society as local and global environmental change accelerates, the committee chose to concentrate its efforts on the geologic record of "ecological dynamics"—the changes and interactions in the earth-life system expressed as alterations in such features as species distributions, species abundance, environment, and climate. While recognizing the significance of evolutionary responses to environmental change throughout the history of life, the committee felt that a study that also treated evolutionary dynamics in great detail would require resources and expertise far beyond those available to it.

This report is the result of many additional hours of discussions, writing, reviewing, and editing by a committee whose breadth and expertise was essential to the quality of the final product. We are also grateful for David Feary's skillful guidance and editorial skills and for the support of National Research Council officials and staff.

Karl Flessa
Chair

Stephen Jackson
Vice Chair

Acknowledgments

This report was greatly enhanced by the participants in the two public committee meetings held as part of this study. The committee would first like to acknowledge the efforts of those who gave presentations at meetings: Enriqueta Barrera, David Blockstein, Lynn Brewster-Wingard, Scott Collins, Rachael Craig, Bruce Fouke, Susan Haseltine, Lars Hedin, Patrick Leahy, Brian Maurer, Michael Meyer, Donald Rice, Craig Schiffries, Steven Stanley, David Verardo, Debra Willard, and Herman Zimmerman. These talks helped set the stage for fruitful discussions in the sessions that followed.

The committee is also grateful to Jill Banfield, Tim Baumgartner, Julio L. Betancourt, Cinzia Cervato, David Jablonski, Dennis H. Knight, Peter Leavitt, Thomas Olszewski, William A. Reiners, Brad Sageman, Bryan Shuman, and John W. Williams, who provided important information, commentary, and material for this report. We also thank Dena Smith and the University of Colorado Museum for providing meeting facilities.

This report has been reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise, in accordance with procedures approved by the National Resarch Council's Report Review Committee. The purpose of this independent review is to provide candid and critical comments that will assist the institution in making its published report as sound as possible and to ensure that the report meets institutional standards for objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process. We wish to thank the following individuals for their participation in the review of this report:

James H. Brown, Department of Biology, University of New Mexico, Albuquerque
Margaret B. Davis, Department of Ecology, Evolution and Behavior (*emeritus*), University of Minnesota
Andrew H. Knoll, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts
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Peter M. Vitousek, Department of Biological Sciences, Stanford University, California

Although the reviewers listed above have provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations nor did they see the final draft of the report before its release. The review of this report was overseen by P. Geoffrey Feiss, College of William and Mary, Williamsburg, Virginia, appointed by the Divison on Earth and Life Studies, who was responsible for making certain that an independent examination of this report was carried out in accordance with institutional procedures and that all review comments were carefully considered. Responsibility for the final content of this report rests entirely with the authoring committee and the institution.

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APPENDIXES

Executive Summary

Earth's environment is in constant flux. Driven by physical processes, biological processes (now including the effects of human activity), and their interactions, incessant changes occur at virtually all temporal and spatial scales. Recent research has greatly increased scientific understanding of the nature and pace of current and past physical environmental changes, and is now also yielding information on the complex ways biological systems contribute to and react to environmental change. Given the diverse roles played by biota in Earth's environmental system, as well as the direct importance of wild and managed biological resources to human welfare, a deeper understanding of the ecological dynamics of environmental change constitutes a critical scientific priority.

Longer-term historical perspectives are essential for answering a host of questions about the ecological dynamics of present day environmental systems and about feedbacks between biotic systems and environmental change, including climate change. The geologic record—the organic remains, biogeochemical signals, and associated sediments of the geological record—provides unique access to environmental and ecological history in regions lacking monitoring data and for periods predating human impacts. It also provides information about a broader range of global environmental conditions than exist today, as well as insights into biological processes and consequences that are expressed only over longer time intervals and the opportunity to discover general principles of ecological organization. Understanding how ecological processes scale up from short-term to evolutionary time frames is critical to a full understanding of the biotic response to environmental change, and thus to developing sound policies to guide future management. Advances during the past 10-20 years have transformed the ability of earth scientists to extract critical biological and environmental information from the geologic record. These advances at the interface of earth and biological sciences—combined with a greatly improved capacity for accurate dating of past events, the development of high-resolution timescales, and new techniques for correlation—set the stage for this assessment of research priorities in geohistorical analysis of biotic systems (see Box ES.1).

The committee recommends a major, decadal-scale scientific commitment to improving our ability to predict the biotic dynamics of environmental change through geohistorical analysis. Given the inherent complexity of biological systems and the increasing footprint of human activities over the last several millennia and centuries, it is critical that geohistorical analysis informs modeling and analysis of present day systems. Such a major effort will require an explicit commitment to innovative and genuinely multidisciplinary research both by agencies and by individuals. It will also require investments in the infrastructure needed to support collaboration between earth scientists and biologists, and new educational opportunities for earth scientists and biologists early in their careers that encourage them to bridge traditional disciplines.

BOX ES.1
Statement of Task

Committee on the Geologic Record of Biosphere Dynamics: The Key to Understanding the Biotic Effects of Future Environmental Change

The committee will describe the potential of the geologic record as a means of understanding biotic interactions with environmental change and the coupling of earth/life processes, and develop strategies for integrating earth and biological sciences and transferring their combined insights to the policy community. In particular, it will undertake the following tasks:

1. Assess the current state of biogeologic analysis relevant to biosphere dynamics;
2. Identify the most promising directions for collaborative research and the sharing of methodologies; and
3. Describe the programmatic themes and research and data infrastructures required to accomplish these objectives.

The committee sees three directions as most promising for significant advances and identifies these as initiatives with the highest scientific and policy value: (1) using the geologic record as a natural laboratory to explore biotic response under a range of past conditions and thereby revealing basic principles of biological organization and behavior; (2) using the record to enhance our ability to predict the response of biological systems to climate change in particular; and (3) exploiting the relatively young geologic record to evaluate the effects of anthropogenic and non-anthropogenic factors in the variability of biotic systems.

INITIATIVE 1: THE GEOLOGIC RECORD AS AN ECOLOGICAL LABORATORY

Most ecological theories are derived from short-term observations and models. Yet we know that past events, and ecological and evolutionary processes operating at timescales beyond direct human observation, affect present day biodiversity and biogeochemical cycling on local, regional, and global scales. The geologic record provides empirical data from longer timescales. This broader perspective both obviates the need to extrapolate ecological behaviors and principles from short-term observations and creates the opportunity to understand the effects of environmental change over an expanded range of temporal and spatial scales. For example, the geologic record is the only source of empirical information on the long-term effects of a broad range of CO_2 concentrations on biotas and climate systems.

Geohistorical analyses are essential to (1) characterize ecological processes and trends that unfold over longer timescales; (2) identify patterns and mechanisms that are masked by the variability inherent in direct, short-term observation; and (3) recognize which aspects of modern ecological systems are contingent on past events. The geologic record of past ecosystems establishes the extent to which conclusions based on modern systems can be extrapolated through time and also permits ecological analysis under global environmental conditions different from those of today. Geohistorical analyses thus permit tests of ecological theories and their underlying assumptions. The geologic record provides access to a wide range of past “alternative worlds” from which truly general principles can be derived. Ecological principles can be considered truly general only if they apply to ancient species and communities as well as to modern ones.

> **Recommendation: A deeper understanding of the origin, maintenance, and distribution of biodiversity and its importance to ecological systems is urgently needed. It is essential to**

> **expand fundamental research using the longer time perspectives of the geologic record to frame and test ecological theories at appropriate scales while encompassing a full range of earth conditions.**

Society needs not only to predict but also to manage the biotic response to future environmental change. Such management can occur only if the principles of large-scale ecology are understood at a level of generality beyond the specifics of a particular time interval. Understanding these fundamental principles of ecological organization and behavior will require significantly increased collaboration across the earth and biological sciences to a degree that traditional funding and administrative structures do not currently encourage or support.

INITIATIVE 2:
ECOLOGICAL RESPONSES TO PAST CLIMATE CHANGE

Climate exerts a dominating influence on the distribution and abundance of organisms, the nature and rates of biogeochemical fluxes, the structure and composition of ecological communities, and the frequency and intensity of ecological disturbances. Climate interacts with and mediates other global change processes, such as biological invasions, human land clearance, anthropogenic alterations of mineral cycles, and disease outbreaks. Because of the importance of climate in governing ecological patterns and processes, documentation of biotic responses to past climate changes is a critical step toward full understanding of ecology. Paleoclimatic studies indicate that Earth's climate is capable of a wide variety of system states and modes of variability and that the past two centuries have experienced only a fraction of the potential variability within the climate system. Therefore, any comprehensive understanding of ecological dynamics requires that we understand how ecological systems have responded to climate change and variability in the past. Just as the instrumental record of the past two centuries provides an inadequate sample of the range and nature of climate variation, ecological studies based on direct observation in present day systems provide an inadequate sample of the array of biotic responses to climate change, and the potential consequences for biodiversity and biogeochemistry. Studies of biotic response to climate change must therefore include insights from geohistorical analysis.

> **Recommendation: Climate change and its consequences are of enormous scientific and societal concern. A significant research initiative to pursue a richer understanding of how biotic sys-**

tems have responded to and interacted with past climate change and variability is needed to provide a sounder basis for forecasting the ecological consequences of future climate change and variability.

Ecology is poised to make great advances by building on the improved understanding of past climate variation and change. In particular, the development of multiple, independent paleoclimate proxies is providing a rich understanding of past climates, while at the same time liberating paleoecological data from being the primary source of paleoclimate inference. Paleoecological data can now be compared to past climate change inferred from other proxies, allowing direct study of biotic responses to climate changes in the geological record. A more sophisticated understanding of the effects of climate change and variability on biodiversity, biogeochemistry, biogeography, community structure, disturbance regimes, and genetic structure of populations requires a concerted effort to link paleoecological and paleoclimatic records.

INITIATIVE 3:
ECOLOGICAL LEGACIES OF SOCIETAL ACTIVITIES

The profound effect of human activities on natural environments and ecosystems is clearly evident, but the consequences are less well understood. In effect, an unintentional global experiment is already in progress. However, the initial conditions of this far-reaching experiment are largely unknown, because the onset of human interactions with natural systems—both intentional and unintentional—predate scientific monitoring efforts, which largely extend back at most to the late 1800s. There is also no "control" in this experiment; completely natural habitats are no longer available either locally or globally to use as a benchmark for comparison with habitats that have been modified. The geohistorical record is thus the only source of information on (1) the natural range of environmental variability and ecosystem function before human impact; (2) how ecosystems functioned in the absence of human influence; (3) how ecosystems have responded to progressive human impacts; and (4) which aspects of present day environmental variability and ecosystems are legacies of past societal activity. Geohistorical records of the past provide an invaluable archive of the state of ecosystems before significant societal impact. They also show how ecosystems have been transformed by human activity.

Recommendation: Societal activities have impinged on the natural world in many ways, but the consequences and possible solutions to these impacts are unclear when some impacts are

> **difficult to distinguish from non-anthropogenic variation. Intensified research on environmental and ecological conditions and variability before human impacts and on the geohistorical records of how societal activities have affected present day ecosystem dynamics is essential.**

Because human activity has already affected natural ecosystems in myriad ways, acquiring knowledge of pre-human baseline states and natural variability is essential for discriminating between anthropogenic and non-anthropogenic change in species, biotas, and ecosystems. Insights into such dynamics from geohistorical analysis are critical in developing strategies for conservation and restoration. In seeking to predict and manage the response of ecosystems to future societally driven perturbations, we must take advantage of the opportunity to understand how these activities have affected ecosystems in the past. Understanding the ecological impact of past human activities is also crucial for the recognition of persistent effects—legacies—that may continue to influence ecosystems long after the causative activities have ceased.

FACILITIES AND INFRASTRUCTURE

Funding

Research on the geologic record as an ecological laboratory, on the ecological responses to past climate change, and on the ecological legacies of societal activities will require additional funding. Current levels of support are inadequate for the increased activities that these three initiatives will generate. High-precision dating, sophisticated geochemical analyses, large numbers of samples, database development, collections maintenance, and the need for collaboration among investigators and students from multiple disciplines are all required, and all will cost money. Increases in funding have not kept pace with society's increasing need to predict and manage future biotic change, or with the increased interest in this topic within the scientific community. The new kinds of research that are needed cannot be pursued without modifying the resource allocation to increase support.

> **Recommendation: Funding levels for research on the geologic record of ecological dynamics must reflect the research's technological needs and the societal importance of understanding the biological response to environmental change. Funding should be structured to ensure that both research and graduate training take full advantage of collaborative opportunities across disciplines.**

Personnel and Training

Research on the geologic record of ecological dynamics should be structured to encourage and support the collaboration of professional biologists and geologists, as well as the training of an increasingly flexible new generation of scientists with the necessary multidisciplinary talents. We recommend establishing a postdoctoral program whereby a new Ph.D. in one discipline would undertake collaborative research with a mentor from the other discipline. This would engage scientists at an early stage in their careers with opportunities for innovation and would have a long period of positive downstream effects.

Laboratories for Geologic Analysis of Ecological Dynamics

Substantial support for research in natural laboratories, and for actual or virtual collaborations and facilities, is needed to focus intellectual efforts and develop research tools for the three initiatives described above.

Natural Laboratories: Long Term Ecological Research Projects

Long Term Ecological Research (LTER) sites have successfully lengthened the time-perspective of ecological studies, generating observations of natural (and in some instances experimentally manipulated) habitats over several to many decades. Nevertheless, LTER event timescales are short relative to many ecological process and environmental change timescales. Existing LTER projects represent a superb opportunity to leverage relatively unusual long-term ecological and environmental monitoring with observations from times before the instrumental record, in order to acquire information on both the character and rates of environmental change and the biotic components of that change. Geohistorical records from lakes, bogs, reefs, or estuaries near or adjacent to LTER sites would provide opportunities to integrate geohistorical data with observations and experiments from the LTER sites. Such integrated records would provide the temporal perspectives necessary to detect decadal and longer ecological trends, and to discriminate between natural and human-driven changes. Activities within the new National Ecological Observatory Network (NEON) program should also go beyond the monitoring, experimentation, and modeling of biotic systems in the present. Geohistorical analysis should be made an integral part of the NEON mandate. Incorporating retrospective data on past biotas and environmental variability is essential to efforts in ecological forecasting.

Natural Laboratories: Geologic Time Ecological Research Projects

The development of Geologic Time Ecological Research (GTER) projects would be a promising platform for research on ecological dynamics. A GTER project would focus on a particular habitat type, critical region, (paleo)latitudinal belt, environmental gradient, or time interval as a natural laboratory for focused, collaborative study for a 5- to 10-year period. The availability of excellent geologic records might motivate the selection of a region for modern-day ecological analysis. For example, a long-lived modern lake basin would provide the opportunity to extend observations of current processes back in time using fossils and environmental data derived from cores to address all three of the initiatives identified here. Similarly, a region known to have experienced biotic invasions in the past (e.g., oceanic islands) would constitute a useful laboratory to examine the controls and consequences of biotic invasions.

Research Collaborations

Research collaborations are envisioned as actual or virtual forums for the analysis, synthesis, and modeling of *existing* data and for the general exchange of intellectual capital. These collaborations might take a form similar to the NCEAS (National Center for Ecological Analysis and Synthesis) model, by providing a setting for collaborative working groups to focus for short periods of time on integrative ecological problems that require synthesis of empirical and model-generated information. The former Pliocene Research, Interpretation, and Synoptic Mapping (PRISM) project of the U.S. Geological Survey (USGS), which targeted global paleoclimates of the Pliocene, demonstrates how federal agencies with intramural researchers can lead collaborative projects, although this particular project emphasized physical environmental reconstruction and improved age determination more than biotic response. This virtual collaboration demonstrated the value of targeting a past interval of geologic time—rather than a geographic site or region—to better understand natural systems with relevance to future change.

Both examples represent innovative ways to foster integrative work among biologists and paleobiologists (as well as other physical scientists), producing immediate scientific results as well as long-term benefits by associating individuals usually separated by administrative and disciplinary barriers.

Databases and Collections

Recommendation: Publicly available databases and natural history collections can promote collaboration, reduce dupli-

cated effort, facilitate large-scale synthetic studies, and provide critical and at times irreplaceable data and research opportunities. Federal agencies should play an important role in sustaining and enhancing community efforts to build and improve such entities.

Data are the currency of research in the geological and biological sciences. The maintenance and accessibility of data in either digital form (e.g., electronic databases) or physical form, including voucher materials (e.g., museum collections, cores, paper records), are essential for the effective and efficient conduct of research in ecological dynamics. The number and size of online databases have grown enormously in the past decade. This increase will continue, thereby providing for greater access to the results of publicly funded research. Previously collected data must be maintained, access must be provided, and repositories for newly collected data should be designated. The key disciplines are being overwhelmed with data even as they labor to find more information relevant to new questions. Enhanced federal support is critical for the expansion and coordination of community-wide database efforts, including the discovery and integration of metadata and the maintenance of key specimens and samples in museum collections. Community-wide databases provide a new research tool for the synthesis and analysis of data at scales that would have been impossible in the past.

Such efforts also add value by promoting the culture of collaboration essential for multidisciplinary research on the geologic record of ecological dynamics. These database efforts will require long-term commitments from agencies, institutions, and professional societies to ensure quality, continuity, and availability of the data and products. Previous recommendations that have focused on geoscience data and collections (NRC, 2002b), including museum collections, also apply to the broadly interdisciplinary data of both the geoscience and bioscience communities that will be needed to address the complex biosphere issues outlined above.

Enhancement of Capabilities for Age Determination and Correlation

Recommendation: The research efforts proposed here require additional support for dating facilities, for the cost of dates in research projects, and for the development of techniques critical for high-resolution age determination and correlation.

High-precision radiometric dates are expensive, time consuming, and frequently constitute the money-limiting or rate-limiting factor in paleobiological research. There is a clear need for support of low-cost, fast-turnaround laboratories for radiometric dating and related chronostratigraphic analyses (e.g., radiocarbon, volcanic ash, geochemical markers). Support is also needed for chronostratigraphic databases and quantitative techniques to facilitate comparison and correlation among geohistorical records. Refining the precision and accuracy of temporal resolution will require improvements in radiometric dating, in our understanding of the temporal resolution of fossil assemblages themselves, and in methods to assign individual geohistorical records to a high-precision geologic timescale. As the resolution of the geologic timescale is progressively refined, there will be a continuing need to improve the accuracy of geochronologic techniques.

Enhancement of Methods for Environmental and Biotic Reconstruction

> **Recommendation: The research efforts proposed here require additional support to develop and refine techniques that can extract high-precision environmental and biotic information from geohistorical records.**

Proxy indicators (environmentally and biotically diagnostic physical, chemical, or biotic features of rocks or fossils) of past environments, biotas, and biotic interactions provide the essential evidence needed to assess the nature, rate, and magnitude of the biotic response to that change. Additional research is needed to develop proxy indicators that can be applied in older geohistorical records, to evaluate the preservation of geochemical and biogeochemical proxies, and to develop measures of short-term environmental variability. Reconstructing the range of natural variation in past environments is needed to detect environmental changes that exceed the natural background.

Proxy indicators are especially needed for determining the characteristics of past biotas that are not preserved as conventional fossils. Proxy indicators for ecological attributes such as abundance, trophic relationships, and growth rates are important for recognizing how ecosystem function changes in response to environmental change. Technological advances now permit the recognition of biotic elements from distinctive organic molecules and stable isotopes preserved in geohistorical records, but this research area is still in an early stage of development. There is enormous potential to use biomolecular and isotopic methods to recognize the presence, abundance, and biochemical significance of biotas that are not preserved as conventional fossils and as records of ecological functioning. Improved understanding of the diagenesis of biomarkers is essential for their application in deeper time.

Only geohistorical data—the organic remains, biogeochemical signals, and associated sediments of the geological record—can provide a time perspective sufficiently long to establish the full range of natural variability of complex biological systems, and to discriminate natural perturbations in such systems from those induced or magnified by humans. Such data are crucial for acquiring the necessary long-term perspective on modern systems. Information from past environmental states, both like and unlike those of the present day, provide the empirical framework needed to discover the general principles of biosphere behavior necessary to predict future change and inform policy managers about the global environment.

1

Introduction

The task of managing ecosystems and biodiversity confronts human society with a host of difficult questions that cannot be answered rigorously without a historic perspective. Are the booms and busts in salmon, sardine, and anchovy populations along the Pacific coast solely the result of fishing practices? How have decades of fire suppression in the western United States altered the frequency and character of fires and the nature of forest communities? How do we set goals for restoration of Florida Everglades and other coastal habitats given the prolonged modification of these complex systems from their original pristine states that existed before human alteration?

In turn, answering these practical questions depends on answers to broader questions: What were the dynamics of fish populations along the Pacific coast before significant human impact? On average, how regularly did forests in the western United States burn over the last millennium? What has been the range of hydrologic and vegetation conditions experienced in Florida's subtropical swamps over the last 10,000 years?

With a still broader perspective, it is also of considerable scientific and policy interest to know the answers to a range of important questions: What are the characteristics of Earth's environments and biotas when the polar regions have little or no permanent ice? How flexible are species, functional groups, and ecosystems in the face of climate and other environmental change under genuinely natural conditions? How do communities reassemble following major perturbations or significant decreases in diversity? Will there be feedbacks from changed biotas that affect the climate system? Are present day losses of biocomplexity significantly different in rate or magnitude than the declines that took place in the absence of any human influence? Are the effects of declines in ecological diversity today likely to have the same effects as those in the past?

The answers to all these questions—whether targeting site-specific problems or exploring general principles of ecological dynamics—require detailed, reliable information on past species abundances and environmental conditions from time intervals predating the last century of direct observation by scientists. Although the past decade has seen major advances in understanding the global climate system by a combination of real-time observations, modeling, and paleoclimate records, predicting and planning for the future depends upon our ability to understand not only how and why environments change but also how and why biological systems react. We also need to understand how biological systems themselves mediate important elements of environmental change ranging from key climatic parameters to biogeochemical cycles. Ecological dynamics (see Box 1.1), whether at the single-species, community, or global scale, generally have been studied by biologists over relatively brief timescales (one to two decades at most) and almost always in systems already highly altered by human activities.

There is thus a growing realization that only geohistorical data—the organic remains, biogeochemical signals, and associated sediments of the geological record—can provide a time perspective sufficiently long to establish the full range of natural variability of complex biological systems, and to discriminate human perturbations from natural cycles (e.g., Jablonski and Sepkoski, 1996; Swetnam et al., 1999; Lawton, 1999; McDonald and Chure, 2001; Woodruff, 2001; Hubbell, 2001; Barnosky et al., 2004). Such data are crucial for acquiring the necessary long-term perspective on modern systems and, by sampling past environmental states both like and unlike those of the present day, for providing the empirical framework needed to discover the general principles of biosphere behavior that would permit prediction and management of future change. This time perspective, which is outside the reach of conventional ecological monitoring (e.g., Long Term Ecological Research [LTER] sites; see Chapter 4), is readily accessible through geohistorical records. The rigorous evaluation of such records by earth scientists over the last few decades has shown that both the character and the rate of biotic response to environmental change can be determined with confidence. Advances in the development of proxy environmental indicators, the reconstruction of species ecologies, and sophisticated dating methods, are changing the way biologists view the world and have prompted a series of workshops on how to best capitalize upon the unique opportunities that geohistorical records afford for direct analysis and modeling of biological systems (e.g., Cohen et al., 1998; Aubry et al., 2000; Flessa, 2000; Myers and Knoll, 2001). Indeed,

BOX 1.1
Terms and Concepts

The term "biosphere dynamics" is used in this report to refer to the ecological and evolutionary changes that occur as biological systems respond to, and contribute to, environmental change. Organisms respond to environmental change at many scales—from the individual to the entire biosphere, and from near instants in time to the entire record of life on Earth. *Biosphere dynamics* encompasses diverse processes, including growth rates of individuals and populations, shifts in geographic range, alterations in the rates and kinds of biogeochemical cycling, changes in the composition of communities over varied timescales, speciation, and local, regional, and global extinction. With this vast array of phenomena that could be subsumed under the term biosphere dynamics, the committee chose to concentrate its efforts on the geologic record of "ecological dynamics"—the changes and interactions in the earth-life system expressed as alterations in features such as species distributions, species abundance, environment, and climate.

The "geologic record" consists of all the direct lithologic, fossil, and geochemical evidence of Earth's history. Taken together, the geologic record is an incomplete archive because some time intervals and places are absent or less well represented than others. "Geohistorical records," a term commonly used in this report, are the individual stratigraphic sections, sediment or ice cores, tree ring series, fossil collections, specimens, or archaeological remains that provide temporal, environmental, and biological information about a particular place. Such geohistorical records can provide extraordinarily rich, high-resolution information about how changes of past biotas are connected to other aspects of environmental change. Collectively, the geologic record is incomplete, but individual geohistorical records (e.g., subannual growth increments in skeletal remains, annual- to decadal-resolution sediment layers, assemblages of skeletal remains before and after critical environmental changes) are more than adequate to document past ecological dynamics and are a key to understanding the biotic effects of future environmental change.

analyses of geohistorical records have already proven critical to understanding the origin, maintenance, and distribution of biodiversity; the character of biotic response to climate change; and the effects of societal activities on biotic systems (see Chapters 2 and 3). Such research, at the interface of the geological and biological sciences, holds enormous promise for both basic and applied research on the nature of biotic change.

BACKGROUND TO THIS REPORT

Previous federally sponsored reports have called for greater collaboration between geologists and biologists in efforts to understand how biotic systems respond to environmental change. Indeed, some of the recommendations in this report can be traced to discussions and promising research themes identified in earlier reports. This fact is evidence of the broad, community-level interest in these issues, the continuing necessity for priority setting within the research community, and the need for substantive support from funding agencies, mission agencies, and academic institutions. These earlier reports include:

- *Effects of Past Global Changes in Life* (NRC, 1995) reported the scientific findings of a symposium held at the Geological Society of America meeting in 1989. This volume called for expanded interdisciplinary research on the response of life to global environmental changes, the identification of secular changes in biogeochemical cycles, the construction of conceptual and numerical models of geosphere-biosphere interactions, and improvements in proxy environmental indicators, ecological indicators, and geochronological techniques.
- A subsequent National Science Foundation (NSF) supported white paper *Geobiology of Critical Intervals* (Stanley, 1997) proposed an initiative to foster research on intervals of geologic time that constituted natural experiments on the structure and dynamics of the earth-life system. Such an initiative would take advantage of the deep-time perspective available in the geologic record to elucidate the biotic responses to environmental change across a broad range of temporal and spatial scales. This report also addressed strategies to improve temporal resolution, foster the development of proxy indicators for environmental and biotic parameters, and develop quantitative models of the earth-life system.
- The 1999 report to the NSF on research directions in paleontology (Flessa, 2000) provided input to the NRC (2001a) report *Basic Research Opportunities in Earth Science*. Flessa (2000) identified four related research themes focused on understanding the rates and mechanisms of change in the earth-life system: (1) the rules of biodiversity dynamics at a full range of temporal and spatial scales; (2) the triggers and characteristics of major evolutionary innovations; (3) how biological systems have affected the physical and chemical nature of the earth's surface and changes in biogeochemical cycling through time; and (4) how the biosphere responds to environmental perturbation. The report also noted the potential of paleontological data and approaches to providing baseline information on environmental and biotic variability before human impact. Recommendations included increased support for single investigators and for

focused, interdisciplinary themes; an initiative to support the development of databases to integrate information on the history of the earth-life system; and linking active research to education and public outreach. These recommendations were strongly endorsed by the international paleontological community (Flessa and Steininger, 2000).

- NRC's (2001a) report on *Basic Research Opportunities in Earth Science* considered these and other research themes in the context of the entire earth science discipline and noted, among other issues, the importance of (1) increased understanding of the interactions between earth systems and biologic processes; and (2) the importance of basic research on the origin and evolution of life. The report called for increased funding for the long-term support of geobiology and the further integration of geobiological research with ongoing efforts to address critical research questions in the environmental sciences.

This present report not only builds on these earlier efforts but also explicitly seeks to find common ground with the biological sciences in identifying research areas in which interdisciplinary collaborations will be most productive. In addition, this report seeks to address ways the mission of the U.S. Geological Survey—providing scientific knowledge that can be applied to address the nation's critical needs in natural resource and environmental management—can be accomplished through research efforts that integrate biological and geological approaches to understanding the past and future development of ecological systems.

This report differs from its precursors in its focus on the ecological consequences of environmental change. In light of the charge (see Box 1.2) to assess the prospects for the use of the geologic record as a key for understanding the biotic effects of future environmental change, the committee made a strategic decision to focus its efforts on the processes and biotic consequences that would most likely be expressed over the next decades, centuries, and millennia. This decision was made in recognition of the imminent impact of environmental change on ecosystem services provided to society, and the need for society to manage and mitigate change and its consequences in the very near future.

The geologic record is also an extraordinarily valuable resource for the study of diversification and extinction, how these evolutionary processes both mediate the biotic response to environmental change and cause change itself, and how the emergence of life and its subsequent evolution and diversification have affected the earth's land surface, oceans, and atmosphere over very long timescales. The committee recognizes both the importance of these types of response and the significant opportunities for collaboration between biologists and geologists they provide. Such promise has been noted in many recent national reports and reviews (e.g., NRC, 1995, 2001a; Richardson, 1996; Reaka-Kudla et al., 1997; Gastaldo and DiMichele, 2000; NAS Colloquium, 2000). However, a report that would also consider the evolutionary dimensions of the biotic response to environmental change was far beyond the resources available to this committee; a similar study focused on the geologic record of the evolutionary consequences of environmental change is urgently needed.

ENVIRONMENTAL SCIENCES AND THE GEOLOGIC RECORD OF ECOLOGICAL DYNAMICS

Analysis of the geologic record of ecological dynamics is a critical means of addressing many aspects of the challenging environmental problems that confront society. Recent National Research Council (NRC) committees on Grand Challenges in Environmental Sciences (NRC, 2001c) and on the National Ecological Observatory Network (NRC, 2004) have identified six major environmental challenges, listed below. Insights provided by geohistorical records would be valuable for each effort and are required for most.

1. **Biological diversity, species composition, and ecosystem functioning.** "This challenge is to improve understanding of the factors affecting biological diversity and ecosystem functioning, including the role of human activity" (NRC, 2001c, p. 3).
2. **Biogeochemical cycles.** "The challenge is to further our understanding of the Earth's major biogeochemical cycles, [and to] evaluate how they are being perturbed by human activities . . ." (NRC, 2001c, p. 2).
3. **Ecological impacts of climate variability.** "The challenge is to increase our ability to predict climate variations, from extreme events to decadal timescales, . . . and to assess realistically the resulting impacts. Important research areas include . . . extending the record of observations back into the Earth's history, [and] improving diagnostic process studies . . ." (NRC, 2001c, p. 3).
4. **Infectious disease and the environment.** "The challenge is to understand ecological and evolutionary aspects of infectious diseases . . ." (NRC, 2001c, p. 3). The scientific community needs to "develop a comprehensive ecological and evolutionary understanding of infectious diseases affecting human, plant, and animal health" (NRC, 2001c, p. 60).
5. **Land use and habitat alteration.** "The challenge is to develop a systematic understanding of changes in human land uses and land covers that are critical to ecosystem functioning and services and human welfare" (NRC, 2001c, p. 4).

The National Ecological Observatory Network (NEON) report (NRC, 2004) identified a sixth area of critical importance:

6. Invasive species. "The identification of potentially harmful invasive species, the early detection of new species as invasion begins, and the knowledge base needed to prevent their spread require . . . a mechanistic understanding of the interplay of invader, ecosystem traits, and other factors including climate and land use that determine invasiveness" (NRC, 2004, p. 25).

The geological record of biosphere dynamics provides the opportunity to assess the origin, rates, and development of evolutionary and ecological processes and past events that affect each of these six major themes. Importantly, the geologic record has the unique advantage of providing evidence for how ecological systems behave in the absence of human influence, thus allowing the discrimination of human-induced variability from other causes of biotic change, and of providing evidence for how ecological systems behave under a range of natural conditions different from those of the present day.

The geologic record permits two complementary approaches to basic research in the environmental and ecological sciences. One is to use the relatively recent past (intervals of time extending from the present back to as many as a few million years ago) as a dynamic context for present day conditions. The high-resolution data available in the most recent ~100,000 years have been exploited very effectively in the last decade of global change research, especially with analyses of sediment and ice cores for geochemical and other proxies for atmospheric and ocean behavior. This recent-past time frame has received less attention as a source of baseline information on species and ecosystems as biological entities, or as a means of investigating and understanding changes in biosphere behavior. As discussed in Chapter 3, opportunities abound in this area.

The second approach, equally valuable but less systematically pursued, is to take advantage of the entire past to investigate biosphere dynamics. This approach uses geologic records of all ages (i.e., time intervals that may be far older and longer than the past few million years) (1) as a source of replicate natural experiments (e.g., to determine variance in the biotic response to multiple instances of global or regional warming and fluctuating ice and sea levels); (2) to test the biosphere response to perturbations that differ in kind, rate, or magnitude, or when ecosystems are in different initial states (e.g., ecosystems that have suffered more degradation than found today—a situation relevant to issues of ecological recovery on a variety of temporal and spatial scales); and (3) to explore feedbacks between earth and life systems on longer timescales and in response to larger perturbations than afforded in the recent past, permitting a more fundamental exploration of the abilities of organisms to modulate and respond to the inorganic world.

Importantly, paleoenvironmental and paleobiological analyses do not necessarily require that the geologic record provide time series data in a strict sense, much less high-resolution time series (i.e., with a closely and evenly spaced series of comparable samples). Isolated snap shots—or even time-averaged samples—can provide immensely valuable insights into the behavior of ancient biological systems. For example, maps of time-averaged pollen percentages at continental scales have revealed the dynamic nature of late Quaternary vegetation and the underlying climatic controls (e.g., Huntley and Birks, 1983; Webb et al., 2004); snapshot fossil assemblages from rodent middens have shown unexpected shifts in plant distributions (Betancourt et al., 1990; Latorre et al., 2002); and analyses of historical, archaeological, and paleontological records have demonstrated the impact of overfishing on coastal ecosystems (J.B.C. Jackson et al., 2001). It is clear that data from even a single, crude pre-impact census would be valuable to a biologist studying a system where no monitoring program had been in place.

UNDERSTANDING PROCESSES—DIFFERENT PERCEPTIONS

Full use of geohistorical records in the analysis of ecological dynamics must overcome several challenges. Some of these challenges are scientific, for example, continuing to improve proxies for environmental conditions and species abundances, refining our ability to establish relative and absolute ages of deposits, and developing statistical treatments of incomplete or biased information (see Chapter 2). However, equally important is the task of bridging the methodological, cultural, and administrative gulfs between biological scientists and earth scientists, and among real-time, recent-past, and deep-past approaches that have hindered both basic research and applications to policy issues.

For the last three decades, many ecologists have studied how biotic systems work, primarily through a combination of short-term, relatively small-scale manipulative experiments and modeling. This necessarily has been largely reductive, with individual projects focusing on the roles or behaviors of limited numbers of species (both biological and biochemical), functional groups, or environmental parameters. Geologists and paleobiologists, on the other hand, have traditionally used observation and statistical pattern analysis of the fossil record to infer cause-and-effect relationships in past systems. Manipulative experiments are far less common, and modeling has focused more on evolutionary and macroevolutionary rather than ecological questions.

The parallel development of macroecology—the analysis of how the ecological attributes of large numbers of individuals and species varies over geography (e.g., Brown, 1995; Gaston and Blackburn, 2000; Hubbell, 2001)—and evolutionary paleoecology—the analysis of the ecological attributes of large numbers of individuals and species in time (e.g., Valentine, 1973; Jablonski and Sepkoski, 1996; Allmon and Bottjer, 2001)—is now providing common ground for ecologists and paleobiologists interested in inferring large-scale ecological processes from ecological and paleoecological patterns. Indeed, the biological community, which has become increasingly aware of the limitations of short-term, local experiments in understanding ecological systems, is increasingly open and eager to pursue ecosystems analysis on broader spatial and temporal scales. Pioneering paleobiologic analyses of geohistorical records already are having a tangible effect on the biosciences, in ecology, evolution, and conservation biology (e.g., Smith et al., 2004; Jablonski, 2001, 2002; Erwin, 2001; Hadly et al., 2003; Pääbo, 2000; and see examples in Chapter 3), in part because so many biological attributes critical to larger-scale phenomena are amenable to analysis in geologic records (e.g., richness, evenness, body size, habitat type, functional/trophic group, geographic range, raw speciation, and extinction rates). However, the fundamental differences in approach of the biological and earth sciences, and their reliance on different sources for research support and outlets for communication of results, will require special effort to overcome impediments to integrating the expertise and data from the two fields.

STATUS OF RESEARCH SUPPORT

Several federal agencies conduct or support research in one or more aspects of the geologic record of biosphere dynamics. These include the National Science Foundation (NSF), U.S. Geological Survey (USGS), National Oceanographic and Atmospheric Administration (NOAA), Environmental Protection Agency (EPA), and National Aeronautics and Space Administration (NASA). This committee was not charged to review the programs of these agencies, and data from the public record are inadequate for a quantitative evaluation of effort, including the funding success of proposals by topic. Budget information—whether for research by agency scientists, grants to fund academic scientists, or from the private sector—is difficult to obtain and interpret because of varying funding periods, funding split among several programs within an agency (especially true for crosscutting initiatives), limited information about successful and unsuccessful research proposals, and many other factors.

Nevertheless, it is clear that the extraction, analysis, and synthesis of paleontologic, geologic, and geochemical evidence relevant to biosphere dynamics in the broadest sense have not yet been major priorities within federal agencies. Two of the agencies with greatest current effort on the geologic record of biosphere dynamics are NSF and USGS. These agencies are the de facto leaders in advancing knowledge of geologic records and in applying that knowledge to understanding the likely biotic effects of future environmental change. Nevertheless, this topic forms only a small part of their missions.

The NSF and USGS differ greatly in their overall goals and methods:

- The NSF is the principal federal agency charged with promoting the progress of the nation's efforts in science and engineering exclusive of the health sciences. NSF achieves its mission largely though funding research grants to scientists and engineers in academic or non-governmental organizations. Although accountable to NSF, the actual research is overseen by the principal investigators. NSF officials are not involved in the research itself. Most funding is allocated though NSF's traditional disciplinary programs. Proposals are initiated by the investigator rather than invited by the agency and funding decisions are based on peer reviews. In some cases, NSF officials, after consultation with the research community, allocate funds to stimulate research in a particular area. Such initiatives help focus efforts in highly promising areas. NSF's criteria for evaluating research proposals include consideration of the potential benefits to society, but the agency is principally focused on enhancing the quality of basic research.
- The USGS is "the Nation's principal natural science and information agency [and] conducts research, monitoring and assessments to contribute to understanding the natural world" (USGS, 2000; p. 2). Although the USGS mission includes fundamental research on the natural world, much of the agency's research is designed and directed to be applicable to society's need to predict, prevent, and mitigate loss from natural hazards and to manage its natural and environmental resources in a sustainable fashion. These resources include mineral, energy, and water resources traditional to the USGS mission. Since the mid-1990s environmental issues such as contaminated environments, effects of climate change, and status of biological resources have been added to the agency's mission (USGS, 1996; Bohlen et al., 1998). The USGS achieves its mission largely through the directed activities of its scientists and collaborating agencies on specific projects. Projects are reviewed and prioritized, largely internally, within the Geology, Biology, and Water Disciplines, each of which establishes its own strategic plan in the context of broader USGS and Department of the Interior strategic plans.

That both agencies support research on the geologic record of biosphere dynamics attests to the importance of this topic in both applied and basic research. Each agency provides instructive cases of successful modes of integrating earth science and bioscience efforts, as well as examples of obstacles to multidisciplinary, multi-scale research. Such research requires intellectual receptivity (of review panels and managers), adequate funding levels (to overcome resistance from traditionalists and discouragement among investigators), funding targeted for new techniques and specialized equipment, and an organizational mandate to foster new directions and overcome structural impediments.

NSF Activities on Geologic Records

Research on the geologic record of biosphere dynamics is supported at NSF through core programs in the Directorate for Geosciences (GEO), which includes the Divisions of Atmospheric Sciences (ATM), Ocean Sciences (OCE), and Earth Sciences (EAR); the Directorate for Biosciences (BIO), particularly the Division of Environmental Biology (DEB); the Office of Polar Programs; and several of NSF's crosscutting programs. These latter programs include (1) Biocomplexity in the Environment, administered out of the director's office and containing Coupled Human-Natural Systems and Coupled Biogeochemical Cycles (initiated in FY1999); and (2) the Biogeosciences Initiative, administered by EAR (initiated FY2003).

Based on NSF data for FY2003 (public websites listing active projects as of December 2003), the number of awards in these programs that examine the response of biotas or ecosystems to climate or other environmental change, and that use the historic or geologic record in some way, is very small. For example, only 5 of 152 awards in ATM's Paleoclimate initiative in OCE, ~10 out of 338 in Biological Oceanography, and ~10 out of 394 in Marine Geology and Geophysics are relevant by these criteria; and within the Ecological Studies cluster within DEB, only ~15 out of 175 are relevant (including only one out of 25 current awards for LTER).

The National Center for Ecological Analysis and Synthesis (NCEAS), also supported by DEB, facilitates interdisciplinary research—including between the biological and physical sciences—through working groups, sabbaticals, and postdoctoral fellowships. Despite the lack of funding from GEO programs, NCEAS has supported a few projects involving geohistorical analysis (1 of 56 total current research awards, 10 of 207 past awards). Limited funds have caused overall funding rates to be very low across the breadth of topics considered by NCEAS.

Programs that could fund integrated analyses of environmental change and biotic response include Marine Aspects of Earth System History (MESH), the marine LTER program, and programs on Ecological Rates of Change (EROC) and Ecological Diversity. Such programs either lack the mandate to include the biotic response to past environmental change (MESH) or focus largely on biotic processes currently operating on annual to decadal timescales.

The majority of projects that investigate the behavior of biological systems on time frames beyond the last few decades have been funded by the Geology and Paleontology Program (GE)[1] within EAR, constituting ~20 percent of a total of 268 funded projects for that core program in FY2003. GE's broad portfolio also includes biogeochemistry, land-use dynamics, geomorphology, stratigraphy, and sedimentology. This core science program is thus the de facto home of geohistorical analysis within NSF. However, internal and external reviews (e.g., Knox et al., 1996; NRC, 2001a) have identified GE as severely oversubscribed and unable to adequately fund the breadth of disciplines for which it is responsible within the earth sciences. Between 1995 and 2000, GE received approximately 290 proposals per year, with a success rate of 20-25 percent, compared with an overall EAR success rate of 31 percent (NRC, 2001a), and it has consistently had one of the lowest funding rates of the core disciplines in GEO. Although GE has been reorganized to reduce the breadth of expertise required of individual panels and staff, total funding has not changed and thus success rates remain low. As concluded by NRC (2001a, p. 92), "None of the existing core programs [in EAR] have the intellectual scope or sufficient resources to accommodate a prolonged emphasis on geobiology."

Other programs that fund research on, or are relevant to, geologic records of biosphere dynamics are the crosscutting Earth Systems History program (ESH), administered by ATM (no award data available); Biocomplexity in the Environment (BE; 9 out of 116); and the Biogeosciences Initiative (no award data available; calls for proposals so far have focused exclusively on microbe-mineral interactions).

Beyond the issue of funding levels is the relatively narrow temporal scope of successful projects. Across NSF, few relevant projects take advantage of more than the very youngest portion of the available geologic record (e.g., last few millennia at most). Moreover, among successful grants on geohistorical topics, the amount of research on developing proxy indicators of climate change or documenting the character and history of climate change overwhelms the amount of research on the biotic consequences of those changes.

Establishing crosscutting programs such as BE and ESH is an effective means of developing interdisciplinary collaborative efforts that make good use of the temporal scope available in the geologic record. However,

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[1] In August 2004, as this report was being completed, reorganization within EAR resulted in GE being replaced by new programs in Sedimentary Geology and Paleobiology (SGP), Geobiology and Environmental Geochemistry (GEG), and Geomorphology and Land Use Dynamics (GLD).

even EAR's Biogeosciences Initiative, which integrates across biology and geology, has insufficient funds to focus on more than mineral-microbe interactions and consequently cannot support research on the other classes of interactions, trophic levels, and scales of biological organization that are of extraordinary importance to the biosphere—and to society.

USGS Activities on Geologic Records

USGS research relevant to the geologic record of ecological dynamics is conducted largely within its Geology and Biology Disciplines. The existing programs with greatest potential to advance—through geohistorical analysis—the USGS missions in natural and environmental resources are the Earth Surface Dynamics Program and the Coastal and Marine Geology Program administered by the Geology Discipline, and the Terrestrial, Freshwater and Marine Ecosystems Program of the Biology Discipline.

Further increased coordination and collaboration between these two divisions is an important priority, as articulated both by USGS strategic plans (USGS, 1996; Bohlen et al., 1998) and by recent external advice to the agency (NRC, 2001b). Such collaborative projects are increasing. The USGS has the opportunity to integrate these scientific communities and pursue research that combines their strengths to greatest advantage. The situation results from the relative novelty of having biological resources as part of the USGS portfolio (the National Biological Service was consolidated with the USGS only in 1996), and by the 1995 congressional directive to recast the agency's mission more clearly in terms of societal needs. This has required the USGS to transform itself from a loosely linked cluster of independent units of research, monitoring, and assessment in the *earth* sciences (geology, water, and mapping), into an agency that conducts more applied research in environmental and *natural* sciences, which now includes the nation's natural biological resources. As described by former USGS Director Eaton (Eaton, 2000), the incorporation of the ~1,600 scientists from the National Biological Service (individuals formerly employed by the Fish and Wildlife Service, National Park Service, and Bureau of Land Management) into the USGS earth science community was in itself a more radical change than any in the 120-year history of the USGS (see also NRC, 2001b).

The application of earth science methods and materials—specifically geohistorical records—to understand, manage, and conserve the nation's biological resources is a promising vehicle for integrating the biological and geological sciences across the organizational divisions of the USGS. Such integration provides an important means to advance elements of the Biology Discipline goal to provide accurate, comprehensive, and timely information on populations, communities, and ecosystems (NRC, 2001b).

At present, relatively few projects explicitly combine these fields in this way, perhaps because of the scientific challenge of bringing geohistorical evidence to bear on these issues.

Some modes of research collaboration for bridging these internal divisions have been successful. One highly successful mode has been where USGS scientists with appropriate expertise are embedded or otherwise placed in close geographic proximity to a university research campus, much as in the long-standing cooperative units of the Fish and Wildlife Service. In this arrangement, USGS research scientists are often housed within university facilities, have courtesy academic appointments, and often serve as research advisers or committee members for graduate students. This provides USGS researchers with more immediate and continuous interactions with collaborating partners, access to additional facilities and expertise, and invaluable informal, and in some instances formal, external review and feedback from a larger community of research colleagues. The university community benefits from collaborative research efforts, additional expertise and facilities, and employment and research opportunities for students.

In the earth sciences, the planned USGS Earth Surface Processes Research Institute (ESPRI) in Tucson is also a promising model. ESPRI will assemble 80-90 full-time researchers and support staff on the University of Arizona campus to investigate landscape change and ecosystems response. Researchers from several disciplines within ESPRI, often in collaboration with related, ongoing research at the University of Arizona, will be able to examine the interactions among climatic variability, landscape change, and ecosystem response across a spectrum of timescales. This effort will assist the USGS mission by developing criteria to distinguish between natural and anthropogenic influences on the landscape, predict potential hazards, and avoid degradation of natural resources.

Judging from existing arrangements of this type, federal personnel in such positions commonly develop formal associations with the university (e.g., adjunct faculty appointments), and thus contribute directly to the graduate and postdoctoral training of new scientists. The intellectual and logistical advantages of such arrangements also contribute to the recruitment and retention of excellent researchers within the USGS.

Site-specific projects—those in which the conditions of a particular location are the subject of investigation—are another good means of fostering collaborations across organizational boundaries. These projects have the advantages of being established as the need arises, without the commitment to physical facilities, and with clear time limits. Current examples include efforts by the Geology and Biology Disciplines, and various combinations of these and state agencies, to evaluate the legacy and present day levels of human impact in U.S. coastal areas, including southern Florida, the Chesapeake Bay, Long Island Sound, and San Francisco Bay. Not all these projects include a biotic component (beyond using particular species as environmental proxies), and not all include the full breadth or depth of geohistorical information that might be valuable to understand the system of interest. Nevertheless, such projects have the potential to focus the talents of a broad array of USGS scientists on a common theme: the nature of biosphere response to environmental change.

Impediments to such collaborations in the USGS, as in other research and public service organizations, potentially include limited expertise available within the organization, limited funds or time made available by the external agency mandating the study, competing demands for instrumentation or personnel, and the physical separation of collaborators from different disciplines. Most of these impediments are beyond the power of the scientists themselves to modify or counterbalance to any meaningful extent. It thus falls upon the agency itself to consider ways to eliminate or minimize these effects. Outsourcing of some portions of the work to universities may, in some instances, make the most sense, both scientifically and logistically.

A productive strategy that the USGS has adopted, and that has broad value for the agency as a research entity, is the Mendenhall Postdoctoral Fellowship Program. This fellowship program brings new expertise to the USGS itself, and is very much like the previous USGS/NRC postdoctoral fellowships. Although the positions are temporary (two-year duration), the associations have potential to produce longer-term professional collaborations and expanded research networks. They also develop a better knowledge base in identifying the appropriate disciplines for future appointments. Each Mendenhall Fellow is attached to a particular project, designed by USGS personnel (in some instances with collaboration from the prospective fellow) to meet agency needs. The selection of proposed projects for advertisement, and of fellows to fill those positions, is based on internal review. These appointments also can be used to foster and reward efforts at integrative science, for example, if criteria for evaluation include whether the fellow is matched to a USGS scientist from the counterpart discipline. Fellowship programs such as this, the earlier NRC postdoctoral fellowships, and enlargement of support for graduate-student research, are excellent means of improving the effectiveness of the USGS effort by broadening and continuously updating the agency's intellectual community.

Other Agency Activities

In general, other federal agencies play complementary roles in support of research on the geologic record of biosphere dynamics.

- NOAA's Paleoclimatology Program, based at the National Climatic Data Center, provides a rich source of paleoclimatic data for research on environmental change and biotic response.[2] Climate reconstructions are typically limited to the Holocene and Pleistocene.
- PAGES (Past Global Changes) is a core activity of the International Geosphere-Biosphere Programme[3] that receives funding support from NOAA, NSF, and the Swiss National Science Foundation. PAGES "seeks to provide a quantitative understanding of the Earth's environment in the geologically recent past and to define the envelope of natural environmental variability against which anthropogenic impacts on the Earth System may be assessed."[4] Research activities include work in terrestrial, lacustrine, and marine systems and are largely restricted to the Quaternary. Its primary focus has been on paleoclimate reconstruction and biosphere-atmosphere-ocean feedbacks, with relatively little attention to the biotic consequences of climate change. PAGES funds workshops and publications.
- NASA's Office of Earth Science seeks a global-scale understanding of the earth system, including how the component parts have evolved and how they will respond to future changes. Some individual awards and components of NASA's Astrobiology Institute[5] support analyses of early environments and early life on earth, the emergence of multicellular organisms, and the evolution of diversity. Little, if any, support examines the record of ecosystem response to past environmental change. In addition, the Exobiology Branch[6] within NASA has funded a limited number of studies of biotic responses to mass extinctions.
- The Department of Energy's Program for Ecosystem Research supports experimental work on the "mechanistic understanding and quantification of ecosystem-scale responses to ongoing and potential future environmental changes associated with energy production."[7] Support for examining the record of past ecosystem response to environmental change is weak.
- The Environmental Protection Agency (EPA) supports both intramural research by its employees and, since 1995, an extramural funding program for individual investigators, graduate students, and research centers (STAR, Science to Achieve Results; see NRC, 2003a). Both problem-driven and core research are supported across the breadth of issues within

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[2] See http://www.ngdc.noaa.gov/paleo/paleo.html.

[3] See http://www.igbp.kva.se/cgi-bin/php/frameset.php.

[4] See http://www.pages.unibe.ch/about/about.html.

[5] See http://nai.arc.nasa.gov/index.cfm.

[6] See http://exobiology.arc.nasa.gov/index.html.

[7] See http://www.science.doe.gov/ober/CCRD/per.html.

the agency's mission, including environmental biology, regional assessments of ecosystems, and ecological indicators. Although STAR has previously funded graduate fellowships that include geohistorical approaches, no projects with a geohistorical approach were funded in FYs 2001-2003.

Private organizations such as the National Geographic Society, the Petroleum Research Fund of the American Chemical Society, Environmental Defense, and the Eppley Foundation for Research have funded evaluations of past environments and biotas. However, such subjects are only a small part of these organizations' missions, and support levels are typically small—at most a few thousand or tens of thousand dollars per year for one to three years. Such funding is sufficient only for modest field or lab analysis and/or partial support for one graduate student's dissertation project.

The extraction and analysis of paleontologic, geologic, and geochemical evidence relevant to biosphere dynamics has not been a major funding priority to date. Furthermore, methodological and administrative gulfs between biological and earth scientists, and among real-time, recent-past, and deep-past approaches, hinder both basic research and the transfer of geohistorical insights to policy on biological resources and global change. New collaborations among earth scientists and biologists are required to advance analysis of biosphere dynamics based on the geologic record, and to increase the engagement of the earth sciences in issues of environmental change.

COMMITTEE CHARGE AND SCOPE OF THE STUDY

Despite the considerable efforts of academic and federal researchers within the broad scope of the geologic record of ecological dynamics, there is insufficient collaboration between the earth science and biological research communities. Recognizing the enormous potential benefits, as well as the significant challenges, involved with promoting truly interdisciplinary research at the interface of earth science and biology, the NSF and USGS requested that the NRC undertake a study to identify the significant research questions and priorities and to provide advice on optimum ways to promote interdisciplinary research (see Box 1.2).

The committee assembled by the NRC to address this task held two open information-gathering meetings where representatives from federal agencies and the academic research community provided their perspectives on the committee's task. An additional closed meeting was held for the committee to deliberate and write its report. As a result of this input and its internal deliberations, the committee has assessed the potential of the geological record to describe past interactions between biotas and

BOX 1.2
Statement of Task

Committee on the Geologic Record of Biosphere Dynamics: The Key to Understanding the Biotic Effects of Future Environmental Change

The committee will describe the potential of the geologic record as a means of understanding biotic interactions with environmental change and the coupling of earth/life processes, and develop strategies for integrating earth and biological sciences and transferring their combined insights to the policy community. In particular, it will undertake the following tasks:

1. Assess the current state of biogeologic analysis relevant to biosphere dynamics;
2. Identify the most promising directions for collaborative research and the sharing of methodologies; and
3. Describe the programmatic themes and research and data infrastructures required to accomplish these objectives.

environmental parameters (Chapter 2), described three research themes where the rich and detailed geological record provides information on the response of past ecosystems to environmental and climatic change at a variety of timescales (Chapter 3), described the collaborative culture that will be required to make optimum use of the considerable capabilities of these two communities (Chapter 4), and made a series of conclusions and recommendations designed to achieve enhanced integration of the geological and biological sciences (Chapter 5).

2

The Nature and Value of Geohistorical Information

THE RATIONALE OF GEOHISTORICAL ANALYSIS

The study of ecological dynamics would benefit greatly from a tripartite research effort similar to that used so successfully in climate and ocean dynamics (see Figure 2.1), where information about past systems—their variability in rates, states, and composition; apparent boundary conditions (including those without modern analogs); spatial scaling effects; correlated relationships evident only over periods longer than modern monitoring programs—has proven to be an essential partner to modeling and studies of present day conditions. In fact, it is difficult to imagine understanding climate and ocean systems as well as we do today without the insights gained from geohistorical data. In the study of climate and ocean dynamics, geohistorical records—including ice cores, sediment cores, tree rings, and coral skeletons—have provided the first evidence for the existence of many important phenomena, including climate flickers and other abrupt climate change, the reorganization of deepwater circulation patterns, and Milankovitch oscillations in temperature and atmospheric composition. Geohistorical records also have provided the impetus and an essential empirical framework for modeling and experiments (see Box 2.1). The intellectual impact of individuals and projects that cross methodological interfaces—using some combination of geohistorical data, modeling, and present day observation and experimentation—has been at least as important as original research within subdisciplines in propelling our understanding of these complex environmental systems, including

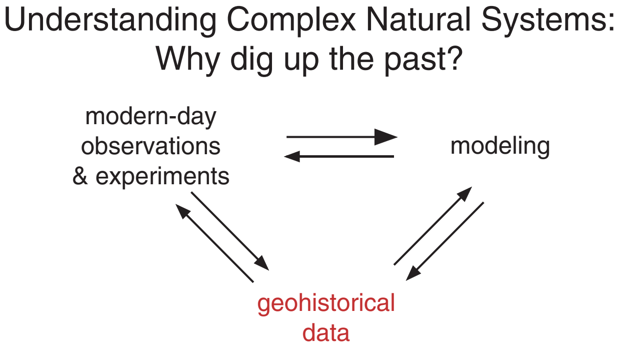


FIGURE 2.1 Schematic illustration showing how interactions among geohistorical data, observations and experiments, and modeling serve to increase understanding of the biotic response to environmental change. Until recently, geohistorical data have not been used extensively by biologists.

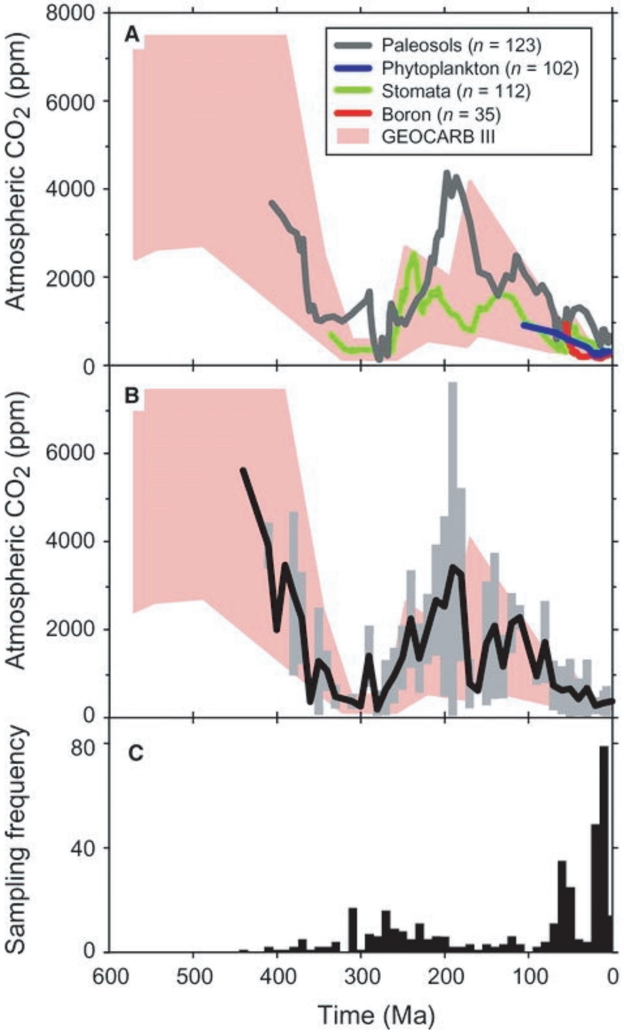
BOX 2.1
CO_2 Through Geologic Time: Observations, Models, and Geohistorical Data

Royer et al. (2004) illustrated the strength of model-data comparisons in their analysis of the role of CO_2 in driving climate during the past 600 Ma. How CO_2 functions as a greenhouse gas is now well established through observations, experiments, and modeling of the present day atmosphere as well as the analysis of climatic proxies and CO_2 in the Quaternary geohistorical record. However, substantiating CO_2's role in the regulation of pre-Quaternary climate is difficult because of the lack of direct information on the composition of the atmosphere through most of geologic time. Geochemical models, based primarily on sedimentary weathering rates, have been devised to predict the evolution of CO_2 through geologic time (e.g., Berner, 2004; Berner and Kothavala, 2001). These predictions can be evaluated by comparing the model results to estimates of past CO_2 based on geochemical and paleobotanical indicators in the rock record. Such indicators are said to be "proxy indicators," in that they substitute for direct measurements. The development and calibration of these and other proxy indicators depends on observations and experiments with modern systems.

Royer et al.'s (2004) review of proxy records indicates a consistent relationship between various CO_2 indicators, geologic evidence of glaciations, and CO_2 predictions from geochemical models. Accordingly, model-proxy comparisons support the hypothesis that CO_2 has acted as the primary driver of climate during the past 600 Ma, identifies key time intervals in which proxy indicators and model predictions do not agree, and evaluates the extent to which proxy indicators differ.

continued

BOX 2.1 Continued



Comparison of atmospheric CO_2 composition predicted by GEOCARB III model calculations (range shown in pink) and proxy indicators. A. Individual proxy indicators (paleosols = fossil soil $\delta^{13}C$; phytoplankton = $\delta^{13}C$ of phytoplankton remains; Stomata = density of stomatal pores in leaves of plants; Boron = $\delta^{11}B$ in remains of planktonic foraminifera. B. Mean (black line) and $\pm 1\sigma$ (gray bars) of proxy estimates in 10 Ma time steps. C. Frequency distribution of proxy data through time. SOURCE: Royer et al. (2004); used with permission.

the especially critical issue of the relative roles of anthropogenic and nonanthropogenic processes in causing biotic change.

The biosphere is an extremely complex system—analogous to climate and ocean systems—with great diversity and variability in the behavior of its components, an enormous variety of interactions and feedbacks that are context specific and probabilistic, and a long memory and residence time for many of its components. Despite this complexity, improved techniques for extracting information on the environments, biotas, and ages of geohistorical records now combine to ensure that geohistorical analysis is well positioned to become a full and essential partner in the analysis of ecological dynamics.

Here, following a brief discussion of strategies for working with incomplete records, we review some of the techniques used to acquire geohistorical data on ecological dynamics, organizing the discussion around questions that are commonly raised by workers unfamiliar with this topic:

- With what detail and confidence can environmental conditions be inferred for the past?
- What kinds of biological information are obtainable from the geologic record?
- How precisely and accurately can the ages of past records be determined?

COMPLETENESS OF THE GEOLOGIC RECORD

Taken as a whole, the geological record is incomplete—not every individual or species that ever lived is preserved, all the environmental conditions for every part of the globe are not recorded in the sediments, and deposition of rocks has not been continuous everywhere on the face of the earth and throughout geologic time. This heterogeneity in the quality of geohistorical data is a fundamental property of the geologic record, just as completeness and bias in written documents and instrumental records are properties that must be considered in the analysis of human cultural history and instrument-based environmental histories. Research over the last ~20 years (e.g., Kidwell and Flessa, 1995; Foote and Raup, 1996; Koch, 1998; Foote et al., 1999; Foote and Sepkoski, 1999; Behrensmeyer et al., 2000; Briggs et al., 2000; Alroy et al., 2001; Kidwell and Holland, 2002) has demonstrated that uniquely valuable data can be extracted from geohistorical records of diverse quality, thus increasing the effective availability of geohistorical information for biosphere analysis. Some of the key elements of this modern strategy, and the stereotypes that are being overturned, are summarized below.

Valuable insights can be gained from sparsely sampled time series and from isolated samples that are well positioned before and after significant biotic or environmental events or transitions. Although long, closely sampled time series may provide important geohistorical information, they are not always required. For example, ecological monitoring programs for modern environments may not have begun before human impact. Under these circumstances, geohistorical records of known age—but not directly connected to the present by a continuous series of comparable samples—are unique and valuable sources of information on local pre-monitoring conditions (e.g., the species composition or dominance structure of a benthic or forest community before an environmental change or an extinction bottleneck, or the typical body sizes of animals before commercial extraction or exploitation). This strategy of opportunism—using such records for their unique insights and aggressively seeking out geohistorical records from previously little-explored areas—has proved remarkably productive in bringing valuable geohistorical perspective on modern management issues in both terrestrial (e.g., Steadman, 1995; Swetnam et al., 1999) and marine settings (Kowalewski et al., 2000; J.B.C. Jackson et al., 2001; Pandolfi et al., 2003; Aronson et al., 2003).

Similarly, biotic response to events in the deeper past can be analyzed in the absence of complete time series by using geohistorical records that are appropriately positioned in time or space, for example by comparing samples from before and after mass extinctions (e.g., Raup and Jablonski, 1993; Jablonski and Raup, 1995; Jablonski, 1995; Erwin, 1996; Foote, 2003). In fact, widely spaced samples over longer periods can be superior to closely spaced samples over shorter time series for the analysis of phenomena that occur over periods greater than a few years, and indeed many important biological processes unfold on timescales of millennia or even millions of years. Paleontologic samples of relatively coarse scale (i.e., millions of years) have revealed striking patterns in the loss and subsequent recovery of morphological richness, a measure of biodiversity that may capture functional variety far more effectively than simple counts of higher taxa (e.g., Foote, 1997, 1999; Lockwood, 2003).

For many purposes, time-averaged (time-exposure) information—as is typically captured by sedimentary records—is adequate to the questions being addressed and may be better than instantaneous snapshot samples. Few geohistorical samples represent instants in time (snapshots) comparable to ecological samples but instead represent accumulations of individuals and species over some period (time exposures, or time averaged). Such time-averaged samples tend to filter out short-term (seasons to centuries) variation in composition, relative abundance, and diversity. If such samples are large enough to encompass the full range of variability (e.g., Olszewski [1999] indicates that samples of as few as 29 individuals may be sufficient), they can be employed to characterize long-term, average conditions (Kowalewski et al., 1998; Olszewski, 1999; Hadly, 1999). In addition, if the time-averaged specimens can be directly dated (e.g., by radiocarbon dating or amino acid racemization), then a continuous temporal record of specimens can be reconstructed (Kowalewski et al., 1998).

When the goal is an understanding of larger-scale trends and general principles relevant to developing realistic conservation and management policies, time-averaged geohistorical data provide essential biological data. For example, the richness and dominance structure of most communities are inherited in part from periods predating scientific study. Dominant species in some communities may be relict populations whose dominance reflects incumbency and lifespan rather than present day conditions. In such situations, a one-time or very short-term sample could reflect ephemeral conditions, whereas a time-averaged sample is more likely to reflect average conditions of local diversity and structure. Because standing diversity may be the product of long-term as well as short-term processes, and because local populations are highly volatile, combining data from both living communities and geohistorical records allows tests of hypotheses, provides strength to the interpretations, and supplies new insights into ecological processes.

The need for truly long-term geohistorical perspectives on species is especially critical in understanding extinction risks and the potential for speciation and other evolutionary innovation. Raw rates of speciation and extinction (numbers of taxa per unit time), as well as variability in raw rates and the frequency distributions of evolutionary durations, can all only be determined using the fossil record of evolutionary first and last appearances. Without such empirical information, rates of speciation, for example, would have to be assumed to be correlated with present day standing diversity, whereas high standing diversity could reflect either high speciation rates in that region, low extinction rates, high immigration of species that originated elsewhere, or some combination of these variables. Similarly, in the absence of geohistorical information on species ranges, extinction risk would have to be evaluated only in light of the population dynamics measurable today. These are examples in which the unique qualities of time-averaged paleobiological information permit questions to be answered that—if only modern-day biological data were available—could only be addressed indirectly.

High-quality geohistorical records are present throughout the ~4 billion year record of Earth, although the total quantity of records decreases with increasing age. Geohistorical records from the relatively recent past contain a wider variety of extractable information (e.g., ancient DNA is more likely to be preserved, and isotopic signatures are less likely to be overprinted), than more ancient records. The taxonomic and functional characteristics of biological remains are more readily inferred by direct comparison to living forms, and dating resolution is better. Because interpretations based on agreement of multiple lines of evidence (whether direct or proxy) are judged more robust than inferences based on single lines of evidence (Mann, 2002), younger records are more likely to yield high-quality information about both environmental change and its biotic response.

Variation in the quantity and quality of data through time occurs over all timescales. For example, archived materials are subject to loss and deterioration even under the best of conditions, and—due simply to scientific and technological progress—workers during the last decades generally have used more precise and diverse means of characterizing and analyzing objects and systems than workers of 50 to 100 years ago. In Earth history—as in other areas—such variation does not invalidate historical analysis but only requires that analysis be done thoughtfully and with standard scientific rigor.

Both biologically and geohistorically, some regions, habitats, and kinds of organisms are better known than others at any moment in time. Information quality is not randomly distributed with respect to geographic region, environment, or taxonomic group; for example, biotic systems and geohistorical records are better known in regions with longstanding academic programs or field stations (e.g., Western Europe and North America); some groups are better known because of their economic importance (e.g., insects as pests and vectors of disease, or benthic mollusks as food for commercial finfish); and some habitats and systems are better understood because of the greater ease of surveys and experiments (e.g., rocky intertidal settings, rodents and insect population dynamics). This unevenness can persist into more mature stages of data acquisition, because additional work on an already well-studied group or area benefits from past insights and investments. As a consequence, some systems are not as well explored as others despite the likely existence of materials (living communities, geohistorical records) that could yield valuable insights.

In any empirical scientific analysis, the ideal is for sampling to be at regular intervals along a gradient, or through time over the course of an experiment, at the same time holding other conditions constant. The greater the density of sample points along the gradient or during time, the greater the confidence in recognizing the effects of processes operating at fine spatial or temporal scales, discovering correlated relationships among the variables and the greater the likelihood of understanding their underlying significance. Such regular sampling is not always possible in natural systems; instead, it is often necessary to interpolate among irregularly spaced points or forced to compare the end points of a suspected spatial gradient or temporal trend. Geological analysis of ecological dynamics is as subject to these challenges as is field-based biology, where for example, the availability of rocky shores would determine the spacing of samples in a latitudinal analysis between Baja California and Oregon. Whether such limitations on continuous sampling constitute a significant impediment depends on the question at hand, but clearly continuous sampling is not required to answer all questions, nor is it always possible.

What is most important in comparative analyses, whether biological or geohistorical, is to (1) have a good match between the question and the quality and quantity of samples that can be acquired; (2) identify the specific variables to be explored (e.g., gradients in environment, variation over geologic age or geographic region); (3) hold other variables constant (for example, sampling protocol—in geohistorical analysis this would also include the preservation quality of the local records sampled); and (4) have a reasonable number of replicate samples per treatment (i.e., per site, per region, per geologic period). With appropriate diligence, together with adjustment of questions as necessary, these challenges can be met in geohistorical analyses with a success rate that is similar to that achieved in field biology experiments.

INFERRING ENVIRONMENTAL CONDITIONS—RESOLUTION AND CONFIDENCE

Various elements of the geologic record capture environmental information in indirect, or "proxy," form. For example, variations in air temperature and rainfall affect the width of tree rings and, accordingly, variations in the widths of tree rings are proxy indicators of variation in temperature and moisture. Similarly, variation in sea-surface temperature and ice cap volume are reflected in fluctuations of oxygen isotope ratios in skeletal remains preserved in marine sediments.

In many cases, proxy indicators can be calibrated based on experiments or on their observed variation in known environments, allowing their use for the determination of precise quantitative measures of environmental conditions. The composition of biotic assemblages has long been used as a basis for quantitative inference of climate, salinity, redox, pH, water depth, productivity, and a variety of other environmental factors (e.g., Imbrie and Kipp, 1971; Bartlein et al., 1986; Fritz et al., 1991; Charles et al., 1994; Charman, 2001; Smol et al., 2002a,b). The discrimination of paleotemperatures with a standard error of only ± 2°C using shape and size characteristics of leaves is a good example of a proxy with relatively high precision based on modern calibration (Wilf, 1997), and the Stomatal Index (SI) of fossil leaves can provide historical records of past levels of CO_2 (Wagner et al., 1999). Similarly, stable isotopes incorporated into fossils and other geohistorical records are providing extraordinarily detailed insights into population size (e.g., Finney et al., 2000), home ranges (Hoppe et al., 1999), diet (e.g., Burton et al., 2001), photosynthetic pathways (e.g., Fox and Koch, 2003), river discharge (e.g., Dettman et al., 2004), salinity (e.g., Rodriguez et al., 2001), climate (e.g., Edwards et al., 1996; Huang et al., 2002), ocean pH (Lemarchand et al., 2000), and elevation (Morrill and Koch, 2002), and effects of CO_2 and climate on vegetation (Huang et al., 2001; Street-Perrott et al., 2004).

Some proxies provide only semi-quantitative or qualitative measures of environmental conditions. For example, sediment grain size, bedforms, and associated paleocurrent evidence for the frequency and magnitude of fairweather and storm reworking permit the confident—but qualitative and comparatively coarse—determination of shallow-, intermediate-, and deep-water paleodepth estimates for continental shelf deposits. Because water depth is rarely an environmental parameter per se (compared, for example, with sediment grain size, frequency of disturbance, or organic content), the recognition of semi-quantitative depth categories in the geologic record is sufficient in most instances. In the terrestrial fossil record, geologists can similarly discriminate among the fluvial sub-habitats of main channel, channel bar, levee, and flood plain by using sedimentary features (e.g., grain size distribution, sediment color, presence and type of root traces) characteristic of water content and soil development. States of preservation of fossil material provide additional information on environmental conditions at and immediately below the depositional interface, including the frequency and agent of burial events. Preservational condition also provides insights as to whether the fossil material is indigenous or exotic to the depositional site and thus whether the inferred ecological tolerances of fossil taxa can be used as proxy environmental information (see next section).

Environmental proxies thus may be based on physical, chemical, or biological features of the geologic record (see Table 2.1). The fossilized remains of organisms—shells, bones, non-mineralized organic tissues—typically carry several kinds of proxy information. For example, the abundance of fossils can reflect original population size, predatory damage can indicate trophic role, and the isotopic composition of their hard parts can capture information on growth temperatures, and ambient salinities (see Box 2.2). Proxy indicators can, of course, be affected by post-depositional alteration and destruction. Some have proven utility through much of the geologic record (e.g., carbon isotopes), some are limited to the Mesozoic and Cenozoic (e.g., stomatal density), and others can be used only in very young deposits under special circumstances (e.g., fossil DNA).

TABLE 2.1 Examples of Proxy Indicators and Their Interpretation

Source	Proxy	Type of Information
Individual fossils	Number and variation of growth rings/bands, size	Seasonality, growth rates, growth conditions, generation times, biomass, age, and season of death
	Fire scars in tree rings	Fire intensity and frequency
	Stomatal density in leaves	Atmospheric CO_2
	Herbivore or predator damage	Intensity of herbivory or predation, herbivore or predator preferences, evolution of herbivore feeding strategies and plant responses
	Leaf shape and size	Mean annual temperature, elevation
	Overgrowth relationships in encrusters	Competitive relationships
	Larval shell type	Mode of dispersal, mode of development, evolutionary history
	Body size	Body size, biomass, size frequency distribution
	Density	Individuals per unit area, biomass
	Location	Habitat, dispersal history, geographic distribution
	Tooth wear	Diet in mammals
	Preservational condition	Exposure, hydraulic energy, sedimentation rate
	Fossil DNA (generally limited to deposits <130 Ka)	Presence of species not otherwise preserved, evolutionary relationships and rates
Composition and structure of fossil assemblages	Taxonomic composition	Taxa present, guild structure, environmental tolerances, diverse climatological, hydrological, and other environmental variables

continued

TABLE 2.1 Continued

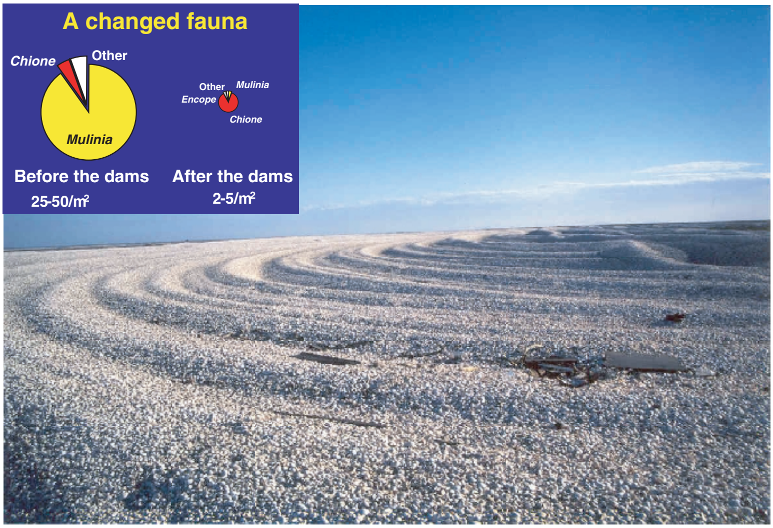
Source	Proxy	Type of Information
Composition and structure of fossil assemblages (continued)	Presence/absence and relative abundance of plant functional types	Physical structure of vegetation—albedo, surface roughness, evapo-transpiration
	Species richness, diversity, and evenness	Species richness, diversity, and evenness
	Relative abundance of taxa	Relative abundance of taxa, dominance, shape of abundance frequency distribution
	Geographic distribution	Geographic distribution, climate
	Presence/absence and relative abundance of animal guilds	Sediment consistency, suspended food supply, presence and structure of vegetation
Geochemical and isotopic composition of skeletal hard parts	Strontium isotopes	Source and amount of freshwater, migration histories, home range
	Oxygen isotopes	Temperature range and variability, salinity, ice volume, source of moisture
	Carbon isotopes	Source of food, vegetation type, productivity, atmospheric CO_2, humidity, temperature
	Nitrogen isotopes	Source of food, trophic level
	Boron isotopes	pCO_2 concentrations
	Hydrogen isotopes	Temperature, source of moisture
	Multi-isotope systematics	Climate, hydrologic conditions, source of organic compounds, biogeochemical cycling
	Ba/Ca ratios	Productivity
	Mg/Ca ratios	Temperature
	Sr/N ratios	Trophic level in mammals
	Sr/Ca ratios	Temperature range and variability

TABLE 2.1 Continued

Source	Proxy	Type of Information
Biogeochemical and geochemical evidence in sediments	Biomarkers and other molecular fossils	Presence of species, trophic groups, or guilds not otherwise preserved
	Chlorophyll levels in sediments	Productivity, sedimentation rate
	Nitrogen and carbon isotopes in organic compounds	Source and level of productivity
	Anthropogenic heavy metals and toxins	Human disturbance
	Evaporite minerals	Evaporation rates
	Authigenic minerals such as phosphorites and glauconites	Productivity
	Mn, Fe, Mo, U, V, and Cr trace elements	Redox conditions
	Sulphur isotopes	Redox conditions, atmospheric oxygen, microbial activity
Lithologic evidence	Sediment grain size and sedimentary structures	Hydraulic energy, storm/bottom disturbance, current direction, substrate character
	Paleosols	Soil development and climate
	Peats and coals	Wetlands hydrology
	Trace fossils	Behavior, surface stability, sediment reworking rates, presence of biota not otherwise preserved, water table position

The abundance of fossil species whose living representatives are restricted to particular environmental conditions often has been used as a proxy for those same conditions in the geologic past. For example, the relative abundance in sedimentary cores of warm- versus cool-water species of planktic foraminifera was used through the 1970s to infer water temperatures using factor analysis, integrating knowledge of these

BOX 2.2
Historical Ecology of the Colorado River Delta



Shell accumulations on the Colorado River delta provide evidence of environmental and ecological conditions before the construction of upstream dams. Inset shows differences in the relative abundance and density of the shelly fauna. SOURCE: Photograph and data by Karl W. Flessa; used with permission.

As a result of the construction of the Hoover Dam and the Glen Canyon Dam, the now-controlled flow of the lower Colorado River permits diversion of its water for the farms and cities of the Southwest. In most years since 1960, the river no longer reaches the sea. In the northern Gulf of California, the Colorado Delta and estuary have been transformed by

species' present day ecological and environmental tolerances, until the problems inherent with non-analog associations were appreciated. This information permitted the history of Quaternary climate change to be reconstructed at a then-unprecedented level of temporal detail and environmental precision (e.g., CLIMAP, 1976, 1984), fueling a generation of climate and ocean modeling.

The diversity and sophistication of non-biotic, primarily geochemical proxy indicators that are now available for use is increasingly liberating human activity. But directly measuring that impact was thought impossible, because no surveys of the delta and estuary had been made before upstream dams and diversions.

With analyses of the age, abundance, species composition, and geochemistry of shells and other remains at the mouth of the river, it has proven possible to construct a baseline by which to measure the ecological impact of the river's diversion (Flessa, 2002). Radiocarbon-calibrated, amino acid dating of shells provides 50-year resolution, indicating that the shells at the river's mouth date from before the river's diversion and back to approximately 1,000 years ago. Comparisons of shelly mollusks in the era before the dams to those alive today document a decrease of as much as 90 percent in population density and the near disappearance of *Mulinia coloradoensis,* a once dominant bivalve (Kowalewski et al., 2000). Analyses of predatory damage on shells of *M. coloradoensis* indicate that it was an important source of food in the trophic web of the estuary before the dam (Cintra-Buenrostro et al., in press). The oxygen isotope composition of shells of *M. coloradoensis* show that it inhabited brackish water and that the freshwater plume of the river extended at least 70 km from the river's mouth (Rodriguez et al., 2001). Oxygen isotope values in the otoliths of two species of endangered fish reveal that they used the brackish waters of the estuary as nursery grounds (Rowell et al., 2004). The analyses of shelly remains have now become a powerful forensic tool in the study of environmental and ecological change.

The case of the Colorado River delta is not unique. In most circumstances, habitats have been modified by human activity long before they could be studied in their pristine condition. The historical record provided by the observations of early explorers, museum collections, or the natural accumulations of resistant remains can now be used to provide a benchmark to measure the effects of human activity.

paleoenvironmental analysis from the potential circular reasoning of using fossils both to indicate environmental change and to measure biotic response to that change. In fact, it is now often possible to apply more than one proxy method to reconstruct the record of many environmental variables (see Box 2.3). Local histories of environmental change that can be reconstructed using such cross-checks—that is, that are robust to several independent proxy methods—are especially compelling (e.g., Mann, 2002).

BOX 2.3

Multiple Proxies at Minden Bog: Peatland Paleohydrology, Forest Composition, and Disturbance Regimes

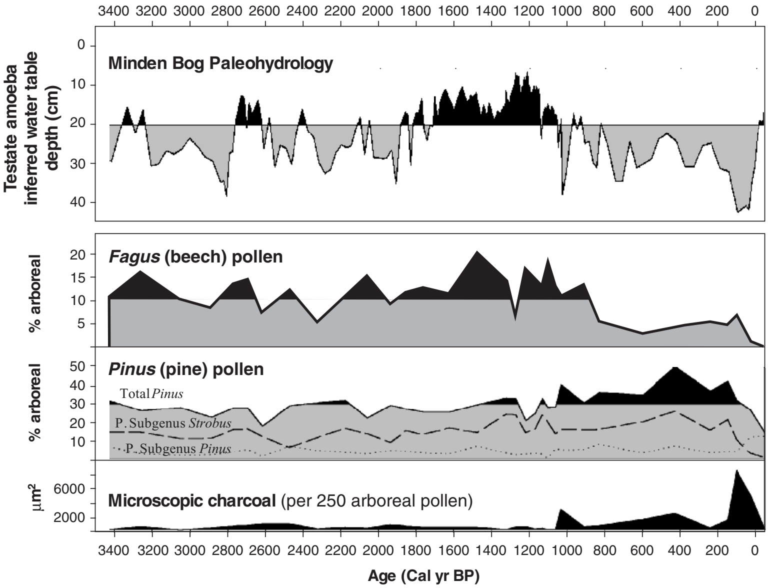
Sediments of peatlands contain paleohydrological and paleoecological records that can be used in tandem to investigate climate variability and its ecological consequences. Ombrotrophic bogs, which receive all their water and minerals directly from the atmosphere, are widespread in the Northern Hemisphere between 45ºN and 55ºN. Because their water tables are perched above the regional groundwater table, they respond rapidly to variations in precipitation and evaporation. European scientists have exploited archives from ombrotrophic bogs to obtain high-resolution paleohydrological records over much of northwestern Europe (e.g., Charman, 2002; Mauquoy et al., 2002).

A recent study indicates the potential for using ombrotrophic bog archives in North America. Minden Bog, 150 km north of Detroit, Michigan, contains a 3,300-year record of hydrological variation with subcentennial resolution (Booth and Jackson, 2003). The record indicates dry but fluctuating conditions from 3,300 to 1,800 years ago, a wet period 1,800 to 1,000 years ago, and uniformly dry conditions for the past 1,000 years (see figure below). These patterns, inferred from fossil assemblages of testate amoebae, are corroborated by other paleohydrological indicators from the peats (humification, plant macrofossils) and other records from the region (lake levels).

Pollen and charcoal data, representing vegetation and fire history from the regional uplands surrounding the bog, indicate a major change in forest composition and fire regime 1,000 years ago. The shift towards drier climate led to a decline in regional beech (*Fagus*) populations, an increase in pine (*Pinus*) populations, and an increase in regional fire incidence (microscopic charcoal). Beech trees are more sensitive to drought and to surface fires than pine trees, and surface fires in humid, forested regions are more frequent during dry periods. This study illustrates the influence of climate change on forest composition and disturbance regime, and the power of using independent paleoclimate proxies together with paleoecological data.

BIOLOGICAL INSIGHTS CONTAINED IN THE GEOLOGIC RECORD

The geologic record contains information on past biotas in many forms, including fossils (the remains of individual bodies), tracks and burrows (trace fossils), and various isotopic and biomolecular (biomarker) proxies for the former existence of species or functional groups. The



Upper diagram shows paleohydrological history of Minden Bog, Michigan, during the past 3,300 years, as inferred from testate amoeba assemblages in sediments. Black-shaded portions represent wet periods (water levels above the 3,300-year mean), while gray portions represent dry periods. Lower diagrams show pollen percentages for beech (*Fagus*) and pine (*Pinus*), and microscopic charcoal deposition. Black-shaded portions of pollen plots represent values exceeding the 3,300-year mean. SOURCE: Modified from Booth and Jackson (2003); copyright Hodder Arnold, used with permission.

combined information from these diverse sources is known as the fossil record of life on Earth.

The fossil record is widely appreciated as a source of valuable, and in many ways unique, information on the evolutionary relationships and dynamics of taxa. Paleontological data are the most robust basis—in readily fossilized groups—for quantifying key evolutionary variables such as species durations, speciation rates, and extinction rates, and how those relate to external factors such as climate change and such internal factors as body size or feeding strategy (e.g., Stanley, 1979; Jablonski, 1995; McKinney, 1997; Sepkoski, 1998; Kidwell and Holland, 2002). Such paleontological analyses have had, and continue to have, major impacts on evolutionary biology, for example in quantifying stasis and punctuation in species histories (e.g., Gould and Eldredge, 1993, 1997; J.B.C. Jackson and Cheetham, 1999; Gould 2002), large-scale evolutionary trends and their underlying dynamics (e.g., Stanley, 1979; Jablonski, 2000; Alroy, 2001a; Gould, 2002), the nature of evolutionary radiations and rebounds in terms of both taxonomic richness and morphological disparity (e.g., Foote, 1997; Lupia, 1999; Eble, 2000), and even the kinds of changes in embryological development that have fueled major evolutionary transitions and diversifications (e.g., Knoll and Carroll, 1999; Shubin and Marshall, 2000; Valentine, 2004). Paleontology is now an integral part of evolutionary biology (Maynard Smith, 1984; Ruse and Sepkoski, 2005), and macroevolution as conceived from the geohistorical record is becoming a part of the educational and research canon (e.g., inclusion in such general works as Raff, 1996; Ridley, 2003; Freeman and Herron, 2003; Coyne and Orr, 2004).

Less well appreciated—especially outside the specialty—is the enormous value of the fossil record for ecological and biogeographic analysis across a range of temporal and spatial scales, including those directly comparable to modern-day studies. These are the biological insights that are the primary focus of this report on the nature and value of geohistorical records.

Many of the biotic variables that are widely analyzed in biology are commonly captured by body fossils in the geologic record, especially for the higher (multicellular) organisms that constitute an important component of lower trophic levels (photosynthetic primary producers, detritivores, deposit feeders) and the entire middle and upper portions of food webs (herbivores; omnivores, including filter feeders; multiple tiers of carnivores). This readily acquired information includes the taxonomic affinity, body size, sexual dimorphism, habitat preferences, ecophenotypic variability, geographic range, functional group (feeding mode, pollination syndrome, spatial tier), and in many instances, the ontogenetic age and rank abundance of fossil species. Such information can yield information on various aspects of the species' biology (e.g., growth rates and likely generation times) and ecological roles (e.g., dominance, trophic position). Multispecies assemblages of fossils can provide information on community composition, species richness, diversity, evenness, predator-prey relationships, food-web structure, and species body-size distributions. Indeed, much of the data needed to determine ecological scaling relationships (e.g., Brown and West, 2000) is obtainable from geohistorical records.

In addition, some kinds of data used in biological analysis are at present rarely extracted from geologic records, with DNA being perhaps the most notable example (see Box 2.4). DNA in living species is extremely valuable in testing genetic divergence among populations and species under conditions of habitat fragmentation and environmental change, and is an important partner to morphologic data in phylogenetic analysis. Unfortunately, DNA degrades rapidly even before burial, and has been extracted from sedimentary records in an intact (readable) form only from specimens younger than ~150 Ka (Poinar et al., 1996; Poinar and Stankiewicz, 1999). This window for DNA preservation is very narrow compared to the evolutionary duration of most species (e.g., ~5 Ma average duration for metazoans). However, within the window of geologic time where it can be extracted successfully, fossil DNA has great, largely untapped potential for detecting the presence of species that did not contribute body fossils or trace fossils (e.g., Kuch et al., 2002; Willerslev et al., 2003) and for studying among-species variation in population-level responses to climate changes at the centennial to millennial scale (e.g., Orlando et al., 2002; Hadly et al., 2003).

BOX 2.4
Ancient DNA from Arid South America

Outside the microenvironment of a living cell, DNA is an unstable molecule and its high nitrogen and phosphorus content make it subject to rapid degradation and utilization by microbes. Accordingly, ancient DNA is preserved only in a restricted set of environments. Some of the greatest successes in ancient DNA analysis have come from desiccated or mummified organic remains preserved in caves and rock shelters of arid and semiarid regions. In an international collaborative effort, scientists from the United States, Germany, Argentina, and Chile have extracted, amplified, and sequenced ancient DNA from rodent middens and herbivore dung from sites on the arid western slope of the central Andes and the semiarid eastern slope of the southern Andes (Kuch et al., 2002; Hofreiter et al., 2003).

Mitochondrial DNA extracted from late Pleistocene herbivore dung at Cuchillo Curá, southwestern Argentina, represents a previously undescribed, extinct species of ground sloth (Hofreiter et al., 2003). Chloroplast DNA revealed several different plant species in the ground sloth's diet; many of the same plant taxa were identified in morphological analyses of plant cuticle from the dung.

continued

BOX 2.4 Continued

The photo on the left shows the Cuchillo Curá site. Ground-sloth dung is from the base of the large crack, just left of center. The photo on the right shows the interior of the Cuchillo Curá rock shelter; the rock hammer rests on the partly eroded dung layer and rodent midden. Dung from which DNA was extracted was radiocarbon dated at 17,300 years BP. SOURCE: Photographs by J.L. Betancourt, USGS; used with permission.

An 11,700-year-old rodent midden from the central Atacama Desert of northeastern Chile yielded mitochondrial DNA of a midden-forming rodent (leaf-eared mouse) and chloroplast DNA representing at least eight plant taxa (Kuch et al., 2002). The mitochondrial DNA not only permitted identification of the rodent species responsible for building the midden but also provided clues to its biogeographic and evolutionary history.

These and other recent studies clearly show that fossil DNA, far from being a mere curiosity, can provide important information on past biotic communities, environments, animal diets, and species occurrences, and can be used to develop and test specific hypotheses on the evolutionary responses of plant and animal populations to environmental change (see also Poinar et al., 2003; Hadly et al., 2004; Willerslev et al., 2003).

Some important paleobiologic information that at present is largely unknown but extremely important is quantitative information on species' metabolic rates and reproductive success. Information about reproductive rates, dispersal capability, source-sink budgets, and absolute population size or density is essential for energetic analyses, including evaluations of competitive success and adaptive strategies. This information is possibly knowable, but at present can be estimated only by extrapolation from living analogs, and deserves much more vigorous investigation.

The application of new technologies from outside paleobiology has already greatly enhanced the power and sophistication of biological information that can be extracted from geohistorical records. For example, accelerator mass spectrometry now permits ^{14}C dating of very small specimens, microsampling of growth increments and improvements in sample processing now allow stable isotope analyses at daily resolution, computerized tomography of fossil specimens reveals previously hidden morphological details, and database and geographic information system technologies allow new analyses of the temporal and geographic distribution of fossils.

Information on Multicellular Life

The multicellular fossil record has a long history of study, and the kinds of biological information sought from the record continues to increase (as noted above, ranging from information on growth rates and dispersal modes to trends in community structure and diversity over geologic time). Intensifying research over the last two decades is transforming our understanding of the quality and power of these many kinds of paleobiological data, especially actualistic studies in modern environments, rapidly developing chemical proxies (summarized in the section on microbial life below, and illustrated in Box 2.5), meta-analysis and other statistical syntheses of existing data, and model simulations. Research programs in this general area—determining how to extract more and better biological information from geologic records—routinely integrate approaches and information from both the biological and geological sciences, and frequently involve collaborations between biologists and geoscientists. Consequently, they not only provide vital information into the fidelity (faithfulness) and acuity (fineness of resolution) of paleontologic data but also provide models for collaborations between the disciplines.

An improved understanding of the controls and selectivity of fossilization does not in itself alter the quality of the record, but quantitative assessments of bias and acuity provide a more rigorous basis for designing paleobiologic research, including improving protocols for sampling and analysis, and for judging which biological questions are tractable for

BOX 2.5
Natural and Human-Caused Variation in Salmon Populations

Salmon are a valuable resource in the Pacific Northwest, and fluctuations in their abundance have both economic and cultural impact. How much of this fluctuation is driven directly by human activity and how much is linked to variations in climate?

The ability to look back in time to estimate both the size of salmon populations from $\delta^{15}N$ values and the productivity of lake systems from indicator species of plankton, reveals not only important ecological feedbacks but also serves to differentiate between human-caused and natural variation in these ecosystems. Variations in salmon populations in several Alaskan lakes over the past 2,000 years were documented by Finney et al. (2000, 2002) by examining variations in $\delta^{15}N$ in lake sediments. Sedimentary $\delta^{15}N$ acts as a proxy indicator of salmon population size, because in contrast to the 0‰ value of terrestrial nitrogen sources, sockeye salmon tissues have $\delta^{15}N$ values of +12‰, reflecting their marine food diet during growth. Adult salmon migrate from the marine environment to their natal lake to spawn and die, adding their distinctive marine $\delta^{15}N$ isotopic signature in lake sediments.

Salmon carcasses are an important source of nutrients to these Alaskan lakes, and a natural positive feedback exists between salmon abundance and lake productivity. Analysis of lake sediments indicates that the abundance of diatom and zooplankton remains—proxy indicators of lake productivity—fluctuate with $\delta^{15}N$. Productive lakes support larger salmon populations, because zooplankton are essential for juvenile salmon growth and, in turn, larger salmon populations result in more productive lakes as a result of greater nutrient loadings.

Fishing activity can disrupt this natural feedback. Finney et al. (2000) showed that the $\delta^{15}N$ of lake sediments has decreased since the 1880s, when commercial fishing began to lower the number of salmon returning to the lakes. The recent decrease in $\delta^{15}N$ values is greater than at any time in the past 300 years, and is despite warming marine waters that should lead to increased abundance. This decline tracks the history of commercial fishing and is only found in lakes having salmon runs, suggesting a disruption of the salmon-based nutrient cycle, which may hinder the recovery of salmon populations in such lakes.

Fluctuations in $\delta^{15}N$ and lake productivity are also evident during the ~2,000 years before commercial fishing (Finney et al., 2000, 2002; Gregory-Eaves et al., 2003). Clearly, natural factors can cause significant variations in salmon abundance. Temporal variations in multiple lakes are similar to those of proxy paleoclimate information for the North Pacific region, and thus consistent with climatic change being an important driver of salmon abundances. Temporal changes in Alaskan salmon abundance also match those in other marine proxy records, such as sardine and anchovy populations off southern California, highlighting the widespread effect of climatic change on marine and coastal ecosystems in the North Pacific region.

study. Some new insights relevant to the multicellular fossil record are highlighted below.

1. What proportion of local and regional diversity is captured by the fossil record? In marine benthic systems, actualistic studies indicate that 75-100 percent of living marine macrobenthic invertebrate species that have biomineralized hard parts (e.g., shelled invertebrates such as most mollusks, sea urchins, barnacles, and corals as well as mineral-secreting algae and various unicellular benthos) are present as dead skeletal material in immediately surrounding sediments, and a similar proportion of living genera have known fossil records (Schopf, 1978; Valentine, 1989; Kidwell and Flessa, 1995; Kidwell, 2002a). These numbers are quite high, given that the likely preservation potential of any given shelled individual is probably quite low. However, a better estimate of the genus-level completeness of the entire macrobenthic fauna is ~40 percent, which is a much-cited determination of the proportion of shelled taxa, as opposed to taxa that are only sparsely mineralized (e.g., starfish and some polychaetes, arthropods, and sponges; ~30 percent of these genera have a fossil record), and taxa composed exclusively of soft tissues (very few modern genera are known in the fossil record [Schopf, 1978]). Few comparable studies have been attempted for terrestrial animal communities, although one regional study of land mammals found a high overall fidelity but a strong correlation with body size (Behrensmeyer and Dechant Boaz, 1980; and see review in Kidwell and Flessa, 1995; Behrensmeyer et al., 2000). Thus, although more research is needed on how these percentages vary among environments and groups, modern death assemblages as well as the fossil record can capture a significant proportion of biological diversity among mineralized metazoans.

Animal and plant groups having only refractory organic coats and skeletons (e.g., pollen, cystate microbes, woody plants, arthropods) are less durable and require particular conditions for preservation, but individual instances of good fossil preservation can be highly resolved (in taxonomy, morphology, and temporal precision). Some intervals of good fossil preservation can be both temporally extensive and highly detailed. For example, sedimentary cores of lakes provide centennial resolution of vegetation changes for the last 12,000 years using a combination of pollen and plant macrofossils; lake records are sufficiently abundant to provide 100-km geographic resolution of vegetational and biogeographic patterns for most of eastern North America; and high-elevation lake records together with low-elevation packrat midden records provide similar resolution in the western United States (Betancourt et al., 1990; Webb, 1993; S.T. Jackson et al., 1997; Williams et al., 2004). Truly extraordinary conditions are required to fossilize soft tissues for geologically significant periods of time (pre-Quaternary), but dozens of such "Fossil Lagerstätten" are known (e.g., Allison, 1988; Selden and Nudds, 2004; Allison and Briggs, 1993). Although generally only sparsely fossiliferous in terms of numbers or density of specimens, they can be invaluable sources of novel morphologic, ecologic (e.g., preserved gut contents, pollen on fur), biogeographic (e.g., hummingbirds in the Eocene of Germany, whereas today they are strictly a New World group), and evolutionary information (Gould, 1989).

2. How common is the transport of dead remains to settings outside the species' original habitat or geographic range? Homogenization of the original spatial distributions of taxa due to postmortem transport and mixing is a persistent concern among paleontologists. Such transport does occur, but its effects are predictable and quantifiable. For example, pollen of wind-pollinated plants is more readily and widely transported than that of animal-pollinated plants, but the area of source forest whose pollen is sampled by the sedimentary record of a given lake is proportional to the surface area of the lake—more detailed understanding of vegetation type and distribution can only be acquired from small basins (S.T. Jackson, 1994; Davis, 2000) or by using plant macrofossils. Out-of-habitat transport and mixing of benthic macro- and microfauna in shallow marine (estuarine to continental shelf) settings is less significant than might be predicted—facies-scale differences in fauna typically persist even in relatively high-energy, level-bottom settings. Environments having high proportions of allochthonous taxa are steep-gradient seafloors and narrow shelves, high-energy tidal channels, and deepwater turbidite fans, which are readily recognized from independent geologic evidence (e.g., Parsons and Brett, 1991; Kidwell and Bosence, 1991; Kidwell and Flessa, 1996). Transport among level-bottom habitats does occur, but "exotic" taxa are more likely (1) to be small-bodied than large-bodied, (2) to have lived attached to the seafloor rather than burrowed within it, and (3) to be represented by relatively few individual specimens. Actualistic research further indicates that many taxa that are "suspicious" because they are poor ecological fits to modern environmental conditions are instead non-transported ecological relicts from former community states (e.g., persistence of epiphytic benthic foraminifers in surficial sediments of seafloors that are no longer vegetated; presence of intertidal mollusks in subtidal sediments in the wake of rapid marine transgression [Anderson et al., 1997; Flessa, 1998; Roy et al., 2001]). Among terrestrial vertebrates, predators and scavengers can be as important—or more important—than physical processes in transporting bones, but again most taxa are found within or close to their original habitats (e.g., Dunwiddie, 1987; Greenwood, 1991; Hadly, 1999; Behrensmeyer et al., 2000; Birks, 2003).

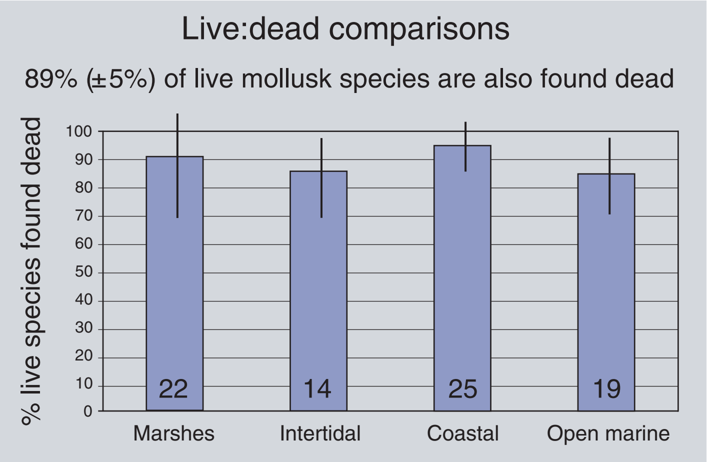
The record of the broader geographic distribution of fossil species is affected by the uneven distribution, preservation, and sampling of sedimentary environments in the geologic record. Nevertheless, shifts in the geographic range of species in response to climate change are readily detected in many fossil records, with most study focused on Quaternary pollen, mammals, and planktonic foraminifera (e.g., COHMAP, 1988; Faunmap Working Group, 1994; CLIMAP, 1976; Roy et al., 2001). The geographic distribution of pre-Quaternary fossils has frequently been used to recognize major immigration events in both the marine and terrestrial realms (e.g., Stehli and Webb, 1985; Vermeij, 1991; Jablonski and Sepkoski, 1996; Clark et al., 1998); to examine the responses of terrestrial faunas to tectonic and climate change (e.g., Carrasco et al., 2005); and to track the geographic patterns in recovery from mass extinction (e.g., Jablonski, 1998). Biases caused by incomplete preservation and or incomplete sampling of geographic regions can be recognized by careful consideration of the expected statistical distribution of fossil samples under varying degrees of completeness (e.g., Holland, 2000; Smith et al., 2001).

3. How faithful are the density and relative abundances of species, and the relative frequencies of feeding types, life histories, and body sizes in fossil assemblages relative to those in the original biota? Organisms composed exclusively of soft (non-mineralized, volatile) tissues require unusual and rapidly acting processes to be preserved, and thus assemblages rich in such specimens should be virtual snapshot records of standing communities. Assemblages composed of taxa having refractory (chitinous, woody) or mineralized skeletal parts have greater potential to be biased by differential preservation processes, including postmortem transport among taxa and age classes, as well as mixing of generations from time-averaging (see below). In what detail can community structure and change be recognized by tracking only one comparably preserved portion (e.g., only pollen and wood, or only well-mineralized taxa); and among the preserved fraction, how faithful are quantitative data to that portion of the original source community? Studies in modern depositional environments comparing local death assemblages with surrounding live communities indicate that among the intrinsically preservable taxa, the original proportions of taxa—and thus many aspects of community structure—are surprisingly well recorded, even by the time-averaged death assemblages that dominate the fossil record of many groups (Kidwell and Flessa, 1995; Kidwell, 2001a; 2002a; see Box 2.6). Mollusks, pollen, and mineralizing microbial groups (e.g., foraminifera, diatoms, and radiolarians) have been the subjects of extensive research on this issue (e.g., Donovan, 1991; S.T. Jackson, 1994; Sugita, 1994; Donovan and Paul,

BOX 2.6
Ecological Information from Time-Averaged Death Assemblages

The fidelity of the taxonomic composition, spatial distribution, and abundance of taxa in fossil assemblages relative to the source living populations is particularly problematic in assemblages of the well-mineralized taxa that dominate the fossil record. Such taxa have generally high preservation potential, but their hard parts are consequently also likely to survive postmortem transport and—whether transported or not—accumulate in time-averaged death assemblages where the number and relative abundance of taxa might be distorted by their differing rates of mortality and relative postmortem fragility (Vermeij and Herbert, 2004).

Paleoecological fidelity has been tested for many decades primarily by estimating the live-dead agreement in modern environments; dead data are generated by sieving dead remains from sediments accumulating in the target habitat or region, and live data may be derived from the same samples (e.g., benthic organisms) or from various kinds of line-transect, quadrant, trap, or aerial surveys of the surrounding area. Shelled mollusks (bivalves and gastropods) have been the subject of an especially large number of such studies (e.g., see figure below).



Percentage of live species of shelled mollusks also found as dead remains in marsh, intertidal, coastal, and open marine habitats. Vertical line at top of bar indicates standard error; number above habitat name indicates the number of studies analyzed. SOURCE: Kidwell (2001b); used with permission.

To acquire a quantitative estimate of these effects, as well as a robust estimate of true death assemblage fidelity, Kidwell (2001b, 2002a,b) reanalyzed raw data from 19 molluscan live-dead studies using a standard set of measures of live-dead agreement, and then subjected these to both conventional statistics and meta-analysis.

The analysis yields fundamentally good news about marine sedimentary environments as sinks of locally produced molluscan hardparts (Kidwell, 2002b):

1. Much previously reported variation among datasets is due to differences in sample size—where data are based on at least 100 live and 100 dead individuals, live-dead agreement for all metrics becomes far more consistent among datasets.
2. Death assemblages capture local live diversity efficiently—88 percent of species documented living in a habitat are also present dead in the same set of samples.
3. Seventy-six percent of all dead individuals are from these same species, that is, species that are only found as dead remains (and thus that might be transported exotics) are each represented by very few individuals.
4. Despite the high variability among studies, species' dominance in death assemblages is in fact highly correlated with those species' dominance or rarity alive.
5. Sediment grainsize and other measures of environment fail to bias preservation in any strong or consistent way, contrary to expectations.
6. All ecological metrics tested so far show a strong, mesh-size effect; the fidelity of molluscan death assemblages to their local live communities is significantly higher if the analysis focuses only on the late juvenile to adult individuals, rather than if it includes ecologically and taphonomically volatile larvae and early juveniles.

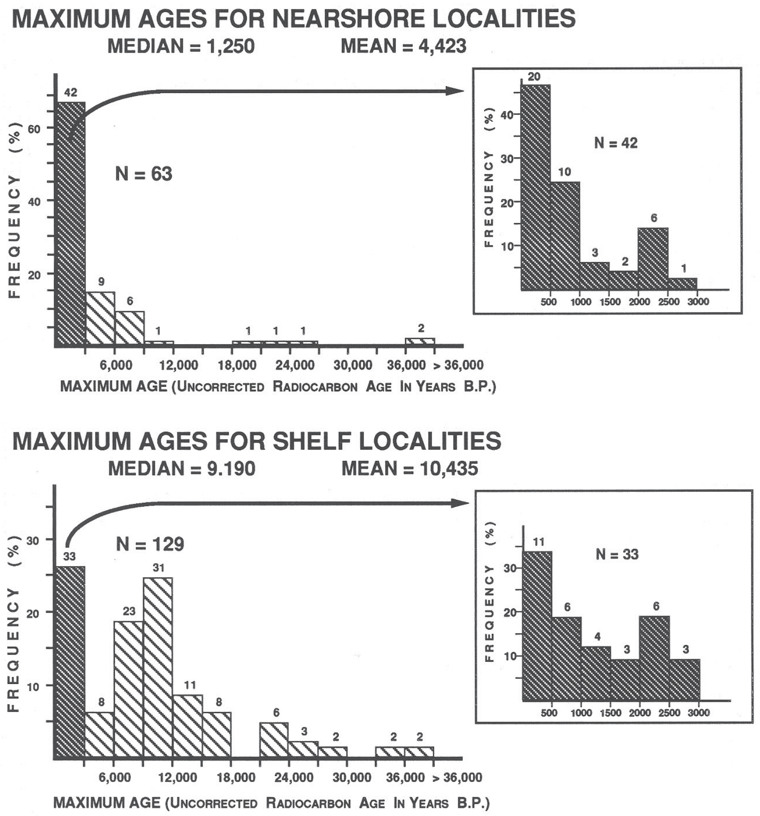
The pervasiveness and magnitude of the mesh-size effect suggests a simple protocol for improving the recovery of accurate ecological data from molluscan death assemblages, namely, target the late juvenile to adult segment of the age- and body-size frequency distribution, which is ecologically and taphonomically relatively stable. This basic approach may well prove useful in other animal groups, inasmuch as mortality and postmortem destruction both tend to be focused on the ontogenetically youngest members of populations. These results are very encouraging, both for using dead remains for rapid biodiversity assessment in modern environments, and for building prehistoric time series using sedimentary records.

1998; Martin, 1999; Behrensmeyer et al., 2000; Davis, 2000). Detailed investigations of the taphonomy of woodrat middens (e.g., Betancourt et al., 1990; Frase and Sera, 1993; Lyford et al., 2004) have validated their utility in reconstructing Quaternary vegetation change in arid regions, and leaf litter captures the richness of surrounding woody plants to moderate to high degrees (Burnham, 1993; Meldahl et al., 1995). Although other major mineralizing groups (corals, echinoderms, land mammals, reef and freshwater mollusks; see Kidwell and Flessa, 1995; Behrensmeyer et al., 2000) have received less attention, results so far are very encouraging. The ability to reconstruct the characteristics of ecological relationships, relative abundances, and biomass is important, because such information is the key to answering many important questions about the structure of communities and the persistence of species under the stress of environmental change.

4. To what extent are the remains of multiple generations or successive community states mixed into single fossil assemblages, thereby blurring the details of events and transitions? Studies of modern communities and environments have been critical to quantifying these values, and despite the complexities the results are encouraging. For example, radiocarbon dating and other chronologic methods indicate that individual cm-scale samples in Quaternary lake records represent only approximately one decade of time-averaging of pollen input from the local community; in many instances, annual resolution is possible, but as in modern monitoring time series, it is often easier to analyze trends when annual data are blurred into decadal time-windows (running averages). Decadal resolution in sedimentary cores can therefore be highly valuable. Annual to decadal resolution is not uncommon in estuarine settings (e.g., Brewster-Wingard and Ishman, 1999), even in rocks that are hundreds of millions of years old (e.g., Lanier et al., 1993). In fully marine settings characterized by slower sediment accumulation or more vigorous postmortem mixing, time-averaging is more prolonged; for example, specimens from shelled-mollusk assemblages can range up to a few thousand (in nearshore settings such as bays and lagoons) to ~10,000 years old (on sediment-poor continental shelves), due to the strong mixing of shell generations by burrowing organisms and storm reworking of the seafloor (Flessa and Kowalewski, 1994; and see Martin et al., 1996, for mixed mollusk-foraminifer assemblages) (see Box 2.7). However, even in such time-averaged samples, most specimens are quite young (at most a few hundred years), and thus the effective time-averaging of information on species' isotopic signatures and relative abundance is probably much less than predicted from the maximum shell age in the collection (Olszewski, 1999; Kidwell, 2002b). Again, mollusks, pollen, and foraminifera have

BOX 2.7
How Much Time Is Represented in Accumulations of Shells in Modern Marine Environments?

Flessa and Kowalewski (1994) surveyed published radiocarbon dates for shells from nearshore and offshore habitats on today's continental shelves. They found that nearshore accumulations generally represented a total of ~1,000 years of accumulation while those from shelf habitats had shells averaging ~10,000 years in age (see figure below). These results provide estimates of the degree of time-averaging in comparable fossil deposits.



Histograms showing differences in the time-averaged age distribution of shells from modern nearshore and shelf environments. SOURCE: Reprinted from Flessa and Kowalewski (1994)[1]; by permission of Taylor & Francis AS.

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[1] "Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature" by K.W. Flessa and M. Kowalewski, from Lethaia www.tandf.no/leth, 1994, vol 27, pp 153-165.

received the greatest research attention, but preliminary results for other major groups are promising.

5. How faithful are observed appearances in the fossil record to the actual evolutionary duration and temporal sequence of species? What is the likelihood that the observed first or last appearance of a species in the fossil record reflects its true time of origination or extinction? Thus, what are the confidence limits on our knowledge of species' evolutionary durations and temporal sequence? Such information is critical for relating particular paleoenvironmental changes to their evolutionary effects. Knowledge of raw extinction and speciation rates allows the ranking of clades, functional groups, and habitats for relative extinction risk; permits the discrimination of pulsed and non-pulsed nature of biotic originations and extinction; and addresses many other questions of biosphere dynamics on evolutionary timescales. These issues have been examined aggressively over the last 15 years by a combination of statistical analysis of large empirical datasets and model simulations that use increasingly realistic assumptions for biases in geohistorical records (Marshall, 1990, 1997; Holland, 1995, 2000, 2003; Foote, 2003). Indeed, even when confidence limits cannot be assigned, cohort analysis (e.g., Foote, 2001a,b) provides valuable estimates of evolutionary rates that are relatively insensitive to incomplete stratigraphic ranges. Despite concerns about continent-to-continent differences in environmental history, and an increase in the volume of fossiliferous rocks toward the present, many of the first-order features of the fossil record (repeated mass extinctions of global biota, secular increase in global diversity, differences in evolutionary rates, bursts of diversification) are robust to sampling and taphonomic biases (e.g., Foote, 2003).

6. To what extent are isotopic, biomolecular, and other chemical signatures of particular taxa or functional groups (e.g., plankton, eukaryotes, C_3 photosynthesizers) modified by postmortem and burial processes? And what factors determine the fidelity of the chemical proxy record of past species and communities? The comparatively easy preservation of refractory and mineralized skeletons favors the preservation of biological and environmental information, including extremely high-resolution isotopic data from single skeletons as a result of the accretionary growth of corals, mollusks, and trees, and including isotopic variation in tree rings (e.g., Poussart et al., 2003). Concern with the post-depositional stability of these signatures dates to their first application in the 1950s, and this remains an important aspect of research into the development of new methods and appropriate selection of samples (Grossman et al., 1996; Kohn et al., 1999; Pearson et al., 2001). Improvements in instruments increasingly permit analysis of single skeletons or accretionary skeletal layers rather than bulk samples, and analysis of single organic compounds, most notably the comparatively stable lipids. These methodological improvements are dramatically increasing the resolving power and confidence in paleoecological and paleoenvironmental reconstruction from chemical proxies in general (e.g., Norris and Corfield, 1998; Hinrichs et al., 2001), as are efforts to develop criteria for selecting materials for analysis (Koch, 1998; Dawson et al., 2002).

In addition, the original mineralogy of hard parts is sometimes completely altered, although such alteration is more common in older sediments. For example, taxa whose skeletons were originally composed of the biomineral aragonite are rarely preserved in that form in Paleozoic age rocks, but instead are usually demineralized (occur as open molds in the rock), recrystallized to more stable calcite, or replaced by some other mineral; Schubert et al. (1997) note that as much as 20 percent of Paleozoic fossils are preserved as silica rather than their original mineralogies. While such alteration precludes isotopic analyses of the hard parts, and is thought to shorten observed stratigraphic ranges (e.g., Briggs and Crowther, 2001; Donovan and Paul, 1998) and bias proportional abundances within individual assemblages (e.g., Cherns and Wright, 2000; Wright et al., 2003), the quantitative impacts are not yet fully explored and other paleoecological information (e.g., geographic distribution, relative abundance, ontogenetic age, repair scars) may still be obtainable.

Information on Microbial Life

The past decade has seen an increased appreciation for the importance of microorganisms in Earth's biotic systems. Microorganisms—microscopic, often unicellular organisms, both prokaryotic (exclusively clonal) and eukaryotic (capable of sexual reproduction)—were virtually the only form of life during the first four-fifths of Earth history, and their biogeochemical conditioning of Earth's surface environments was critical to the evolution of higher life as it is known on this planet, including the evolution of multicellular animals (in the late Precambrian) and the invasion of land (in the early Phanerozoic). Microbial organisms still dominate primary productivity on Earth today (that is, photosynthetic and other autotrophic means of synthesizing organic matter from inorganic compounds) despite the evolutionary diversification and prominence of higher plants. Microbial life also dominates the recycling of organic detritus (breakdown of dead or discarded biological tissues into simpler organic and inorganic compounds) (Fenchel, 1988; Perry et al., 2002).

Although multicellular plants and animals participate significantly at lower trophic levels and dominate all higher trophic levels (herbivores, carnivores, omnivores) that we exploit directly for food and other sustenance, microbes are critical components in the functioning of Earth's biosphere, and in biogeochemical cycling in particular. Understanding the functioning of microbial communities, especially in systems that include multicellular life, is an important aspect of understanding ecological dynamics. A major direction of research lies in the development of techniques to identify, from geohistorical records, the presence and role of microorganisms in ecosystems. As an essential aid to interpreting that record we also need to know how the organic and mineral records of microbial activity are modified by subsequent burial, diagenesis, and metamorphism.

Most of life on Earth over the history of the planet has been microbial. Certainly, all early recognizable life was unicellular, but the evidence for this from rock textures (>3 Ga) as well as microfossils and isotopic signatures has remained controversial (Grotzinger and Rothman, 1996; Reid et al., 2000; Brasier et al., 2002; Garcia-Ruiz et al., 2003; Schopf et al., 2002). The record of Proterozoic microbial life is much better, providing an increasingly rich record of the diversification of both prokaryotic and early eukaryotic lineages.

In contrast, microbial groups having biomineralized tests (including photosynthetic diatoms and calcareous nannoplankton, and heterotrophic [animal-like] radiolarians, silicoflagellates, and foraminifers) have an excellent fossil record. With the exception of diatoms and benthic foraminifera, these Phanerozoic groups largely have been exploited for their usefulness in biostratigraphic correlation and as carriers of isotopic-proxy information on environments, rather than to gain insights into their roles in ecological dynamics. Analysis of calcareous and siliceous microfossils continues to be of incalculable value for paleoceanographic investigations (particularly by the ocean drilling community), providing much of the chronostratigraphic framework and environmental information for the recognition of climate change, productivity, changes in circulation, and major evolutionary events. As many studies illustrate, the attributes that make these microfossils ideal for biostratigraphic and environmental analysis of small-volume, high-resolution core samples—their microscopic individual size, relatively large population sizes, widespread occurrence, mineralized skeletons identifiable to species level, and skeletal capture of isotopic signatures—also make them valuable sources of ecological insights. These insights range from the local and regional to the global-scale shifts of planetary respiration associated with mass extinctions and other extraordinary episodes (e.g., Falkowski et al., 2004). Furthermore, most of these biomineralizing groups already have been subject to taphonomic evaluation in modern environments (discussed above in the section on multicellular life).

Although the record of non-mineralizing microbial life is better in the more recent record, organic molecules of definite biological origin can be well preserved even in the pre-Phanerozoic record. Much of what is known about the timing of major microbial innovations in the deep past and allied changes in biogeochemical cycling comes from the geologic record of lipid biomarkers and isotope signatures. For example, data for lipids recovered from the rock record have made it possible to establish the first appearance of the Archaea and of eukaryotes (Brocks et al., 1999; Summons et al., 1999), and allowed recognition of some significant evolutionary expansions (e.g., of marine Archaea in the mid-Cretaceous). Lipids make excellent molecular fossils and proxies for biogeochemical processes because their structures are resistant to degradation. Some have molecular structures that are unique to the organisms that make them (that is, serve as biomarkers; e.g., Brocks et al., 1999; Huang et al., 1999; Pancost et al., 2002), and most can preserve C- and H-isotope signatures.

Biomarkers are proving to be increasingly valuable in reconstructing the input of organic matter and microbial dynamics of ecosystem change in Quaternary environments, especially in lakes and coastal estuaries of high societal and economic value (e.g., Boon et al., 1979; Laureillard and Saliot, 1993; Canuel et al., 1995; Mudge and Norris, 1997). There, high levels of primary production, caused by elevated nutrient loading (eutrophication) and/or diminished ability of herbivores to crop production (because of overfishing and top-down stresses), can lead to increased delivery of organic matter to the lake bottoms or seafloors and a cascading series of responses (the Baltic Sea, Adriatic Sea, and Chesapeake Bay are good illustrative examples where considerable controversy exists over both natural versus human, and bottom-up versus top-down drivers; see Malone et al., 1999; J.B.C. Jackson et al., 2001; Boesch et al., 2001). Biomarkers now permit the terrestrial, algal, and bacterial components of the total organic rain to be differentiated and tracked over time (e.g., in the Chesapeake; see Zimmerman and Canuel, 2000, 2002). These components change in absolute and relative abundance as the microbial loop grows to dominate the food web, eventually leading to low-oxygen conditions at the lake bottom or seafloor and in some portion of the water column. Such low-oxygen conditions are recognizable by laminated sediments, dark sediment color, biomarkers of anaerobic bacteria, carbon and nitrogen isotopic changes, iron and other metal speciation chemistry, and—in estuarine environments—by distinctive sulfur chemistry (Jonsson et al., 1990; Cornwell et al., 1996; Struck et al., 2000; Voss et al., 2000; Shen et al., 2002). Establishing when these transitions from complex food webs to much simpler Precambrian-like microbial loops occur relative to human activities (e.g., the onset of intense agricultural fertilization, commercial shell or fin fisheries, urbanization) is critical for evaluating the roles of anthropogenic and other stresses in estuarine and lacustrine deterioration, as well as for achieving a more general understanding of the dynamics of microbial communities in ecosystems containing higher organisms.

There is potential to use these biomolecular methods in deeper time both in these and other environments and to develop proxies for a larger array of organisms, both microbial and multicellular. Conclusions based on lipid biosignatures are still limited by incomplete knowledge of how lipids are transformed upon burial (lipid diagenesis), which organisms make various lipid types (taxonomic or metabolic specificity), and the extent to which these organisms might fractionate associated isotopes (vital effects). Nevertheless, these questions are tractable, and improved understanding of the diagenesis of biomarkers and the development of new biomarkers, especially to diagnose the arrival and expansion of invasive and harmful taxa, deserve priority in future research.

Isotopic signatures can be preserved in organic molecules from geohistorical records that range from decades to billions of years in age. For those signatures that are biological in origin, the magnitude of the isotopic fractionation potentially can discriminate among a variety of candidate organisms. For example, bacteria that aerobically oxidize methane can use one of two enzymes, and the isotopic fractionation depends upon the enzyme used. At present we do not yet completely understand the full array and combined effects of the many complex factors that determine the isotopic signatures preserved in the rock record, and thus this remains an important area for future research. For example, considerable progress is being made in the analysis of isotopic fractionation by higher organisms (e.g., distinguishing C_3 versus C_4 photosynthesis in plants), but further work is required to understand the trophic significance of fractionation and its post-burial preservation, for both microbial and multicellular organisms.

Genomic data should facilitate a more complete analysis of the diversity and distribution of enzymes involved in important biogeochemical processes today, and permit their calibration to isotopic signatures. Because gene sequences also contain within them a record of phylogenetic relationships among microbial groups (and thus implicitly their temporal order of appearance), genomic data have the potential to greatly improve our understanding of the evolution of biogeochemical pathways and their isotopic signatures. This is a valuable tool to combine with the preserved geologic record of molecular fossils, from which the absolute timing of microbiological and biogeochemical innovations can be deduced.

PRECISION AND ACCURACY OF GEOHISTORICAL RECORDS

Measuring and documenting rates of change are some of the primary goals of both biology and paleontology, and thus the fineness (precision) and truth (accuracy) with which the relative timing and absolute ages of events can be determined are critical. Techniques for measuring geologic age vary greatly in the materials dated, the methodology, and the temporal range. Figure 2.2 shows the time depth and resolution of a variety of useful techniques, and each has power in a particular set of sample materials, environments, and depth of time. It is useful to distinguish among methods that directly date the biological materials themselves, those that date associated inorganic materials, and those that establish the contemporaneity of events.

Direct Dating of Biological Materials

Tree rings and their analogs in coral, mollusk, and other accretionary hard parts provide a chronology based on the periodicity of accretionary growth in these organisms. In addition, variation in growth rates or biogeochemical composition can document environmental variation at annual and subannual temporal scales. In effect, the preserved remains themselves provide a clock and a calendar that can be used to date the remains directly. The use of dendrochronology (tree ring dating) is currently restricted to habitats with strong seasonal variation in growth, and can be extended through cross-dating to thousands of years before present. Corals are largely limited to tropical, shallow marine habitats, with individual sclerochronologies able to be taken as far back as a few centuries, and older time series able to be developed using radiometric dating. Decadal-, centennial-, and millennial-scale modalities generally can be recognized from these annual records. The development of chronologies based on accretionary growth in mollusks are in their infancy, but long-lived species show promise for ~1,000 year chronologies (Marchitto et al., 2000), and even short-lived species provide useful decadal-scale chronologies (Jones et al., 1989; Schöne, 2003). What chronologies based on rapidly growing species lack in total duration, they often make up for in sub-annual resolution.

Although the use of internal growth periodicities for absolute chronologies is restricted to the late Quaternary (e.g., dendrochronology), most of these methods can be applied in the deeper past where appropriate materials are preserved. These high-resolution time series are not always tied to a comparably resolved absolute timescale, but they do provide valuable estimates of past seasonal and environmental variability in temperature, salinity, and nutrient cycling (e.g., Purton and Brasier, 1999; Steuber, 1996).

Radiocarbon analysis, using the unstable ^{14}C isotope, is the primary method for direct dating of organic materials less than 40,000-50,000 years old. Radiocarbon ages traditionally have been based upon measurement

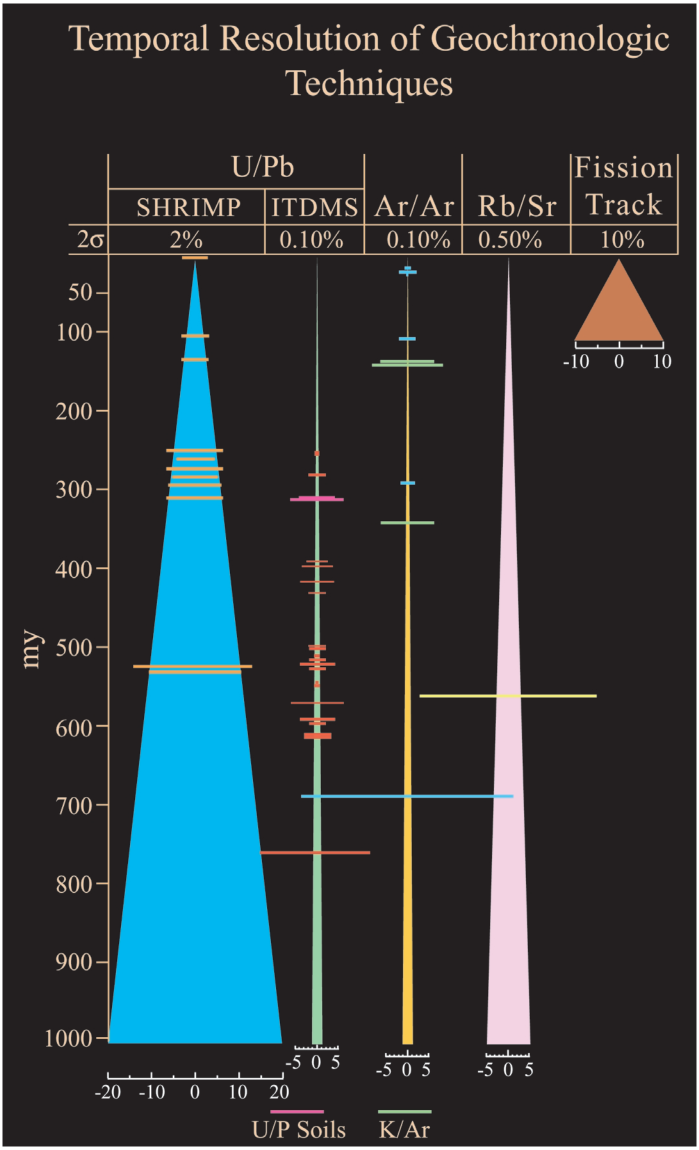

FIGURE 2.2 Effective temporal range (vertical axis shows millions of years into the past) and precision (width of horizontal bars represents 2-sigma confidence intervals) of some dating techniques commonly used to date geologic materials. The numbers below each technique indicate 2σ variation expressed as a percent of calculated age; horizontal scale bars below each expanding triangle express the 2σ variation in millions of years. SOURCE: Doug Erwin, National Museum of Natural History; used with permission.

of β-particle emission during decay of ^{14}C isotopes. Such measurement requires large amounts (usually ≥1 g) of carbon, which often necessitates mixing of sediment constituents or organic materials of different ages. Some aquatic plants and algae use HCO_3^- and $CO_3^=$ in photosynthesis, which may derive from dissolution of ancient carbonate-rich bedrock or surficial materials. Many organic-rich materials (bone, peat, shell) can be contaminated by intrusion and replacement by younger or older carbon. Thus, conventional β-decay dates are subject to imprecision and error beyond the standard counting error. Development of accelerator mass spectrometry (AMS) as an alternative means of assessing isotopic composition of carbon samples helps circumvent some of these problems. Much smaller quantities of carbon are required (as little as 10 μg), which minimizes time-averaging , and has other practical advantages:

1. Dates can be obtained on compound-specific organic fractions from samples, using the most stable organic molecules and avoiding those most likely to exchange carbon with the surrounding environment. This has been especially useful in the dating of bone, shells, and concentrations of pollen and other microfossils.
2. Dates can be obtained on one or a few specimens (plant fossils, bones, shells), separate portions of long-lived individuals, and even individual carbon compounds (e.g., Ohkouchi et al., 2003).
3. Dating can be restricted to materials that are most likely to yield reliable dates (e.g., terrestrial plant macrofossils, charcoal).
4. Dates can be obtained on sediment samples spanning as little as a few mm of deposition, rather than several cm.

The advent of AMS dating has yielded more precise and accurate sediment chronologies and age estimates for fossils, and has made it possible to assess whether fossils occurring in the same stratum were truly contemporaneous (or, alternatively, represent contamination or time-averaging).

Because the production rate of ^{14}C atoms in the atmosphere varies owing to variation in cosmic radiation, the ^{14}C content of the atmosphere varies through time. Radiocarbon dates are thus not equivalent to calendar-year dates. However, variations in atmospheric ^{14}C content for the past 20,000 years are well characterized, and so it is possible to estimate the calendar-year age of a sample given its radiocarbon age[2] (Stuiver and Reimer, 1993).

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[2] See also http://radiocarbon.pa.qub.ac.uk/calib/.

Uranium/thorium techniques also can be used to date fossil material as old as ~300,000 years. Although molluscan aragonite does not appear to provide a closed system and often yields unreliable dates, coral skeletons have proven to be especially suitable for U-series dating. The technique also has been applied to tooth enamel and bone, but additional work is needed to refine the analyses of these materials.

Amino acid racemization techniques (Wehmiller, 1993; Rutter and Blackwell, 1995; Goodfriend et al., 2000) also can be applied directly to skeletal materials (bone, shell, eggshell), and when calibrated (typically with radiocarbon or uranium/thorium techniques) can yield estimates of calendar age (e.g., Kaufman, 2003; Kowalewski et al., 1998). Within the range of radiocarbon dating, calibrated amino acid dates can be reliable and economical alternatives to radiocarbon dating for particular sites. Amino acid racemization dating is also valuable beyond the range of the radiocarbon technique, although precision is lower. Electron spin resonance can also be applied directly to fossil materials, such as shell and enamel, but the method requires further calibration and dates are rarely as precise as those produced by radiocarbon dating (Blackwell, 1996).

Dating Associated Geologic Materials

Other techniques of dating (luminescence, lichenometry, cosmogenic nuclides, paleomagnetism, astronomical cyclicity, radiometric other than radiocarbon and uranium/thorium) cannot be applied directly to fossil specimens but can date material associated with the fossil in some way, and this is the primary means of age determination for fossils that cannot be dated directly. For example, cave deposits (speleothems) associated with fossils can be dated using uranium/thorium.

Age estimation of sediments spanning the past two to five centuries using radiocarbon-based models is rendered difficult by several factors. First, landscape disturbance frequently causes changes in sediment accumulation rates in lake and wetland basins, and most parts of the world have been cleared or cultivated in the past few centuries. Second, the precision of radiocarbon age estimates has a finite limit, typically ± 50-100 years except in a few unusual cases. However, other dating methods can be applied. For example, varve counts can provide precise chronologies for lakes with annually laminated sediments. Certain short-lived isotopes that accumulate in sediments can be used for dating. Primary among these is ^{210}Pb, which can provide reliable age models for sediments of the last 100-150 years (Noller, 2000). Cesium-137, which is produced during nuclear explosions, is useful for very recent sediments. Microscopic and macroscopic carbonaceous/metallic particles produced by industrial combustion can sometimes be used as stratigraphic markers, as can biostratigraphic markers (e.g., *Ambrosia*, *Plantago*, *Salsola*, *Cannabis*, and other indicators of land clearance or cultivation).

Uranium-lead and argon-argon are two of the more widely used systems for absolute age determination in older, pre-Quaternary rocks. Both generally depend on samples of detrital volcanic materials, generally from ash falls preserved in the sedimentary rock record. Minerals studied include monzanite, zircon, apatite, and uraninite. Both systems are highly accurate, and the two techniques complement each other by providing important cross-checks on dates. U/Pb encompasses two decay systems (uranium-235 and uranium-238), thus providing an internal check on the reliability of results; argon lacks this ability. Rocks amenable to argon dating are somewhat more common, increasing the scope of the technique. There is also the prospect that continuing uncertainties about the precise potassium-40 decay constant will be resolved in the next few years, thereby opening up a further technique for developing accurate chronologies.

Two distinct techniques are applied to the U/Pb system—Super High-Resolution Ion Microprobe (SHRIMP) and Isotope Dilution Mass Spectrometry (ITDMS). SHRIMP studies have the advantage of analyzing extremely small areas on single zircon grains, allowing identification of later overgrowths on the rim of grains, a complication that can reduce the precision of results. SHRIMP studies are particularly powerful for Archean and Proterozoic rocks, although they are also useful through much of the Phanerozoic.

Where dates are not available for every level in a local sedimentary sequence, it is generally possible to develop an age model to estimate the ages of intervening levels, especially when the record is from depositional systems that have generally uniform sedimentation rates (most notably lake and deep marine sediments). Rates of sedimentation are calculated by interpolation between the few dates that are available. This rate then can be used to model the chronology for intervening intervals and, by extrapolation, through deeper parts of the local record if this extends beyond the limits of a single dating technique (e.g., radiocarbon).

Milankovitch periodicities (periodic oscillations induced by changes in orbital parameters occurring at 23 Ka, 41 Ka, 100 Ka, and 400 Ka timescales; see Hays et al., 1976) have been recognized in sedimentation patterns, isotopic ratios, and other features back in time to at least the Miocene (and sporadically to the Triassic). Such variations have been very useful for calibrating many long-term records, and are now routinely employed in paleoclimatology and have been successfully employed in paleoceanography and stratigraphy (e.g., Zachos et al., 2001; House and Gale, 1995; Hinnov, 2000).

Correlation Techniques

Even when absolute ages cannot be determined for fossil deposits, it is often possible to correlate intervals between localities and to establish contemporaneity. When absolute ages are known in one location, correlation allows projection of those dates to a different location. Techniques used in correlation between localities are varied.

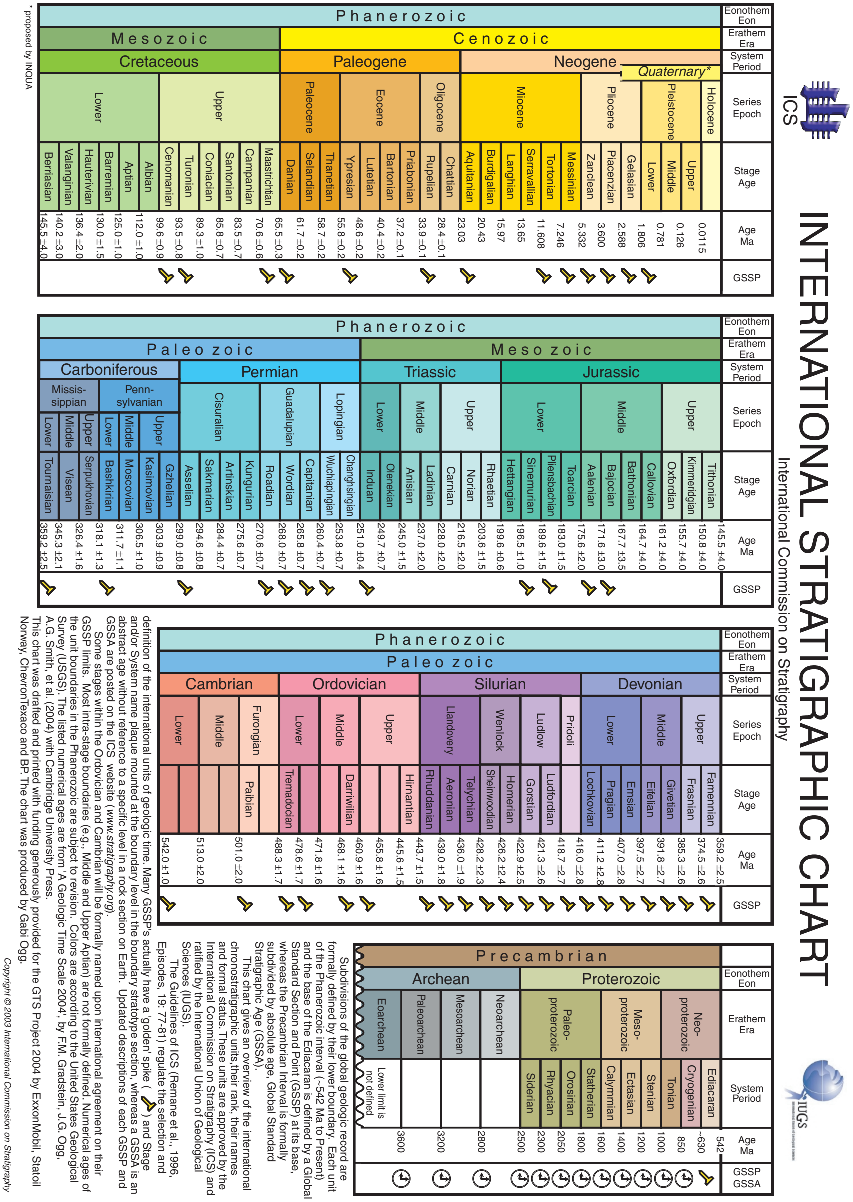
Biostratigraphy relies on broadly distributed, short-ranging species that allow correlation between rock units deposited during the same interval of time. Pelagic marine microfossils and to a lesser extent pollen are the most useful such fossils because of their broad geographic range and rapid evolutionary turnover, but a wide variety of fossils have been used. Biozonation schemes are well established for some fossils (e.g. pollen, foraminifera, radiolarians, nannofossils), in large part because of the immense efforts during the Deep Sea Drilling Project (DSDP, from 1968 to 1983) and Ocean Drilling Program (ODP, from 1985 to 2003). In continental deposits of the Cenozoic and latest Cretaceous, land-mammal ages—intervals of time characterized by distinctive assemblages of mammals (Lindsay, 2003; Woodburne, 2004)—have proven especially useful. Many biozonation schemes are increasingly well integrated with radiometric age determinations of associated rocks and with zonations of relative time based on past reversals in Earth's magnetic field.

More recently, other correlation techniques have been applied: (1) using distinctive isochronous events (isochrons) that occurred at a single, discrete point in time; (2) wiggle matching; and (3) quantitative biostratigraphy. These approaches are especially valuable tools because they permit correlation between marine and terrestrial sequences, resolve the ordering of events, and greatly improve the fidelity of correlation over standard zonations.

Isochrons are a powerful tool because if correctly identified, they represent a single time horizon. Examples include volcanic ash beds and rapid shifts in carbon isotopes that permit correlation over large distances. The boundaries of magnetic reversal intervals can also serve as isochrons; although individual reversals are probably drawn out over hundreds to thousands of years, this fuzziness will in many cases be insignificant given the level of resolution that is otherwise possible. Epiboles—thin, widespread beds of a single species—can similarly serve as time horizons (Brett and Baird, 1997), but are typically restricted to intra-basinal rather than global correlation. In those rare instances where the horizon of interest contains material that can be dated to a high level of resolution (e.g., the volcanic ashes that coincide with the latest Permian mass extinction in south China [Bowring et al., 1998]), the isochrons also provide constraints on the rates of ecological or evolutionary response to environmental change. Long-term records of changing isotopic values (typically of oxygen, carbon, sulfur, or strontium) in stratigraphic sequences have proven to be especially valuable for correlation because many such shifts are global. Variations in isotopic values in a new sequence are matched to corresponding isotopic variations in a well-dated (calibrated) sequence using a procedure informally known as wiggle matching (e.g., Hoek and Bohncke, 2001). In the Quaternary, variation in atmospheric ^{14}C concentrations can be used to increase dating precision in some circumstances. Such wiggle matching, in which a tightly spaced series of AMS ^{14}C ages is plotted against sediment depth, and then matched to the ^{14}C-calendar-year curve, can yield subdecadal precision for *Sphagnum* peats (Kilian et al., 2000; Blaauw et al., 2004). However, this application requires large numbers of AMS dates (10 to 100 or more per core), at high expense. Strontium isotopes in the oceans have varied through time as a result of changes in the composition of continental rocks, the extent of hydrothermal activity, and rates of continental weathering. However, because the change in strontium isotope composition was not monotonic during the Phanerozoic, and isotopic values show some scatter at any particular time, this approach does not yet yield high-resolution dates, and it cannot be used for high-resolution correlation.

Newly developed techniques and applications in geochronology and quantitative biostratigraphy (see Agterberg and Gradstein, 1999; Buck and Millard, 2003; Sadler, 2004) seek to both order and correlate by integrating, sequencing, and calibrating a large number of events. These approaches are based on algorithms that emphasize the temporal ordering of events occurring in different locations, rather than the establishment of simultaneity of events, as with the search for isochrons. Thus, the principal result is an integrated stratigraphy that can then be assigned a temporal framework using high-precision dating. Such ordination techniques have been used with a variety of taxonomic groups in a variety of stratigraphic settings (e.g., Guex, 1991; Alroy, 1994; Sadler and Cooper, 2003). These approaches have the potential to improve temporal resolution to 10,000 to 50,000 years over time spans from 50 million to 100 million years (Sadler, 2004). As biostratigraphic databases increase in number and size, a growing challenge will be the provision of computing facilities to handle these computationally intensive procedures.

The most recent geologic timescale (see Figure 2.3; Gradstein and Ogg, 2004; Gradstein et al., 2004) integrates currently available geochronologic and stratigraphic information and represents perhaps a two-fold increase in refinement over the timescale available 20 years ago. For example, 40-Ka resolution is now available in the Neogene, more than 200 radiometric dates provide calibration points, and error bars are now provided to estimate uncertainties associated with boundaries. Continued refinement of



INTERNATIONAL STRATIGRAPHIC CHART

International Commission on Stratigraphy

ICS

Eonothem Eon	Erathem Era	System Period	Series Epoch	Stage Age	Age Ma	GSSP
Phanerozoic	Cenozoic	Neogene Quaternary*	Holocene		0.0115	
			Pleistocene	Upper	0.126	
				Middle	0.781	
				Lower	1.806	✓
			Pliocene	Gelasian	2.588	✓
				Piacenzian	3.600	✓
				Zanclean	5.332	✓
			Miocene	Messinian	7.246	✓
				Tortonian	11.608	✓
				Serravallian	13.65	
				Langhian	15.97	
				Burdigalian	20.43	
				Aquitanian	23.03	✓
		Paleogene	Oligocene	Chattian	28.4 ±0.1	
				Rupelian	33.9 ±0.1	✓
			Eocene	Priabonian	37.2 ±0.1	
				Bartonian	40.4 ±0.2	
				Lutetian	48.6 ±0.2	
				Ypresian	55.8 ±0.2	✓
			Paleocene	Thanetian	58.7 ±0.2	
				Selandian	61.7 ±0.2	
				Danian	65.5 ±0.3	✓
	Mesozoic	Cretaceous	Upper	Maastrichtian	70.6 ±0.6	✓
				Campanian	83.5 ±0.7	
				Santonian	85.8 ±0.7	
				Coniacian	89.3 ±1.0	
				Turonian	93.5 ±0.8	✓
				Cenomanian	99.6 ±0.9	✓
			Lower	Albian	112.0 ±1.0	
				Aptian	125.0 ±1.0	
				Barremian	130.0 ±1.5	
				Hauterivian	136.4 ±2.0	
				Valanginian	140.2 ±3.0	
				Berriasian	145.5 ±4.0	

*proposed by INQUA

Eonothem Eon	Erathem Era	System Period	Series Epoch	Stage Age	Age Ma	GSSP
					145.5 ±4.0	
Phanerozoic	Meso zoic	Jurassic	Upper	Tithonian	150.8 ±4.0	
				Kimmeridgian	155.7 ±4.0	
				Oxfordian	161.2 ±4.0	
			Middle	Callovian	164.7 ±4.0	
				Bathonian	167.7 ±3.5	
				Bajocian	171.6 ±3.0	✓
				Aalenian	175.6 ±2.0	✓
			Lower	Toarcian	183.0 ±1.5	
				Pliensbachian	189.6 ±1.5	✓
				Sinemurian	196.5 ±1.0	✓
				Hettangian	199.6 ±0.6	
		Triassic	Upper	Rhaetian	203.6 ±1.5	
				Norian	216.5 ±2.0	
				Carnian	228.0 ±2.0	
			Middle	Ladinian	237.0 ±2.0	
				Anisian	245.0 ±1.5	
			Lower	Olenekian	249.7 ±0.7	
				Induan	251.0 ±0.4	✓
	Paleo zoic	Permian	Lopingian	Changhsingian	253.8 ±0.7	
				Wuchiapingian	260.4 ±0.7	✓
			Guadalupian	Capitanian	265.8 ±0.7	✓
				Wordian	268.0 ±0.7	✓
				Roadian	270.6 ±0.7	✓
			Cisuralian	Kungurian	275.6 ±0.7	
				Artinskian	284.4 ±0.7	
				Sakmarian	294.6 ±0.8	
				Asselian	299.0 ±0.8	✓
		Carboniferous	Penn- sylvanian Upper	Gzhelian	303.9 ±0.9	
				Kasimovian	306.5 ±1.0	
			Penn- sylvanian Middle	Moscovian	311.7 ±1.1	
			Penn- sylvanian Lower	Bashkirian	318.1 ±1.3	✓
			Missis- sippian Upper	Serpukhovian	326.4 ±1.6	
			Missis- sippian Middle	Visean	345.3 ±2.1	
			Missis- sippian Lower	Tournaisian	359.2 ±2.5	✓

Eonothem Eon	Erathem Era	System Period	Series Epoch	Stage Age	Age Ma	GSSP
					359.2 ±2.5	
Phanerozoic	Paleo zoic	Devonian	Upper	Famennian	374.5 ±2.6	✓
				Frasnian	385.3 ±2.6	✓
			Middle	Givetian	391.8 ±2.7	✓
				Eifelian	397.5 ±2.7	✓
			Lower	Emsian	407.0 ±2.8	✓
				Pragian	411.2 ±2.8	✓
				Lochkovian	416.0 ±2.8	✓
		Silurian	Pridoli		418.7 ±2.7	✓
			Ludlow	Ludfordian	421.3 ±2.6	✓
				Gorstian	422.9 ±2.5	✓
			Wenlock	Homerian	426.2 ±2.4	✓
				Sheinwoodian	428.2 ±2.3	✓
			Llandovery	Telychian	436.0 ±1.9	✓
				Aeronian	439.0 ±1.8	✓
				Rhuddanian	443.7 ±1.5	✓
		Ordovician	Upper	Hirnantian	445.6 ±1.5	
					455.8 ±1.6	
					460.9 ±1.6	✓
			Middle	Darriwilian	468.1 ±1.6	✓
					471.8 ±1.6	
			Lower		478.6 ±1.7	✓
				Tremadocian	488.3 ±1.7	✓
		Cambrian	Furongian			
				Paibian	501.0 ±2.0	✓
			Middle			
					513.0 ±2.0	
			Lower			
					542.0 ±1.0	✓

Eonothem Eon	Erathem Era	System Period	Age Ma	GSSP GSSA
			542	
Precambrian Proterozoic	Neo- proterozoic	Ediacaran	~630	✓
		Cryogenian	850	◷
		Tonian	1000	◷
	Meso- proterozoic	Stenian	1200	◷
		Ectasian	1400	◷
		Calymmian	1600	◷
	Paleo- proterozoic	Statherian	1800	◷
		Orosirian	2050	◷
		Rhyacian	2300	◷
		Siderian	2500	◷
Archean	Neoarchean		2800	◷
	Mesoarchean		3200	◷
	Paleoarchean		3600	◷
	Eoarchean	Lower limit is not defined		

Subdivisions of the global geologic record are formally defined by their lower boundary. Each unit of the Phanerozoic interval (~542 Ma to Present) and the base of the Ediacaran is defined by a Global Standard Section and Point (GSSP) at its base, whereas the Precambrian Interval is formally subdivided by absolute age, Global Standard Stratigraphic Age (GSSA).

This chart gives an overview of the international chronostratigraphic units,their rank, their names and formal status. These units are approved by the International Commission on Stratigraphy (ICS) and ratified by the International Union of Geological Sciences (IUGS).

The Guidelines of ICS (Remane et al., 1996, Episodes, 19: 77-81) regulate the selection and definition of the international units of geologic time. Many GSSP's actually have a 'golden' spike (✓) and Stage and/or System name plaque mounted at the boundary level in the boundary stratotype section, whereas a GSSA is an abstract age without reference to a specific level in a rock section on Earth. Updated descriptions of each GSSP and GSSA are posted on the ICS website (*www.stratigraphy.org*).

Some stages within the Ordovician and Cambrian will be formally named upon international agreement on their GSSP limits. Most intra-stage boundaries (e.g., Middle and Upper Aptian) are not formally defined. Numerical ages of the unit boundaries in the Phanerozoic are subject to revision. Colors are according to the United States Geological Survey (USGS). The listed numerical ages are from 'A Geologic Time Scale 2004', by F.M. Gradstein, J.G. Ogg, A.G. Smith, et al. (2004) with Cambridge University Press.

This chart was drafted and printed with funding generously provided for the GTS Project 2004 by ExxonMobil, Statoil Norway, ChevronTexaco and BP. The chart was produced by Gabi Ogg.

IUGS

FIGURE 2.3 The geologic timescale of Gradstein and Ogg (2004), with numerical ages from Gradstein et al. (2004). The "golden spikes" represent stratigraphic unit boundaries that are located by a particular point in an actual stratigraphic section. SOURCE: International Commission on Stratigraphy; used with permission.

the geologic timescale is now being systematically pursued[3] and is likely to provide even greater precision and accuracy for future studies of the geologic record of ecological dynamics.

IMPACT OF DATABASE TECHNOLOGIES AND SYNTHETIC STUDIES

The development of databases and database technologies during the past 20 years has facilitated analyses and syntheses at broad geographic and temporal scales, stimulated broad, community-based research projects, and enabled cross-disciplinary work. The addition of web-based technologies for rapid data transfer and communication has greatly improved scientific communication and dramatically improved the dissemination of research results.

Databases and associated research projects abound in both the biological and geological sciences. Examples in the biological sciences most relevant to this report are databases on the distribution of plants (e.g., SALVIAS—Spatial Analysis of Local Vegetation Inventories Across Scales[4]), fish (FishBase[5]), phylogenetic analyses (e.g., Tree of Life[6]), and many others available through links from the Natural Science Collections Alliance.[7] The importance of the analysis and synthesis of wide-ranging datasets and databases to the ecological and evolutionary sciences has been recognized by the establishment of the NSF-supported National Center for Ecological Analysis and Synthesis (NCEAS—see Chapter 4) and the recent NSF funding of a Center for Synthesis in Biological Evolution (CSBE). In the geological sciences most relevant to this report, examples include databases for paleoclimatic reconstructions (National Oceanic and Atmospheric Administration's [NOAA] World Data Center for Paleoclimatology[8]), the JANUS[9] database of results from the Ocean Drilling Program (see Chapter 4), resources for paleogeographic reconstructions (e.g., Paleogeographic Atlas Project[10] and PALEOMAP project[11]), data on the diversity of fossils through geologic time (Paleobiology Database[12]—

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[3] See http://www.stratigraphy.org.

[4] See http://eeb37.biosci.arizona.edu/~salvias/mission.html.

[5] See http://www.fishbase.org/home.htm.

[6] See http://www.tolweb.org/tree/phylogeny.html.

[7] See http://www.nscalliance.org/bioinformatics/index.asp.

[8] See http://www.ngdc.noaa.gov/paleo/paleo.html.

[9] See http://www-odp.tamu.edu/database/.

[10] See http://pgap.uchicago.edu/PGAPhome.html.

[11] See http://www.scotese.com/.

[12] See http://paleodb.org.

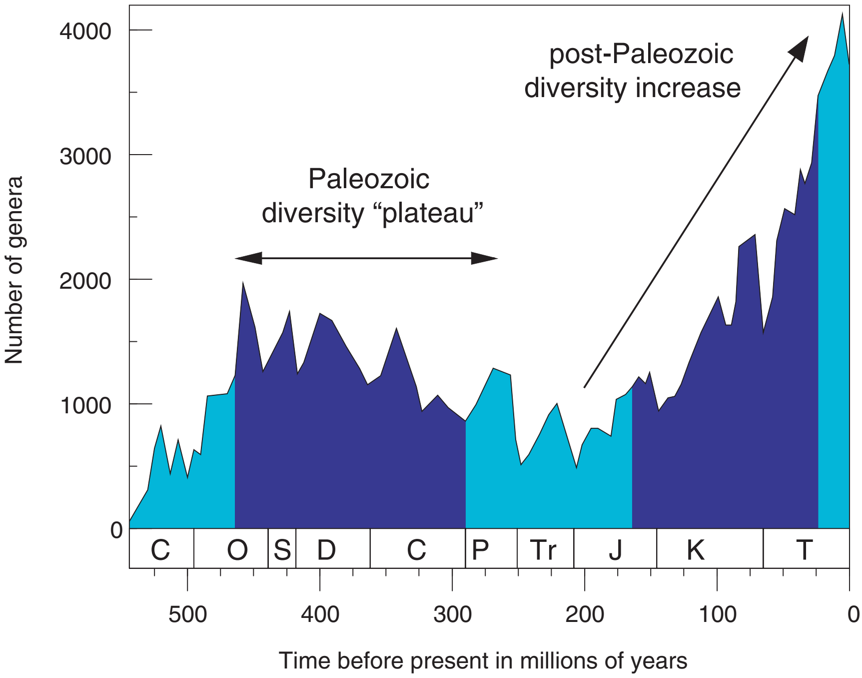

FIGURE 2.4 The "Sepkoski curve" showing numbers of genera of marine animal fossils through Phanerozoic time. The blue portions of the curve indicate time intervals chosen for more detailed study of diversity change by Alroy et al. (2001). SOURCE: Newman (2001); used with permission.

see Chapter 4), information on the stratigraphic distribution of fossils (e.g., NEPTUNE[13] and Paleostrat[14]), and many more specialized databases (e.g., Panama Paleontology Project[15] and Neogene fossil mammals of the Old World[16]).

There is probably no better example of how data compilations and syntheses can shape entire disciplines than the graphs illustrating the diversity of families and genera of marine fossils through geologic time (e.g., see Figure 2.4). Laboriously assembled from the print literature by Sepkoski (1982, 1993, 2002), these simple figures summarized the state of

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[13] See http://services.chronos.org/databases/neptune/index.html.

[14] See http://www.paleostrat.org/.

[15] See http://www.fiu.edu/~collinsl/pppimagemapnew.htm.

[16] See http://www.helsinki.fi/science/now/.

knowledge of diversity change though geologic time, and in many regards they have proven robust to taxonomic revision and phylogenetic approaches (e.g., Sepkoski and Kendrick, 1993; Robeck et al., 2000; Adrain and Westrop, 2000). They have attracted broad attention in the biological sciences because of the near-plateau in diversity over several hundred million years in the Paleozoic, the abrupt extinctions and rapid rebounds that punctuate the time series, and the dramatic post-Paleozoic diversity increase to the present day. Interpretation of all these features remains controversial, and countless research projects have been engendered by new approaches to the biological and geological factors underlying the entire curve and its many taxonomic and ecologic components (e.g., Sepkoski, 1984, 1996; Raup and Boyajian, 1988; Valentine et al., 1991; Eble, 1999; Bambach et al., 2002; Alroy et al., 2001; Foote, 2003; Jablonski et al., 2003). Sepkoski's efforts helped launch a new, integrative, and synthetic style of research in paleontology, and were instrumental in the formation of the community-based Paleobiology Database, which has initiated a next-generation compilation using spatially explicit occurrence data.

SUMMARY AND OUTLOOK—STRATEGIES FOR GEOHISTORICAL ANALYSIS

Geohistorical data are essential for answering many kinds of questions, especially when the aims are either to discriminate between anthropogenic and non-anthropogenic effects or to understand phenomena that cycle or emerge over periods greater than a few years. Such discrimination is extremely difficult without recourse to historic records in the broadest sense—pre-scientific documents, archaeological materials, natural sedimentary records. Therefore, a rigorous strategy for evaluating ecological dynamics using geohistorical records—and for integrating geological and biological methods and insights—is essential.

Intensified research on these issues over the last 15-20 years now enables the exploitation of uniquely valuable data lodged in geohistorical records (summarized from above):

- Important environments (notably lakes, peatlands, estuaries, and deep ocean basins) typically yield high-resolution time series data ideal for tracking ecosystem change. Valuable and unique data also can be acquired even from isolated before-and-after sample sets, and the time-averaging that characterizes many geological samples of past ecosystems is advantageous for statistical analyses of broad-scale changes and patterns.
- Newly developed geological and, especially, geochemical methods provide an increasing number of proxy indicators of environmental change. Thus, changes in the composition, relative abundance, distribu-

tion, and diversity of fossil biotas can now be used as measures of the biotic response to environmental change, rather than indicators of both the change and the response.

- An increasing number of ecologically valuable metrics can now be evaluated confidently, either using the conventional fossil record of preserved individuals, or using various chemical proxies of former biological populations (biomarkers, isotopic signatures).
- Relative and absolute age dating of geologic materials and time series has improved greatly in the last 20 years, and has crossed a key threshold with respect to analyzing ecological dynamics. Resolution now matches or exceeds what would be possible using conventional biostratigraphic methods, liberating geohistorical analysis of ecological dynamics from pitfalls of circularity in age and rate determinations.
- New database and web technologies have stimulated community-based efforts to assemble and analyze large amounts of ecological, paleoecological, and evolutionary data relevant to understanding the geologic record of ecological dynamics. Such efforts at synthesis are essential partners in efforts to acquire new data.

The geologic column provides a wealth of geohistorical records that are ready to yield important data on ecological dynamics. It is not the record that is inadequate but rather the availability of resources to extract and analyze the record. Using geohistorical records to their fullest potential will require an effort focused on the biological analysis of groups known to have reasonable fossil records, and on the development of proxy methods for groups of great biological interest but poor fossilization potential. Biologists and earth scientists, working together, will need to frame research questions so that the answers take maximum advantage of the great potential of geohistorical analysis to provide major insights.

3

Research Opportunities

Six major research initiatives for the environmental sciences have been identified in recent NRC reports (NRC, 2001c, 2004), the first four of which cannot be met without using the geologic record of ecological dynamics:

1. Biological diversity
2. Biogeochemistry
3. Ecological impacts of climate variability
4. Habitat alteration
5. Invasive species
6. Infectious diseases

The current state of the biosphere is a consequence of both present day processes and prior conditions. A full understanding of current patterns and processes, therefore, requires geohistorical analysis to supplement knowledge based on shorter-term observations, experiments, and modeling. The geological record provides the rich source of information that is essential for developing an understanding of the origin and controls of biological diversity, the controls and dynamics of biogeochemical cycling, the ecological impacts of climate change and variability, and the extent and consequences of habitat alteration. It also has the potential to provide important insights into the dynamics of invasive species and the environmental context of infectious diseases.

There are three general areas of environmental science research in which addressing the historical antecedents of present day patterns and processes will be especially important. Each takes advantage of the rich and detailed geological record of how past ecosystems responded to environmental change at a variety of timescales. Together they provide the basic knowledge needed to predict and manage the response of the biosphere to likely change in the future.

1. **The Geologic Record as an Ecological Laboratory.** The geological record comprises an immense array of natural laboratories for studying how ecological systems operate under diverse conditions and at broad timescales. Using these laboratories to answer fundamental questions about biological diversity and biogeochemical processes is both possible and urgently needed. Ecological and evolutionary processes at timescales beyond direct human observation have influenced biodiversity and biogeochemistry at all scales (see examples described below). Currently, most ecological theory is based on short-term observations and mechanics, which are then extrapolated to longer timescales. Ecological studies using geohistorical records are needed to characterize ecological processes that occur over longer timescales; identify patterns and mechanisms that are masked by the short timespans of direct observation; and recognize those aspects of modern ecological systems that are contingent on past events. The geologic record also contains a series of "alternative worlds" suitable for testing the universality of ecological theory.

2. **Ecological Responses to Past Climate Change.** The geologic record contains information on how ecological systems—from individual species to biomes—have responded to a wide array of climate changes in the past. Just as paleoclimatological studies have revealed sensitivities and vulnerabilities in the global climate system that could not have been identified from analysis of modern systems alone (NRC, 2002a), so too are paleoecological studies revealing ecological responses to past climate changes that could not have been predicted solely from modern ecological investigations and theory (see examples described below). Studies that link paleobiological and paleoclimatic records are urgently needed to assess the ecological consequences of ongoing and future climate changes. The past two centuries have experienced only a fraction of the potential variability within the global climate system. Therefore, direct observations of biotic responses to climate variability and change provide only a limited view of the full range of possible changes and responses. Parallel to the call for "extending the record of [climate] observations" using the geological record (NRC, 2001c), a concerted effort is needed to use geohistorical records to gather critical information on how ecosystems will respond to future change. Specific time intervals can also serve as model systems for understanding effects of climate changes of particular magnitude, rate, extent, and duration.

3. Ecological Legacies of Societal Activities. The geologic record contains a rich store of information on ecological changes occurring during periods of past societal activity. The relative timing and nature of these correlations provide abundant material for evaluating direct and indirect causation—such records are important for gauging the extent to which our modern world has already been altered by human activities (see examples described below). They are also needed to predict effects of future societal modification of habitats and biological systems themselves. Determining whether particular ecological phenomena are induced by ongoing societal activity, comprise legacies of past human activities, or would have occurred in the absence of societal activity is a vital first step toward appropriate management. Determining how societal activities have shaped modern ecological systems at local, regional, and global scales is essential for understanding the world we have inherited, for assessing ecological theory developed within altered ecosystems, and for predicting how ecosystems will change in the face of ongoing and future societal activities. It is also necessary for determining baselines of natural ecological variability against which human activities and management decisions can be evaluated.

THE GEOLOGIC RECORD AS AN ECOLOGICAL LABORATORY

Ecological studies have tended to focus on patterns and processes that are observable on the timescales of direct human experience—weeks to decades, and occasionally centuries. Although ecological succession, one of the core concepts of ecology, is concerned with changes occurring over timescales of decades to millennia (Cowles, 1899, 1901; Clements, 1916; Glenn-Lewin et al., 1992), successional studies have only rarely taken advantage of geohistorical records of actual change at individual sites. Instead, ecologists have relied on space-for-time substitution (Pickett, 1989) or direct observations of successional change at shorter timescales. Chronosequence studies have pitfalls, however (S.T. Jackson et al., 1988; Davis, 1989; Fastie, 1996), and the oldest "permanent plots" where long-term changes can be monitored systematically date only to the mid-19th century (Pickrell, 2001). Most of the remaining conceptual and empirical core of ecology, whether at the organismal, population, community, ecosystem, or global level, tends to be focused on the "here and now," with only nominal acknowledgment of longer-term patterns and dynamics. Thus, we are building our understanding of ecology on a very small sample, comprising an ultra-thin and perhaps unrepresentative slice of the history of the biosphere.

Ecologists now recognize that many important ecological processes operate at timescales far beyond human life spans and that in many cases we cannot simply scale up in a linear fashion from studies spanning a few years to phenomena spanning thousands to millions of years (see Box 3.1). Many recent trends in ecology are concerned with the search for general rules that govern ecological systems, for example, in the areas of community assembly (Weiher and Keddy, 1999), biodiversity dynamics (Rosenzweig, 1995; Hubbell, 2001), macroecology (Brown, 1995; Maurer, 1999), scaling (Brown and West, 2000; Enquist et al., 2003; Smith et al., 2004), biodiversity/productivity relationships (Loreau et al., 2001; Tilman et al., 2001), global biogeochemical cycles (Schlesinger, 1997), trophic interactions (Williams and Martinez, 2000; Brose et al., 2004), and ecological stoichiometry (Sterner and Elser, 2002). Rigorous and definitive testing of general theory of this kind in ecology can be extraordinarily difficult but the past, as represented in the fossil record, provides a potentially powerful means for assessing and refining such ecological hypotheses. So far, the considerable potential of the geologic record has not been fully exploited by ecologists. Furthermore, although ecological rules identified from modern observation and theory are generally treated as universal, they may be contingent on the modern environment and biota. They may have relict, non-equilibrium features from both natural events and human activities of the past. Subjecting these hypothesized rules to rigorous tests involving both “natural,” pre-human conditions as well as various “alternative worlds” of the recent and deep past will determine the extent to which ecological laws are analogous to physical laws, or whether they evolve as the biosphere evolves. Observations in deep time can help determine whether deep structure and principles exist in ecological systems.

Opportunities for Scientific Advance

Major opportunities exist for increased interactions between ecology and the geosciences, particularly paleoecology and paleobiology. Future research efforts should be particularly focused on studies and syntheses that have the capacity for:

1. testing fundamental ecological theory and principles at timescales greater than the past two centuries;
2. identifying important ecological patterns and processes that emerge only at timescales beyond those of direct human observation; and
3. determining whether the basic laws and principles identified in ecology today are universal and thus applicable throughout geologic time, or are contingent on the modern biosphere, and thus evolve through time as environments and biota change. If the latter, we need to know whether such evolution proceeds in a predictable and systematic fashion, and which major ecological concepts are universal and which are subject to change.

BOX 3.1
Fast and Slow Processes in Ecology

Ecological processes occur over a vast array of temporal scales, comprising at least 16 orders of magnitude. For example, a phosphate ion released into solution in the photic zone of the ocean may be absorbed by phytoplankton in less than a second (10^{-8} year), while an organically bound phosphate incorporated into ocean sediments may be locked up for 10^8 years or more and then released only after subduction, metamorphism, uplift, and ultimate release by weathering (Ruttenberg, 2004). The mean generation time of a single-celled prokaryote may be less than a day, while that of many tree species is more than a century. With a constant environment, interspecific competition may take days, years, or centuries to reach equilibrium, respectively, in communities of microbes, intertidal mollusks, or forest trees.

Ecologists are increasingly recognizing that ecological systems are influenced by both “fast” and “slow” processes, and that many ecological patterns are dictated by interactions between processes operating at very different rates (Carpenter and Turner, 2001). Developing theoretical, observational, and experimental frameworks for understanding these interactions is a major challenge for ecology and related sciences. In practice, ecologists have dealt with this problem by focusing on particular timescales (usually short), treating slow processes as constants (parameters), and calculating equilibrium values for the faster variables (Carpenter and Turner, 2001). However, this approach has limitations. Because of disturbances, climate variability, and other factors, ecosystems are in a state of continual flux. Although ecologists have addressed this problem by incorporating random fluctuations or disturbances into their models, such variations may not be simple random variation about a constant mean. For example, climate variability is non-stationary at timescales from interannual to multimillennial and beyond. Disturbances (e.g., fire, windstorms, hurricanes, flood and wave events) are often tied to climate, and consequently disturbance frequencies and amplitudes cannot necessarily be modeled as random variables, even at routine ecological timescales of 10^1-10^3 years. Some events may be so infrequent (e.g., impacts, volcanic eruptions, methane releases from the seafloor) or slow-acting (e.g., sea-level change) that observation and experimentation are essentially out of the question.

Many ecological processes, particularly biogeochemical, biogeographic, and evolutionary processes, occur over even longer timescales, ranging from 10^3-10^8 years (i.e., at geologic timescales). Such slow processes can be accelerated, decelerated, reversed, shunted to alternative pathways, or (in the case of phyletic evolution) terminated, as a consequence of climatic, tectonic, macroevolutionary, and other events. The controls on slow processes and the long-term effects of rare events can be understood only by using the geologic record.

These issues cut across a wide range of timescales, ranging from recent millennia to the entire record of life on Earth. They are vitally important to appropriate application of ecological knowledge and theory to conservation biology, biosphere maintenance, and global change biology. As we enter a period of potentially rapid environmental change, with extensive biological invasions and impoverishment of biodiversity, we need to know which ecological rules will apply and which are likely to be altered.

A critical goal will be to improve dialogue between paleobiologists and ecologists, particularly in the realm of theory and concepts. But this must be accompanied by integrated studies aimed at addressing the central questions of ecology across a range of timescales. For example, use of the geologic record is vital to addressing national ecological research priorities in the areas of biodiversity and biogeochemical cycles. It can also provide important perspectives on infectious diseases and invasive species. One major goal is to integrate paleobiological studies with ecological experimentation and modeling.

Both communities will benefit from increased interactions. A danger in the traditional ecological focus on the "here and now" of experiments on existing systems and environments is that the role of historical contingency and long-term processes can be overlooked. On the other hand, paleoecologists may discount the implications of short-term ecological experiments simply because short-term events are often difficult to resolve in the geologic record. Greater collaboration and coordination between these disciplines can help determine where observable short-term processes can scale up to explain long-term patterns, suggest experimental tests of paleoecologically generated hypotheses, and identify the ecological consequences of past environmental events.

Biodiversity

While understanding patterns of extant biological diversity is one of the central themes of ecology, the factors and processes that govern it are still inadequately understood. Consequences of biodiversity loss are not fully known but may be substantial, ranging from elimination of potentially useful species to loss of ecosystem services and even collapse of ecosystem function. The geologic record provides information on speciation and extinction rates as well as biogeographic changes that regulate biodiversity. Resolving one of the *Grand Challenges in Environmental Sciences* (NRC, 2001c; p. 26)—"Produce a quantitative, process-based theory of biological diversity at the largest possible variety of spatial and temporal scales"—requires use of the geologic record.

The Evolutionary Dynamics of Biodiversity. Biodiversity is shaped by biogeographic and evolutionary dynamics that occur over thousands to millions of years. Although the formation, invasion, migration, substitution, and even extinction of species can potentially be inferred from phylogenetic structure, the fossil record is a direct and rich source of data needed to discover the biological principles underlying the origin, maintenance, collapse, recovery, and extinction of species. Paleobiological time series leading to the present day, together with time series embedded entirely in the geologic record provide opportunities to identify and test fundamental ecological principles underlying biodiversity (see Box 3.2). Isolated but well-situated snapshots and brief time exposures in the geologic record provide additional opportunities.

Virtually all the key variables in conventional "macroecological" analysis of species assemblages in the present day—namely, species composition, richness, relative abundance, geographic range, body size and many life history factors, growth or metabolic rates, environmental tolerance, trophic or functional group, speciation and extinction rate—are measurable in the fossil record (see Chapter 2). Moreover, some kinds of information can only be determined using paleobiological data. For example, although net diversification rates can be inferred from species richness in clades and communities without a long historic record, the more useful raw speciation and extinction rates can only be determined from the fossil record. Only data on raw rates can reveal whether the striking variation in richness observed among ecological communities reflects differences in the production of species, in rates of species loss, or some combination of the two. These are qualitatively different dynamics, and call for completely different management strategies. These issues can be addressed by studies in deep time (e.g., Valentine, 1990; Sepkoski, 1998; Jablonski and Roy, 2003) as well as in the late Quaternary (e.g., Colinvaux, 1997; Hooghiemstra, 1997; Willis and Niklas, 2004).

Ecological theory and experimentation has led to the recognition that certain species are "community keystones," whose extinction might have profound and long-lasting effects (Paine, 1966; Chase and Leibold, 2003). However, other studies—including a number of paleoecological studies—suggest that communities can retain fundamental structure and function despite continual turnover in species composition driven by routine geographic range shifts and extinctions (Valentine and Jablonski, 1993; Holland and Patzkowsky, 2004; S.T. Jackson and Overpeck, 2000; Webb et al., 2004). This suggests that there can be considerable interchangeability among species within ecological and functional categories. Are these apparently conflicting perspectives an artifact of scale? Paleoecological studies can take advantage of natural experiments in which community

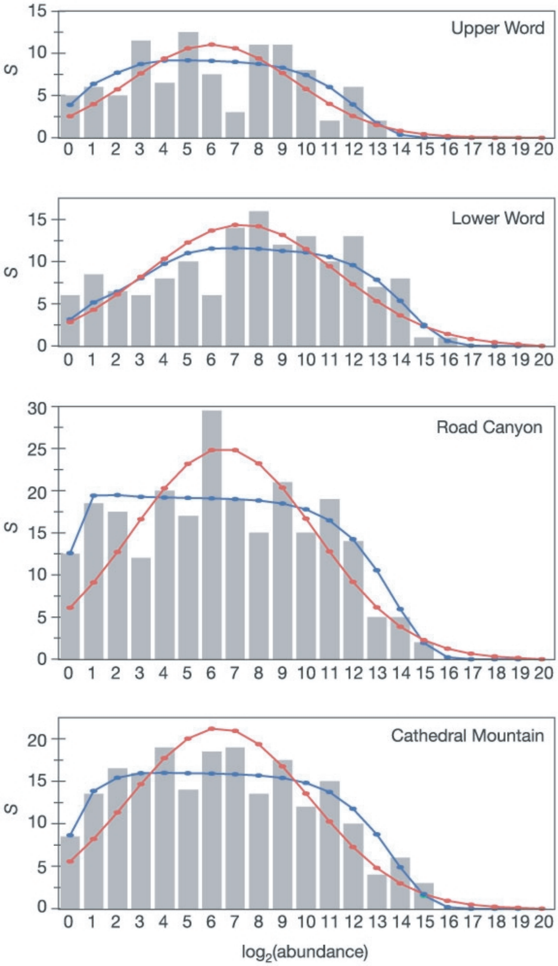
BOX 3.2
Changing Community Structure in Permian Brachiopods

Paleobiological data can be used to provide tests of fundamental ecological theory. Permian rocks in west Texas, deposited 275-265 Ma ago, contain well-preserved and well-studied assemblages of brachiopods. More than 850,000 specimens are now housed at the National Museum of Natural History in Washington, D.C. Olszewski and Erwin (2004) tallied these specimens in order to determine the species abundance distributions and how these distributions changed through the 10-million year interval. Maximum likelihood fits to the species abundance curves (shown below) were closer to the zero-sum multinomial distribution predicted by Hubbell's (2001) neutral model of ecological communities than to the classic log-normal distribution.

The shapes of the distributions of the lower two intervals differ significantly from those of the upper two intervals, and these differences are attributed to restrictions in population size, decreased isolation, and decreased chances of immigration resulting from lower sea levels in the upper two intervals. Accordingly, the geologic record of Permian fossils in this area preserves the results of a natural experiment on how environmental change affects ecological community structure over long time periods.

Species abundance distributions of brachiopods from Permian rocks of west Texas. Youngest time interval (Upper Word) on top, oldest interval (Cathedral Mountain) on bottom; S = number of species. The red line is maximum likelihood fit to log-normal distribution; blue line is maximum likelihood fit to zero-sum multinomial distribution. SOURCE: Olszewski and Erwin (2004); used with permission.

composition has changed with range shift or extirpation to assess this question. Similarly, little is known about the timescales and patterns of survival in remnant populations and the consequences for community structure. Is richness conserved? Do new species substitute for lost ones? Are functional groups thinned proportionally? Understanding these dynamics in terms of general principles, and at the timescales at which



species migrations and community turnover actually occur, will contribute significantly to our understanding of individual species behavior and the net outcomes for biodiversity and community structure in habitat fragments—an understanding that has obvious practical implications for management of natural systems in the face of human activities and impacts.

One reason why migration has emerged as such an important species response to environmental change is that species often exhibit evolutionary stasis, and are insufficiently malleable in an evolutionary sense to adapt to radically altered conditions. The fossil record clearly indicates pervasive evolutionary stasis in diverse groups in the face of substantial environmental change (Huntley et al., 1989; Coope 1995; J.B.C. Jackson and Cheetham, 1999; J.B.C. Jackson and Johnson, 2000). However, evolutionary responses have been documented in several cases (e.g., Smith et al., 1995; Rousseau, 1997; Benton and Pearson, 2001). What permits or drives some species to depart from stasis and thus adjust to changing physical and biological environments? Do the evolutionary responses observed represent expansion into new niche space or redistribution of existing variation (Huntley, 1999; S.T. Jackson and Overpeck, 2000)? These questions are particularly pressing in the tropics, where many species are linked in close ecological partnerships. What intrinsic biological or environmental factors promote the coevolution of "mutualists"[1] or of producers and consumers? Paleoecological records suggest that coevolutionary adjustments may have been very rapid, given the rapid pace of Quaternary climatic change and community response documented in the tropics, but it is also possible that the coevolutionary associations observed today comprise a limited subset—those where the partners happened to migrate together over repeated glacial/interglacial cycles. These alternative explanations suggest radically different potentials for the regeneration capacity of coevolutionary partnerships that have been disrupted. This can only be tested—using the fossil record—by determining the antiquity of such partnerships. Although molecular data can provide information on the age of taxa, their mutual readjustments can only be documented using morphological and paleobiogeographic data from geohistorical records (e.g., Labandeira, 2002).

Rules of Extinction. When the rate or magnitude of the environmental change exceeds the ability of a species to adapt or migrate, the result is local, regional, or global extinction. Because global extinction is irreversible and because even local extinction can remove key genetic resources and severely perturb communities, one fundamental aim of conservation is to minimize extinction or at least to minimize its effects. Consequently, a high priority for managing the present day biota is a set

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[1] Mutualists are organisms or species that are involved in "mutualistic" interspecific relationships in which both species benefit. Examples are plants and pollinators (plants feed insects in exchange for pollen transport), and mycorrhizae (fungi provide hard-to-get dissolved minerals in exchange for sugars from plant root).

of predictive rules for species extinction and survival—both the overall rates (what proportion lost?) as well as patterns of selectivity (which species or kinds of species, which habitats, which precursor states?). In a given situation, these rules probably vary according to the magnitude and kind of disturbance, the intrinsic characteristics of the species involved (e.g., reproductive rates, geographic range sizes, niche parameters), or the original richness, spatial extent, and productivity of the community (i.e., the ecological context). The fossil record affords an opportunity to test these factors across a range of extinction intensities and drivers. Some commonalities are beginning to emerge among taxa and across time intervals (e.g., the effect of geographic range, body size, relative abundance; see Jablonski, 1995; McKinney, 1997; Purvis et al., 2000; Manne and Pimm, 2001; Harcourt et al., 2002), but more comparative work is needed to expand both taxonomic and ecological coverage, and to test whether survivorship patterns change qualitatively with disturbance intensity or type. This is an area where modeling efforts and simulations, through collaborations between paleontologists and ecologists could be particularly productive. Such models could act as a spur and guide for paleontological field work to iteratively refine the models. Determining the characteristics of demonstrably resilient systems or groups, particularly in relation to biotic or environmental crises, will be critical for effective management of diversity as a whole. Resilient groups may not have characteristics considered desirable from a human perspective.

Community Structure: Unity, Anarchy, or Both? Geologic records of different ecosystems and time periods often yield contrasting views of community unity and integrity. Paleobiological records indicate that terrestrial and temperate marine communities did not migrate as cohesive, integrated units in response to Quaternary environmental changes. Instead, species shifted their geographic ranges individualistically, producing species associations that do not occur today (Box 3.3). This fluid pattern of community assembly and disassembly was unexpected by ecologists, and speaks to fundamental questions of the inertia of community structure, the strength and particularity of biotic interactions among species, and the likely consequences of species extinctions and invasions for community resilience. Some systems, however, such as tropical coral reefs, show greater stability of community composition during the Quaternary (J.B.C. Jackson, 1995; Pandolfi, 1999; Pandolfi and Jackson, 2001), and many pre-Quaternary paleobiological studies suggest long intervals of community stability (Brett et al., 1996; Ivany, 1996; Schopf and Ivany, 1998). Assessment of the origin of this variation—whether it stems from the nature of the physical environment (S.T. Jackson, 2000; S.T. Jackson and Overpeck, 2000), differential resilience of communities to

BOX 3.3
Singular Communities in the Recent Past

One of the most important insights to emerge from the late Quaternary fossil record is the existence in the recent past of biotic assemblages that have no modern counterparts. For example, sediments of Cheek Bend Cave in Tennessee that date to 17,500-17,000 years ago contain bones of yellow-cheeked voles, a tundra/boreal-forest rodent of northwest Canada and central Alaska, and plains pocket gophers, a grassland rodent of the central United States. Today, populations of these species do not occur within 1,000 km of each other. High-precision dating of the bones confirms that these species lived near the cave at the same time during the last glacial/interglacial transition (Stafford et al., 1999).

Vertebrate faunal records from Cheek Bend Cave and numerous other sites contain diverse examples of communities with no modern analogs, and similarly singular assemblages have been documented for terrestrial insects (Coope, 1994) and marine mollusks (Roy et al., 1995). Similar results come from studies of past terrestrial vegetation; pollen and plant macrofossil assemblages with no modern analogs are well documented in a variety of continental settings (S.T. Jackson and Williams, 2004). For example, vegetation of the upper Midwest was occupied during the last deglaciation by forests dominated by boreal conifers (spruce) and cool-temperate hardwoods (elm, oak, ash, hornbeam) (Williams et al., 2001). Such forests do not occur anywhere in North America today.

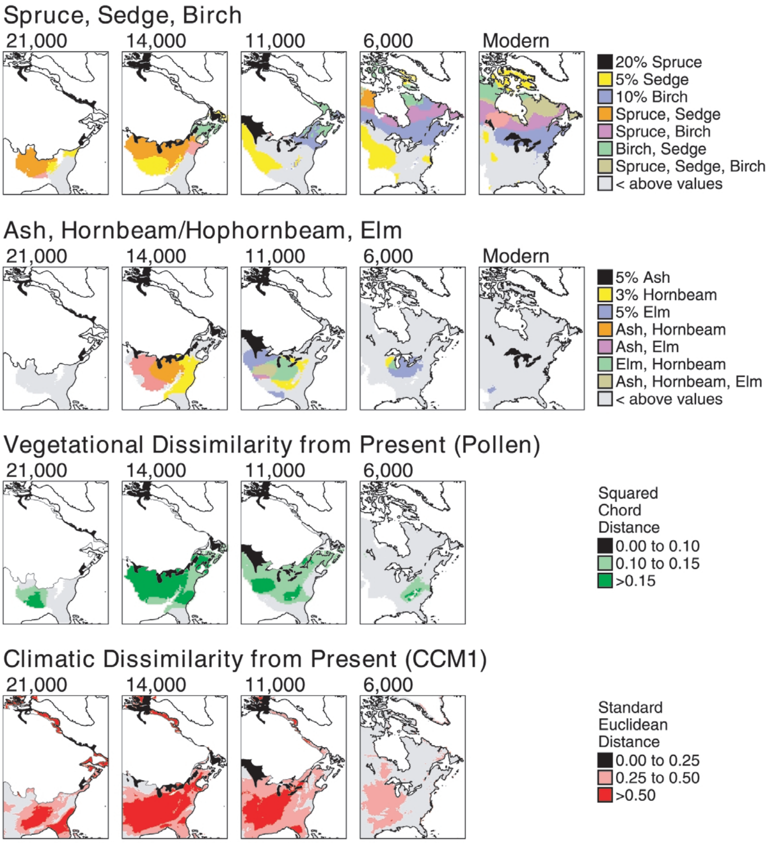
A critical question for both ecology and conservation biology is how these singular communities arise. Their existence in the past indicates that animal and plant species have responded individualistically to environmental changes of the late Quaternary, and that communities may be ephemeral at timescales beyond a few thousand years. Did they develop because species range adjustments through dispersal and colonization could not keep pace with the rate of environmental change? Or did they arise as a result of unique combinations of environmental variables? Paleoecologists have pursued these questions vigorously during the past two decades. A recent study by Williams et al. (2001) comparing fossil pollen data with paleoclimate simulations has supported the latter hypothesis (see figure below). Regions and time periods characterized by pollen assemblages lacking modern analogs closely match those with simulated climate regimes lacking modern analogs. Simulated climates of the late glacial period (18,000-10,000 years ago) were drier and had greater temperature seasonality than modern climates of the region.

From this perspective, the modern suite of species associations is not fixed, and novel associations may be expected to arise if future climatic conditions move outside the modern range. Recent climatic trends and climate simulations all suggest that 21st century climates may have smaller diurnal and annual seasonal ranges, and the synoptic pattern of precipitation intensity and variability is likely to change (Easterling et al., 1997; IPCC, 2001; S.T. Jackson and Williams, 2004). An important question is whether we have sufficient ecological knowledge to predict which communities will be most sensitive to these changes, and which sorts of new communities will arise to replace them. Paleoecological studies can play two roles here. First, examination of the history of particular communities can indicate which communities have been most sensitive to climate changes of the recent past. Second, the no-analog communities of the past can serve as a laboratory for testing models relating modern biogeographic distributions and community composition to climate. Numerous opportunities exist for collaboration among ecologists, paleoecologists, paleoclimatologists, and modelers to determine whether past community composition can be predicted accurately from modern ecological observations and paleoclimate information. Such collaborations will help assess whether we have adequate knowledge to predict biotic responses to ongoing and future climate change.

Transient effects are likely to dominate in the near term, and another pressing question is how rapidly communities will respond to climate change in the coming decades. Again, the past may serve as a guide. Analyses of high-resolution lacustrine records suggest that plant communities responded to past abrupt climate changes with lag times less than a century (Birks and Ammann, 2000; Tinner and Lotter, 2001; Williams et al., 2002) and that these responses were spatially complex (Shuman et al., 2002a). Response times of a few decades are short from a geological perspective, but highly significant on human and ecological timescales. Based on these findings, we can expect disruption of existing communities and emergence of new combinations of species associations in the near future in response to climate change, although other anthropogenic effects (land use, invasive species) will also contribute. More broadly, these studies underscore the value of Quaternary research for studying linkages between biological and physical systems at timescales intermediate between the human life span and the deep-time perspectives afforded by longer-term geohistorical records (S.T. Jackson, 2000).

continued

BOX 3.3 Continued



Rows 1 and 2 are plant associations over time for (row 1) spruce, sedge, and birch and (row 2) ash, hornbeam/hophornbeam, and elm. Each plant taxon is represented by a single pollen percentage contour, and each possible combination of plant taxa is represented by a different color. Color combinations present in the ancient time periods but absent in the modern maps mark the distribution of no-analog plant associations. Rows 3 and 4 are dissimilarity maps for fossil pollen assemblages (Row 3) and CCM-1 (Community Climate Model-1) climates (Row 4), interpolated to a common 50 km grid. Each dissimilarity value represents the minimum distance between a pollen or climate gridpoint and its corresponding modern dataset. High dissimilarities indicate the absence of any close modern analog. SOURCE: Modified from Williams et al. (2001); used with permission.

physical perturbation (J.B.C. Jackson, 1992), the taxonomic level of the investigation (species vs. genus vs. family vs. functional group), or alternations between stable and unstable environmental regimes in geologic time (Brett et al., 1996)—has important implications for ecological and evolutionary theory as well as for conservation strategies.

Recovery after Biotic Disturbance. Disturbance occurs on a variety of temporal and spatial scales. Many such disturbances are not amenable to contemporary analysis but require paleobiological data. An important unresolved issue is whether biotic response to perturbation scales from ecological to evolutionary events. Do the processes involved in response to ecological disturbances also apply to response to mass extinctions, or is there a threshold beyond which the processes differ? The variety and intensity of disturbances that species and communities can tolerate or withstand is best evaluated through the paleobiological record of past disturbances. This allows definition of the limits to disturbances beyond which the system may collapse. Repeated disturbances might weaken communities by, for example, reducing the number of connections within food webs, or may harden communities through progressive subtraction of more narrowly adapted species. Evidence for such behavior and its net consequences for community diversity and structure, and predictions for present day communities, can be acquired only from historical analysis.

In the historical analysis of recoveries, it is clear that some species that appear to be adapted for particular disturbance regimes may in reality simply have fortuitous exaptations (or pre-adaptations) that happen to be useful. For example, long-leaf pines in southeastern forests occur in a fire regime that paleobiological data suggest has only existed for the last 6-8 Ka, and to which they could not have evolved. Fire adaptations may have arisen in a very different environment. Similarly, high carbon-use efficiency in conifers—an adaptation to cold environments—may also confer advantages in the low-CO_2 environments that arose during Quaternary glaciations (S.T. Jackson et al., 2000). The preferential survival of dinoflagellates relative to other phytoplankton during the end-Cretaceous extinction events may be attributable to their characteristic resting cysts, which appear to have evolved to permit dormancy under much less extreme stresses (Kitchell et al., 1986). These examples underscore that only paleobiological analysis can reveal the behavior of species over the timescales—and through the repeated natural experiments—that permit assessment of the relative importance of the different environmental and biological factors affecting biotic recovery.

Biogeochemistry

Biogeochemical cycles of carbon, oxygen, nitrogen, phosphorus, sulfur, and other elements play critical roles in the earth system, ranging from effects on local productivity to global biosphere functioning. Understanding these cycles and how they are influenced by heterogeneity in space and variability in time is a critical goal for ecology. It is also vitally important as human activities disrupt these cycles, altering their rates, pathways, and chemical transformations. Many of the processes involved in these cycles occur at timescales of hundreds to millions of years, and so geological perspectives are necessary. Two of the four "important areas of [biogeochemical] research" identified in the NRC *Grand Challenges in Environmental Sciences* report—"(1) Improve the quantification of sources and sinks of the nutrient elements, and gain a better understanding of the biological, chemical, and physical factors regulating transformations of nutrient reservoirs, and (2) Improve understanding of the interactions among the various biogeochemical cycles" (NRC, 2001c; p.19)—will require integration of information from the geologic record to facilitate improved understanding. Biogeochemical cycles are global in nature, but the underlying processes, particularly biological ones, are inherently local. Geohistorical records can address fundamental biogeochemical questions at spatial scales ranging from local to global, and temporal scales ranging from the recent past to the entirety of geobiological history.

Biogeochemical Fluxes and Controls: Retrospective Experiments and Chronosequences. Ecologists are concerned with understanding the processes governing biogeochemical cycles, and with assessing the sensitivity of biogeochemical reservoirs and fluxes to a wide array of perturbations—from local disturbances to global climate change. Their efforts are hampered by the wide range of temporal scales at which relevant processes occur and the limited array and duration of observational and experimental studies available. Geohistorical records can be exploited to solve some of these problems; in particular, they can be used to design retrospective experiments and for chronosequence analysis.

Retrospective experiments take advantage of natural or human-caused situations in which treatment effects and controls can be assessed using geohistorical records. Sedimentary basins—lakes, estuaries, marine basins, peatlands—provide a record of a variety of biogeochemical processes and fluxes in the form of fossil organisms, biomarkers, and sediment geochemistry. They simultaneously record information about adjacent terrestrial ecosystems (e.g., vegetation, soils) and climate. Quasi-experimental pairs or arrays of basins can be used to examine *treatment* versus *control* effects of perturbations (e.g., see Box 3.4), assess sensitivity of different systems to perturbations, and identify dominant controls by examining differential responses of sites in contrasting environments (e.g., Whitehead et al., 1989; Ford, 1990; Ewing, 2002; Leavitt et al., 2003). This approach can even be used to provide estimates for variables not measured in long-term monitoring programs (e.g., Leavitt et al., 1989). The retrospective-experimental approach greatly extends our ability to understand the controls on biogeochemical processes.

The chronosequence approach—in which variation in space is substituted for change in time—is one of the oldest and most powerful tools employed by ecologists for studying temporal change. Historically, its primary applications have involved geological or disturbance-based contexts (respectively referring to the time since geologic origination of the land surfaces, and time since the last severe disturbance). The wide range in ages of the volcanic islands of the Hawaiian archipelago, for instance, have been used to identify rates of nutrient leaching, sources and rates of nutrient supply, and the climatic controls on these processes (Chadwick et al., 1999; Hotchkiss et al., 2000). Information from paleoecological studies comprises a vastly underutilized context for chronosequence studies of biogeochemical flux. Such studies provide site-specific information on the timing of immigration of dominant species, conversion of one vegetation type to another (e.g., steppe to woodland, tundra to forest), and invasion of new plant functional types (e.g., conifers into hardwood forests) (e.g., Björkman and Bradshaw, 1996; Peñalba and Payette, 1997; Davis et al., 1998; Lyford et al., 2003; Betancourt, 2004). Ecologists can utilize this information to devise sampling arrays to assess the effects of a range of factors (e.g., species composition, plant functional types, and vegetation physiognomy) on soil chemistry, watershed hydrology, decomposition rates, disturbance regimes, and other ecosystem properties important to biogeochemical cycling. Abundant opportunities exist for collaboration between ecologists, paleoecologists, and geologists to identify appropriate chronosequences at a broad range of scales.

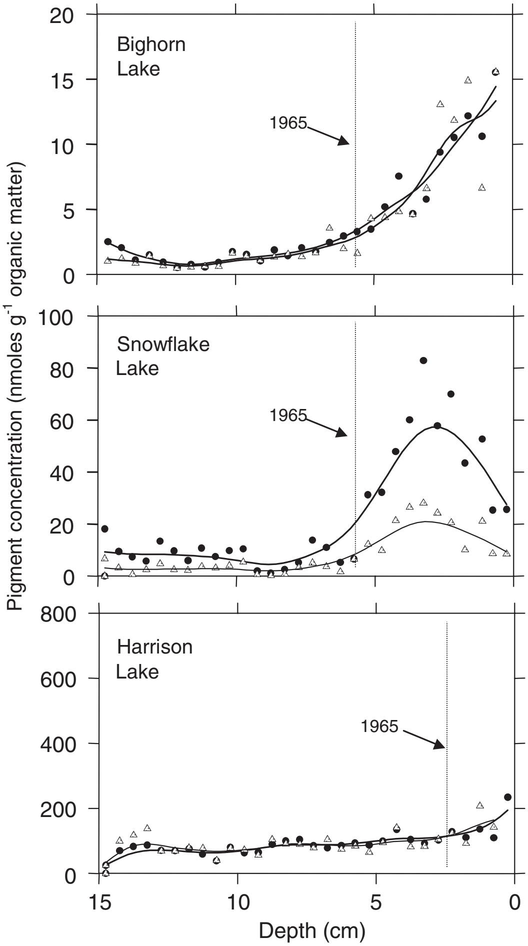
The Evolution of Global Biogeochemical Cycles. The fundamental understanding of the dynamics and controls of biogeochemical cycles must rest on a foundation composed of the entire history of the biosphere (Schlesinger, 2004). Biogeochemical cycles have evolved together with the biota of the planet, and the evolution of these cycles has involved reciprocal effects of biogeochemical and environmental changes on the biota. Furthermore, because of the diversity of rates and response times among the various components of the earth system, these effects have played out over a vast array of timescales. Determining how these cycles have changed—and why—constitutes a major scientific challenge that requires

BOX 3.4
Assessing the Biogeochemical Consequences of Fish Introductions

Fish introductions and invasions are widespread in North America, and they will continue as management agencies continue to stock lakes and streams, and as fish invade new waters as a result of human activities or by natural means (Rahel, 2000). Fish introductions can alter food-web structure and extirpate native amphibians, zooplankton, and benthic macroinvertebrates.

A recent collaborative study involving surveys, experiments, modeling, and paleolimnology has revealed that trout introductions to oligotrophic lakes (i.e., clear lakes with low primary productivity as a result of nutrient limitations) can have important biogeochemical effects, ultimately leading to increased primary productivity in planktonic algae (Schindler et al., 2001). Trout feed on amphibians and benthic macroinvertebrates along the shallow margins of lakes, and they excrete phosphorus-rich wastes into the water column throughout the lake. In doing so, the fish transfer phosphorus from terrestrial ecosystems and the benthos—which would normally be recycled within the benthos or trapped in sediments—to the pelagic system. Experimental and observational studies in lakes indicate that this transfer can lead to a significant increase in phosphorus availability to phytoplankton (Schindler et al., 2001). A retrospective experiment was performed, using algal biomarkers in sediments to test whether fish stocking in the 1960s influenced primary productivity. Paleolimnological studies of three lakes, each with a different fish-stocking history, show clear responses consistent with the nutrient-transfer hypothesis: the unstocked lake (Harrison Lake; see figure below) showed no change, whereas a lake with successful stocking (Bighorn Lake) showed a persistent increase in algal productivity. Fish were stocked in a third lake (Snowflake Lake), but disappeared within two decades. The return of algal productivity to pre-stocking levels indicated that lakes can recover when fish populations decline or are removed. Schindler et al. (2001) concluded that management and restoration of historically fishless lakes should begin with a moratorium on additional stocking.

Trout were introduced for the first time to Bighorn Lake in 1965, and brook trout populations have been self-sustaining in the lake ever since. Trout were also introduced repeatedly to Snowflake Lake in the early to mid-1960s. However, these populations were not self-sustaining and were extinct by the early 1980s. Harrison Lake has never been stocked, but it sustains a native population of bull trout. The unstocked lake—Harrison Lake—shows little change in algal productivity during recent decades. Bighorn Lake, with fish populations since 1965, shows a steady increase in productivity following the original stocking. Snowflake Lake shows an initial increase in productivity, followed by a decline to near pre-1965 levels, evidently tracking the introduction, increase, decrease, and eventual extinction of trout populations.



The stratigraphic profiles of algal-pigment biomarkers in sediments of three lakes in the Canadian Rockies with differing fish introduction histories demonstrate how net primary productivity is influenced by fish populations as a result of their effects on nutrient cycling. Closed circles represent sedimentary concentrations of β-carotene (produced by all algae) and open triangles represent lutein-zeaxanthin (which is specific to chlorophyte [green] algae). SOURCE: Schindler et al. (2001); used with permission.

the marshaling of resources and fostering of collaborations among the earth and life science communities.

Great progress in understanding the biogeochemical evolution of the biosphere has been made in the past two decades. Carbon cycling has been a particular focus of attention (e.g., see Box 3.5), both because biogeochemical cycles of other elements are tied to it, and because of the need to understand controls of global carbon fluxes and reservoirs in the context of the anthropogenic CO_2 increase (Berner and Konthava, 2001; Sundquist and Visser, 2004). However, many critical questions remain, and the biogeochemical history of other elements is more poorly known. Is it possible to predict past dynamics of oxygen, phosphorus, iron, and nitrogen cycles based on knowledge of past carbon cycling? Are interactions among these cycles contingent on particular configurations of climate, sea level, and continental position? Are couplings among cycles contingent on the existence (or absence) of particular types of organisms or metabolic pathways? Furthermore, development of improved paleobiogeochemical proxies is needed to extend our understanding in deep time.

Scientific advance in addressing these and other questions will proceed most rapidly and effectively using a "critical intervals" approach, in which resources are focused on particular periods of time that are likely to be particularly revealing (Stanley, 1997). These can include periods for which diverse, detailed information is readily available, periods with important system transitions or excursions, periods with unique configurations of the earth system, and periods for which processes can be linked with understanding and modeling of modern systems or biota. The latter can range from anaerobic, prokaryotic systems of the Proterozoic, to the modern biota of the late Quaternary. For the Phanerozoic, periods in which correlations of events or time series between marine and terrestrial domains should be emphasized. A hierarchical, "zoom-lens" approach can be taken in many cases. For example, the Eocene-Oligocene interval might be studied at a coarse scale, with intensified efforts focused on specific events such as the early Eocene thermal maximum and the rapid cooling event at the Eocene-Oligocene boundary (Zachos et al., 2001).

These efforts will require collaborations spanning much of the earth and environmental sciences, and integrating data collection, database development, and modeling. Some initial efforts at such collaborations have been made for some geologic intervals, notably the Proterozoic, Cenozoic, and Quaternary (e.g., Anbar and Knoll, 2002; Bigelow et al., 2003; Kaplan et al., 2003; Knoll, 2003; Rothman et al., 2003; Wing et al. 2003).

Dynamics of Biotic Invasions

Species introductions, both deliberate and accidental, are having dramatic ecological effects across the globe (Mooney and Hobbs, 2000; Mack et al., 2003; NRC, 2004). The long-term ecological and evolutionary consequences of these exchanges are as yet poorly understood. Geohistorical records of past invasions induced by climate change, dispersal, and continental drift provide a series of natural experiments that can help assess future community and ecosystem consequences of biotic invasions. For example, the past biotic interchanges from North Pacific to North Atlantic, between North America and South America, and between eastern Asia and western North America, recognized on the basis of phylogenetic and biogeographic analyses of pre- and post-interchange biotas, are rich in insights into the asymmetry seen in most biotic interchanges, the differential invasive properties of species, phylads,[2] and functional groups, and the contrasting regional biotic histories of donor and recipient areas (Vermeij, 1991; Jablonski and Sepkoski, 1996). Paleobiological records of species expansions into new territory following climatic changes of the late Quaternary provide lessons relevant to modern invasions, including the relative rapidity and underlying mechanisms (Davis, 1981a; Webb, 1988; Clark et al., 1998; Lyford et al., 2003). Paleobiological approaches can also be used to investigate species introductions that occurred before adequate historical documentation (Parkes et al., 1992; S.T. Jackson, 1997; Egan and Howell, 2001).

Infectious Diseases

There is increasing awareness of the risks of outbreaks of infectious diseases in humans and other species that are important for human use or conservation (NRC, 2001c). Although epidemiological studies will likely be central to this topic, the role of environmental change and human activities in triggering disease outbreaks is being increasingly appreciated. Our ability to identify past disease outbreaks and their consequences using the geologic record is certainly limited. Nevertheless, we should be alert to the opportunities that may exist for useful investigations on this topic. For example, sedimentary records of dinoflagellate tests or biomarkers in selected areas may help determine whether recent outbreaks of *Pfiesteria* red tides—harmful algal blooms—are unprecedented and presumably related to human activities, or have occurred in the past with

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[2] Phylad—an evolutionary lineage; a group of species, genera, or families that share a common ancestor.

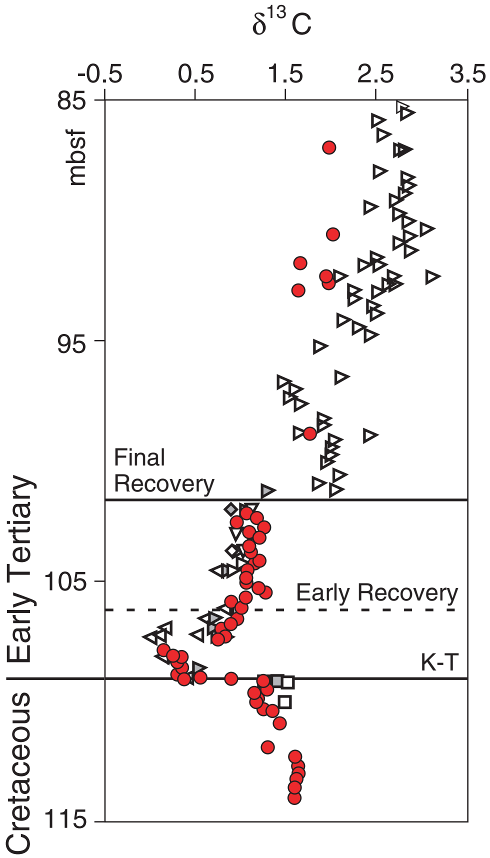
BOX 3.5
Carbon Cycling and the Delayed Ecological Recovery of the Oceans after the Cretaceous-Tertiary Extinction

The ecological effects of the Cretaceous-Tertiary extinction in the oceans persisted for millions of years. D'Hondt et al. (1998) used carbon stable isotopes in the calcium carbonate hard parts of planktonic and benthic foraminifera to track the recovery of oceanic productivity and the flux of carbon to the deep sea. Although the productivity of surface waters was restored quickly, full recovery to pre-extinction levels of organic carbon flux to the deep sea was delayed by at least three million years.

The figure above shows a sharp decrease in $\delta^{13}C$ at the Cretaceous-Tertiary (K/T) boundary, suggesting that surface productivity was greatly reduced as a consequence of the events and extinctions occurring at the end of the Cretaceous. In the "Strangelove Ocean" (Hsü and McKenzie, 1985) that existed after the K/T event, the normal sinking of organic matter to the deep sea ceased and the difference in the $\delta^{13}C$ composition of shallow planktic foraminifera and deep sea benthic foraminifera hard parts disappeared.

D'Hondt et al. (1998) suggest that despite the return of surface productivity to pre-extinction levels within a few thousands of years (shown by the "Early Recovery" zone in the figure), final recovery to pre-extinction $\delta^{13}C$ differences was delayed by for almost 3 million years by reduced fluxes of organic carbon. They argue that the delayed recovery was either a consequence of the small size of the surviving phytoplankton or the small size of phytoplankton grazers. The organic matter of very small phytoplankton is more likely to be recycled within the surface waters than exported to deeper water, and larger grazers are needed to aggregate biomass (as carcasses or fecal material) for rapid delivery to the deep sea. The "Final Recovery" of $\delta^{13}C$ may reflect the evolution of larger species of phytoplankton and their grazers in the post-K/T ocean, and the consequent recovery of ecological mechanisms for the delivery of organic matter to the deep sea. The end-Cretaceous extinctions affected not only the composition of the earth's biotas but also its ecological dynamics and carbon cycling—the ecological legacy of this mass extinction lingered in the oceans for millions of years.

BOX 3.5 Continued



Cretaceous-Tertiary δ^{13}C records from DSDP Site 577 in the Central Pacific Ocean, with red circles showing the difference between δ^{13}C values from bulk carbonate and benthic foraminfers. "mbsf" = meters below sea floor. SOURCE: D'Hondt et al. (1998); used with permission.

similar extent and magnitude. Similarly, molecular or serological analysis of debris from fossil rodent middens and archeological sites may provide clues on the antiquity, extent, and evolution of hantavirus. Prehistoric outbreaks of forest pathogens in North America (Davis, 1981b; Allison et al., 1986; Fuller, 1998) and Europe (Peglar, 1993) are well documented. Application of molecular techniques to the sedimentary record may help resolve the causal agents, and high-resolution paleoclimatological studies may help identify whether climate variations interacted with pathogens or vectors (e.g., Speer et al., 2001; Acuna-Soto et al., 2002). Late Quaternary megafaunal extinctions have been attributed to microbial pathogens spread by migrating humans (MacPhee and Marx, 1997), and attempts are being made to test this hypothesis using molecular analysis of fossil material (Greenwood et al., 2001).

ECOLOGICAL RESPONSES TO PAST CLIMATE CHANGE

Climate has an overarching effect on Earth's biota—biodiversity and biogeochemistry are strongly influenced by temperature and precipitation at local to global scales. Geographic distributions and population sizes of organisms are constrained to varying degrees by climate. The tempo and pattern of biological invasions and disease outbreaks are frequently determined by climate, and effects of human land use and habitat alteration are contingent on climate. Atmospheric accretion of greenhouse gases, together with extensive land-cover changes by human activities, are raising concerns about human-induced climate change (IPCC, 2000, 2001; Pielke et al., 2002; Marland et al., 2003). However, the paleoclimate record indicates that, even in the absence of human influences on climate, climate change and variability are natural components of Earth's system. Historical data have been crucial to disentangling potential anthropogenic and non-anthropogenic impacts.

Management of modern ecosystems (e.g., for maintenance of biodiversity, sequestration of carbon, utilization of timber, forage, fisheries, and other resources) in the face of ongoing and future climate change must be informed by knowledge of how such systems have responded to climatic variations in the past. Understanding how ecological systems have responded to past climatic and other environmental changes is necessary because the geologic record of ecological dynamics includes a vastly greater range of climatic conditions than are present today, or that are recorded in the instrumental and archival records of the past two centuries. Indeed, paleoclimatological studies of the past two decades have revealed properties of Earth's climate system, including variability, sensitivity, control, feedbacks, and susceptibility to abrupt change, that would have otherwise gone unnoticed (NRC, 2001c, 2002a). We would be utterly ignorant of the rates of abrupt climate change in the absence of paleoclimate data (NRC, 2002a).

The rapid, ongoing development of paleoclimatic and other paleoenvironmental records, at local to global scales, and from the Proterozoic to the late Holocene, provides important opportunities for linking records of biotic changes to the existing paleoclimatic and paleobiological datasets and records. Such opportunities exist throughout the entire geologic column. Most depositional settings where high-quality, well-dated paleoclimatic records can be extracted—whether these are high-resolution time series or more scattered samples across time—can also yield paleobiological records. Recent improvements in dating and chronostratigraphy have opened additional opportunities for correlating these records across different localities, regions, continents, and oceans, allowing climatic, environmental, and biotic dynamics to be studied together within a spatial framework. Finally, the recent and continuing development of a multitude of paleoclimate proxies (Parrish, 1998; Bradley, 1999) is driving an important transition in paleoclimatology and paleoecology. Paleoclimate inference is no longer heavily dependent on biological proxies, but can now draw on a greater variety of both biological and non-biological data. Thus, paleontological data on past distribution and abundance of organisms can now be used as response variables in studies in which climate change has been independently inferred (see Box 3.6).

Opportunities for Scientific Advance

Particular emphasis should be given to research efforts that focus on particularly well-documented and revealing time intervals in Earth history, and to work that contributes to our ability to forecast ecological responses to ongoing and future climate change. Integrated studies of paleoclimate, paleoenvironment, and paleobiology are not practical for every interval of Earth history. With limited resources and in light of variation in the quality of the geologic record at different time periods, efforts should be targeted at selected intervals in Earth history that:

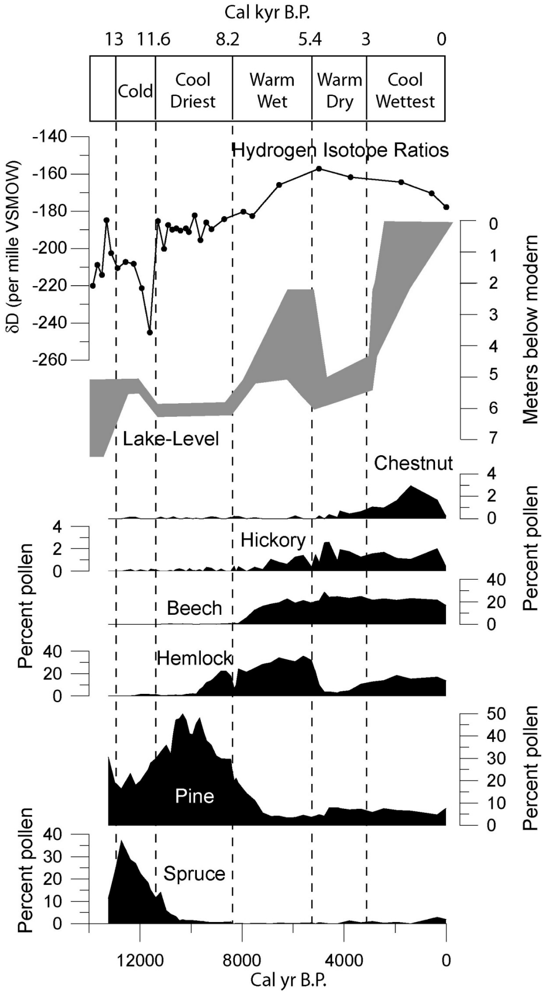
1. provide high temporal resolution and easy correlation over broad areas and among terrestrial and marine records;
2. have existing or potential high-quality paleoclimate records, preferably involving multiple proxies and multiple inferred variables (e.g., temperature and precipitation; warm-season and cool-season temperatures, means and extremes);

BOX 3.6

Linking Independent Records of Climate Change and Biotic Response

Efforts to use geohistorical records to understand biotic responses to environmental change have often been hampered because the same data—pollen percentages, occurrences of plant or animal fossils—were used to infer both paleoenvironments and composition of past biotic communities. The proliferation of multiple paleoenvironmental proxies in the past two decades has now made it possible to link biotic responses to past environmental changes with greater confidence and precision. For example, pollen percentages from lake and peatland sediments—long a dominant source of paleoclimatic inferences for continental regions—are now being complemented by a variety of paleoclimatological and paleohydrological proxies, including stable isotopes, geochemical, mineralogical, and molecular markers, and microfossils of aquatic organisms (e.g., diatoms, chironomids, testate amoebae, chrysophytes).

In the figure below, postglacial pollen percentages of several important forest trees are plotted for a pond in the Berkshires of western Massachusetts, together with independently derived estimates of paleoclimate from lake levels (paleohydrology) and hydrogen isotopes (paleotemperature) from a lake 200 km to the east in southeastern Massachusetts. Major vegetation transitions in the Berkshires coincide with climatic transitions recorded in southeastern Massachusetts, demonstrating the climatic control of vegetational composition and spatial coherence of climatic change at millennial scales (Shuman et al., 2004).



Climate and vegetation history of central New England since deglaciation. Hydrogen isotope ratios (Huang et al., 2002) indicate regional changes in temperature (low values indicate colder temperatures), and lake levels inferred from sedimentological indicators (Shuman et al., 2001) indicate moisture balance. Changing pollen percentages indicate changing composition of regional forests in western Massachusetts (Whitehead and Crisman, 1978). Radiocarbon dating is sufficiently precise to allow correlation of events at the two sites at multicentennial scales. Greater dating precision is possible using higher density of dating together with accelerator mass spectroscopy (AMS) dating of individual macrofossils. SOURCE: Shuman et al. (2004); used with permission.

3. contain existing or potential paleobiological records of adequate quality;
4. have potential for linking or nesting ecosystem dynamics across a range of timescales; and
5. provide opportunities for testing theory and integrating knowledge from ecology, evolutionary biology, and biogeochemistry.

These time intervals should collectively encompass a range of past climatic variations, both quantitative (magnitude and rate of change) and qualitative (nature of change; earth-system boundary conditions). The ideal suite of time intervals and studies can be envisioned as a set of natural experiments that together reveal the dynamics of biotic response in a wide range of habitats as driven by gradual, abrupt, and cyclical climatic changes at timescales ranging from years to millions of years.

The late Quaternary is particularly well suited for studies of biotic response to climate change because of high temporal precision, ease of precise correlation among sites, and opportunities to link past dynamics with modern ecosystems. It also provides the clearest links to ecological forecasting and risk assessment in the face of current global change. However, earlier intervals in the geologic record also provide important opportunities for studying biotic responses to climatic changes of different magnitude, quality, and duration. The pre-Quaternary record is a rich source of information on how biological diversity and biogeochemical cycling responded to changes in climate at different scales (e.g., transitions from greenhouse to icehouse worlds) and rates. Furthermore, because biodiversity and biogeochemistry both interact with climate change (NRC, 2001c), they must be studied in an integrated fashion.

Integrating Ecology and Climate Change

Ecologists have long recognized the influence of climate on global biodiversity, primary productivity, species distributions, and biogeochemical cycles. Although other ecological phenomena, including population size, population dynamics, community structure, and evolutionary adaptations have been traditionally ascribed to biotic interactions (competition, predation, mutualism), there is increasing recognition that climate plays an important, often dominating role (Post and Stenseth, 1999; Post et al., 1999; Ackerly, 2003; Hengeveld, 1990; Stenseth et al., 2002; Chavez et al., 2003). Because climate varies significantly at ecological and evolutionary timescales, and because climate exerts direct and indirect influences on ecological systems at all levels of organization (organismal to global), a clear need exists for studies targeting climatic influences across a wide array of ecological systems, timescales, time periods, and spatial scales.

Biotic systems also affect climate through their effects on parts of the climate system such as carbon cycling, albedo, and the production of naturally occurring greenhouse gases. Geohistorical records provide abundant opportunities for learning about how the physical environment, particularly climate, constrains or determines features of the biosphere at scales ranging from genomic to global biogeochemistry and about how biotic systems affect climate. Following are select examples of how geohistorical approaches are contributing to fundamental understanding of ecological systems in the context of climate change and variability.

Climate Change and Community Reorganization. Studies of climate change during the last deglaciation reveal that millennial-scale climatic change leads to recombinations of climate variables at individual sites (e.g., different combinations of seasonal temperatures, or temperature and precipitation), and qualitative alteration of geographic and elevational gradients in climate (e.g., changes in the slope of the relationship between seasonal temperatures) (Kutzbach and Webb, 1993; Kutzbach et al., 1998). These patterns of change have profound ecological implications (Webb, 1987; S.T. Jackson and Overpeck, 2000; Webb et al., 2004). Paleoecologists had long recognized late Quaternary biotic assemblages that lacked modern counterparts (see Box 3.3). The existence of past climates lacking modern analogs provided a powerful potential explanation, which was corroborated by the demonstration that peculiar communities were concentrated in regions and time periods where prevailing climate was unlike any existing today (Williams et al., 2001; S.T. Jackson and Williams, 2004). It is now becoming increasingly evident that many—perhaps most—communities undergo extensive reorganizations in response to climatic changes at millennial timescales and beyond. The full ecological and evolutionary implications of this phenomenon have yet to be explored.

Community-level response to climate change represents a potentially fruitful area for integrated studies of climate change and paleontology both in the Quaternary and earlier in Earth's history. Some communities may be less likely than others to undergo disassembly in response to environmental change and whether such differential responses show systematic patterns as a function of latitude, diversity, food-web structure, environmental plasticity, or other properties deserves further study. For communities that do undergo disassembly, we need to explore the underlying patterns and processes. For example, does disassembly consist of gradual turnover as local populations of some species are extirpated and other species colonize? Or do communities persist until some threshold is reached, undergoing collapse and rapid replacement? What roles do disturbances and climate extremes play in these responses? Studies focused on these questions are needed to assess the role of non-linearities and threshold effects, and determine the roles of climate extremes, disturbance, and ecological properties (population size and connectedness, generation time, dispersal capacity) in governing community responses to climate change. They will also help assess community-level consequences of disassembly. Are there predictable consequences for species richness, representation of functional groups, or food-web structure? Understanding these dynamics will enrich our fundamental understanding of ecology as well as determine risks and consequences associated with future climate change.

Climate Change and Ecosystem Function. Ecosystem function depends on the prevailing climate regime (including variability) and on structure and composition of biotic communities, particularly vegetation. A central goal of global change biology is to develop capacity to predict how climate change will affect—both directly and indirectly—such ecosystem properties and services as primary productivity, carbon storage, biogeochemical cycles, disturbance regimes, atmospheric feedbacks, and soil stability. Climate exerts direct control on many of these properties for terrestrial systems, and influences physical properties of vegetation and composition of the biota, which influence other ecosystem functions. Aquatic ecosystems are also directly influenced by climate (temperature, hydrology) and by properties (productivity, disturbance, biogeochemical flux) of terrestrial ecosystems in catchment basins.

Changes in ecosystem function resulting from climate change and/or vegetational change are well documented from paleoecological records in both terrestrial and aquatic ecosystems. Climate changes of the recent past have often had dramatic ecosystem consequences, some far-reaching in nature. Fire regimes have undergone shifts in ecosystems across North America during the past 12,000 years (Clark et al., 1996, 2001b; Carcaillet et al., 2001; Veblen et al., 2003), with consequent changes in watershed hydrology and geomorphology (Meyer et al., 1995; Meyer and Pierce, 2003). Vegetation shifts involving major changes in important plant traits (Lavorel and Garnier, 2002; Chapin, 2003) have led to changes in landscape stability and biogeochemical flux. For example, early Holocene soil stabilization and humification associated with climate-driven replacement of tundra woodland by coniferous forests led within a few centuries to widespread ecosystem acidification (Whitehead et al., 1989; Ford, 1990), providing a baseline against which to evaluate industrial acidification (from "acid rain") of the 20th century. More subtle changes in biogeochemical flux are associated with Holocene shifts in forest dominants

(Whitehead et al., 1989; Willis et al., 1997; Ewing, 2002; Ewing and Nater, 2002). Finally, climate-driven vegetational shifts have synergistic effects with the climate system, owing to vegetation/atmosphere feedbacks (Kabat et al., 2004). For example, such feedbacks were responsible for deep penetration of early Holocene monsoons into the African continent (Kutzbach et al., 2001).

Many of these ecosystem-level responses took several centuries to play out, owing to the slow rates of many biogeochemical and other processes and system-response lags. Such slow changes are difficult to fully understand in the absence of geohistorical records, and changes of the past century or two are confounded by direct human impacts (e.g., land clearance, damming/diversions, pollutants). Opportunities abound for further exploitation of the fossil record to understand climatic influences on ecosystem function, particularly with the rapid recent development of proxies for paleoclimatic inference, tools for paleoecological assessment, and ability to obtain precise dating of sediments and events. Furthermore, ongoing activity in studying and modeling ecosystem function in relation to climate change provides a rich source of theory and hypotheses for testing using the fossil record. The extent to which ecosystem function is directly controlled by climate versus indirectly influenced via vegetation dominants or individual species is still being debated. Geohistorical records provide opportunities for teasing apart the respective roles of climate and biota in controlling ecosystem properties. A variety of natural experiments exist in the past that can be studied to address these questions and test models of future climate-change impacts on ecosystems.

Evolutionary Effects of Climate Change—Integrating Paleobiology and Genetics. Biotic responses to climatic changes of the Quaternary have involved large- and small-scale shifts in geographic distributions, expansions and reductions in population sizes, and fragmentation and coalescence of populations. These responses have long been recognized as having significant evolutionary and genetic consequences, and Quaternary events have traditionally been viewed as key to explaining speciation events and patterns of genetic diversity within species. The past decade's advances in molecular and mathematical tools for genetic analysis (Avise, 2000; Hewitt, 1999, 2000), together with the increasingly detailed records of biogeographical and ecological changes of the late Quaternary, are providing opportunities for synthesis of evolution, ecology, and climate change (Petit et al., 2002a,b). We are now in position to apply paleobiological and molecular-genetic approaches in an integrated fashion to track population-level dynamics in response to climatic change, and to assess the roles of isolation, bottle-necking, dispersal, migration, and other events in shaping the genetic structure and ecology of existing populations (Hewitt, 2000;

Jacobs et al., 2004). These efforts can shed light on how climate variation and change have influenced the evolutionary dynamics of populations and species, and provide a basis for forecasting genetic and conservation implications of future change.

Studies of DNA from fossil material, although apparently limited to a handful of paleontological settings in the late Quaternary, can reveal spatiotemporal patterns of genetic and evolutionary responses to environmental change (Poinar et al., 1998, 2001, 2003; Kuch et al., 2002; Hofreiter et al., 2003; Willerslev et al., 2003; Hadly et al., 2004). Application of these kinds of studies to sensitive species during past periods of abrupt climate change can determine the role of environmental extremes in shaping evolution and adaptation (Ackerly et al., 2000; Gutschick and BassiriRad, 2003). Similar efforts aimed at periods of non-analog climates and communities can be used to test whether novel environmental changes lead to predictable adaptive responses (Ackerly, 2003).

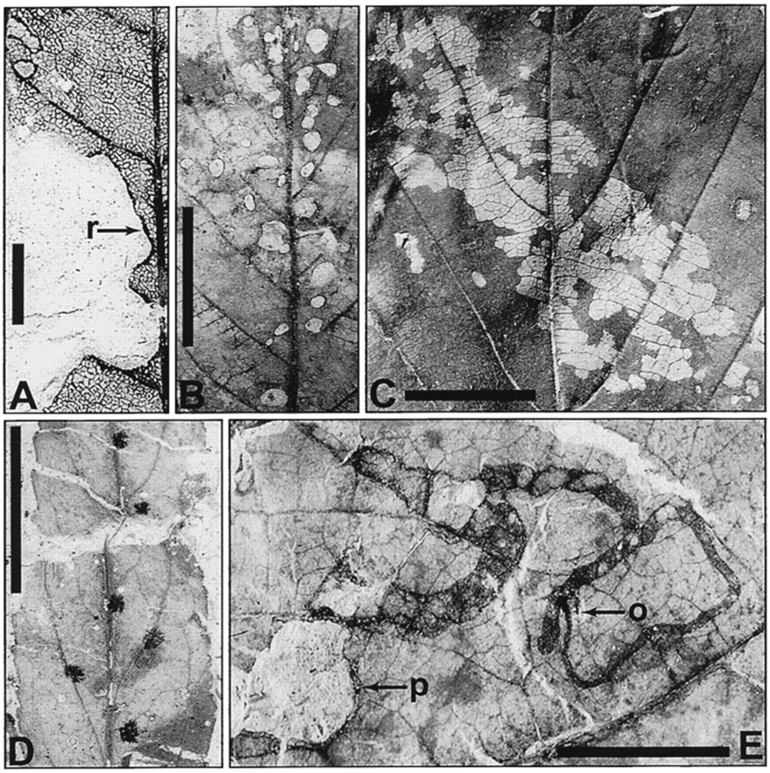
The fossil record of the pre-Quaternary provides important opportunities for learning about the impact of climate change on evolution and ecology (e.g., see Box 3.7). The modern biotas have evolutionary origins in the pre-Quaternary, with most intergeneric divergences and many species divergences dating to the Tertiary (Avise, 2000). Understanding how these divergences and associated adaptations arose in relation to pre-Quaternary climate changes is necessary to understand the ecological and genetic properties of extant species. Furthermore, the pre-Quaternary record contains a vast number of natural experiments in which the effects of climate changes varying widely in rate, magnitude, duration, and global context can be explored. These experiments can be utilized to answer fundamental questions about ecological and evolutionary patterns and theory (e.g., McKinney and Drake, 1998; Erwin and Wing, 2000; Gastaldo and DiMichele, 2000; J.B.C. Jackson and Johnson, 2000, 2001; Wilf et al., 2001).

Forecasting Biotic Responses to Future Climate Change

Climate change represents one of the great environmental challenges faced by human society, and successful planning and decision-making depends on our ability to anticipate future changes and their consequences (NRC, 2001c). A science of ecological forecasting is developing rapidly, focusing on predicting effects of climate, human activities, invasive species, and other factors on ecosystems, ecosystem services, and biological resources (Clark et al., 2001a). To date, with a few notable exceptions (e.g., Swetnam et al., 1999), ecological forecasting has made little explicit use of historical perspectives.

BOX 3.7
Plant-Insect Interactions during Global Warming 56 Ma Ago

The traces of plant-insect interactions are recorded in fossil leaves, providing insight into how insect herbivory changes in response to climate change. Wilf and Labandeira (1999) and Wilf et al. (2001) examined insect damage on fossil leaves during the Paleocene-Eocene episode of global warming, approximately 56 Ma ago. They identified 41 types of feeding damage from the leaves of 88 species of angiosperms preserved in Paleocene and Eocene deposits from Wyoming.



Examples of insect damage in Paleocene (A,C) and Eocene (B,D,E) leaves. Scale bars are 1 cm. Reaction tissue (r) shown in panel A; galls shown in D; oviposition site (o) and pupation chamber (p) shown in E. SOURCE: Wilf et al. (2001). Copyright (2001) The National Academy of Sciences, U.S.A; used with permission.

continued

BOX 3.7 Continued

As the mean annual temperature of the site increased from an estimated 14.4 ± 2.5°C in the Paleocene to 21.3 ± 2.2°C in the Eocene, both the diversity of insect damage and the frequency of herbivory increased. The geologic record of global warming during the Paleocene-Eocene provides a laboratory in which to examine the response of plant-insect interactions to climate change.

Paleoclimatological data and perspectives are playing an increasingly important role in climate forecasting and risk assessment, particularly in context of the ongoing severe drought in the western United States. Climate scientists have recognized that the instrumental record of the past century provides a miniscule sample of the range of natural climate variability and is too short to evaluate dynamics at decadal timescales and beyond. Furthermore, climate variations of the 20th century have been clouded by human activity, including trace gas emissions (e.g., carbon dioxide, methane), aerosols, and land-use/land-cover change, so it is difficult to differentiate non-anthropogenic influences from human ones. Thus, paleoclimate studies, ranging from records spanning the past few centuries to records covering the last few glacial/interglacial cycles, are central to climate forecasting. In fact, current concerns in climate policy over abrupt changes driven by non-linearities in the climate system (NRC, 2002a) have arisen entirely from paleoclimate records which indicate that such changes and responses are intrinsic features of the earth system.

The rich geologic record of biotic responses to past climate changes is an essential component of ecological forecasting. In its absence, we are left with a depauperate view of the full range of ecological consequences of climate change, and are hampered in separating direct effects of climate from other factors (e.g., human activities, direct response to trace gas concentrations). We discuss three areas of particularly critical need for historical and geohistorical perspectives: (1) natural resource management, (2) abrupt climate change, and (3) conservation of biodiversity. Paleobiological studies are already making substantial contributions in a fourth key area, the parameterization and testing of models of regional and global climate change (Kohfeld and Harrison, 2000; Kutzbach et al., 2001; Kaplan et al., 2003).

Climate Variability and Management of Natural Resources

Just as climate scientists have come to recognize that the instrumental records spanning the past century or two fails to include the full range of climate variability relevant to planning and risk assessment, applied ecologists and resource managers are realizing that 20th-century monitoring provides an inadequate baseline for assessing variability in population size, disturbance frequency, and productivity in ecosystems. Furthermore, human activities such as timber harvesting, fire suppression, and livestock grazing have altered natural variation and distorted baselines. Resource managers are turning to the concept of "range of natural variability" or "historic range of variability," as a baseline for management (Swanson et al., 1993; Kaufmann et al., 1994; Landres et al., 1999). These applications often focus on the mid-19th century, or the decades immediately preceding extensive Euro-American settlement, as the natural baseline for management targets. However, most of the properties of interest to managers (e.g., population size, disturbance frequency, regeneration rate, discharge) are tied to climate, and climate variability of the 19th century is as unrepresentative of the preceding several centuries as it is of the 20th century (Bradley and Jones, 1992; Cook et al., 1999). Furthermore, some ecological phenomena vary at lower frequencies that require records spanning multiple centuries to detect. Resource management will benefit from records spanning several centuries or more to identify the controls on ecosystem properties and to assess the full range of inherent variability.

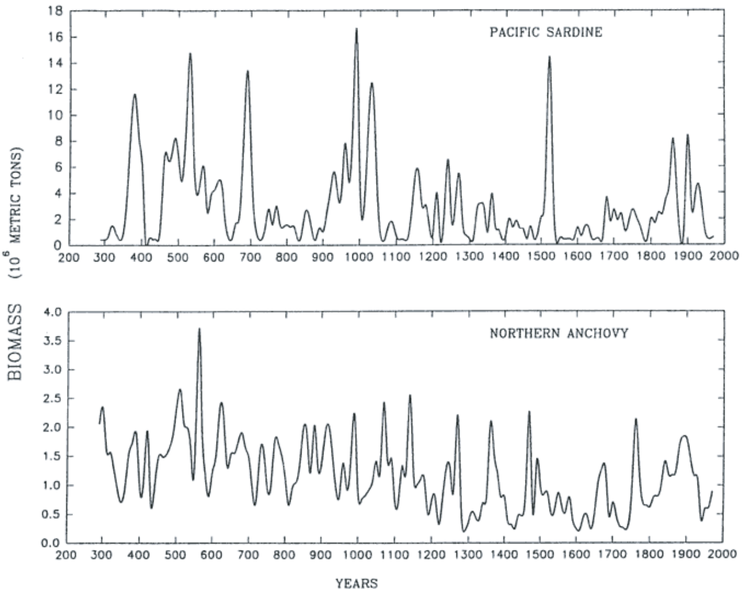
Perspectives spanning hundreds to thousands of years are being applied in fisheries management and vegetation management in a few areas. Fire scar, woodrat midden, sedimentary charcoal, and paleoclimate studies are influencing management of forests and woodlands in parts of western North America (Millar and Woolfenden, 1999; Swetnam et al., 1999). Reconstructions of marine fish populations (e.g., sardines, anchovies) from fish scales accumulated in sediments are being used in tandem with paleoclimatological, paleoceanographic, and modern ecological studies to develop predictive frameworks for fisheries management (Baumgartner et al., 1992; Schwartzlose et al., 1999; see Box 3.8). These syntheses and applications are important because they allow identification of the relative impacts of climate variability and human impacts (e.g., harvesting, fire suppression) on natural resources, and provide a great deal of predictive power by linking resource properties (population size, productivity, fire risk) to climate variability at interannual, decadal, and multidecadal timescales. Diverse ecological phenomena, ranging from population size to vertebrate sex ratios to food web structure are being linked to interannual climate variation (El Niño-Southern Oscillation [ENSO], North Atlantic Oscillation [NAO], Arctic Oscillation [AO]) (Lima

BOX 3.8
Fish Scales, Climate Variation, and Fisheries Management

Many marine fisheries have undergone catastrophic declines in the past four decades. These events are often attributed to overfishing or poor management practices. The 1972-1973 collapse of the Peruvian anchoveta fishery is one of the most celebrated cases. This event, however, coincided with an unusually strong El Niño event, and the plummet of the anchoveta populations is now regarded as resulting from a combination of fishing practices and the interruption of nutrient upwelling during the El Niño event. Populations of fish and other marine organisms change in size and location in response to climate variations; for example, marine fish fluctuations of the past century have been linked to ENSO (El Niño-Southern Oscillation) variation as well as lower-frequency variations in the Pacific Basin (e.g., Pacific Decadal Oscillation [PDO]) (Mantua et al., 1997; Chavez et al., 2003; Lehodey et al., 2003).

Pelagic fishes—such as sardines and anchovies—slough off scales as they grow, and these scales are preserved in sediments of deep, anoxic basins. Fish scales from sediment cores of these basins provide high-resolution (often annual) records of changing biomass, species composition, and age structure of pelagic fish communities, spanning hundreds to thousands of years. These geohistorical records are providing information on the natural variability and climatic controls of marine fisheries.

In the Santa Barbara Basin off the California coast, sardine and anchovy production has fluctuated tenfold during the past 1,700 years, with rapid increases and equally rapid declines (see figure below). Spectral analysis of these records reveal high-frequency variation (period of 50-60 years), possibly linked to PDO variation, and lower-frequency trends, which are correlated with the Medieval Warm Period (10th to 14th centuries) and the Little Ice Age (15th to 19th centuries) (Baumgartner et al., 2004).

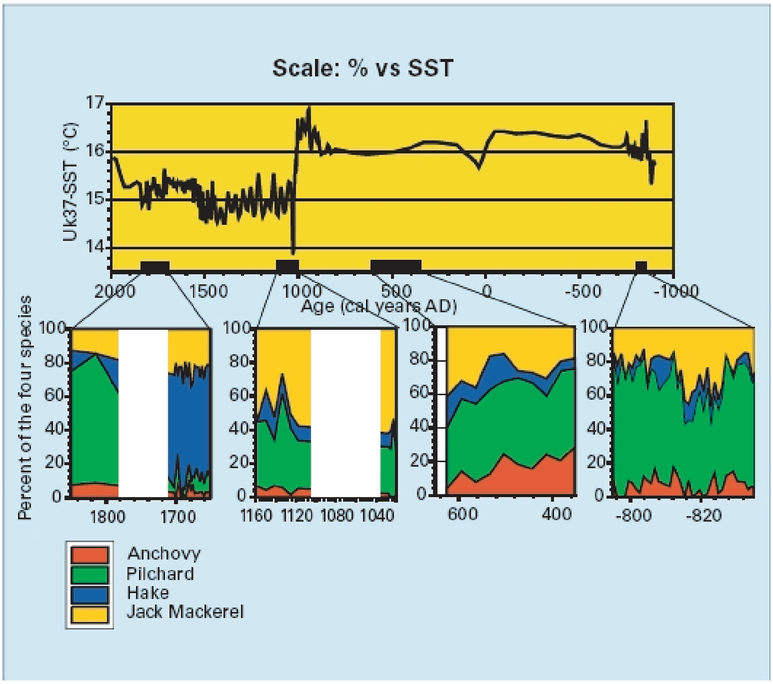


1,700-year record of sardine and anchovy biomass off the California coast, inferred from fish scale deposition in laminated sediments from the Santa Barbara Basin. SOURCE: Baumgartner et al. (1992); courtesy California Cooperative Oceanic Fisheries Investigations; used with permission.

Similar time series are under development from several ocean basins. A record spanning the past 3,000 years is being developed from the upwelling zone off the coast of Namibia in southwest Africa (see figure below). Estimates of sea-surface temperature (SST) from a biomarker proxy provide an independent baseline for environmental change. The record indicates an abrupt shift in mean and variance of SSTs around 1,000 years ago. Changes in absolute and relative abundances of economically important fish species may be attributable to this regime shift, as well as SST trends and variations at higher (centennial to multidecadal) frequencies.

continued

BOX 3.8 Continued



3,000-year record of SST (estimated from alkenone undersaturation) and relative abundance of fish scales from anchovy, sardine (pilchard), hake, and jack mackerel from a sediment core obtained off Walvis Bay, Namibia, in the Benguela Current upwelling zone. SOURCE: Baumgartner et al. (2004); courtesy California Cooperative Oceanic Fisheries Investigations; used with permission.

Sediments from deep basins preserve other paleoenvironmental proxies (e.g., stable isotopes, biomarkers) as well as other biological information (diatoms, radiolarians, foraminifera). Integrated studies of individual cores can provide rich records of pelagic fish communities, primary productivity, and environmental variability. Development of networks of these geohistorical records within and among basins will reveal the spatial and temporal patterns of environmental variability and ecological response, providing a sound baseline for fisheries management and forecasting.

et al., 2001; Post and Stenseth, 1999; Post et al., 1999; Grant et al., 2000). These interannual variations are superimposed upon lower-frequency variations, and their regional expressions are often contingent on the lower-frequency dynamics (e.g., Dettinger et al., 2001; Enfield et al., 2001). Thus, scaling up of ecological responses in a forecasting framework may not be straightforward, and will require longer-term data and perspectives. Forecasting must be supported wherever possible by longer-term historical studies. For many important ecological phenomena, it may be impossible to obtain appropriate paleontological records, so integration of ecological modeling with paleoclimate records will be necessary. But such applications will need to be validated, and opportunities for directly linking geohistorical studies to ecological and paleoclimatological studies should be exploited when they arise.

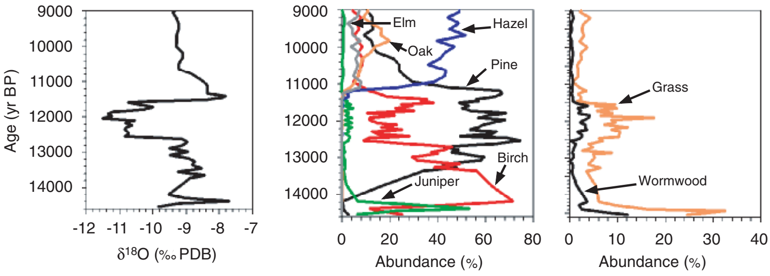
Ecological Consequences of Abrupt Climate Change

Earth's recent climatic history has been punctuated by abrupt, high-magnitude changes, ranging from temperature shifts of up to 16°C and twofold changes in precipitation spanning decades during the last deglaciation to widespread multidecadal droughts during the past 2,000 years (NRC, 2002a). Documentation of these abrupt changes demonstrates that Earth's climate system is strongly influenced by nonlinear effects, and that it is capable of rapid shifts that are likely to have vast societal, economic, and ecological consequences (NRC, 2002a; Alley et al., 2003). Abrupt climate change has become a major research focus in the context of global change, and paleoclimate studies continue to play a major role in understanding mechanisms of abrupt change as well as assessing risks.

Ecological consequences of abrupt climate changes have received comparatively little attention, even though such changes were first identified from paleontological records (Younger Dryas interval) and tree ring studies (late Holocene droughts). Yet the evidence available indicates that ecological impacts were large and widespread. The Younger Dryas interval, an abrupt cooling concentrated in the North Atlantic region 12,800-11,600 BP, resulted in vegetation changes over much of the globe (Peteet, 1995), many of them occurring within a century of the climate change (Birks and Ammann, 2000; Shuman et al., 2002a,b; Williams et al., 2002). The Younger Dryas represents a model system for exploring the biotic implications of large-magnitude, rapid change (see Box 3.9). Did widespread mortality of tree and shrub populations lead to subsequent wildfires? Did vegetational transitions involve rapid migration (e.g., Webb et al., 2004), or alternatively opportunistic expansion of local populations capable of tolerating the new conditions? Did local and regional population extirpations

BOX 3.9
Biotic Responses to Abrupt Climate Change: A Case Study from the Younger Dryas Interval

Abrupt climate changes are a characteristic feature of recent earth history and are nowhere better illustrated than the Younger Dryas interval (YDI), an abrupt cooling event between 12,800 and 11,600 years ago during the last deglaciation (NRC, 2002a). A high-resolution study of oxygen isotopes and pollen from Rotsee, a deep lake in central Switzerland, reveals the impacts on vegetation (Lotter et al., 1992; Williams et al., 2002). The YDI is clearly delineated in the carbonate oxygen-isotope record as an excursion toward more negative values. Before the YDI, climatic warming led to replacement of open, tundra-like vegetation (dominated by juniper, wormwood, and grasses) by forests of birch, joined a few centuries later by pine. Rapid cooling at the inception of the YDI led to a severe decline in birch populations, an increase in pine, and resurgence of juniper, grass, and wormwood, indicating replacement of birch/pine forest by open woodlands with patches of tundra. Rapid warming at the end of the YDI resulted in declines of all the YDI dominants, and development of temperate forests (oak, hazel, elm).



Oxygen-isotope record from sedimentary carbonates of Rotsee, Switzerland, together with pollen percentages for selected taxa. SOURCE: Figure by Andre F. Lotter; used with permission.

increase risk of global extinction for species? How did populations and species survive abrupt changes of the past? These questions bear directly on the likely consequences of abrupt changes in the future (NRC, 2002a).

Abrupt changes in the Holocene are also suitable model systems for studying how climatic changes of smaller magnitude and shorter duration influenced ecosystems. A transient climate anomaly associated with collapse of the Laurentide ice sheet 8200 BP had effects in the North Atlantic region and possibly beyond (Tinner and Lotter, 2001; Shuman et al., 2002a). Other events are documented from geohistorical records in the mid- to late Holocene at regional to global scales (van Geel et al., 1996, 2000; NRC, 2002a; Booth et al., 2004). Severe droughts and other abrupt events of the past 1,000-2,000 years can be documented from both sedimentary records and tree ring analyses (Woodhouse and Overpeck, 1998). These events provide unique opportunities for linking demographic studies of extant populations (Swetnam and Betancourt, 1998; Allen and Breshears, 1998; Swetnam et al., 1999) with high-resolution paleoclimate records and paleobiological records from sediments. Such integrated studies will be valuable both in forecasting ecological changes associated with future abrupt climate change and in examining the mechanisms underlying responses recorded in sedimentary records predating the past 1,000-2,000 years.

Maintaining Biodiversity in a Changing World

Conserving biological diversity and maintaining critical ecosystem services in a time of global climate change, possibly including abrupt changes and climate "surprises" (Overpeck and Webb, 2000; NRC, 2002a), is an immense challenge for scientists, managers, and policy makers. Climate-driven disruption of community structure as incumbent species populations decline and new species immigrate may compromise ecosystem services, and put many species at risk of extinction. These problems are compounded by human activities and introduced species. Habitat fragmentation may inhibit dispersal of native species to suitable habitats, and climate change may interact with wildfire, exotic invasions, and pathogen or disease outbreaks in creating stress on species, populations, and communities.

The species living on Earth today have obviously been subjected to the effects of climate change repeatedly in the late Quaternary, and past climate changes have been accompanied by disturbances, invasions, and other stresses. However, we are almost completely ignorant of what may have been lost in terms of biodiversity—both species diversity and genetic diversity—during these past episodes, and hence are severely handicapped in assessing risks and vulnerabilities for ecological impacts of ongoing and future change. The fossil record has much to contribute to evaluating the potential losses in genetic diversity, species diversity, community stability, and ecosystem services owing to climate change, as well as (conversely) understand the potential role of climate change in generating genetic diversity and ecological novelty.

A wide variety of questions of both fundamental scientific interest and practical value can be addressed using the fossil record. Have species extinctions or genetic bottlenecking been concentrated during past periods of rapid or abrupt climate change? What are the relative capacities for adaptation to environmental changes versus extinction or migration (S.T. Jackson and Overpeck, 2000; Davis and Shaw, 2001; Ackerly 2003)? Does capacity for adaptive response vary predictably among species (Hadly et al., 2004)? Does rapid migration inevitably lead to attenuation of genetic diversity (Cwynar and McDonald, 1987)? Have severe pathogen outbreaks in the past (e.g., Davis, 1981b; Peglar, 1993) been triggered by climate anomalies? Are species-based, community-based, or habitat-based strategies for biodiversity conservation most likely to be effective during a period of climate change (e.g., Hunter et al., 1988)? We know that many species that are widespread and abundant today have been rare and restricted in the past (e.g., *Pinus ponderosa* var. *ponderosa*), while species that are rare and restricted today have been widespread and abundant in the recent past (e.g., *Pinus remota*) (Betancourt et al., 1990; Lanner and Van Devender, 1998). We also know that abundant and widespread species can undergo complete extinction within a few thousand years (S.T. Jackson and Weng, 1999). What are the extinction risks in the face of environmental change?

An important lesson from paleoecological studies of the late Quaternary is that most terrestrial communities and ecosystems have developed within the past 800 to 8,000 years, and that most species have attained their modern distributions within that same period. Thus, the geographic ranges of species, the composition of ecological communities, and the properties of ecosystems (including diversity, productivity, and disturbance regimes) are all contingent on particular climatic regimes that have prevailed for a few thousand years at most. Understanding the causal relations between ecological properties and climate regimes, and delineating the range of climatic conditions that existing systems are capable of tolerating, is critical to ecological forecasting in the context of global change. However, modern spatial patterns of species and communities, and modern climatic gradients provide an insufficient basis for inferring the climatic limits of existing systems.

Macroclimatic regimes as recent as 9000-6000 BP have no modern counterparts (see Box 3.3), and the climate changes—even those of the past few thousand years—that led to development of modern ecosystems are poorly documented. At least some modern communities developed rapidly, suggesting either non-linear relationships between climate change and community composition or a major role of abrupt or rapid climate change. In most cases we do not know how much, nor what kind of, climatic change might lead to collapse of natural populations, communities, or ecosystems in the future. Because climatic change within the next century may yield climate regimes as different as those of today from those of the last deglaciation 14,000-11,000 years ago (e.g., see figure 10 in S.T. Jackson and Williams, 2004), we cannot yet assess the resilience of biotic systems in the face of future change.

Historical and geohistorical studies are essential to address these questions. Integrated studies involving retrospective approaches (e.g., paleoecology, paleoclimatology, demographic reconstructions of population history) in tandem with ecological studies (long-term monitoring; experimentation in field, greenhouse, and laboratory; modeling) would accelerate progress in both ecology and paleoecology, and provide a firm foundation for ecological forecasting related to climate change.

ECOLOGICAL LEGACIES OF SOCIETAL ACTIVITIES

During the past few centuries, and possibly for the past several millennia, the biosphere has been experiencing a situation unprecedented in its history: the dominant ecological influence of a single eukaryotic species at a global scale. Human societies have undoubtedly affected the environment and biota at local scales since the emergence of *Homo sapiens* some 100,000 years ago, and other hominids had ecological effects as well. However, the spread of modern humans across the globe, the increase in their populations with the development of agriculture, and the proliferation of new technologies and life styles, have led to expansion of human ecological influences from highly localized to regional and, ultimately, global in scale.

The development of ecology and other environmental sciences during the past two centuries has led to recognition of these impacts, which has led in turn to a concern with identifying ecological baselines—systems, past or present, that show no discernible human influence—with which to compare modern systems for impact assessment. Restoration ecology, conservation biology, and ecosystem management all rely on these baselines, which often include estimates of past natural variability. However, geohistorical records are providing abundant evidence of widespread human impacts on populations, communities, and ecosystems, even in places long thought to be relatively unaffected by human activities (Douglas et al., 2004; Willis et al., 2004) (see Box 3.10). Recent evidence suggests that agricultural societies had global effects on biogeochemistry at least 5,000 years ago (Ruddiman and Thomson, 2001; Ruddiman, 2003).

Although a strong case has been made for the role of humans in the extinction of large mammals in North America starting about 13,000 years ago (Martin, 1967; Alroy, 2001b), evidence for a human role in such ancient extinctions remains mixed (e.g., Guthrie, 2003, 2004) and a scientific con-

BOX 3.10
The Ecological Effects of Prehistoric Whaling

Even some remote lakes of the high Arctic have been altered by human activity long before the advent of industrial society. Douglas et al. (2004) examined the sedimentary and fossil record of a high Arctic lake adjacent to an AD ~1200-1600 Thule Inuit whaling settlement on Somerset Island, Canada. The lake differs from most other isolated Arctic lakes in having unusually high concentrations of total phosphorus, organic carbon, and calcium. The site is scattered with whale bones, including bones used in the construction of dwellings, 10 bowhead whale crania that may have been used in ceremonies, and scattered bones, baleen, and skin of other marine mammals.

A detailed chronology of the lake sediments was provided by ^{210}Pb dating, and archaeological materials were dated with AMS radiocarbon dating. Strongly positive δ^{15}N values in lake sediments indicate the influence of decaying marine organic matter on the lake while the relative abundance of several diagnostic species of diatoms document the response of the lake's flora to the human-caused influx of nutrients from decaying whale carcasses.

An increase in δ^{15}N values in the lake sediments follows the initial Thule Inuit settlement in AD ~1200, and the increase in abundance of an epiphytic diatom marks the development of moss vegetation in the lake. Clearly, decaying whale carcasses provided the unusually high nutrients that characterize this lake. Despite the site's abandonment in AD ~1600, the decay of carcasses and continuing decay of bones has sustained the lake's high levels of phosphorous and high δ^{15}N values for the past 400 years. Human impact on this high Arctic lake system long preceded the influence of Europeans and lingered long after the abandonment of the settlement.

sensus has proven elusive (Grayson et al., 2001, Cardillo and Lister, 2002; Barnosky et al., 2004; see Figure 3.1). Regardless of the role of humans in Pleistocene extinctions, there is a growing realization that we have inherited a world that has already been profoundly altered by human activities.

Organized, systematic monitoring and documentation of ecological systems date only to the 19th century, although fragmentary information can be gleaned from documentary sources and museum collections dating back a few centuries. Even for the 20th century, important gaps remain in our observational network for ecology. Failure to recognize the extent to

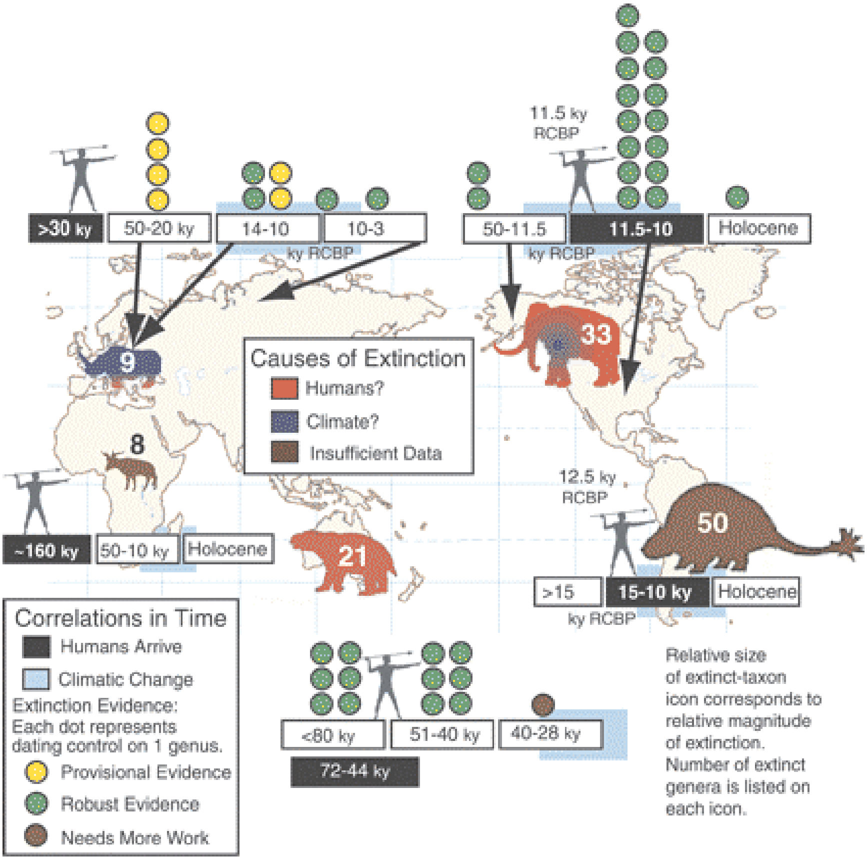


FIGURE 3.1 Summary of the numbers of megafaunal genera (genera consisting of species with body sizes >44 kg) that became extinct on each continent, the strength of the extinction chronology, and a comparison of the timing of extinction with the timing of human arrival and late Pleistocene climatic change. SOURCE: Barnosky et al. (2004); used with permission.

which ecological systems have been altered by human activities can lead to confusion and error in ecological theory and application. The pioneers of ecology often overlooked the fact that systems they studied were far from pristine, leading them to misattribute patterns arising from human disturbance to processes such as succession (e.g., S.T. Jackson et al., 1988). We are not immune from this problem today, given the widespread impacts of humans throughout the globe.

Populations, communities, ecosystems, and the biosphere all have "memory;" they carry vestiges of past events and trends, owing to delayed response to forcings or perturbations, persistence of physical entities, and the contingent nature of many ecological phenomena on previous states or events. This "ecological memory" is encapsulated in the concept of ecological legacies, defined as current properties of an ecological system that can be explained only by events or conditions that are not present in the system today (see Box 3.11). Thus, many features of modern systems, from the absence of large size classes in coastal fish populations to the high fire risk in many western forests to the relatively high pre-industrial methane concentrations in the earth's atmosphere, may all be regarded as legacies of past societal activities (respectively, fishing, fire prevention, and rice cultivation) (J.B.C. Jackson et al., 2001, Swetnam et al., 1999; Ruddiman and Thomson, 2001).

We can neither understand nor manage the ecological systems of our planet adequately without determining which features are ascribable to natural processes and patterns and which are ecological legacies of societal origin. The geologic record can and must play a critical role in assessing such legacies. In nearly all cases, geohistorical records provide the only source of information on ecological history that extends to pre-human (i.e., true baseline) conditions.

Opportunities for Scientific Advance

Geohistorical records can contribute to understanding of human impacts and legacies in innumerable ways, from individual lakes, wetlands, and forest stands to regional, continental, and global scales. Particular demands will arise at the local level as resource managers and restoration ecologists come to appreciate the need for historical information and context (Egan and Howell, 2001). Greatly improved understanding and application can come from studies that integrate ecological, paleoecological, and archaeological approaches to:

1. discriminate effects of human activities from those of climate variability;
2. assess the magnitude and extent of impacts on specific ecological systems under different societies, cultures, and technologies;
3. determine how local effects of human land use and habitat alteration scale up to aggregated effects across heterogeneous regions, including entire catchment basins;
4. exploit opportunities to use past or ongoing human activities (e.g., top predator removal, landscape alteration, nutrient enrichment) to evaluate fundamental ecological theory;

BOX 3.11
Ecological Legacies

The legacy concept in ecology originated from the observation that ecosystem recovery following large natural disturbances (e.g., the 1980 Mt. St. Helens eruption and the 1988 Yellowstone fires) was influenced by organisms that survived the disturbance as well as physical and biotic structures (windthrow mounds, dead trees, soil carbon, coarse woody debris) that persisted from the previous community (Franklin and Halpern, 1989; Foster et al., 1998). The concept has since been expanded to incorporate any property of an ecosystem that is attributable to a past event (e.g., a wildfire) or system state (e.g., a previous community at the site). For example, age structure of a forest or woodland stand may be linked to a disturbance event centuries ago (Swetnam and Betancourt, 1998; Frelich, 2002), soil structure of a forest stand may be attributable to occupancy of the site by prairie vegetation several thousand years ago, and nitrogen reservoirs in Antarctic lakes may be attributable to high lake levels of the Pleistocene (Moorhead et al., 1999). Human activities, including management practices, also impose legacies across a wide range of spatial scales (Wallin et al., 1994; Swetnam et al., 1999; Foster et al., 2003).

Ecological systems carry these historical signatures for a variety of reasons. First, ecological processes occur across a wide range of timescales, so one component of a system may change rapidly in response to disturbance or environmental change while another may change very slowly. For instance, a crown fire kills most trees and burns most fine fuels in a forest stand within minutes, while coarse woody debris and soil carbon can persist for decades after the fire (Foster et al., 1998). Plant species composition can change in response to climate change within decades, while soil carbon reservoirs may require centuries or millennia to respond. Second, ecological systems can leave a strong imprint on the environment that may persist long after the originating system has disappeared or been replaced by another. For example, vegetation influences the physical and chemical structure of soils, and many species, ranging from prokaryotes to trees and mammals, have bioengineering properties, creating landforms that can persist for decades to millennia (Jones et al., 1994; Crooks, 2002). Third, many properties of biological systems are contingent on history. The genetic structure of populations contain overprints of population history (Hewitt, 2000; Petit et al., 2003), age structure of populations is often governed by previous mortality, recruitment, and/or dispersal events (Swetnam and Betancourt, 1998), and soil nutrient reservoirs are influenced by the climatic and vegetation history of the site. Human land use imposes legacies in soil and vegetation that can persist for hundreds to thousands of years (Motzkin et al., 1996; Dupouey et al., 2002; Foster and Aber, 2004). The concept of ecological legacies provides a vital link between ecology and the historical sciences.

5. identify the differential sensitivity of ecosystems to persistent legacies of human activities; and
6. address human legacies that affect species, habitats, and ecosystems of particular management concern and societal value.

The kinds of systems and timescales at which geohistorical records can be applied to these problems are legion. Humans affect ecosystems in a variety of ways, ranging from inadvertent introduction of diseases and invasive organisms to direct utilization of native species to appropriation of entire habitats for conversion to agricultural or urban landscapes. Hunter/fisher/gatherer societies have different impacts from pastoral/agricultural societies, which differ again from industrial/urban ones. There is considerable diversity among cultural groups within each of these broad categories. And impacts of any given culture should be contingent on the local ecosystems and the prevailing environment, including climate and climate variability. All ecological studies and management efforts should be preceded or accompanied by serious investigation of the extent to which system properties represent legacies of past human activities (Hamburg and Sanford, 1986). Well-focused, integrative studies of the kind described above will put us in position to use the past to manage for the future.

Natural Variability and Shifting Baselines

Environments and biotas vary naturally around some ever-shifting mean value. The magnitude of this variation depends on characteristics of the environment as well as the frequency, duration, and temporal resolution of observations. Documenting this natural variability is important because the demonstration of human impact requires that we separate the "signal" of human action from the "noise" of non-anthropogenic variation.

Assessing the natural range of variability requires geohistorical perspectives because observational environmental and ecological records do not nearly encompass the full range of natural variability over the past few centuries, and there is abundant evidence for human impact on the environment throughout the entire observational record. Similar problems plague all ecological investigations because no living systems can be considered pristine. Completely "natural" systems (in the sense that they are unaffected by the consequences of human activity) are only available in the geologic record. Fortunately, as described earlier, the quality of environmental and biotic information in the record often allows the reconstruction of environmental variation with seasonal and annual resolution.

A common problem in measuring human impact is what fisheries biologist Daniel Pauly (1995) called the "Shifting Baseline Syndrome."

Scientists and the general public alike tend to define a "natural" or "pristine" baseline as the way things were either when they were first observed, or from descriptions of the very recent past. Human impacts are then measured from this baseline of personal, short-term experience, despite the likelihood of prior human-caused change. For example, in fisheries, each new generation of fishers tends to resist limits to their catch because they consider the present day catch as the norm, rather than the enormous catches of the previous generations. The now-classic example concerns codfish from the Gulf of Maine—for the 5,000 years leading up to the 20th century, the average size of fish caught and eaten was about 1 m, whereas the average size steadily decreased in the 20th century (J.B.C. Jackson et al., 2001; see Figure 3.2). Ignorance of this change allowed continued fishing when the average size had already dropped by two thirds in the 1970s and 1980s, leading to the subsequent total collapse of the fishery.

We can still unambiguously define an environment and its associated biota as pristine based on the way things were at that place—plus or minus the natural range of variation—immediately before the first arrival of modern *Homo sapiens*. This admittedly discounts the environmental effects

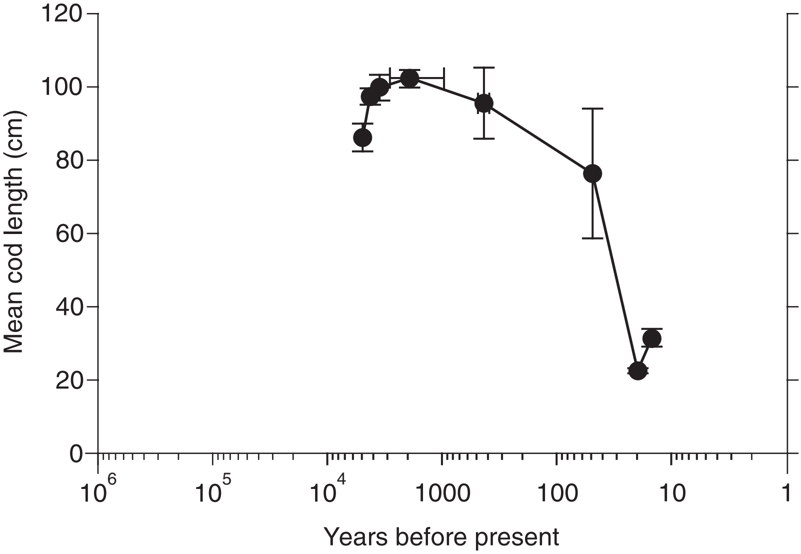


FIGURE 3.2 Time series of mean body length of Atlantic cod from kelp forests in the coastal Gulf of Maine. The earlier five data points are derived from archaeological records, whereas the last three points are from fisheries data. SOURCE: J.B.C. Jackson et al. (2001); used with permission.

of pre-modern humans in Africa before 150 Ka, but for our purposes here we can probably dismiss these effects as relatively minor. All other definitions of pristine depend on more arbitrary assessments of a lack of "significant" human impact, despite the presence of human populations, and are subject to the problem of shifting baselines noted above.

The value of recognizing the pristine condition of an environment and biota is that it provides a basic frame of reference to assess all subsequent human and natural environmental change. Most interestingly, such true baselines allow us to ask the question: "What was the world like just before the arrival of modern humans?" Of course, the first arrival of people around the world was not synchronous, and required almost the entirety of human existence from first origins in Africa approximately 150-100 Ka. Very approximately, modern humans arrived in Europe and Asia between about 100-50 Ka, in Melanesia and Australia about 60-40 Ka, in the Americas about 20-12 Ka, in Polynesia 2 Ka, and less than 1,000 years ago in New Zealand and Madagascar. This delayed arrival of people in progressively remote locations from Africa provides a powerful tool to distinguish between changes in climate and human impacts as causes for biotic change.

Assessing Human Impact

A reliable frame of reference needs to be established for evaluating human impacts over many timescales throughout the Holocene. Human land use and habitat alteration have left signatures on the landscape and in geohistorical records dating in many cases to the first human colonizations. Sedimentary charcoal indicates increased incidence and extent of wildfires upon colonization of Australia by aboriginal hunter-gatherers ~40,000 years ago. Hunter-gatherer societies throughout the world have used fire as a tool to manipulate habitat, with effects on vegetation composition and structure detectable in geohistorical records at local to regional scales (e.g., McGlone, 1989; Burney, 1999). Agricultural societies have had even greater impacts, converting natural vegetation to agricultural lands. Such conversions in the prehistoric record have ranged from transient and local (e.g., Iversen, 1973; McAndrews, 1988; McAndrews and Boyko-Diakonow, 1989) to persistent and regional (Berglund, 1992; Binford et al., 1987; Brenner et al., 2002). Societies with large populations and advanced technologies, both agricultural and industrial, have tended to have even greater and more persistent effects.

Because aquatic systems accumulate sediments and are influenced by land use in surrounding catchment basins, they are particularly effective recorders of human impacts. Lakes accumulate sediments continuously and thus are especially effective recorders of human activities in the surrounding watershed (e.g., Smol, 2002; Alin et al., 1999, 2002; Cohen, 2003) as well as distant regions. For example, paleontological and geochemical studies of lake sediments in the Adirondacks and other regions provided critical confirmation that regional ecosystem acidification was a result of mineral acids from distant industrial sources (Charles et al., 1990, 1994; Battarbee and Charles, 1994). Signatures of human activities also show up in fluvial, wetland, and estuarine sediments, even though deposition may be irregular or discontinuous. Studies of estuarine sediments have revealed the extent to which coastal ecosystems have been altered by human agricultural, industrial, and fisheries activities (J.B.C. Jackson et al., 2001; Curtin et al., 2001; Cooper and Brush, 1991; Brush, 1997). Sediments of lakes and peat bogs have been used to document onset of metal mining and smelting (e.g., Shotyk et al., 1998; Martinez-Cortizas et al., 1999), providing biogeochemical baselines.

Human impacts on Holocene environments and biotas are generally much more closely related to cultural, technological, and economic attributes of societies than to the simple presence of humans (see Box 3.12). This is often most clearly evident from comparisons of human activities and their consequences during the rapid economic transitions associated with colonial occupation (e.g., the Americas before and after European conquest and colonization, Australia before and after British colonization). Other critical transitions include the advent of intensive agriculture, industrialization and resource exploitation based on fossil fuels, and transitions from local to regional to global markets.

Documentation of human-caused changes in the distribution, abundance, and size of species and the distribution and composition of communities offers the potential for reconstructing the structure and function of natural communities. This is fundamental for understanding the adaptations and limits of species that now inhabit strikingly different habitats than those lived in previously. Some possibly general patterns of the consequences of human activities have been identified, but require considerable further examination in a wide variety of settings:

- the loss or ecological extinction of megafauna;
- shortening of food webs;
- distortion of biogeochemical cycles;
- shifts from heterogeneous to homogeneous biogeographic distributions due to invasive species;
- general loss of biodiversity; and
- replacement of eukaryotes in the oceans by bacteria and archaea.

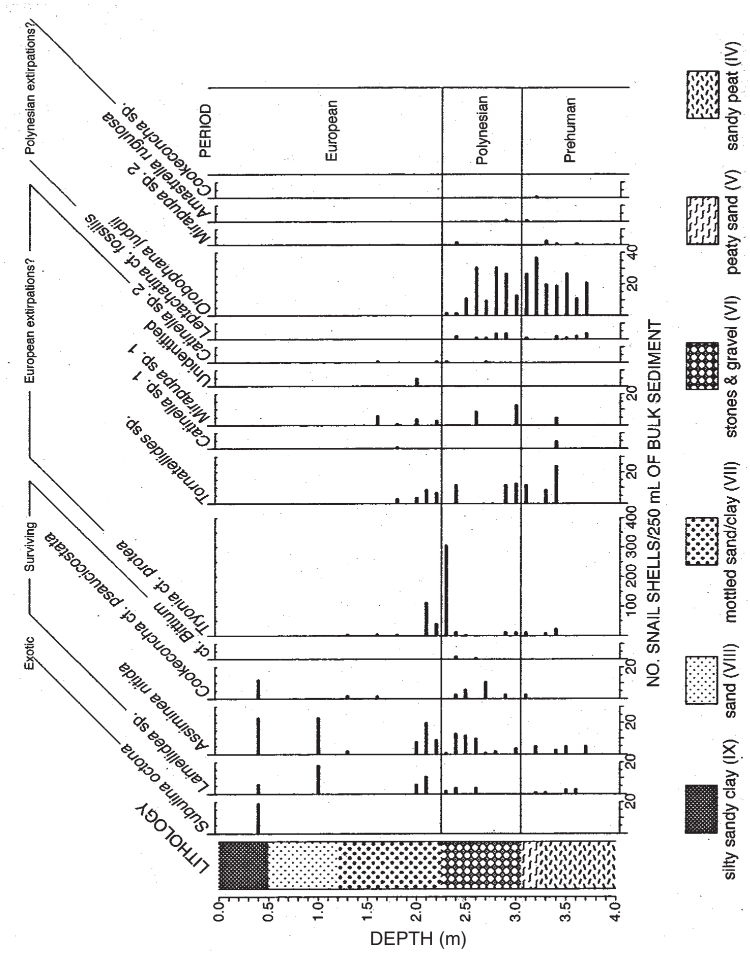
As pointed out by Margalef (1968), all these processes may act to reverse ecological succession while at the same time increasing produc-

BOX 3.12
Prehistoric (and Historic) Impacts of Humans on Polynesian Faunas

Islands of the central tropical Pacific—Polynesia—have been invaded by two successive waves of human culture. The prehistoric Polynesian (or Lapita) culture swept westward across the region beginning about 4,000 years ago, reaching the most remote islands (Hawaii, Easter Island, New Zealand) in the past 1,000-2,000 years. The Polynesians cultivated imported crops, tended domesticated livestock (pigs, chickens), and foraged for wild plant and animal foods. They also imported dogs and rats. The late 18th and 19th centuries saw secondary colonization and conquest of the Pacific islands by European and Euro-American cultures. On the larger islands (e.g., Hawaiian islands, New Zealand), these latter cultures implemented extensive and intensive grazing (cattle, sheep) and cultivation (sugar cane) in the 19th century, as well as imported a wide variety of non-native plants and animal species.

Paleontological studies provide rich records of the impacts of these activities on native fauna and flora. Easter Island saw particularly devastating impacts of Polynesians, with deforestation leading to extinction of all the native trees (Dransfield et al., 1984; Flenley et al., 1991). Native bird communities throughout Polynesia underwent rapid species extinctions as the Polynesians arrived; as many as 2,000 species of birds, comprising some 20 percent of global avian diversity, may have disappeared during the Polynesian invasions (Steadman, 1995).

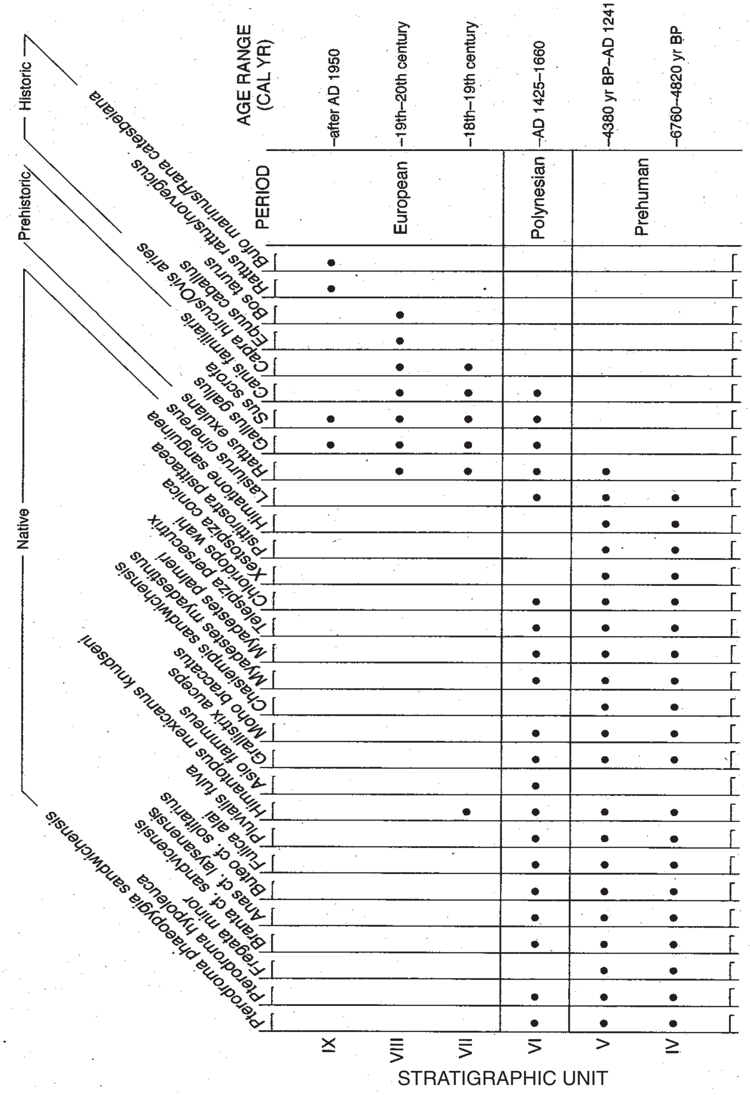
A recent integrated paleontological excavation on the island of Kauai (Hawaii) illustrates the severity of the losses associated with Polynesian activities, as well as the impacts of the second, European, colonization wave (Burney et al., 2001). Native species of crabs, marine mollusks, land snails, and birds that survived the Polynesian invasion were exterminated during the 19th century (see figures below). Pollen and macrobotanical data indicate that plant species that are now rare and restricted to remote montane sites were widespread in the coastal lowlands before human colonization. Few of the native vertebrate and invertebrate animals recorded in the pre-Polynesian sediments remain today. As Burney et al. (2001) observed, the paleontological record at their site “documents the purloined riches of a truly lost world.”



Abundance of fossil snails in sediments of the Mahaulepu Sinkhole, Kauai. Note apparent extinctions of at least five native species during the Polynesian period, extinction of six species since European and Euro-American colonization, survival of three native species, and introduction of one exotic species. SOURCE: Burney et al. (2001); used with permission.

continued

BOX 3.12 Continued



Occurrence of vertebrate bones in sediments of the Mahaulepu Sinkhole, Kauai. Note the severe loss of native bird species (11 species portrayed are extinct on the island, as are other species not on this diagram), Polynesian introductions of rats (*Rattus*), fowl (*Gallus*), pigs (*Sus*), and dogs (*Canis*), and European introductions of rats and toads (*Bufo*). SOURCE: Burney et al. (2001); used with permission.

tivity. Although this increases food supplies on land in the case of agriculture, the process greatly decreases food supplies in the ocean because microbes and jellyfish come to dominate the resulting communities. Simple food-web models can be employed to estimate the standing crops of species at different trophic levels using historical data for estimated abundances of apex predators that have greatly declined before ecological observations began (Christensen and Pauly, 1993). Historical data describing the composition and structure of communities offer powerful but under utilized tools for estimating the ecosystem consequences of human impacts.

Historical Ecology and Restoration Ecology

Truly pristine pre-human conditions may not provide realistic targets for resource management or ecosystem restoration. Such pristine conditions have not occurred more recently than centuries to thousands of years ago, depending on the ecosystem and its location, and the world is already in a different climate regime. Nevertheless, they are an essential frame of reference for evaluating the natural geographic ranges and habitat distributions of species, their characteristic size frequency distributions, and a host of other parameters that are the essentials of basic ecological research. Furthermore, such fundamental baselines provide goals for ecological restoration, to the extent that prevailing climatic conditions allow. And by allowing us to differentiate natural phenomena from legacies of human activities, and to determine the specific human activities to which particular legacies are attributable, they provide a sounder basis for determining realistic and appropriate management and restoration targets. Knowing whether a particular vegetation pattern or disturbance regime is attributable to natural conditions, pre-European Native American land use, or Euro-American impacts, for example, is an essential first step in management decisions. Decisions ultimately rest on a number of social, scientific, economic, and political considerations, but historical knowledge can provide more informed judgments. As an example, pinyon pines (*Pinus edulis*) do not grow at Chaco Canyon National Monument today. Yet paleontological studies indicate that they occurred there naturally from ~6,000 years ago until the populations were exterminated by Anasazi fuel harvesting 1,000-800 years ago (Betancourt and van Devender, 1981). This information complicates, but also enriches, decisions.

One of the greatest values of historical data describing ecological conditions before substantial human impacts is the formulation of goals for ecological restoration. This is particularly important in the case of habitats and ecosystems that were not described or monitored before human disturbance. Although much restoration can be guided by conditions in nearby, relatively undisturbed settings, there is an increasing appreciation for the value of historical data from both documentary evidence and natural biotic and environmental archives (i.e., the proxy data described in Chapter 2) (e.g., Brenner et al., 1993; Brush, 1997). Indeed, for long-lived species such as trees, the long temporal framework provided by tree ring analysis is essential for understanding such important phenomena as fire frequency and migration rates (Swetnam et al., 1999). This historical approach to restoration has now matured to the point where techniques for reconstructing reference ecosystems and their historic range of variation are well established for a variety of terrestrial and coastal ecosystems (see Egan and Howell, 2001).

The application of historical ecology to issues of ecosystem restoration and management has enormous potential for both basic and applied research. In basic research, the integration and cross-calibration of observational, documentary, and proxy ecological data provides both a near-continuous and long-term ecological record as well as the opportunity to develop confidence limits for proxy indicators farther back in the geologic record. In applied research, the approaches of historical ecology demand close collaboration among biologists, geologists, and archaeologists engaged in ecosystem management and restoration—practical issues that are an increasingly important focus of the U.S. Geological Survey.

4

The Culture of Collaborative Research

While recent technological and conceptual progress makes positive collaborations between biologists and geologists especially promising, organizational frameworks and traditions have the potential to either promote or retard such collaborations. Scientists, whether in academic or agency settings, are sensitive to institutional reward systems and the opinions of their peers as well as new research opportunities.

As new scientific disciplines and subdisciplines emerge, they follow a variety of paths. Frequently, initial efforts focus on the core elements of their new field of inquiry. Scientists record observations, take measurements, and seek patterns and processes that characterize their field. This phase of information and data accumulation tends to focus on the fine points of the discipline, in many cases adopting a reductionist approach that provides great detail about the subject. Then—as a discipline matures—scientists often reach out to adjacent fields to provide new insights and opportunities for investigation. Efforts to organize and synthesize data from disparate observations and experiments also begin to develop. This may start with the search for new tools or with comparisons between different systems, and eventually leads to more conceptual or theoretical considerations about the relationships between issues at hand. This intellectual expansion yields even greater interactions as the web of scholarship expands in all directions.

This same intellectual trajectory happens in many individual scientists over the course of their careers. Initial training usually focuses on collection of data and their analysis. Scientists seek research support for these activities, publish the research results, and generate solutions based on those results. As they mature individually, some researchers begin to look for patterns and seek the broader implications of their research and thus many senior scientists reach out beyond their own expertise to collaborate with colleagues in allied disciplines, taking advantage of synergistic interactions to seek answers to important questions. A few scientists seek even broader collaborations that synthesize information across extensive areas of expertise in search of comprehensive understanding of the nature and scope of their discipline. Truly exceptional scientists can manage broad syntheses single-handedly, but such individuals are so rare that the scientific community must also develop team-based strategies to yield the insights that emerge from cross-disciplinary syntheses.

Our reward systems tend to promote individual scholarship and its products over the processes required for broader, more synthetic, activities. In many institutions, the order of authorship and even the number of authors is viewed as an important characteristic of published work such that being sole author, first author, or an author among few co-authors is viewed as especially worthy. Individual grants and the number of graduate students in one's own laboratory are important evaluation criteria rather than the development of multidisciplinary projects with dispersed resources and intellectual capital.

Synthetic, interdisciplinary research requires efforts that can be viewed as unproductive and even onerous (such as increased efforts at communication, data sharing). Furthermore, results emerging from large projects with many authors may be devalued (i.e., divided by the number of authors) in our current reward system, even though it may lead to insights that an individual scientist might not have been able to conceive or might not have had the standing to promote or publish.

These issues arise in many disciplines and are becoming increasingly common as teams of research scientists organize to address issues from different perspectives. Such "team science" requires explicit reconsideration of funding schemes, measures of academic performance, protocols for authorship, and policies for sharing data. For example, the National Institutes of Health (NIH) has established initiatives to facilitate interdisciplinary research,[1] NIH's Bioengineering Consortium has recently reported on the nature and implications of team science,[2] and Altshuler and Altshuler (2004) discuss the challenges in combining genome science and human clinical research. Thus, while the issues discussed below are not unique to the integration of biological and geological approaches to understanding biosphere dynamics, they are important to progress on the topic.

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[1] See http://nihroadmap.nih.gov/interdisciplinary/index.asp.

[2] See http://www.becon.nih.gov/symposia_2003/becon2003_symposium_final.pdf.

PROMOTING THE CULTURE OF COLLABORATION

Opportunities for collaboration begin with the notion that the results of collaborative, synthetic research are important and yield results that would otherwise be difficult or impossible to achieve. Because of the nature of the research we envision here, we must develop a reward system with an appreciation of the collateral responsibilities, time commitments, and costs associated with collaboration—from data sharing to increased respect for large-scale projects that may appear to dilute the role of individuals.

New forms of collaboration, driven by the need to bring together broad expertise to address multidisciplinary questions, must be encouraged and facilitated. Although individual research will always be important, substantial or comprehensive collaborations are needed to address truly large and complex issues. A topic as broad as the biosphere and involving complex dynamics must include consideration of diverse topics requiring associations among researchers from the disciplines of ecology, microbiology, geology, paleobiology, oceanography, climatology, archaeology, geography, and biogeochemistry. Collaborations need to overlap sufficiently to ensure that the full array of issues under consideration are being addressed, but also be broad enough so that each collaborator has distinctive contributions to make.

Minimizing hurdles to collaboration. Institutional structures and processes that inhibit collaboration must be addressed. While some interdisciplinary programs (programs in systems biology to foster collaborative efforts in molecular biology, for example), have flourished in universities, many opportunities are inhibited by department- or institution-specific requirements and accounting systems for both funds and academic credit.

There is no ideal organizational structure for institutions that facilitates collaboration and coordination of activities. However, institutions can develop specific intellectual bridges for interdisciplinary research and actively promote them. Within, and especially among, academic institutions this may mean breaking down the notion that the "winner" in a collaboration is the person or institution that receives the largest share of a project. This means moving toward a system that recognizes that being a contributor to several or many successful projects is at least as valuable as being the major recipient of support for an individual project.

Within the federal system, this may mean ensuring that the most appropriate people are engaged in research projects, regardless of which agency, division, or research facility they are associated with. This requires a means to use or transfer funds that is not easily accomplished in the current system.

Collaborative research requires additional infrastructure, funding,

and effort. Effective collaboration engenders specific additional costs in both time and money (meetings, communications, resolution of misunderstandings or conflicts) that are not associated with individual research. Collaborators, funding sources, and host institutions must recognize that additional communication and coordination results in a net gain in understanding and knowledge that can be greater than the sum of results from smaller projects undertaken over the same amount of time. Participants in large or diverse collaborative projects may need to develop formal or informal management plans to promote effective interaction. Furthermore, funding agencies must be willing to support the extra infrastructure (in the form of salary, personnel, hardware, and travel for face-to-face communication) needed to support collaborative efforts. While all involved may understand the concept of the division of labor, explicit efforts must be made to ensure that scientists are focusing on the intellectual components of a project while being assisted by able project managers, technicians, and other support staff.

Reward systems. Current academic reward systems tend to depreciate the value of collaborative research. The time spent in coordination may be viewed as unproductive, and the activities required for collaboration (e.g., data integration, developing and employing data standards) may not be judged valuable in their own right by peers or administrators. Papers with many authors, or even synthetic results in a book (versus individual research) may be undervalued. While we must continue to place high value on individual research, we should also accept that the activities associated with collaboration and synthesis are especially valid contributions to scholarship and not a simple form of community service.

Our current reward system embodies a complex, but well-known, system of credit. In smaller projects, the role of multiple authors is fairly transparent, and assigning the order of authorship can be straightforward. In highly collaborative projects, there may be many authors with different responsibilities, and their order of precedence may be difficult to ascertain (see Kennedy, 2003). This circumstance is exacerbated by certain journals that arbitrarily limit the number of authors on a paper, further complicating the reward structure of research efforts.

Protecting intellectual property. There is an apparent conflict between making information broadly available and protecting the intellectual property of those who generated it. However, while some information generated by ecologists and geologists might have economic value, most of the value is perceived by scientists as intrinsic to a greater understanding of the processes of nature. In this case, economic value is replaced by the value of recognition and acknowledgement from peers. Nevertheless, just as individuals and corporations may be unwilling to share information with inherent economic value, scientists often are concerned that if they make their data broadly available before it has been fully explored intellectually, someone else may take advantage of the effort. For example, a scientist might collect deep-time samples from many locations and make the data broadly available. It may be possible for someone, as the project nears completion, to interpret what is already available, thereby pre-empting the primary researcher. The problem is especially acute for new researchers just beginning to build a reputation for originality and productivity. Scientists must be assured that the potential benefits of open access to data outweigh the risks of misuse.

Although community standards are emerging on these issues (NRC, 2003b), individual scientists will need to find intellectual satisfactions in shared projects that outweigh the overhead associated with such research. Some solutions will emerge from modified reward systems that nudge us into accepting the costs, and benefits, of collaboration.

OPPORTUNITIES FOR COLLABORATION

Developing new cultural and technological infrastructure for promoting and enhancing interactions will help provide the foundation for increased collaboration. We must also support, and encourage the use of, specific opportunities for training, analysis, integration, synthesis, and widespread sharing of information. These opportunities should be supported as distinct entities whose specific purpose is to facilitate those processes that promote collaboration.

Some existing programs are good models for efforts to promote interdisciplinary, collaborative research projects. The National Science Foundation (NSF) supports collaborative efforts at several points along the research track. For example, the Integrative Graduate Education and Research Traineeship (IGERT) Program has as its goal "to catalyze a cultural change in graduate education, for students, faculty, and universities by establishing new, innovative models for graduate education in a fertile environment for collaborative research that transcends traditional disciplinary boundaries. It is also intended to facilitate greater diversity in student participation and preparation and to contribute to the development of a diverse, globally aware, science and engineering workforce." These awards support graduate students in interdisciplinary studies across and between campuses, with the goal of producing young scientists who embrace collaboration and synthesis. Breadth in NSF-sponsored research is fostered through cross-cutting initiatives such as Biocomplexity in the Environment, division-scale efforts such as the Division of Earth Sciences (EAR) Biogeosciences Initiative, Directorate for Biosciences (BIO)-funded centers such as the National Center for Ecological Analysis and Synthesis and the planned Center for Synthesis in Biological Evolution, and the BIO-funded Long Term Ecological Research (LTER) sites. NSF also has a long record of support for ocean drilling, perhaps the foremost geoscience collaborative research activity (see Box 4.1). Proposal development, shipboard participation, and postcruise scientific interaction have enabled generations of young researchers to collaborate closely with senior scientists in an intense, multidisciplinary environment.

Research Laboratories

The Long Term Ecological Research (LTER) program at the National Science Foundation supports integrated ecosystems-level research at

BOX 4.1
A Model for Successful Collaboration: National and International Ocean Drilling

Almost 40 years ago, testing the seafloor spreading hypothesis was the impetus for a group of four U.S. marine geoscience institutions to collaborate on a proposal to collect seafloor core from the world's oceans. This proposal resulted in the Deep Sea Drilling Project (DSDP), which existed solely as a U.S. program from its first drilling leg in 1968 until 1973, when the first international partner (Soviet Union) joined. By 1975, DSDP was being supported by five international participants and involved nine U.S. institutions.

In the early 1980s it was clear not only that ocean coring using the DSDP drilling platform—the *Glomar Challenger*—had been immensely successful, but also that there continued to be considerable potential for additional scientific discoveries from the world's oceans. DSDP terminated in 1983, but a new program—the Ocean Drilling Program (ODP) with a more advanced drillship, the *JOIDES Resolution*—commenced in 1985. From this time until it terminated in 2003, ODP drilled almost 1,800 holes at more than 650 sites around the globe, ranging from shallow reef depths (40 m) to the deepest ocean (5.9 km). ODP evolved from an initial scientific collaboration involving 10 U.S. institutions and 17 international partners to a partnership involving 18 U.S. institutions with funding support and scientific participation from 22 international partners. As a consequence, many hundreds of individual scientists from around the world participated in ODP collaborative science. One theme that persisted through this history of strikingly successful national and international scientific collaboration was that the broadest possible participation would be sought to maximize the intellectual stimulus available to the program.

BOX 4.1 Continued

The Ocean Drilling Program drillship R/V *JOIDES Resolution* departing from Townsville, Australia, for a drilling leg in the South Pacific. Following their two months of close collaboration onboard the drillship, the 28 members of the shipboard scientific party—from nine different countries—spent several years collaborating onshore to produce more than 50 scientific papers. SOURCE: Photograph by David A. Feary; used with permission.

In 2004 the international ocean drilling community took the next step with the establishment of the Integrated Ocean Drilling Program (IODP), with plans to use multiple drilling platforms to ensure that an even greater proportion of the global ocean would be able to yield scientific results. At least three platforms would be used, with shallow continental shelves and the Arctic Ocean high on the list of scientific targets.

During the last 40 years, the ocean drilling programs—DSDP, ODP, and IODP—provided the impetus and platform for development and testing of a broad range of scientific hypotheses and concepts, including the movement of the world's continents described by plate tectonics, the dramatic history of global climate change from the Cretaceous world with polar forests to the modern world with its melting ice caps, the immense global thermohaline circulation system that moves water from shallow seas into the deep ocean, and the metabolic functions of microorganisms in the deep biosphere ecosystem far below the seafloor.

multiple sites in North America and Antarctica (see Box 4.2). The sites emphasize ecological studies across many subdisciplines and regional scales. These projects, which concentrate on ecosystem patterns and processes, have been collaborative, incorporating a wide range of disciplines. Similar programs, focusing on other levels of biological organization (e.g., communities, populations) would expand the high value of programs such as LTER. Furthermore, developing new field research programs that support the technically sophisticated techniques and instruments required for contemporary ecological and geological field research would further promote collaboration between scientists from different disciplines.

BOX 4.2
The Long Term Ecological Research Network

Many ecological research projects occur on short timescales governed by budget and granting cycles or academic calendars, even though most important ecological processes take place over decades, centuries, and millennia. Recognizing this, the National Science Foundation sponsored a series of workshops in the late 1970s to develop concepts for a program supporting long-term ecological research and promoting forms of collaboration required to sustain a comprehensive research agenda. The program that emerged, the Long Term Ecological Research Network,[3] took as it core mission and central intellectual theme the **understanding of long-term patterns and processes of ecological systems at multiple spatial scales.**

To accomplish this mission, the network initially focused on field research at sites representing many habitats in the United States. Ecological processes at all sites were to be investigated by directing observations, measurements, monitoring, and experiments toward five major areas:

- Pattern and control of primary production;
- Spatial and temporal distribution of populations selected to represent trophic structure;
- Pattern and control of organic matter accumulation in surface layers and sediments;
- Patterns of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters; and
- Patterns and frequency of site disturbances.

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BOX 4.2 Continued

In addition to new sites, NSF supported expanding the breadth of research at some sites to include social sciences. Furthermore, the Network began to promote international collaborations such that a number of other countries have instituted programs similar to LTER. SOURCE: Long Term Ecological Research Network[4]; used with permission.

Although all the 26 LTER sites focus on the core objectives of the network, each site has distinctive themes associated with each habitat type. For example, Konza Prairie (KNZ)[5] maintains watershed-level manipulation of fire frequency and bison grazing to determine the role these historically

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BOX 4.2 Continued

important factors play in maintaining diversity of tallgrass communities. The H.J. Andrews site (AND), managed by the U.S. Forest Service, focuses on successional changes in ecosystems, forest-stream interactions, population dynamics of forest stands, patterns and rates of decomposition, and disturbance regimes in forest landscapes. The two urban sites, Central Arizona[6] (Phoenix - CAP) and Baltimore Ecosystem Study (BES)[7] are investigating the relationship between ecological, sociological, and economic factors in major urban areas. The other sites contribute equally to core areas while also addressing local and regional issues.

Because the scope of research at LTER sites is quite broad, it is inherently multidisciplinary. This feature is reinforced by the emphasis on the five core areas of research, each of which relies on a wide array of scientists for a comprehensive understanding of the underlying principles. With regard to interactions and collaborations between geologists and biologists, those core areas pertaining to biogeochemistry, soil formation, and surface and subsurface water are particularly reliant on broad field research and intellectual engagement.

As the LTER Network has matured, opportunities have emerged from the core research areas. These include education training and outreach, information management and dissemination, and providing data and ecological insight to the wise management of natural resources. The sites and their network office are also heavily involved with developing research tools, and are actively promoting synthesis between sites.

The LTER Network now represents an important element in the research and intellectual infrastructure of ecology. Ecological research, which has both core elements emerging from theoretical and empirical approaches, and a scope that incorporates many allied disciplines, has flourished in response to the LTER Network. It is clear that this is an effective model that could be embellished or adapted for other forms of collaboration between disciplines.

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[3] See http://lternet.edu/.

[4] See http://lternet.edu/sites/.

[5] See http://www.lternet.edu/sites/knz.

[6] See http://www.lternet.edu/sites/cap.

[7] See http://www.lternet.edu/sites/bes.

The proposed National Ecological Observatory Network[8] (NEON) would address regional and continental-scale issues in ecology and evolutionary biology through a network of sites focused either on critical environmental challenges or ecosystem types (NRC, 2004). Such a network would certainly facilitate collaboration between ecologists and environmental biologists. However, current plans focus primarily on real-time monitoring and experimentation and do not call for the sort of integration across timescales envisioned in this report. A geohistorical approach could extend NEON's observational reach to encompass hundreds to thousands of years. This would add value by providing historical context for modern systems, and by providing opportunities for linked modeling, experimental, and geohistorical studies. The availability—or potential for development—of geohistorical records should be considered in selecting NEON study sites, particularly those focusing on climate change, land-use effects, biodiversity, and biogeochemistry.

The National Center for Ecological Analysis and Synthesis

The goal of the National Center for Ecological Analysis and Synthesis (NCEAS)[9] is to use existing data from a broad range of disciplines to address important ecological questions. By taking a broad view of ecology, the center has involved many scientists who would not consider themselves ecologists, including geologists, hydrologists, and paleontologists. NCEAS facilitates collaboration by hosting meetings and supporting postdoctoral and sabbatical researchers conducting synthetic research. Furthermore, because the center relies on existing data, it has developed significant research efforts directed toward generic access to data.

Field research in ecology often requires work in distant and isolated locations. One result is that many scientists and students are isolated from intellectual interactions with disciplines peripheral to the particular topic being investigated in the field. Recognizing this, the ecological community has supported the notion of a center for synthesis where ecologists and scientists from allied disciplines could congregate to address important questions.

NCEAS focuses on using existing data to address important ecological questions, and employs three main types of research approaches. The most distinctive are the working groups, teams of up to 20 researchers who conduct meetings lasting three days to three weeks several times over the course of a year or two. Working groups actually conduct research at the center, synthesizing data, developing theories and models,

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[8] See http://www.nsf.gov/bio/neon/start.htm.

[9] See http://www.nceas.ucsb.edu/.

and testing them with data. Approximately 700 visiting scientists a year participate in working groups. NCEAS also supports four to six center Fellows (sabbatical visitors) each year from around the world. The fellows are in residence for 4-12 months, and typically become engaged in working group activities. Finally, NCEAS supports 15-20 postdoctoral associates for one to three years. About one-third are formally associated with working groups, but even the others, who come to NCEAS to work on their own projects, become involved with one or more working groups. The postdoctoral associates are unusual in that they have no formal mentors. Rather, they interact with the hundreds of visiting scientists at the Center. This yields young scientists with the important skills and appreciation for creative, collaborative, multidisciplinary research. Most projects are initiated by research proposals that are reviewed by a Science Advisory Board composed of 19 members from many disciplines and several countries.

The physical facility consists of meeting rooms and offices for visiting and resident scientists and comprehensive computing capabilities. The atmosphere is promoted by a staff dedicated to minimizing the extra effort required to travel to the center and work collaboratively. A key feature of the center is the breadth of participation. Participants are highly diverse with regard to nationality, academic rank, institutional affiliation, and importantly, scientific discipline. The 3,200 participants belong to more than 180 scientific societies, have published their results in 140 journals, and many come from departments that are not biology-based. The dynamics among the resident scientists (postdoctoral associates and fellows) and the hundreds of visiting scientists each year generate an intellectual ambience that is quite productive (e.g., ~1,000 publications in 10 years, with an average impact factor more than twice that of the top 20 journals in ecology). The NCEAS model is successful in promoting creativity and interdisciplinary research.

While detailed sociological studies are being conducted on NCEAS to characterize how scientists interact effectively, there are also a few obvious features that contribute to collaboration. In the first place, the center was formed at a time when many scientists knew they wanted or would benefit from the opportunities it provides. Perhaps the most important resource the center provides is the opportunity to interact, primarily mediated through specific time set aside to focus on the issues under consideration. Furthermore, scientists are in close proximity and are there explicitly to interact. Another important feature is the center's pleasant, neutral location; it is not on a campus, freeing participants in unanticipated ways to interact effectively. The facility, logistic support, and comprehensive computing and analytical support lower the activation energy to conduct interdisciplinary research and yield an intellectual ambience that promotes creativity and productivity.

Collaboration, synthesis, and analysis of existing data provide added value to research conducted by individual scientists. The model of collaboration at NCEAS is simple. Attempts are made to choose good projects and productive, creative scientists and then to facilitate their endeavors. It is a highly portable model, and could easily be employed in other circumstances to promote the interdisciplinary efforts envisioned in this report.

Community-wide Databases and Collaborative Research

Science benefits from technological advances that promote information sharing and collaboration. Increased and speedier travel and communication enhancements spurred the sharing of information and development of ideas. Scientists are now approaching the capability to share actual data, even in real time, in a manner that will lead to another quantum leap in the opportunity for integration, synthesis, and understanding. Specifically, we must develop access to the wide array of highly distributed and heterogeneous data that characterize the disciplines of interest—information pertaining to ecological dynamics might range from genetics to global change. This is not only an enormous breadth of data types, but in addition much of the data across this spectrum is gathered, stored, analyzed, and modeled in different ways. The traditional approach to this circumstance is to develop application-specific solutions, particularly databases that are customized for the topics under consideration. While effective to an extent, the data may not be more generally accessible in this form, severely limiting its usefulness. Thus, generic data access and integration tools are essential so that data can be effectively reconfigured for uses other than for which they were originally intended. This requires data management and higher-order access concepts to promote integration across disciplines that have inherently different semantics.

True generic access requires a distinct data management model that provides access to information in place of a uniform database structure. Rather than standardizing inputs and outputs, the solution lies in developing ontologies (complex synonymies of fields and attributes) and metadata (information about the data itself). Information, once linked through ontologies or characterized with metadata, can be made accessible in context-dependent ways that are both comprehensive and efficient. With a community-based web portal to the database, hundreds of thousands of data resources, from small compilations (doctoral dissertations, individual researchers' results) to large, well-known data sources (weather, ocean temperatures, remotely sensed data) can be incorporated in research, planning, and resource management. The key tools are efficient and flexible ways to describe and enter ecological and geological information, powerful searching capability, and tools for data visualization and analysis.

Effective collaboration requires more than access to pertinent data. Collaborating scientists must be able to quickly analyze data, and transport it into appropriate visualization tools that make the data understandable to the array of collaborators from several fields. Once user-friendly tools to acquire and analyze data are available, it will be possible to quickly find, download, and analyze disparate datasets to test an idea much in the way we now use abstracts of articles to get a sense of whether a new idea warrants further consideration.

Existing community-wide database efforts. An extraordinary amount of ecological, environmental, geochronological, and paleobiological information is becoming available electronically. Many individuals, research groups, and institutions are providing access to vast amounts of data online in the form of customized datasets generated to address specific questions or issues. These efforts to turn data into datasets add value that can be useful in unanticipated ways. We note here some ongoing efforts that will be important to the successful analysis of the geologic record of ecological dynamics.

- **The Paleobiology Database**[10] is an NSF-funded project that provides global, collection-based occurrence and taxonomic data for marine and terrestrial animals and plants of any geological age, as well as web-based software for statistical analysis of the data. This project currently has 133 participants from 57 institutions in 11 countries and promotes collaborative efforts to answer large-scale paleobiological questions by developing a useful database infrastructure and bringing together large datasets. It presently contains 409,210 occurrences (documented presence of a taxon at a geographic-stratigraphic site) among 39,721 collections.
- **FAUNMAP**[11] is a relational database that documents the temporal and spatial distribution of mammals for the last 2 million years in Canada and the United States (Faunmap Working Group, 1994). Entries in the database are based on collections in a public repository with precise geographic location and a fine-scale chronological framework. FAUNMAP is linked to a Geographic Information System equipped with ARC/INFO software that allows for the geographic distribution of more than 200 individual species to be mapped for 11 distinct time periods. Statistical parameters derived from manipulation of the database and other treatments can also be mapped at a variety of scales.
- The **Chronos Project**[12] is an NSF-funded effort to assemble, integrate, analyze, and disseminate geologic and paleontological data relating

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[10] See http://paleodb.org/.

[11] See http://www.museum.state.il.us/research/faunmap/.

[12] See http://www.chronos.org.

to geologic time with a platform that links to a variety of chronostratigraphic, paleogeographic, paleoclimatic, paleontological, and geochemical databases. Chronos will be a “federation” of databases. Chronos will also provide individual researchers with web-based tools to search for information relevant to research questions, Geographic Information System and Time Information System capabilities, correlation routines that can be remotely run on the San Diego Supercomputer, and the visualization tools necessary for the effective display and integration of information about the history of life on Earth. Still in its early stages of development, Chronos is also designed to provide outreach to students and the general public.

- **EARTHTIME**[13] is an NSF-funded project involving geochronologists, paleontologists, and stratigraphers to produce the highly resolved geological timescale necessary for the rigorous analysis of evolutionary and geological rates. Current geochronological information, particularly in deep time, is insufficient to adequately constrain rates and thus processes of change. This effort will work closely with Chronos and other projects.
- The **North American Pollen Database**[14] (NAPD) is a cooperative database of Quaternary pollen data from North America and is one of several continental databases that together constitute the Global Pollen Database[15] (GPD). The NAPD is funded by the National Oceanic and Atmospheric Administration (NOAA), whose primary goal is to facilitate the application of fossil pollen data to paleoclimatic inference and model testing. However, the NAPD has been widely used in ecological and biogeographic studies (e.g., Williams et al., 2001, 2004). The NAPD, GPD, and other paleontological databases administered by the NOAA’s World Data Center for Paleoclimatology (e.g., North American Plant Macrofossil Database, Western North American Packrat Midden Database, Insect Database, International Multiproxy Paleofire Database) deserve continued support, particularly from agencies charged with supporting research in biosphere and ecological history. NOAA’s Paleoclimatology program has recently been targeted for elimination or severe downsizing; such action would be disastrous for these vital databases. Increasing research emphasis on biosphere responses will place more demands on paleoclimatic reconstructions, and in many cases will require development of paleoclimate records and analytical capabilities that are specifically geared to biological questions. Although the NOAA paleoclimate databases are

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[13] See http://www-eaps.mit.edu/earthtime/.

[14] See http://www.ngdc.noaa.gov/paleo/napd.html.

[15] See http://www.ngdc.noaa.gov/paleo/gpd.html.

managed specifically for paleoclimatic applications, many are of major importance for paleoecology (e.g., pollen, plant macrofossils, tree rings).

- The **Geosciences Network** (GEON) research project,[16] supported by NSF, is a collaboration between information scientists and geoscientists to develop ontologies and portals to link datasets and provide analytical and visualization tools to the geosciences community at large. The central Appalachians and the Rocky Mountains are being used as "test beds" to demonstrate how existing geophysical, structural, geochemical, paleontological, and paleogeographic databases can be linked to examine the tectonic, sedimentary, and biotic evolution of the two regions. Integration of the heterogeneous datasets in these two areas will provide a model for the even broader range of geosciences datasets necessary to understand the complex dynamics of the earth system.
- **Deep Time**[17] is a collaborative project between paleobotanists and molecular systematists focused on the evolutionary history of plants. It is funded through the NSF's Division of Biological Infrastructure and involves more than 100 participants as well as postdoctoral support. The project addresses common interest areas related to molecular clocks, integration of molecular and morphological data, examples of cladistic analysis of particular datasets, and the agreement and discordance of the molecular and paleontological datasets. These interest areas often cross boundaries between plant- and animal-based data, so both are included.

The development of these community databases provides some important general lessons for the future:

1. The most successful databases appear to be those that are motivated by closely related scientific questions generated at the community level. Such grassroots efforts ensure the "buy-in" of contributors, the rapid generation of research results, and the continued growth and evolution of the effort.
2. Development and management of databases involves interactions between natural scientists and information scientists, whose research strategies and objectives may not always converge. The problems that may stymie natural scientists may be routine and uninteresting to information scientists, and vice versa. Communication between these cultures is essential, and creative ways to facilitate it are needed.
3. Databases require commitments from one or more funding sources to ensure that they continue to be maintained and to assimilate data as

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[16] See http://www.geongrid.org/index.html.
[17] See http://www.flmnh.ufl.edu/deeptime/.

long as they are scientifically useful. They also require long-term commitments from scientists and institutions to house them. Research museums may be particularly well suited as homes for databases because curatorial and archiving activities are routine functions in these institutions.

4. Databases involve trade-offs between posterity-driven archival functions and the immediate needs of scientific users. There is a risk that shortcuts taken in data formatting, database architecture, and metadata assimilation may facilitate short-term and ongoing applications at the expense of future applications that may have different requirements.

SUMMARY

The various models discussed in this chapter (e.g., IGERT, LTER, NCEAS, and community-wide databases) promote collaboration through training, research, and analysis and synthesis. Although most of these particular examples are supported by NSF, they—and other models that encourage collaborative research—are easily exportable to other research and education entities, from individual campuses to government agencies. Indeed, successful large-scale multidisciplinary efforts in genetic sciences (e.g., National Center for Biotechnology's GenBank,[18] the Human Genome Project[19]) and NASA's Astrobiology Institute[20] demonstrate that effective collaborations among disciplines can be stimulated and supported though the creation of appropriate programs, centers, and other community-based efforts. Future progress in understanding the geologic record of ecological dynamics will require not only new and better data but also better capacity for analyzing and synthesizing the data that we already possess. Although the collective cultures of the relevant disciplines are evolving in this direction, much more can be done to facilitate this evolution at levels ranging from individual institutions to funding agencies.

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[18] See http://www.ncbi.nlm.nih.gov/.

[19] See http://www.ornl.gov/sci/techresources/Human_Genome/project/about.shtml.

[20] See http://nai.arc.nasa.gov/.

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Conclusions and Recommendations

Environmental variability, driven both by natural processes and by human forces, is pervasive at virtually all temporal and spatial scales. We can observe environmental change in local neighborhoods over individual lifespans, infer it from stories told by grandparents, and recognize it in both historical documents and in the data captured by geohistorical records. In a changing world, understanding the patterns, processes, and principles governing the participation of biological systems in environmental change—and understanding how those systems respond—is a scientific and societal priority of the highest rank. Our growing understanding of physical environmental change must be linked with a major effort to understand the response of biotic systems to environmental change. Both wild and managed biological resources are of extraordinary significance for human welfare, and consequently how they change in response to climatic and other environmental change is of great importance. If we are to achieve this goal, analysis of the geologic record needs to become a full partner to the empirical analysis and modeling of present day biological systems.

To promote significant and timely progress in understanding the geologic record of ecological dynamics, we recommend that a substantive new research effort be focused on the three research initiatives described below, in order to (1) further our understanding of the basic principles of ecological organization and dynamics; (2) enhance our ability to predict the response of biological systems to climate change in particular; and (3) provide a means to distinguish between anthropogenically- and non-anthropogenically-caused changes in biological systems. These topics are ripe for scientific exploration, and have great societal relevance. Success will require new investment in the general field of biogeosciences, as well as support for infrastructure that encourages research integration, collaboration, and coordination among earth scientists and biologists.

Research efforts will require substantial material support because biological systems are complex entities with dynamics spanning a broad range of scales that are affected by chance and historical contingency. The inherent complexity of biological systems at all scales—individual species, guilds, communities, biomes, biosphere—and the increasing footprint of human activities over the last several millennia and centuries—requires that we bring the full panoply of scientific approaches to the problem of understanding ecological dynamics. In the past, geohistorical analysis has received little effort compared with that expended on ecological modeling, modern observations, and manipulative experiments. This is despite the extraordinary potential of the geologic record for yielding essential information on patterns and processes of biotic response to environmental change. As outlined in the preceding chapters, advances over the past two decades have revolutionized earth scientists' ability to date and extract critical biological and environmental information from the geologic record. Moreover, biologists increasingly realize that long-term historical perspectives are vital for answering a host of biological questions, both fundamental (e.g., principles of community organization and individual species response) and particular (e.g., timing of biotic change relative to natural and human stressors in a given region).

Until now, limited use of the geologic record reflects long-standing uncertainties about the adequacy of geohistorical information for answering ecological questions. These uncertainties are now largely resolved—a broad and diverse array of geohistorical records are demonstrably suitable for addressing ecological questions. The limited use of the geologic record also reflects the cultural, disciplinary, and administrative barriers that separate the earth and biological sciences. Analysis of the geologic record of ecological dynamics cannot be tackled without a significant commitment in effort and funds, and without renewed emphasis on genuinely multidisciplinary research both by agencies and by individuals. Without such change, only a few earth scientists (researchers, reviewers, supervisors, fund managers) will identify biological problems as falling under their disciplinary mandate. Similarly only a few biological scientists will find it practicable to acquire the skills needed to analyze geohistorical records, no matter how important geohistorical data are to the questions being addressed. However, like several previous national committees (e.g., NRC, 2001c, 2004; NSB, 2000), this committee considers that a deeper understanding of ecological dynamics should have a high scientific priority. As a matter of policy, federal agencies should take the lead in facilitating and establishing means of achieving success in the analysis of the geologic record of ecological dynamics.

We identify the following three initiatives as being ripe for intensified exploration and having the highest scientific and societal relevance.

INITIATIVE 1:
THE GEOLOGIC RECORD AS AN ECOLOGICAL LABORATORY

> **Recommendation: A deeper understanding of the origin, maintenance, and distribution of biodiversity and its importance to ecological systems is urgently needed. It is essential to expand fundamental research using the longer time perspectives of the geologic record to frame and test ecological theories at appropriate scales while encompassing a full range of earth conditions.**

Most ecological theories are derived from short-term observations and models. But the ecological and evolutionary processes operating at timescales beyond direct human observation have driven, and continue to drive, changes in biodiversity and biogeochemical cycling on local, regional, and global scales. A fundamentally important role of geohistorical data in ecological analysis is to provide empirical data from longer timescales. An understanding that extends beyond short-term observations is essential to (1) characterize longer-term ecological processes; (2) identify patterns and mechanisms that are masked by the variability inherent in direct, short-term observations; (3) identify which aspects of modern ecological systems are contingent on past events; and (4) permit ecological analysis under conditions different from those of today. Such tests of ecological theories, and their underlying assumptions, are necessary because ecological principles can be considered truly general only if they apply to ancient species and communities as well as to modern ones. The geologic record is thus an ecological laboratory providing access to a wide range of past "alternative worlds" from which truly general principles can be derived regarding the triggers, character, and rates of change of ecological properties and functions.

An understanding of these general principles is necessary not only to understand ecological response to past climate change and legacies of societal activities (Initiatives 2 and 3 below) but also to address basic questions concerning the dynamics of biodiversity at all spatial and temporal scales. Are the macroecological properties of communities across modern and ancient settings (including those lacking modern analogs) constant? Can taxa within guilds or trophic levels be substituted—in the face of local extinction and immigration—without changing ecosystem properties? To what degree is spatial ecological variation comparable to temporal ecological variation? What is the impact on local diversity patterns of regional species pools that have been assembled over evolutionary timescales? Are areas of high diversity characterized by high speciation rates, or are they simply long-term accumulators (characterized by low extinction rates)? What is the role of local extinction on the influx of biotic invaders? What is the relative importance of physical environmental and biotic forcing on ecological and evolutionary change?

INITIATIVE 2:
ECOLOGICAL RESPONSES TO PAST CLIMATE CHANGE

> **Recommendation: Climate change and its consequences are of enormous scientific and societal concern. A significant research initiative to pursue a richer understanding of how biotic systems have responded to and interacted with past climate change and variability is needed to provide a sounder basis for forecasting the ecological consequences of future climate change and variability.**

Climate is a dominating influence on the distribution and abundance of organisms, the nature and rates of biogeochemical fluxes, the structure and composition of ecological communities, and the frequency and intensity of ecological disturbance. Geohistorical data show that Earth's climate is capable of a wide variety of system states and modes of variability. To understand how biological systems are likely to react in the future, we need to understand how ecological systems have responded to climate change and variability in the past. Paleoclimate studies of ice cores, sedimentary records, tree ring series, and other records clearly indicate that the past two centuries have experienced only a fraction of the potential variability within the climate system. This is an inadequate sample of the range and nature of climate variation. As a result, ecological studies based on direct observation of current systems provide an inadequate sample of the array of biotic responses to climate change and of the potential consequences for biodiversity and biogeochemistry.

Understanding biotic responses to climate changes of the past is pivotal to forecasting how ecological systems are likely to respond to ongoing and future climate changes, whether natural or anthropogenic. Paleoclimate studies reveal that, just within the past 10,000 years, climates with no modern counterparts have prevailed over much of the globe, and abrupt changes in climate have occurred with unexpected magnitude and rapidity. The near future is likely to include climate states with no modern analogs as well as abrupt climate changes. Just as paleoclimate records were critical to identifying important properties of Earth's climate system and assessing risks and vulnerabilities to future change, paleoecological records of biotic responses to past climate change are critical to forecasting ecological responses to future change and assessing risks and vulnerabilities.

INITIATIVE 3:
ECOLOGICAL LEGACIES OF SOCIETAL ACTIVITIES

> **Recommendation: Societal activities have impinged on the natural world in many ways, but the consequences and possible solutions to these impacts are unclear when some impacts are difficult to distinguish from non-anthropogenic variation. Intensified research on environmental and ecological conditions and variability before human impacts and on the geohistorical records of how societal activities have affected present day ecosystem dynamics is essential.**

Environments and ecosystems have been profoundly affected by societal activities. Because the effects are far-reaching and began long before the advent of direct observations, the geohistorical record is the only source of information on (1) how ecosystems functioned in the absence of human influence; (2) the natural range of environmental variability and ecosystem function; (3) how ecosystems have responded to progressive human impacts; and (4) which aspects of present day environmental variability and ecosystems are a legacy of past societal activity. Geohistorical records constitute an archive of the natural state of ecosystems before significant societal impact, and of how ecosystems have been transformed by past and ongoing human activity.

The effect of societal activity on natural environments and ecosystems is an unintentional global experiment already in progress. However, the initial conditions of this experiment are largely unknown because the onset of human interactions with these systems—both intentional and unintentional—predate scientific monitoring efforts. There is thus no control for time in this experiment; completely natural habitats are no longer available either locally or globally to use as benchmarks for comparison with habitats or regions of known impact. Similarly, so-called natural variability (i.e., unaffected by societal activity) in environments and ecosystems can be rigorously estimated only by reference to the geological record.

Acquiring such knowledge of pre-human baseline states and natural variability is essential for discriminating between anthropogenic and non-anthropogenic change in species, biotas, and ecosystems. Insights into the sensitivity and response of ecosystems to human activities are critical in developing strategies for conservation and restoration; thus this initiative has significant potential for practical benefits to society. In seeking to predict and manage ecosystems in the face of future environmental perturbations, whether natural or societally driven, we must take advantage of the opportunity to understand how societal activities have affected ecosystems in the past. Understanding the ecological impact of past societal activities is also crucial for the recognition of persistent effects—legacies—that may continue to influence ecosystems long after the causative societal activities have ceased.

FACILITIES AND INFRASTRUCTURE

Funding and Personnel

> **Recommendation: Funding levels for research on the geologic record of ecological dynamics must reflect the research's technological needs and the societal importance of understanding the biological response to environmental change. Funding should be structured to ensure that both research and graduate training take full advantage of collaborative opportunities across disciplines.**

Federal research funding on the geologic record of ecological dynamics has not kept pace with the increased costs of geochemical analyses, high-precision dating, large numbers of samples, the establishment of databases vital to synthetic studies, and the need for collaboration among investigators and students from multiple disciplines. In addition, funding has not kept pace with the increased interest in this topic within the scientific community that has resulted from society's increasing need to predict and manage future biotic change.

Although it may be predictable that a review committee will call for increased funding or other commitment of new resources to a field, it is a fact that new kinds of research cannot be pursued without changing the resource allocation. Within the National Science Foundation (NSF), support for core programs in the Division of Earth Sciences (EAR) and the Directorate for Biosciences (BIO) should be increased. Such programs have supported the development of many of the innovative concepts and techniques essential for research in ecological dynamics and have supported the training of students now poised to conduct research in this area. Continued low proposal success rates will stifle further innovation and discourage research just as the disciplines have reached a critical point. The need for integrative studies, almost certainly requiring the collaboration of researchers from both directorates, also requires the investment of funds into cross-directorate initiatives such as those proposed above. Some existing cross-program and cross-directorate efforts could incorporate and foster geohistorical analysis of ecological dynamics with relatively little modification of their mandate by adoption of one or more of the initiatives identified above (e.g., as an initiative under the Biogeosciences Program, or the Biocomplexity in the Environment Program). The review panels for these programs and the Advisory Committee for Environmental Research and Education (ERE), which has oversight over the Foundation's environmental science portfolio, should include one or more individuals with expertise in geohistorical records relevant to biosphere analysis. Accordingly, we see two modes of support within NSF for geohistorical analysis of ecological dynamics, one through core programs for smaller projects, and the other through cross-divisional and cross-directorate initiatives intended to stimulate collaborative research on this topic. Assessing the ecological consequences of past climate change and variability is a critical missing element of NSF's component of the U.S. Climate Change Science Program (CCSP). The closest existing program, Earth Systems History (ESH), cannot accommodate an expanded mandate to include biotic responses without erosion of its current activities and commitments. A significant increase in funding to ESH, together with participation on panels and administration of individuals with expertise in geohistorical analysis of biotic responses to climate change, would be one potential solution. Such an expansion could take advantage of the paleoclimate expertise of the ESH community and fuse it with the ecological perspectives of the paleobiology community. Alternatively, a companion program to ESH, concentrating on biotic responses to past environmental change, could be developed within NSF.

Other federal agencies should also be able to support research in this area, particularly in those topics especially appropriate to their missions. The Environmental Protection Agency's STAR (Science to Achieve Results) graduate fellowship and grant programs are especially relevant and effective. The National Oceanographic and Atmospheric Administration (NOAA) can build on its strengths in paleoclimate reconstructions to incorporate biotic responses to climate change as an explicit part of its research mandate. NOAA already has a long tradition of involvement in research on paleoclimate and in research and management of marine fisheries. While this has led to some productive interactions between Quaternary scientists, biologists, and physical oceanographers, little of this research has used geohistorical data or methods to analyze past ecosystems in the context of NOAA's mandate to provide climate forecasting.

The existence within the U.S. Geological Survey (USGS) of both geologic and biologic expertise is highly favorable for integrative, collaborative efforts using geologic records of biological systems, and, in particular, Initiative III (Ecological Legacies of Societal Activities) is in close accord with the agency's environmental missions. The USGS has both the facilities and the expertise for coring and for the sedimentary and paleontologic analysis of those cores, and it would be logical for geohistorical analysis to be a standard portion of many, if not most, place-based research studies having an environmental component. At present many of these studies sample only surficial sedimentary deposits or conduct only real-time monitoring to acquire environmental and biological information. For example, the South Florida ecosystem and Chesapeake Bay projects of the USGS could easily extract ecosystem information as well as proxy indicators of prior conditions. Systematic paleoenvironmental and paleobiologic analysis will enable the USGS to meet its goal of providing science for a changing world. For settings, methods, and taxonomic groups for which it lacks expertise, the USGS could partner effectively with other agencies having common research and management interests as well as with research universities and institutes. For example, very few NSF-funded Long Term Ecological Research (LTER) sites have used geohistorical data on environmental change and biotic response, although these represent superb opportunities for the nation to leverage long-term investments of biological effort and funds. Some structures for partnering with academia already exist within the USGS in the form of cooperative units.

The nature of research on the geologic record of ecological dynamics should be structured to encourage and support the collaboration of professional biologists and geologists, as well as the training of a highly flexible next generation of scientists who take such interactions for granted. To foster this, we recommend establishing a postdoctoral program by the NSF whereby new Ph.D.s would collaborate and have as their mentors PIs from other directorates—such matches have the advantage of engaging scientists very early in their careers, with potential for a longer period of positive downstream effects. The USGS already has a postdoctoral program to bring new ideas and expertise to the agency, and this could be modified, enlarged, or partially committed to specifically match biologists and geologists on integrative geohistorical projects. We also recommend the introduction of Doctoral Dissertation Improvement Grants (DDIGs) to NSF's Directorate for Geosciences (GEO). These grants in the Directorate for Biosciences are a proven means of encouraging graduate students to go beyond traditional approaches to a research topic.

Laboratories for Geologic Analysis of Ecological Dynamics

Substantial support for research in natural laboratories and for actual or virtual collaborations and facilities is needed to focus intellectual efforts and research tools on the three initiatives described above.

Natural laboratories: Long Term Ecological Research (LTER) and Geologic Time Ecological Research (GTER) Projects. Among existing programs, Long Term Ecological Research sites (LTERs, funded by the Biosciences Directorate) have been one of the most successful for lengthening the time perspective of ecological studies—over the 24 years of the program, 26 sites have been established and are generating observations of natural (and in some instances experimentally manipulated or extensively societally modified) habitats. Existing LTER projects represent a superb opportunity to couple systematic long-term biological monitoring with ecological and environmental observations from times before the instrumental record. Support should be provided for collection and analysis of geohistorical information at or near these sites, using sediment cores from lakes, peatlands, and estuaries, tree ring analyses, cave deposits, skeletal accumulations, and packrat middens to acquire information on both the character and rates of environmental change and the biotic response to that change. Integration of such geohistorical data with the LTER site's observational record and with the results of on-site experiments will build the temporal perspective necessary to detect decadal and longer ecological trends and to discriminate between natural and human-driven changes. In many cases, the best potential areas for obtaining geohistorical records may be outside the boundaries of specific LTER sites, but such geohistorical records can provide representative case studies or regional perspectives relevant to the individual LTER missions. Notwithstanding the potential advantages of connecting LTER observations to adjacent geohistorical records, excellent geohistorical records should be sought in places where they can address critical ecological problems—in estuaries, reefs, tropical lakes, and habitats now strongly affected by societal activities.

Activities within the new National Ecological Observatory Network (NEON) program should go beyond the monitoring, experimentation, and modeling of biotic systems in present day real time. Incorporation of retrospective data describing both past biotas and environmental variability is essential to efforts in ecological forecasting, and thus geohistorical analysis should be made a formal and integral part of the network's mandate.

The committee also recommends Geologic Time Ecological Research (GTER) projects as a promising platform for research on ecological dynamics. A GTER project would designate a particular habitat type, critical region (e.g., land bridge, oceanographic gateway), (paleo)latitudinal belt, environmental gradient, or time interval as a natural laboratory for focused, collaborative study for a five- to ten-year period. Comparable to LTER sites, the Plate Boundary Observatory of EarthScope, or an Ocean Drilling Program cruise, a GTER program would invite proposals for research on one or more of the initiatives proposed here. For example, a long-lived modern lake basin would provide the opportunity to extend observations of current processes back in time—using the fossils and proxy environmental data derived from cores—to address all three of the initiatives identified here. A region known to have undergone past habitat fragmentation (e.g., as a result of tectonic creation of a broad region of complex topography) would constitute a useful laboratory to examine the effects of tectonics on non-analogous faunas. The Panama Paleontology Project[1] (focused on the marine biotic response to the Neogene uplift of the isthmus; funded by NSF and the Smithsonian Institution) is a useful example of a collaborative project that targeted a critical area and time interval in order to explore fundamental principles of biosphere behavior. The project involved a major investment in new geologic and paleobiologic fieldwork and analysis, and provides a valuable temporal framework for understanding the historical events that shape present day biological systems in both oceans. Acquisition of geohistorical data on the South Florida ecosystem by the USGS and partner agency scientists as part of the effort to restore this ecosystem is an excellent example of an applied project of this type.

Research collaborations. Research collaborations are envisioned as actual or virtual forums for the analysis, synthesis, and modeling of *existing* data and for the general exchange of intellectual capital. These collaborations might take a form similar to the NCEAS (National Center for Ecological Analysis and Synthesis) funded by NSF's Biosciences Directorate. In such a setting, collaborative working groups could focus for short periods (multiple meetings over one to two years) on integrative ecological and paleoecological problems that require meta-analysis or synthesis of some combination of empirical and model-generated information. The former Pliocene Research, Interpretation, and Synoptic Mapping (PRISM) project of the USGS, which targeted global paleoclimates of the Pliocene, demonstrates how federal agencies with intramural researchers can lead collaborative projects, although the focus of this particular project was more on physical environmental reconstruction and improved age determination than biotic response. This collaboration demonstrates the con-

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[1] See http://www.stri.org/english/research/programs/programs_information/panama_paleoecology.php.

cept of using a past interval of geologic time—rather than a geographic site or region—as a laboratory to better understand natural systems with relevance to future change.

Synthesis centers and virtual collaborations represent innovative ways to foster integrative work among biologists, paleobiologists, and physical scientists. Resident postdoctoral students associated with such efforts can provide both interdisciplinary training and continuity for ongoing projects.

The committee also recommends support for annual or biannual, multi-day research workshops focused on these interdisciplinary research initiatives. Such workshops could be in conjunction with existing professional meetings or take the form of gatherings like Penrose or Chapman conferences. Such meetings are extremely valuable for intellectual exchange, networking, and the formation of new research collaborations, and will be essential for breaking down some of the administrative and cultural barriers that exist between the biological and earth sciences. For example, the cross-directorate Biocomplexity in the Environment Program at NSF, the Exobiology Program at the National Aeronautics and Space Administration (NASA), and the STAR Program at the Environmental Protection Agency (EPA) all require their current Principal Investigators and graduate fellows to attend annual meetings in order to exchange research results and to network. We recommend forums that are similar in style, but that are not limited to individuals funded by a particular program or agency. Private, non-profit, federal, and state organizations are all potential sponsors of such efforts.

Databases and Collections

Recommendation: Publicly available databases and natural history collections can promote collaboration, reduce duplicated effort, facilitate large-scale synthetic studies, and provide critical and at times irreplaceable data and research opportunities. Federal agencies should play an important role in sustaining and enhancing community efforts to build and improve such entities.

Data are the currency of research in the geological and biological sciences. For this reason, the maintenance and accessibility of data in either digital form (e.g., electronic databases) or physical form (e.g., museum collections, cores, paper records) are essential for the effective and efficient conduct of ecological dynamics research. The number and size of online databases have grown enormously in the past decade, and are sure to increase even more in the next decade as the pressure increases for greater access to the results of publicly funded research. Previously collected data and natural history collections must be maintained and accessible, and repositories for newly collected data should be provided. We are being overwhelmed with data even as we labor to find more. Enhanced federal support is therefore critical for the expansion of community-wide database efforts and for the maintenance of existing collections and archives, including the discovery and integration of metadata. In addition to their archival function, databases provide a vital platform for the synthesis and analysis of data at scales that would have been impossible in the past—they are a powerful new research tool.

Natural history and geoscience collections often provide vital information on environmental and biotic conditions before human impact, access to materials that can be used to test critical hypotheses in the earth and life sciences, and fossil and live-collected specimens no longer available in the field. An important attribute of natural history and geoscience collections is that they have lasting value. Collections are frequently studied by new investigators to answer questions that had not been previously anticipated. These unanticipated uses often arise when new analytical techniques make it possible to acquire different or improved information from previously studied material. In addition, collections are especially important when re-sampling is either impossible or impractical. The original sites of many collections are no longer accessible and live-collected specimens from periods before extensive human impact provide irreplaceable and invaluable baselines. Preserving and curating existing collections will require significant allocations of space as well as some ongoing input of curatorial resources, but without such collections, attempts to characterize past biotic and environmental change and understand their interconnections will be severely compromised. Previous recommendations that have focused on geoscience data and collections (NRC, 2002b), including museum collections, have equal applicability to the broadly interdisciplinary data that will be needed by the geoscience and bioscience communities to address the complex biosphere issues outlined above.

Enhancement of Capabilities for Age Determination and Correlation

> **Recommendation: The research efforts proposed here require additional support for dating facilities, for the cost of dates in research projects, and for the development of techniques critical for high-resolution age determination and correlation.**

Improvement in the application of geohistorical records to understanding ecological dynamics requires improvement in three aspects of geochronology: (1) enhanced resolution of radiometric dates; (2) greater understanding of the temporal resolution of fossil assemblages themselves; and (3) improved tools for correlation—the assignment of isolated geohistorical records to a high-precision timescale.

High-precision radiometric dating is expensive, time consuming, and frequently constitutes the money-limiting or rate-limiting factor in paleobiological research. There is a clear need for support of low-cost, fast-turnaround laboratories for radiometric dating and related chronostratigraphic analyses (e.g., radiocarbon, volcanic ash, geochemical markers). The existing geological timescale also lacks sufficient resolution in many places to adequately determine rates of biological and geological processes. Targeted research aimed at providing a high-resolution (better than 0.1 percent accuracy) timescale is needed. As the resolution of the geologic timescale is progressively refined, there is a continuing need to improve the accuracy of geochronologic techniques. Pertinent issues here include resolving differences between labs in data standardization and handling, decay constants, and other aspects that limit inter-laboratory comparison of results. Additionally, the number of groups pursuing extremely high-resolution analyses is very small, which suggests a need to either establish national facilities for this work or spread best practices to a greater number of facilities. Attention is also needed to provide improved statistical techniques—e.g., where a series of dated horizons are available in a single section, the overlapping uncertainties should allow refinement of error estimates; however, the statistical basis for such refinement has yet to be developed.

Late Quaternary researchers will benefit particularly from access to low-cost, quick-turnaround radiocarbon dating, and from development and dissemination of statistical tools for age-model development. Accelerator Mass Spectrometry (AMS) dating is opening up many new questions and applications, making high-precision dating (decadal to centennial scale) possible in a number of contexts. Such precision requires large numbers of dates for each site, as well as rapid turnaround. Investment in AMS dating facilities that will provide rapid dates at low cost would enable a wide array of questions to be addressed by the community. Although calibration of radiocarbon age estimates to calendar years Before Present (BP) is now routine, the available tools and software are primitive and inadequate for community needs. Statistical tools for age calibration and calculation of age-depth models for sediment sequences are urgently needed. A modest investment aimed at developing these tools and incorporating them into freely available and user-friendly software would yield a major return in quality and quantity of high-precision paleoecological studies.

How much time is represented in a bedding plane full of fossils? Even when strata can be dated to a high precision, the fossils contained within those strata may represent an accumulation over hundreds to thousands of years. It is necessary to determine whether there are any general rules for the degree of time-averaging in different depositional systems and environments. If such rules can be discovered, they would help determine the best age-dating systems for particular types of studies. Extensive application of radiocarbon or calibrated amino acid dating is vital for such work. The new NSF-funded amino acid racemization dating laboratory at Northern Arizona University may serve as a model for a facility that provides dates at a cost-effective price to a broad community of users.

Increased attention is also needed for improved high-resolution correlation between stratigraphic sections, allowing the assignment of isolated geohistorical records to a high-precision geologic timescale. As geochronology improves, the temporal diachroneity and other difficulties associated with traditional biostratigraphy for relative age correlation will become limiting constraints. Advances in geochronologic resolution must be matched by improved methods of correlation based on rigorous and quantitative biostratigraphy (e.g., ordination and optimization) and better statistical analyses of the quality of the fossil record (e.g., confidence intervals). Support is needed for chronostratigraphic databases that will facilitate comparison and correlation among records. A critical issue for understanding many biotic and environmental events in the geologic record, and testing hypotheses for their causes, is the temporal relationship between marine and terrestrial events. Determining whether particular marine and terrestrial events were simultaneous will require more accurate and more comprehensive high-resolution correlations between marine and terrestrial sections. Cross-correlation is an especially important issue during critical biotic events such as mass extinctions. For such important intervals in Earth history, attaining high-resolution correlation between marine and terrestrial sections will require targeted, collaborative efforts.

Enhancement of dating techniques, and new developments in methods for the correlation of geohistorical records—both with one another and with a high-precision timescale—suggest that very high levels of temporal resolution are readily achievable. We envision a correlated geologic timescale with a resolution of better than 1 million years through the Paleozoic, 0.25 Ma for all stage-level boundaries through the post-Paleozoic, with higher resolution through the Cenozoic. Centennial-scale resolution should be routinely possible for the past 25,000-35,000 years, with annual to decadal resolution and correlation possible for many sites within the past 15,000 years.

Enhancement of Methods for Environmental and Biotic Reconstruction

> **Recommendation: The research efforts proposed here require additional support to develop and refine techniques that can extract high-precision environmental and biotic information from geohistorical records.**

Proxy indicators of past environmental change provide the essential evidence needed to assess the nature, rate, and magnitude of the biotic response to that change. Additional research is needed to develop proxy indicators that can be applied in older geohistorical records, to evaluate the preservation of geochemical proxies, and to develop measures of short-term environmental variability. Reconstructing the range of natural variation in past environments is needed to detect environmental changes that exceed the natural background.

Proxy indicators are also needed to recognize microscopic and macroscopic components of past biotas that are not preserved as conventional fossils (e.g., biomarkers, stable isotopes). Proxy indicators for ecological attributes such as abundance, trophic relationships, and growth rates are important for recognizing how ecosystem function changes in response to environmental change. Although impressive technological advances now permit the recognition of biotic elements based on distinctive organic molecules preserved in geohistorical records, this research area is still in an early stage of development. There is enormous potential to use biomolecular methods to recognize the presence, abundance, and biochemical significance of biotas that are not preserved as conventional fossils. Improved understanding of biomarker diagenesis is essential for biomarkers to be used in deeper time.

IMPLEMENTATION

Given the importance of an improved understanding of ecological dynamics, the complexities of the scientific problem, and the time that is needed to train individuals and refine methods for merging biological and geological information, the committee recommends a decadal-scale commitment to applying geohistorical methods to address issues of ecological dynamics. Such a coordinated effort would be highly effective both as a means of tackling important problems and as a vehicle for promoting the integration of earth and biological sciences. Judging from other disciplines, a decade is the minimum time frame for sustained support that is realistically needed to cause genuine change in the scientific community. A decade provides time for multiple initiatives to be rotated through calls for proposals, with a round of renewals for each, so that significant numbers of ambitious projects can be undertaken and new careers can be shaped.

Ideally, the combined earth science and biological communities should have opportunities to intensify and diversify research effort in all three of these complementary directions, and we would expect that different federal agencies might take the lead with different initiatives. All of these initiatives should be used as opportunities to increase interactions across the interface of the earth and biological sciences, and whenever possible should be funded across—rather than within—divisions or directorates of agencies (whether research is intramural or extramural). Most would be good vehicles for partnerships among federal agencies or among federal agencies, universities, and museums.

- **Initiative 1 (The Geologic Record as an Ecological Laboratory)** will be of direct interest to the academic community, which is funded primarily by NSF, but is unlike any previous program in proposing that paleo- and neo-biologists focus on ecological rather than exclusively evolutionary issues. The existing Biocomplexity in the Environment (BE) Program, or its successors, would be a natural home for this topic, as would the Biogeosciences Initiative (currently administered out of EAR in the Directorate for Geosciences). This initiative might also be attractive to the USGS as a research topic, requiring the teaming of scientists across disciplinary boundaries or with university and museum scientists (e.g., through LTERs, existing "place-based" projects of the USGS, or newly proposed GTER projects). Research synthesis using databases, meta-analysis, and re-analyses of collections will be important methods for much of this research; and these are common modes of collaboration between scientists from diverse institutions and between empiricists and modelers.
- **Initiative 2 (Ecological Responses to Past Climate Change)** will require close collaboration and coordination between the paleoclimate, paleoecology, and ecology communities. Ongoing federal funding initiatives centered on past climate change and variability do not currently encourage such coordination. ERPCC is an initiative aimed at documenting ecological responses to past climate change and assessing their implications for sustaining biodiversity and ecosystem services in the face of global change. Funding of such work would need to span NSF directorates, USGS disciplines, NASA, and NOAA; it would be an appropriate addition to the U.S. Climate Change Science Program.

- **Initiative 3 (Ecological Legacies of Societal Activities)** is a natural topic for support by a wide range of federal agencies, including both intramural and extramural research programs at EPA, because of its applied as well as basic research aspects. This initiative differs from existing efforts, however, in its explicit focus on bringing geohistorical methods and materials to bear on the issues. Within NSF, this initiative—like the other two initiatives—would be a part of the Environmental Research and Education portfolio, and would find a logical home in the Coupled Human-Natural Systems Program within BE, or its successor program. This is another natural topic for partnerships among agencies or universities through LTERs as well as USGS and EPA programs focused on particular regions or habitats, but would also be appropriate for synthetic analysis or modeling at regional and global scales.

We do not list these agencies and specific programs to be prescriptive, but rather to give examples of how these initiatives that stress geohistorical methods complement—or are natural extensions of—existing programs.

Only geohistorical data—the organic remains, biogeochemical signals, and associated sediments of the geological record—can provide a time perspective sufficiently long to establish the full range of natural variability of complex biological systems, and to discriminate natural perturbations in such systems from those induced or magnified by humans. Such data are crucial for acquiring the necessary long-term perspective on modern systems. Information from past environmental states, both like and unlike those of the present day, provide the empirical framework needed to discover the general principles of biosphere behavior necessary to predict future change and inform policy managers about the global environment.

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Appendixes

APPENDIX A

Committee and Staff Biographies

Karl W. Flessa (Chair) holds a joint appointment as professor in the Department of Geosciences and the Department of Ecology and Evolutionary Biology at the University of Arizona. He was a Humboldt Fellow at Universität Tübingen, Germany, served as a program officer at the National Science Foundation, was chair of the Department of Ecology and Evolutionary Biology, and a visiting professor at the Universidad Autónoma de Baja California, Mexico. His current research interests focus on the conservation biology and environmental history of the Colorado River delta, the taphonomy, paleoecology, and stable isotope geochemistry of Recent and Pleistocene invertebrates, and the quality of the fossil record. Dr. Flessa is a fellow of the Geological Society of America. He received an A.B. degree in geology from Lafayette College (1968) and a Ph.D. from Brown University (1973).

Stephen T. Jackson (Vice Chair) is professor of botany and director of the Program in Ecology at the University of Wyoming. His research focuses on ecological, evolutionary, and biogeographic effects of environmental change. He is particularly interested in linking patterns and processes at timescales studied by ecologists (months to decades) with those of Quaternary geohistorical records (centuries to millennia). Educational background includes a B.A. and M.S. in botany from Southern Illinois University (Carbondale) and a Ph.D. in ecology and evolutionary biology from Indiana University (1983). He was a National Science Foundation postdoctoral fellow in environmental biology at Brown University and has also served on the Biological Sciences faculties at Idaho State University and Northern Arizona University.

John D. Aber is professor and chair of the Department of Natural Resources at the Institute for the Study of Earth, Oceans, and Space of the University of New Hampshire. Since August of 2003, he has also served as vice president for research and public service. Dr. Aber studies forest ecosystems, with particular focus on nitrogen cycling and the process of nitrogen saturation in forests in response to acid deposition. He earned a bachelor's degree in engineering and applied science (computer science) from Yale University in 1971, and master's and Ph.D. degrees in 1973 and 1976 from Yale in forestry and environmental studies.

Michael A. Arthur is a professor of geosciences in the Department of Geosciences at Pennsylvania State University. Dr. Arthur's research interests focus on sedimentary and stable isotope geochemistry of the marine record to understand paleoenvironments and environmental interactions. Prior to his present appointment, Dr. Arthur taught at the University of South Carolina and the Graduate School of Oceanography at the University of Rhode Island, following periods at Scripps Institution of Oceanography and the U.S. Geological Survey. He has contributed extensively to Ocean Drilling Program science planning committees. Dr. Arthur has received the American Association of Petroleum Geologists President's Award and the F.P. Shepard Medal, and is a fellow of the Geological Society of America

Peter R. Crane (NAS) is the director of the Royal Botanic Gardens, Kew. His current research interests focus on large-scale patterns in the history and diversity of living plants. He is also increasingly concerned with how plant diversity can best be conserved for the future, and how it can be used in sustainable ways for human benefit. Professor Crane has studied plants and vegetation in several parts of the world and has undertaken research on living plants in numerous families in order to establish a secure basis for comparison with fossil material. He was awarded the Bicentenary Medal of the Linnean Society of London in 1984, and was elected as a fellow of the Royal Society in 1998. He was knighted by Her Majesty the Queen in 2004.

Douglas H. Erwin is a research paleobiologist and senior scientist in the Department of Paleobiology at the Smithsonian Institutions National Museum of Natural History. His interests range from the causes and consequences of the end-Permian mass extinction, to the role of ecology and development in the Cambrian radiation of metazoa, to the evolutionary history of Paleozoic gastropods. He received the 1996 Charles Schuchert Award of the Paleontological Society, given to a scientist under age 40 who has done outstanding work in the field of paleontology. He is also an external faculty member of the Santa Fe Institute and former interim director of the National Museum of Natural History.

Russell W. Graham is director of the Earth and Mineral Sciences Museum and associate professor of geosciences at the Pennsylvania State University. Dr. Graham's research focuses on the evolution, biogeography, and extinction of Quaternary mammals. He has edited three books and published more than 50 professional papers on these topics. Dr. Graham was elected a fellow of the American Association for the Advancement of Science in 1996 for his studies of the spatial response of mammals to environmental change. He graduated from the University of Iowa with a B.S. in zoology in 1969 and an M.S. in geology in 1972. He received his Ph.D. in geology from the University of Texas at Austin in 1976.

Jeremy B.C. Jackson is a professor of oceanography at the Scripps Institution of Oceanography (Geosciences Research Division and Marine Biology Research Division) at the University of California, San Diego. Previously, he was the senior scientist at the Smithsonian Tropical Research Institute in Panama, where he was also director of its Center for Tropical Paleoecology and Archaeology. Before that, he was professor of ecology at Johns Hopkins University. He received his Ph.D. from Yale University in 1971. His current research interests include paleobiology and macroevolution, speciation and extinction, ecology and paleoecology of coral reefs, marine conservation, and bryozoans and mollusks. His past research interests included historical patterns of diversity and extinction in tropical America in relation to the formation of the Isthmus of Panama and the ecology and conservation of tropical coastal communities.

Susan M. Kidwell is the William Rainey Harper Professor in the Department of Geophysical Sciences and the Committee on Evolutionary Biology at the University of Chicago. Her research expertise is in taphonomy and stratigraphy, particularly of marine records, and she is particularly interested in the recognition and evaluation of preservational biases in biological and geologic information. Dr. Kidwell was a member of the National Academy of Sciences' Delegation on Sedimentary Basins to the Peoples' Republic of China in 1985. She is a past member of the Board on Earth Sciences and Resources. She received the Presidential Young Investigator Award (1986) from the National Science Foundation, the Charles Schuchert Award from the Paleontological Society (1995), and is a fellow of the American Academy of Arts and Sciences (2002).

Christopher G. Maples is the vice president for research at the Desert Research Institute in Las Vegas and Reno, Nevada. His current research involves field- and literature-based studies of invertebrates or invertebrate traces. He uses these data to address questions that link paleontology and geology. Other current research includes several projects on Late Devonian through Permian echinoderm extinctions, extinction rebound, and biogeography from various parts of the world. Dr. Maples served as program director for geology and paleontology and other programs at the National Science Foundation from 1995-1998. He received the 1994 Charles Schuchert Award of the Paleontological Society, awarded to a scientist under age 40 who has done outstanding work in the field of paleontology.

Charles H. Peterson is Alumni Distinguished Professor of Marine Sciences, Biology, and Ecology at the University of North Carolina at Chapel Hill. Dr. Peterson's research is focused on the organization of soft-sediment benthic communities in estuaries and lagoons, with particular interest in predation and intra- and inter-specific competition, the influence of hydrodynamics on ecological processes, and the role of resource limitation in suspension-feeding bivalve populations. In addition to his experimental approach to testing hypotheses concerning benthic systems, he conducts research in paleoecology, invertebrate fisheries management, estuarine habitat evaluation, and barrier island ecology. He earned his Ph.D. from the University of California, Santa Barbara, in 1972.

O. James Reichman is director of the National Center for Ecological Analysis and Synthesis and professor in the Department of Ecology, Evolution, and Marine Biology at the University of California, Santa Barbara. His research focuses on the influence of the spatial patterns of animal disturbances on the structure, function, and restoration of plant communities and natural landscapes. A second area of research involves an analysis of long-term food storage strategies by animals that cache food during periods when it is unavailable or costly to obtain. Dr. Reichman has been a program officer in the ecology program at the National Science Foundation, associate vice provost for research and director of Konza Prairie Research Natural Area at Kansas State University, and assistant director for research in the National Biological Service in the Department of the Interior. Dr. Reichman received a Ph.D. from Northern Arizona University in 1974.

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David L. Dilcher (NAS) is a Graduate Research Professor in the Florida Museum of Natural History at the University of Florida. He was professor in biology and geology at Indiana University for 24 years. His research activities focus on the history of CO_2 in relation to climate change in the past, and the evolution of land plants as revealed by the fossil record—the nature of the earliest flowering plants, the reproductive biology of flowering plants, and the historical diversity and paleogeography of flowering plants. Professor Dilcher has been president of the Botanical Society of America, and is an honorary professor of Jilin University and Nanjing University in China and a corresponding member of the Senckenberg Museum in Germany.

NATIONAL RESEARCH COUNCIL STAFF

David A. Feary is a senior program officer with the NRC's Board on Earth Sciences and Resources. He earned his Ph.D. at the Australian National University before spending 15 years as a research scientist with the marine program at the Australian Geological Survey Organisation. During this time he participated in numerous research cruises—many as chief or co-chief scientist—and most recently was co-chief scientist for Ocean Drilling Program Leg 182. His research activities have focused on the role of climate as a primary control on carbonate reef formation and improved understanding of cool-water carbonate depositional processes.

Robin A. Schoen is the director of the Board on Agriculture and Natural Resources (BANR). Before joining BANR, she was senior program officer for the Board on Life Sciences, where she directed a range of studies that included stem cell research, the plant genome initiative, and invasive plants. Her earlier work focused on involving U.S. scientists in efforts to strengthen biology internationally, and in addressing policy issues that affect progress in microbiology, neuroscience, biophysics, cancer research, physiology, and biodiversity. Robin received a B.S. in biology and chemistry from Frostburg State College (Maryland) and an M.A. in science and technology policy from George Washington University.

Radhika S. Chari was a senior project assistant with the Board on Earth Sciences and Resources until April 2004, before moving to a position as administrative coordinator for the Board on Assessment of NIST Programs and the Army Research Laboratory Technical Assessment Board. Ms. Chari received her B.A. degree in philosophy from Fordham University.

Amanda M. Roberts is a program assistant with the Board on Earth Sciences and Resources. Before coming to the National Academies she interned at the Fund for Peace in Washington, D.C., working on the Human Rights and Business Roundtable. Amanda also worked in

Equatorial Guinea, Africa, with the Bioko Biodiversity Protection Program. She received her B.A from the University of Oklahoma and her M.A. in international peace and conflict resolution from Arcadia University, specializing in resource extraction and conflict in sub-Sahara Africa.

APPENDIX B

Acronyms and Abbreviations

AMS	Accelerator Mass Spectrometry
AO	Arctic Oscillation
ATM	Division of Atmospheric Sciences
BE	Biocomplexity in the Environment
BIO	Directorate for Biosciences
BP	Before Present
CCM-1	Community Climate Model-1
CCSP	Climate Change Science Program
CSBE	Center for Synthesis in Biological Evolution
DDIG	Doctoral Dissertation Improvement Grant
DEB	Division of Environmental Biology
DSDP	Deep Sea Drilling Project
EAR	Division of Earth Sciences
ENSO	El Niño-Southern Oscillation
EPA	Environmental Protection Agency
ERE	Environmental Research and Education
EROC	Ecological Rates of Change
ESH	Earth Systems History Program
ESPRI	Earth Surface Processes Research Institute

GE	Geology and Paleontology Program
GEG	Geobiology and Environmental Geochemistry
GEO	Directorate for Geosciences
GEON	Geosciences Network
GLD	Geomorphology and Land Use Dynamics
GPD	Global Pollen Database
GTER	Geologic Time Ecological Research
IGERT	Integrative Graduate Education and Research Traineeship
IODP	Integrated Ocean Drilling Program
ITDMS	Isotope Dilution Mass Spectrometry
LTER	Long Term Ecological Research
MESH	Marine Aspects of Earth Systems History
NAO	North Atlantic Oscillation
NAPD	North American Pollen Database
NASA	National Aeronautics and Space Administration
NCEAS	National Center for Ecological Analysis and Synthesis
NEON	National Ecological Observatory Network
NOAA	National Oceanographic and Atmospheric Administration
NRC	National Research Council
NSF	National Science Foundation
OCE	Division of Ocean Sciences
ODP	Ocean Drilling Program
PAGES	Past Global Changes
PDO	Pacific Decadal Oscillation
PRISM	Pliocene Research, Interpretation, and Synoptic Mapping
SALVIAS	Spatial Analysis of Local Vegetation Inventories Across Scales
SGP	Sedimentary Geology and Paleobiology Program
SHRIMP	Super High-Resolution Ion Microbe
SI	Stomatal Index
SST	sea-surface temperature
STAR	Science to Achieve Results
USGS	U.S. Geological Survey
YDI	Younger Dryas Interval