CHAPTER 1

Background and Framework for Long-Term Ecological Research

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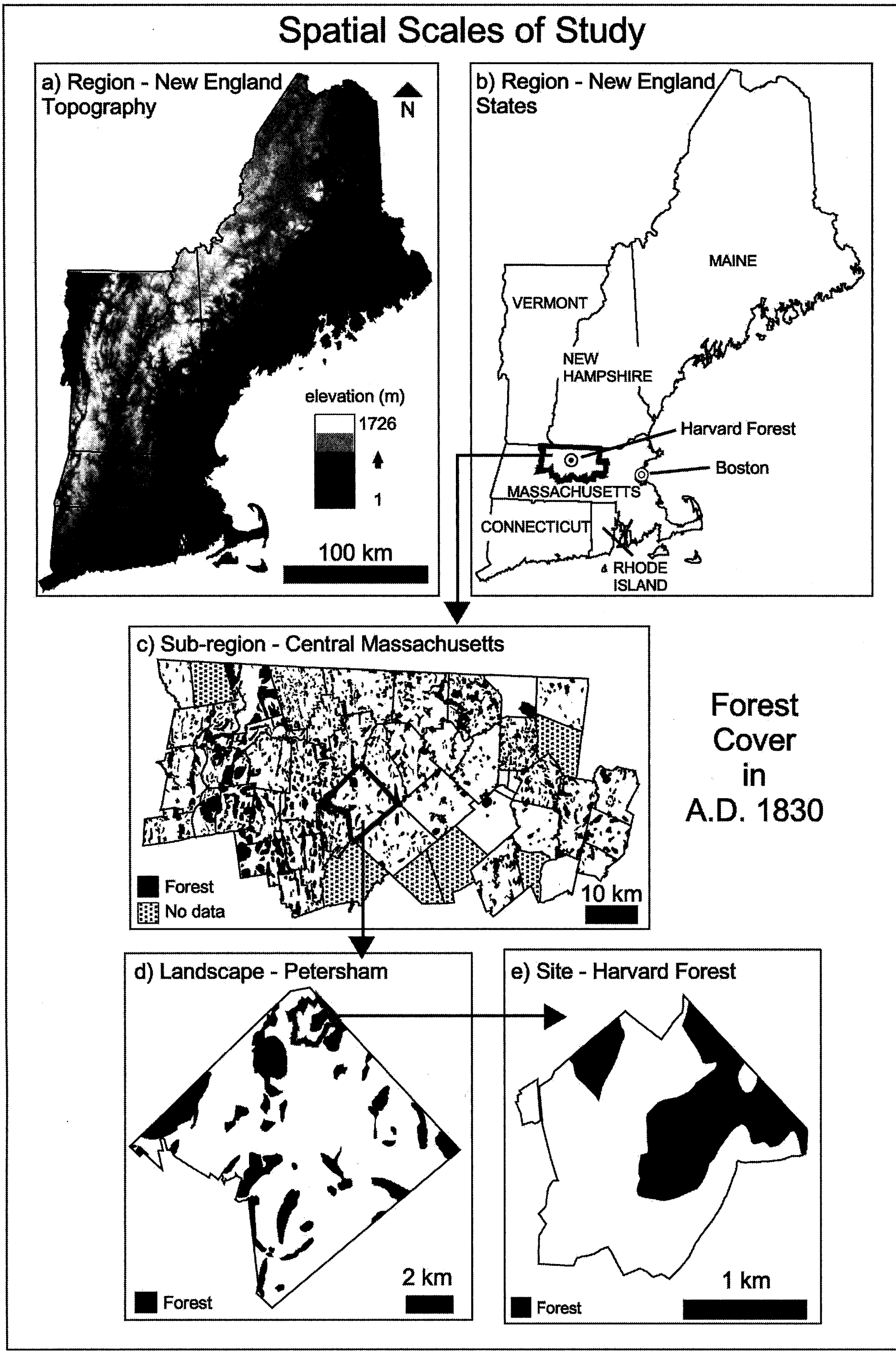
In 1907 Harvard University acquired nearly 3,000 acres of land in the central Massachusetts town of Petersham to establish the Harvard Forest as a center for research and education in forest ecology, conservation, and management. In the ensuing century of investigations, students, faculty, and visiting researchers came to rely heavily on accumulated and continuing historical studies as a complement to intensive field and laboratory work and as a source of insight into important processes that have shaped the land, its people, and its biota. By developing long-term studies of the past and present, we can uncover events and processes that are infrequent in occurrence, we can examine physical and biological processes that unfold over long periods of time, and we can sift through the many changes and factors that have operated in the landscape over time in order to identify those that are critical for interpreting modern conditions and dynamics (Figure 1.1).

This long-term approach to ecological research was a central driver in the selection of research directions when we teamed together with colleagues from several Harvard departments, the University of New Hampshire, the Ecosystem Center at the Marine Biological Laboratory, and the University of Massachusetts in 1988 to form the Harvard Forest Long Term Ecological Research (LTER) program. In particular, we applied our understanding of the history of the land, modern forest dynamics, and projections for future changes in the regional and global environment to select a suite of important disturbances, stresses, and forest ecosystem processes to investigate in detail. The broad objective of these studies was to develop information and approaches that will answer fundamental ecological questions and to generate data and perspectives that have broad application to major environmental and conservation issues.

A sketch of the history of New England's land and people highlights the major changes that shape the present landscape and the key objectives of our investigations.


Spatial Scales of Study
a) Region - New England Topography
N
elevation (m)
1726
1
100 km
b) Region - New England States
MAINE
VERMONT
NEW HAMPSHIRE
Harvard Forest
Boston
MASSACHUSETTS
CONNECTICUT
RHODE ISLAND
c) Sub-region - Central Massachusetts
Forest
No data
10 km
Forest Cover in A.D. 1830
d) Landscape - Petersham
2 km
Forest
e) Site - Harvard Forest
1 km
Forest

Overview of Environmental and Forest Dynamics in Central New England

Over the past few thousand years, New England's landscape has been remarkably dynamic in response to varied changes in environmental, cultural, and biological factors that control the structure, composition, and function of forest ecosystems (Figure 1.2). The broadscale geological and physiographic structure of the region has been relatively unaltered since the last wave of glaciation overran the gentle hill and valley topography and blanketed it with shallow deposits of silt, sand, clay, and rock some 14,000 years ago. In contrast, the region's climate has evolved continually on a time frame of decades to millennia. Relatively warm conditions in the mid-Holocene period approximately 5,000 years ago gave way to cooler conditions about 2,000 years ago that persisted until the recent past. Subtle changes in the composition of New England forests throughout this time and increasingly in the few hundred years before European settlement suggest that significant shifts occurred in the amount and seasonal distribution of precipitation and temperature. As a consequence, the abundance of important trees, including beech, hemlock, spruce, and chestnut, has shifted in pronounced though poorly understood ways.

When we examine any forest's history more closely, it is apparent that natural disturbances ranging from frequent, small events to infrequent, broadscale and intense impacts are important in structuring the New England landscape. Nearly 5,000 years ago, an insect pest caused hemlock to decline abruptly throughout its range in eastern North America. Over the ensuing thousand-year period, forest and lake ecosystems changed as this long-lived and shade-tolerant tree species declined and then gradually rebounded, albeit with considerable geographic variation in the rate and extent of recovery. The details of this episode continue to emerge through new studies and are clearly relevant to modern questions concerning the importance of individual species to ecosystem function and the potential impacts of introduced organisms, such as the hemlock woolly adelgid, on our forests.

In contrast to the solitary occurrence of a natural pest, the historical record of powerful hurricanes leads us to suspect that tropical storms episodically disrupt and shape New England forests (Figures 1.3 and

Figure 1.1. Primary spatial scales of investigation in the Harvard Forest Long Term Ecological Research program. The New England–wide maps depict topography and state boundaries as well as the location of the Harvard Forest. Other maps show the distribution of forest area (black) remaining in the mid-nineteenth century at the height of agricultural activity and deforestation. Areas in white were predominantly open pastureland, other agricultural fields, and village areas. Compiled and modified from U.S. Geological Survey (unpublished), Foster, Motzkin, and Slater 1998, Foster 1992, and Hall et al. 2002.

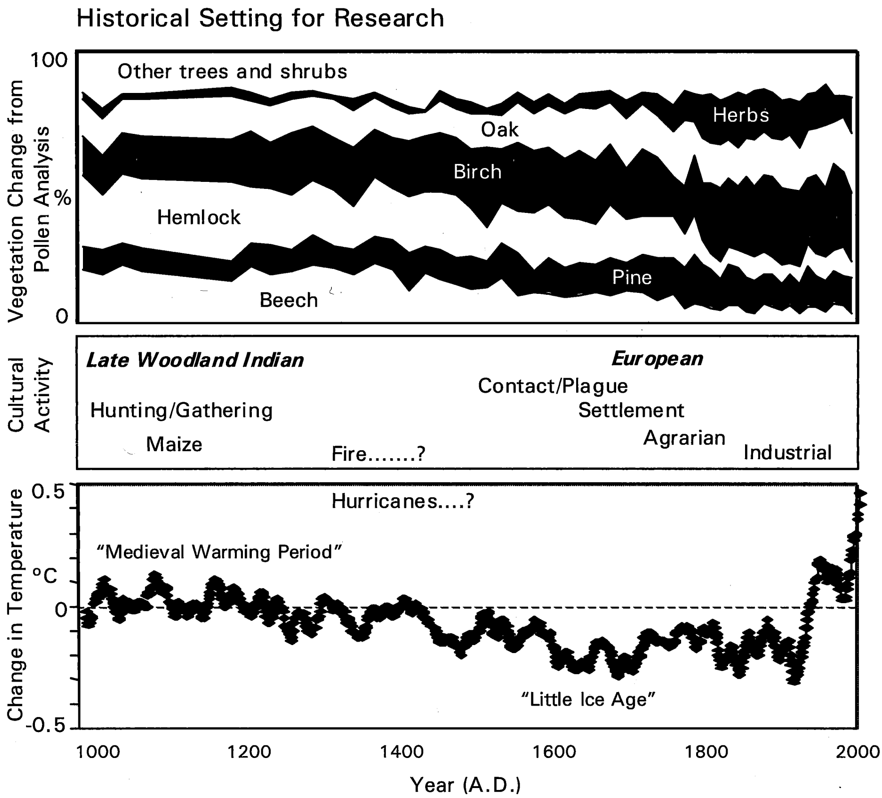


Figure 1.2. The temporal setting for long-term studies in New England in relation to important biotic, cultural, and environmental changes. Biotic (vegetation) change (top) is illustrated by the varying percentages of pollen of major plant taxa from Aino Pond in north central Massachusetts (Fuller et al. 1998). Major cultural changes (middle) highlight the shift from native hunting, gathering, and horticulture to European agriculture and industry. Climate dynamics (bottom) are depicted by the long-term change in Northern Hemisphere temperature over the past 1,000 years, as reconstructed from tree-ring records and other proxies (adapted from Crowley 2000, data archived at the World Data Center for Paleoclimatology, Boulder, Colorado, USA).

1.4). Severe storms tend to follow similar paths across New England, and therefore it is possible that distinct regional gradients and repeatable landscape patterns of windthrow and damage may exist. Long-term records and historical studies also suggest that less intense disturbance resulting from northeasterlies, downbursts, ice storms, and late-season snowstorms are important drivers of forest gap dynamics, processes that may diversify forest landscape patterns over time. Understanding the relative role of these different types and scales of physical disturbance and their distribution across New England has remained an elusive goal of ecologists.

Figure 1.3. The 1938 hurricane damaged more than 70 percent of the volume of timber on the Harvard Forest and exerted a profound effect on ecological thought, forest planning, and interpretations of New England's environmental history. Photograph of Albert Cline, Harvard Forest director who was faced with coping with this unanticipated event, from the Harvard Forest Archives.

Fire is less frequent in the temperate forests of New England than in the boreal region, midwestern grasslands, or western woodlands. However, fire may have a long-lasting effect on forest composition and function, so interpreting its frequency, intensity, type, and variability through time remains a great challenge. This subject is especially relevant to modern conservation and land management as fire is increasingly viewed as a critical tool for maintaining important plant or animal assemblages. Discussion of fire, which is often placed in the category of "natural" disturbances, invariably introduces the issue of cultural influences on our landscape as most New England fires are ignited by people. Indeed, fire

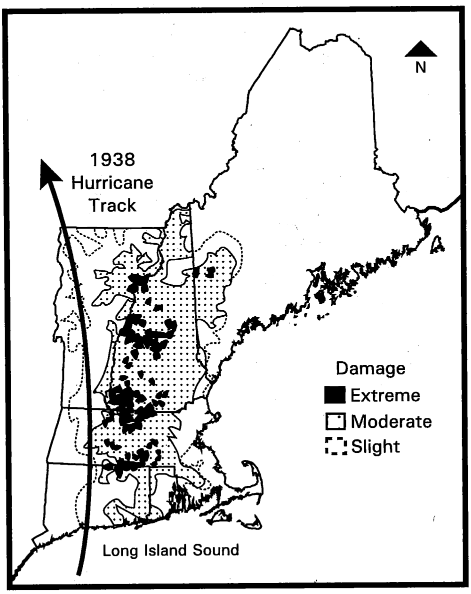


Figure 1.4. The 1938 hurricane damaged forests in a 100-kilometer-wide swath that extended from Long Island Sound to northern Vermont. Damage was concentrated to the east of the storm track due to the counterclockwise rotation and forward velocity of the storm. The track was reconstructed from meteorological records, whereas damage estimates are based on town-wide assessments of salvaged timber by the New England Timber Salvage Administration (unpublished data). The low damage values in southern New England are due to the relatively small amount of merchantable timber-size trees in that region in 1938. Modified from Foster 1988a, published by Blackwell Scientific Publications, by permission of the British Ecological Society.

represents the major means by which a relatively small population of Native Americans might have exerted a widespread effect on natural vegetation (Figure 1.5).

For New England, the general patterns of Indian activity are broadly understood: concentrated coastal and river valley populations and much lower densities in upland areas; cultural patterns, seasonal activities, and densities that varied historically with the availability of resources; the late arrival of maize (corn) horticulture circa A.D. 1000; and a transformation of subsistence patterns and culture with the arrival of European people. However, many major questions remain concerning the type and spatial extent of human effects on natural ecosystem patterns, and these motivate our ongoing studies.

Over the nearly 400 years since European settlement, the rate of ecosystem change has accelerated. Across New England, extensive de-

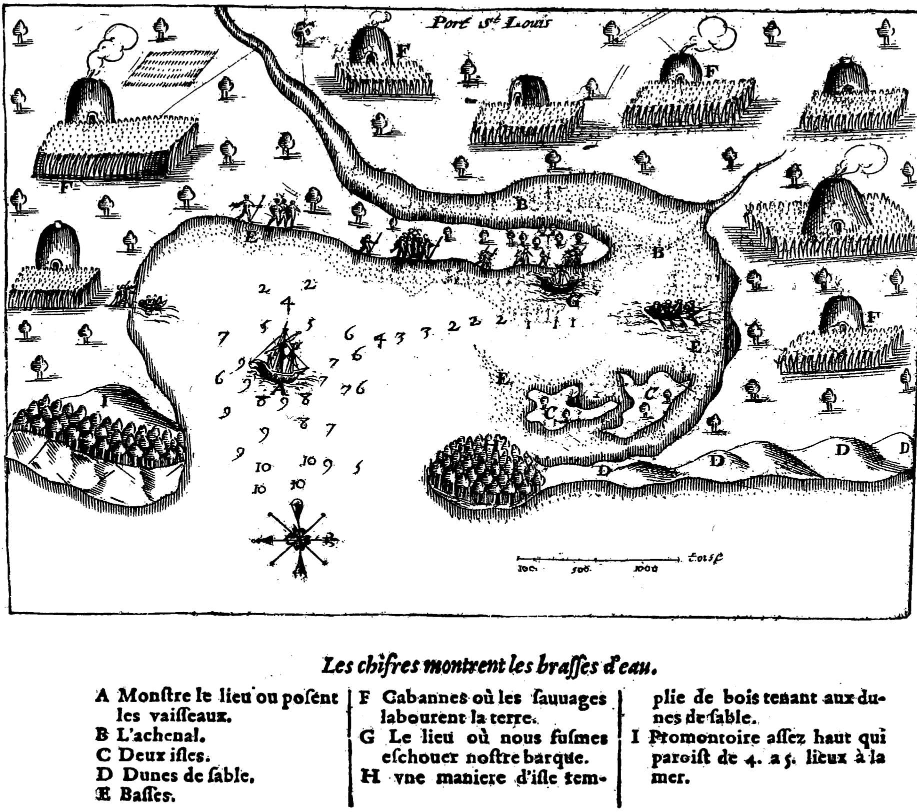


Figure 1.5. Champlain's map of Indian lodges, cornfields, and the landscape around Plymouth Bay, Massachusetts, in 1605. Although evidence for Indian encampments and local effects on the landscape is especially abundant near the coast and in major river valleys, the details of this activity and the extent of Indian influence on the interior countryside remain a matter of debate. In particular, archaeological evidence for large agricultural fields, extensive corn consumption, fortified settlements, and sizable villages in the region is lacking. Map originally printed in "The Voyages of Samuel de Champlain" (S. de Champlain, 1613).

forestation for agriculture peaked after 1850 and was followed by broad-scale abandonment of farming and reforestation through natural succession (Figures 1.6 and 1.7). Vast areas that supported scattered woodlots in a panorama of fields and pastures only 150 years ago are now covered with a mosaic of maturing second-growth forests that support natural ecosystem processes and native wildlife populations (Figure 1.8). Consequently, a central question looms over all environmental studies in the region: what are the enduring consequences of land-use history?

During the past century the forests and environment of New England

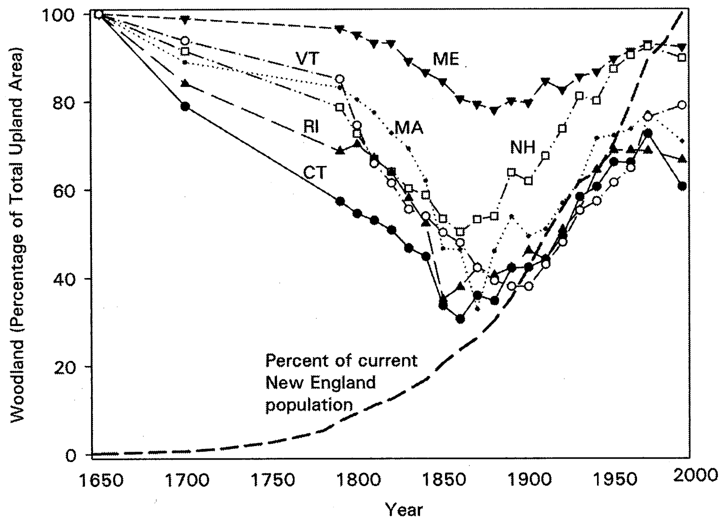


Figure 1.6. Historical changes in the New England population (heavy dashed line) and forest cover for each of the individual states. Excluding Maine, where the northern forest region was never settled and remained forested, the states share a common history of deforestation for agriculture followed by farm abandonment and natural reforestation. The extent to which these secondary forests differ in structure and function from permanently wooded areas or the forests of the presettlement period forms a major research emphasis of Harvard Forest studies. Population data compiled from U.S. censuses; forest cover data from Baldwin 1942 and U.S. Forest Service 1958, 1965, 1973, and 1990.

have also been exposed to new stresses induced through human activity. A series of introduced insects and diseases—chestnut blight, Dutch elm disease, gypsy moth, beech bark disease, and hemlock woolly adelgid—has selectively weakened, defoliated, or decimated major tree species across the region. Industrialization has changed the earth's atmosphere, which among other things has increased the deposition of nitrogen, a major limiting nutrient in most terrestrial ecosystems, as well as sulfur, in forms that acidify the rain and the region's ecosystems. Photochemical processes in the earth's upper atmosphere are depleting the tropospheric ozone (O_3) layer that shields nature and humans from ultraviolet radiation. Meanwhile, during the summer growing season, stagnant air circulation along the industrialized eastern seaboard brings damaging ozone and other pollutants to New England forests.

Increases in major greenhouse gases—including carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O)—may be initiating a global increase of temperature that could reach 3° to 4°C in the north-

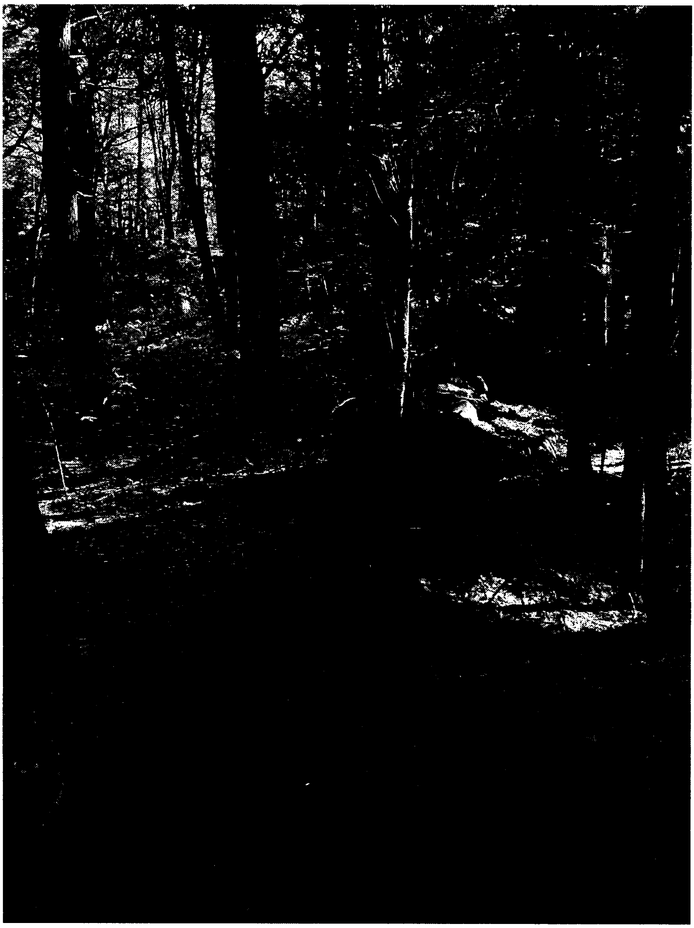


Figure 1.7. A stone wall built in the eighteenth century to separate a tilled field from an adjacent pasture winds through a second-growth hardwood stand in central Massachusetts. Despite the natural appearance of the vast forest area in New England, most of the region bears subtle clues to its cultural past. Photograph by D. R. Foster.

eastern United States by the end of the century. Increases in CO_2, nitrogen, and ozone in the atmosphere may also have subtle, though important, consequences for plant growth and competition, plant-animal interactions, and ecosystem processes. Evaluating the comparative effects of these novel stresses and the potential interactions that they may have with historically important disturbances is a challenge for ecologists and an important focus for conservationists and natural resource managers.

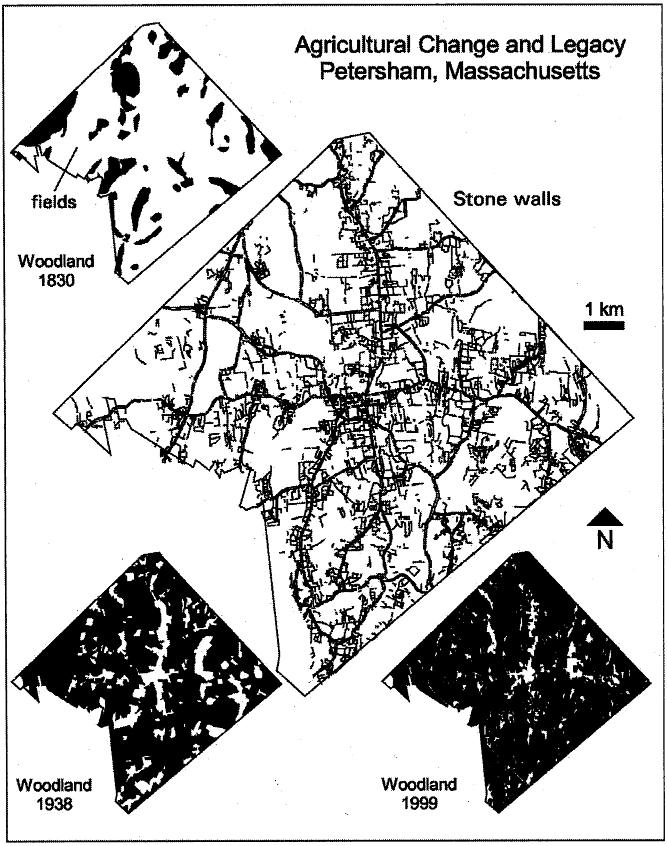


Figure 1.8. The pattern of stone walls bordering colonial fields and roads in the central Massachusetts town of Petersham (center) documents the extent and intensity of agriculture in New England's history. The approximately 380 kilometers of stone walls run through a landscape that is now nearly completely forested (bottom right) as a result of forest succession on abandoned farmland (top and bottom left). Maps compiled from the Worcester County White Pine Blister Rust project (1938–39; Harvard Forest Archives), 1830 land-use maps (Massachusetts State Archives, Harvard Forest Archives, and Hall et al. 2002), 1938 aerial photographs, and MassGIS 2002.

Broad Ecological Questions Concerning New England Forests

Our brief historical overview highlights many changes in the physical, biotic, and human environment of New England that have initiated a range of forest dynamics and have set the vegetation and landscape on a long-term trajectory. This overview also raises broad questions that drive our research as we seek to understand, conserve, and manage the modern landscape and anticipate future changes. Not surprisingly, these questions address fundamental issues relevant to many natural ecosystems worldwide.

1. *How does the array of environmental factors and disturbance processes interact to shape forest ecosystems over time?* The preceding section identified major uncertainties concerning the ways in which climate change, natural disturbance, and human activities have operated at local to regional scales through time. Of specific interest are details of the natural disturbance regimes, especially variations in wind, pathogens, and fire and the way in which these have interacted with prehistoric and historical human activity and environmental change.
2. *What are the contrasting effects of natural, physical disturbance versus novel, anthropogenic stress on the function of forest ecosystems?* Increasingly, forest ecosystems are exposed to chemical and climatic stresses that are qualitatively different from the types of impacts that forests have experienced for millennia. Recognizing that forest species evolved within a context of natural disturbance and environmental change, it is important to assess whether forests retain the same degree of control over ecosystem processes (for example, nutrient cycling, hydrology, and forest growth) under these novel conditions as they do under historically important stresses. Specifically, we are interested in contrasting the relative effects of physical disturbance, such as hurricanes, with important new stresses such as nitrogen additions and rapid climate change.
3. *What changes in forest patterns and processes were generated by the history of intensive land use since European settlement, and how persistent are the physical and biological legacies of this historical disturbance in New England's reforested landscape?* Large areas of northwestern Europe, Latin America, and eastern North America have experienced or are currently undergoing landscape transformations analogous to the forest–deforestation–reforestation history of New England, and thus lessons from our region should have general relevance. Major questions remain concerning the initial effects of colonial land-use activity, the ability of forest ecosystems to return to predisturbance conditions, and the legacy of historical changes on modern forest characteristics. For example, is the history of sites that were in agriculture 150 years ago reflected in the modern forest composition, soils, and fertility, or in the way that the forest will respond to the next hurricane or to acid rain?
4. *What application do answers to these questions have for environmental policy issues such as (a) designing effective local and regional conservation strategies, (b) anticipating forest ecosystem response to modern stresses and disturbances, and (c) developing global strategies to mitigate future climate change?* As we develop an improved understanding of modern forest ecosystems and their history of change, we can bring this information to bear on fundamental ecological questions concerning the patterns and processes of natural ecosystem organization and dynamics. We can also assist in the application of this information to education and the management of our natural environment and resources.

Design of the Harvard Forest Research Program

In order to address the broad ecological questions raised above, our research effort has been organized to integrate studies across disciplines, scientific approaches, and a range of spatial and temporal scales. By augmenting the lengthy record of ecosystem change that had developed over nearly a century of study at the Harvard Forest, we have selected historically important and relevant processes for investigation. We have also expanded existing programs in order to make education and public outreach a major goal of our program (Table 1.1).

We use a suite of scientific approaches in order to identify important ecological processes, to create a long-term series of measurements, and to assess ecosystem response and dynamics.

Ecological history provides information on the range of environmental conditions and types of natural and human disturbance processes that have been historically important in a landscape (Figure 1.9). This information identifies processes that are critical to study in order to understand ecosystem structure and function, and it contributes to our understanding of the relative role of historical factors versus environmental factors in controlling modern conditions. In addition, many key

Table 1.1. Design of the Harvard Forest Long Term Ecological Research Program

Research Approaches
1. Reconstruction of ecosystem dynamics using paleoecology, historical ecology, and modeling to evaluate long-term trends, to study infrequent processes, and to interpret the development of modern conditions
2. Measurement of modern ecosystem structure, composition, processes, and dynamics on permanent plots, through remote sensing and through eddy flux measurements of atmosphere-biosphere exchanges to define current conditions and rates
3. Experimental manipulations of ecosystems to evaluate and compare patterns of response and to collect integrated measurements on multiple processes
4. Controlled environment studies of plant and population responses to specific environmental changes
5. Integration through modeling, comparative studies, monthly meetings, annual symposia, and synthetic products, including coordination with other research programs
6. Application to ecological theory, conservation biology, environmental policy, and forest management

Spatial Scales of Investigation
1. Plot: 0.1 km
2. Site: 1 km—Harvard Forest
3. Landscape: 10 km—Petersham, Massachusetts
4. Subregion: 100 km—e.g., central Massachusetts, Cape Cod and islands, White Mountains
5. Region: 1,000 km—New England and adjacent New York

Disturbances, Stresses, and Environmental Processes Investigated
1. Climate change
2. Windstorms and other environmental extremes
3. Fire
4. Native and introduced pathogens and pests
5. Land use: aboriginal, historical, and current
6. Changes in atmospheric chemistry

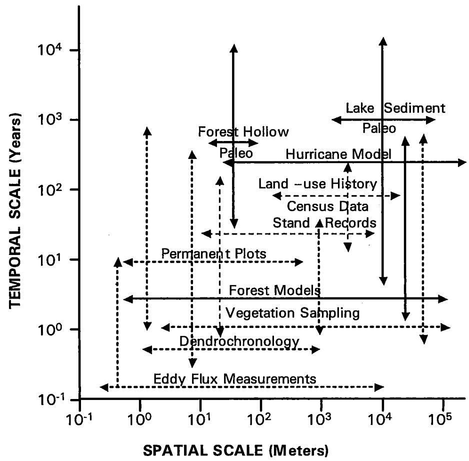


Figure 1.9. The relationship between the temporal and spatial scales of many of the ecological methods used in the Harvard Forest research program. Approaches include field studies (dotted lines), historical research (dashed lines), paleoecological and other retrospective studies (solid lines), and modeling (also solid). For each approach, vertical and horizontal lines approximate the temporal and spatial coverage achieved. Based on Foster et al. 1990.

ecological processes, such as succession, ecosystem development, large disturbances, species invasion, and ecosystem response to environmental change, operate on decadal to millennial timescales or with such great temporal variability that they are difficult or impossible to measure through conventional studies. Historical techniques enable the evaluation of such processes and allow these observations to be placed within the context of long-term trends and cycles of environmental change.

Experimental field manipulations allow us to evaluate infrequent though historically important processes as well as to anticipate future ecosystem response to predicted changes in climate or chemical stresses. At the Harvard Forest, we have focused large experiments on a subset of important though contrasting disturbances and stresses, including simulation of windthrow from an intense hurricane, timber harvesting, chronic nitrogen amendments to simulate enhanced deposition of nitrogen, soil warming as a component of climate change, and alteration of organic matter inputs to soils to examine basic soil processes linked to carbon and nitrogen dynamics. In the case of historically important processes such as hurricanes and forest logging, results from the experimental manipulations are compared directly with long-term studies of "natural experiments," such as the 1938 hurricane or historical logging that occurred throughout central New England. Many of the experiments are compared with parallel studies in different ecosystems. For example, the nitrogen saturation experiment has counterparts at the

Bear Brooks watershed in Maine maintained by the U.S. Forest Service and in the enhanced deposition of nitrogen that is occurring at high elevations in New England and in central Europe; the soil warming experiment has been replicated in the subarctic region at the Abisko Research Station in northern Sweden; organic matter manipulation experiments have been undertaken at the University of Wisconsin and other sites within the U.S. LTER network; and results from the experimental hurricane have been compared with those from natural events in many temperate and tropical forests. In all cases, the integrated measurements of ecosystem structure and pattern enable comparison among these important manipulations.

Long-term measurements of ecosystem patterns and processes in a range of natural forests carry forward observations of current conditions and results from reconstructive studies. In particular, measurements continued over decades assess seasonal and interannual variation, long-term trends and trajectories, and ecosystem function under highly varied sets of conditions. Permanent plots and repeated sampling of forest stands at five- to ten-year intervals continue long-term experiments and observations that were initiated in the early 1900s by the first faculty and students at the Harvard Forest. Remote sensing, using modern and historical aerial photographs or satellite images, increases the coverage of many measurements across two or more of our spatial scales of observation (for example, from plots in a forest to the landscape or region) and over many decades. Control areas, which are the undisturbed but monitored parts of our experimental manipulations, provide baseline measurements that may be linked with other data sets, such as the studies of atmosphere-biosphere exchange at our Environmental Measurement Station. The coupling of retrospective historical studies and long-term measurements of intact and experimentally manipulated ecosystems provides an integrated assessment of ecosystem dynamics and function under a range of historical, modern, and simulated conditions.

Harvard Forest research operates at four primary spatial scales of investigation: site (approximately 1 kilometer), landscape (approximately 10 kilometers), subregion (approximately 100 kilometers), and region (approximately 1,000 kilometers) (Figure 1.1). Intensive site studies at the scale of individual organisms, forests, or sample plots represent the heart of our long-term effort. Most of our studies at this scale occur on Harvard Forest land (approximately 1,200 hectares) in central Massachusetts, where varied vegetation, site conditions, and history, along with nearly 100 years of study, provide an ideal setting for long-term measurements and experiments. Infrastructure improvements, such as access to electrical and telecommunications cables at major experiments, erection of a series of canopy access and environmental measurement towers, the use of mobile lifts to reach into the crowns of mature trees, and surveyed grid points, enable diverse studies. Geographic information system–based data-management systems allow field sampling to be integrated with other sources of information such as low-elevation aerial photography, satellite imagery, radiotelemetry, historical surveys, and vegetation maps.

Many important processes, including natural and human disturbance, wildlife movement, and hydrologic flows, occur at a *landscape* scale, where physiography, slope position, vegetation structure, and soil variation interact to form complex patterns. In central New England, the area of an individual town (often approximately 10 by 10 kilometers) captures substantial landscape variation of the characteristic hill and valley topography. Consequently, the town of Petersham, Massachusetts, serves as one focus for many landscape studies because it includes the main tracts of the Harvard Forest and represents a typical rural village in the New England uplands. Given the politically independent structure of New England town governments, much of the geographical, social, and environmental data relevant to ecological studies are collected or aggregated by public agencies at a town level, making this political unit a particularly convenient scale of study.

To place site- and landscape-level studies in a broader context and to examine variation in environmental, social, and biotic processes, we conduct a considerable amount of research at the *subregional* scale (for example, central Massachusetts, Cape Cod and the Islands, the White Mountains of New Hampshire, the Connecticut Valley), and the *regional* scale of New England, oftentimes including adjacent New York. Selection of these areas is based on ecological, cultural, and pragmatic considerations. For example, the central Massachusetts subregion (approximately 5,000 square kilometers) extends 100 kilometers east from the Connecticut Valley Lowland through the Central Uplands physiographic region to the Eastern Lowlands west of Boston, and 50 kilometers south from the New Hampshire border approximately halfway to the Connecticut border. Petersham and the Harvard Forest lie directly in the center of this diverse subregion, which encompasses a wide range of the physical and biological variation in central New England, as well as a substantial amount of the cultural variation that has occurred from precolonial to modern times. The ability to place intensive studies within the context of these major cultural and environmental gradients is extremely useful for interpreting the generality of results and for understanding the broadscale controls over major ecological processes. On the practical side, this subregion consists of fifty townships in four counties of one state, which presents a manageable, though considerable, challenge for the collection and archiving of archaeological, historical, environmental, and biological data. Information for this region comes in three primary forms—continuous spatial coverage (for example, elevation, land-cover maps, and remote sensing imagery), township-level data (for example, population, agricultural, and forestry statistics), and networks of site-specific data (for example, sample plots, archaeological sites, and intensive measurement locations).

Considerably greater variation in environmental and cultural conditions occurs across the New England region, and the dynamics and effects of many of the broadscale disturbances and anthropogenic stresses can be understood only at this scale. In order to evaluate processes that are relevant at the regional scale, we conducted select studies utilizing diverse historical, modern, and modeling approaches. These studies yield data that may be continuous, aggregated at the county scale, or site specific. Importantly, these studies also enable us to see how well our approaches and results translate to other areas.

Thus, the research approach followed by the Harvard Forest LTER program is a continuation of the long-standing approach to understanding the New England landscape that Harvard Forest researchers have used for nearly a century. We use historical studies to understand the development of modern forests and to study infrequent and variable events and slow processes; we integrate our understanding of modern measurements and experiments with results from retrospective studies; we emphasize long-term experiments with an informative and secure data management structure; and we attempt to synthesize the results of all of these studies such that they address fundamental ecological questions and provide insights into societally relevant management issues.