CHAPTER 5

Broadscale Forest Response to Land Use and Climate Change

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Questions Concerning the Regional Patterns of the Forest in New England

In New England, where the landscape has been shaped by four centuries of intensive land use following European settlement, a history of environmental, human, and vegetational change over the past millennium or more has great relevance to the study, conservation, and management of modern ecosystems. As ecologists investigate current relationships between forest ecosystems and the environment in order to anticipate future changes, it is important to understand the factors that control current landscape conditions and the rate at which these are changing. Similarly, as conservationists or forest managers work to preserve, restore, or manage species and ecosystems, they frequently seek to base their management decisions on a knowledge of the conditions and processes that have existed in the past. Therefore, in our desire to understand the modern landscape of central New England, we used approaches from paleoecology, archaeology, and history, in addition to modern vegetation and environmental research, to investigate the long-term consequences of the environmental, cultural, and disturbance processes described in the previous chapter. In our attempt to evaluate the factors that control the rates and patterns of change in ecological systems and to provide practical information concerning past conditions and the development of the modern landscape, we centered on several fundamental questions:

- What were the regional patterns of forest composition and dynamics before European settlement, and how did these relate to broadscale variation in climate, soils, and human activity?
- What was the vegetation response to broadscale human disturbance, particularly deforestation, agriculture, and intensive woodlot management?
- How have forest patterns changed since European settlement? To what extent are their regional characteristics determined by the modern environment versus historical factors?

Although our studies focus on characteristics of the New England landscape and the peculiarities of its land-use history, the questions addressed and our framework for integrated historical and ecological study are relevant to other parts of the world. Much of the eastern United States, along with portions of the Caribbean, Central America, northwestern Europe, and even parts of Southeast Asia, share a history of recent declines in human activity following intensive land use. Moreover, studies from areas with such a history of changing land use have application to regions that are currently subject to intensive forestry and agriculture. How do natural systems respond, on a broad scale, to new disturbance? And if we choose to restore disturbed landscapes to more "natural" conditions by ceasing these activities, how will the regional patterns of vegetation respond and recover? As we set about examining modern patterns of vegetation across broad areas, information about the history and trajectory of forest change as well as the factors that have controlled these will provide fundamental information for planning research and interpreting results.

Research Approaches and Considerations

In order to evaluate broadscale vegetation patterns and dynamics, we focused on the central Massachusetts subregion surrounding the town of Petersham, integrating historical approaches with the analysis of modern conditions (Figure 5.1). We designed our study so we could examine vegetation and human history across natural gradients in climate and physiography, moving from the Connecticut River Valley to the Central Uplands where the Harvard Forest is located, and down onto the gentle Eastern Lowlands (see Chapter 2).

Paleoecology: Extending Our Long-Term Studies

To extend the record of vegetation and environmental change back through the period preceding European settlement, we used a wide range of paleoecological methods, including pollen, chemical, and physical analyses of lake sediments. We focused especially on the past 1,000 years in order to have a lengthy record of the conditions before European arrival as a background for evaluating subsequent changes. In particular, we were interested in documenting the pre-European fire and disturbance regimes and the long-term rates of vegetation change. Because the pollen records from small, closed lakes (that is, water bodies with no inlet or outlet streams) sample the vegetation from approximately a 10-kilometer distance, we selected ten such lakes for comparative study.

Paleoecological studies provide some unique advantages over other historical methods as they yield continuous, long-term records in which

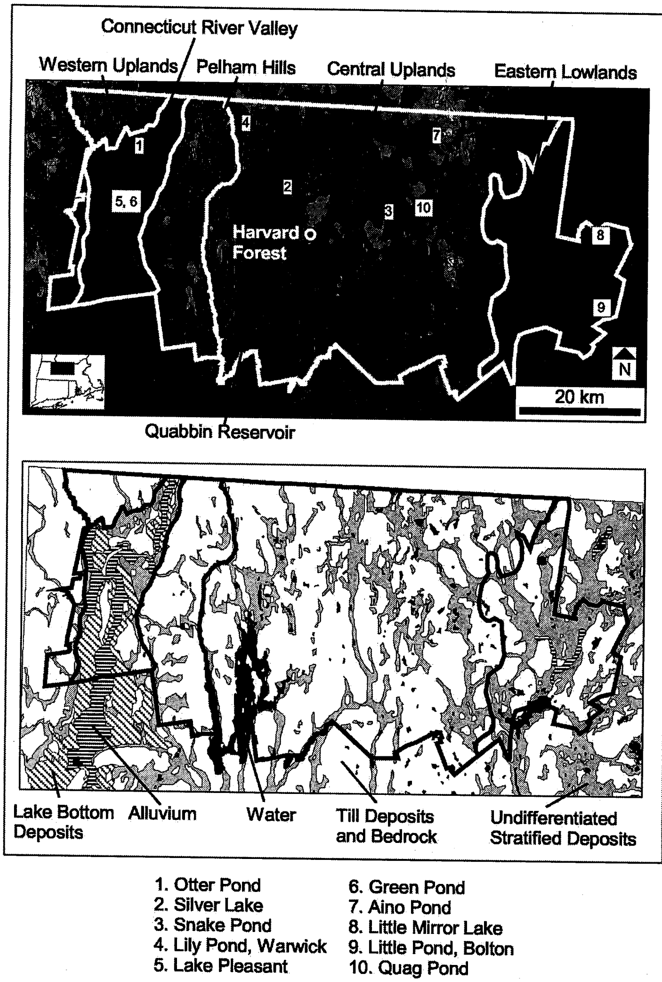


Figure 5.1. The central Massachusetts subregion showing topography, major physiographic regions, and the location of the small lakes sampled in the paleoecological study (top) and surficial geology (bottom). See inset and Figure 1.1 for location information. Compiled from Foster, Motzkin, and Slater 1998, 98: fig. 2 (surficial geology data from Heeley and Motts 1973), and Fuller et al. 1998, 78: fig. 1, with permission from Springer-Verlag (copyright 1998) (elevation data from U.S. Geological Survey 1993).

the resolution of vegetation pattern and composition remains relatively constant through time. In contrast, most of our historical vegetation records are restricted to the past 100 years, and the methods, details, and resolution of each historical survey often vary considerably. Nonetheless, paleoecological approaches have inherent limitations. Each of the different types of fossil analyses may actually record phenomena at somewhat different spatial scales. For example, pollen may be derived largely from vegetation within 5 to 10 kilometers of the lake, most large charcoal fragments come from within the watershed, and organic matter may originate from organisms in the lake (for example, plankton, zooplankton, and macrophytic plants) as well as vegetation along the lake shore and through the watershed. The taxonomic resolution and abundance of the different fossil materials also vary; with some notable exceptions, pollen is primarily identifiable at the level of genus, such as birch and oak. Different growth forms of plants, such as herbs, shrubs, and trees, and different species also vary in the amount of pollen that they produce and its dispersibility. Necessarily, all of our interpretations must attempt to take these factors into account.

Historical Sources: A Range of Sources and Insights

The analysis of historical land use generally entails utilizing many sources. These include state and federal censuses collected according to politically defined sampling units (often towns, roughly 10 by 10 kilometers) at regular intervals (generally ten years) for primarily economic purposes, and according to guidelines and regulatory needs that may vary through time. We then combine these long time series with information derived from town histories and sporadic additional surveys and maps in order to interpret European settlement patterns, land-use history, and land-cover changes. Despite some obvious limitations, these data provide many remarkable insights.

Most useful are decadal census data on population, livestock, crops, and land cover and infrequent tallies of forest cutting activities and products. In addition, and most fortuitous for our investigations, there is the statewide map series from 1830 that depicts forest and landscape patterns at approximately the peak of deforestation and intensive agriculture (Figure 5.2). These maps underscore the opportunistic nature of all historical research and the important role that serendipity plays in scientific endeavors (see Box 5.1). Commissioned by an act of the state legislature that required each town to produce a map showing cultural features (such as roads, houses, churches, and mills), physiography, and water bodies, these maps also depict forests, open land, and lowland meadows that were an important source of hay for colonial livestock. By transferring these nineteenth-century maps to modern base maps and then digitizing them onto a geographic information system (GIS), it is possible to piece together regional maps that are suitable for qualitative and (with caution) quantitative analysis. The resulting maps provide a perspective on the patterns of vegetation and human activity, as well as insights into the decision-making processes of the inhabitants, at the period of the most intensive land use in the region's history. The 1830 series therefore provides one of our most important regional perspectives on land cover before the twentieth century.

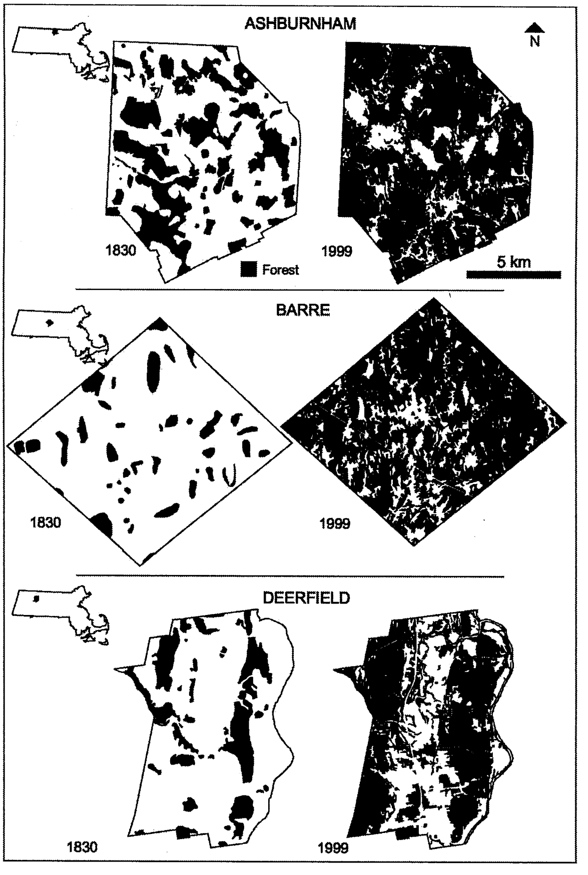


Figure 5.2. The availability of town maps from the 1830s enables us to explore variation in the patterns of vegetation and land-use history among towns across the state. These three central Massachusetts towns exhibit major differences in the amount and distribution of forest in the mid-nineteenth century and equally striking variation in patterns of reforestation. Ashburnham is a rural hill town with rugged topography; Barre occupies more gentle terrain and progressed from strongly agricultural to industrial (see Figure 4.20); and Deerfield lies largely in the Connecticut River Valley where rich, level terrain supported early settlement and extensive agriculture. See inset maps for locations in Massachusetts. Modified from O'Keefe and Foster 1998b; forest cover data for 1999 from MassGIS 2002.

Data on the Modern Landscape: Surprisingly Weak

One of the consequences of the twentieth-century growth of New England's industrial, commercial, and technological economy and the decreased dependence on local agriculture and natural resources is that the data characterizing modern vegetation and land cover are of lower quality than the best historical data. Similarly, information on soils, surficial geology, and many environmental variables are less reli-

Box 5.1.

The Art and Serendipity of Historical Studies

Much of the challenge and excitement in designing long-term studies lie in the development of strategies for identifying, collecting, and integrating diverse types of modern and historical data. Inevitably, this process involves ingenuity and compromise as we attempt to compare sources of information that vary considerably in their spatial, temporal, and taxonomic resolutions and as we seek to adapt data to our specific ecological interests that were originally collected for a wide range of mostly economic or regulatory purposes. In our regional study of forest dynamics, one good illustration of this process of data mining and adaptation comes from the piecing together of very different historical sources to interpret changes in vegetation and land cover.

At the time of the establishment of most towns across the Commonwealth of Massachusetts (as well as other New England states), the original settlers, called "proprietors," commissioned surveyors to delimit the town boundaries and major property divisions through so-called "lotting" surveys and to lay out roadways. Although these surveys were based on geography rather than on vegetation, the surveyors blazed "witness" trees and recorded the tree species at the intersecting corner of each property line. If we assume that these trees were selected objectively and without bias (that is, for species or size) and that the survey lines are numerous enough to sample the towns representatively (large and oftentimes rather uncertain assumptions), then a compilation of the recorded trees should offer an extraordinary opportunity for us to assess compositional variation of forests across the region at the time of European settlement.

Were the surveys biased with regards to particular species, tree sizes, or forest types? Were the surveyors accurate in their tree identifications? Are the samples of trees large enough and sufficiently independent to yield accurate assessments? And can samples defined by political and ownership boundaries provide information that can be reconciled with other forestry data and with ecological scales of variation? To answer these questions, we initially collected proprietors' data from more than fifty towns and examined the resulting patterns with these questions in mind (see Figure 5.3). To our satisfaction, the data formed a remarkably consistent geographical pattern that closely parallels underlying environmental gradients and the vegetation records from pollen in lake sediments across the region. A similar conclusion was reached in a larger companion study that we undertook in collaboration with Charlie Cogbill from the Hubbard Brook LTER site. In this subsequent effort we assembled proprietors' data for nearly the entire New England region. Having confirmed the general accuracy of these data, we gathered other later sources of vegetation, land-use, and environmental information that could be collected or aggregated to a town scale. In each case, we went through a similar process of searching sources, developing methodologies, and then checking results. In the end, by utilizing diverse sources of historical information in new ways, we emerged with a valuable perspective on centuries of change in New England.

able and detailed in New England and many eastern states than in other parts of the country, where natural resources are an important part of the economy. For forests, the most comprehensive statewide data are for 1985, and these provide only broad height and cover classes, with no information on forest composition. In fact, there are no reliable maps of forest types (that is, based on forest composition) in the state for the past half century. Consequently, and ironically, a major hurdle in our studies was to develop modern vegetation data that were commensurate with the species-specific data that are available from historical sources such as proprietors' survey records (see Box 5.1), which date from the seventeenth and eighteenth centuries. We accomplished this by sampling more than 450 plots distributed randomly in forests across central Massachusetts. The paucity of biological and environmental information for one of the wealthiest states in the United States unfortunately leaves us with a limited ability to assess current ecological conditions, let alone to predict or shape future ones.

Data: Strengths and Weaknesses

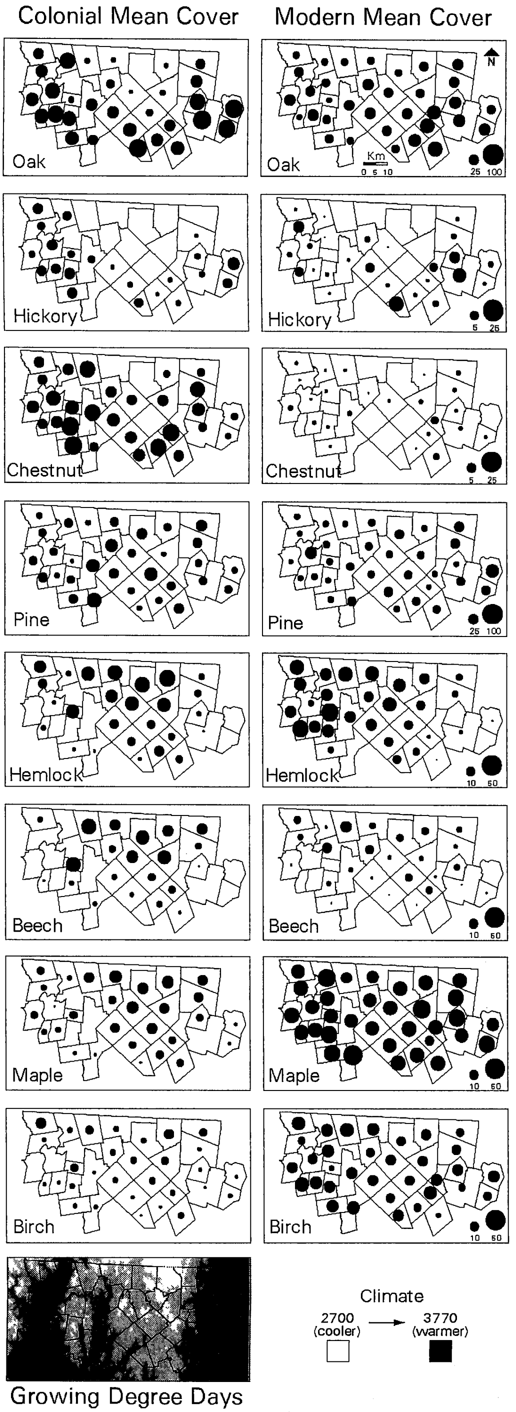
In comparing the historical and modern vegetation data with the paleoecological record, we can see some complementary strengths and weaknesses. Whereas we often have a good idea of the spatial and temporal precision of each data set, the resolution of data from different sources is often quite different. In fact, the scale, methods, and objectives vary among almost all historical and modern sources. Unlike sediment analyses in which we can control (with some limitation) the temporal frequency and resolution of the sampling, with historical data we generally have little control over these factors and need to evaluate whatever data are available. As a result, our reconstructions of past landscapes are based on irregular sampling intervals and offer ample opportunity for ongoing discussion and refinement.

Presettlement Vegetation and Landscape Dynamics

Historical and paleoecological sources provide consistent and complementary pictures of the landscape that the earliest European explorers and settlers encountered. From both perspectives, we see strong variation in forest composition that corresponds to physiographic and elevational variation across the region (Figures 5.3 and 5.4). The cooler upland areas in the north-central part of the region were dominated by hemlock, white pine, and such northern hardwood species as beech, yellow birch, and lesser amounts of red oak, whereas the lower elevation and warmer Connecticut River Valley and Eastern Lowlands had considerably more oak (presumably all three major species—red, black, and white oak) and hickory. White pine, ash, and chestnut were rather evenly distributed across the landscape. Red maple, paper birch, and gray birch, which are important today, were not common.

Identifying the factors that were responsible for controlling this pronounced geographic pattern across a relatively small geographic area warrants discussion, however. The strong similarity in the dominant tree species in the two lowland portions of the study area, which vary considerably in soils, physiography, and geology, suggests that the primary factor controlling vegetation variation was climate, which is roughly similar in the two areas. In support of this interpretation, analy-

Figure 5.3. Witness tree surveys from early European colonial history were compiled to examine changes in the distribution and abundance of tree species over the past three centuries. Regional variation was striking in the early eighteenth century and corresponded closely to elevational and climatic gradients (growing degree days). However, after more than 200 years of land use and reforestation, tree species abundances show little variation in the modern landscape. Modified from Foster, Motzkin, and Slater 1998, 110: fig. 11, with permission from Springer-Verlag (copyright 1998).


Colonial Mean Cover
Modern Mean Cover
N
Oak
Oak
Km
0 5 10
25 100
Hickory
Hickory
5 25
Chestnut
Chestnut
5 25
Pine
Pine
25 100
Hemlock
Hemlock
10 50
Beech
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Growing Degree Days
Climate
2700 (cooler)
3770 (warmer)

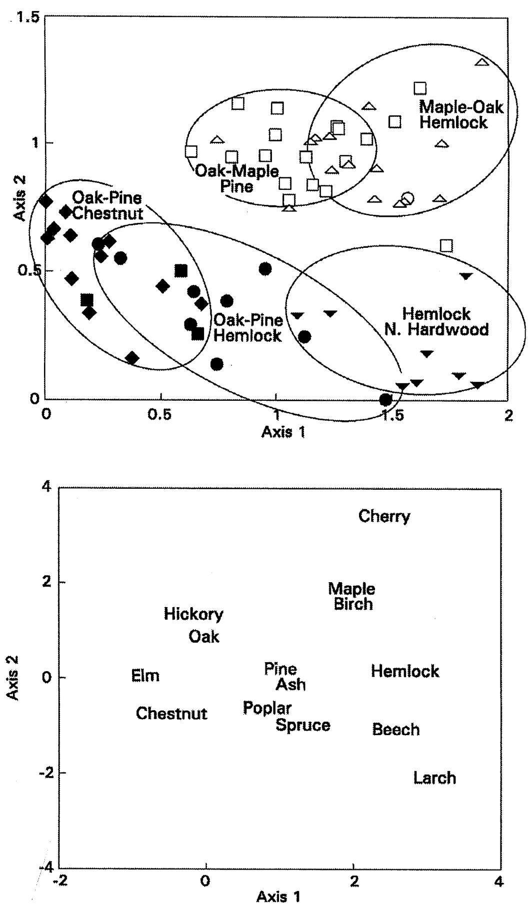

Figure 5.4. Detrended correspondence analysis (DCA) of early settlement (closed symbols) and modern (open symbols) vegetation for the central Massachusetts region (top); and the DCA loadings for major tree species (bottom). At the time of settlement, the vegetation varied along a compositional gradient corresponding to elevation and climate, whereas the modern vegetation is distinctly different and much more homogeneous in composition. Modified from Foster, Motzkin, and Slater 1998, 111: fig. 12, with permission from Springer-Verlag (copyright 1998).

sis of the relationship between vegetation and climate based on both historical and paleoecological data demonstrates that the abundance of each of the major tree species is strongly correlated with the modern variation in the length of the growing season across the region (Table 5.1). Thus, there appears to be a strong correlation, if not a direct cause-and-effect relationship, between variation in forest composition and climatic variables known to control broad biogeographic patterns.

However, the interpretation is not completely straightforward, as other factors, including disturbance regimes and cultural activity, covary with these physiographic and climatic gradients. In the uplands, the abundance of long-lived and shade-tolerant species, which are characteristic of mature forests, implies that disturbance, especially fire, was probably infrequent. Hemlock, in particular, is quite intolerant of burning, and our studies of individual woodlands show that it may take many centuries for hemlock to recover its former abundance after intense surface fires. During such prolonged postfire periods, hemlock is generally replaced by sprouting and early- to mid-successional hardwood species, including birch, oak, chestnut, and maple, or by the fire-tolerant white pine. Therefore, the consistently high pollen and witness tree values for hemlock and low values for oak and chestnut from across the uplands suggests a low incidence of fire at the time of European settlement. Indeed, charcoal levels in lake sediments at all uplands sites are low throughout the pre-European period, bolstering this interpretation. The low abundance of early successional species such as paper birch and red maple suggests that other disturbances, including windstorms, pathogens, or human activity, were either infrequent or local in extent.

In contrast, oak and hickory were more abundant in the lowlands,

Table 5.1. Results of Simple Linear Regression of Tree Abundance (Percent Occurrence) and Climate (Growing Degree Days) for the Colonial Period

	Colonial Forest		Modern Forest	
	r^2	Slope	r^2	Slope
Oak	0.53	0.121‡	0.00	0.004
Hickory	0.44	0.013‡	0.01	0.008*
Hemlock	0.57	−0.052‡	0.06	−0.017
Beech	0.53	−0.043‡	0.16	−0.011*
Maple	0.47	−0.028‡	0.04	0.010
Birch	0.18	−0.010*	0.00	0.001
Ash	0.03	−0.004	0.00	0.001
Chestnut	0.02	0.005	0.01	0.001
Pine	0.00	−0.002	0.05	0.012
Cherry	0.06	−0.002	0.12	−0.010*
Larch	0.06	−0.002	?	?
Poplar	0.02	−0.002	0.05	0.002
Spruce	0.03	−0.002	0.23	−0.004
Elm	0.06	0.003	0.19	0.001*
Oak-hickory	0.55	0.133‡	0.02	0.012
Northern hardwood-hemlock	0.61	−0.122‡	0.05	−0.018

Source: Reprinted from Foster, Motzkin, and Slater 1998, table 3, p. 110, with permission from Springer-Verlag (copyright 1998).

Note: Based on proprietors' survey data (approximately 1700–1800) and modern forests (1993–96) for each township in north-central Massachusetts. Northern hardwoods include birch, maple, and beech. Climate was based on the parameter that provided the best regression fit for each period, which was maximum degree growing days in a township for the colonial period and average degree growing days for the modern period. Significance levels: *$p < .05$, ‡$p < .001$

where it appears that more fire accompanied the warmer temperatures and longer growing seasons. Charcoal levels in lake sediments are generally higher in the Connecticut River Valley and Eastern Lowlands than in the uplands. In fact, charcoal abundances from lakes on the flat, dry Montague sand plain in the Connecticut River Valley approach the very high values observed from sandy outwash plains along the southeastern coast of Massachusetts and on Cape Cod. Archaeological studies reveal a consistent Native American presence throughout the Connecticut River Valley and Eastern Lowlands, and these landscapes have always been interpreted as providing diverse resources for a fairly high human population. Although the uplands are not as well-studied, the available evidence indicates many fewer Native Americans, primarily bands from the lowlands engaged in seasonal activity, and very scattered settlement. Thus, although the climatic gradient may have been a primary factor controlling the vegetation pattern, this climatic influence was apparently reinforced by greater fire frequency. Certainly, the absence of hemlock and northern hardwoods and the abundance of fire-tolerant and sprouting oak and hickory in the lowlands are consistent with regional patterns of climate, fire, and human activity.

In this regard, it is important to underscore that the inertia inherent in forest ecosystems may enable even slight variation in regional disturbance patterns to exert a rather pronounced effect on vegetation patterns. Specifically, if fire was extremely uncommon across much of the uplands, occurring a few times a millennium or so as indicated by our admittedly limited studies in Petersham, or even less frequently as suggested by studies in the Berkshire Uplands, then it may not require a particularly active fire regime in the lowlands to favor species like oak and other hardwoods over hemlock. Because hardwood species are capable of sprouting and hemlock cannot tolerate fire or invade new sites rapidly, surface fires every century may be all that is required to maintain the oak-hickory forest. This is an important consideration, as much of the discussion on fire in New England has focused on reconciling references from early settlers suggesting that frequent fires maintained open forest conditions with historical and fire ecology studies suggesting a low incidence of fire. Clearly, we would be well-advised to consider the potential importance of infrequent disturbances.

Patterns of Forest Response to European Activity

Before considering the role of pre-European fire and Indian activity in more detail, we may come forward to the present and ask how 300 years of land use, including extensive deforestation, agriculture, repeated cutting of the remaining forests, and widespread reforestation, have changed the pattern of vegetation that occurred in the seventeenth century. The answer is twofold: forests per se have proved to be ex-

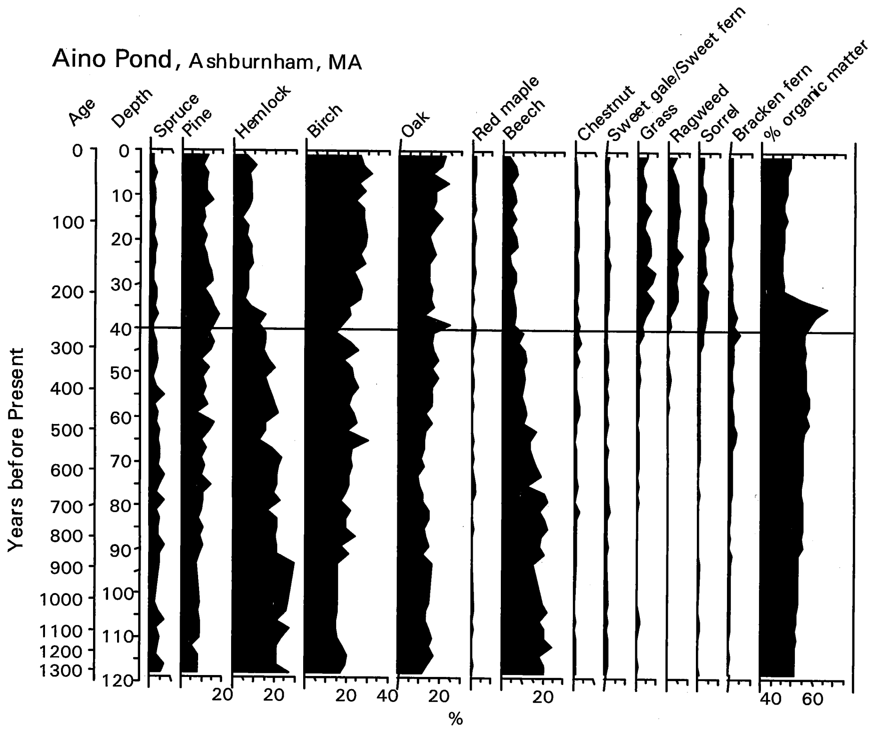

Figure 5.5. Pollen diagram from Aino Pond in north-central Massachusetts. Vegetation change has occurred continuously but was most rapid just after European settlement. The pre-European declines in hemlock and beech during the Little Ice Age (beginning approximately 500 years B.P.) are quite apparent. Pollen diagram, by N. Drake, modified from Fuller et al. 1998, 82: fig. 2a, with permission from Springer-Verlag (copyright 1998).

tremely resilient to intensive human activity and have reestablished widely throughout the region after agriculture and other intensive land-use practices ceased. However, the abundance and distributional patterns of major tree species, as well as their relationship to underlying environmental factors, have been substantially altered over the past 300 years (Figures 5.3, 5.4, 5.5). In fact, across north-central Massachusetts today the abundance of tree species varies remarkably little as one moves from the Connecticut River Valley up through the hilly uplands and down into the Eastern Lowlands (Figure 5.3). From the pre-European pattern in which hemlock and northern hardwood species dominated in the uplands and oaks and hickory dominated the lowlands, the landscape has changed to one in which oak, red maple, and black birch are ubiquitous across the region, with lesser amounts of white pine and hemlock and very little beech.

The relatively uniform composition of forests across the region shows no statistical relationship to the regional climate (for example, growing degree days or average temperature) nor to the variation in specific land-use practices that exists among the three physiographic areas (Table 5.1). Instead, it appears that current forest composition and structure at this scale are largely the products of the relatively brief, intense, and novel disturbance regime that originated with the arrival of Europeans. The detailed patterns of land use and land cover do exhibit a degree of regional variation that is quite striking: as we drive through the Connecticut River Valley we view large, open expanses with tobacco sheds, cornfields, and vegetable stands that contrast with the few remaining dairy farms in the more forested uplands and with the apple orchards, market gardens, and suburbs of the Eastern Lowland. Nonetheless, the overwhelming similarity in the history of land clearance, intense logging, and old-field succession across the entire region evidently outweighs the influence of environmental factors, fire, or modest land-use differences that controlled the vegetation in the pre-European period. The consequence of the massive land-use transformation of New England over the past 300 years is the fairly uniform distribution of mid-successional and sprouting species that dominate the landscape today.

The major changes in composition that occurred in the past 300 years lend support to the interpretation of broadscale land-use history as a major determinant of modern forest geography. The species that were most important at the time of European settlement and that declined most abruptly after European settlement are beech and hemlock, both of which are susceptible to disturbances such as fire and compaction of the soil surface by grazing animals. Similarly, field studies and demographic modeling of beech and hemlock highlight the fact that these slow-growing and shade-tolerant species are slow to reinvade sites from which they have been removed by agricultural activity or fire. Relative to other species, both are also slow to recover and dominate sites where they have been heavily cut. In contrast, the species that have increased across the region, including red maple, gray and paper birch, and the oaks, exhibit distinctly different behavior. Each of these responds well to disturbance by fire, cutting, and field abandonment as they sprout prolifically, grow relatively rapidly, and disperse and establish relatively easily in open sites. Consequently, and perhaps not surprisingly, the imposition of a regime of frequent and high-intensity disturbance in the uplands, which previously were dominated by slow-growing, shade-tolerant tree species, resulted in a shift to rapid-growing, moderately tolerant to shade-intolerant species that are more typical of young and early-successional forests. Thus, the composition of the upland areas became more compositionally similar to that of the lowlands over the past few centuries.

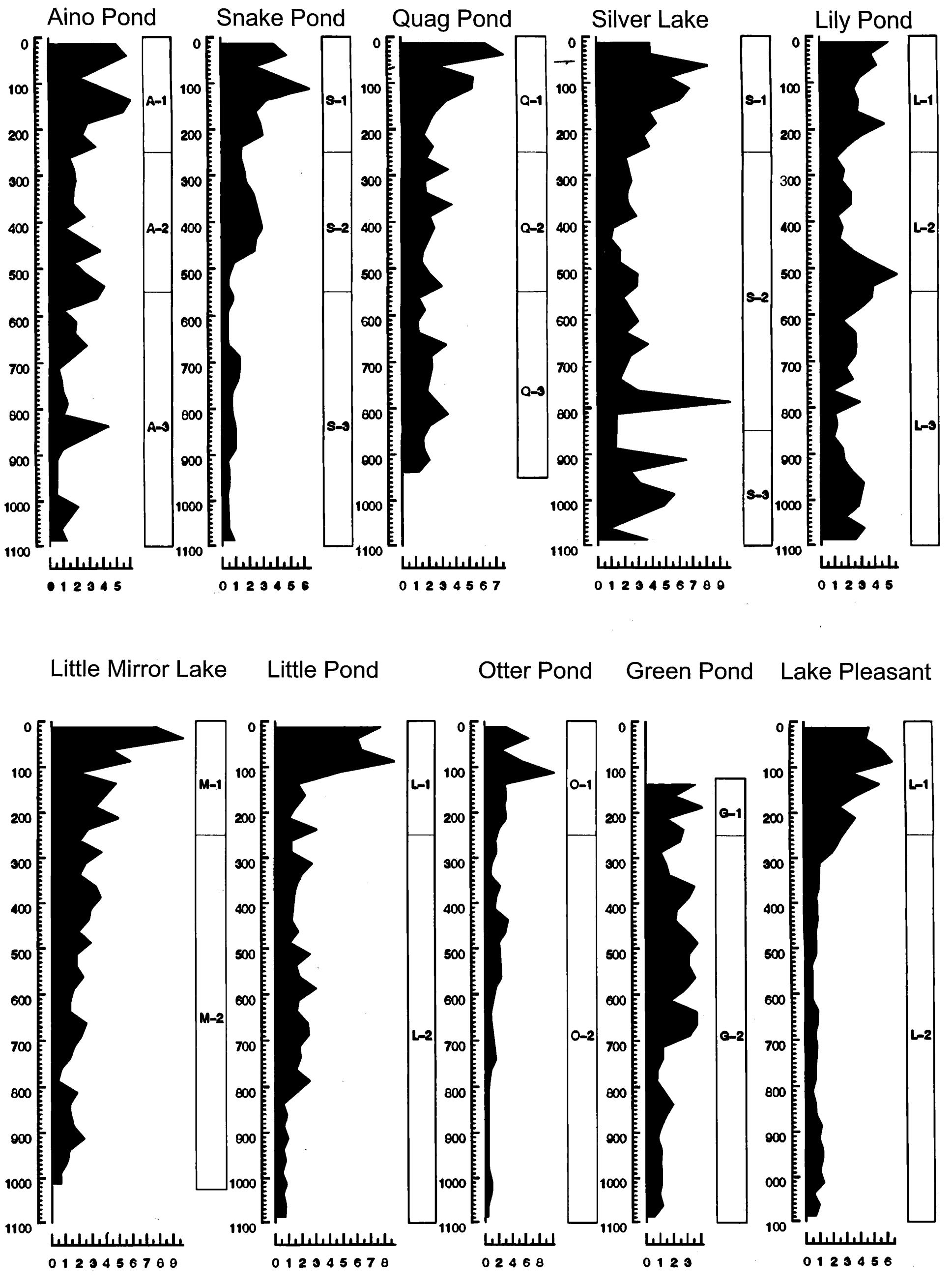

Figure 5.6. Rates of vegetation change around ten lakes in central Massachusetts based on multivariate analyses of pollen data. All sites exhibit continual though varying rates of change, underscoring the inherent dynamics in vegetation. However, most sites exhibit the highest rates of change during the period of European settlement (labeled with top rectangle showing zone 1,250–0 years B.P.). Modified from Fuller et al. 1998, 86: fig. 4, with permission from Springer-Verlag (copyright 1998).

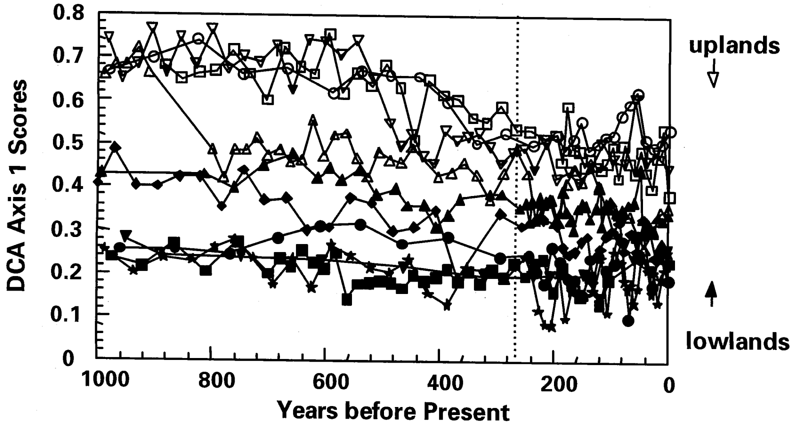

Figure 5.7. Long-term vegetation trends in central Massachusetts over the past 1,000 years based on detrended correspondence analysis (DCA) of pollen data. Samples that have similar scores are similar in vegetation composition. Although vegetation differences were great 1,000 years ago, they have lessened over time as a consequence of climate change and European land use. Currently, sites from the hilly uplands of central Massachusetts (see Figure 5.1) are quite similar to those in the Connecticut River Valley. Modified from Fuller et al. 1998, 88: fig. 7, with permission from Springer-Verlag (copyright 1998).

The Long-Term Perspective on Change in the Vegetation, Environment, and People

Knowing the extent of the differences between modern forests and those that the first European settlers encountered, a series of questions arises that can only be answered by a longer and more continuous record. How do the extent and rate of these changes compare with presettlement dynamics? What was the actual timing of shifts in major tree species? Is the modern forest composition gradually reverting to its earlier, presettlement composition? And are all of the changes that occurred over the past few centuries the result of human activity? For such a long and continuous perspective on landscape dynamics, we necessarily turn to the paleoecological record.

The story that emerges from our network of ten lake sites provides some interesting insights and a few unexpected observations on long-term vegetation dynamics. Not surprisingly, our results also raise new questions that will challenge and motivate our research through the next decades. An analysis of the overall rate of vegetation change over the past 1,000 years, which is largely driven by variation in the abundance of pollen from trees, indicates that vegetation has changed continuously, though at highly variable rates (Figure 5.6). Forest ecosystems, whether analyzed at the landscape level from an individual pollen diagram or at a regional scale using many lake sites, are characterized by constant change. Nevertheless, the rate of change increased greatly at essentially all sites after European settlement and has been maintained at enhanced levels to the present. Thus, the background levels of vegetation change generated by change in climate and possibly by Native American activity have been greatly exceeded by the effects of European land use.

Our pollen stratigraphies also indicate the rather unexpected result that a considerable amount of the regional change and convergence in tree composition occurred before and very shortly after European settlement (Figures 5.5 and 5.7). During this time, beech and hemlock declined and birch, oak, and red maple (which is insect pollinated and therefore underrepresented in the pollen rain) increased. The rapidity and timing of this shift in tree composition are notable, for at many sites it precedes the intense and broadscale disturbance associated with the peak of agriculture in the mid-nineteenth century. Subsequent to this early change, agricultural activity followed by natural succession, reforestation, widespread logging of white pine, the chestnut blight, the 1938 hurricane, and ongoing forest cutting have kept the regional vegetation in a mode of continual readjustment that has sustained high rates of forest change. This history of ongoing, albeit varied, disturbance is undoubtedly a major factor promoting the persistent dominance of mid-successional species and inhibiting the return of forest composition to presettlement conditions.

An examination of our pollen records, which extend back nearly a millennium before the establishment of Plymouth Plantation in 1620, implicates another environmental factor contributing to the compositional change that occurred with European settlement. Forest composition was actually changing and becoming more homogeneous on a subregional scale before European settlement (Figure 5.7). Notably, in the uplands there are two distinct pre-European periods that are differentiated at approximately A.D. 1400. At this time, bracken fern *(Pteridium aquilinum)* and grasses increase, whereas beech and hemlock begin a marked, though gradual, decline (Figure 5.5). Thus the subsequent decline in these two prominent late-successional tree species at the time of European settlement was preceded by a period of more than two centuries during which they were already decreasing in abundance. Explanations for this early change are based largely on circumstantial evidence and rely on comparisons with studies and data from other regions. However, these results fit an emerging pattern of forest dynamics seen from Cape Cod and the coastal islands to eastern Canada and beyond.

Interpretations of pre-European vegetation dynamics, especially the increase in bracken and decline in beech and hemlock, may be split into environmental and cultural arguments. However, as we have seen previously these two factors often act together and are not mutually exclusive. The *environmental argument* for the fifteenth-century change in vegetation focuses on the so-called Little Ice Age, a subtle but broadscale change in climate that has been recorded at sites around the globe (see Figure 1.2). This climatic anomaly occurred from the fifteenth century or earlier until the mid-nineteenth century and was responsible for the advance of mountain glaciers in the Alps, the Andes, and southeastern Alaska; the annual freezing of the Thames River in London during the Elizabethan era; and extreme weather conditions in the North Atlantic throughout the period of European exploration of North America. This approximately 400-year period was characterized by colder temperatures and more highly variable temperature, precipitation, and length of growing season than occur today. However, the exact mechanism linking Little Ice Age climate conditions with the decline in hemlock and beech and open forest conditions favoring bracken fern is unclear. In fact, a decrease of northern species with the onset of apparently cooler conditions appears to be counterintuitive. Nonetheless, if greater variation in annual and growing-season precipitation accompanied these changes, then a decline in drought-sensitive hemlock and beech is more understandable. In fact, although there is little independent climatic evidence for the Little Ice Age in New England, historical records from agricultural diaries indicate a greater frequency of extreme winters and cool summers as well as more variable growing seasons in the seventeenth and eighteenth centuries. In any case, the temporal synchronicity between widespread vegetation changes in New England and Little Ice Age phenomena noted elsewhere is striking. A similar shift in forest composition appears at a number of sites throughout northeastern North America, again arguing for a regional driver like climate.

The *cultural argument* notes that important changes in Native American subsistence activities may have followed the arrival of maize agriculture in New England around A.D. 1100 and that these could have initiated regional vegetation changes. More intensive and broadscale human impacts including increased sedentarism, village expansion, and widespread forest burning could be associated with an increase in horticulture and population. In turn, these disturbances could have encouraged weedy species locally and bracken and oak regionally because they are more tolerant to fire than long-lived trees such as hemlock and beech. Under this scenario, upland areas would respond strongly because of the abundance of hemlock and northern hardwoods and the historically low frequency of fire. Forests in the lowlands would exhibit less change in response to a slight increase in fire frequency because of the ongoing presence of fire-tolerant species.

Evaluating the cultural argument requires examining both the archaeological evidence for change in human subsistence patterns and the paleoecological record for evidence of a corresponding change in disturbance regimes accompanying the shift in forest composition. Evidence for the arrival of maize into the Connecticut River Valley by the eleventh century A.D. appears to fit established chronologies and evidence. There is, however, meager support for the notion that this was accompanied by any major and broadscale shift in cultural patterns. Indeed, the interpretation currently forwarded by our collaborator Elizabeth Chilton at the University of Massachusetts is for a "mobile farmer," essentially a seasonally mobile lifestyle based on hunting and gathering in which limited horticulture played an important though subsidiary role. In the absence of archeological sites in the valley or elsewhere indicating large permanent settlements, it appears that although Indian activity may have had local effects on the vegetation, widespread clearing or depletion of wood resources associated with a sedentary lifestyle is unsubstantiated.

Likewise, there is little evidence in the charcoal and pollen records that fire activity changed at this time and became important on a broad scale in southern New England. Charcoal abundance does rise after A.D. 1100 at a few lowland sites and is notably high at the few Connecticut River Valley sites; however, at the majority of upland sites, charcoal values remain low through the pre-European period. Most important, the abundances of charcoal, beech, and hemlock do not exhibit any consistent relationships.

After we examine the evidence from across New England and results from central Massachusetts, it appears clear that the major driver of change during the pre-European period is broadscale climate. Although the exact nature and magnitude of Little Ice Age climate change remain poorly understood, the widespread and temporally consistent nature of changes occurring from the coastal region through central Massachusetts to the Berkshires and northern Vermont implicates regional drivers. As we look across this region, the extent of vegetation change and the species involved vary. But there are few obvious mechanisms, other than fire, by which a relatively small human population could trigger such broadscale dynamics. Indeed, although there is every reason to expect that the New England Indian populations did affect their local habitats as well as specific resources, including fish and wildlife populations, little evidence remains for their impact at the landscape to regional scale that pollen analysis can sense. Though this result differs from many other parts of the globe where indigenous populations had a controlling influence on vegetation patterns and dynamics, it fits well with current archaeological data and supports the interpretation of the early historical landscape as one largely dominated by mature forests composed of long-lived species.

On the other hand, these results identify major gaps in our knowledge about the nature, timing, and specific mechanisms of pre-European landscape and environmental change. The direction of future research is clearly defined. In order to identify the timing and spatial variation in the extent and nature of vegetation change, we need a dense network of detailed pollen diagrams. These may well show, for example, that species vary considerably in their dynamics and that even the amount of change in a single species like beech varies across its range. To tease apart the relative role of climate change, fire, or other human activity in initiating these forest dynamics, we need to work with paleolimnologists, dendrochronologists, and archaeologists to develop independent records of physical, biological, and cultural factors.

The Other Vascular Plants: Effects of Regional History on Modern Distributions

One striking characteristic of most long-term assessments of forest change, including much of the work discussed above, is that it focuses on the major tree species to the exclusion of most other biota. Thus, as ecologists debate fundamental processes, such as the integrity of plant communities, the rates of postglacial migration, or, in our case, the regional response of forests to changes in climate and land use, much of the discussion is based on only a meager subset of the species that occur in the landscape. The explanation for this is largely pragmatic: paleoecological and historical records are primarily restricted to trees. In addition, there is some ecological and practical argument for focusing on the dominant constituents of the forest, as they largely control many important ecosystem characteristics because of their great size and biomass. However, in order to assess many important ecological processes and to consider some of the dramatic transformations that are occurring on our landscape today, we need to broaden our considerations to other biota. For example, we are very interested in knowing whether the process of regional homogenization, which characterizes the history of the major tree species in central Massachusetts, has occurred in the shrubs, herbs, and ferns.

Limitations in historical and modern data restrict the scope of inquiry considerably. Almost no information exists on the prehistoric or historical changes in the distribution of most species of herbs, shrubs, or other plants, and therefore we are not able to follow changes for these species as we did for trees. However, for the central Massachusetts study region, our sample of vascular plants in more than 450 randomly placed plots allows us to evaluate broad patterns of current distribution and abundance of many plants and to contrast these with tree patterns. At a regional scale, do these species vary with gradients in physiography, climate, or land use?

As was expected, a large number of herb and shrub species occur infrequently, so that even with several hundred plots, it is difficult to discern distinct geographic patterns of distribution. Other species such as clubmoss *(Lycopodium obscurum)*, partridgeberry *(Mitchella repens)*, star flower *(Trientalis borealis)*, wild oats *(Uvularia sessilifolia)*, and blueberry *(Vaccinium angustifolium)* are distributed fairly uniformly

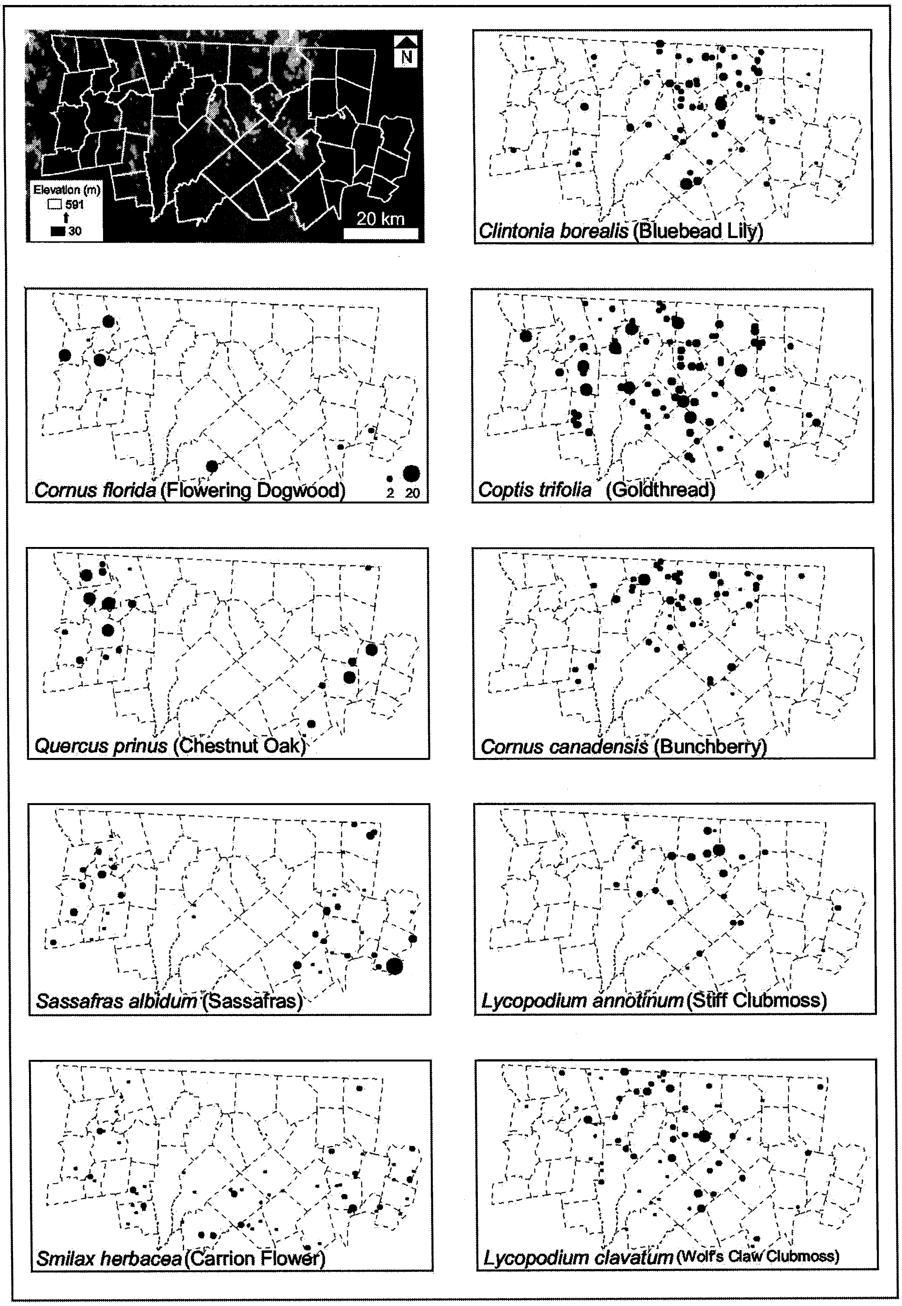

Figure 5.8. Distribution of nine minor trees and understory plants in central Massachusetts. Unlike the major tree species, which are rather homogeneous in their geographical distributions, these species show an apparent strong link to climatic and elevational variation. Species on the left preferentially occur at warmer, low elevations and southern sites, whereas those on the right are more common to the north and at higher elevations. Unpublished vegetation data from the Harvard Forest Archives; elevation data from U.S. Geological Survey 1993.

across the region and do not display strong patterns that are easily related to the physiographic subregions or regional variation in disturbance history. However, the modern distributions of many species do appear to be strongly related to physiographic and climatic variation across the region (Figure 5.8). Several species, including bunchberry *(Cornus canadensis),* bluebead lily *(Clintonia borealis),* goldthread *(Coptis trifolia),* dewdrop *(Dalibarda repens),* some clubmosses *(Lycopodium annotinum, L. clavatum),* Canada yew *(Taxus canadensis),* painted trillium *(Trillium undulatum),* and southern wild raisin *(Viburnum nudum),* are much more common in the northern portion of the Central Uplands than in the Connecticut River Valley, Eastern Lowlands, or southern portion of the Central Uplands. In contrast, species such as carrion flower *(Smilax herbacea),* flowering dogwood *(Cornus florida),* sassafras *(Sassafras albidum),* and chestnut oak *(Quercus prinus)* are more characteristic of the lowlands or the southern portion of the Central Uplands and are infrequent in the northern portion of the Central Uplands.

These results suggest that for at least some species, patterns of modern distribution at the subregional scale are related to variation in physiography and climate. In many cases these regional distributions fit the broader patterns of the species' geographic ranges, as in the case of bunchberry and Canada yew, which extend well into the boreal forest; or dogwood, sassafras, and chestnut oak, which have a corresponding southern range into the Appalachians. It is quite likely that these primarily "field layer" species may therefore serve as more useful indicators of site conditions and environment than many tree species that are apparently tolerant of a wide range of physical conditions and whose modern distributions appear more closely linked with disturbance history. In fact, this rationale is what has led researchers in Fennoscandia and elsewhere to base their vegetation classification and forest site evaluations on a combination of understory and overstory species. Although locally the distribution and abundance of even these restricted field layer species have undoubtedly been influenced by historical land use and other disturbances (see Chapter 8), these local effects have not obscured the broader environmental controls over their distribution patterns. A few of the less common tree species also have distinct subregional distributions, as, for example, red spruce, which is much more abundant in the north-central uplands, and chestnut oak, which is more abundant in the lowlands.

Dynamics of Some Vascular Species in Response to Land-Use History

We can gain some insight into how some herb and shrub species have responded to regional land use for those species where herbarium specimens and other sources are available to document historical distri-

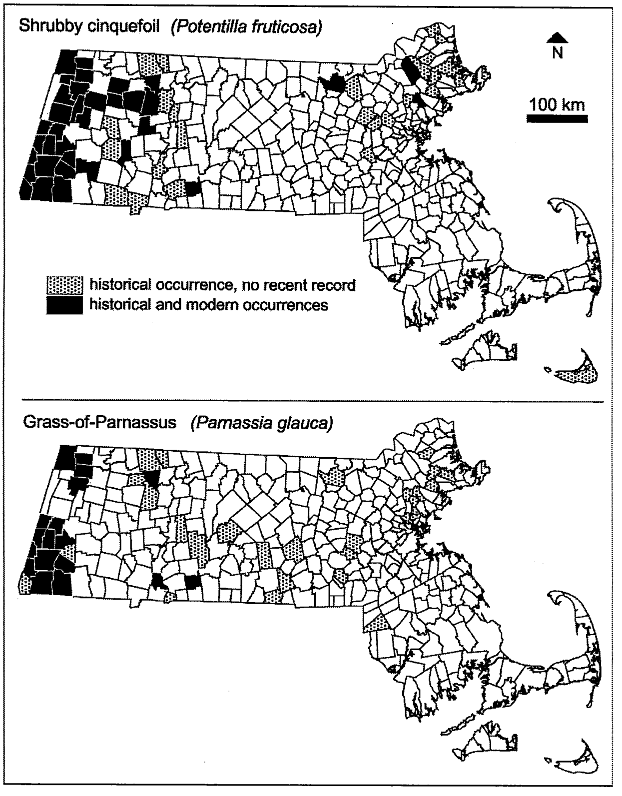

Figure 5.9. The approximate historical (late nineteenth to mid-twentieth centuries) and modern (since 1978) distributions of two uncommon plant species in Massachusetts. Both species declined in geographic extent and abundance during the twentieth century and are representative of a group of species that have become conservation concerns. Many plants and animals increased and thrived under open agricultural conditions during the nineteenth century but declined as grazing, mowing, and burning declined and the landscape reforested. Unpublished data from Glenn Motzkin and the Harvard Forest Archives.

butions. We searched for such cases with a particular focus on the historical and modern distributions of several species that are uncommon in Massachusetts and that occur today in habitats that are priorities for conservation. In particular, we examined a group that is thought to include good indicators of nutrient-rich, calcareous wetland conditions that frequently support unusual plant associations. A sequence of historical maps makes it clear that some species distributions have changed dramatically over the past several hundred years. A notable example is shrubby cinquefoil *(Potentilla fruticosa)*, a plant that is of considerable conservation interest and that today is largely restricted to Berkshire County and the hill towns west of the Connecticut River on circumneutral or calcareous soils (Figure 5.9). This species, however, formerly occurred fairly commonly in the Connecticut River Valley as well as in northeastern Massachusetts. Indeed, as recently as the early twentieth century, this shrub was widespread and seen frequently in old fields, where it was considered a "noxious weed" that warranted eradication by farmers. Referring to the distribution of this species in Vermont, L. R. Jones and F. V. Rand stated in 1909 that "shrubby cinquefoil was originally found only occasionally bordering swamps and in a few cool, rocky gorges or cliffs. During the last generation, however, it has been spreading persistently over pastures in certain sections until today it must be ranked as the most aggressive invader among the shrubby weeds, quite outclassing the hardhacks [i.e., *Spiraea* species]. Plowing and close pasturing have been used to successfully check its progress. . . . Reforestation of any kind, however, will soon suppress it."

Thus, we see that a species that is becoming uncommon in the modern landscape and is often used as an indicator of unusual soil conditions that may support rare species was formerly much more widespread and viewed as an undesirable weed. Several other uncommon species show similar dramatic shifts in their distributions during the past century, including grass-of-Parnassus *(Parnassia glauca)* (Figure 5.9) and yellow sedge *(Carex flava)*. Similar to shrubby cinquefoil, these species have disappeared from the wet meadows and pastures that they had colonized during the agricultural period but that have since reforested.

Thus, although data are frequently lacking, there is good reason to believe that the distribution and abundance of many taxa have changed substantially throughout the historical period in response to historical land-use activities. Because each species responds to such disturbances individualistically, the current landscape is characterized by species at differing points in their response to historical factors, and we may assume that substantial changes in species distributions and assemblages will continue to occur. These conclusions not only are interesting ecologically but have major implications for the development and implementation of conservation policies.