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Land-Use History as Long-Term Broad-Scale Disturbance: Regional Forest Dynamics in Central New England

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Abstract

Human land-use activities differ from natural disturbance processes and may elicit novel biotic responses and disrupt existing biotic-environmental relationships. The widespread prevalence of land use requires that human activity be addressed as a fundamental ecological process and that lessons from investigations of land-use history be applied to landscape conservation and management. Changes in the intensity of land use and extent of forest cover in New England over the past 3 centuries provide the opportunity to evaluate the nature of forest response and reorganization to such broad-scale disturbance. Using a range of archival data and modern studies, we assessed historical changes in forest vegetation and land use from the Colonial period (early 17th century) to the present across a 5000 km^2 area in central Massachusetts in order to evaluate the effects of this novel disturbance regime on the structure, composition, and pattern of vegetation and its relationship to regional climatic gradients. At the time of European settlement, the distribution of tree taxa and forest assemblages showed pronounced regional variation and corresponded strongly to climate gradients, especially variation in growing degree days. The dominance of hemlock and northern hardwoods (maple, beech, and birch) in the cooler Central Uplands and oak and hickory at lower elevations in the Connecticut Valley and Eastern Lowlands is consistent with the regional distribution of these taxa and suggests a strong climatic control over broad-scale vegetation patterns. We infer from historical and paleoecological data that intensive natural or aboriginal disturbance was minimal in the Uplands, whereas infrequent surface fires in the Lowlands may have helped to maintain the abundance of central hardwoods and to restrict the abundance of hemlock, beech, and sugar maple in these areas. The modern vegetation is compositionally distinct from Colonial vegetation, exhibits less regional variation in the distribution of tree taxa or forest assemblages defined by tree taxa, and shows little relationship to broad climatic gradients. The homogenization of the vegetation, disruption of vegetation-environment relationships, and formation of new assemblages appear to be the result of (a) a massive, novel disturbance regime; (b) ongoing low-intensity human and natural disturbance throughout the reforestation period to the present; (c) permanent changes in some aspects of the biotic and abiotic environment; and (d) a relatively short period for forest recovery (100–150 years). These factors have maintained the regional abundance of shade intolerant and moderately tolerant taxa (for example, birch, red maple, oak, and pine) and restricted the spread and increase of shade-tolerant, long-lived taxa such as hemlock and beech. These results raise the possibility that historical land use has similarly altered vegetation-environment relationships across broader geographic regions and should be considered in all contemporary studies of global change.

Key words: land use; history; vegetation dynamics; disturbance; New England landscape.

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Introduction

Ecologists have increasingly investigated natural disturbance as an important factor controlling vegetation dynamics and organization at community, landscape, and regional scales (Dayton and others 1992; Boose and others 1994; Turner and others 1997). Interest in human disturbance has come more unevenly and centers primarily within the disciplines of conservation biology, natural resource management, and applied ecology despite recognition that most landscapes worldwide are impacted by cultural activities (Turner and others 1990). However, acknowledgment of the impact and legacy of prehistoric and historical human activity on ecosystem structure and function (Northrop and Horn 1996; Binford and others 1997) and concern with the accelerating rate of human impacts require that the history and consequences of land use be addressed as fundamental ecological issues and major components of global change (IGBP 1990; Sundquist 1993).

Land use differs from natural disturbances in important ways and may therefore elicit novel biotic responses (CEES 1990). Human disturbance may be new within the evolutionary context of organisms (Foster and others 1997); may reach intensities rivaling the most severe natural disturbances (Turner and others 1990); may be relatively homogeneous across broad areas that differ naturally in environment, disturbance regimes, and patterns of biotic variation (Mladenoff and others 1993; Likens and others 1996); and may alter the biotic and abiotic environment and natural disturbance processes (Foster and others 1997a). These qualities may cause human impact to disrupt existing relationships between the biota and the environment and may result in significant shifts in community composition and dynamics (Foster and others 1997).

In many regions, human disturbance has not increased monotonically with time or even with expanding human density (Turner and others 1990). For example, extensive tropical and temperate areas have undergone episodes of deforestation and agriculture followed by agricultural abandonment and widespread natural reforestation. This pattern has been documented from prehistory and the historical period in Europe (Watkins 1993), Latin America (Gomez-Pompa and Kaus 1992; Binford and others 1997), the Caribbean, and eastern North America (Williams 1982; Foster 1992), and continues to be an important landscape dynamic in some tropical and temperate regions (Lugo and Brown 1980; Watkins 1993). Consequently, many forested areas that are managed, conserved, and studied intensively today may still be experiencing major community-to-landscape dynamics as a consequence of recovery from intense historical land use (Bormann and Likens 1979; Lugo and Brown 1980; Foster and others 1997b; Golodetz and Foster 1997). The history of these regions offers the opportunity to evaluate patterns of regional vegetation response to broad-scale, long-term human disturbance. By detailing the history of human activity and the resulting changes in forest structure, composition, and pattern, we can examine biotic response to novel, regional-scale disturbance processes. Such an understanding is a critical component in studies of global change. In addition, documentation of historical shifts in patterns of land use, land cover, and forest distribution also provides the temporal context necessary for framing modern ecological studies and making policy decisions on management and conservation (Foster and others 1993, 1996; Motzkin and others 1996).

Across New England, as in much of the eastern United States, the landscape has undergone a complete transformation within the past 350 years (Williams 1982). Deforestation and agriculture by European colonists transformed a landscape that was initially almost completely forested into an agrarian countryside dominated by tilled fields, pastures, and woodlots (Foster 1998). Subsequent farm abandonment and natural reforestation led to the development of the modern, largely forested landscape (Whitney 1994; Foster 1995). In our central Massachusetts study region, the agricultural landscape of the mid-19th century contained less than 40% woodland in contrast to more than 85% forest today. As forests have expanded and grown in height and age, the countryside has increasingly assumed the appearance, composition, and function of a natural forest landscape (McKibben 1995). However, no studies have documented this regional history of land use and forest change in detail while simultaneously assessing the consequences for modern forest composition, structure, and dynamics [compare Fuller and others (1998)].

Our regional study was designed in conjunction with a parallel paleoecological study (Fuller and others 1998) to evaluate composition and variation in the pre-Colonial forest, the history and pattern of land-use activity by European colonists, and the forest response to changing intensity of broad-scale disturbance. The study embraced a 350-year-long historical period, and the central Massachusetts study region was selected because it encompasses

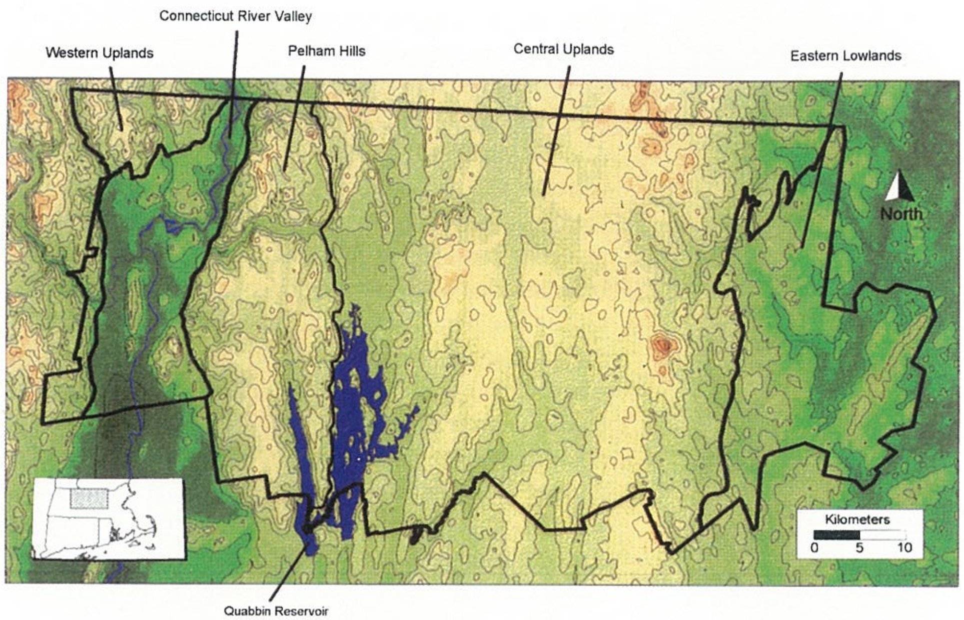


Figure 1. Study region showing elevation (50-m contours), major physiographic divisions (heavy black lines), and location of the Quabbin Reservoir and the Connecticut River. The Pelham Hills is a rugged area within the Central Uplands. Elevation ranges from 30 m (green) in the Connecticut River Valley and Eastern Lowlands to 609 m (orange/brown) in the Central Uplands.

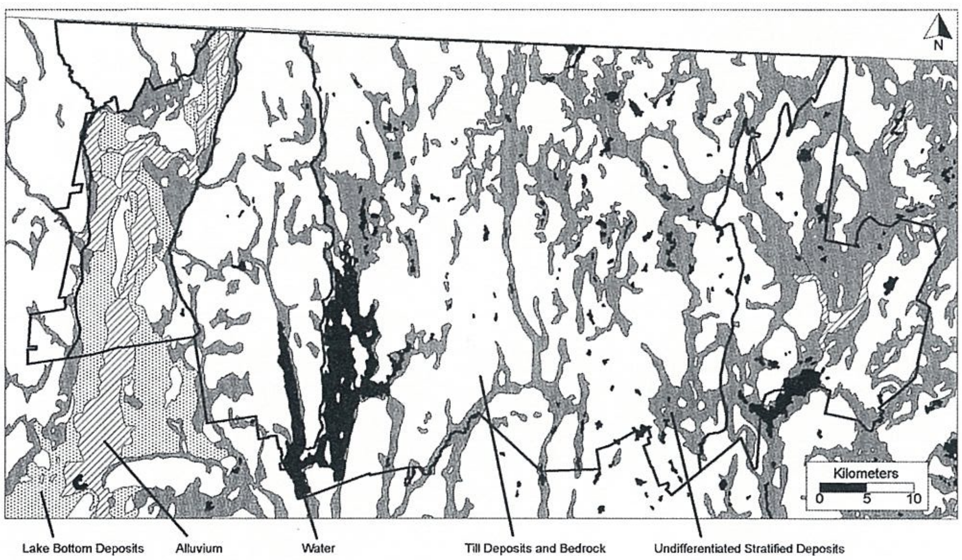


Figure 2. Surficial geology of the study region showing the physiographic divisions (black lines) and distinctive regional variation in surficial deposits. Outwash and till predominate in the Eastern Lowlands, whereas the Connecticut River Valley, which has a similar elevational range, contains extensive areas of glacial lake deposits and alluvium. Modified from Heeley (1973).

regional variation in physiography and climate that allowed us to evaluate land-use history and vegetation dynamics across environmental gradients. This study design enabled us to address four distinct, though closely related questions: (a) How did forest composition within the region vary at the time of European settlement and did this variation correspond to broad-scale environmental gradients? (b) What were the patterns and extent of historical land-use and land-cover change and how was this related to regional environmental variation? (c) Did historical land use lead to the development of modern vegetation that is distinct in composition, structure, and pattern? (d) In what ways were the relationships between forest vegetation and environmental gradients altered by this regional disturbance and vegetation response? Answers to the first two questions are essential to interpret the causes of any subsequent vegetation changes and patterns. The third question has generated contrasting views in ecological literature. Many studies, including local paleoecological studies, suggest that intensive human impacts can change forest composition substantially (Whitney 1990; Foster and Zebryk 1993; Palik and Pregitzer 1994; White and Mladenoff 1994). However, other ecologists have suggested that the native species and forests of the region have developed a strong resilience to disturbance through

Table 1. Surficial Geology and Historical and Modern Land Cover Characteristics of the Central Massachusetts Study Region by Physiographic Region and Entire Area

	Connecticut River Valley	Pelham Hills	Central Uplands	Eastern Lowlands	Entire Region
Surficial geology (%)					
Stratified deposits	21	17	27	42	27
Till and bedrock	22	83	73	55	67
Lake bottom	31	0	0	0	3
Alluvium	26	0	0	3	3
1830 Land cover (%)					
Open agriculture	65	65	79	77	75
Forest/swamp	24	34	18	18	21
Meadow	7	<1	2	3	2
Water	4	<1	1	2	2
1985 Land cover (%)					
Agriculture	27	3	7	13	10
Urban	15	3	8	22	9
Forest	53	92	81	58	76
Meadow	1	1	2	2	2
Water	4	1	2	2	2
Climate					
Mean January temp. (°C)	−4.5	−5.6	−5.6	−4.6	−5.4
Mean July temp. (°C)	21.8	20.6	20.5	21.5	20.8
Growing degree days	3585	3291	3263	3508	3344

repeated episodes of hurricane and fire that should enable them to recover from human impact and maintain a consistent regional composition (Nichols 1913; Raup 1964; E. Russell 1980).

The fourth major question is whether broad-scale human disturbance has altered regional relationships between vegetation and environmental gradients. Three possibilities exist: (a) regional vegetation-environment correlations could be enhanced as variation in land use along physiographic and climatic gradients reinforces natural patterns, (b) regional patterns could weaken due to regional constancy in land use and inadequate time for species to reassume an equilibrium with climate, and (c) regional variation could remain unchanged as species respond differentially to human disturbance across gradients of environment, physiography, and original vegetation.

Our historical study is paralleled by paleoecological research within the same region such that independent assessments of vegetation composition and change could be derived and compared, and so that vegetation response to land use could be analyzed in relationship to forest dynamics during the pre-European period (Fuller and others 1998). This coordinated project is grounded in the belief that ecologists need to evaluate modern conditions and anticipate future changes with an understanding of the extent, magnitude, and consequences of past dynamics.

Study Region

The study region, which occupies a 100 × 50-km area of Worcester, Franklin, and Hampshire counties in north-central Massachusetts (Figure 1), covers a relatively broad range of environmental and cultural variation across three physiographic areas that are distinguished by elevation and relief, geology and soils, climate, Native American activity, and European land-use history (Figure 2 and Table 1). The largest physiographic area is the Central Uplands, which forms part of the broad Central Highlands that run nearly the length of central New England (Denny 1982). This area is distinguished by an undulating topography of north-south-trending hills and narrow valleys with a general relief of 150–430 m above sea level (a.s.l.). Metasedimentary and metavolcanic gneisses, schists, and granites of Paleozoic age are overlain by thin till deposits on the uplands and deep, level outwash deposits in the narrow valleys (Table 1 and Figure 2) (Heeley and Motts 1973; Denny 1982; Griffith and others 1994). Upland till soils are typically acid sandy loams of relatively low nutrient status. With the exception of small urban areas, lakes, and open wetlands, the area is extensively forested, with only limited active farmland. Within the western part of the Central Uplands, the Pelham Hills sub-area is characterized by more rugged hills, steeper terrain, and even greater forest cover. The Quabbin Reservoir, created in the 1930s to provide water for the Boston metropolitan area, occupies portions of the former townships of Dana, Prescott, Greenwich, and Enfield in the Swift River Valley, an area of lower elevation and more extensive outwash soils than the surrounding uplands (Figure 1).

The Connecticut River Valley, a broad lowland west of the Central Uplands, is distinct with respect to geology and physiography (Denny 1982). The level-to-rolling plains at 30–75 m a.s.l. are underlain by sedimentary siltstone, sandstone, shale, and conglomerate and relatively thick deposits of outwash, alluvium, and glacial lake sediments (Figures 1 and 2). Soils include well-drained, coarse-silty Hadley, poorly drained Limerick, and excessively drained sandy soils of the Hinckley series. The plains are interrupted by steep basalt ridges of Mesozoic age that reach 250 m and are overlain by thin till soils. The relatively rich soils, level terrain, and long settlement history of the valley bottom have led to a modern land cover of agricultural land, urban and industrial areas, concentrated housing, and forest, in contrast to the ridges that are heavily wooded.

In the eastern part of the study area, the Central Uplands grade into the Eastern Lowlands, which is part of the extensive Coastal Lowlands of New England (Denny 1982). This area of hills and irregular relief at 40–200 m a.s.l. is formed by granite, schist, and gneisses of Proterozoic age overlain by glacial till, extensive areas of stratified deposits, and lesser amounts of alluvium. Modern land cover includes forest, wetlands, urban areas, housing, and agriculture.

Comparison among the physiographic areas indicates that the Connecticut River Valley and Eastern Lowlands occur at lower elevations and have gentler relief than the intervening Central Uplands (Table 1). In general, the Connecticut River Valley is lower in elevation, has more nutrient-rich soils, and has retained more open agricultural land than the Eastern Lowlands. Across the region, there is substantial variation in surficial geology, with glacial till dominating the Uplands, lake deposits and alluvium in the Connecticut River Valley, and stratified deposits and till in the Eastern Lowlands. The Connecticut River Valley and Eastern Lowlands have milder climates than the Central Uplands, with average summer and winter temperatures 2-3° C lower. This climatic gradient encompasses a range in township average growing degree days from nearly 3600 in the Connecticut River Valley and Eastern Lowlands to 3300–3400 in the southern part of the Uplands to only 3100–3200 in the northern Uplands.

Methods

Environmental Data

Regional environmental data were compiled to interpret spatial and temporal patterns of forest vegetation. Soil data included regional maps of soil series and a generalized map (1:250,000) of surficial deposits depicting four broad types (Heeley and Motts 1973). Geographic variables (elevation, latitude, and longitude) were compiled from a digital elevation model (DEM; see GIS Development and Data Analysis below) and climatic parameters (mean annual temperature and precipitation, January and July temperature and precipitation, and growing degree days) were derived by using an empirical climate model developed by Ollinger and others (1993) for New England. These modern climate parameters were used for all analyses, with no attempt to adjust for possible historical changes in climate [see Baron and Smith (1996)] when examining historical vegetation patterns. This approach was based on the belief that although climate may change through time, over a 350-year period we would not expect any change in magnitude or geography of the climatic gradient.

History of Land Use, Land Cover, and Human Population

Historical land-use and land-cover data were obtained from town valuation records for 1791–1860, state census records for 1865–1905, the Massachusetts MapDown project for 1951 and 1971 (MacConnell 1973), and MassGIS for 1985 (MassGIS 1991). All data are stored permanently in the Harvard Forest Archives. For 1985, the 21 original land-cover categories were grouped into four types: Agriculture/Open, Urban, Forest (including orchards) and Water (including nonforested wetlands). Dates of township incorporation and settlement are based on White (1966) and WPA (unpublished data), respectively. A wide array of cultural data extending back to 1791 was compiled from the US census on a township and decadal basis, including statistics on land cover and population. Population figures were extended back to 1650 by using the Massachusetts census. Due to changes in recording and reporting methods [Black and Wescott (1959)], land-cover data before 1801 were deemed too uncertain for use. An extensive archaeological data base for the region (Mulholland 1984) was made current through an exhaustive search of all known professional and amateur collections (M. Mulholland and D. Foster unpublished)

Colonial Period Vegetation

At the time of settlement, surveys were conducted to establish the physical boundaries of each township, to delimit land grants to initial proprietors or owners, and to lay out road networks. Although variable in design, density, and detail, these surveys used trees as boundary or witness markers to provide secure geographic reference; a tabulation of the trees recorded therefore provides a record of forest composition preceding widespread European disturbance in each township (Siccama 1971; Whitney 1994; Cogbill 1996).

For the present study, we compiled all available witness tree data (32 townships total) from four primary sources: (a) Proprietors' Record Books, which list each tree used to mark property boundaries for the first settlers; (b) maps and deeds describing the land of individual settlers; (c) plan maps and boundary descriptions of land grants and purchases; and (d) road surveys.

Forest Pattern at the Height of Deforestation (1830 AD)

In 1830, the General Court of Massachusetts passed legislation requiring each town to produce a town plan at a scale of 1 inch = 100 rods showing features such as roads, boundaries, meadows, and woodlands. To assess the pattern of forest area near the height of agricultural activity, these maps were compiled from the Massachusetts State Archives, transferred to 1:25,000 topographic quad sheets with a zoom transfer scope, digitized as vector images, and analyzed in raster format in Idrisi (Eastman 1992). Of the 49 towns in the study area, 43 maps from 1830 indicated woodlands; 5 distinguished softwood, hardwood, or mixed woodlots; 29 included meadows; and 5 indicated the location of swamps.

Modern Forest Composition

Modern vegetation composition was sampled in 461 plots (each 20 × 20 m) randomly located within the 45 modern towns in the study area. This sampling density represents one plot per approximately 775 ha, with 8–15 plots per town, proportional to town area. Locations with less than 50% canopy cover were not sampled, and plots were occasionally moved to the nearest forested stand in order to avoid stand boundaries and cultural features. At each plot, percent cover within height strata was estimated for each vascular species in eight cover-abundance classes (1 = rare, <1%; 2 = few, <5%; 3 = numerous, <5%; 4 = 5%–15%; 5 = 16%–25%; 6 = 26%–50%; 7 = 51%–75%; and 8 = >75%). In order to compare these data with Colonial data on tree distribution, analyses for the current study are restricted to overstory trees which are represented as average percent cover on a township basis.

GIS Development and Data Analysis

A DEM was assembled by combining 7.5-minute US Geological Survey DEMs in Idrisi, converting the resulting DEM to 60-m resolution, and changing the projection to Massachusetts State Plane. Surface roughness was calculated by sampling every fourth pixel on the DEM and running a high-pass filter in Idrisi to identify areas of abrupt change versus gradual change (Eastman 1992). Modern township boundaries were derived from MassGIS (1991), boundaries for 1830 were digitized from township plans, and intervening changes in boundaries were digitized from contemporary maps.

Colonial period and modern forest data were analyzed separately and collectively. Spatial patterns of the distribution and abundance of individual taxa were depicted on a township basis by using GIS, and detrended correspondence analysis (DCA) (Hill 1979) was subsequently used to examine species and township relationships. Regression of DCA axis scores versus townshipwide environmental variables was used to explore the environmental controls over vegetation variation across the region. Relationships between individual taxa abundance and geographic (elevation, latitude, and longitude) and climatic (temperature, growing degree days, and precipitation) variables were assessed through linear regression. Regional forest assemblages were identified through cluster analysis of the combined Colonial and modern data by using Ward's method, an agglomerative algorithm (Tongeren 1995), with the Goodman-Kruskal gamma coefficient to calibrate distances between clusters.

RESULTS

Prehistorical Indian Activity

Aboriginal peoples in the region had adopted maize agriculture by approximately 1200 BP and were utilizing a mixture of hunting, food gathering, and small-scale agriculture at the time of European contact (Mulholland 1988). The largest concentrations of indigenous people occurred in broad valleys and along streams and wetlands in the Eastern Lowlands and Connecticut River Valley, with much

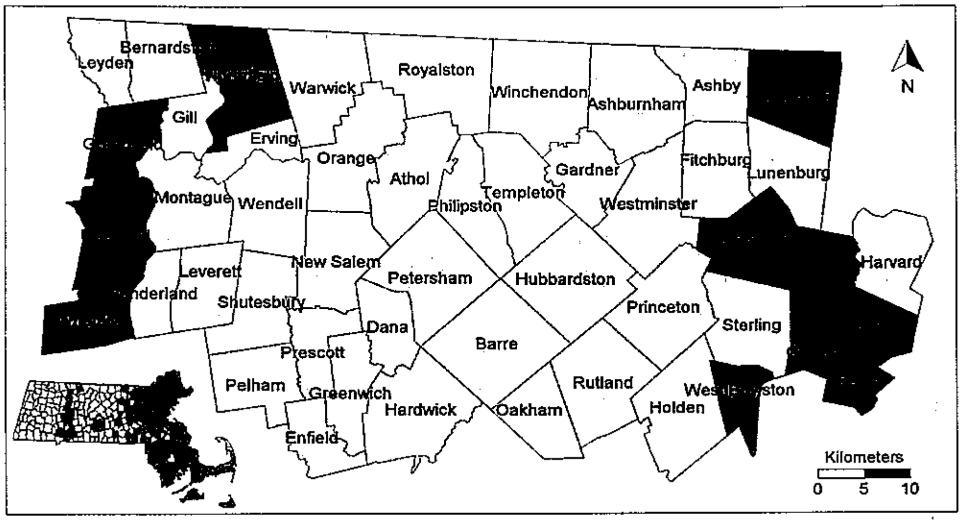


Figure 3. The central Massachusetts study area indicating the settlement date of townships within the state of Massachusetts. Settlement periods include dark gray, before 1700; gray, 1700–50; and white, after 1750.

smaller populations in the Uplands and to the north (M. Mulholland unpublished data). Major Indian settlements occurred to the east at Lancaster, in the Connecticut River Valley, and just south of the region in Sturbridge, and trails crossed the region (Mulholland 1984). Although archaeological and historical evidence for agricultural fields and clearing occurs throughout the region [for example, see Whitney (1793), Coolidge (1948), and H. Russell (1980)], the extent, duration, and intensity of use of such fields are unclear. One potential broad-scale Indian impact was the use of fire to clear settlements, to maintain fields, and to improve wildlife habitat. Paleoecological data suggest that fire activity was generally low across the study region but was greater in the lowland areas of denser Indian settlement and somewhat warmer climate (Fuller and others 1998).

Historical Changes in Land Use and Land Cover

New England Colonial settlement involved population expansion from coastal areas northward and inland along major river valleys, reaching the study area in the mid-17th century with the establishment of West Boylston (1642) and Lancaster (1643) in the Eastern Lowlands, and Whately (1672) and Deerfield (1673) in the Connecticut River Valley (Figure 3). Indian confrontations restricted English populations and township establishment through the early 1700s. From 1700 to 1750, however, two-thirds of the region was settled and, by the late 18th century, towns in the north-central area and more rugged Pelham Hills were occupied. The population grew at a relatively constant rate through the mid-19th century while maintaining a homogeneous distribution (Figure 4). Beginning about 1850, however, population growth increased sharply, rural densities declined, and industrial towns emerged (Figures 4 and 5). Although industries subsided following World War II and manufacturing towns often stagnated, the population continues to rise through suburbanization of the Connecticut River Valley, Eastern Lowlands, and adjoining towns (Figure 4).

European settlement initiated a 250-year process of forest clearance and environmental change that transformed the New England landscape (Cronon 1983) (Figures 5 and 6). Colonial agriculture provided both subsistence and commercial enterprise through export from ports near Boston and along the Connecticut River. In the 18th and 19th centuries, farms were small (about 20–75 ha); grew diverse grains such as corn, oats, rye, and wheat; and supported extensive pasture and hay for cattle. Three agricultural land-use or cover classes can be ranked by intensity of environmental impact: woodland that was cut for wood products and often grazed or burned; pasture that was grassy, mostly treeless, and grazed intensively; and cultivated land that was cleared and plowed, homogenizing the top 15–25 cm of soil (Foster 1992; Motzkin and others 1996).

The historical abundance of these cover types was controlled by temporal and geographic changes in agricultural type and intensity (Figure 6). Spatial variation developed by the 1790s when agricultural land (pasture and cultivated) comprised approximately 50% of the Connecticut River Valley and Eastern Lowland regions and 75% of the Central Uplands. For nearly 75 years (1800–1875), intensive agriculture thrived, with 60%–80% of most townships in open land (Figure 5). The Central Uplands and broad plains of the Connecticut River

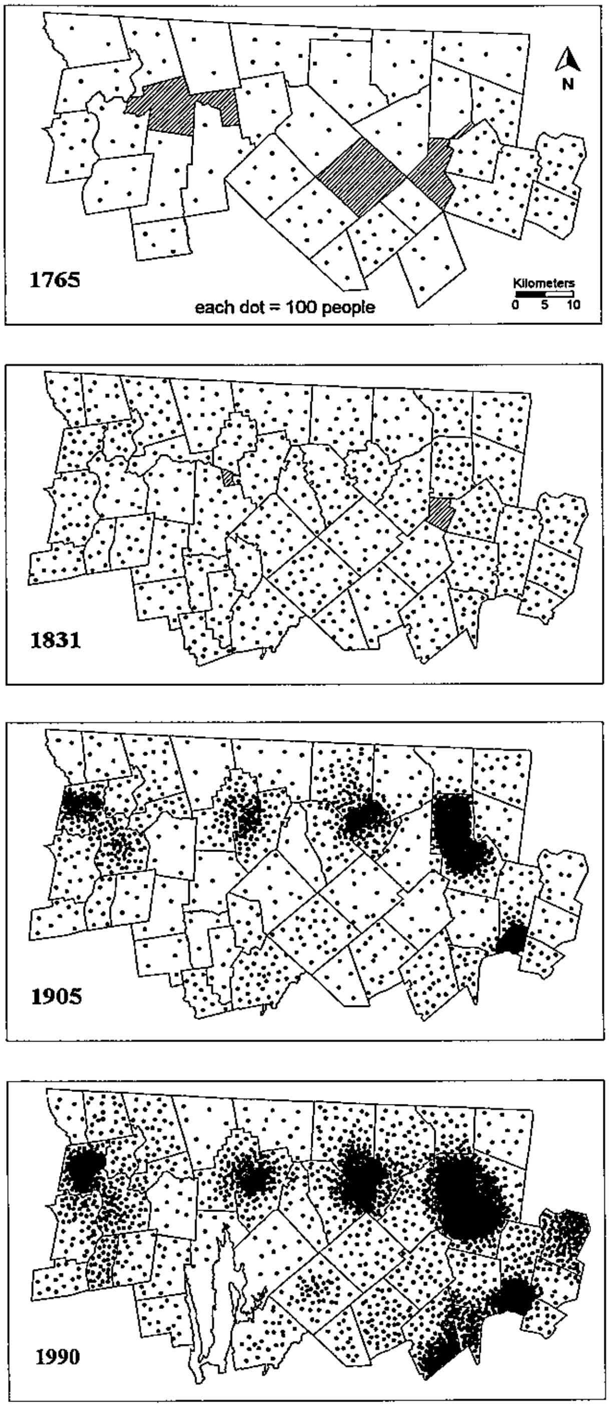


Figure 4. Changes in population density across the study region from the Colonial period to the present. Through the peak of agricultural activity in the mid-19th century, the population was distributed in rural towns of remarkably homogeneous density. With industrialization and major population growth, rural populations declined as people migrated to urban centers. In more recent decades, suburban populations have expanded. Diagonal lines indicate towns for which data are unavailable.

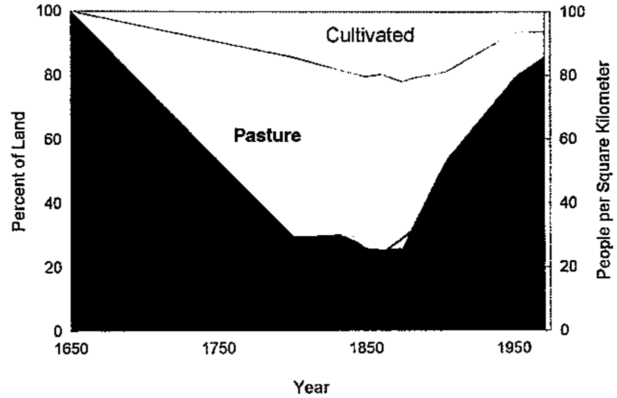


Figure 5. Changes in land use (dark gray, woodland; gray, pasture; and white, cultivated) and human population (dark solid line) through the historical period in central Massachusetts. Population increases in slope in the mid-1700s, mid-1800s, and early 1900s, whereas land use exhibits three contrasting phases: deforestation through 1800, intensive agriculture (1800–75), and rapid reforestation (1875–1985).

Valley were most intensively deforested (Figures 6 and 7), with somewhat more forest occurring in the Pelham Hills (30%–50% forest), Eastern Lowlands (25%–35%), and along bedrock ridges in the Connecticut River Valley. Pasture was 2–4 times as abundant as tillage, with an agricultural emphasis on grazing animals, particularly beef cattle.

Industrialization in the middle to late 19th century brought agricultural decline and a shift to perishable crops such as vegetables and milk that could be transported to urban centers (Black and Wescott 1959). Land abandonment and natural reforestation commenced with marginal farmlands in the Pelham Hills and Central Uplands and then spread across the region (Figure 6). During the 1920s and 1930s, construction of the Quabbin Reservoir and dissolution of four townships (Dana, Prescott, Enfield, and Greenwich) in the Swift River Valley increased the local rate of reforestation and created the largest water body (approximately 10,000 ha) in southern New England. Through the 20th century, central Massachusetts has become increasingly wooded, with the Pelham Hills and Quabbin area supporting approximately 90% forest, the rest of the Central Uplands ranging from 80% to 90% forest, and the Eastern Lowlands and Connecticut River Valley towns supporting less forest and more cultivated land. Recent increases in population in these two areas has been accompanied by concentrated housing and industrial development.

Overall, the study area typifies the changing relationship between population and land-use history across large parts of the eastern United States

(Whitney 1994). Population and agricultural land both increased through the early 19th century, but population continued to rise through the mid-19th-century period of agricultural stability, and increased with industrialization and farm abandonment. Reforestation was most rapid through the end of the 19th century and has slowed subsequently. Regional patterns of land use emerged early and persist: intensive cultivation in the broad lowlands and extensive deforestation, pasturing, and reforestation in the rougher uplands.

Forest Pattern at the Height of Agriculture

Agricultural statistics and other cartographic sources confirm that the forest pattern on 1830 maps is representative of the mid-19th-century period of intensive agriculture (Whitney and Davis 1986; Foster 1995; G. Motzkin and D. Foster unpublished). Analysis of these patterns identifies factors controlling landscape to regional variation in land-use intensity. It also provides insight into modern forest characteristics. Forests in 1830 comprise the current "primary" forests that have remained wooded throughout the historical period (Foster 1992; Gerhardt 1993; Motzkin and others 1996).

Comparison through linear regression of township census data in 1830 and forest area on the 1830 map indicates agreement between the latter and the sum of "woodland" and "unimprovable lands" in the census (G. Motzkin unpublished). Thus, forest on the 1830 map apparently includes wooded areas, cut-over and regrowing forest, and wooded wetlands and rocky areas unsuitable for agriculture. It does not include shrubby pasture, grass-dominated wetland ("meadow"), or areas being converted to agriculture. This analysis also confirms the comparability of two independent, historical assessments of forest cover at a township scale.

The 19th-century landscape was characterized by scattered woodlots in a matrix of agricultural land (Figure 7). The forest pattern that emerged in the mid-19th century and continues to control many modern characteristics of vegetation, ownership, and land use (Motzkin and others 1996) resulted from an interplay between land use and physiography that varied across the region. Physiographic

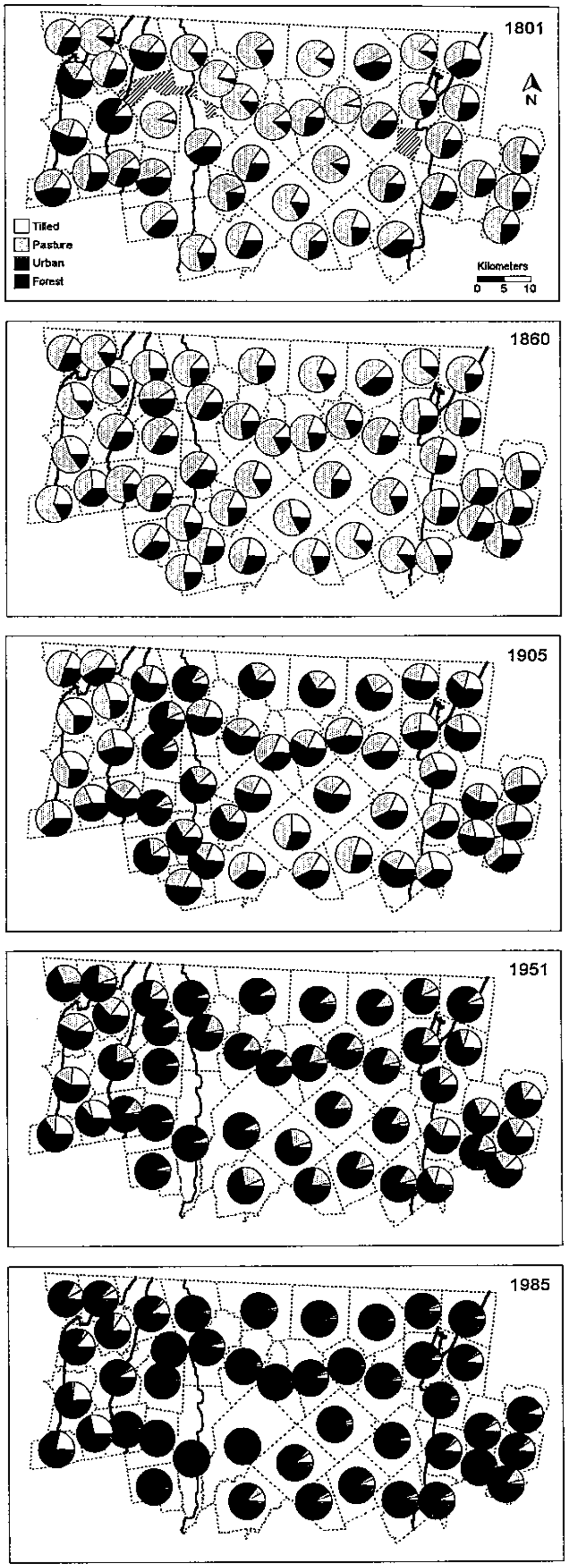


Figure 6. Change in land cover on a township basis across central Massachusetts from 1801 to the present. Physiographic regions are indicated and unincorporated towns in 1801 are marked with diagonal lines. Categories include forest (black), tilled (white), pasture (light gray), and urban (dark gray) in 1985. In 1801, active conversion of forest to open agricultural land and pasture was still occurring, leading to a peak of deforestation around 1860.

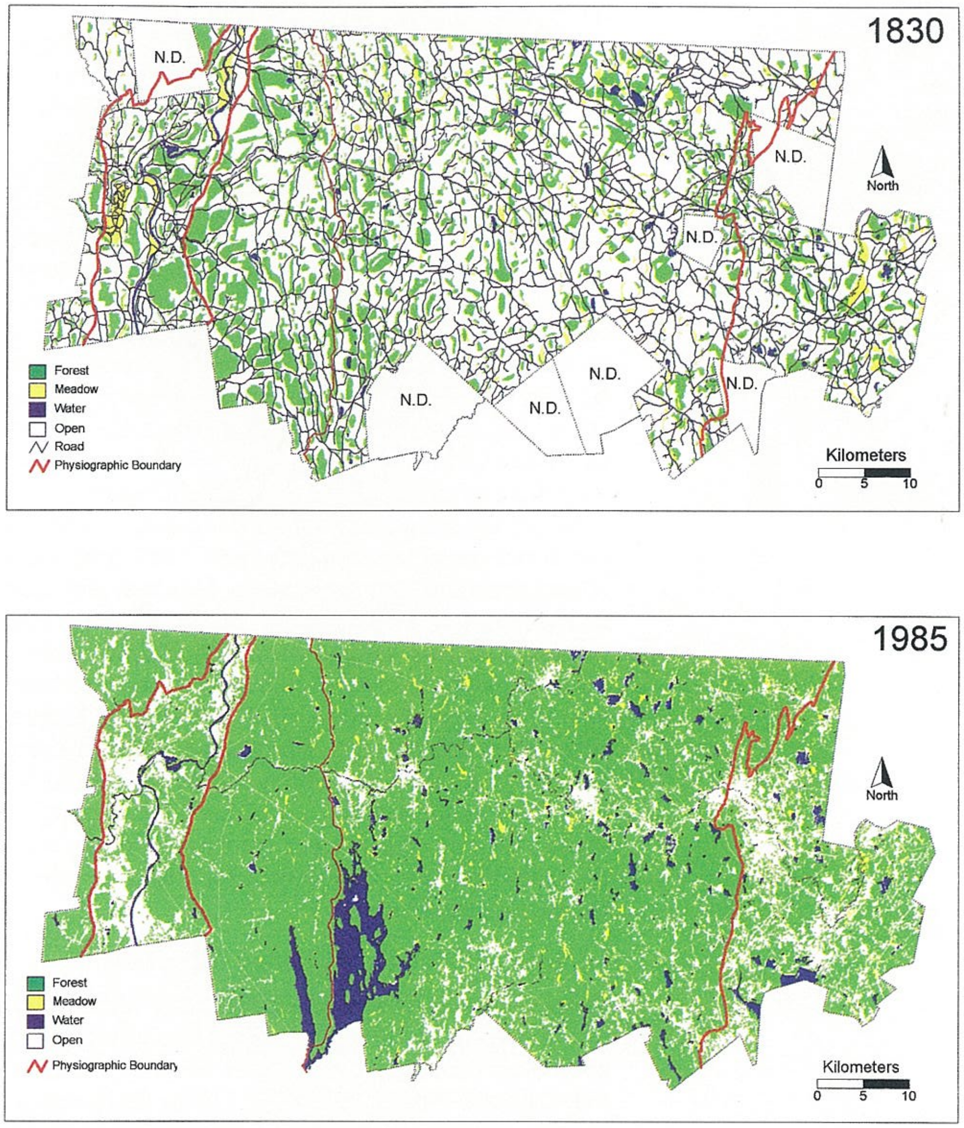


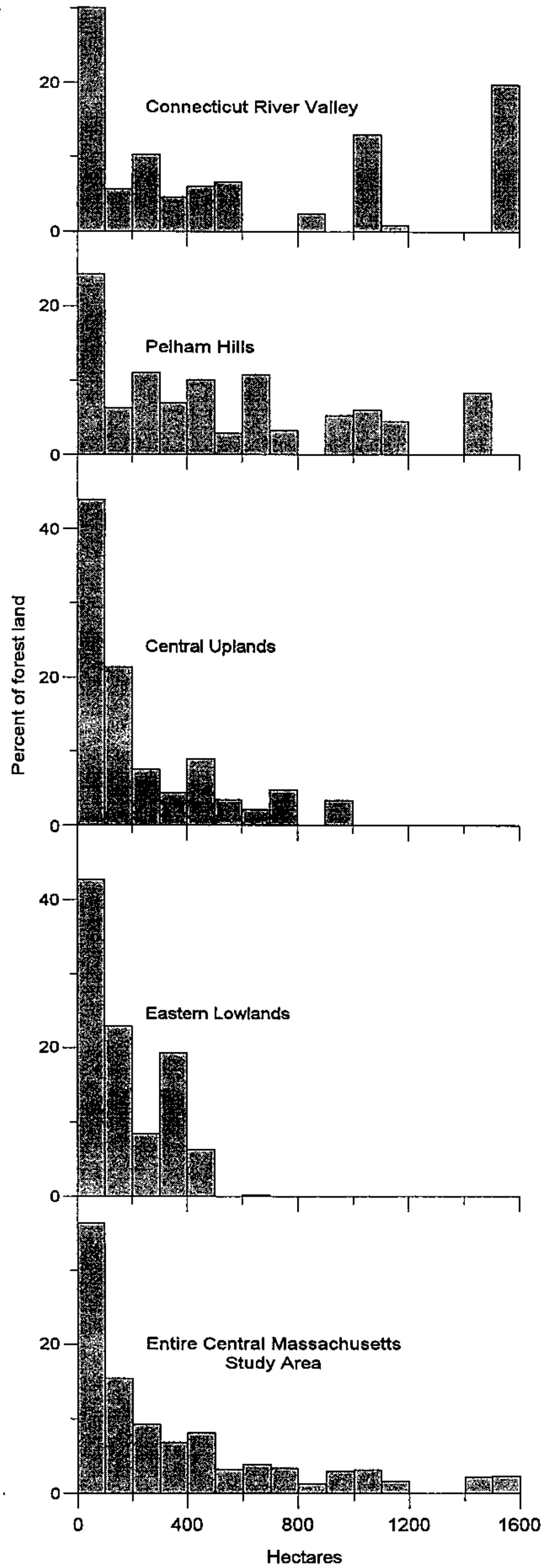
Figure 7. Changes in forest cover in central Massachusetts from 1830 (the height of the agricultural period when open fields predominated and woodlots were small, isolated, and heavily utilized for diverse wood products) and 1985 (forest dominated the region). The decline in agriculture, abandonment of farms, and movement of people into urban areas allowed the natural reforestation of most of the study area. Urban areas combined with agricultural areas in the Connecticut River Valley and Eastern Lowlands provide the major nonforested areas in the modern landscape.

features, topography, and soils vary within the different subregions and consequently exerted a variable influence on land use across the larger region. For instance, in 1830 the Connecticut River Valley had extensive field (65%) and meadow (7%) overlying level soils along the Connecticut and Deerfield Rivers and large forested areas on bedrock ridges and domes, wetlands, and coarse sandy outwash deposits (Table 1 and Figure 7). Forest areas in the Connecticut River Valley exhibited the widest range in size (from less than 1 ha to more than 1500 ha) in the study area (Figure 8).

The Pelham Hills supported a distinctive pattern, with forests predominantly restricted to steep slopes and agricultural areas (66%) on outwash soils and north-south bedrock ridges (Figure 7). Forest size distribution was remarkably similar to the physiographically distinct Connecticut River Valley (Figure 8). The rest of the Central Uplands supported very little forest area (18%) in a fine-grained pattern of small woodlots within an agricultural matrix. Forests were predominantly in narrow lowlands, steep slopes, and wetlands (Figures 7 and 8). The Eastern Lowlands paralleled the Central Uplands in the amount (approximately 18%) and forest size distribution and relationship to physiography. Till-covered areas and well-drained glacial materials were farmed, and excessively well-drained sands and poorly drained wetlands were forested.

Forest-Cutting Activity

The US census for 1885 and 1895 indicates the intensity and size of logging activities and type and age of forests cut during this period of regional reforestation (Figure 9). Across the region in the late 19th century, stands 25–40 years in age comprised



more than half of the reported harvest, suggesting a dearth of old forests and reliance on small hardwoods for fuel, railroad ties, poles, and posts, and white pine for boxes, barrels, and crates (Fisher 1933). In the Eastern Lowlands and adjoining Central Uplands, up to 50% of cutting occurred in stands less than 20 years of age and little occurred in stands more than 40 years old. In contrast, in the Pelham Hills, few cut stands were less than 20 years old, many were 25–60 years old, and some exceeded 65 years of age. Oak and chestnut were cut heavily in the Connecticut River Valley and Eastern Lowlands, whereas birch and beech (lumped in the census) were most frequently cut across the Central Uplands and to the north (Figure 9). Pine and maple were harvested extensively across the region.

In the modern landscape, approximately 16% of the forest area was cut between 1985 and 1995 (Department of Environmental Management and D. Kittredge, D. Foster, and B. Slater unpublished). Harvest intensity ranged from light selective thinnings to patch clear-cuts, and areas cut ranged from less than 5 ha to more than 100 ha as loggers concentrated on larger, older forests (that is, more than 65 years old), selectively removing merchantable trees while leaving a residual, tall canopy of scattered trees. This pattern contrasts strongly with the common late-19th-century practice of clear-cutting young stands.

Historical Changes in Forest Structure

Based on historical accounts and the size of construction materials from the 17th and 18th centuries, it can be surmised that large trees were common in the Colonial forests (Whitney 1793). Estimates of natural and human disturbance (for example, wind, fire, and indigenous activity) suggest that extensive areas of forest more than 100 years old would have been widespread (Stephens 1955; Foster and Zebryk 1993; Boose and others 1994; Foster and Boose 1995; Fuller and others 1998). In contrast, 19th-century descriptions of forests, fuelwood consumption, and wood utilization suggest that woodlands of the intense agricultural period (that is, 1790–1880) were young and dominated by multiple-stemmed sprouts that were cut frequently and maintained in a sproutland or coppice condition [compare Emerson (1846), Peterken (1996), and Foster (1998)]. Data from 1885–95 indicate that more than 75% of the forest was less than 30 years of age (Figure 10) and was comprised of the first generation of trees on

Figure 8. Variation in the size distribution of forest stands in 1830 within the physiographic areas and for the entire study region in central Massachusetts.

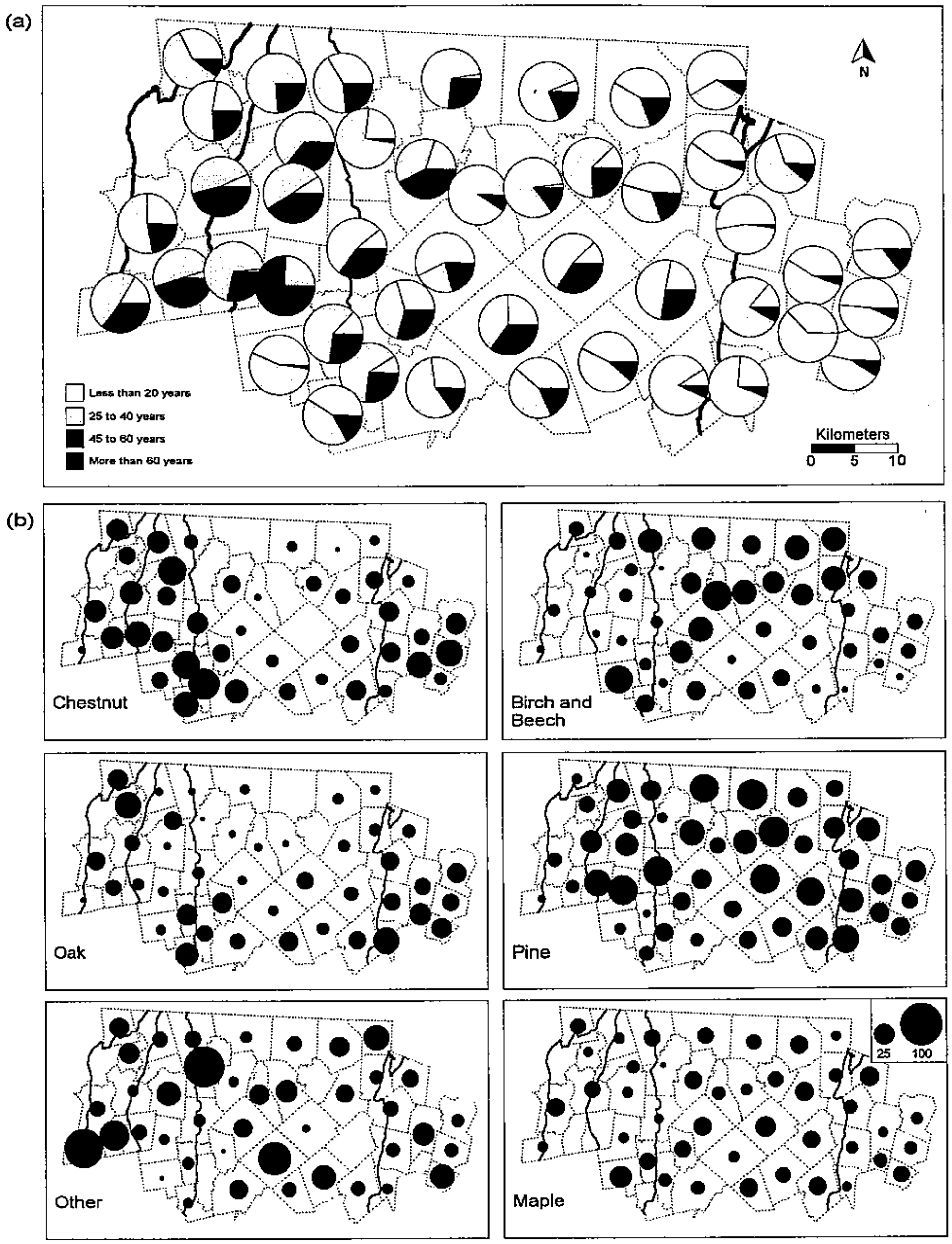


Figure 9. Forest logging activities in 1885 depicting the age distribution of forest stands that were harvested (a), and the relative number (%) of cuttings of different tree species (b). The majority of forests cut were less than 40 years old, although many younger forests were cut in the east and older forests were cut in the west. Species selection parallels their Colonial distribution, with oak and chestnut preferred in the Connecticut River Valley and Eastern Lowlands, and birch and beech cut more frequently in the northern Central Uplands.

abandoned fields and cut-over primary and secondary forests. According to surveys from the early (1916–29) and mid-1900s (1951), the small size (less than 35–40 feet tall) and young age of forests were maintained until the last few decades. By 1971, forest structure increased toward taller, older stands, with 75% of the forest exceeding 40 feet in height and townships in the Pelham Hills supporting more tall forest than elsewhere in the study region (Figure 10) (MacConnell 1973). The trend of increasing forest size and age continues today (Brooks and others 1992).

Thus, from the late 1700s through the mid-1900s forests were comprised predominantly of small, young trees. Despite the increase in forest area that occurred after 1850, tree size and age remained low, presumably due to ongoing forest cutting and the effect of the 1938 hurricane. Extensive tall and old forest is a relatively recent phenomenon that has emerged as growth has exceeded forest cutting. The modern practice of selection rather than clear cutting maintains tall, uneven-aged stands.

Colonial Period Vegetation

The number of witness trees tallied from proprietor's records varied from 35 to 538 per town, with a mean of 161. Data were analyzed as relative abundance, calculated for each taxon as a percentage of the total number of trees tallied within Colonial

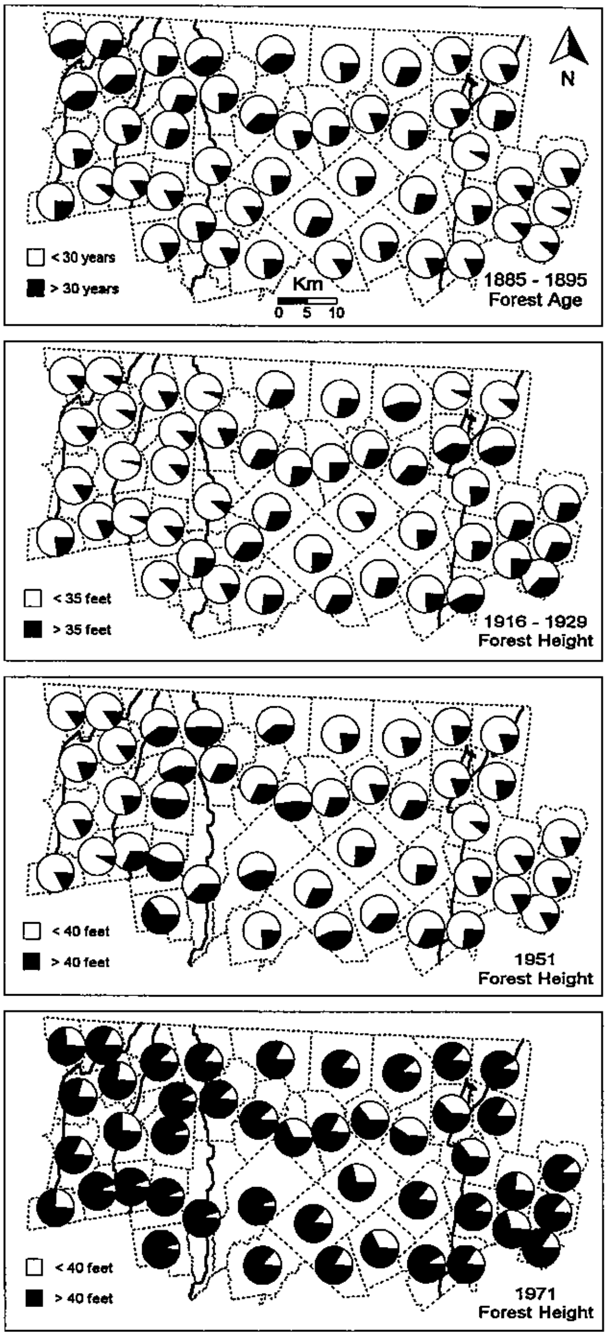


Figure 10. Changes in forest age and height structure since the late 19th century. In 1885–95, the majority of forests were less than 30 years old, with younger forests in the east than northwest. From 1916–29 to 1951, forests remained short in stature, with a general trend toward increased growth especially in the Pelham Hills. However, a regionwide increase in height has occurred since 1951.

(17th-18th century) township boundaries (Table 2 and Figure 11). A total of 58 tree names were recorded and examined for synonomy. Initial analysis indicated that results at a taxonomic level below genus provided little additional information, and consequently 14 tree genera occurring in more than 20% of the townships were included for statistical analysis. Less common trees are discussed below, but their distributional patterns were not analyzed quantitatively.

Three distributional patterns emerge for common trees: southern taxa (oak and hickory) were most abundant at low elevations in the southern Central Uplands, the Connecticut River Valley, and the Eastern Lowlands, and their abundance is positively correlated with increasing growing degree days (Figure 11 and Table 3); northern taxa (hemlock, beech, maple, and birch) increase with elevation and decreasing annual temperature, and reach their greatest abundance in the northern Central Uplands; and other taxa are either less abundant (poplar, ash, and spruce), less common (cherry, elm, and larch), or exhibit little geographic relationship to elevation, climate, or physiography (pine and chestnut). The regional distribution of individual taxa during the Colonial period was most strongly related to climate expressed as growing degree days (GDD) (township maximum and mean). Oak (r^2 = 0.53) and hickory (r^2 = 0.44) were uncommon or absent in cool northern townships and increased greatly to the south and at lower elevations. Oak was the most abundant taxon, reaching a maximum value of 75%, exceeding 30% in more than half of the townships, and occurring in 97% of the townships. Among northern taxa, hemlock (r^2 = 0.57), beech (r^2 = 0.53), and maple (r^2 = 0.47) had stronger relationships with climate than did birch (r^2 = 0.18). Hemlock was most abundant, reaching a maximum of 31% and frequency of 81%. Beech (frequency, 66%) was abundant in the north and exceeded 20% in four towns. Maple and birch were less abundant (maximum value of 18% and 13%, respectively) but occurred in more than 90% of the towns. Pine and chestnut were very common (frequency within towns of 100% and 91%) and abundant (maximum of 52% and 20%) but showed no strong distributional pattern. Chestnut was absent from three towns in the Central Uplands and was more abundant around the Uplands margins, whereas pine was somewhat more abundant in the Central Uplands. Patterns were variable among less abundant and less common taxa. For instance, ash had two areas of abundance in the southern Central Uplands and Connecticut River Valley, spruce was more abundant in the western and northern part of the study area, poplar was more common in the south, and elm and larch were scattered.

Table 2. Mean Abundance (Percentage) for Each Taxon in the Colonial and Modern Periods for the Entire Study Region and the Major Physiographic Areas

	Whole region		Connecticut Valley		Pelham Hills		Central Uplands		Eastern Lowlands	
	Colonial	Modern	Colonial	Modern	Colonial	Modern	Colonial	Modern	Colonial	Modern
Maple	7.6	24.8	3.9	30.4	3.3	27.2	10.3	23.9	3.7	23.1
Beech	6.7	2.9	0.3	1.0	5.6	3.9	9.6	3.3	1.9	1.1
Hemlock	9.9	11.6	4.8	15.3	5.2	14.8	13.9	11.9	1.7	1.3
Oak	32.6	24.1	44.7	22.1	38.1	20.8	21.2	23.5	59.4	34.9
Hickory	2.2	2.0	4.6	3.8	4.2	0.4	0.7	1.5	2.9	4.1
Chestnut	7.7	0.6	7.7	0.7	13.8	0.8	6.6	0.5	6.0	1.0
Pine	19.9	15.2	16.5	10.9	18.4	10.9	22.1	16.1	16.8	20.8
Birch	3.7	12.3	2.0	10.8	3.4	14.8	4.2	12.6	1.6	8.2
Ash	2.9	2.3	4.5	1.3	3.1	3.2	3.3	2.3	0.5	2.1
Cherry	0.5	2.1	0.8	1.2	0.1	2.6	0.6	2.4	0.4	1.4
Spruce	1.4	0.6	2.7	0.0	2.0	0.0	1.4	1.0	0.0	0.0
Elm	1.0	0.1	2.7	0.2	0.6	0.0	0.8	0.6	1.0	0.3
Poplar	2.0	0.5	1.1	1.1	1.3	0.0	2.2	0.6	1.4	0.4
Larch	0.6	0.0	0.0	0.0	0.0	6.0	1.0	0.0	<.1	0.0

Vegetation Change from the Colonial Period to the Modern Period

Despite broad similarities in species composition through time, we document considerable changes in the relative abundance and distribution of several dominant taxa at a regional scale from the Colonial period to the present (Figure 11 and Tables 2 and 3). The most striking change is the pronounced shift toward regional homogeneity in composition and a nearly complete loss of relationship between taxa abundances and the regional climate gradient. Although regional homogenization was a consequence of changes among all taxa, the process was strongly influenced by a few taxa. During Colonial times, oak and hickory had pronounced southern and lowland distributions, with strong positive relationships to GDD. Through ensuing centuries, oak increased slightly in relative abundance in the Uplands; declined in the south, Connecticut River Valley, and Eastern Lowlands; and developed a uniform regional abundance. Hickory became less abundant and common while remaining most common in the Connecticut River Valley and Eastern Lowlands. Among northern species that were strongly and negatively related to GDD during Colonial times, maple and birch have increased greatly, beech is much less important today, especially in the Central Uplands where it was formerly abundant, and hemlock is more abundant in the west. These trends have obscured the original relationship with climate (Table 3). Other changes include a tremendous decline in the relative importance of chestnut due to introduced blight, a small decrease in pine in some Central Uplands townships, and declines in elm, ash, spruce, and poplar. Cherry has increased in relative abundance and frequency.

Combined ordination of Colonial and modern vegetation data highlights the patterns of regional homogenization and change in species composition (Figure 12 and Table 4). Colonial towns form a distinct grouping from modern towns and spread out along the first axis, whereas modern towns form a dense grouping. Modern township position in ordination space is largely controlled by increases in maple and birch, declines in hickory and beech, and increasing township similarity. An analysis of position along the first DCA axis indicates a strongly positive relationship to growing degree days primarily due to the massive increases in red maple and birch in southern townships.

Separate ordination of the Colonial and modern data confirms the decline in the environmental patterning of the vegetation. The separation of Colonial townships along the first DCA axis corresponds to a strong relationship with climate (GDD; $r^2 = 0.58$, $P < 0.001$; Table 4), whereas the modern ordination is only weakly related ($r^2 = 0.14$, $P > 0.05$). Groups of townships that were distinctly separated in the Colonial vegetation (for example, northern Uplands towns like Royalston, Winchendon, Westminster, Templeton, and Warwick versus southern and Lowland towns such as Harvard, Bolton, Lancaster, Leverett, Oakham, Deerfield, Sunderland, and Northfield) overlap in their modern distribution with Central Uplands towns.

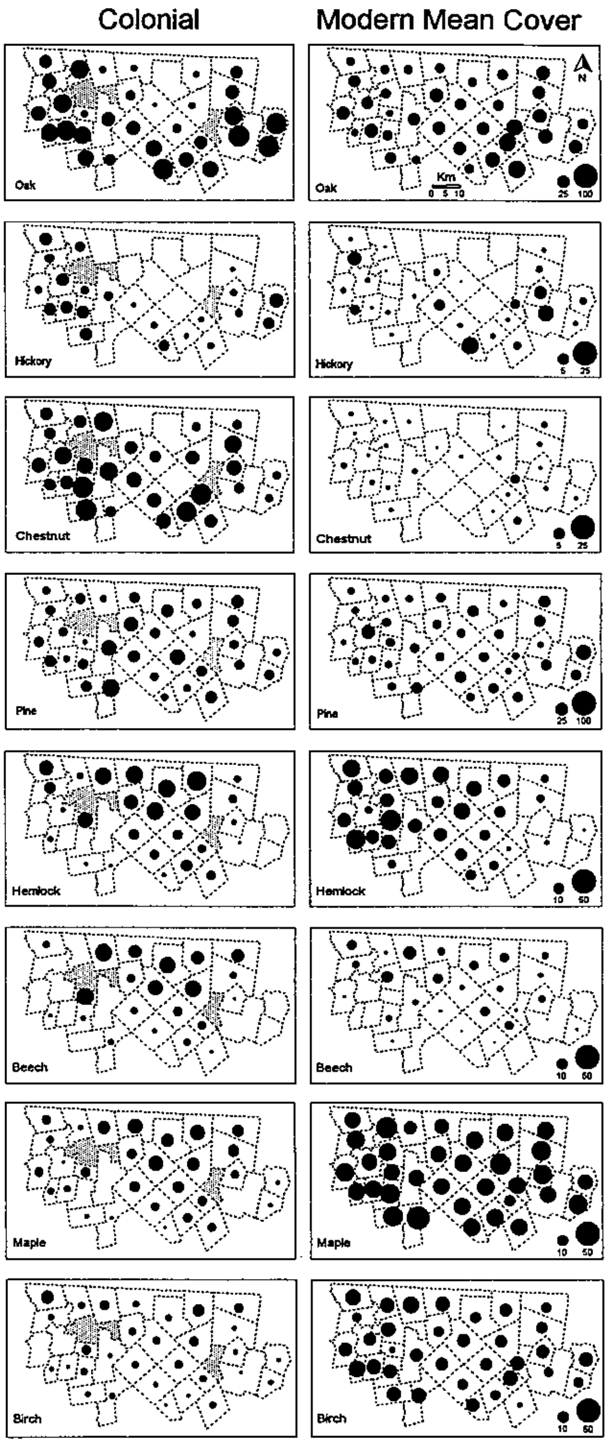


Figure 11. The relative abundance (%) of major tree taxa in the Colonial period before forest clearance and today. The pattern of regional variation in species that existed during the Colonial period has been obscured in the modern landscape, and overall abundances have changed, with birch and maple increasing and chestnut, hickory, and beech declining. Towns for which proprietor's data were unavailable are shaded. Note that maps for different taxa are scaled differently.

Table 3. Results of Simple Linear Regression of Tree Abundance (Percent Occurrence) and Climate* (Growing Degree Days) for the Colonial Period Based on Proprietors' Survey Data (ca. 1700-1800) and Modern Forests (1993–1996) For Each Township in North Central Massachusetts. Northern Hardwoods Include Birch, Maple and Beech

	Colonial Forest		Modern Forest	
	r^2	slope	r^2	slope
Oak	.53	.121***	.00	.004
Hickory	.44	.013***	.01	.008*
Hemlock	.57	−.052***	.06	−.017
Beech	.53	−.043***	.16	−.011*
Maple	.47	−.028***	.04	.010
Birch	.18	−.010*	.00	.001
Ash	.03	−.004	.00	.001
Chestnut	.02	−.005	.01	.001
Pine	.00	−.002	.05	.012
Cherry	.06	−.002	.12	−.010*
Larch	.06	−.002	?	?
Poplar	.02	−.002	.05	.002
Spruce	.03	−.002	.23	−.004
Elm	.06	.003	.19	.001*
Oak-Hickory	.55	.133***	.02	.012
Northern Hardwood-Hemlock	.61	−.122***	.05	−.018

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 are indicated as * < .05, ** < .01, * < .001.*

A parallel result is obtained when the combined Colonial and modern data sets are classified through cluster analysis (Table 5). Three predominantly Colonial assemblages are identified (oak-pine-chestnut, oak-pine-hemlock, hemlock-northern hardwoods) that are compositionally distinct and form a clear geographic pattern, with hemlock-northern hardwoods in the northern Central Uplands, oak-pine-hemlock in adjoining lower towns, and oak-pine-chestnut in the Connecticut River Valley, Eastern Lowlands, and southern portion of the Central Uplands. Two primarily modern assemblages (oak-maple-pine and maple-oak-hemlock) are compositionally similar and occur equally in all physiographic regions and across the elevational and climate range. The lack of overlap in Colonial and modern vegetation is underscored by this analysis (Table 5).

Discussion

The structure, composition, and pattern of forest vegetation in the New England landscape have been

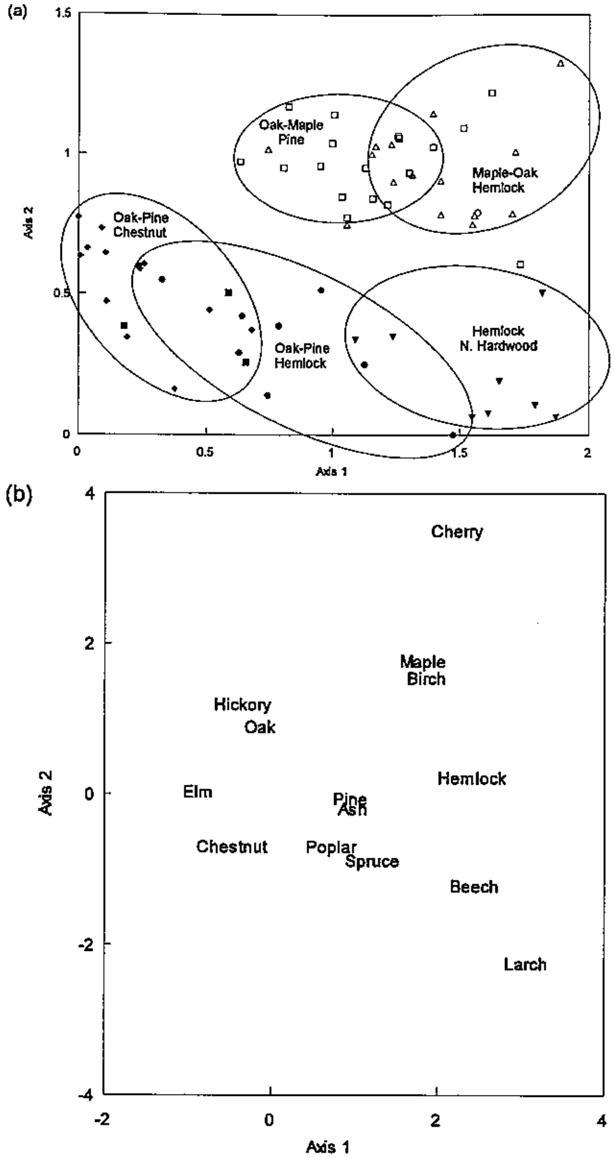


Figure 12. Detrended correspondence analysis of Colonial (solid symbols) and modern (open symbols) forest vegetation showing the distribution of township samples (a) and taxa (b) on the first two axes. The modern samples form a more tightly clustered pattern that is less elongated along the first axis. This change toward a distinct and more homogenous regional vegetation is a consequence of increasing maple and birch, declining hickory, and increase in oak in the Central Uplands.

dynamic over the past 3 centuries in response to major changes in the intensity and quality of land use (Fig. 13) (Fuller and others 1998). By examining these biotic and cultural dynamics across a region that encompasses major environmental gradients, we have been able to assess the spatial details of human activity and vegetation pattern and to evaluate their changing relationship to the physical

Table 4. Results of Regressions of Township Positions on the First Two DCA Axes Versus Climate Calculated as Average, Maximum or Forest-Weighted Growing Degree Days (GDD) for the Township. Significance Levels Include * < .05, *** < .001

	Axis 1 r^2	Axis 2 r^2
Colonial data		
Average GDD	0.576***	0.112*
Maximum GDD	0.623***	0.026
Modern data		
Average GDD	0.139*	0.018
Maximum GDD	0.089	0.003
Forest weighted GDD	0.182*	0.019*

and climatic characteristics of the landscape. To place these dynamics in a historical context, we begin with an evaluation of the pre-European vegetation, assess the magnitude and direction of forest change to the present, and then evaluate land use and other factors that have controlled these dynamics and may determine ongoing changes in the cultural landscape of New England.

Evaluation of Data Sources

Although witness tree data have been used to reconstruct vegetation and disturbance histories across the eastern United States (Siccama 1971; Seischab and Orwig 1991; Smith and others 1993), no systematic use has been made of the more diverse town survey, road survey, and proprietors' data that exist for many New England towns (Whitney 1994). Local studies suggest that these sources provide reliable and informative insights into landscape-to-township vegetation patterns (Whitney 1994; Cogbill 1996). When interpreting these "Colonial data," their qualities and potential limitations must be considered, particularly (a) the number of trees for each township (538 or fewer in the current study); (b) the time-transgressive nature of the data across a region (approximately 150 years in central Massachusetts), determined by the timing of settlement and land divisions; (c) loss of some records; (d) uneven sampling of vegetation along contemporary (that is, 17th and 18th century) boundaries; and (e) questions regarding bias and error [see Bourdo (1956), Grimm (1984), and Schwarz (1995)]. Nonetheless, the geographic consistency in Colonial tree data documented in this and other studies [see Siccama (1971) and Whitney (1994)] and similarity with contemporary pollen data (Fuller and others 1998; D. Foster and J. Fuller unpublished) confirm the representativeness and utility of

Table 5. Forest Types for the Central Massachusetts Study Area Based on Cluster Analysis of the Colonial and Modern Forest Data Combined. Species and Forest Types are Arranged to Display Major Variation in Species Abundance. A Comparison of Forest Type Distribution Between Modern and Colonial Township Indicates That Very Little Overlap in Forest Composition Occurs Between the Two Time Periods. Abundance Values are Percentage of All Tree Taxa

	Hemlock N. Hardwood	Maple-Oak Hemlock	Oak-Pine Hemlock	Pine-Chestnut	
				Oak-Maple-Pine	Oak-Pine-Chestnut
Hemlock	20	16	10	8	2
Beech	17	3	6	3	0
Maple	15	25	8	23	2
Birch	6	14	6	11	1
Cherry	1	3	1	2	0
Pine	19	14	20	15	16
Poplar	2	0	2	1	1
Spruce	2	1	1	0	2
Ash	3	3	4	2	3
Elm	0	0	1	0	2
Chestnut	4	0	8	3	8
Hickory	0	3	2	2	5
Oak	8	19	30	29	55
Modern towns (%)	0	44	3	53	0
Colonial towns (%)	25	0	28	9	38

these historical data. Our analysis of Colonial data from 32 townships across central Massachusetts documents regional patterns in taxa abundance that are spatially consistent and structured along environmental gradients. However, limitations in these data do warrant consideration. The surveys span a short time period and therefore provide a static sample of vegetation that may be dynamic at stand to regional scales due to disturbance or climate change (Foster and Zebryk 1993; Fuller and others 1998). Taxonomic resolution is variable but primarily at the generic level, and differs somewhat from that of pollen analysis. Finally, the data provide spatial resolution at a township level and may be ambiguous for townships crossing major substrate, disturbance, or environmental boundaries. In summary, survey data lack the temporal continuity but provide more consistent and finer spatial resolution than lake-level paleoecological data, and they provide more extensive information on regional vegetation patterns than township or county histories that may contain higher taxonomic resolution (Raup 1937; Foster 1992).

Regional Variation in Colonial Forest Vegetation

At the time of European settlement, individual taxa and tree assemblages exhibited a regional pattern that varied consistently with climatic gradients and physiography. Three broad spatial patterns of variation included (a) southern taxa such as oak and hickory increased with growing season and across the lower elevations in the Connecticut River Valley, Eastern Lowlands, and southern part of the Central Uplands; (b) northern hardwoods (beech, maple, and birch) and hemlock increased in the higher, cooler Central Uplands; and (c) pine and chestnut were abundant and variable across the region. These distributions led to a strong sorting of township-level vegetation across environmental gradients as documented in regional maps, DCA, and cluster analyses (Figures 11 and 12). The northern Central Uplands was largely dominated by hemlock-northern hardwoods. Hemlock, beech, and maple reached their greatest Colonial abundance in this assemblage, and pine and birch were near peak abundance. The ability to infer the species involved is variable and necessarily induces some circularity in interpretations of species biology and disturbance histories. Palynological data and local histories suggest that sugar maple was more important in the Colonial period than red maple (Whitney 1793; Fuller and others 1998). This interpretation is consistent with the greater longevity, shade tolerance, and northern distribution of sugar maple, which parallels beech and hemlock (Pacala and others 1996). Based on longevity and shade tolerance, yellow birch was probably most abundant in the northern

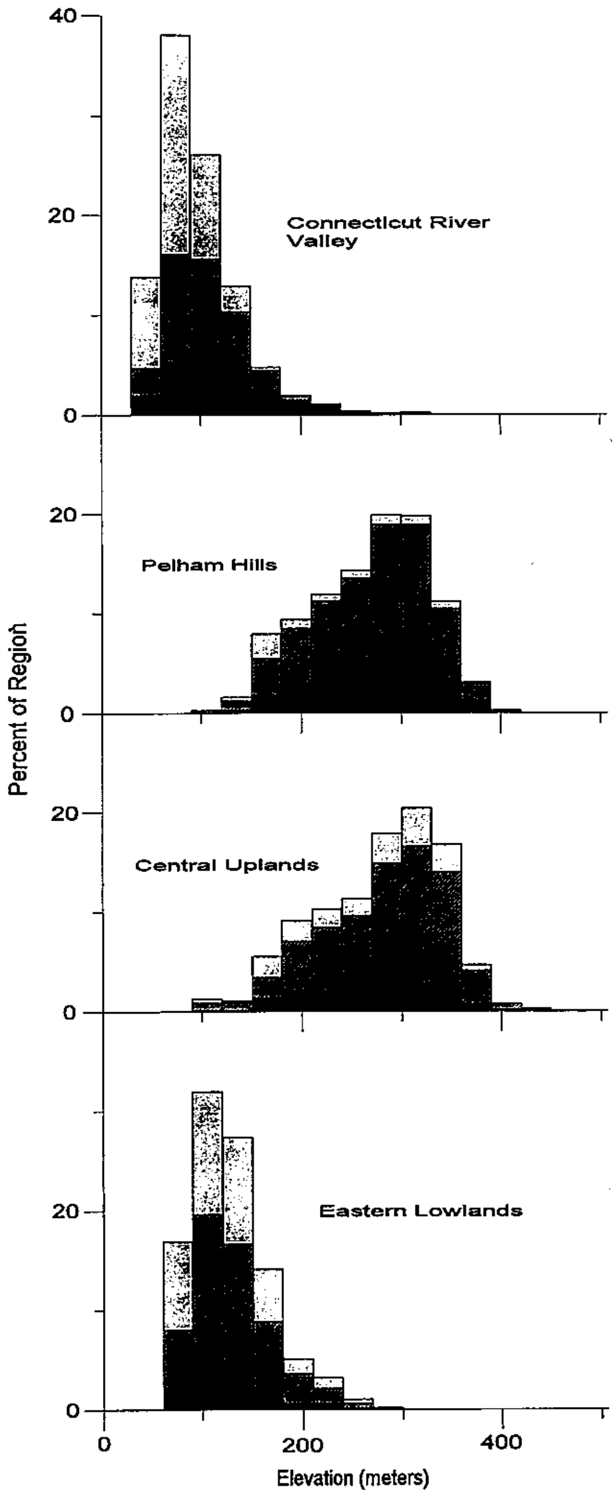


Figure 13. The relative abundance of forest in 1830 (black) and 1985 (dark gray) by elevational distribution in the study area. The light gray portions of each bar represent current nonforested areas.

hardwoods (Hough and Forbes 1943; Fowells 1965; Forcier 1973; Pacala and others 1996). This vegetation type is similar to the hemlock-northern hardwood climax postulated and reconstructed across the broad uplands of New England (Nichols 1913; Lutz 1930; Hawes 1933; Winer 1955; Spurr 1956; Filip and others 1960; Siccama 1974; Backman 1984). The abundance of hemlock, beech, and sugar maple and relatively low abundance of early to midsuccessional taxa suggest that disturbance by fire, hurricanes, and human activity was low in frequency and intensity or localized to specific substrates or landscape positions (Fisher 1933; McIntosh 1972; Foster and Zebryk 1993). The abundance of pine is notable. Based on historical sources (Whitney 1793) and palynological evidence (Fuller and others 1998), white pine was much more abundant than pitch pine across the till-dominated uplands. White pine is a moderately shade tolerant but long-lived species (250–300 years) that is dependent for establishment on canopy openings. Thus, its high abundance across the uplands may have been due to infrequent large disturbance, local abundance on open or droughty sites (for example, pond shores, beaver meadows, and well-drained sandy soils), or local disturbance by fire or humans such as abandonment of Indian fields (Fisher 1933; Gordon 1940; H. Russell 1980; Bernstein 1993).

In the lower elevations in the southern portion of the Central Uplands, the Connecticut River Valley, and Eastern Lowlands, there was a rather abrupt transition as hemlock and northern hardwoods gave way to increasing oak and chestnut. A transitional assemblage (oak-pine-hemlock) with intermediate values of all taxa (Table 5) is identified for townships that include two physiographic areas or a wide elevation range. In lower, warmer townships, oak was predominant, joined by white pine, chestnut, and hickory (Botts 1934; Bromley 1935). This assemblage occurs across a wide range of surficial materials and topographic roughness and therefore is presumably not controlled directly by soils or physiography (Griffith and others 1994); strong agreement with temperature and growing season suggests climatic control. However, the climatic gradient was paralleled by prehistorical human activity, and greater concentrations of people in the Connecticut Valley, Eastern Lowlands, and southern Uplands may have led to increased clearing and fire activity (Mulholland 1984, 1988; unpublished data). The low abundance of birch (for example, gray, black, or white) or red maple, which are successional taxa that increase with frequent disturbance such as windthrow or fire, and the dominance of midsuccessional but long-lived taxa such as oak, pine, chestnut, and hickory suggest that disturbance frequency was low to moderate in this Colonial landscape (Raup 1937). Rather, climate, perhaps reinforced by infrequent fire (for example, every 100–200 years), may have maintained the midsuccessional and relatively fire-tolerant taxa while excluding late successional fire-intolerant taxa such as beech and hemlock, without favoring shorter-lived pioneer species [Merrill and Hawley (1924), Lorimer (1989), Marks and Smith (1989), Abrams (1992); but see Clark and others (1996), Abrams and Seischab (1997), and Clark (1997)]. This interpretation is consistent with paleoecological charcoal data that indicate an increasing though moderate frequency of fires in oak-dominated sites and the archaeological evidence (Fuller and others 1998; M. Mulholland unpublished data).

Overall, the regional vegetation pattern indicating that taxa and assemblages were strongly controlled by a broad, though relatively modest climatic gradient is in accord with other landscape reconstructions in the northeastern United States (Gordon 1940; Winer 1955; McIntosh 1972; Spear and Miller 1976; Marks and Gardescu 1992). Composition data are consistent with an interpretation of a relatively unimportant role of frequent or broad-scale disturbance by wind or humans across the Uplands and an extremely low frequency of fire (Foster and Zebryk 1993). A somewhat higher frequency of fire in the Lowlands may have reinforced the climatic control over vegetation composition. Based on the apparent low frequency of disturbance, it is assumed that older-growth, large-stature forests would have predominated across the Uplands and Lowlands. A major challenge remains in sorting out the relative importance of the interrelated effects of climate, fire, and people in determining the sharpness and controls of spatial patterns in vegetation (Fuller and others 1998).

Modern Vegetation Composition and Pattern

Despite the extensive process of natural reforestation and forest maturation that has occurred over the past 100–150 years, the modern forest vegetation of central Massachusetts is surprisingly dissimilar to the Colonial forests in terms of composition, inferred structure, and relationship to regional environmental gradients. Whereas forest vegetation per se has proven to be highly resilient to the human impacts and natural changes that have occurred during historical times, individual taxa have responded in highly variable ways to produce landscape patterns that contrast strongly with those of the Colonial period (Foster 1995; Pacala and others 1996). Unless interpreted carefully and with an understanding of the history of change in land use and forest cover, studies of modern vegetation patterns may lead to erroneous conclusions about forest organization and environmental relationships in this landscape shaped by cultural history.

On the basis of individual taxa and township assemblages, the modern vegetation is distinct from that of the Colonial period. Cluster analysis and DCA indicate separation of township samples from the two periods and a strong tendency toward greater regional similarity (homogeneity) within the modern vegetation. The strong relationship between Colonial vegetation and regional climatic gradients is not apparent in the modern vegetation. The homogenization and decreasing relationship of vegetation to climate appears strongly in the distribution and abundance of individual taxa. Although a few taxa such as hickory, spruce, chestnut, and beech maintain a somewhat similar pattern of distribution in the two periods, substantial changes in abundance have weakened or eliminated modern relationships with climate. Most taxa that were abundant in the Colonial period have undergone major changes in both abundance and distribution. Notably, oak has increased in the north-central region and declined at lower elevations, birch and maple have increased substantially across the region but especially at lower elevations and to the south, and hemlock has declined in the north and increased to the west and south (Figure 11). The modern vegetation has little geographic variation at a species or assemblage level. As the strength of the broad-scale environmental relationship with vegetation patterns has declined, no new pattern relating, for example, to physiography or regional variation in land use, has emerged. These results parallel findings from other areas of the northeastern and upper midwestern United States in which intensive cutting, changing fire regimes, or other land-use practices have altered the vegetation and its relationship to environmental gradients since presettlement times (McIntosh 1972; Whitney 1990b; Palik and Pregitzer 1994; White and Mladenoff 1994).

The regional-level results also parallel three observations noted at a stand scale: (a) modern vegetation assemblages are novel and bear little resemblance to historical assemblages, (b) species have responded in a highly individualistic manner to changes in disturbance regime and the institution of novel land-use disturbances, and (c) the last 300 years have resulted in a weakening of the tight vegetation-climate relationship and an increase in vegetation similarity across sites (Foster and Zebryk 1993).

Factors Controlling Regional Vegetation and Its Dynamics

The magnitude of the vegetation change that occurred over the past 300 years, the shift in regional patterns and decline of environmental control and distribution, and the limited evidence for reversion of the vegetation back toward that of the Colonial period (Fuller and others 1998) indicate the overwhelming influence of land use on past, modern, and future dynamics of the vegetation. Here we evaluate the nature of these land-use activities in an attempt to assess the relevant characteristics controlling this regional vegetation response.

Land use as intensive regional disturbance. Colonial settlers and their successors instituted a regional transformation of the landscape that represented a novel and massive disturbance. In a landscape in which broad-scale disturbance had previously been uncommon and old-growth forests and middle to late successional species were prevalent, Europeans initiated novel impacts as forests were cut and cleared and extensive areas replaced by pasture, crops, and human settlement. Remaining forest areas consisted of highly fragmented woodlots disturbed by cutting, grazing, and burning (Graves and Fisher 1903; Foster 1995), and isolated trees persisted along fencerows, in swamps, and scattered in pastures (Foster 1998). The process of forest conversion to agriculture was both widespread and strongly preferential to specific sites and forest types by which farmers gauged the productivity of the land [Belknap (1792), cited in Lord (1973)]. For instance, Belknap identifies beech and sugar maple as species indicative of good agricultural soils. Thus, through extensive conversion of specific forest types and intensive disturbance of remaining woodlands, Colonial land use exerted a rapid, pronounced, and highly selective impact on species distributions and on forest composition and structure.

In contrast to many natural disturbances in which a pulse of damage is followed by a period of recovery (Pickett and White 1985), the agricultural history of central New England culminated in a 75-year period (around 1800–1875) in which forest cover remained at a minimum. The patterns of intense human disturbance were strongly reinforced by ongoing forest use and agriculture during this period and elicited an unprecedented magnitude and rate of change (Fuller and others 1998). Following the peak of agricultural land use, a century-long period of declining disturbance and natural reforestation led to a remarkable regrowth of forest extent and volume. This process initially favored pioneer species such as birch, red maple, and white pine that were adapted for broad-scale dispersal and rapid establishment and growth on open or grassy sites (Spurr 1956). Revegetation therefore presented another process that selectively promoted species uncommon in the Colonial forest. Once established, these new species and forests generated long-lasting legacies of land use, since initial floristic composition may strongly control community characteristics for many hundreds of years (Foster and Zebryk 1993; Pacala and others 1996). Consequently, the short duration of the reforestation period in New England has been inadequate for late successional species to increase or spread extensively or for the imprint of land use to disappear.

Moreover, the subsequent history of New England has involved changing intensities and types of disturbance rather than a complete cessation of human impacts. Historical evidence suggests that agricultural land often underwent a progressive change in use, for example, from tillage to pasture to wooded pasture to forest, as it was gradually abandoned from intensive use (Foster 1995, 1998). During the process of reforestation and regrowth, forests were often cut at a young age (20–50 years) and frequently burned to produce a sprout hardwood forest. Large-stature forests have become dominant in only the last 50 years as fuelwood demands declined and wood imports increased. Selective forest cutting has affected over 16% of the Uplands in the last 10 years (D. Kittredge, D. Foster, and B. Slater unpublished), which has contributed to the dominance of early successional and spouting species over late successional species. Natural disturbances such as the 1938 hurricane have also impacted this regenerating forest area (Foster and Boose 1995).

Land use has also generated permanent changes in the abiotic and biotic environment that may have created enduring changes in regional vegetation. Wetland and soil drainage, lake and reservoir creation, and commercial, urban, and residential development have altered sites and taken areas permanently out of native vegetation. In addition, changing atmospheric chemistry and nutrient loadings have instilled fundamental changes in the regional environment (Aber and others 1989, 1993). Decimation, and more recent proliferation, of native animal and plant species directly or through the introduction of disease and pathogens have altered the biotic environment in ways that are complex and extremely difficult to assess (Orwig and Foster 1998).

Thus, the substantial and long-lasting changes in vegetation over the last 300 years can be understood in terms of the introduction of an intensive, broad-scale, and novel disturbance regime; ongoing intensive human land use; permanent changes to the biotic and abiotic environment; changes in regional climate (Baron and Smith 1996); and a relatively short period for vegetation recovery. The initial clearing, cutting, and burning favored species resilient to frequent disturbance. Species such as beech and sugar maple, which were common on productive upland sites favored for agriculture, and hemlock and northern hardwoods, which were susceptible to burning, decreased in relationship to fire-tolerant and sprouting species such as oak, chestnut, birch, and red maple (Winer 1955). Widespread field abandonment accelerated the abundance of well-dispersed intolerant taxa such as birch, red maple, and white pine and animal-dispersed taxa such as oak, chestnut, and cherry, which established within the new woods. Ongoing cutting and burning maintained these species and produced the extensive sprout hardwood forests that characterized much of New England in the early part of this century. Hemlock and, to a greater extent, beech, which expand slowly into forested areas and are susceptible to fire, were largely restricted to primary forest sites and mesic, protected locations. However, fire control, a shift to less intensive selective cutting, and gradual forest maturation have enabled a progressive increase of hemlock as an overstory component of primary woods and understory component of secondary woods. Beech continues to have a relatively low abundance due to the extent of its initial decline: its very poor ability to disperse and the advent of the beech-bark disease (Twery and Patterson 1984; Pacala and others 1996).

Despite significant regional variation in the timing, quality, and intensity of land use, the cumulative impact of 300 years of land-use history has been to reduce strongly the regional variation in vegetation and to eliminate the relationship between the vegetation and climatic gradients. This suggests that broad-scale similarities in land use have overwhelmed regional environmental control. Given the broad similarities in land use across most of New England, excluding Maine, this raises questions concerning the regional extent of vegetation homogenization and the extent of environmental variation that may be obscured by the institution of a broad-scale disturbance regime.

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