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Effects of postsettlement human activities on forest composition in the north-eastern United States: a comparative approach

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Abstract

Aim This study compares human impacts and forest ecosystem response across geographical regions. Such a comparison allows us to evaluate the relationship between regional changes in forest composition and regional patterns of human activity.

Location Four study areas in the north-eastern USA were investigated, two of which were dominated by oak-pine forests at the time of European settlement (Central Massachusetts, MA; Pike County, PA), and two of which were dominated by beech and hemlock (South Berkshire, MA; Wayne County, PA).

Methods Trees recorded in early land survey records were compiled and compared with data on modern forest composition obtained from recent forest inventories. To assess the similarity of the four regions with regard to species composition, Euclidean Distances (ED) were calculated between the colonial and modern forest composition for each of the four regions. Information about the history of human impacts in the four study regions was used to interpret the changes in forest composition.

Results General changes in forest composition through the historical period include a decline in beech, hemlock and chestnut, and an increase in maple and birch. Changes in pine and oak were minor by comparison. Supraregional human impacts are generally linked with supraregional trends in species composition, whereas regional patterns of land use caused regional patterns of change in species composition.

Main conclusions These results suggest that human activities do not necessarily lead to more similar species composition between regions, especially if these activities show clear spatial patterns at about the same resolution that species composition is evaluated. Comparing species-specific changes in forest composition with species-specific human activities on the same spatial scale is crucial in order to evaluate human impacts on ecosystems and to make more robust generalizations about the temporal dynamics of landscapes.

Keywords

Disturbance, driving forces, forest dynamics, human impact, land use history, north-eastern USA.

INTRODUCTION

Human impacts on forest ecosystems are ubiquitous, and so must be included in studies of landscape and ecosystem change (e.g. Iverson, 1988; Foster, 1992; Motzkin *et al.*, 1996; Turner, Wear & Flamm, 1996; Russell, 1997; Skanes & Bunce, 1997; Carcaillet, 1998; Cowell, 1998; Foster, Motzkin & Slater, 1998; Roche, Tatoni & Médail, 1998). In the north-eastern USA, human impact on forest composition and function has significantly increased since the arrival of European settlers in the 17th–18th centuries. Comparisons of forest composition, as determined from historical sources, with modern forests document significant changes in several local areas (e.g. Siccama, 1971; Glitzenstein *et al.*, 1990; Abrams & Ruffner, 1995; Cowell, 1998). However, few studies compare human impacts and forest ecosystem change across broader

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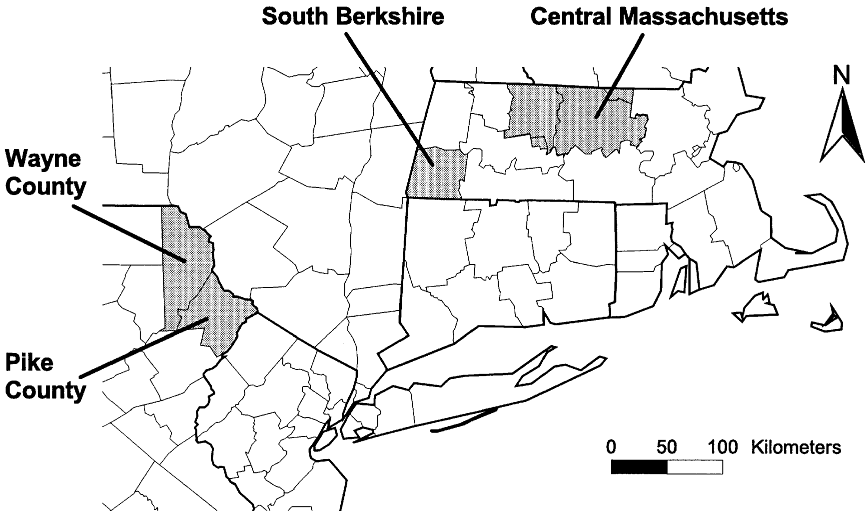

Figure 1 Map showing the location of the four study regions in the north-eastern USA.

geographical regions. Such a comparison allows us to evaluate whether regional changes in forest composition correspond with regional patterns of human activity and to determine whether human activities have caused forest composition to become more or less homogenous across a broad region since European settlement.

Comparing patterns of landscape structure and change is crucial for attempts to develop a general model of landscape change (Simpson *et al.*, 1994). In this study, we compare the relative changes in postcolonial forest composition with differences in human impacts in four regions across the north-eastern USA. Previous studies have documented land use changes and their effects on vegetation patterns in one of these four regions (Foster *et al.*, 1998; Fuller *et al.*, 1998). Three additional regions were selected in order to test and expand the findings of these studies (Fig. 1), and to gain a deeper understanding of the factors driving postcolonial vegetation changes across the Northeast.

STUDY REGIONS

In order to compare the effects of historical land use on vegetation change across the north-eastern USA, we selected study areas with similar colonial vegetation patterns but different land use histories. Sites were also selected that are representative of the major forest types in the north-eastern USA. In particular, we selected 'oak/pine' and 'beech/hemlock' regions in both Massachusetts and Pennsylvania for comparison, thereby adding to a growing database of colonial vegetation reconstruction (Whitney, 1994). All four regions were glaciated in the Wisconsinan glacial advance.

The Central Massachusetts study region covers an area of 3500 km^2 in northern Worcester and eastern Franklin Counties, as well as portions of Hampshire and Middlesex Counties (Fig. 1). Central Massachusetts is the second warmest of the four study regions (Fig. 2), with the coldest climate in the northern central Uplands, and the highest average temperatures in the Connecticut River Valley. In the eastern lowlands, outwash and till predominate, whereas the Connecticut River Valley to the west contains extensive areas of glacial lake deposits and alluvium. Soils in the central uplands are typically acid sandy loams (Foster *et al.*, 1998). The northern part of Central Massachusetts occurs in the mixed forest–coniferous forest province, and the southern part and the lowlands in the Connecticut River Valley and in the east are in the oceanic broad-leaved forest province (Bailey, 1998).

The South Berkshire region covers 1150 km^2, comprising the southern part of Berkshire County. South Berkshire is the coldest of the four study regions (Fig. 2). The lowest average temperature is reached in the Taconic Mountains, although the warmest conditions occur nearby in the town of Sheffield. Loamy soils predominate throughout. Those in the western and north central parts of the study area are derived from schist, gneiss and granite, while those in the eastern and south-central part are derived from limestone (Soil Survey Berkshire, 1988). South Berkshire is part of the oceanic broad-leaved forest province (Bailey, 1998).

Wayne County in the north-eastern corner of Pennsylvania covers an area of 1900 km^2 and is the second coldest of the four regions (Fig. 2). The lowest temperatures occur in the northern part of the county, whereas the warmest areas are located at the border with Pike County. Wayne County is primarily in the Appalachian Plateaus Province, with a small area along its western border in the Ridge and Valley Province. Most of the county is covered by glacial till and glaciofluvial material (Soil Survey Wayne, 1985), and is part of the mixed deciduous-coniferous forest province (Bailey, 1998).

Pike County is situated south of Wayne County in north-eastern Pennsylvania and covers an area of 1420 km^2. It is the warmest of the four study regions (Fig. 2). Whereas the lowest temperatures occur in the west towards Wayne, the highest temperatures are reached in the southern portion of the County along the Delaware River. Pike County lies mainly on the Allegheny Plateau. The county is characterized by rocky ridges covered with undulating glacial till and outwash deposits that have depressions filled with either silts and clays, water

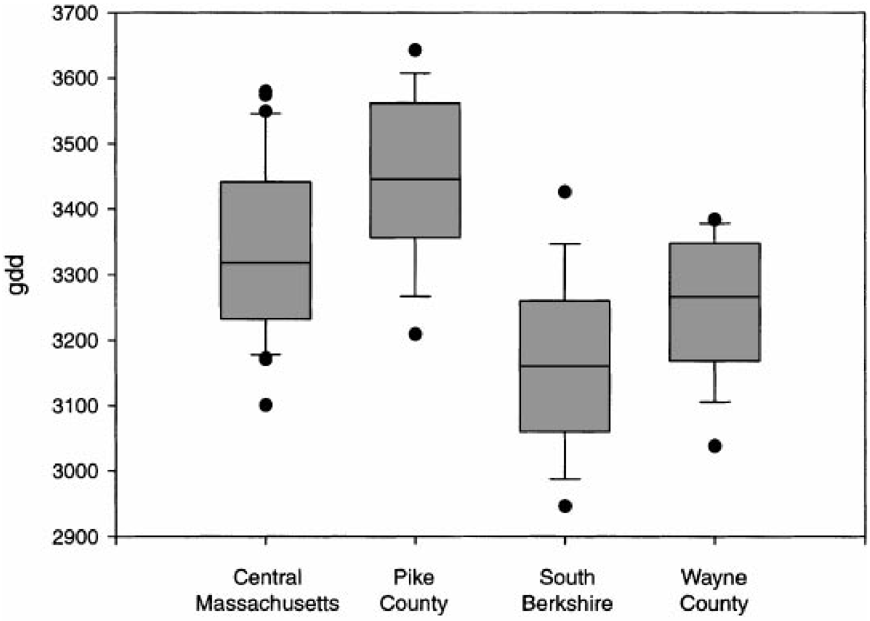

Figure 2 Range of growing degree days for the four study regions based on a grid with 200 × 200 m cell size. Data for the grid were obtained from a regression model developed by Ollinger *et al.* (1993). See text for details.

or organic deposits (Soil Survey Pike, 1995). The northern part of Pike County falls within the mixed deciduous-coniferous forest province (Bailey, 1998), the southern part of the county is in the oceanic broad-leaved forest province.

MATERIALS AND METHODS

Natural impacts on forests

Differences in forest composition across broad geographical regions are partly caused by regional differences in natural impacts on the forests. In their study of forest dynamics in Central Massachusetts, Foster *et al.* (1998) successfully demonstrated that presettlement tree distribution was strongly related to growing degree days (GDDs). Similarly strong and highly significant relationships between climate and forest composition in the early historical period were found for the three other regions that we address in the current study (Bürgi & Russell, 2000).

Thus, GDD values were used to characterize regional climatic differences. Values were calculated based on an empirical climate model developed by Ollinger *et al.* (1993). In the part of this model used in our study, multiple linear regressions were performed for average monthly temperatures against latitude, longitude and elevation. The temperature values were taken from a regional database of 164 weather stations, evenly distributed across New York and New England (Ollinger *et al.*, 1993). GIS coverages were generated based on a digital elevation model (DEM) and a grid cell size of approximately 200 × 200 m. GDDs for every cell were calculated by multiplying the average monthly temperature by the number of days in that month, followed by adding together all monthly GDD values. In order to characterize general climatic differences between the four study regions, summary statistics were calculated for all cells falling within a region. The range of climatic variation within a region is depicted by box-plots of GDD values on a single-cell basis for every region (Fig. 2).

We did not model changes in climate over the past two to three centuries. Although climate has changed somewhat through this period, major changes in the geography of the climatic gradients are not expected (Foster *et al.*, 1998). Using a comparative approach between fairly large regions, we consider this to be an appropriate assumption.

Regional differences in vegetation may also result from variation in disturbance regimes or edaphic factors. In particular, hurricanes are a major natural disturbance factor along the East Coast of the USA. Information about regional differences in frequency of damaging hurricanes was taken from a recent study by Boose, Chamberlin & Foster (2001). Regional differences in soils and geology were determined based on Soil Surveys of the Soil Conservation Service of the USDA. The map of ecoregions of North America (Bailey, 1998) was used to supply information about the general vegetation characteristics of the study regions.

History of human impacts on forests

In evaluating the history of human impacts on ecosystems, we must rely on historical data and be aware of its limitations. Whereas standard techniques for ecological data collection and analyses are well-established, working with historical sources inevitably involves some degree of subjective interpretation (Marcucci, 2000). In order to limit such subjectivity, standards for evaluation of historical data have been promoted, such as the four criteria listed by Forman & Russell (1983). They propose: (a) the distinction of first- and second-hand observation, (b) an evaluation of the purpose or possible bias of the observations, (c) the consideration of the author's knowledge of the subject, and (d) the observation must be put in its historical and ecological context.

It is obvious that for different types of data, these criteria have to be applied in an appropriate manner. In our study, we rely on state and federal census data, which are often used in ecological studies (e.g. Turner, 1987; Foster *et al.*, 1998) as they are collected in a well-defined and consistent manner across time and space. Additional sources used include local histories (Field, 1829; Marvin, 1879; Goodrich, 1880; Smith, 1885; Tague & Kimball, 1961; Lehde, 1989; Barbe & Reed, 1998; Fluhr, 1998) which are much more difficult to interpret, as they often are based on a series of anecdotal observations recorded in chronological order. In taking the limitations of these sources into account, we used information drawn from local histories only in combination with other sources, such as reports by government agencies (Anonymous, 1896, 1906a, b, 1945; Report, 1915; Cook, 1917; Parmenter, no date, 1928, 1933) or scholarly publications (Fedkiw & Stout, 1959; Foster, 1961; Parks, 1967; Pyne, 1982; Connolly, 1985; McGaw, 1987; McGregor, 1988; Kirby, 1995). Combining historical information from different types of sources has proved to be an effective tool for evaluating land use impacts (e.g. Davis, 1973; Christensen, 1989; Russell, 1997; Foster *et al.*, 1998; Bürgi, 1999; Motzkin *et al.*, 1999; Marcucci, 2000).

In order to summarize a wide range of historical sources across broad temporal and spatial scales, we developed timelines of the history of human impacts in the four study regions. These timelines include data about population density, land in forest, human activities and transportation facilities, and indicate the time periods for which data about colonial and modern forest composition were available (Fig. 3a–d).

Population data for Wayne and Pike were obtained from federal census records for 1800–1990. For towns in the Southern Berkshire study area, these data were complemented by data from the federal census for 1790 and, for 1765 and 1776, from the state census for 1885. For Central Massachusetts, population data were from state censuses (Federal Census, 1790–1990; Census of Massachusetts, 1885).

Land area in forest was determined for Central Massachusetts and South Berkshire from tax valuations (Tax valuations, 1791–1860), state censuses (Census of Massachusetts, 1875–1905), forest surveys (Cook, 1917; Parmenter, no date supplied, 1928, 1933), the Massachusetts MapDown project (MacConnell, 1973), MassGIS (1991) and the Berkshire County Databook (Berkshire, 1997). As no state censuses are available for Pennsylvania, federal censuses were used for Wayne and Pike for 1850–1930, and later data come from federal agricultural censuses. In order to get an estimate of the portion of land in forest, estimated areas of land used for transportation, land under water and residential areas were subtracted from the difference between total area and agricultural land. As it is often hard to make a clear distinction between forest land and open land (Black, 1960), the numbers given in Fig. 3 should be regarded as rough estimates.

Information about important forest industries was compiled from local histories, tax valuations and state and federal censuses. Industrial activities were only included if they affected a significant part of a study region. Information about the most important transportation facilities is taken from local and regional histories and other secondary literature.

Forest composition

Early land survey records offer a wealth of information about the landscape from a very early phase of European settlement. The corners of surveyed lots were often marked with trees ('witness trees'), providing useful data on colonial forest composition. For Central Massachusetts, witness tree data were compiled by Foster *et al.* (1998). Road survey data were excluded, as they seem to have different biases from lot surveys (Bürgi & Russell, 2000). Witness tree data for Berkshire county were compiled in the 1920s by Barnes (1920/21, 1930). For Wayne and Pike Counties, warrant maps were used thereby avoiding the bias inherent in written surveys or deeds, as trees marking corners of neighbouring lots are counted once in a compilation based on maps. In cases where trees were apparently the same but identified differently in adjacent lots (e.g. pine, white pine), the more precise name was taken. Trees named very differently (e.g. chestnut, chestnut oak or even oak, hemlock) were counted in both forms. Some smaller towns with < 50 trees were combined with adjacent towns in order to keep the average size of towns similar.

Data on modern forest composition were obtained from the USDA Forest Service Forest Inventory and Analysis (FIA) Eastwide Forest Inventory Data Base (http://www.srsfia.usfs.msstate.edu/scripts/ew.htm; Dickson & McAfee, 1988; Hansen *et al.*, 1992; Alerich, 1993). These are based on data from ground plots (0.4047 ha) sampled in different forest types as identified on aerial photos. In order to make the data about modern forest composition more comparable with witness tree data, all trees < 10 cm d.b.h. were excluded from the analysis (Cowell, 1998).

Species composition for every region was calculated as the average of the percentages by town.

To assess the similarity of the four regions with regard to species composition, Euclidean Distances (EDs) were calculated between all four regions for the colonial and modern forest composition. To determine change over time, EDs were also calculated for the four regions between colonial and modern time.

ED was calculated as:

$$ED_{i,j} = \sqrt{\sum_k (y_{ki} - y_{kj})^2}$$

where y is the percentage of a species k in the data sets i and j, and i and j were different regions or colonial and modern forest composition of the same region.

RESULTS

Natural impacts on forests

In the north-eastern USA, the importance of large-scale windstorms is highly variable. Central Massachusetts experiences severe hurricanes causing extensive blowdowns (F2 on the Fujita scale) about every 150 years, e.g. in 1815 and in 1938, when white pine was particularly susceptible to damage (Foster, 1988; Boose *et al.*, 2001). The frequency of damaging hurricanes is lower in South Berkshire and the study regions

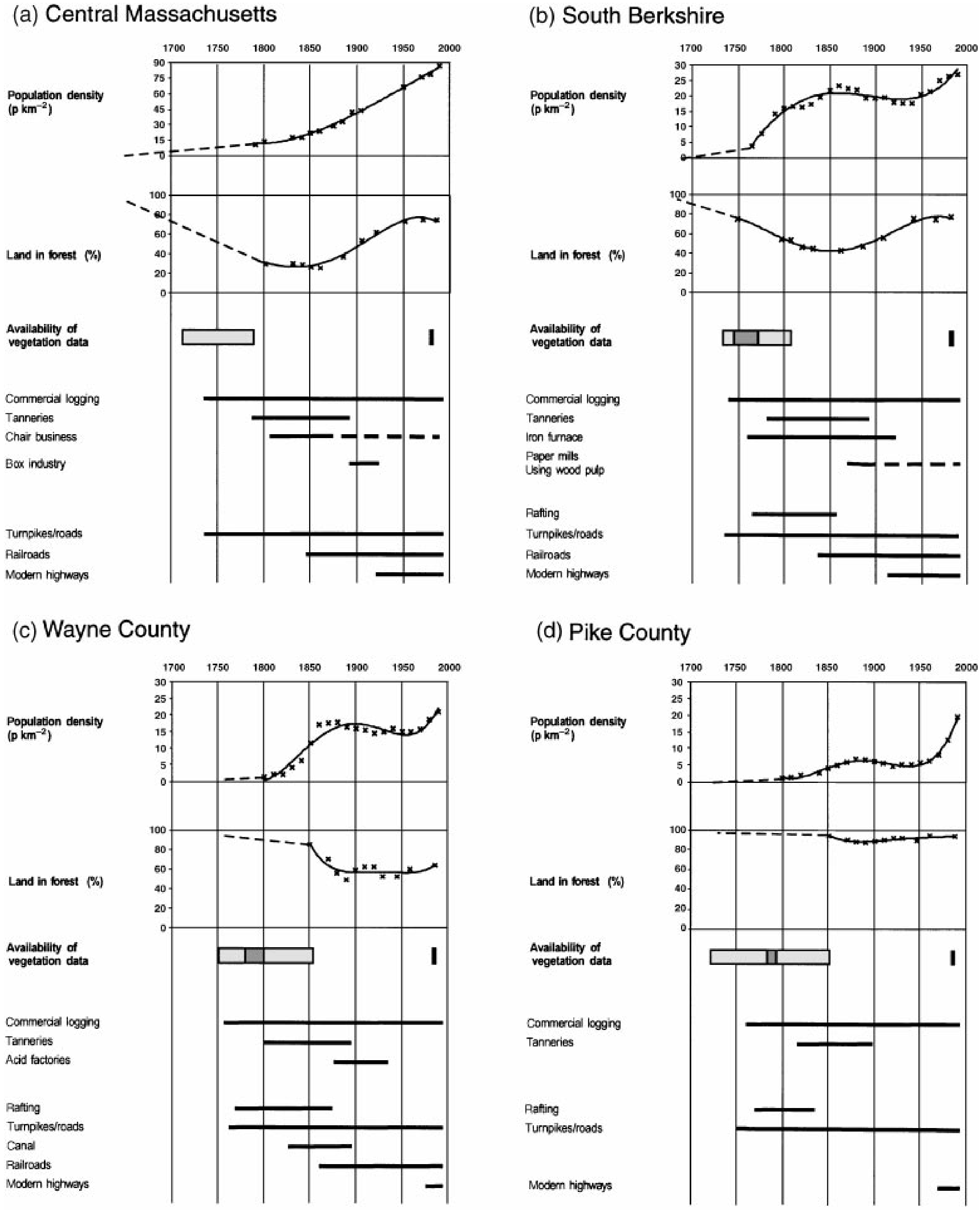

Figure 3 Summary of historical information about human activities with impact on the forests in the four study regions. In (b), (c) and (d), darker shading for availability of vegetation data indicates the period from which most of the data were derived. With improved transportation facilities, especially the extension of the railroad in the mid-19th century, the impact of local industries on local forest resources lessened. Therefore some activities lost their direct local impact in the second half of the 19th century, as indicated by dashed lines. Note the larger scale for population density in Central Massachusetts.

in Pennsylvania are out of the range of regular catastrophic wind damage by hurricanes (Boose *et al.*, 2001).

Another important abiotic disturbance (partly triggered by human activity) is fire. The extent, intensity, frequency and source of ignition (i.e. human vs. lightning) of fires in the precolonial period remain a point of debate (Russell, 1983; Abrams, 1998; Ruffner & Abrams, 1998). In the 19th and 20th centuries, railroads and people (e.g. hunters, campers and berry pickers starting incendiary fires to encourage the younger growth of blueberries and huckleberries) were probably the most frequent causes of forest fires (Rothrock, 1894; Anonymous, 1906b; Report, 1915). Pike was among the counties with the most extensive fires in Pennsylvania, but fire was also frequent in Wayne (Anonymous, 1896) and the study regions located in Massachusetts. In the 20th century, improved fire detection and suppression resulted in a decline in the importance and size of fire (Pyne, 1982).

An impressive example of the impact of a biotic disturbance is the nearly complete loss of chestnuts in all four regions caused by an introduced fungal blight (*Cryphonectaria parasitica*). The killing front for this pathogen passed through all four study regions between 1910 and 1920 (Anderson, 1974).

Comparing the history of human impacts on forests

Population densities

The four regions differ significantly in time of European–American settlement and population trends (Fig. 3a–d). Central Massachusetts was first settled in the middle of the 17th century, and after 1850 industrial towns grew as rural population decreased (Foster *et al.*, 1998). Population density reached 87 people/km^2 in 1990, far higher than in the other regions. Although settlers reached South Berkshire in the late 17th century (Smith, 1885), it was not until after the end of the French and Indian Wars in the 1760s that the population increased substantially. As the study region includes only a few industrial towns, population density between 1860 and 1930 dropped by 24%. Since that time, population has increased to 23.9 people/km^2 in 1990. The first European settlers arrived in Wayne County in 1755 (Goodrich, 1880), but population density remained at only two people/km^2 until 1820. The population rose to 17 people/km^2 between 1820 and 1840, followed by a long period of slow decline until the last two censuses, when the trend reversed. By 1990, population density had reached 21 people/km^2. Even though the first settlers had arrived in the area of Pike County by about 1725, it remained mostly unsettled in the 18th century (Lehde, 1989). In the early 19th century, population density was similar to Wayne (Fig. 3d). In 1920, < five people/km^2 were recorded. After 1960 a sharp increase in population occurred, reaching 20 people/km^2 in 1990.

Forest cover

Prior to industrialization, changes in population were mirrored by changes in the percentage of land in forest (Fig. 3). Forest cover in Central Massachusetts decreased rapidly through the 18th century, with *c.* 30% of the land forested by 1800. Farm abandonment started in the first half of the 19th century and regional forest cover increased after about 1880. Today, forests cover *c.* 75% of the land. In South Berkshire, *c.* 75% of the land remained forested through the late 18th century. Forest cover declined to a minimum of about 40% in 1875 and subsequently increased steadily such that by 1985, 77% of the land was again forested. As late as 1850, forests still covered about 86% of Wayne County, but in the second half of the 19th century forest cover declined to about 50%. Most land that was cleared for agriculture is still in use, and forest cover has only increased to about 65%. Pike County supported more than 85% forest cover throughout the time period covered in this study.

Industrial activities with potential impact on forests

All four study regions have a long tradition of logging. In the early 19th century, a great portion of the pine and hemlock cut in South Berkshire was floated down the Housatonic River to Milford and Derby, CT, where it was converted into boards, planks and shingles for market in Connecticut and New York (Field, 1829). Sawmilling remained the county's major forest product industry up to the middle of the 20th century (Foster, 1961). Rafting of logs was also important in Wayne and Pike; from 1764 to 1869, an estimated 4.7×10^6 m^3 of lumber was rafted out of Wayne to Philadelphia (Goodrich, 1880; Barbe & Reed, 1998). In 1860, 107 sawmills were reported for Wayne County, representing 11% of the aggregate value of all manufacturing in Wayne County (Federal Census, 1860). In Pike, lumbering started in the 1760s and remained by far the largest industry during the 19th century (Anonymous, 1945), with logs rafted down the Delaware (Fluhr, 1998). In 1879, the amount of wood cut in Pike was about 40% of the amount cut in Wayne (Federal Census, 1880). The supply of props for coal mines in Scranton, PA was a major use of pitch pine as well as some oak (Anonymous, 1906a; Report, 1915; Illick & Aughanbaugh, 1930).

In the second half of the 19th century, hemlock bark was the main source of tannins for processing hides in the Northeast. In Central Massachusetts and South Berkshire, tanneries were apparently only of local importance. After about the middle of the 19th century, bark was increasingly imported from northern New England (Connolly, 1985), further reducing the local impact of the tanning process. In contrast, starting in 1800, leather making was a major industry in Wayne. In 1860, 18 leather-producing manufacturers contributed 62% of all products manufactured in Wayne County (Federal Census, 1860). By 1871, Wayne was the leading county in Pennsylvania in leather tanning output (Barbe & Reed, 1998). In Pike, leather tanning was also important, contributing two-thirds of the value of products manufactured in 1860 (Federal Census, 1860), but still less than 11% of the output in Wayne County. The industry declined at the end of the 19th century, with reduced availability of hemlock and the invention of chemical tanning.

Wood was also used in a variety of local industries with distinct regional patterns. In the eastern part of Central Massachusetts, hardwood lumber was used widely in the chair-manufacturing business (Marvin, 1879; Connolly, 1985). Second growth white pine stands that became established as a consequence of farm abandonment throughout Central Massachusetts were used heavily for producing wooden boxes and crates between the 1890s and the 1920s (Fedkiw & Stout, 1959; Irland, 1982). In South Berkshire, paper production was a major industry with increasing impact after 1867, when paper started to be made from wood pulp (McGaw, 1987). Iron furnaces operating in nearly all South Berkshire towns between the 1760s and the 1920s created a significant demand for wood for fuel (Cronon, 1983; Kirby, 1995). In Wayne, wood was also used in acid factories to produce wood alcohol and acetate of lime. The first acid factory was built in Starrucca in 1876 and was in operation until 1924, originally processing the waste of the lumber industry (Barbe & Reed, 1998).

Transportation

In Central Massachusetts, an early network of overland trails was improved in the 18th century by a network of roads. However, the poor quality of many of these early roads limited market access (Parks, 1967). The construction of railroads starting in 1844 resulted in a significant improvement of overland transportation, and interregional automobile highway systems became widespread by the mid-1920s (Connolly, 1985). In the 17th–18th centuries, overland travel from South Berkshire was limited (McGaw, 1987). Transportation was improved in the 18th century by early roads, and since 1842 by railroads (Smith, 1885).

As indicated above, rafting was of great importance for moving logs in the Pennsylvania study regions. In 1762, the first road opened through Wayne; some turnpikes and plank roads followed (Barbe & Reed, 1998). Improvements in the method of burning anthracite coal from the nearby mines in Scranton triggered construction of the Delaware and Hudson Canal in 1827 (Goodrich, 1880), which initiated an increase in population density in Wayne (Fig. 3c). Competition from the railroads forced the canal to cease operations in 1898 (Barbe & Reed, 1998). Railroads became widespread by 1860 and had a considerable influence on the lumber industry and on the location of tanneries. Both industries shifted towards regions with access to the new infrastructure system (McGregor, 1988). In 1975, Route I-84 was completed, causing an increase of second homes in the southern part of Wayne (Barbe & Reed, 1998).

A railroad constructed through Pike in 1849 (Lehde, 1989) did not run along the Delaware River, and thus bypassed the main towns of Pike. By the 1980s, a popular movement to live in Pike and commute to New York or New Jersey (Fluhr, 1998) caused a sharp increase in second homes (Soil Survey Pike, 1995), commuters and retired people living in Pike.

Species composition

Witness trees were compiled by town but data from towns with less than 50 witness trees or data from towns with fewer than two plots or less than 50 trees for modern forest composition were excluded. Only towns with data available for colonial and modern forest composition were included in the analyses. However, for all four study regions this smaller subsample of comparable towns is representative of the species composition of the respective region (see all towns vs. comparable towns in Table 1). The number of witness trees per comparable town ranged from 98 in Wayne County to 1007 in South Berkshire (Table 1). For modern forest composition, an average of 40 plots and 1273 trees was compiled by study region, and the comparable towns contained an average of 4.2 plots with 134 trees.

The oak-pine regions

In Central Massachusetts, a significant increase in maple occurred from the colonial to modern period (8.3 to 26.9%), primarily due to an increase in red maple which today accounts for 25.9% of the trees (Fig. 4, Table 1). Only white pine is more common on the modern landscape (26.7%). Total pine shows only a slight increase from 23.4 to 27.2%. As we do not know how many of the 14.1% of trees classified as 'other pine' in the witness tree data were white pine, no trend in this species can be discerned. The percentage of 'oaks' decreased from 28.6 to 21.7%. Whereas the red oak group showed an increase from 9.5 to 19.3%, white oak decreased from 13.2 to 2.4%. Hemlock decreased from 9.6 to 6.4%, and chestnut which accounted for 8.2% of witness trees, was eliminated by the chestnut blight. Other species declining were beech (6.7 to 0.9%), ash (3.7 to 2.0%) and poplar (2.6 to 0.2%), whereas white birch (0.3 to 5.7%) and cherry (0.6 to 3.1%) increased.

In Pike County, oak increased from 39.0 to 46.5%. Both white oak (19.9 to 17.5%) and red oak (11.4 to 12.2%) remained relatively stable, whereas chestnut oak increased from 7.6 to 16.7%. Pines were abundant in the colonial period, but declined sharply from 26.5 to 7.5% through the historical period. It cannot be determined if this change was caused by a change in pitch pine or in white pine. Maple increased from 7.4 to 26.9%, primarily due to an increase in red maple; the proportion of sugar maple remained small (2.8 to 3.1%). Chestnut was common in the colonial forest (7.1%), but was reduced to 0.4% as a result of the chestnut blight. Other species showing a decline are beech (4.5 to 1.5%) and hemlock (5.5 to 1.9%). Ash remained stable (2.4 to 2.2%), but cherry (0.0 to 1.8%) and poplar (0.1 to 1.4%) increased slightly.

The beech-hemlock regions

The most important tree in South Berkshire today is hemlock (18.6%), which had a similar percentage in the colonial period. However, in colonial forests, beech was much more common, accounting for 27.3% of all trees compared with only 2.7% in modern forests. White pine increased from 3.1 to 16.3%. The increase in red maple from the colonial to modern periods was lower in South Berkshire (1.9 to 13.4%) than in Central Massachusetts, with 6.5% 'other maple' in the witness tree data. Sugar maple increased, rising from 1.4 to 5.6%. White oak decreased from 8.4 to 0.4%, whereas the red oak group increased from 5.0 to 14.3%. Chestnut disappeared completely, but only accounted for 3.5% of witness trees. Whereas ash remained at *c.* 5%, birch increased from 5.0 to 9.1%. Increases are also visible for cherry (0.0 to 4.0%) and poplar (1.4 to 5.7%).

Today, 45.1% of all trees in Wayne's forests are maple,

Table 1 Species composition (percentage) for each taxon in the colonial and modern periods for the four study regions. For Latin names see Appendix. Pine, oak, maple and birches are classified according to the categories given in Appendix 1.

	Central Massachusetts				Pike County				South Berkshire				Wayne County				Mean all four regions	
	Colonial		Modern		Colonial		Modern		Colonial		Modern		Colonial		Modern		Colonial	Modern
	All towns	Comparable towns		All towns	All towns	Comparable towns		All towns	All towns	Comparable towns		All towns	All towns	Comparable towns		All towns	Comparable towns	
No. of trees	4777	3146	1573	1921	1659	1306	1713	1713	6748	5035	550	714	939	787	1251	1635	2568	1272
No. of plots			52	63			51	51			17	22			40	52		40
No. of towns	27	16	16	19	12	9	9	9	12	5	5	7	10	8	8	12	10	10
Tree/plot			30	30	m		34	34			32	32			31	31		32
Tree/town	177	197	98	101	138	145	190	190	562	1007	110	102	94	98	156	136	270	134
Plot/town			3.3	3.3			5.7	5.7			3.4	3.1			5.0	4.3		4.2
White oak	19.0	13.2	2.4	2.4	19.7	19.9	17.5	17.5	8.3	8.4	0.4	1.1	2.5	3.1	2.8	1.9	11.1	5.8
Red oak group	11.4	9.5	19.3	18.0	11.8	11.4	12.2	12.2	7.1	5.0	14.3	16.4	2.0	2.2	3.0	4.9	7.0	12.2
Chestnut oak	0.2	0.1	0.0	0.0	8.8	7.6	16.7	16.7	0.0	0.0	0.7	0.7	1.3	1.7	2.7	1.8	2.4	5.0
Other oak	4.7	5.9	0.0	0.0	0.1	0.1	0.0	0.0	1.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Oak	35.2	28.6	21.7	20.4	40.4	39.0	46.5	46.5	16.5	13.9	15.3	18.2	5.8	7.0	8.5	8.6	22.1	23.0
White pine	4.1	5.7	26.7	27.1	4.2	4.2	5.6	5.6	2.6	3.1	16.3	14.2	2.6	3.1	3.1	2.5	4.0	12.9
Pitch pine	2.3	3.6	0.3	0.2	0.9	0.8	1.9	1.9	0.8	0.7	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.5
Other pine	12.6	14.1	0.2	0.2	21.7	21.5	0.0	0.0	3.7	4.5	0.0	0.0	0.4	0.5	0.0	0.0	10.2	0.1
Pine	19.1	23.4	27.2	27.5	26.9	26.5	7.5	7.5	7.1	8.2	16.3	14.2	3.0	3.6	3.1	2.5	15.4	13.5
Beech	6.6	6.7	0.9	1.4	3.1	4.1	1.5	1.5	22.9	27.3	2.7	3.1	36.1	34.1	6.4	8.3	18.0	2.9
Hemlock	8.8	9.6	6.4	7.8	5.2	5.5	1.9	1.9	18.8	19.0	18.6	18.5	22.0	20.9	6.8	5.7	13.8	8.4
Red maple	0.0	0.0	25.9	25.5	0.0	0.0	23.8	23.8	2.2	1.9	13.4	13.4	0.0	0.0	16.3	19.3	0.5	19.9
Sugar maple	0.0	0.0	1.1	1.0	2.3	2.8	3.1	3.1	1.4	1.4	5.6	5.4	14.3	13.6	28.5	24.3	4.4	9.6
Other maple	6.9	8.2	0.0	0.0	4.4	4.6	0.0	0.0	7.2	6.5	0.0	0.0	1.8	1.8	0.3	0.3	5.3	0.1
Maple	6.9	8.3	26.9	26.4	6.7	7.4	26.9	26.9	10.8	9.7	19.1	18.8	16.1	15.4	45.1	43.9	10.2	29.5
Black birch	1.3	1.4	2.2	2.4	0.2	0.2	2.9	2.9	0.0	0.0	2.1	1.5	0.6	0.6	5.1	6.6	0.6	3.1
White birch	0.2	0.3	5.7	5.3	0.1	0.1	0.2	0.2	0.0	0.0	3.1	4.3	0.2	0.3	0.4	0.2	0.2	2.4
Yellow birch	0.0	0.0	1.3	1.6	0.0	0.0	0.8	0.8	0.0	0.0	3.9	6.1	0.0	0.0	3.4	3.0	0.0	2.3
Other birch	1.9	1.8	0.0	0.0	1.9	2.0	0.0	0.0	4.9	5.0	0.0	0.0	5.4	5.5	0.0	0.0	3.6	0.0
Birch	3.4	3.5	9.2	9.3	2.2	2.4	3.9	3.9	4.9	5.0	9.1	11.9	6.2	6.4	8.8	9.8	4.3	7.8
Ash	3.7	3.7	2.0	1.8	2.2	2.4	2.2	2.2	4.5	5.2	4.5	4.3	2.0	2.0	4.9	6.8	3.3	3.4
Chestnut	8.1	8.2	0.1	0.1	7.5	7.1	0.4	0.4	6.2	3.5	0.0	0.0	1.4	1.8	0.0	0.0	5.2	0.1
Cherry	0.4	0.6	3.1	2.6	0.0	0.0	1.8	1.8	0.1	0.0	4.0	2.9	0.1	0.2	5.1	4.2	0.2	3.5
Poplar	2.0	2.6	0.2	0.2	0.1	0.1	1.4	1.4	1.1	1.4	5.7	4.2	0.0	0.0	3.3	2.3	1.0	2.7
Others	5.8	4.8	2.2	2.5	5.9	5.6	6.0	6.0	7.2	6.6	4.7	3.9	7.3	8.6	8.0	7.9	6.4	5.2

Colonial, colonial forest; modern, modern forest.

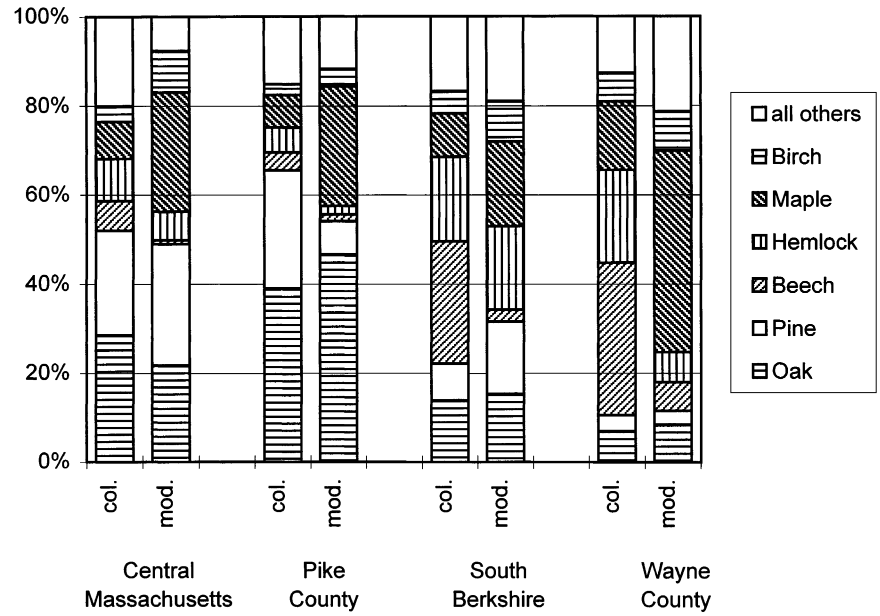

Figure 4 Percentages of the six most-abundant taxa in the colonial and modern periods in the four study regions. See Appendix 1 for scientific names.

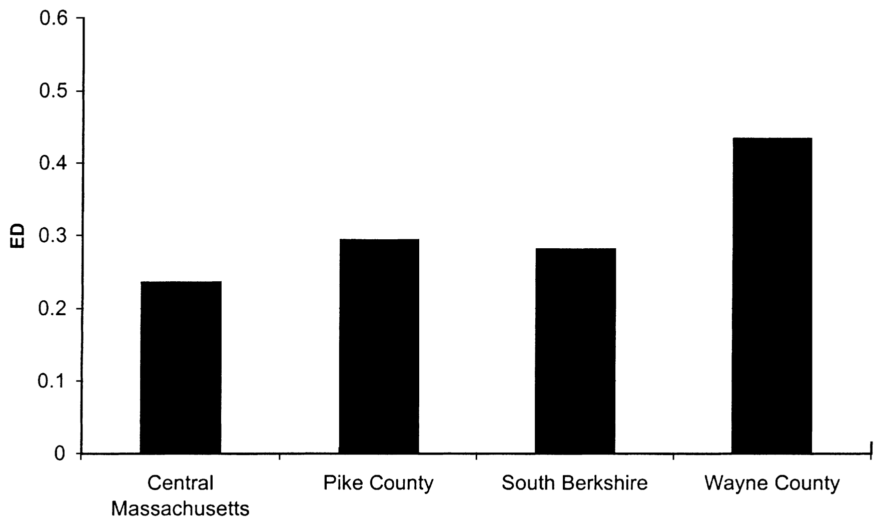

Figure 5 Similarities in forest composition between colonial (col.) and modern (mod.) forests for all four study regions (CM = Central Massachusetts, SB = South Berkshire, WA = Wayne, PI = Pike).

compared with 15.4% in colonial times. Red maple increased from 0.0 to 16.3% and sugar maple increased from 13.6 to 28.5%. Beech decreased from 34.1 to 6.4% and hemlock decreased from 20.9 to 6.8%. Only minor changes occurred in oak (7.0 to 8.5%) and pine (3.6 to 3.1%). Because 5.5% of the 6.4% 'birches' were in the category of 'other birch' in the witness tree data, it cannot be determined if the minor increase in birch includes a change in species composition. Cherry (0.2 to 5.1%), poplar (0.0 to 3.3%), and ash (2.0 to 4.9%) all increased from the colonial to modern period.

By species

Whereas some species show the same trends over time in all four regions, others show distinct regional patterns (Table 1, Fig. 4). Species that generally increase over time in all four regions are maple, birch and cherry. Poplar increased in all regions except Central Massachusetts. Species that did not change significantly in percentages across the four regions are oak and ash, although oak decreased somewhat in Central Massachusetts. Ash decreased somewhat in Central Massachusetts and increased in Wayne, but accounted for < 5% in both the colonial or modern periods. The supraregional percentage of Pine did not change much over time (15.5 to 13.5%), but clear regional differences are discernible. Pine increased in Central Massachusetts (from 23.4 to 27.2%) and even more so in South Berkshire (from 8.2 to 16.3%), but declined heavily in Pike (from 26.5 to 7.5%). Species that declined in all four regions include beech, hemlock and chestnut.

Similarity between regions and changes in time

Changes in tree composition between colonial and modern forests were largest in Wayne County (ED = 0.43) and smallest in Central Massachusetts (ED = 0.24) (Fig. 5). The changes in

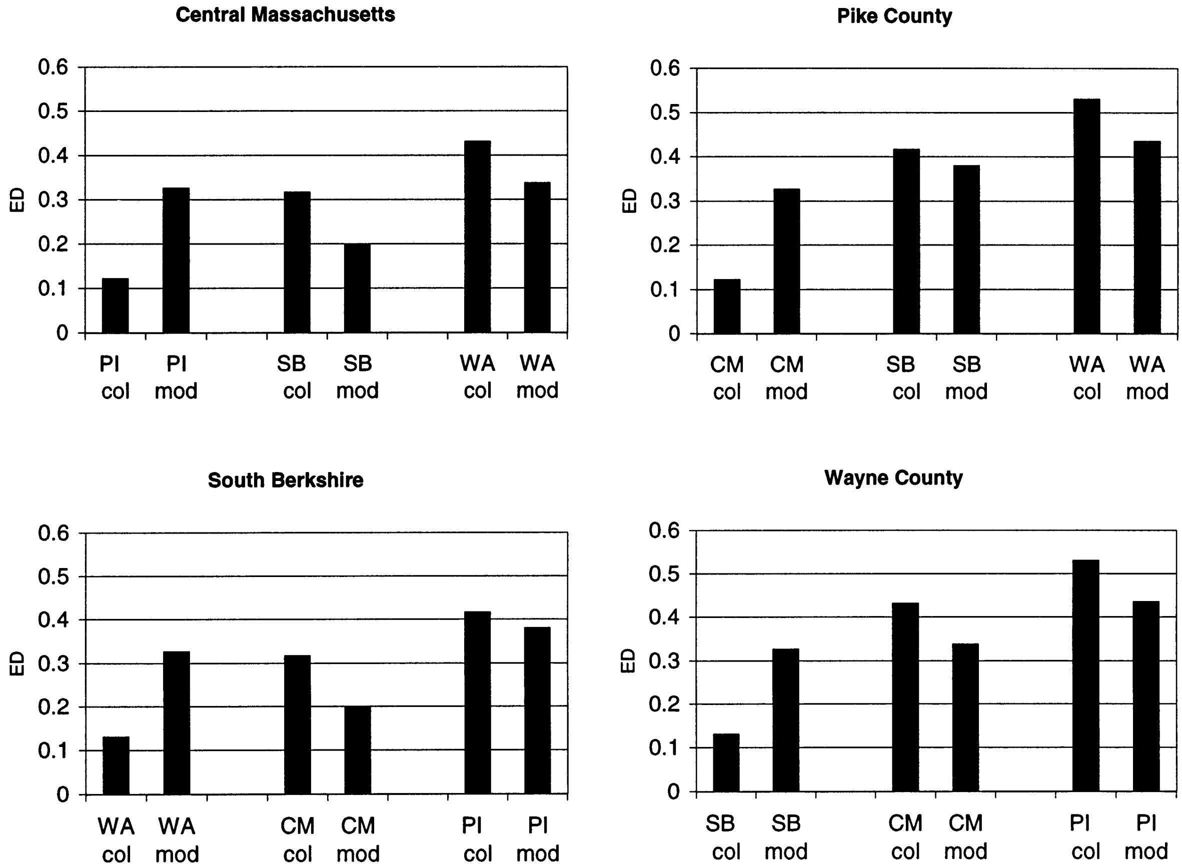

Figure 6 Similarities in forest composition between all regions for colonial (col.) and modern (mod.) forest composition (CM = Central Massachusetts, SB = South Berkshire, WA = Wayne, PI = Pike).

forest composition in South Berkshire (ED = 0.28) and Pike County (ED = 0.29) were only slightly larger than those recorded for Central Massachusetts.

Comparisons of all regions for the colonial period (Fig. 6) indicate that Central Massachusetts was most similar to Pike County (ED = 0.12) and South Berkshire was most similar to Wayne County (ED = 0.13). This reflects the rationale for selecting these four regions. Furthermore, Fig. 6 illustrates that the more similar regions were during the colonial period, the more dissimilar they became over time. This causes a decrease in the variance in similarity during the postcolonial period from Var (EDcol) = 0.38 to Var (EDmod) = 0.11, despite the relatively constant Euclidean Distance between two regions (Av (EDcol) = 0.32, Av (EDmod) = 0.33). Thus, species composition itself did not become more similar, but the average degree of similarity between the regions increased.

DISCUSSION

Evaluation of data on colonial forest composition

How well do these data reflect actual changes in forest composition? Witness tree data have been widely used to reconstruct colonial forest composition. Still, because of potential errors from fraud, early impacts of settlers on the surveyed forests, misidentification of trees species, sampling bias and bias in the selection of trees (Whitney, 1994), the sources must be critically evaluated. Although fraud is difficult to assess, there is no evidence for it in the history of surveying in these regions during these periods of time. To avoid potential impact of settlement on the surveyed vegetation, surveys were included only if they occurred before widespread settlement of a region. Nonetheless, some level of impact of early human activities on colonial forest composition cannot be excluded. This is especially true for Central Massachusetts and for South Berkshire, where settlement started before surveys were made. We also cannot exclude potential impacts of native Americans, which were not evaluated, in part because information about variation in native American activities is not sufficient (e.g. Grumet, 1995).

The bias caused by misidentified trees was minimized by grouping species into distinct taxonomic groups, typically genera (Appendix 1). Sampling bias is a complex question, as the bias might go in very different directions. In towns where one area was divided into small house lots, this part was much more intensively sampled than areas where lots were large. In some areas the lots were laid out in a regular grid, in others they were shaped very irregularly with many corners. In some warrant maps for Wayne and Pike County, gridded and irregular shaped lots were recorded. In these gridded surveys, fewer trees but more posts, piles, and stones were noted as corners. This might have been caused by the smaller freedom of placing the corner close to a tree. Therefore areas surveyed in a grid are probably underrepresented in the compilation. As only towns with > 50 witness trees recorded were included in this study, we are confident that these data cover a significant portion of the physiographical properties at the town level. In summary, despite these limitations, witness tree records are still the best source of information about colonial forest composition (Whitney, 1994; Bürgi & Russell, 2000).

Changes in forest composition

The average change in forest composition across the four study regions indicates a decline in beech, hemlock and chestnut, and an increase in maple, birch and cherry (last column, Table 1). Changes in pine and oak were minor by comparison. These general changes are similar to those recorded in pollen records for the Northeast in the historical period (Russell *et al.*, 1993).

Despite an impressive increase in maple in the historical period, oak-pine forests still dominate the two warmer regions (i.e. Central Massachusetts and Pike). But while in Central Massachusetts the percentages of oak and pine remained about the same over time, they changed in Pike, with oak increasing significantly (39.0 to 46.5%) and pine declining to less than one-third of its importance in colonial times (26.5 to 7.5%). Working in the nearby southern Pocono Plateau, Dando (1996) found a similar decline in pine from 32 to 6%. The decline of oak and pine (66 to 39%), lack of change in beech and hemlock (15 to 17%) and increase in maple (6 to 27%) in Dando's region suggests that forest changes in the southern Pocono Plateau were perhaps driven by factors similar to those important in Pike County.

In the colder regions, South Berkshire and Wayne, beech and hemlock were the most important trees in colonial times. McIntosh (1962), who examined the colonial forest composition for the Catskill Mountains which are situated halfway between Southern Berkshire and Wayne, found similar results. In all three regions beech was the dominant species, representing nearly 50% of all trees recorded for the Catskill Mountains. Hemlock (20%), sugar maple (13%) and birch (7%) were also quite common (McIntosh, 1962). In all three regions, beech declined heavily in the historical period, leading to a change in dominant tree species (McIntosh, 1972). Hemlock also declined in the Catskill Mountains and in Wayne, in contrast to South Berkshire where it remained constant. Today, Wayne's forests are dominated by maple (45.1%), whereas the increase of maple was much less significant in South Berkshire. Instead, white pine and red oak increased, causing South Berkshire's modern forests to be more similar to those in Central Massachusetts than those in Wayne.

Linking changes in forest composition with the history of human impacts

Although climate has warmed somewhat since *c.* 1850, the impacts of this warming on vegetation variation across the region have probably been swamped by changes related to human activities (see, for example, Russell *et al.*, 1993; Bradley & Jones, 1995). A simple classification was applied to compare changes in forest composition with human activities (Table 2). Species were classified according to changes in

Table 2 Classification of changes in forest composition, human activities and natural impacts from the colonial to modern periods in the four study regions.

	Central Massachusetts	Pike County	South Berkshire	Wayne County	Regionality
Species					
Oak	– –	+ +	0	0	4
Pine	+	– – –	+ +	0	5
Beech	– –	–	– – – –	– – – –	3
Hemlock	–	–	0	– – –	3
Maple	+ + +	+ + +	+ +	+ + + +	2
Birch	+ +	0	+	+	2
Human activities					
Agricultural abandonment	+ + +	0	+ +	+	3
Logging	+ +	+ +	+ +	+ +	0
Tanneries	+	+ +	+	+ + +	2
Natural impacts					
Windthrow	+ + +	+	+ +	+	2
Fire	+	+ + +	+	+ +	2

Classification for change in species: x < 2%,0; 2% ≤ x < 5%,+/–; 5% ≤ x < 10%,+ +/– –; 10% ≤ x < 20%,+ + +/– – –; 20% ≤ x,+ + + +/– – – –.
Classification for human activities/natural impacts: negligible, 0; less important, +; important, + +; very important, + + +.

their percentages between colonial and modern times, activities were classified according to their importance. Among human activities farm abandonment, logging and tanning were selected as the most important in terms of potential impact on species composition. A regionality factor was calculated as the difference between the highest and lowest class. Some changes in forest composition were about the same in all four regions under study (i.e. increase in red maple), whereas others were different from region to region (i.e. changes in pine). Similarly, some human activities were significant for all regions (e.g. logging) whereas others show distinct regional patterns (e.g. agriculture). Thus, the question arises as to whether trends in forest composition that are consistent across all study areas are caused by human activities that affected all areas, whereas regional patterns in forest changes resulted from regional differences in the history of human impacts on the forests.

Being a valuable timber, oak was often selectively logged, perhaps contributing to the decrease of white oak in Central Massachusetts (from at least 13.2 to 2.4%) and South Berkshire (from at least 8.4 to 0.4%). Williams (1989) notes the high demand of white oak by railroads, indicating the diverse impacts of railroads on forest composition. In contrast, the increase of oak in Pike is likely to be a consequence of the comparable higher fire frequency in this region.

White pine was probably affected in all regions by selective removal in the early phase of commercial logging. As white pine is the most important old-field successional species in the study regions, regional differences in the percentages of pine on the modern landscape may result from regional importance of farming and farm abandonment. The increase in white pine in Central Massachusetts with farm abandonment in the late 19th and early 20th centuries is well documented (Fisher, 1933). However, in this region the process of abandonment was paralleled by industrial activities specialized in processing white pine (i.e. box industry in Fig. 3a) and the hurricane of 1938 (Foster, 1988), such that the modern forests do not have substantially more white pine than colonial forests. Farm abandonment as a process was not as important in Pike because agriculture was never very important. Consequently no regrowth of white pine was induced to offset the decrease in pine caused by logging.

A substantial decrease in beech occurred across all study regions. Many pollen records for the north-eastern USA show a general decline in beech beginning well before European settlement (e.g. Russell *et al.*, 1993; Fuller *et al.*, 1998). After European settlement, as a late-successional species, beech was probably affected by the general increase in anthropogenic disturbances, including the very probable increase of fire frequency (Russell *et al.*, 1993).

The regional pattern in changes in hemlock mirrors the regional pattern in tanning industry; Wayne, where the lack of hemlock is said to have been the reason for the decline of this industry after 1870, shows by far the biggest decline in hemlock. On the other hand, in South Berkshire, where tanning was not reported to be important, hemlock remained constant. McIntosh (1972) too, links the decline of hemlock to its exploitation for tanbark. Hemlock has limited dispersal capabilities and is known for comparatively slow recovery after its removal from a site (He & Mladenoff, 1999).

The substantial increase in maple across all study regions probably results from an overall increase in forest disturbances, especially cutting. The comparison of species changes across the regions (Table 2) reveals that the massive increase in maple, primarily red maple (Table 1), has a small regionality factor. Thus, the expansion of red maple in eastern forests (Abrams, 1998) is not likely to be linked with a human activity that shows a distinct regional pattern. Instead, red maple may have been favoured by supraregional impacts, such as logging (red maple has never been a highly valued timber species) and fire suppression (being more sensitive to fire than many other forest trees; Abrams, 1998).

Birch increased in Central Massachusetts, less so in South Berkshire and Wayne, and did not show any significant change in Pike. Thus, its regional pattern is similar to pine, with the exception of a larger increase in Central Massachusetts, which is well explained by the fact that, contrary to pine, birch was not selectively logged after regrowth. The patterns of changes in birch thus reflect well the regional patterns of increased disturbances since settlement.

Improved transportation facilities, especially the extension of the railroad in mid-19th century, lessened the impact of local industries on local forest resources. Therefore some activities lost their direct local impact in the second half of the 19th century (e.g. paper mills in South Berkshire, chair manufacturing in Central Massachusetts; Fig. 3) and their spatial patterns are not likely to show any correspondence with patterns of change in species composition. Similarly, the increase of transportation of goods and mobility of people weakened the link between total population and impact on the local forests, as illustrated by the parallel increases in population and forest area in the 20th century.

CONCLUSIONS

For some species, changes in percentages were consistent across all four study regions, whereas for others, change varied from region to region. Similarly, some human activities were recorded for all regions whereas others show a distinct regional pattern. Supraregional activities seem to be generally linked with supraregional trends in the percentages of species, such as red maple and beech, whereas regional patterns of land use caused regional patterns of change in some species percentages.

The two pairs of regions with high similarity in colonial forest composition (Central Massachusetts–Pike/South Berkshire–Wayne) both became less similar over time, but more similar to the other pair. As the original pairs were similar with regard to average temperature (Fig. 1), we conclude that today's forest composition corresponds less with regional patterns of temperature regimes. The decrease in climate signal, noted within the Central Massachusetts region on a town scale by Foster *et al.* (1998), is also visible across different regions. At the same time, regions that were similar in colonial forest composition have become more dissimilar. These, and similar results by Schneider (1996), suggest that human activities do not necessarily lead to more similar species composition between regions, especially if these activities show clear spatial patterns at about the same resolution that species composition is evaluated. Thus, changes in similarity must be evaluated at explicit spatial and temporal scales.

Many impacts and disturbances are species specific and similarly the response of the different species to disturbances is individualistic. Thus, aspects of the interaction of society and nature that affect single species are lost in generalized measures of similarity or diversity. Our approach allowed us to compare species-specific changes directly with species-specific human activities on the same spatial scale. Such an approach is crucial in order to evaluate human impacts on ecosystems and to make more robust generalizations about the temporal dynamics of landscapes.

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Appendix 1 Classification of witness tree names to species and taxa used in the analyses.

Class	Category	Latin name	Names of witness trees
Oak	White oak	*Quercus alba*	White oak
	Red oak group	*Quercus*	Red oak, black oak, spanish oak
	Chestnut oak	*Quercus prinus*	Mountain oak, rock oak, chestnut oak
	Other oak	*Quercus* spp.	Oak, grey oak, yellow oak, swamp oak, swamp white oak
Pine	White pine	*Pinus strobus*	White pine
	Pitch pine	*Pinus rigida*	Pitch pine, yellow pine
	Other pine	*Pinus* spp.	Pine, pine knot
Beech	Beech	*Fagus grandifolia*	Beech, black beech, red beech
Hemlock	Hemlock	*Tsuga canadensis*	Hemlock
Maple	Red maple	*Acer rubrum*	Soft maple, swamp maple
	Sugar maple	*Acer saccharum*	Hard maple, rock maple
	Other maple	*Acer* spp.	Maple, elkwood
Birch	Black birch	*Betula lenta*	Black birch
	White birch	*Betula papyrifera*	White birch
	Yellow birch	*Betula alleghaniensis*	Swamp birch, yellow birch
	Other birch	*Betula* spp.	Birch
Ash	Ash	*Fraxinus* spp.	Hard ash, black ash, white ash, red ash, ash
Chestnut	Chestnut	*Castanea dentata*	Chestnut
Cherry	Cherry	*Prunus* spp.	Cherry, black cherry, red cherry
Poplar	Poplar	*Populus* spp.	Poplar
All others	Alder	*Alnus* spp.	Alder, alderbush, spotted alder, swamp alder
	Apple	*Malus* spp.	Apple, wild pear
	Atlantic white cedar	*Chamaecyparis tyoides*	White cedar
	Basswood	*Tilia americana*	Basswood, bass, linn, lime wood, softwood tree
	Blackgum	*Nyssa sylvatica*	Piperage, peparige, gum
	Boxwood	*Acer negundo*?	Boxwood
	Butternut	*Juglans cinerea*	Butternut, white walnut
	Dogwood	*Cornus florida*	Dogwood
	Eastern red cedar	*Juniperus virginiana*	Juniper, red cedar
	Elm	*Ulmus* spp.	Elm, red elm, witch elm, white elm
	Fir	*Abies balsamea*	Furr, firr, farr
	Hickory	*Carya* spp.	Hickory, walnut
	Hornbeam	*Ostrya/Carpinus*	Hard beam, horn bean, hornbin, hornwood, blue beech, ironwood, leverwood, deerwood
	Sassafras	*Sassafras albidum*	Saxafax
	Serviceberry	*Amelanchier* spp.	Shadbush, shadwood
	Spruce	*Picea* spp.	Spruce, black spruce
	Sycamore	*Platanus occidentalis*	Button wood, button tree
	Tamarack	*Larix laricina*	Tamarack, hackmatack, hackmetack
	Walnut	*Juglans nigra*	Black walnut
	Tulip tree	*Liriodendron*	White wood tree, white tree
	Willow	*Salix nigra*	Willow, black willow
	Others		Horn pine, pinall bech, ballwood, spruce pine, White ash poplar, 'spruce or white pine'

Note: only tree species were included.